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Widespread latitudinal asymmetry in the performance of marginal populations: A meta-analysis

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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 performance in marginal populations are widespread, then populations from the high-latitude margin (HLM) should perform as well as or better than central populations, whereas low-latitude margin (LLM) populations should perform worse.

Location: Global.

Time period: 1995–2019.

Major taxa studied: Plants and animals.

Methods: To test our prediction, we used a meta-analysis to quantify empirical support for asymmetry in the performance of high- and low-latitude margin populations compared to central populations. Performance estimates (survival, reproduction, or lifetime fitness) for populations occurring in their natural environment were derived from 51 papers involving 113 margin-centre comparisons from 54 species and 705 populations from the Americas, Europe, Africa and Australia. 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 realms (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 realms. Differences in performance were weakly ($p = .08$) related to the difference in average temperatures between central and marginal populations.

Main conclusions: The observed asymmetry in performance in marginal populations is consistent with predictions about the effects of global climate change, though further research is needed to confirm the effect of climate. It indicates that changes in demographic rates in marginal populations can serve as early-warning signals of impending range shifts.

KEYWORDS
centre-periphery hypothesis, climate change, demographic rates, population performance, range edge, range margin, range shift

1 | INTRODUCTION

Ongoing climate changes are predicted to increase mismatches between current environmental conditions and the climate to which local populations are adapted ('species-climate disequilibrium'; 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 could presage large-scale geographical range shifts (Lenoir & Svenning, 2015; Parmesan et al., 1999; Sexton et al., 2009). Yet, we know little about how widespread asymmetries in marginal population growth rates are. Population growth rates are hard to estimate 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.

Climate-driven distribution changes have been extensively reported in recent years (Chen et al., 2011; Lenoir et al., 2020; Wiens, 2016). However, causal relationships with recent climate changes are difficult to establish, because range limits can also be constrained by a variety of non-climatic factors such as habitat availability, dispersal limitation, and biotic interactions (Hargreaves et al., 2014; Lee-Yaw et al., 2016; Louthan et al., 2015; Pironon et al., 2017). Notably, long-lived and immobile species may in particular accumulate extensive extinction debts and colonization credits through slow dispersal and demographic responses to climate shifts (Talluto et al., 2017). Changes in the performance (e.g. in terms of

reproduction, survival or lifetime fitness) 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 detection of such events in marginal population dynamics are rare, especially for populations at contracting range margins (Fredston-Hermann et al., 2020; Hastings et al., 2020; Hill et al., 2011; Kunstler et al., 2020). Indirect approaches are therefore required to assess how widespread range-wide asymmetries in population performance are.

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, 2002; Sexton et al., 2009; Figure 1). The CP 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). The comprehensive review of Pironon et al. (2017) found that only about 50% of the studies supported the CP hypothesis for abundance and genetic variation, and only 20–30% for demographic rates, size and population performance. Similar lack of widespread support was also found in two detailed analyses of population abundance (Dallas et al., 2017; Santini et al., 2019). Under the CP paradigm, the optimal climate zones of species would displace polewards with current climate change, so that performance in populations at the high-latitude margin (HLM) would improve, whereas performance at the low-latitude margin (LLM) would worsen. The hypothesized difference in performance between high-latitude and
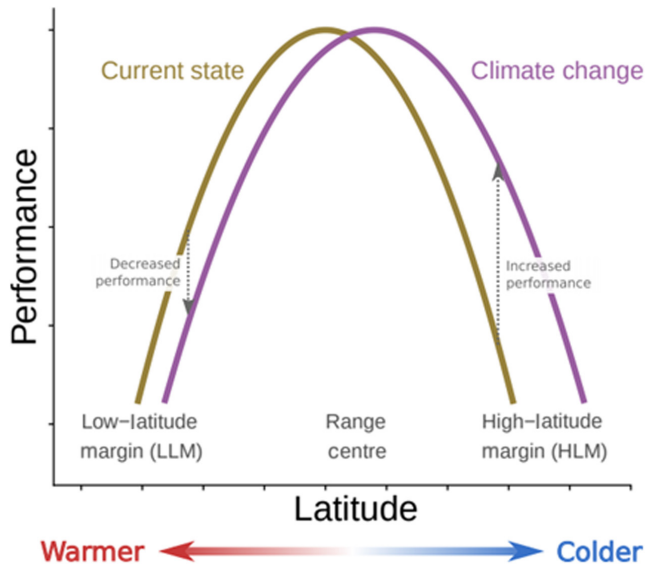
FIGURE 1 The centre-periphery hypothesis postulates that population performance is maximal around the range centre and decreases towards the margins of the distribution range, as environments become less suitable. Under current climate change, the optimal climate zones would displace polewards so that high-latitude populations (HLM) would increase their fitness whereas low-latitude populations (LLM) would 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.

central populations is thus expected to decrease with climate change, while the difference between low-latitude and central populations is expected to increase (Figure 1).

We selected a comprehensive sample of published studies to compare measures of population performance in sites located at the centre and at the HLM or LLM of species ranges. We predicted that if impacts of ongoing climate change on population performance are widespread, then (a) HLM populations should perform as well as or better than central populations, whereas LLM populations should perform worse than central and HLM populations (Figure 1). To test this prediction, we employed information from empirical studies to quantify differences in the performance of HLM, LLM and central populations. We also tested if patterns are consistent across realms (marine vs terrestrial) and across taxonomic kingdoms (plants vs animals), because climate is shifting at different paces in marine and terrestrial environments (Burrows et al., 2011), and the capacity to buffer climatic stress through phenotypic plasticity and persistent life cycle stages differs between plants and animals (Villellas et al., 2015, see also Lloret et al., 2012). We also predicted that if climate is a major driver of differences in population performance, then (b) performance differences should increase with the difference in climate between central and marginal populations (Figure 1). To test this prediction, we relate the observed differences in performance between central and peripheral populations to differences in climate.

2 | MATERIALS AND METHODS

2.1 | Data compilation

We followed the preferred reporting items for systematic reviews and meta-analyses (PRISMA) protocol for data compilation, meta-analysis and reporting of results (Moher et al., 2009, Page et al., 2021; see Appendix S1). First, we searched Web of Science™ and Scopus until 19 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' (see full details and search strings in Appendix S1).

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 explicit and clear information on our 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; see below). 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 are described in detail in Figure S1.

We extracted the reported performance metrics from each primary paper and assigned them to one of three categories: (a) 'survival' (e.g. mortality of individuals or ramets, rates of fruit abortion or germination); (b) 'reproduction' (e.g. proportion of actively reproducing individuals, seed number, gonadal mass, total seed or egg mass); or (c) 'lifetime fitness' (e.g. different estimates of population growth rate). Moreover, we assigned each case study to one of two major taxonomic groups (plants versus animals) and realms (terrestrial versus marine). Two major kinds of papers provided suitable information: (a) explicit CP comparisons of mean performance values from populations classified as central or marginal by the authors, and (b) 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, and then calculated the average performance, sample size and resulting standard deviation for central, high- and low-latitude margins (Pulido et al., 2022).

2.2 | Meta-analysis of differences between marginal and central populations

2.2.1 | Effect sizes

We used Hedges' *d* statistic as our standardized measure of effect size. Hedges' *d* is the most appropriate measure of 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:

$$d = J \frac{\overline{X}_{\text{Margin}} - \overline{X}_{\text{Center}}}{\sqrt{\frac{(n_{\text{Margin}} - 1)s^2_{\text{Margin}} + (n_{\text{Center}} - 1)s^2_{\text{Center}}}{n_{\text{Margin}} + n_{\text{Center}} - 2}}}$$

where

$$J = 1 - \frac{3}{4(n_{\text{Margin}} + n_{\text{Center}} - 2) - 1}$$

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

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:

$$v_d = \frac{n_{\text{Margin}} + n_{\text{Center}}}{n_{\text{Margin}} \times n_{\text{Center}}} + \frac{d^2}{2(n_{\text{Margin}} + n_{\text{Center}})}$$

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 ($n = n_{\text{centre}} + n_{\text{margin}}$), because, for such primary papers, n_{centre} is counted twice. We manually corrected n in all such cases before conducting the analysis.

2.2.2 | 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: (a) among true effect sizes, (b) among CP comparisons stemming from the same primary papers (by computing the variance–covariance matrix among all effect sizes), and (c) 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 (R Core Team, 2021; Viechtbauer, 2010). Primary paper identity was declared as a random factor and individual CP comparisons were nested as random factors 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), that is, 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 effect sizes (weight = $1/(v + \tau^2)$). Then, we used multi-level (hierarchical) meta-analyses to test the effect of three moderators: Margin (HLM versus LLM), Kingdom (animals versus plants) and Realm (marine versus 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 Realm ($n = 10$ models). We ranked these 17 models plus the null model (i.e. intercept only) according to their Akaike's information criterion corrected for small sample sizes (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 ΔAIC$_c < 2$ were considered best, given the data structure and the model set (Table 1). AIC$_c$ weights represent the probability that a given model is the best within 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 (Figure S4). Finally, we estimated model parameters for all competing models with ΔAICc < 2. We reported model parameter estimates for the best model and, whenever necessary, for competing models. Further details of the meta-analysis, including several assessments of its inherent reliability (e.g. publication bias, balanced representation of moderators etc.) are shown in Appendix S1.

2.3 | Relationship between climate and differences in population performance

2.3.1 | Climate data

We gathered the geographical coordinates of all populations included in the meta-analysis from the primary papers ($n = 705$ populations; Figure S5). 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 A) 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 (Appendix S1, Figure S5). 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 the two regions.

TABLE 1 Summary of the five models retained in the set of best models (with $\Delta AIC_c < 2$).

Model	Parameters	Estimate (± 95% CI)	Q_M (p-value)	Q_E (p-value)	Pseudo R^2
Model 1	Intercept (HLM, Aquatic)	0.3 (−0.28 to 0.88)	14.06 (.001)	335.62 (<.001)	.04
	Margin (LLM)	**−0.72 (−1.12 to −0.31)**			
	Realm (Terrestrial)	−0.5 (−1.14 to 0.14)			
Model 2	Intercept (HLM)	−0.07 (−0.41 to 0.27)	11.65 (.001)	342.87 (<.001)	.029
	Margin (LLM)	**−0.71 (−1.11 to −0.30)**			
Model 3	Intercept (HLM, Aquatic)	0.49 (−0.17 to 1.15)	15.45 (.001)	334.47 (<.001)	.048
	Margin (LLM)	**−1.16 (−1.95 to −0.36)**			
	Realm (Terrestrial)	−0.75 (−1.51 to 0.01)			
	Margin (LLM) × Realm (Terrestrial)	0.59 (−0.33 to 1.50)			
Model 4	Intercept (HLM, Aquatic, Animals)	0.23 (−0.36 to 0.82)	15.07 (.002)	334.39 (<.001)	.049
	Margin (LLM)	**−0.73 (−1.13 to −0.32)**			
	Realm (Terrestrial)	−0.69 (−1.43 to 0.04)			
	Kingdom (Plants)	0.35 (−0.32 to 1.02)			
Model 5	Intercept (HLM, Aquatic, Animals)	0.43 (−0.24 to 1.09)	16.69 (.002)	332.96 (<.001)	.057
	Margin (LLM)	**−1.21 (−2.01 to −0.41)**			
	Realm (Terrestrial)	**−0.99 (−1.85 to −0.13)**			
	Kingdom (Plants)	0.40 (−0.29 to 1.08)			
	Margin (LLM) × Realm (Terrestrial)	0.64 (−0.28 to 1.56)			

Note: Margin (bold values) explained a significant amount of heterogeneity in each of the five competing best models whereas neither Kingdom nor Realm explained a significant amount of heterogeneity in any of the five models retained in the set of best models. Q_M 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.

Abbreviations: ΔAIC_c, change in Akaike's information criterion corrected for small sample size; CI, confidence interval; HLM, high-latitude margin; LLM, low-latitude margin.

2.3.2 | Analysis of relationships between climate and population performance

To assess the relationship between differences in performance and differences in climate between marginal and central populations, we used generalized 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 identity as a random effect (to control for lack of independence). We weighted performance effect sizes by their variances so that their influence on 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 Appendix S1 for further details).

3 | RESULTS

Marginal populations performed on average worse than central populations, since grand mean effect size was negative (−0.36; 95% confidence interval [CI]: −0.69 to −0.03). There was a significant amount of heterogeneity, and 58% of total heterogeneity was due to among-study heterogeneity ($\tau^2 = 1.65$, $Q_E = 433.0$, $p < .0001$). Five models received relatively strong support, at the level of $\Delta AIC_c \leq 2.0$ (Table 1, Table S2). All five included margin type as a moderator ($w_H = .99$).

Performance declined more strongly towards the LLM (effect size: −0.81; 95% CI: −1.23 to −0.39; estimated from the model with Margin as the sole moderator) than towards the HLM (effect size: −0.09; 95% CI: −0.45 to 0.27) (Figure 2). Population performance differed detectably between margin types in the five models with $\Delta AICc \leq 2$ (Table 1). The best model only explained 4% of the total heterogeneity. The five models with $\Delta AICc \leq 2$ also included Realm, Kingdom and the Margin × Realm interaction as moderators, but their relative importance was low ($w_H < .78$, as compared to $w_H = .99$ for the Margin moderator); we only detected differences in two of the comparisons between aquatic and terrestrial realms, whereas no differences were noted in the comparisons between plants and animals (Figure 3, Appendix S1).

To test whether heterogeneity among effect sizes was contingent upon the way population performance was estimated, we ran a multi-level hierarchical model with the performance variable (survival, reproduction, lifetime fitness) as a fixed effect. Differences in population performances between central and marginal populations did not differ among performance metrics ($Q_M = 0.51$, $p = .78$). When running models for each population performance parameter separately, we confirmed that population performance was consistently lower at the LLM compared to central populations (survival: 0.56 and −2.08; reproduction: −0.44 and −0.52; lifetime fitness: −0.08 and −0.51 in HLM and LLM, respectively).
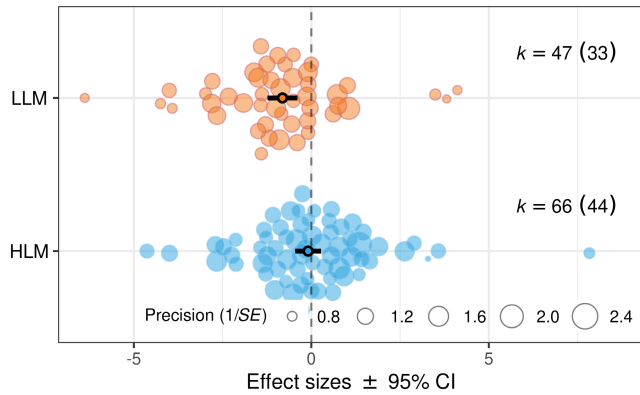
FIGURE 2 Orchard plot showing the distribution of effect sizes and the difference between effect sizes for low- (LLM) and high-latitude margins (HLM). Coloured dots represent individual effect sizes; their size is proportional to the precision of the case study. Black circled dots represent mean coefficient estimates and horizontal black lines extending from them represent 95% confidence interval (CI) from the model with Margin as the sole moderator. CI overlap prediction intervals, indicating that effect sizes of new studies would fall in the range of the currently estimated CI. Negative and positive values indicate lower and higher performance of marginal populations as compared to central populations, respectively. Numbers (*k*) indicate the number of case studies and, within parentheses, the number of primary studies they were extracted from.

The differences in performance between marginal and central populations were weakly related to the difference in their average temperature in the period 1985–2016 (effective degrees of freedom = 2.50, F = 2.33, p = .08; Table S3; total deviance explained by an additive mixed model: 21%). As predicted, performance decreased with increasingly departing temperatures from central populations, but the decline was asymmetric between high- and low-latitude populations (Figure 4): HLM populations experiencing 5 °C colder temperatures than central populations showed similar performance, whereas LLM populations experiencing 5 °C warmer temperatures performed worse (Figure 4). Differences in population performance were unrelated to geographical distance between marginal and central populations (Figure S6). The same asymmetry (i.e. higher overall performance in HLM than LLM for similar temperature deviations) was also observed when analysing terrestrial species alone, but this response was affected by precipitation (effective degrees of freedom = 6.07, F = 2.02, p = .058, total deviance explained = 32.5%; Table S4). With decreasing precipitation, performance decreased faster in low-latitude populations (Figure 5).

4 | DISCUSSION

Overall, our results show that populations from the centre of the range tend to outperform those residing at the range margins, and that this difference is considerably more pronounced at low-latitude margins. Such latitudinal asymmetry is predicted when the
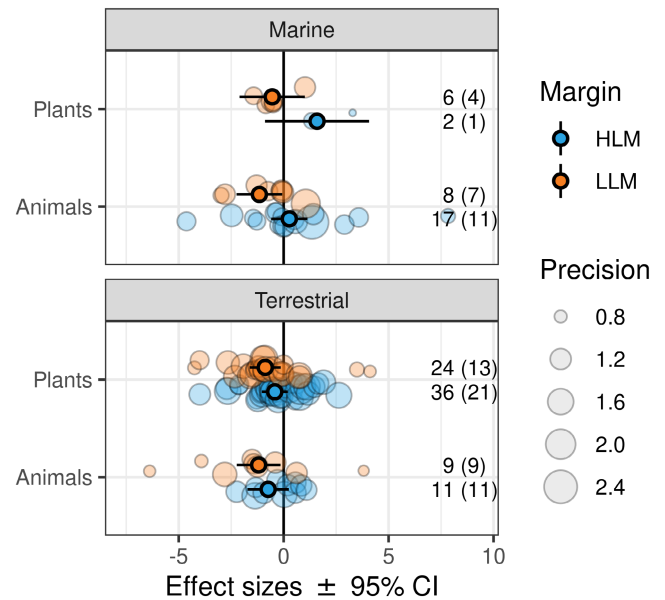

FIGURE 3 Asymmetry in population performance at high- (HLM) and low-latitude margins (LLM) for each Kingdom and Realm. Coloured dots represent individual effect sizes; their size is proportional to the precision of the case study. Black circled dots represent mean coefficient estimates and 95% CI from the model including Margin, Kingdom and Realm as moderators. Negative and positive values indicate lower and higher performance of marginal populations as compared to central populations, respectively. Numbers indicate the number of case studies and, within parentheses, the number of primary studies they were extracted from.
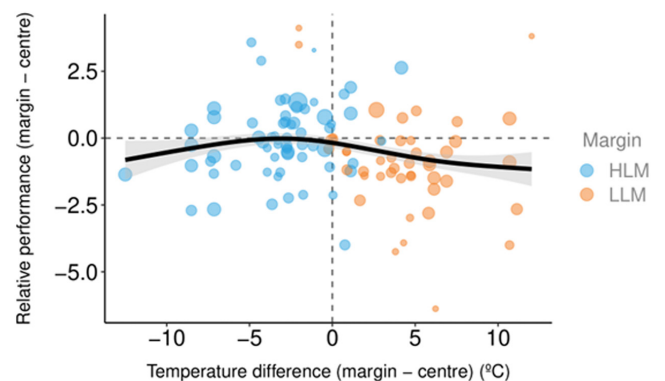

FIGURE 4 Relationship between the observed difference in performance (Hedges' *d*) and the difference in average temperatures between peripheral and central populations for the period 1985–2016 [n = 109 margin-centre comparisons involving 52 species (37 terrestrial and 15 marine)]. Positive values of Hedges' *d* indicate higher 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 higher 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. 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.

environmental conditions relevant for population performance are directionally displaced (Lenoir & Svenning, 2015; Figure 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 result from ongoing climate change, although we cannot exclude eventual effects of post-glacial colonization lags (Hargreaves et al., 2014; Normand et al., 2011). To evaluate the potential role of such long-term colonization lags, we thoroughly searched the literature (including the BIOSHIFTS database; Lenoir et al., 2020) for published evidence on ongoing range shifts of the 54 species included in our meta-analysis. We detected published evidence for a total of 24 ongoing range shifts concerning 15 of our species. Most of these shifts (79%) were polewards and hence in accordance with the range-wide asymmetry in population performance that we are reporting here (see Table 2). According to the authors reporting them, all shifts were directly or indirectly linked to recent climate change (especially rising temperatures), and not to historical factors. Importantly, both these 15 and most of the other species in our meta-analysis represent either highly mobile species or geographically widespread species reaching high latitudes (Figure S5), in other words: species that are unlikely to exhibit persistent, strong post-glacial migrational lags (e.g. Baselga et al., 2012; Seliger et al., 2021). Taken together, this evidence suggests that recent climate change probably plays an important role in the identified asymmetry in marginal population performance. This does however not rule out that current and long-term dynamics may go along with each other in some cases or that historical effects might even be more relevant in species with characteristics less represented here.

The type of range margin (HLM or LLM) only explained a small amount (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 only reported short-term data that are likely to miss relevant periods of (by definition
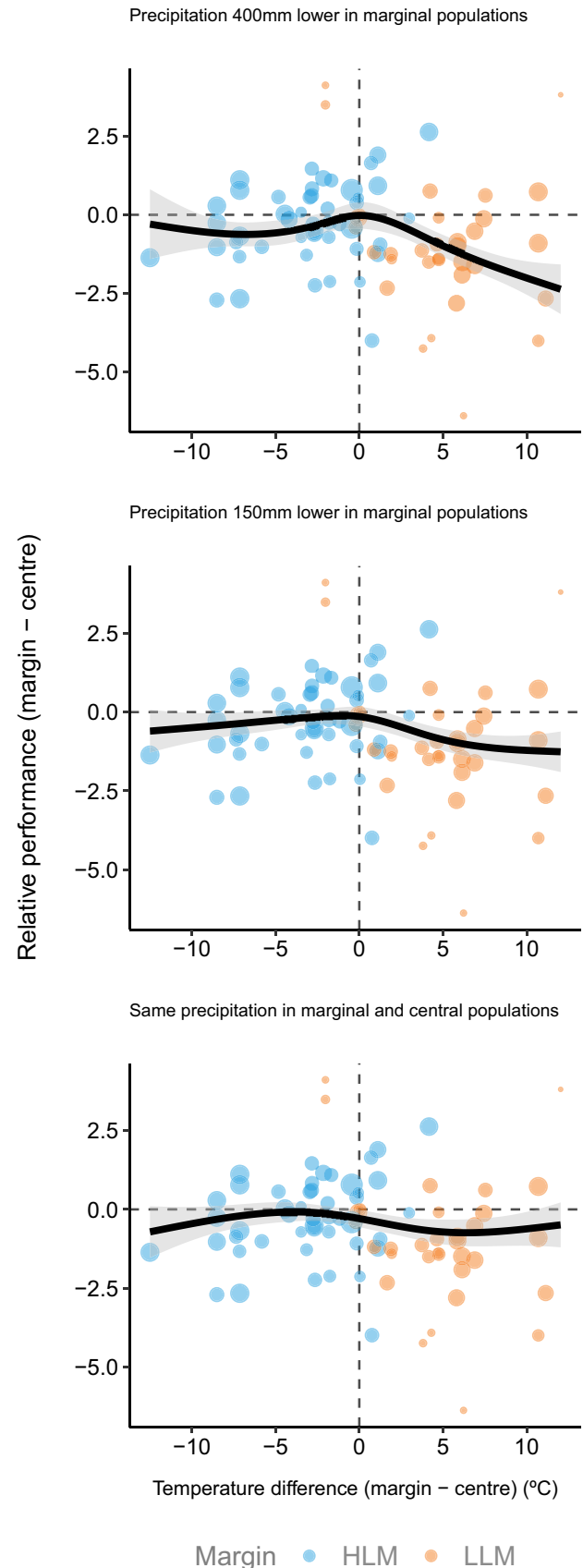
rare) climatic extreme events, and may thus not fully capture long-term trends in those populations. More generally, performance at certain specific life stages is not necessarily a reliable predictor of

TABLE 2 List of species included in the meta-analysis for which information about range shifts has been reported in the scientific literature.

Organism	Species	Type of range shift	Ref.	Study period	Driver
Bird	*Cyanistes caeruleus*	Expansion northwards	1	1994–2009	Temperature
		Expansion northwards	2	1974/79–1986/89	Climate
		Expansion southwards	3	2000/02–2010/12	Temperature
		Expansion northwards	4	1960–2014	Climate
		Expansion northwards	5	1970/80–2006/10	Temperature
	Ficedula hypoleuca	Expansion northwards	5	1970/80–2006/10	Temperature
	Dendroica caerulescens	Expansion northwards	6	1980/85–2000/05	Climate
Fish	*Girella elevata*	Expansion southwards	7	2002–2009	(Temperature)
		Expansion southwards	8	1992/95–2006/07	(Temperature)
Herb	*Plantago coronopus*	Expansion northwards	9	1978/94–1995/2011	(Temperature)
Herb	*Silene acaulis*	Expansion south	9	1978/94–1995/2011	(Temperature)
Herb	*Cirsium heterophyllum*	Expansion northwards	9	1978/94–1995/2011	(Temperature)
	Cirsium acaule	Expansion northwards	10	1930/60–1987/99	(Temperature)
Herb	*Himantoglossum hircinum*	Expansion northwards	11	1991–2006	Temperature
Seaweed	*Fucus guiryi*	Contraction south	12	1970–2012	Temperature
		Contraction south	13	1982–2011	Temperature
	Fucus vesiculosus	Contraction south	14	1982–2011	Temperature
		Expansion southwards	15	1970–2000	Temperature
Tree	*Thuja occidentalis*	Expansion northwards	16	1970–2002	Not analysed
		Expansion northwards	17	1980–2015	Mixed
		Contraction north	18	1970/78–2000/12	Not analysed
	Pinus sylvestris	Expansion southwards	19	1914/87–1997/2013	Climate
	Juniperus communis	Expansion northwards	9	1978/94–1995/2011	(Temperature)
	Taxus baccata	Expansion northwards	10	1930/60–1987/99	(Temperature)

Note: For each shift, the study period and the driver suggested by the authors are shown (drivers in parentheses denote an indirect assessment). All cases but *Girella elevata* are located in the Northern Hemisphere; see Appendix B for full references. 1: Massimo et al. (2015); 2: Brommer (2004); 3: Tayleur et al. (2015); 4: Potvin et al. (2016); 5: Virkkala & Lehikoinen (2017); 6: Zuckerberg et al. (2009); 7: Last et al. (2015); 8: Stuart-Smith et al. (2010); 9: Groom (2013); 10: Amano et al. (2014); 11: Van der Meer et al. (2016); 12: Riera et al. (2015); 13: Lourenço et al. (2016); 14: Nicastro et al. (2013); 15: Lima et al. (2007); 16: Boisvert-Marsh & Périé (2014); 17: Fei et al. (2017); 18: Sittaro et al. (2017); 19: Kuhn et al. (2016).

lifetime fitness and population growth rates (Lee-Yaw et al., 2016; Villellas et al., 2015). Climate-driven trends in our performance measures may also be masked by interferences with biotic interactions (Louthan et al., 2015), which tend to be especially relevant at warm range margins (Paquette & Hargreaves, 2021). And anthropogenic drivers other than recent climate change, such as land use change, pollution, or biotic invasions, may further modify marginal population performance (Vilà-Cabrera et al., 2019). 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 LLM 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 are a widespread phenomenon, 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 potentially allow them to reduce population declines and accumulate higher extinction debts (Jackson & Sax, 2009; Jump et al., 2009). Nevertheless, the vast majority of the studies involving plant species (66 out of 68) reported that plant populations performed worse at the range margins (Figure 3). One possible explanation is that most of the original studies in our meta-analysis targeted demographic variables that are not tightly associated with the major mechanisms enhancing the resilience of plant populations, for example dormancy, resprouting or extended iteroparity (see Hampe & Jump, 2011).

Climate is shifting at different paces in marine and terrestrial environments. The median rate of temperature increase on land is more than triple that in the oceans (0.24 vs 0.07 °C per decade since 1960; Burrows et al., 2011). Climate change velocity – that is, the geographical shift of isotherms over time – is, however,

often considered to be more relevant for species range shifts. Global patterns of climate velocity are quite heterogeneous, but values on land and in the oceans are similar at the latitudes from which most of our original studies stem (Burrows et al., 2011). Still, marine species are on average shifting their range considerably faster polewards than terrestrial ones (Lenoir et al., 2020), probably due to the interplay between their narrower thermal safety margins (Sunday et al., 2012) and more effective dispersal. Given the fast range dynamics of marine species, one might expect that these species would also show stronger asymmetry in marginal population performance than terrestrial ones. Although we were unable to confirm such a difference in our global models, marine organisms experienced slightly, but consistently greater asymmetry than their direct terrestrial counterparts (Figure 3). Our failure to statistically corroborate the expected difference between marine and terrestrial species might therefore be due to lack of statistical power. On the other hand, Figure 3 also illustrates that the only statistically significant reduction in marginal population performance occurred in the LLM populations of terrestrial species (both plants and animals). Such populations tend to be less sensitive than marine populations to temperature fluctuations and rather constrained by water availability than by temperature (Lenoir et al., 2020; Vilà-Cabrera et al., 2019). They often occur in 'microrefugia', that is, enclaves of suitable and relatively stable climate that is locally decoupled from regional trends due to topography or other effects (Hampe & Jump, 2011). The relatively strong signal exhibited by these populations could indicate that their particular refugial environments allow them to persist during a certain period of time even under reduced performance before ultimately going extinct – in other words: to accumulate a greater extinction debt than marine populations (see also Lenoir et al., 2020).

Although purely correlational, the analysis of relationships between differences in population performance and local climates provided 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 partially related to differences in temperature, yet this link was far stronger in LLM 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 (Hastings et al., 2020; Kunstler et al., 2020; Normand et al., 2011). Low levels of precipitation reinforced the observed temperature effect in terrestrial organisms, and this was once again especially true in LLM populations. This trend is likewise expected 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 occurs in combination with low levels of precipitation. Nonetheless, there was extensive unexplained variation

and more, or higher quality, data will be needed to assess these relationships in the future.

5 | CONCLUSIONS

Overall, our results support the notion that the performance of marginal populations – animal or plant, terrestrial or marine – is sensitive to a changing climate, with performance at LLMs being especially negatively affected by warming. Given that differences in marginal population performance can represent an early indicator of impending range shifts (Lenoir & Svenning, 2015; Parmesan et al., 1999), our results indicate that many extant species ranges are not in equilibrium with current climates, but poised to decline at LLMs and increase at HLMs even though they have to date not experienced perceivable shifts. Our results also represent further evidence that an enhanced representation of demographic and dispersal dynamics could increase the realism of population-based approaches to species distribution modelling (Shipley et al., 2022). 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.

CONFLICT OF INTEREST STATEMENT
The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT
Data that support the findings of this study and R script are available at 10.15454/STOJ93.

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BIOSKETCH

The authors have developed joint work in the study of species range dynamics focusing on rangewide geographical asymmetry in population performance and disequilibrium in species ranges with current climate. They are also interested in the impacts of disequilibrium on the future distribution of species and communities and on ecosystem function.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

APPENDIX A

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.

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APPENDIX B

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