MR. JOACHIM PAUL TÖPPER (Orcid ID : 0000-0002-6996-7223)

DR. OLAV SKARPAAS (Orcid ID : 0000-0001-9727-1672)

Article type : Primary Research Articles

The devil is in the detail: non-additive and context-dependent plant population responses to increasing temperature and precipitation

Plant demography in a warmer & wetter climate

J. P. Töpper^{1,2,3*}, E. Meineri^{3,4}, S. L. Olsen⁵, K. Rydgren², O. Skarpaas^{5,6} & V. Vandvik³

1. Norwegian Institute for Nature Research, Thormøhlensgate 55, N-5008 Bergen, Norway

2. Institute of Natural Science, Western Norway University of Applied Sciences, Røyrgata 6, N-6856 Sogndal, Norway

3. Department of Biological Sciences, University of Bergen, P.O. Box 7803, N-5020 Bergen, Norway

4. Aix Marseille University, University of Avignon, CNRS, IRD, IMBE, Marseille, France

5. Norwegian Institute for Nature Research, Gaustadalléen 21, N-0349 Oslo, Norway

6. Natural History Museum, University of Oslo, P.O. Box 1172 Blindern, N-0318 Oslo, Norway

*Corresponding author: J. P. Töpper, email: joachim.topper@nina.no

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/gcb.14336

This article is protected by copyright. All rights reserved.

Key words: climate change, plant demography, Integral Projection Models, transplant experiment, *Veronica alpina*, *Veronica officinalis*, *Viola biflora*, *Viola palustris*

Paper type: Primary Research Article

Abstract

In climate-change ecology, simplistic research approaches may yield unrealistically simplistic answers to often more complicated problems. In particular, the complexity of vegetation responses to global climate change begs a better understanding of the impacts of concomitant changes in several climatic drivers, how these impacts vary across different climatic contexts, and of the demographic processes underlying population changes. Using a replicated, factorial, whole-community transplant experiment, we investigate regional variation in demographic responses of plant populations to increased temperature and/or precipitation. Across four perennial forb species and twelve sites, we found strong responses to both temperature and precipitation change. Changes in population growth rates were mainly due to changes in survival and clonality. In three of the four study species, the combined increase in temperature and precipitation reflected non-additive, antagonistic interactions of the single climatic changes for population growth rate and survival, while the interactions were additive and synergistic for clonality. This disparity affects the persistence of genotypes, but also suggests that the mechanisms behind the responses of the vital rates differ. In addition, survival effects varied systematically with climatic context, with wetter and warmer+wetter transplants showing less positive or more negative responses at warmer sites. The detailed demographic approach yields important mechanistic insights into how concomitant changes

in temperature and precipitation affect plants, which makes our results generalizable beyond the four study species. Our comprehensive study design illustrates the power of replicated field experiments in disentangling the complex relationships and patterns that govern climate change impacts across real-world species and landscapes.

Introduction

The empirical evidence for climate change impacts on plants is rapidly accumulating, including range shifts (Gottfried et al., 2012; Grabherr, Gottfried, & Pauli, 1994; Lenoir, Gegout, Marquet, de Ruffray, & Brisse, 2008; Parmesan & Yohe, 2003; Pauli et al., 2012), increased productivity (Wu, Dijkstra, Koch, Peñuelas, & Hungate, 2011), phenological shifts (Oberbauer et al., 2013), and changes in biotic interactions (Alexander, Diez, & Levine, 2015). This list is by no means exhaustive, but illustrates that our understanding of the basic impacts of climate change on plant life is developing rapidly. Many climate-change impact studies measure responses at the community or ecosystem level (Elmendorf et al., 2012; Wu et al., 2011). While this is important for assessing effects and consequences for ecosystem functions and services, our mechanistic understanding of climate-change impacts is hampered by a lack of knowledge of the demographic processes behind changes in species abundance. It is, for instance, not trivial whether a population decline is driven by reductions in survival or reproduction, given the different implications that changes in these vital rates may have for population size, gene-pool size, selection processes, and spatial dynamics, as these rates differentially impact population extinction probabilities and hence biodiversity (Ehrlén & Morris, 2015; Pearson et al., 2014). Demographic studies can further such mechanistic insights into how specific climatic drivers affect local population dynamics.

In addition to global warming, regionally varying changes in precipitation are predicted for significant areas across the globe (IPCC, 2014). The interplay between these two climatic changes is complex and may even vary across climatic gradients (Luo et al., 2008). For assessments of future vegetation changes, it is vital to know how plants respond to simultaneous changes in temperature and precipitation – can the single effects simply be added (additive interaction) or does the response to combined change deviate from that sum (non-additive interaction), either in an enforcing manner (synergistic interaction) or in a counteractive manner (antagonistic interaction) (Darling & Côté, 2008)? However, as single-factor and local climate experiments still dominate the literature, we have only limited knowledge about the interaction effect of changes in temperature and precipitation (Barnett & Facey, 2016; Mundim & Bruna, 2016; Wu et al., 2011) and the climatic context-dependency (Dunne, Saleska, Fischer, & Harte, 2004; Root & Schneider, 1995; Rustad, 2008) of climate-change impacts, which can be expected to vary within a species' niche (Hampe & Petit, 2005).

Here we present the results of a turf transplant experiment in which we assess the effects of single and combined changes in temperature and precipitation on the population dynamics of four common forbs – two alpine-specialist species (*Viola biflora* and *Veronica alpina*) and two temperature-generalist species (*Viola palustris* and *Veronica officinalis*) – across broad bioclimatic gradients in Norway. To mimic the regional climate change projections, predicting increases in temperature and precipitation (IPCC, 2014), vegetation turfs were transplanted to sites that were warmer, wetter, and warmer+wetter, as well as at 'home' for control. In our system, precipitation falls during the entire year, but a significant amount as snow during winter, and the turfs transplanted to wetter sites will thus experience more and longer snow cover. The experiment was replicated across a climatic grid of 12 sites arrayed in three levels of mean summer temperature and four levels of annual precipitation

(Figure 1, Table S2). This experimental design allows us to disentangle the effects of concomitant changes in temperature and precipitation, and to assess how climate-change effects vary across climatic contexts. We followed all individuals of the target species in transplanted and control turfs over four years and parameterized size-structured population models for all species and treatments, yielding population growth rates (λ) for all treatments and populations as well as vital rate contributions to differences in λ (Merow et al., 2014).

For the single-factor climatic changes, several appropriately founded hypotheses can be formulated. *Hypothesis #1*: we expect warming to be positive for the overall productivity of the vegetation sward in our alpine and sub-alpine sites, but detrimental for weak competitors such as the alpine species *Viola biflora* and *Veronica alpina*, but also for *Viola palustris* (cf. Klanderud, 2005). *Hypothesis #2*: for increased precipitation, we generally expect negative responses as the climatic context of our climate grid already is quite humid (Schuur, 2003). *Hypothesis #3*: in line with niche theory (Hampe & Petit, 2005), we expect the proposed negative effects of increased temperature and precipitation to be strongest in the warmest and wettest sites, respectively. *Hypothesis #4*: for additive vs. non-additive outcomes of the fully factorial experiment, we generally expect antagonistic responses (cf. Darling & Côté, 2008), especially since warming and increased precipitation are of an inherently counteractive nature with respect to water balance.

Materials and methods

Study area and species. The study was carried out over four years (2009–2012) as part of the SEEDCLIM climate change experiment performed in twelve grassland sites in Norway (Klanderud, Vandvik, & Goldberg, 2015). The sites were selected to fit within a systematic, orthogonal climate grid composed of three levels of summer temperature (boreal ~10.5°C, sub-alpine ~8.5°C, and alpine ~6.5°C at 440–590 m, 780–820 m, and 1100–1200 m above

sea level, respectively) and four levels of annual precipitation (ca. 600, 1200, 2000, 2700 mm), where summer temperature (mean of June to September) and annual precipitation are not correlated (Figure 1, Table S2). The climate grid is based on long-term monthly means from the current ‘normal period’ 1961–1990 provided by the Norwegian Meteorological Institute (met.no). The sites were selected to be as similar as possible in all aspects other than climate (grazed, species-rich grasslands situated on south-facing, shallow slopes on calcareous bedrock).

For the demographic study, we selected four study species: two alpine specialists, *Viola biflora* L and *Veronica alpina* L, and two temperature-generalist species, *Viola palustris* L and *Veronica officinalis* L (hereafter simply referred to as ‘generalist’). All study species are perennial and reproduce both sexually and clonally. The study species were common throughout the climate grid, although not all species occurred in all sites (Figure S1).

Experimental design. At each site, we established five experimental blocks, and in each block four 25 × 25 cm plots were placed semi-randomly to contain the study species. In September 2009, three plots from each block were transplanted to the sites either one step warmer, wetter, or warmer+wetter (Figure 1). This constituted a summer temperature increase of ca. 2–3 °C and an annual precipitation increase of ca. 700–800 mm (Table S2), mimicking climate change projections for the study region (IPCC, 2014). As plots from the warmest sites could not be transplanted to a warmer site, nor plots from the wettest sites to a wetter site, and neither of the two to warmer+wetter, the design resulted in 5 replicates from each of 8 communities transplanted to warmer sites, 9 communities to wetter, and 6 communities to warmer+wetter (Figure 1). The fourth plot of a block was transplanted within its original block as a control. The transplanted turfs measured 29 × 29 cm (i.e. the plot

dimensions plus 2 cm at each side, to reduce edge effects) and were 5–10 cm deep. As an estimate of competition for light within the community, we measured overall vegetation height in all plots as the average of five measurements of the foliage height per plot at peak season (end of July) prior to transplanting in 2009, and in 2011, 2012, and 2013. To assess whether vegetation height changed in response to the climate transplant treatments, we analyzed the difference in vegetation height between transplant plots and controls from each block separately for each transplant treatment using linear mixed effects models with Gaussian error structure, year as fixed effect, and random intercepts for site ($n = 151, 171$, and 118 for warmer, wetter, and warmer+wetter, respectively; model and data satisfied linear-model assumptions of normal errors and homoscedasticity).

Data collection. In July/August 2009, prior to transplanting, we tagged all ramets of the study species within each plot and recorded a selected set of vegetative and reproductive traits (e.g. leaf number and length, shoot height, fruit number; see Methods S4) allowing estimation of dry biomass, our estimate of plant size (biomass regression based on destructive samples; see Meineri, Skarpaas, Spindelböck, Bargmann, & Vandvik, 2014), and fecundity. In the summers of 2010, 2011, and 2012, we recorded the survival of the previous years' ramets, tagged new clonal ramets and seedlings, and repeated the measures of vegetative and of reproductive traits for all live ramets (Methods S4). In total over the course of the experiment, we recorded 2501 ramets of *Viola palustris*, 2713 ramets of *Viola biflora*, 3920 ramets of *Veronica officinalis* and 897 ramets of *Veronica alpina*.

Population modeling and statistical analyses. To analyze population dynamics and estimate population growth rates (λ) of the different populations and treatments, we used integral projection models (IPMs), which are based on regressions of vital rates (survival,

growth, clonality, fecundity) against a continuous state variable describing each individuals' state (here plant size) (Easterling, Ellner, & Dixon, 2000). All regressions were performed separately for each species and treatment using generalized linear mixed effects models (Bates, Maechler, Bolker, & Walker, 2015) in R version 3.3.1 (R Core Team, 2016). This method allows the stochastic modeling of temporal and spatial variability arising from the study design by specifying site and annual transition as random effects. Using the fixed effects coefficients from these regressions we built IPMs for every species and treatment using the R-package 'IPMpack' (Metcalf, McMahon, Salguero-Gomez, & Jongejans, 2013). As the underlying mixed-effect models include random effects for site and annual transition, the 'deterministic' λ s of our resulting IPMs account for temporal and spatial stochasticity. We calculated vital rate contributions to the differences in λ between the transplants and their respective controls (at their 'home' sites) through separate one-way life table response experiments (LTRE) for each treatment (Caswell, 2001). Uncertainties for λ and vital rate contributions were obtained by bootstrapping the original data (separately for each species and treatment) 10,000 times (Manly, 1997): individual ramets were sampled with replacement to construct a resampled dataset containing the same number of observations as the original dataset. Regression modeling, construction of IPMs, and calculation of λ were then repeated for each of the 10,000 resampled datasets. To assess the effects of climatic context on the population responses to increased temperature and precipitation, we built site-specific IPMs based on the random site effects of the vital rate regressions for each bootstrap sample. We then regressed the differences in site-specific λ values between climate transplants and controls, and the respective vital rate contributions from the LTREs with site temperature and precipitation across all species 10,000 times in linear mixed effects models. Here, we used a Gaussian error distribution with an identity link and specified summer temperature and precipitation (in two separate models) as fixed effects and species as a

random intercept. For more detailed information on regressions, population models, and their analyses please refer to Methods S4.

Results

All four species had stable or growing populations in the control turfs during the timeframe of the experiment. The transplants showed three principal response patterns in population growth rate (λ) to the climatic change treatments. For *Veronica alpina* and *Viola palustris*, λ decreased in all three treatments; *Viola biflora* showed decreased λ in the wetter transplants; and for *Veronica officinalis*, λ decreased in the wetter and warmer+wetter transplants (Figure 2a). The effect of the combined warmer+wetter transplant treatment on λ resembled the effect in the transplants that received only warming in the alpine species (*Viola biflora* and *Veronica alpina*), whereas it was more comparable to the effect in the transplants with only higher precipitation in the generalist species (*Viola palustris* and *Veronica officinalis*) (Figure 2a, see Table S4 for the original λ values). The changes in λ in the climate transplant were mainly caused by reduced survival and reduced clonality, whereas growth and fecundity hardly changed (Figure 2b). In contrast, the height of the extant vegetation increased under warmer and warmer+wetter climates, although less so in the latter, while it stayed largely constant in the wetter transplants (Figure 3). When comparing the vital rate contributions to changes in λ from the added single treatments and the combined warmer+wetter treatment, we found negligible differences for clonality (indicating additivity) across all species, but considerable differences for survival (indicating non-additivity) (Figure 4). The survival contributions in the combined treatments were generally less negative than expected for *Veronica alpina* and *Viola palustris* and less positive than expected for *Viola biflora* (antagonistic effects). For *Veronica officinalis*, both clonality and survival contributions to changes in λ were additive. The magnitude of the decrease in λ and changes in all vital rates

in response to warming was constant along the temperature gradient (Figure 5), as were the responses to increased precipitation along the precipitation gradient (not shown). However, the response to increased precipitation, whether it occurred alone or in combination with increased temperature, varied over the temperature gradient. In alpine populations, increased precipitation generally had positive or neutral effects on λ and survival, whereas the effects became increasingly negative towards sub-alpine and boreal populations (Figure 5).

Discussion

Supporting *hypothesis #4*, three of the four study species showed non-additive effects of concomitant changes in temperature and precipitation on λ , illustrating that impacts of multiple global change drivers largely do not act independently (Parmesan & Hanley, 2015).

In fact, our study mirrors the general pattern of non-additivity being more common than additive responses in factorial climate-change experiments, with a ratio of occurrence at 3:1 (Darling & Côté, 2008). Interestingly, the main underlying contributors to the observed changes in λ – survival and clonality – responded in different ways. Whereas survival mirrored the antagonistic non-additivity seen in λ in *Viola biflora*, *Viola palustris*, and *Veronica alpina*, the clonality effects were additive and synergistic in all species. This is important, as these antagonistic effects (of temperature and precipitation increase) on survival reduction translate into higher survival under the combined increase in temperature and precipitation relative to warming alone. Clonal reproduction, on the other hand, is even more reduced due to synergistic negative effects on clonality. Together, this implies a higher retention of different genotypes and hence an improved chance of long-term population persistence (Morris & Doak, 2002) under combined increases in temperature and precipitation, even though population growth rates and thus population-size trajectories change similarly under warming alone.

Furthermore, non-additive effects on survival and additive effects on clonality suggest that there are differences in the mechanisms behind the effects of the tested climatic changes on these vital rates. For survival, the negative effects of warming for both *Viola palustris* and *Veronica alpina* likely relate to the observed simultaneous increase in competitive interactions in our experiment (Fig. 3; see also Guittar, Goldberg, Klanderud, Telford, & Vandvik, 2016). This is in line with *hypothesis #1* and is supported by both these species being relatively weak competitors for light (Jensen & Meyer, 2001; Kollmann & Rasmussen, 2012; Olsen, Töpper, Skarpaas, Vandvik, & Klanderud, 2016) and by other studies that find changes in biotic interactions in response to climate warming (Alexander et al., 2015). Reduced survival under increased precipitation might be a more direct, physiological response to excess water in an already humid study region (supporting *hypothesis #2*; see also Schuur, 2003), although some species may benefit, as exemplified by *Viola biflora*, due to high moisture affinity (Lenoir et al., 2010). Together, the weaker effects on survival in the warmer+wetter transplants might reflect the lower increase in competition for light in this treatment compared to warming alone (*cf.* Figure 3), but also an alleviation of the excess-water effect through higher evapotranspiration in a warmer climate (Harte & Shaw, 1995). Therefore, the effects on the survival of our study species seem to be plastic realizations of the net-outcome of the concomitant climatic changes, acting either directly via soil moisture, indirectly via biotic interactions, or via a combination of both. In contrast to survival, the largely additive effects on clonal growth suggest that increases in temperature and precipitation affect this vital rate independently of one another. The largest decreases in clonal growth in our study occurred under increased precipitation, which contrasts with the general pattern of an increasing proportion of clonal plant species towards wetter habitats (Herben, Šerá, & Klimešová, 2015; Klimešová & Herben, 2015; Ye et al., 2014). This indicates that not precipitation *per se* but a related climatic factor might be the driving force

behind the reduced clonality in our wetter transplants. For instance, transplants to more oceanic sites with higher rainfall would also experience an increase in cloudiness, and thus a decrease in light availability, which has been shown to reduce the production of clonal ramets (Guo et al., 2016; Méthy, Alpert, & Roy, 1990; M. T. Wang, Zhao, Du, & He, 2008; P. Wang, Lei, Li, & Yu, 2012; Xie, Zhang, Zhao, Du, & He, 2014). Our experimental setup allows us to address this effect independent of any change in temperature, which otherwise may have masked this response.

As the net-effects of a warmer+wetter climate clearly reflect the responses to warming alone in *Viola biflora* and *Veronica alpina* – both alpine species and weak competitors – our results underline the susceptibility of alpine systems to increased stress from competition as a biotic consequence of climate warming (Klanderud, 2005; Klanderud & Totland, 2005).

Generalist species with higher competitive abilities could, however, be expected to show a dominance of precipitation increase effects (compared to warming effects). *Veronica officinalis* exemplifies this in our study with a neutral effect of warming whereas the wetter and warmer+wetter treatments reduced λ , reflecting the species' affinity to low-moisture environments (Mossberg & Stenberg, 2007). In contrast to the other species, the negative survival contribution to changes in λ was not reduced in the combined treatment. The consequent steep drops in population size under any wetter climate suggest a realistic risk of local extinctions for this species in the nearer future (Morris & Doak, 2002). Also *Viola palustris* showed a stronger similarity between the responses to the wetter and warmer+wetter treatments, especially so for survival. However, while the combined response in *Veronica officinalis* is clearly driven by precipitation increase, it seems more like a mixture of both warming- and precipitation-increase responses in *Viola palustris*. Given the differences in the two species' ecology – *Viola palustris* being moisture adapted and a weak

competitor vs. *Veronica officinalis* being dry-adapted and a better competitor (see above) – our results do not qualify for deducting a common pattern for generalist species.

Non-additive synergistic effects of the individual climatic drivers (i.e. stronger than predicted from summed single effects) did not occur in our experiment, which likely is due to inherent counteractive effects of warming and increased precipitation (Luo et al., 2008; Wu et al., 2011). Thus, quantitative predictions based on single effects would at least not have underestimated the impacts of the combined climatic change. However, such non-additive synergistic effects are anything than rare, occurring about as regularly as antagonistic effects (Darling & Côté, 2008). This highlights that factorial experiments are vital for reasonably precise quantitative predictions of combined climate-change responses (Barnett & Facey, 2016; Darling & Côté, 2008), even when well-known biotic and abiotic affinities of the focal species may tempt one to make predictions based on single factor effects, as is commonly done in the literature (Mundim & Bruna, 2016; Wu et al., 2011).

Plant population responses to climate change have been hypothesized to vary across different climatic contexts throughout the species' range and realized bioclimatic niches (Grime et al., 2000; Holub, Fabsicova, Tuma, Zahora, & Fiala, 2013), but this has rarely been tested empirically (Ehrlén & Morris, 2015; Ehrlén, Morris, von Euler, & Dahlgren, 2016). From niche theory, we could have expected (*hypothesis #3*) stronger negative responses of our alpine species to climate warming in the sub-alpine sites, which are near the 'rear edge' of the species' temperature niche (Hampe & Petit, 2005), as well as generally more negative (or less positive) effects of increased precipitation towards the wettest sites (Schuur, 2003). Our experiment did not support these expectations. In contrast, our study documents less negative effects of increased precipitation, with and without increased temperature, on λ and survival towards lower ambient temperatures in *Viola biflora*, *Viola palustris*, and *Veronica alpina* (Figure 4). A possible reason, why increased precipitation did not impede the alpine

species, could be that a large amount of the precipitation in the alpine falls as snow during the winter. For *Viola biflora*, a snowbed species, λ and survival increased under wetter conditions in the alpine, which might reflect a competitive advantage relative to other species under prolonged snow cover (Reinhardt, Odland, & Pedersen, 2013). In addition, poorly developed alpine soil types, with typically low water retention and high runoff, could buffer against higher precipitation and explain weaker impacts than in the warmer sites with better developed and stronger water-retaining soils (Rawls, Pachepsky, Ritchie, Sobecki, & Bloodworth, 2003).

In summary, our results illustrate important benefits of choosing a more complex experimental design and measuring responses at a more detailed level. The demographic approach allowed us to identify which vital rates were most responsive to the tested climatic changes, the factorial experiment separated non-additive from additive effects, and both approaches together revealed that the mechanisms behind the effects of the climatic changes varied between the vital rates. This illustrates that the links between a changing environmental variable and an affected species are rarely simple and *uni-causal*, which can also be generalized to communities or ecosystems (Emmett et al., 2004; Parmesan & Yohe, 2003). We also demonstrate that including context dependency in the design of a climate change study is a strong approach for achieving results that are both precise and ecologically generalizable (Borer et al., 2014; De Boeck et al., 2015; Fraser et al., 2013; Parmesan & Hanley, 2015), which is important for the development of good spatial predictions for the effects of future environmental changes.

Acknowledgements

We thank T. Bargmann, A. Chételat, F. Duckert, M. Evju, S. Fariñas, K. Ferter, M. Hamacher, K. Klanderud, S. Le Mellec, N. Mahler, E. M. C. Meineri, P. Michel, C. Pötsch, B. Töpper and I. Tween and for assistance in the field and lab, the land-owners for granting us access to their grasslands, and Y. Buckley, J. Alexander, and D. Goldberg for valuable feedback on an earlier version of the manuscript. Financial support came from the Norwegian Research Council (NORKLIMA grant #184912/230) and Olav Grolle Olsens fund at the University of Bergen.

References

- Alexander, J. M., Diez, J. M., & Levine, J. M. (2015). Novel competitors shape species' responses to climate change. *Nature*, 525(7570), 515-518. doi:10.1038/nature14952
- Barnett, K. L., & Facey, S. L. (2016). Grasslands, invertebrates, and precipitation: a review of the effects of climate change. *Frontiers in Plant Science*, 7, 1-8. doi:10.3389/fpls.2016.01196
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1-48. doi:10.18637/jss.v067.i01
- Borer, E. T., Harpole, W. S., Adler, P. B., Lind, E. M., Orrock, J. L., Seabloom, E. W., & Smith, M. D. (2014). Finding generality in ecology: a model for globally distributed experiments. *Methods in Ecology and Evolution*, 5(1), 65-73. doi:10.1111/2041-210x.12125
- Caswell, H. (2001). *Matrix population models: construction, analysis, and interpretation*. (2nd ed.). Sunderland, Massachusetts: Sinauer Associates, Inc. Publishers.
- Darling, E. S., & Côté, I. M. (2008). Quantifying the evidence for ecological synergies. *Ecology Letters*, 11(12), 1278-1286. doi:10.1111/j.1461-0248.2008.01243.x
- De Boeck, H. J., Vicca, S., Roy, J., Nijs, I., Milcu, A., Kreyling, J., . . . Beier, C. (2015). Global change experiments: challenges and opportunities. *Bioscience*, 65(9), 922-931. doi:10.1093/biosci/biv099
- Dunne, J. A., Saleska, S. R., Fischer, M. L., & Harte, J. (2004). Integrating experimental and gradient methods in ecological climate change research. *Ecology*, 85(4), 904-916. doi:10.1890/03-8003
- Easterling, M. R., Ellner, S. P., & Dixon, P. M. (2000). Size-specific sensitivity: Applying a new structured population model. *Ecology*, 81(3), 694-708.
- Ehrlén, J., & Morris, W. F. (2015). Predicting changes in the distribution and abundance of species under environmental change. *Ecology Letters*, 18(3), 303-314. doi:10.1111/ele.12410
- Ehrlén, J., Morris, W. F., von Euler, T., & Dahlgren, J. P. (2016). Advancing environmentally explicit structured population models of plants. *Journal of Ecology*, 104(2), 292-305. doi:10.1111/1365-2745.12523
- Elmendorf, S. C., Henry, G. H. R., Hollister, R. D., Björk, R. G., Bjorkman, A. D., Callaghan, T. V., . . . Wookey, P. A. (2012). Global assessment of experimental climate warming on tundra

- vegetation: heterogeneity over space and time. *Ecology Letters*, 15(2), 164-175. doi:10.1111/j.1461-0248.2011.01716.x
- Emmett, B. A., Beier, C., Estiarte, M., Tietema, A., Kristensen, H. L., Williams, D., . . . Sowerby, A. (2004). The response of soil processes to climate change: results from manipulation studies of shrublands across an environmental gradient. *Ecosystems*, 7(6), 625-637. doi:10.1007/s10021-004-0220-x
- Fraser, L. H., Henry, H. A. L., Carlyle, C. N., White, S. R., Beierkuhnlein, C., Cahill, J. F., . . . Turkington, R. (2013). Coordinated distributed experiments: an emerging tool for testing global hypotheses in ecology and environmental science. *Frontiers in Ecology and the Environment*, 11(3), 147-155. doi:10.1890/110279
- Gottfried, M., Pauli, H., Futschik, A., Akhalkatsi, M., Barancok, P., Alonso, J. L. B., . . . Grabherr, G. (2012). Continent-wide response of mountain vegetation to climate change. *Nature Climate Change*, 2(2), 111-115. doi:10.1038/nclimate1329
- Grabherr, G., Gottfried, M., & Pauli, H. (1994). Climate effects on mountain plants. *Nature*, 369(6480), 448-448. doi:10.1038/369448a0
- Grime, J. P., Brown, V. K., Thompson, K., Masters, G. J., Hillier, S. H., Clarke, I. P., . . . Kiely, J. P. (2000). The response of two contrasting limestone grasslands to simulated climate change. *Science*, 289(5480), 762-765. doi:10.1126/science.289.5480.762
- Guittar, J., Goldberg, D., Klanderud, K., Telford, R. J., & Vandvik, V. (2016). Can trait patterns along gradients predict plant community responses to climate change? *Ecology*, 97(10), 2791-2801. doi:10.1002/ecy.1500
- Guo, Y. H., Yuan, C., Tang, L., Peng, J. M., Zhang, K. L., Li, G., & Ma, X. J. (2016). Responses of clonal growth and photosynthesis in *Amomum villosum* to different light environments. *Photosynthetica*, 54(3), 396-404. doi:10.1007/s11099-016-0194-x
- Hampe, A., & Petit, R. J. (2005). Conserving biodiversity under climate change: the rear edge matters. *Ecology Letters*, 8(5), 461-467. doi:10.1111/j.1461-0248.2005.00739.x
- Harte, J., & Shaw, R. (1995). Shifting dominance within a montane vegetation community - results of a climate-warming experiment. *Science*, 267(5199), 876-880. doi:10.1126/science.267.5199.876
- Herben, T., Šerá, B., & Klimešová, J. (2015). Clonal growth and sexual reproduction: tradeoffs and environmental constraints. *Oikos*, 124(4), 469-476. doi:10.1111/oik.01692
- Holub, P., Fabsicova, M., Tuma, I., Zahora, J., & Fiala, K. (2013). Effects of artificially varying amounts of rainfall on two semi-natural grassland types. *Journal of Vegetation Science*, 24(3), 518-529. doi:10.1111/j.1654-1103.2012.01487.x
- IPCC (2014). *Climate Change 2014: Fifth Assessment Report of the Intergovernmental Panel on Climate Change, Summary for Policymakers*.
- Jensen, K., & Meyer, C. (2001). Effects of light competition and litter on the performance of *Viola palustris* and on species composition and diversity of an abandoned fen meadow. *Plant Ecology*, 155(2), 169-181. doi:10.1023/a:1013270628964
- Klanderud, K. (2005). Climate change effects on species interactions in an alpine plant community. *Journal of Ecology*, 93(1), 127-137. doi:10.1111/j.1365-2745.2004.00944.x
- Klanderud, K., & Totland, Ø. (2005). Simulated climate change altered dominance hierarchies and diversity of an alpine biodiversity hotspot. *Ecology*, 86(8), 2047-2054. doi:10.1890/04-1563
- Klanderud, K., Vandvik, V., & Goldberg, D. (2015). The Importance of biotic vs. abiotic drivers of local plant community composition along regional bioclimatic gradients. *PLoS One*, 10(6). doi:10.1371/journal.pone.0130205
- Klimešová, J., & Herben, T. (2015). Clonal and bud bank traits: patterns across temperate plant communities. *Journal of Vegetation Science*, 26(2), 243-253. doi:10.1111/jvs.12228
- Kollmann, J., & Rasmussen, K. K. (2012). Succession of a degraded bog in NE Denmark over 164 years - monitoring one of the earliest restoration experiments. *Tuexenia*(32), 67-85.

- Lenoir, J., Gegout, J. C., Guisan, A., Vittoz, P., Wohlgemuth, T., Zimmermann, N. E., . . . Svenning, J. C. (2010). Cross-scale analysis of the region effect on vascular plant species diversity in southern and northern European mountain ranges. *PLoS One*, 5(12). doi:10.1371/journal.pone.0015734
- Lenoir, J., Gegout, J. C., Marquet, P. A., de Ruffray, P., & Brisse, H. (2008). A significant upward shift in plant species optimum elevation during the 20th century. *Science*, 320(5884), 1768-1771. doi:10.1126/science.1156831
- Luo, Y., Gerten, D., Le Maire, G., Parton, W. J., Weng, E., Zhou, X., . . . Rustad, L. (2008). Modeled interactive effects of precipitation, temperature, and [CO₂] on ecosystem carbon and water dynamics in different climatic zones. *Global Change Biology*, 14(9), 1986-1999. doi:10.1111/j.1365-2486.2008.01629.x
- Manly, B. F. J. (1997). *Randomization, bootstrap and Monte Carlo methods in biology*. London: Chapman & Hall.
- Meineri, E., Skarpaas, O., Spindelböck, J., Bargmann, T., & Vandvik, V. (2014). Direct and size-dependent effects of climate on flowering performance in alpine and lowland herbaceous species. *Journal of Vegetation Science*, 25(1), 275-286. doi:10.1111/jvs.12062
- Merow, C., Dahlgren, J. P., Metcalf, C. J. E., Childs, D. Z., Evans, M. E. K., Jongejans, E., . . . McMahon, S. M. (2014). Advancing population ecology with integral projection models: a practical guide. *Methods in Ecology and Evolution*, 5(2), 99-110.
- Metcalf, C. J. E., McMahon, S. M., Salguero-Gomez, R., & Jongejans, E. (2013). IPMPack: an R package for integral projection models. *Methods in Ecology and Evolution*, 4(2), 195-200. doi:10.1111/2041-210x.12001
- Méthy, M., Alpert, P., & Roy, J. (1990). Effects of light quality and quantity on growth of the clonal plant *Eichhornia crassipes*. *Oecologia*, 84(2), 265-271. doi:10.1007/bf00318283
- Morris, W. F., & Doak, D. F. (2002). *Quantitative conservation biology: theory and practice of population viability*. Massachusetts, USA: Sinauer.
- Mossberg, B., & Stenberg, L. (2007). *Gyldendals store nordiske flora* (2 ed.). Stockholm: Gyldendal.
- Mundim, F. M., & Bruna, E. M. (2016). Is there a temperate bias in our understanding of how climate change will alter plant-herbivore interactions? A meta-analysis of experimental studies. *American Naturalist*, 188, S74-S89. doi:10.1086/687530
- Oberbauer, S. F., Elmendorf, S. C., Troxler, T. G., Hollister, R. D., Rocha, A. V., Bret-Harte, M. S., . . . Welker, J. M. (2013). Phenological response of tundra plants to background climate variation tested using the International Tundra Experiment. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 368(1624). doi:10.1098/rstb.2012.0481
- Olsen, S. L., Töpper, J. P., Skarpaas, O., Vandvik, V., & Klanderud, K. (2016). From facilitation to competition: temperature-driven shift in dominant plant interactions affects population dynamics in semi-natural grasslands. *Global Change Biology*, 22, 1915-1926. doi:10.1111/gcb.13241
- Parmesan, C., & Hanley, M. E. (2015). Plants and climate change: complexities and surprises. *Annals of Botany*, 116(6), 849-864. doi:10.1093/aob/mcv169
- Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421(6918), 37-42. doi:10.1038/nature01286
- Pauli, H., Gottfried, M., Dullinger, S., Abdaladze, O., Akhalkatsi, M., Alonso, J. L. B., . . . Grabherr, G. (2012). Recent plant diversity changes on Europe's mountain summits. *Science*, 336(6079), 353-355. doi:10.1126/science.1219033
- Pearson, R. G., Stanton, J. C., Shoemaker, K. T., Aiello-Lammens, M. E., Ersts, P. J., Horning, N., . . . Akçakaya, H. R. (2014). Life history and spatial traits predict extinction risk due to climate change. *Nature Climate Change*, 4(3), 217-221. doi:10.1038/nclimate2113
- R Development Core Team. (2016). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <http://www.R-project.org>

- Rawls, W. J., Pachepsky, Y. A., Ritchie, J. C., Sobecki, T. M., & Bloodworth, H. (2003). Effect of soil organic carbon on soil water retention. *Geoderma*, 116(1-2), 61-76. doi:10.1016/s0016-7061(03)00094-6
- Reinhardt, S., Odland, A., & Pedersen, A. (2013). Calciphile alpine vegetation in Southern Norway: importance of snow and possible effects of climate change. *Phytocoenologia*, 43(3-4), 207-223. doi:10.1127/0340-269x/2013/0043-0534
- Root, T. L., & Schneider, S. H. (1995). Ecology and climate - research strategies and implications. *Science*, 269(5222), 334-341. doi:10.1126/science.269.5222.334
- Rustad, L. E. (2008). The response of terrestrial ecosystems to global climate change: towards an integrated approach. *Science of the Total Environment*, 404(2-3), 222-235. doi:10.1016/j.scitotenv.2008.04.050
- Schuur, E. A. G. (2003). Productivity and global climate revisited: the sensitivity of tropical forest growth to precipitation. *Ecology*, 84(5), 1165-1170. doi:10.1890/0012-9658(2003)084[1165:pagcrt]2.0.co;2
- Wang, M. T., Zhao, Z. G., Du, G. Z., & He, Y. L. (2008). Effects of light on the growth and clonal reproduction of *Ligularia virgaurea*. *Journal of Integrative Plant Biology*, 50(8), 1015-1023. doi:10.1111/j.1744-7909.2008.00645.x
- Wang, P., Lei, J. P., Li, M. H., & Yu, F. H. (2012). Spatial heterogeneity in light supply affects intraspecific competition of a stoloniferous clonal plant. *PLoS One*, 7(6). doi:10.1371/journal.pone.0039105
- Wu, Z., Dijkstra, P., Koch, G. W., Peñuelas, J., & Hungate, B. A. (2011). Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. *Global Change Biology*, 17(2), 927-942. doi:10.1111/j.1365-2486.2010.02302.x
- Xie, T. P., Zhang, G. F., Zhao, Z. G., Du, G. Z., & He, G. Y. (2014). Intraspecific competition and light effect on reproduction of *Ligularia virgaurea*, an invasive native alpine grassland clonal herb. *Ecology and Evolution*, 4(6), 817-825. doi:10.1002/ece3.975
- Ye, D., Hu, Y. K., Song, M. H., Pan, X., Xie, X. F., Liu, G. F., . . . Dong, M. (2014). Clonality-climate relationships along latitudinal gradient across China: adaptation of clonality to environments. *PLoS One*, 9(4). doi:10.1371/journal.pone.0094009

Figure captions

Figure 1. **Experimental design and geographical location of the study area and study sites.** Point-up triangles are alpine, circles are sub-alpine, and point-down triangles are boreal sites. Increasing precipitation level indicated by increasingly saturated blue. Colored arrows indicate direction of transplantation: red = warmer, blue = wetter, purple = warmer+wetter, black = control.

Figure 2. **Effects of increased temperature and precipitation on population growth rates (a) and vital rates (b).** Shown are (a) the median differences in population growth rates ($\Delta\lambda$) between climate transplants and controls and (b) the median vital rate contributions to $\Delta\lambda$ for all species and treatments. Error bars in (a) indicate bootstrap confidence intervals (0.025 and 0.975 quantiles of 10,000 bootstrapped $\Delta\lambda$). Numbers in (a) indicate percentage of bootstrap $\Delta\lambda$ values that are lower or higher (as indicated by the direction of the bar) than zero.

Figure 3. **Effects of increased temperature and precipitation on overall vegetation height.** Shown is the mean difference in overall vegetation height between the respective climate transplants and the home controls in each block. Error bars indicate 95% confidence intervals. Significant differences to values in 2009 indicated by stars: *** < 0.001 < ** < 0.01 < * < 0.05 < ° < 0.1.

Figure 4. **Non-additivity vs. additivity of effects of increased temperature and precipitation.** Predicted values for changes in population growth rate ($\Delta\lambda$), survival, and clonality from added single treatment (x-axes) plotted against observed values from the combined treatment (y-axes) in all study species. The dashed line represents the perfect match between prediction and observation. Hence, a data cloud placed symmetrically on the dashed line indicates additivity, while non-symmetry indicates non-additivity. The area above the line indicates less negative (or more positive) effects than predicted, the area below the opposite. The numbers shown in the larger area (above or below the dashed line) of the respective data clouds indicate the percentage of 10,000 bootstraps lying in that area.

Figure 5. **Temperature context dependency.** Changes in population growth rate ($\Delta\lambda$) and survival in response to warming, increased precipitation, and the combined treatment as a function of mean site summer temperature across *Viola biflora*, *Viola palustris*, and *Veronica alpina*. The fourth study species, *Veronica officinalis*, was omitted from the analysis as it occurs at only one temperature level in the warmer and warmer+wetter climate transplants, but is indicated by '×'. The colored lines represent regression predictions from 10,000 linear mixed effect models with the bootstrapped $\Delta\lambda$ or survival contribution per site as response variable, home site temperature as fixed effect explanatory variable, and species identity as random effect. The bold black line represents the regression prediction based on the median $\Delta\lambda$ or survival contribution per site. The number in the upper right corner indicates the percentage of negative bootstrap slopes.