Widespread latitudinal asymmetry in marginal population performance

Running title: *Asymmetry in marginal population performance*

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Abstract

Aim

Range shifts are expected to occur when populations at one range margin perform better than those at the other margin, yet no global trend in population performances at range margins has been demonstrated empirically across a wide range of taxa and biomes. Here we test the prediction that, if impacts of ongoing climate change on population performance are widespread, then populations from the high-latitude margin (HLM) should perform as well as or better than central populations, whereas populations at low-latitude margins (LLM) populations should perform worse.

Location

Global

Time period

1898–2020

Major taxa studied

Plants and animals

Methods

To test our prediction, we used a meta-analysis quantifying the empirical support for asymmetry in the performance of high- and low-latitude margin populations compared to central populations. Performance estimates were derived from 51 papers involving 113 margin-centre comparisons from 54 species and 705 populations. We then related these performance differences to climatic differences among populations. We also tested whether patterns are consistent across taxonomic kingdoms (plants *vs*. animals) and across habitats (marine *vs*. terrestrial).

Results

Populations at margins performed significantly worse than central populations and this trend was primarily driven by the low-latitude margin. Although the difference was of small magnitude, it was largely consistent across biological kingdoms and habitats. The differences in performance were positively related to the difference in average temperatures between populations during the period 1985–2016.

Major conclusions

The observed asymmetry in marginal population performance confirms predictions about the effects of global climate change. It indicates that changes in demographic rates in marginal populations, despite extensive short-term variation, can serve as early-warning signals of impending range shifts.

Keywords: centre-periphery hypothesis, demographic rates, latitudinal asymmetry, marginal populations, population performance, range margin, range shift.

Introduction

Ongoing climate changes are predicted to increase mismatches between current environmental conditions and the climate to which local populations are adapted (Svenning & Sandel 2013). These mismatches should in turn result in range-wide asymmetries in population growth rates with positive rates at the upper latitudinal or altitudinal range edges, and negative ones at low-latitude or altitude edges. Such asymmetries in population growth rates have been hypothesized to be the main driver of large-scale geographical range shifts (Parmesan et al. 1999, Sexton et al. 2009, Lenoir & Svenning 2015). Yet, we know little about how generalised asymmetries in marginal population growth rates are globally. Population growth rates are difficult to monitor directly, but the demographic processes underlying these rates, such as survival and fecundity, are more accessible to short-term observation. Quantifying the global extent of asymmetry in demographic processes should thus allow us to assess existing disequilibrium of species ranges with climate and hence the propensity of species to shift their range. Such knowledge is crucial to accurately forecast future climate-driven range shifts (Dullinger et al. 2012, Normand et al. 2013) and changes in ecosystem functioning, and for informing resource and conservation planning.

Putatively climate-driven distribution changes have been extensively reported in recent years (Chen et al. 2011, Wiens 2016, Lenoir et al. 2020). However, causal relationships with recent climate changes are difficult to establish because range limits can

also be constrained by diverse non-climatic factors, such as habitat availability, dispersal limitation or biotic interactions (Louthan et al. 2015, Hargreaves et al. 2014, Lee-Yaw et al. 2016, Pironon et al. 2017), and especially long-lived and immobile species may accumulate extensive extinction debts and colonisation credits (Talluto et al. 2017). Changes in the performance of marginal populations should hence represent a much more direct and immediate indicator of species' response to climate warming than distribution changes (Vilà-Cabrera et al. 2019). Still, the effects of climate on population performance will often be difficult to detect except in meteorologically extreme years. Long-term observations that enable detecting such events in marginal population dynamics are, however, rare, especially for populations at contracting range margins (Hill et al. 2011, James et al. 2015, Fredston-Hermann et al. 2020, Hastings et al. 2020, Kunstler et al. 2021). Hence, we need other approaches to assess if range-wide asymmetries in population performances occur.

Here, we use the abundant empirical literature spawned by the so-called centre-periphery (CP) paradigm to examine differences in population performance between the range centre and the high- and low-latitude margins for a wide range of taxa. This paradigm states that the size, density and long-term growth rate of populations tend to decrease from the centre towards the periphery of the range as environmental conditions become increasingly less favourable (Brown 1984, Sagarin & Gaines 2006, Sexton et al. 2009) (Fig. 1). The centre-periphery paradigm has motivated hundreds of comparisons of various indicators of population performance (including measures of individual survival or fecundity, population viability and others) in central and marginal populations (Pironon et al. 2017).

We selected a comprehensive sample of published studies to compare measures of population performance in sites located at the centre and at the high-latitude margins

(HLM) or low-latitude margins (LLM) of species ranges. We predicted that if impacts of ongoing climate change on population performance are widespread, then (i) HLM populations should perform as well as or better than central populations, whereas LLM populations should perform worse than central and HLM populations (Fig. 1). To test this prediction, we employed information from empirical studies to quantify differences in the performance of HLM, LLM and central populations, and to test if patterns are consistent across taxonomic kingdoms (plants *vs*. animals) and across habitats (marine *vs*. terrestrial). We also predicted that if climate is a major driver of differences in population performance, then (ii) performance differences should increase with the difference in climate between central and marginal populations (Fig. 1). To test this prediction, we relate the observed differences in performance between central and peripheral populations to differences in climate.

Materials and methods

Data compilation

We searched Web of Knowledge® and Scopus until 19th April 2020 for publications in peer-reviewed international scientific journals using key search terms in the title or the abstract. In addition, we searched Google Scholar using the same terms in the full text of scientific publications, and restricting our selection to the first 200 references found. The terms 'centre/center-periphery', 'central-marginal', 'abundant centre/center', and 'latitudinal cline' were introduced in combination with performance related terms including 'fecundity', 'performance', 'survival', 'recruitment' and 'population growth rate'. Three filters were then applied to the initial subset of papers. First, we only considered studies

reporting field data from natural populations, including control populations of transplant experiments if these were measured at their home sites and met all other criteria. Second, we only considered studies with at least two central and two peripheral populations (i.e., true replicates). Third, we only considered papers that provided sufficiently clear criteria for the definition of central and peripheral range parts relative to the global range of the target species (and not only parts of it). This filtering procedure resulted in a total of 51 publications, with 113 centre-periphery contrasts of 54 species. The workflow and output of our compilation and selection process is described in Supplementary Information 1.

We extracted the reported performance metrics from each primary paper and assigned them to one of three categories: (i) 'Survival' (e.g., mortality of individuals or ramets, rates of fruit abortion or germination), (ii) 'Reproduction' (e.g., proportion of actively reproducing individuals, seed number, gonadal mass, total seed or egg mass), or (iii) 'Lifetime fitness' (e.g., different estimates of population growth rate). Moreover, we assigned each case study to one of two major taxonomic groups (plants *vs*. animals) and habitat (terrestrial *vs*. marine). Two major kinds of papers provided suitable information: (i) explicit CP comparisons of mean performance values from populations classified as central or marginal by the authors, and (ii) papers reporting on latitudinal clines. In the first case, we followed the criteria of the original authors for classifying populations as central or marginal. In the second case, we selected the three most central and the three most marginal populations along the gradient (rarely more if several populations were located closely together). We extracted quantitative data for our target metrics either manually from text and tables or from figures with Dagra digitizing software version 2.0.12 (Blue Leaf Software 2016). We recorded mean values for each individual population (Fig. S3), and

then calculated the average performance, sample size and resulting standard deviation for central, high- and low-latitude margins, respectively.

Meta-analysis of differences between marginal and central populations

Effect Sizes – We used Hedges' *d* statistic as our standardised measure of effect size. Hedges' *d* is the most appropriate effect size to compare raw means when both positive and negative values are present in data (Koricheva et al. 2013). Hedges' *d* was calculated as:

$$d = J\frac{\overline{X_{margin}} - \overline{X_{center}}}{\sqrt{\frac{(n_{margin} - 1)\, s^2_{margin} + (n_{center} - 1)\, s^2_{center}}{n_{margin} + n_{center} - 2}}}$$

where

$$J = 1 - \frac{3}{4\,(n_{margin} + n_{center} - 2) - 1}$$

and $\overline{X}$, n and s^2 the mean, sample size and sampling variance.

Negative values of *d* indicate lower performance in marginal (either HLM or LLM) populations than in central populations (consistent with the CP paradigm), whereas positive values indicate higher performance. The sampling variance of effect sizes was:

$$v_d = \frac{n_{center} + n_{margin}}{n_{center} \times n_{margin}} + \frac{d^2}{2\,(n_{center} + n_{margin})}$$

Note that v_d contains information about both the sample size and the standard deviation (within d^2) of the original studies; it hence can be used to weight the relative importance of studies within the meta-analysis. In some papers, both HLM populations and LLM populations were compared to the same central populations, resulting in an overestimated pooled sample size ($N = n_{center} + n_{margin}$) because, for such primary papers, n_{center} is counted twice. We manually corrected N in all such cases before conducting the analysis.

Meta-analytical models – Our dataset had a hierarchical structure as some primary papers contained several case studies. We accounted for this potential non-independence of cases by estimating model heterogeneity from multiple sources: (i) among true effect sizes, (ii) among CP comparisons stemming from the same primary papers (by computing the variance-covariance matrix among all effect sizes), and (iii) among groups of moderators. This was done using multi-level error meta-analysis with the *rma.mv* function of the R package *metafor* v. 2.0-0 (Viechtbauer 2010). Primary paper identity was declared as a random factor and individual CP comparisons were nested as random factor within primary papers. We estimated variance components for primary papers (σ_1^2) and case studies (σ_2^2) together with intra-class correlations (ρ), i.e., correlations between true effect sizes from the same study (such that $\rho = \sigma_1^2 / (\sigma_1^2 + \sigma_2^2)$).

We first calculated grand mean effect size as the overall weighted mean across all effect sizes (Borenstein et al. 2007). This corresponds to a random-effects meta-analysis, where heterogeneity among true effect sizes (τ^2) is used to weight individual effects sizes (weight = $1/(v + \tau^2)$). Then, we used multi-level (hierarchical) meta-analyses to test the effect of three moderators: Margin (HLM vs. LLM), Kingdom (animals vs. plants) and Habitat (marine vs. terrestrial). We built a set of the 17 possible models including all possible combinations of simple effects (n = 7 models) and two-way interactions among

Margin, Kingdom and Habitat (n = 10 models). We ranked these 17 models plus the null model (i.e., intercept only) according to their AIC_c using the R package *glmulti* v. 1.0.7 (Calcagno 2013). For each model, we calculated ΔAIC_c and AIC_c weight (w_i). Models within $\Delta AIC_c < 2$ were considered as best models, given the data structure and the model set (Table 1). AIC_c weights represent the probability that a given model is the best model in the set of models considered. For each moderator, we then estimated its relative importance (w_H) by summing all w_i of the models including this moderator ($w_H = \Sigma w_i$); w_H can be interpreted as the probability that a given moderator is included in the best model (Fig. S2). Finally, we estimated model parameters for all competing models with $\Delta AICc < 2$. We reported model parameter estimates for the best model and, whenever necessary, for competing models. Further details upon the meta-analysis, including several assessments of its inherent reliability (e.g., publication bias, balanced representation of moderators, etc.) are shown in Supplementary Information 2.

Relationship between climate and differences in population performance

Climate data – We gathered the geographical coordinates of all populations included in the meta-analysis from the primary papers (n = 705 populations). For each population, we calculated the average annual temperature between 1985 and 2016 (i.e., when most studies were performed) based on monthly temperature data from CRU TS 4.04 (Harris et al. 2020) for terrestrial species and HadISST 1.1 (Rayner et al. 2003) for marine species. For terrestrial taxa, we also extracted average annual precipitation at each site, again from CRU TS 4.04. We could not match climate data for two fish species (Heibo et al. 2005, Power et al. 2005; Appendix 1) and hence excluded these species from the analyses. The final dataset for the climatic analysis contained 683 populations from 52 species (37

terrestrial, 15 marine) and 109 margin–centre comparisons (Fig. S3). We then aggregated populations to calculate average temperature and precipitation for each combination of study, species, performance variable, and region (either central, HLM, or LLM). We could then relate each comparison of performance between a margin (HLM or LLM) and the central range (i.e., Hedges' *d*) with the difference in average temperatures or precipitation between both regions.

Analysis of relationships between climate and population performance – To assess the relationship between the differences in performance and the differences in climate between marginal and central populations, we used generalised additive mixed models (function gam in the R package *mgcv*, version 1.8-17 [Wood 2006]) using the temperature differences as predictor, and the study as random effect (to control for lack of independence). We weighted performance effect sizes by their variances so that their influence in model calibration was inversely related to their uncertainty. For the terrestrial taxa, we also fitted a similar model including precipitation and its interaction with temperature as predictors (see Supplementary Information 3 for further details).

Results

Marginal populations performed on average worse than central populations, since grand mean effect size was negative (-0.35; 95% CI: -0.66, -0.04). There was a significant amount of heterogeneity, and 58% of the total heterogeneity was due to among-study heterogeneity ($\tau^2 = 1.29$, $Q_E = 362.48$, $P < 0.0001$). Five models received relatively strong support, at the level of $\Delta AIC_c \leq 2.0$. All five included margin type as a moderator ($w_H = 0.99$).

Performance declined more strongly towards the low-latitude margin (effect size: -0.94; 95% CI: -1.42, -0.46; estimated from the model with Margin as the sole moderator) than towards the high-latitude margin (effect size: -0.37; 95% CI: -0.80, 0.07) (Fig. 2). The difference between population performance in both margins was significant in the five models with ΔAICc ≤ 2 (Table 1). The best model explained only 5% of the total heterogeneity. The five models with ΔAICc ≤ 2 also included Habitat, Kingdom and the Margin × Habitat interaction as moderators, but their relative importance was low (w_H < 0.75); only one of the differences between aquatic and terrestrial habitats was significant, whereas none of the comparisons between plants and animals were significant (Fig. 3).

The differences in performance between marginal and central populations were significantly related to the difference in their average temperature in the period 1985–2016 (F = 3.39, P = 0.017; Table S3; total deviance explained by an additive mixed model: 20.8%). As predicted, performance decreased with increasingly departing temperatures from central populations, although the decline was asymmetric between high- and low-latitude populations (Fig. 4): HLM populations experiencing 5 ºC colder temperatures than central populations showed similar performance, whereas LLM populations experiencing 5°C warmer temperatures performed significantly worse (Fig. 4). Differences in population performance were not related to geographical distance between marginal and central populations (Fig. S4). In terrestrial species, population performance showed a similar asymmetric response to temperature (i.e., higher overall performance in HLM than LLM for similar temperature deviations), although there was a significant interactive effect of precipitation (F = 2.70, P = 0.024, total deviance explained = 29.5%; Table S4). With decreasing precipitation, relative performance in marginal populations decreased faster at both margins, albeit more so in low-latitude populations (Fig. 5).

Discussion

Overall, our results show that populations from the centre of the range tend to outperform those residing at the range margins, and that these differences are more pronounced at low-latitude margins. Such latitudinal asymmetry is predicted when the environmental conditions relevant for population performance are directionally displaced (Lenoir & Svenning 2015; Fig. 1). Global warming has provoked a rapid large-scale poleward displacement of climatic zones since the 1970s, and the trend is predicted to further accelerate through the coming decades (IPCC 2013). The observed difference is therefore likely to largely result from ongoing climate change, although we cannot exclude effects of changes in factors unrelated with current climate, such as historical colonisation lags or biotic interactions (Normand et al. 2011, Hargreaves et al. 2014, Louthan et al. 2015). To achieve further insights into this question, we thoroughly searched the literature (including the BIOSHIFT database, Lenoir et al. 2020) for reports on observed range shifts of the species included in our meta-analysis. We detected a total of 26 range shifts concerning 16 of our species; most shifts (19 out of 26) were polewards (see Table 2). Although limited, this evidence suggests that demographic rates in marginal populations act indeed as early-warning signals of impending range shifts.

The type of range margin (HLM or LLM) explained only a moderate 4% of the overall variation in the relative performance of marginal populations. This is unsurprising given the great variety of organisms, response variables, and ecological contexts considered in our analysis. In addition, most primary studies reported only short-term data that are likely to miss relevant periods of (by definition rare) climatic extreme events and may thus

not fully capture long-term trends in those populations. Finally, performance at certain specific life stages is not necessarily a reliable predictor of lifetime fitness and population growth rates (Villellas et al. 2015, Lee-Yaw et al. 2016). Despite these diverse limitations, the type of range margin still was the main predictor of performance in marginal populations. Thirty-seven (82%) of the 45 comparisons available for the low-latitude margin showed worse performance in LLM than central populations, compared to 34 (53%) of 64 comparisons for HLM populations.

Our findings suggest that latitudinal asymmetries in demographic performance exist worldwide, and occur in both animals and plants and in both terrestrial and marine species. This ubiquity is particularly striking given the great diversity of ecological strategies to cope with environmental stresses and hazards. For instance, plants generally have a greater capacity to buffer climatic stress through phenotypic plasticity and persistent life cycle stages than animals (Villellas et al. 2015, see also Lloret et al. 2012), which would allow them to slow population declines and accumulate a higher extinction debt (Jackson & Sax 2009, Jump et al. 2009). Moreover, climate is shifting at different pace in marine and terrestrial environments, with median temperatures increasing more than three times faster on land than at sea (Burrows et al. 2011). Water temperature and related properties typically drive population dynamics of marine species, whereas many LLM populations of terrestrial species are primarily constrained by water balance (Hampe & Jump 2011; Vilà-Cabrera et al. 2019). This difference may also explain why marine ectothermic animals tend to more fully occupy the latitudinal ranges situated within their thermal tolerance limits than terrestrial ectotherms (Sunday et al. 2012).

Although purely correlational, the analysis of relationships between differences in population performance and local climates provides interesting insights that add further

support to our climate-change based interpretation of geographical trends in marginal population performance. First, centre-margin differences in population performance were generally related to differences in temperature, yet this link was far stronger in LLM populations than in HLM populations. Such an asymmetry is expected under recent global climate warming which tends to exacerbate temperature-related climatic constraints for LLM population performance, while relaxing them in HLM populations (Normand et al. 2009, Hastings et al. 2020, Kuntsler et al. 2020). Low levels of precipitation reinforced the observed temperature effect, and this was once again especially true in LLM populations. This trend is likewise expectable under recent climate warming, given that many LLM populations of terrestrial organisms experience constraints from water availability (Vilà-Cabrera et al. 2019) and their performance should hence suffer most strongly when a temperature increase goes along with low levels of precipitation.

Conclusions

Given that differences in population performance can represent a powerful early indicator of impending range shifts (Parmesan et al. 1999, Lenoir & Svenning 2015), our results indicate that many extant species ranges are not in equilibrium with current climates even though they to date have not experienced perceivable shifts. Considering empirical fitness trends in marginal populations will substantially increase the realism of population-based approaches to species distribution modelling (Anderson et al. 2009, Maier et al. 2014). Given that latitudinal range shifts are likely to be ongoing or impending for many species, such improved predictive capacity is needed if we are to forecast their implications for biodiversity and ecosystem function.

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References

Anderson, B. J., Akçakaya, H. R., Araújo, M. B., Fordham, D. A., Martinez-Meyer, E., Thuiller, W., & Brook, B. W. (2009). Dynamics of range margins for metapopulations under climate change. *Proceedings of the Royal Society B*, 276, 1415-1420.

Blue Leaf Software (2016). Dagra digitizing software version 2.0.12. http://www.blueleafsoftware.com/Products/Dagra/

Borenstein, M., Hedges, L., & Rothstein, H. (2007). Comprehensive Meta-analysis. (http://www.meta-analysis.com/downloads.

Brown, J. H. (1984). On the relationship between abundance and distribution of species. *American Naturalist*, 124, 255-279.

Burrows, M. T., Schoeman, D. S., Buckley, L. B., Moore, P., Poloczanska, E. S., & Brander, K. M. (2011). The pace of shifting climate in marine and terrestrial ecosystems. *Science*, 334, 652-655.

Calcagno, V. (2013). glmulti: Model selection and multimodel inference made easy. R package version 1.0.7. (https://CRAN-R-project.org/package=glmulti).

Chen, I. C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, 333, 1024-1026.

Dullinger, S., Gattringer, A., Thuiller, W., Moser, D., Zimmermann, N. E., Guisan, A., Willner, W., Plutzar, C., Leitner, M., Mang, T., Caccianiga, M., Dirnböck, T., Ertl, S., Fischer, A., Lenoir, J., Svenning, J. C., Psomas, A., Schmatz, D. R., Silc, U., Vittoz, P., & Hülber, K. (2012). Extinction debt of high-mountain plants under twenty-first-century climate change. *Nature Climate Change*, 2, 619-622.

Fredston-Hermann, A., Selden, R., Pinsky, M., Gaines, S. D., & Halpern, B. S. (2020). Cold range edges of marine fishes track climate change better than warm edges. *Global Change Biology*, 26, 2908-2922.

Hampe, A., & Jump, A. S. (2011). Climate relicts: past, present, future. *Annual Review of Ecology, Evolution & Systematics*, 42, 313-333.

Hargreaves, A. L., Samis, S. E., & Eckert, C.G. (2014). Are species' range limits simply niche limits writ large? A review of transplant experiments beyond the range. *American Naturalist*, 183, 157-173.

Harris, I. C., Jones, P. D., & Osborn, T. (2020). CRU TS4.04: Climatic Research Unit (CRU) Time-Series (TS) version 4.04 of high-resolution gridded data of month-by-month variation in climate (Jan. 1901- Dec. 2019). Centre for Environmental Data Analysis, https://catalogue.ceda.ac.uk/uuid/89e1e34ec3554dc98594a5732622bce9

Hastings, R. A., Rutterford, L. A., Freer, J. J., Collins, R. A., Simpson, S. D., & Genner, M. J. (2020). Climate change drives poleward increases and equatorward declines in marine species. *Current Biology*, 30, 1572-1577.

Hill, J. K., Griffiths, H. M., & Thomas, C. D. (2011). Climate change and evolutionary adaptations at species' range margins. *Annual Review of Entomology*, 56, 143-159.

IPCC (2013). Climate Change 2013 – The Physical Science Basis. Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. T. F. Stocker et al. Eds., Cambridge University Press.

Jackson, S. T., & Sax, D. J. (2009). Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. *Trends in Ecology and Evolution*, 25, 153-160.

Jump, A. S., Mátyás, C., & Peñuelas, J. (2009). The altitude-for-latitude disparity in the range retractions of woody species. *Trends in Ecology and Evolution*, 24, 694-701.

Koricheva, J., Gurevith, K., & Mengersen, K. (2013). Handbook of meta-analysis in ecology and evolution. Princeton University Press, Princeton.

Kunstler, G., Guyennon, A., Ratcliffe, S., Rüger, N., Ruiz-Benito, P., Childs, D. Z., ... & Salguero-Gomez, R. (2020). Demographic performance of European tree species at their hot and cold climatic edges. *Journal of Ecology*, 109, 1041-1054.

Lee-Yaw, J. A., Kharouba, H. M., Bontrager, M., Mahony, C., Csergo, A. M., Noreen, A. M. E., Li, Q., Schuster, R., & Angert, A.L. (2016). A synthesis of transplant experiments and ecological niche models suggests that range limits are often niche limits. *Ecology Letters*, 19, 710-722.

Lenoir, J., Bertrand, R., Comte, L., Bourgeaud, L., Hattab, T., Murienne, J., & Grenouillet, G. (2020). Species better track climate warming in the oceans than on land. *Nature Ecology & Evolution*, 4, 1044-1059.

Lenoir, L., & Svenning, J. C. (2015). Climate-related range shifts – a global multidimensional synthesis and new research directions. *Ecography*, 38, 15-28.

Lloret, F., Escudero, A., Iriondo, J. M., Martínez-Vilalta, J., & Valladares, F. (2012). Extreme climatic events and vegetation: the role of stabilizing processes. *Global Change Biology*, 18, 797-805.

Louthan, A. M., Doak, D. F., & Angert, A. L. (2015). Where and when do species interactions set range limits? *Trends in Ecology and Evolution*, 30, 780-792.

Mair, L., Hill, J. K., Fox, R., Botham, M., & Thomas, C. D. (2014). Abundance changes and habitat availability drive species' responses to climate change. *Nature Climate Change*, 4, 127-131.

Normand, S., Randin, C., Ohlemüller, R., Bay, C., Høye, T. T., Kjær, E. D., Körner, C., Lischke, H., Maiorano, L., Paulsen, J., Pearman, P. B., Psomas, A., Treier, U. A.,

Zimmermann, N. E., & Svenning, J. C. (2013). A greener Greenland? Climatic potential and long-term constraints on future expansions of trees and shrubs. *Philosophical Transactions of the Royal Society B*, 368, 2012047.

Normand, S., Ricklefs, R. E., Skov, F., Bladt, J., Tackenberg, O., & Svenning, J.C. (2011). Postglacial migration supplements climate in determining plant species ranges in Europe. *Proceedings of the Royal Society B*, 278, 3644-3653.

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J. K., Thomas, C. D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W. J., Thomas, J. A., & Warren, M. (1999). Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, 399, 579-583.

Pironon, S., Papuga, G., Villellas, J., Angert, A. L., García, M. B., & Thompson, J. D. (2017). Geographic variation in genetic and demographic performance: new insights from an old biogeographical paradigm. *Biological Reviews*, 92, 1877-1909.

Rayner, N. A., Parker, D. E., Horton, E. B., Folland, C. K., Alexander, L. V., Rowell, D. P., Kent, E. C., & Kaplan, A. (2003). Global analyses of sea surface temperature, sea ice, and night marine air temperature since the late nineteenth century. *Journal of Geophysical Research*, 108, 4407.

Sagarin, R. D., Gaines, S. D., & Gaylord, B. (2006). Moving beyond assumptions to understand abundance distributions across the ranges of species. *Trends in Ecology and Evolution*, 21, 524-530.

Sexton, J. P., McIntyre, P. J., Angert, A. L., & Rice, K. J. (2009). Evolution and ecology of species range limits. *Annual Review of Ecology, Evolution and Systematics*, 40, 415-436.

Sunday, J. M., Bates, A. E., & Dulvey, N. K. (2012). Thermal tolerance and the global redistribution of animals. *Nature Climate Change*, 2, 686-690.

Svenning, J. C., & Sandel, B. (2013). Disequilibrium vegetation dynamics under future climate change. *American Journal of Botany*, 100, 1266-1286.

Talluto, M. V., Boulangeat, I., Vissault, S., Thuiller, W., & Gravel, D. (2017). Extinction debt and colonization credit delay range shifts of eastern North American trees. *Nature Ecology & Evolution*, 1, 182.

Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, 36, 1-48.

Vilà-Cabrera, A., Premoli, A. C., & Jump, A. S. (2019). Refining predictions of population decline at species' rear edges. *Global Change Biology*, 25, 1549-1560.

Villellas, J., Doak, D. F., García, M. B., & Morris, W. F. (2015). Demographic compensation among populations: what is it, how does it arise and what are its implications? *Ecology Letters*, 18, 1139-1152.

Wiens, J. J. (2016). Climate-related local extinctions are already widespread among plant and animal species. *PLoS Biology*, 14, e2001104.

Wood, S. N. (2006). Generalized Additive Models: An Introduction with R. Chapman and Hall/CRC.

Data and materials availability

Data and code that support the findings of this study have been archived at https://doi.org/10.15454/STOJ93.

Table 1. Summary of the five models retained in the set of best models (i.e., with $\Delta AIC_c < 2$). Margin explained a significant amount of heterogeneity in each of the five competing best models whereas neither Kingdom nor Habitat explained a significant amount of heterogeneity in any of the five models retained in the set of best models. QM and associated P-values represent the test associated with each moderator, separately. Pseudo R^2 were calculated as 1 – LLR, where LLR is the ratio between the log-likelihood of model i and the log-likelihood of the null model.

Models	Parameters	Estimate (± 95% CI)	Q_M	Q_E	pseudoR2
Model 1	Intercept (HLM, Aquatic)	0.3 (-0.28, 0.88)	14.06 (0.001)	335.62 (< 0.001)	0.04
	Margin (LMM)	**-0.72 (-1.12, -0.31)**			
	Habitat (Terrestrial)	-0.5 (-1.14, 0.14)			
Model 2	Intercept (HLM)	-0.07 (-0.41, 0.27)	11.65 (0.001)	342.87 (< 0.001)	0.029
	Margin (LLM)	**-0.71 (-1.11, -0.30)**			
Model 3	Intercept (HLM, Aquatic)	0.49 (-0.17, 1.15)	15.45 (0.001)	334.47 (< 0.001)	0.048
	Margin (LLM)	**-1.16 (-1.95, -0.36)**			
	Habitat (Terrestrial)	-0.75 (-1.51, 0.01)			
	Margin (LMM) × Habitat (Terrestrial)	0.59 (-0.33, 1.50)			
Model 4	Intercept (HLM, Aquatic, Animals))	0.23 (-0.36, 0.82)	15.07 (0.002)	334.39 (< 0.001)	0.049
	Margin (LLM)	**-0.73 (-1.13, -0.32)**			
	Habitat (Terrestrial)	-0.69 (-1.43, 0.04)			
	Kingdom (Plants)	0.35 (-0.32, 1.02)			
Model 5	Intercept (HLM, Aquatic, Animals))	0.43 (-0.24, 1.09)	16.69 (0.002)	332.96 (< 0.001)	0.057
	Margin (LLM)	**-1.21 (-2.01, -0.41)**			
	Habitat (Terrestrial)	**-0.99 (-1.85, -0.13)**			
	Kingdom (Plants)	0.4 (-0.29, 1.08)			
	Margin (LMM) × Habitat (Terrestrial)	0.64 (-0.28, 1.56)			

Table 2. List of species included in the meta-analysis for which information about ongoing range shifts has been reported in the scientific literature. All cases stem from the northern hemisphere. See Appendix 2 for full references.

Organism	Species	Type of range shift	Reference
Bird	*Cyanistes caeruleus*	expansion northwards	Massimino et al. 2015
		expansion northwards	Bromer 2004
		shift southwards	Tayleur et al. 2015
		shift northwards	Potvin et al. 2017
		shift northwards	Virkkala & Lehikoinen 2017
	Ficedula hypoleuca	expansion northwards	Virkkala & Lehikoinen 2017
	Dendroica caerulescens	expansion northwards	Zuckerberg et al. 2009
Fish	*Girella elevata*	expansion northwards	Last et al. 2015
		expansion northwards	Stuart-Smith et al. 2010
Herb	*Plantago coronopus*	expansion northwards	Groom 2013
Herb	*Silene acaulis*	expansion south	Groom 2013
Herb	*Cirsium heterophyllum*	expansion northwards	Groom 2013
	Cirsium acaule	expansion northwards	Amano et al. 2014
Herb	*Himantoglossum hircinum*	expansion northwards	Van der Meer at al. 2016
		contraction south	Pfeifer et al. 2010
Herb	*Cypripedium calceolus*	contraction south	Lesica & Crone 2017
Seaweed	*Fucus guiryi*	contraction south	Riera et al. 2015
		contraction south	Lourenço et al. 2016
	Fucus vesiculosus	contraction south	Nicastro et al. 2013
		expansion southwards	Lima et al. 2007
Tree	*Thuja occidentalis*	expansion northwards	Boisvert & Périé 2014
		expansion northwards	Fei et al. 2017
		contraction north	Sittaro et al. 2017
	Pinus sylvestris	expansion southwards	Kuhn et al. 2016
	Juniperus communis	expansion northwards	Groom 2013
	Taxus baccata	expansion northwards	Amano et al. 2014

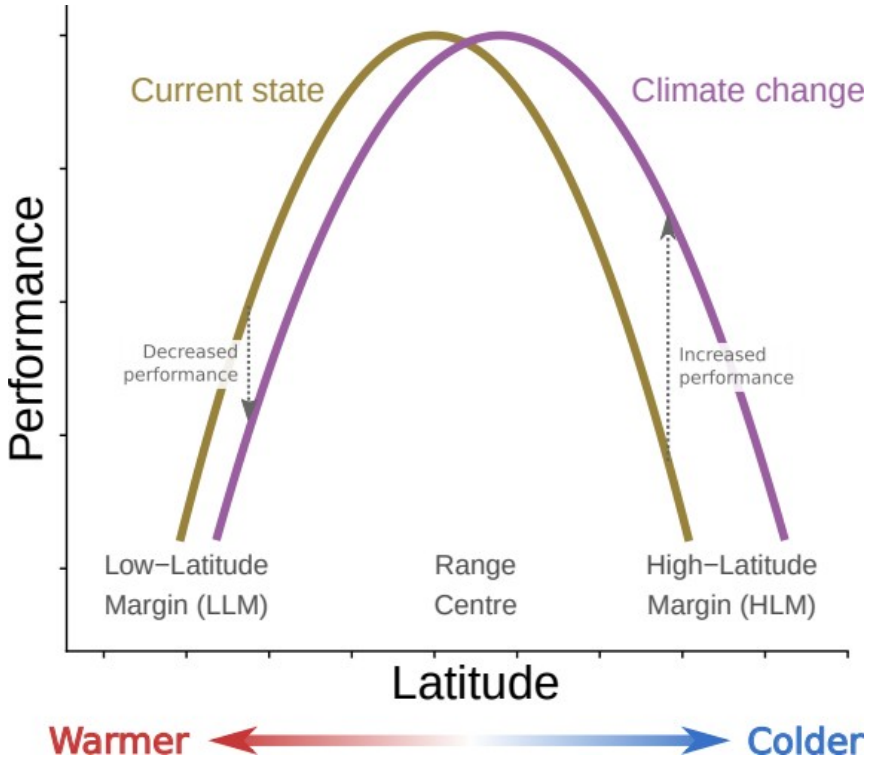

Figure 1. The centre-periphery hypothesis postulates that population performance is maximal around the range centre and decreases towards the margins of the distribution range, as environments become less suitable. Under current climate change, the optimal climate zones would displace polewards so that high-latitude populations (HLM) would increase their fitness whereas low-latitude populations (LLM) experience a decrease. Hence, the difference in performance between high-latitude and central populations would reduce with climate change, while low-latitude populations would show greater differences to central populations.

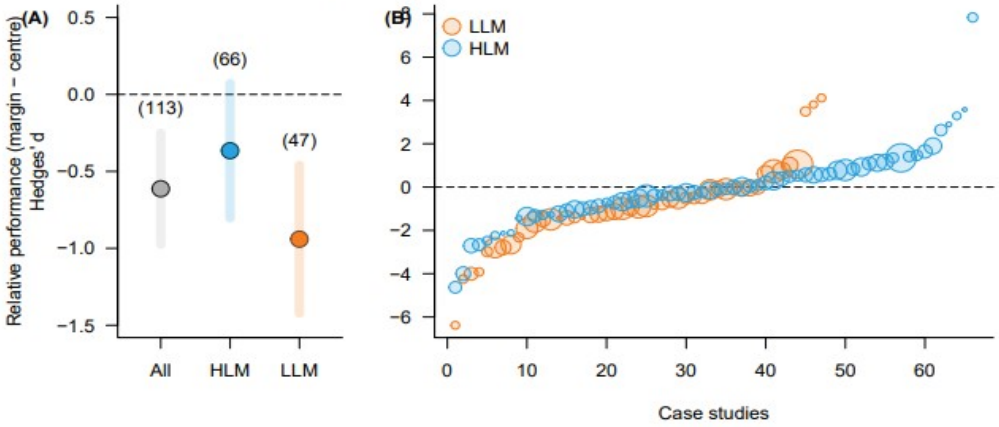

Figure 2. Observed differences in performance (Hedges'*d* effect sizes) between marginal (high-latitude, HLM, and low-latitude, LLM) and central populations across all species and studies. **(A)** Grand mean (grey) and margin-specific (blue and orange) combined effect sizes. Error bars represent 95% confidence intervals. Numbers in parentheses correspond to the number of case studies. **(B)** Individual effect sizes for HLM and LLM case studies ranked from the lowest to the highest value. Dot size is proportional to the weight of individual effect sizes in the meta-analysis. Both in **(A)** and **(B)**, positive and negative values indicate higher and lower performances in marginal than in central populations, respectively. Horizontal dashed lines represent the null hypothesis of no difference in the performance of central vs. marginal populations.

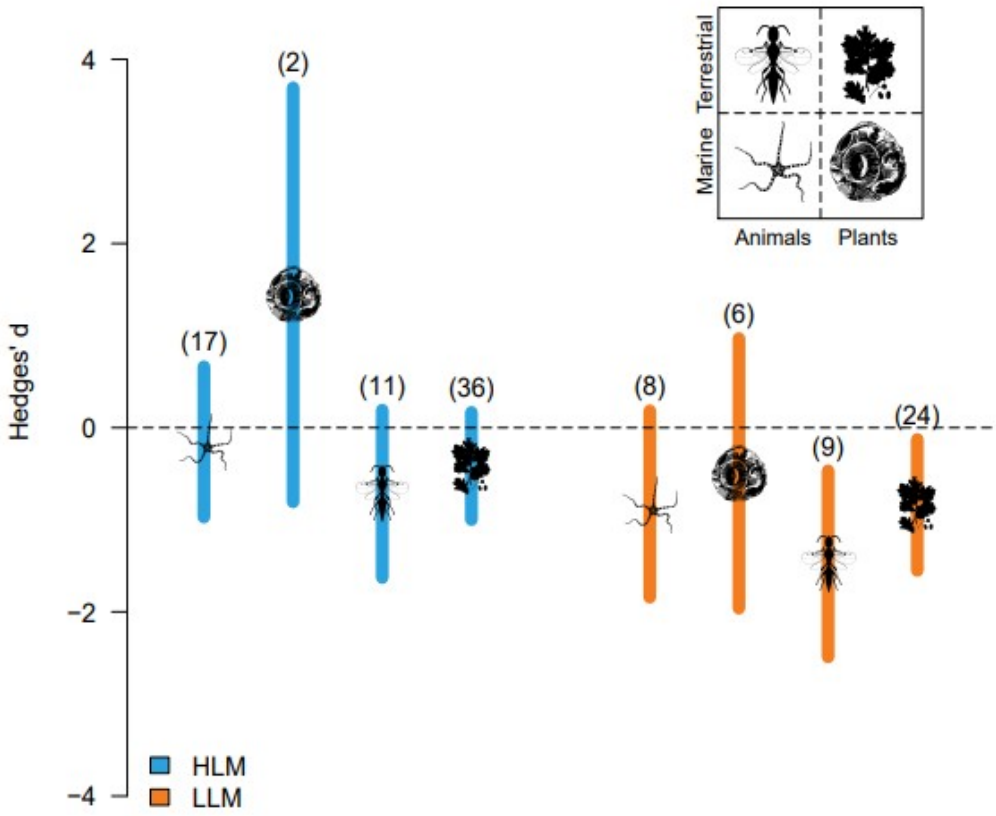

Figure 3. Asymmetry in population performance at High Latitude Margins (HLM) and Low Latitude Margins (LLM) for each Kingdom and Habitat. Symbols representing Habitats and Kingdoms are centred on the mean estimate. Vertical bars represent 95% CI estimated from the multi-level meta-analysis. Negative and positive values indicate lower and higher performance of marginal populations as compared to central populations, respectively. Numbers within parentheses indicate the number of case studies for each category.

Figure 4. Relationship between the observed difference in performance (Hedges' *d*) and the difference in average temperatures between peripheral and central populations for the period 1985-2016 for all studied species (52 species: 37 terrestrial and 15 marine; n = 109 margin-centre comparisons). Positive values of Hedges' *d* indicate better performance in the margin compared to central populations, and vice versa. Point size is inversely related to Hedges' *d* variance for each contrast (i.e., bigger points represent stronger effect sizes). The curve represents the fit of a generalized additive mixed model (GAMM) with temperature as predictor (and study as random effect to control for lack of independence). The shaded area around the GAMM curve represents the standard error of the prediction. HLM = high-latitude margin, LLM = low-latitude margin.

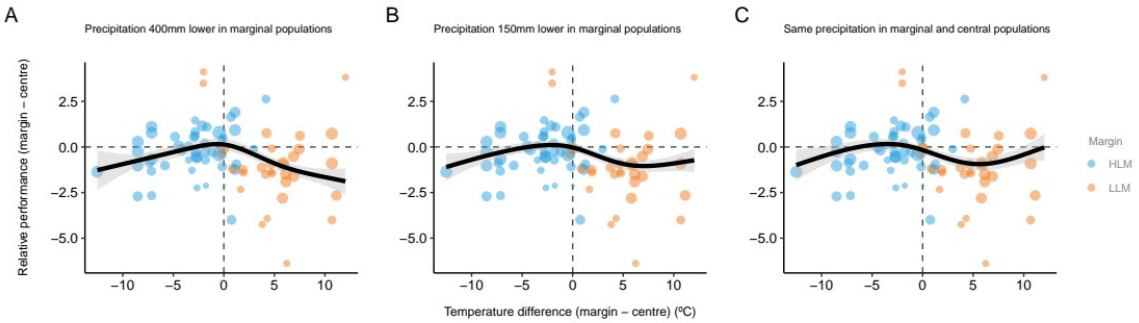

Figure 5. Relationship between the observed difference in performance (Hedges' *d*) and the difference in average temperatures between peripheral and central populations for the period 1985–2016 for 37 terrestrial species (n = 80 margin-centre comparisons). Positive values of Hedges' *d* indicate better performance in the margin compared to central populations, and vice versa. Point size is inversely related to Hedges' *d* variance for each contrast (i.e., bigger points represent stronger effect sizes). The black curve represents the fit of a generalized additive mixed model (GAMM) with temperature, precipitation and their interaction as predictors (and study as random effect to control for lack of independence). The shaded area around the GAMM curve represents the standard error of the prediction. As the interaction between temperature and precipitation was significant, results are shown for three scenarios (annual precipitation 400 mm lower, 150 mm lower, or same in marginal as in central populations). These values approximate the first, second, and third quartiles, respectively, of precipitation differences between marginal and central populations observed in our dataset. HLM = high-latitude margin, LLM = low-latitude margin.

Appendix 1. List of the 51 papers contributing data on population performance for the analysis.

Aikens, M. L., & Roach, D. A. (2014). Population dynamics in central and edge populations of a narrowly endemic plant. *Ecology*, *95*, 1850-1860.

Angilletta Jr, M. J., Niewiarowski, P. H., Dunham, A. E., Leach, A. D., & Porter, W. P. (2004). Bergmann´s clines in ectotherms: illustrating a life history perspective with sceloporine lizards. *The American Naturalist*, *164*, E168-E183.

Araújo, R. M., Serrao, E. A. & Sousa-Pinto I., & Aberg, P. (2014). Spatial and temporal dynamics of fucoid populations (*Ascophyllum nodosum* and *Fucus serratus*): a comparison between central and range edge populations. *PLoS ONE*, *9*, e92177.

Baer, K. C., & Maron, J. L. (2019). Declining demographic performance and dispersal limitation influence the geographic distribution of the perennial forb *Astragalus utahensis* (Fabaceae). *Journal of Ecology*, *107*, 1250-1262.

Brante, A., Cifuentes, S., Partner, H. O., Arntz, W., & Fernandez, M. (2004). Latitudinal comparisons of reproductive traits in five brachyuran species along the Chilean coast. *Revista Chilena de Historia Natural*, *77*, 15-27

Cardoso, R. S., & Defeo, O. (2003). Geographical patterns in reproductive biology of the Pan-American sandy beach isopod *Excirolana braziliensis*. *Marine Biology*, *143*, 573-581.

Carey, P. D., Watkinson, A.R., & Gerard, F.F.O. (1995). The determinants of the distribution and abundance of the winter annual grass *Vulpia ciliata* ssp. *ambigua*. *Journal of Ecology*, 83, 177-187.

Derocher, A. E. (1999). Latitudinal variation in litter size of polar bears: ecology or methodology? *Polar Biology*, *22*, 350-356.

Dixon, A. L., Herlihy, C. R., & Busch, J. W. (2013). Demographic and population genetic tests provide mixed support for the abundant centre hypothesis in the endemic plant *Leavenworthia stylosa*. *Molecular Ecology*, *22*, 1777-1791.

Doak, D. F., & Morris, W. F. (2010). Demographic compensation and tipping points in climate-induced range shifts. *Nature, 467*, 959-962.

Ebert, T. A. (2010). Demographic patterns of the purple sea urchin *Strongylocentrotus purpuratus* along a latitudinal gradient, 1985-1987. *Marine Ecology Progress Series*, *406*, 105-120.

Ebert, T. A., Dixon, J. D., Schroeter, S. C., Kalvass, P. E., Richmond, N. T., Bradbury, W. A., & Woodby, D. A. (1999). Growth and mortality of red sea urchins *Strongylocentrotus franciscanus* across a latitudinal gradient. *Marine Ecology Progress Series, 190*, 189-209.

Fargallo, J. A. (2004). Latitudinal trends of reproductive traits in the Blue Tit *Parus caeruleus*. *Ardeola*, *51*, 177-190.

Ferreira, J. G., Hawkins, S. J., & Jenkins, S. R. (2015). Patterns of reproductive traits of fucoid species in core and marginal populations. *European Journal of Phycology*, *50*, 457-468.

Foden, W., Midgley, G. F., Hughes, G., Bond, W. J., Thuiller, W., Hoffman, M. T., ... & Hannah, L. (2007). A changing climate is eroding the geographical range of the Namib Desert tree *Aloe* through population declines and dispersal lags. *Diversity and Distributions*, *13*, 645-653.

García, D., Zamora, R., Gómez, J.M., Jordano, P., & Hódar, J.A. (2000). Geographical variation in seed production, predation and abortion in *Juniperus communis* throughout its range in Europe. *Journal of Ecology*, *88*, 436-446.

García, M. B., Goñi, D., & Guzmán, D. (2010). Living at the edge: local versus positional

factors in the long-term population dynamics of an endangered orchid. *Conservation Biology*, *24*, 1219-1229.

Graves, G. (1997). Geographic clines of age ratio of black-throated blue warblers (*Dendroica caerulescens*). *Ecology*, 78, 2524-2531.

Heibo, E., Magnhagen, C., & Vøllestad, L. A. (2005). Latitudinal variation in life-history traits in Eurasian perch. *Ecology*, *86*, 3377-3386.

Hidas, E. Z., Russell, K. G., Ayre, D. J., & Minchinton, T. E. (2013). Abundance of *Tesseropora rosea* at the margins of its biogeographic range is closely linked to recruitment, but not fecundity. *Marine Ecology Progress Series*, *483*, 199-208

Jump, A. S., & Woodward, F. I. (2003). Seed production and population density decline approaching the range-edge of *Cirsium* species. *New Phytologist*, *160*, 349-358.

Koski, M. H., Grossenbacher, D. L., Busch, J. W., & Galloway, L. F. (2017). A geographic cline in the ability to self-fertilize is unrelated to the pollination environment. *Ecology*, *98*, 2930-2939.

Lammi, A., Siikamäki, P., & Mustajärvi, K. (1999). Genetic diversity, population size, and fitness in central and peripheral populations of a rare plant *Lychnis viscaria.* *Conservation Biology*, *13*, 1069-1078.

Lardies, M. A., Arias, M. B., & Bacigalupe, L. D. (2010). Phenotypic covariance matrix in life-history traits along a latitudinal gradient: a study case in a geographically widespread crab on the coast of Chile. *Marine Ecology Progress Series*, *412*, 179-187.

Lathlean, J. A., Ayre, D. J., & Minchinton, T. E. 2010. Supply-side biogeography: Geographic patterns of settlement and early mortality for a barnacle approaching its range limit. *Marine Ecology Progress Series*, *412*, 141-150

Lester, S. E., Gaines, S. D., & Kinlan, B. P. (2007). Reproduction on the edge: large-scale

patterns of individual performance in a marine invertebrate. *Ecology*, *88*, 2229-2239.

Matías, L., & Jump, A. S. (2015). Asymmetric changes of growth and reproductive investment herald altitudinal and latitudinal range shifts of two woody species. *Global Change Biology*, *21*, 882-896.

Nantel, P., Gagnon, D., & Montreal, A. (1999). Variability in the dynamics of northern peripheral versus southern populations of two clonal plant species, *Helianthus divaricatus* and *Rhus aromatica. Journal of Ecology*, *87*, 748-760.

Parry, D., Goyer, R. A., & Lenhard, G. J. (2001). Macrogeographic clines in fecundity, reproductive allocation, and offspring size of the forest tent caterpillar *Malacosoma disstria*. *Ecological Entomology*, *26*, 281-291.

Paul, V., Bergeron, Y., & Tremblay, F. (2014). Does climate control the northern range limit of eastern white cedar (*Thuja occidentalis* L.)? *Plant Ecology*, *215*, 181-194.

Pfeifer, M., Passalacqua, N. G., Bartram, S., Schatz, B., Croce, A., Carey, P. D., ... & Jeltsch, F. (2010). Conservation priorities differ at opposing species borders of a European orchid. *Biological Conservation*, *143*, 2207-2220.

Power, M., Dempson, J. B., Reist, J. D., Schwarz, C. J., & Power, G. (2005). Latitudinal variation in fecundity among Arctic charr populations in eastern North America. *Journal of Fish Biology*, *67*, 255-273.

Rhainds, M., & Fagan, W. F. (2010) Broad-scale latitudinal variation in female reproductive success contributes to the maintenance of a geographic range boundary in bagworms (Lepidoptera: *Psychidae*). *PLoS ONE, 5*, e14166.

Rivadeneira, M. M., Hernández, P., Antonio Baeza, J., Boltana, S., Cifuentes, M., Correa, C., ... & Valdivia, N. (2010). Testing the abundant-centre hypothesis using intertidal porcelain crabs along the Chilean coast: linking abundance and life-history variation. *Journal of*

Biogeography, *37*, 486-498.

Ruskin, K. J., Etterson, M. A., Hodgman, T. P., Borowske, A. C., Cohen, J. B., Elphick, C. S., ... & Kovach, A. I. (2017). Seasonal fecundity is not related to geographic position across a species' global range despite a central peak in abundance. *Oecologia*, *183*, 291-301.

Sanz, J. J. (1997). Geographic variation in breeding parameters of the Pied Flycatcher *Ficedula hypoleuca*. *Ibis*, *139*, 107-114.

Sanz, R., Pulido, F., & Nogués-Bravo, D. (2009). Predicting mechanisms across scales: amplified effects of abiotic constraints on the recruitment of yew *Taxus baccata.* *Ecography*, *32*, 993-1000.

Sheth, S. N., & Angert, A. L. (2018). Demographic compensation does not rescue populations at a trailing range edge. *Proceedings of the National Academy of Sciences*, *115*, 2413-2418.

Silva-Montellano, A., & Eguiarte, L. E. (2003). Geographic patterns in the reproductive ecology of Ag*ave lechuguilla* (Agavaceae) in the Chihuahuan desert. I. Floral characteristics, visitors, and fecundity. *American Journal of Botany*, *90*, 377-387.

Simoncini, M., Piña, C. I., & Siroski, P. A. (2009). Clutch size of *Caiman latirostris* (Crocodylia: *Alligatoridae*) varies on a latitudinal gradient. *North-Western Journal of Zoology*, *5*, 191-196.

Stanton-Gedes, J., Tiffin, P., & Shaw, R.G. (2012). Role of climate and competitors in limiting fitness across range edges of an annual plant. *Ecology*, *93*, 1604-1613.

Starmer, W. T., Wolf, L. L., Barker, J. S. F., Bowles, J. M., & Lachance, M. A. (1997). Reproductive characteristics of the flower breeding *Drosophila hibisci* Bock (*Drosophilidae*) along a latitudinal gradient in eastern Australia: relation to flower and habitat features. *Biological Journal of the Linnean Society*, *62*, 459-473.

Stocks, J. R., Gray, C. A., & Taylor, M. D. (2015). Intra-population trends in the maturation and

reproduction of a temperate marine herbivore *Girella elevata* across latitudinal clines. *Journal of Fish Biology*, *86*, 463-483.

Viejo, R. M., Martinez, B., Arrontes, J., Astudillo, C., & Hernandez, L. (2011). Reproductive patterns in central and marginal populations of a large brown seaweed: drastic changes at the southern range limit. *Ecography*, *34*, 75-84.

Villellas, J., Ehrlén, J., Olesen, J. M., Braza, R., & García, M. B. (2013). Plant performance in central and northern peripheral populations of the widespread *Plantago coronopus*. *Ecography*, *36*, 136-145.

Villellas, J., Morris, W. F., & Garcia, M. B. (2013). Variation in stochastic demography between and within central and peripheral regions in a widespread short-lived herb. *Ecology*, *94*, 1378-1388.

Vogler, F., & Reisch, C. (2013). Vital survivors: low genetic variation but high germination in glacial relict populations of the typical rock plant *Draba aizoides*. *Biodiversity and Conservation*, *22*, 1301-1316.

Willemsen, R. E., & Hailey, A. (2001). Variation in adult survival rate of the tortoise *Testudo hermanni* in Greece: implications for evolution of body size. *Journal of Zoology*, *255*, 43-53.

Wilson, B. S., & Cooke, D. E. (2004). Latitudinal variation in rates of overwinter mortality in the lizard *Uta stansburiana*. *Ecology*, *85*, 3406-3417.

Yakimowski, S. B., & Eckert, C. G. (2007). Threatened peripheral populations in context: geographical variation in population frequency and size and sexual reproduction in a clonal woody shrub. *Conservation Biology*, *21*, 811-822.

Zardi, G. I., Nicastro, K. R., Serrano, E. A., Jacinto, R., Monteiro, C. A., & Pearson, G. A. (2015). Closer to the rear edge: ecology and genetic diversity down the core-edge

gradient of a marine macroalga. *Ecosphere*, *6*, 1-25.

Appendix 2. References cited in Table 2.

Amano, T., Freckleton, R. P., Queenborough, S. A., Doxford, S. W., Smithers, R. J., Sparks, T.H., & Sutherland, W. J. (2014). Links between plant species' spatial and temporal responses to a warming climate. *Proceedings of the Royal Society B*, *281*, 20133017.

Boisvert-Marsh, L., & Périé, C. (2014). Shifting with climate? Evidence for recent changes in tree species distribution at high latitudes. *Ecosphere, 5*, 1-33.

Brommer, J. E. (2004). The range margins of northern birds shift poleward. *Annales Zoologici Fennici, 41*, 391–397.

Fei, S., Desprez, J. M., Potter, K. M., Jo, I., Knott, J. A., & Oswalt, C. M. (2017). Divergence of species responses to climate change. *Science Advances*, *3*, e1603055.

Groom, Q. J. (2013). Some poleward movement of British native vascular plants is occurring, but the fingerprint of climate change is not evident. *PeerJ*, *1*, e77.

Kuhn, E., Lenoir, J., Piedallu, C., & Gégout, J. C. (2016). Early signs of range disjunction of submountainous plant species: an unexplored consequence of future and contemporary climate changes. *Global Change Biology*, *22*, 2094-2105.

Last, P. R., White, W. T., Gledhill, D. C., Hobday, A. J., Brown, R., Edgar, G. J., & Pecl, G. (2015). Long-term shifts in abundance and distribution of a temperate fish fauna: a response to climate change and fishing practices. *Global Ecology and Biogeography, 20*, 58-72.

Lesica, P., & Crone, E. E. (2017). Arctic and boreal plant species decline at their southern range limits in the Rocky Mountains. *Ecology Letters, 20*, 166-174.

Lima, F. P., Ribeiro, P. A., Queiroz, N., Hawkins, S. J., & Santos, A. M. (2007). Do distributional shifts of northern and southern species of algae match the warming pattern? *Global Change Biology*, *13*, 2592-2604.

Lourenço, C. R., Zardi, G. I., McQuaid, C. D., Serrao, E. A., Pearson, G. A., Jacinto, R., & Nicastro, K. R. (2016). Upwelling areas as climate change refugia for the distribution and genetic diversity of a marine macroalga. *Journal of Biogeography, 43*, 1595-1607.

Massimino, D., Johnston, A., & Pearce-Higgins, J. W. (2015). The geographical range of British birds expands during 15 years of warming. *Bird Study, 62*, 523-534.

Nicastro, K. R., Zardi, G. I., Teixeira, S., Neiva, J., Serrão, E. A., & Pearson, G. A. (2013). Shift happens: trailing edge contraction associated with recent warming trends threatens a distinct genetic lineage in the marine macroalga *Fucus vesiculosus*. *BMC Biology*, *11*, 6.

Pfeifer, M., Passalcqua, N. D., Bartram, S., Schatz, B., Croce, A., Carey, P. D., Kraudel, H., & Jeltsch, F. (2010). Conservation priorities differ at opposing species borders of a European orchid. *Biological Conservation, 143*, 2207-2220.

Potvin, D. A., Välimäki, K., & Lehikoinen, A. (2016). Differences in shifts of wintering and breeding ranges lead to changing migration distances in European birds. *Journal of Avian Biology*, *47*, 619-628.

Riera, R., Sangil, C., & Sansón, M. (2015). Long-term herbarium data reveal the decline of a temperate-water algae at its southern range. *Estuarine, Coastal and Shelf Science, 165*, 159-165.

Sittaro, F., Paquette, A., Messier, C., & Nock, C. A. (2017). Tree range expansion in eastern North America fails to keep pace with climate warming at northern range limits. *Global Change Biology*, *23*, 3292-3301.

Stuart-Smith, R. D., Barrett, N. S., Stevenson, D. G., & Edgar, G. J. (2010). Stability in temperate reef communities over a decadal time scale despite concurrent ocean warming. *Global Change Biology*, *16*, 122-134.

Tayleur, C., Caplat, P., Massimino, D., Johnston, A., Jonzén, N., Smith, H. G., & Lindström, Å. (2015). Swedish birds are tracking temperature but not rainfall: evidence from a decade of abundance changes. *Global Ecology and Biogeography*, *24*, 859-872.

Van der Meer, S., Jacquemyn, H., Carey, P. D., & Jongejans, E. (2016). Recent range expansion of a terrestrial orchid corresponds with climate-driven variation in its population dynamics. *Oecologia, 181*, 435-448.

Virkkala, R., & Lehikoinen, A. (2017). Birds on the move in the face of climate change: High species turnover in northern Europe. *Ecology and Evolution*, *7*, 8201-8209.

Zuckerberg, B., Woods, A. M., & Porter, W. F. (2009). Poleward shifts in breeding bird distributions in New York State. *Global Change Biology*, *15*, 1866-1883.