LETTER

Coexistence barriers confine the poleward range of a globally distributed plant

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Abstract

In the study of factors shaping species' poleward range boundaries, climatic constraints are often assigned greater importance than biotic interactions such as competition. However, theory suggests competition can truncate a species' fundamental niche in harsh environments. We test this by challenging a mechanistic niche model – containing explicit competition terms – to predict the poleward range boundaries of two globally distributed, ecologically similar aquatic plant species. Mechanistic competition models accurately predicted the northern range limits of our study species, outperforming competition-free mechanistic models and matching the predictive ability of statistical niche models fit to occurrence records. Using the framework of modern coexistence theory, we found that relative nonlinearity in competitors' responses to temperature fluctuations maintains their coexistence boundary, highlighting the importance of this fluctuation-dependent mechanism. Our results support a more nuanced, interactive role of climate and competition in determining range boundaries, and illustrate a practical, process-based approach to understanding the determinants of range limits.

Keywords

Coexistence, competition, geographic distribution, invasibility, niche model, range limit.

Ecology Letters (2020)

INTRODUCTION

Ecologists have long embraced Darwin's hypothesis that species' range limits are determined by biotic interactions towards the equator and by climatic harshness towards the poles (Darwin, 1859; Dobzhansky, 1950; MacArthur, 1972; Brown, 1995). This hypothesis assumes that the number of other species or individuals with which a species interacts increases towards the equator, eventually reaching a latitude where the effects of competition, predation or disease curb further expansion. Because species richness and population densities often decline towards the poles, environmental stress is thought to have primacy over interspecific interactions in determining species' poleward boundaries. However, empirical support for this century-old hypothesis – variously called *stress gradient hypothesis* or the *species interactions–abiotic stress hypothesis* (SIASH) (Louthan *et al.*, 2015) – remains mixed (Wethey, 2002; Maestre *et al.*, 2005; Hargreaves *et al.*, 2014; Cunningham *et al.*, 2016; Morris *et al.*, 2020).

These hypotheses commonly posit that the *per capita* magnitude (Grime, 1979; Louthan *et al.*, 2015) or relative frequency (Bertness and Callaway, 1994; Maestre *et al.*, 2009) of negative interactions, such as competition, should decrease with environmental stress, resulting in weaker competitive regulation of populations in harsher environments. While this prediction often holds (reviewed in Louthan *et al.*, 2015), a population's *tolerance* of competition can also decrease in harshening environments, where even weak competition can drive an already-low *per capita* growth rate, r ($= dN/Ndt$, where N is population size), below zero (Holt, 1985; Chesson and Huntly, 1997). The relative importance of competition or other negative interactions in shaping range margins may therefore hinge on a delicate balance between the overall intensity of competition experienced by a marginal population and the extent to which competition suppresses its environmentally determined *per capita* growth rate.

Assuming that species' geographical distributions are manifestations of their ecological niches (Hutchinson, 1957; Pulliam, 2000; Soberón, 2007), it becomes possible to study factors shaping these distributions using the quantitative tools of population ecology (Holt, 2009; Godsoe *et al.*, 2017). A species' biotically reduced or realised niche can be defined by the combined abiotic and biotic states over which its intrinsic *per capita* growth rate, r, is greater than zero, indicating persistence is possible. This rate can be expressed as a function, $r(E, C)$, of the both the local abiotic environment (E) and the effects of biotic interactions such as competition (C) (Chesson, 1989). For a species that does not interact with any others nor experience dispersal limitation, its geographical range is limited solely by its growth response to the abiotic environment, $r(E)$ (i.e. its fundamental niche) (Hutchinson, 1957) (Fig. 1a). Under a SIASH scenario, stressful abiotic conditions at a species' poleward margin will cause a zero net-growth boundary, beyond which persistence cannot be sustained ($r(\bar{E}) \leq 0$, where the overbar indicates a long-term average over environmental fluctuations). However, if $r(\bar{E})$ cannot sufficiently predict an observed range boundary, then we are left to consider alternative range-limiting mechanisms such as competition, predation, mutualism and dispersal limitation or lags following environmental change – the effects of which can modify or limit the niche in a variety of ways (Soberón, 2007; Godsoe *et al.*, 2017; Alexander *et al.*, 2018) (Fig. 1b and c).
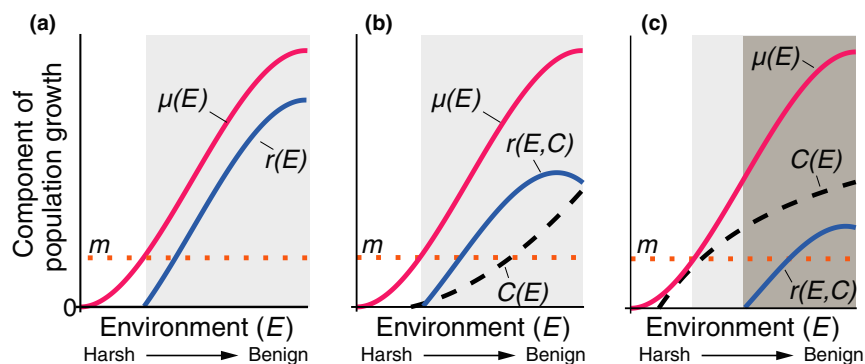
Figure 1 A species' intrinsic growth rate, r $(=dN/Ndt)$, can be expressed as a function of its birth rate, μ, the impacts of competition from other species, C, and a mortality term, m, such that $r = \mu - m - C$. We can define a species' niche breadth as the conditions where $r > 0$ (Godsoe *et al.*, 2017). (a) In the absence of interspecific interactions, the grey area shows the fundamental niche for a species with a monotonic growth response across an environmental gradient E. For simplicity, we assume mortality m is constant over E. (b) Consistent with the SIASH pattern (Louthan *et al.*, 2015), including a competition term $C(E)$ that decreases in harshening environments suppresses *per capita* growth but does not affect the niche limit. (c) Slightly adjusting the functional form of $C(E)$ causes the niche to be truncated by competition in harsh environments by negating the positive effects of $\mu(E)$ (Chesson and Huntly, 1997). The darker grey region shows the new biotically limited niche breadth. Range boundaries can therefore occur where interspecific competition truncates the niche. In a community context, this boundary is the coexistence boundary – across which stable coexistence between two or more competitors is no longer possible.

Quantifying the joint, interactive effects of the abiotic environment and competition on species' growth rates are challenging, but can be accomplished using the tools of modern coexistence theory (MCT) (Chesson, 2000a). If a species' latitudinal range margin is limited by competition, it is incapable of stably coexisting with resident competitor species at and beyond the latitude where its long-term *invasion growth rate*, $\bar{r}_{\text{inv}}$, switches sign from positive to negative. This growth rate quantifies a species' ability to invade and therefore coexist with a community of resident competitors, and can be partitioned into the relative contributions of various coexistence mechanisms (Ellner *et al.*, 2019). These mechanisms reduce species' niche overlap and growth advantages to prevent competitive exclusion, and are defined by their degree of dependence on fluctuations in environmental and competitive factors (Chesson, 2000a). In a geographical context, coexistence outcomes are expected to vary over space if the environment covaries with latitude, leading to the prediction that competition-limited species' ranges manifest where the joint effects of the environment and competition prohibit coexistence (Godsoe *et al.*, 2015). Bringing the MCT framework to bear on niche models permits an explicit quantification of mechanisms causing competitor-limited range margins, although this has yet to be attempted using real distributional data (Godsoe *et al.*, 2017, 2018; Alexander *et al.*, 2018).

Here, we ask whether a process-based (also called mechanistic) niche model (Kearney and Porter, 2009) can accurately predict the poleward range margins of two of the most broadly distributed plants on Earth – the duckweeds *Lemna minor* and *Spirodela polyrhiza*. These minute floating plants widely coexist in fresh waters across N. America, Eurasia, Africa and Australia (Figs S1 and S2), although competition limits their stable coexistence under certain conditions (Armitage and Jones, 2019; Hart *et al.*, 2019). Our objective was to test whether species' laboratory-measured growth responses to temperature and competition can be used to accurately predict their range margins. This approach has successfully predicted species distributions over various abiotic and dietary niche dimensions (Birch, 1953; Buckley, 2008; Hooper *et al.*, 2008; Eckhart *et al.*, 2011; Kearney *et al.*, 2018), but has yet to be used in a multispecies context to evaluate how competition influences range limits and coexistence. Although multispecies statistical niche models attempt to recover the independent biotic and abiotic determinants of species distributions (Pollock *et al.*, 2014), these correlative approaches cannot yet reliably attribute co-occurrence patterns to competitive interactions (Blanchet et. al, 2020). A process-based, or mechanistic niche modelling approach – which includes experimentally measured competition terms – permits us to ask whether predicted poleward range limits are more or less accurate when we account for interspecific competition. We then partition our model's geographically explicit invasion growth rates into their constituent coexistence mechanisms to identify how these mechanisms vary over space to maintain competitors' range boundaries.

MATERIALS AND METHODS

Detailed methods are described in the Supporting Information Appendix.

Mechanistic niche model

We use a previously developed stage-structured differential equation model describing the population growth rates of our focal duckweed species. The process for developing and fitting this model is detailed in (Armitage and Jones, 2019). The model describes the temporal dynamics of the focal species' (j) clonal vegetative and dormant (turion) forms (N_j and S_j respectively) according to the equations.

$$\frac{dN_j}{dt} = N_j\mu_j(T)\left[1 - d_j(T)\right]\left[1 - \sum_{k=1}^{2}\alpha_{jk}(T)\log(N_k+1)\right] - N_j m_j + S_j g_j(T)$$

$$\frac{dS_j}{dt} = N_j\mu_j(T)d_j(T)\left[1 - \sum_{k=1}^{2}\alpha_{jk}(T)\log(N_k+1)\right] - S_j g_j(T),$$

(1)

where m_j is a constant *per capita* mortality rate for each species. We do not include mortality spikes at $T \leq 0$ C because this would assume that all duckweed perish when temperatures drop below freezing. Although this is indeed possible, many plants escape mortality in ice-free refuges that remain unfrozen at our spatial scale of inference (10–20 km^2). Nonetheless, adding such a term does not change the qualitative outcomes of our subsequent invasion analyses. The maximum daily *per capita* growth rate, $\mu_j(T)$, is a unimodal function of temperature following the expression.

$$\mu_j(T) = c_j T\left(T - T_{\min,j}\right)\left(T_{\max,j} - T\right), \quad 0 \leq T_{\min,j} < T_{\max,j}. \quad (2)$$

Here, the parameters $T_{\min,j}$ and $T_{\max,j}$ describe the minimum and maximum temperatures at which growth is possible (C), and c_j is a shape constant. We assume growth is not possible at temperatures less than 0 C and so require $T_{\min,j}$ to remain positive. Inter- and intraspecific competition were modelled using the temperature-dependent parameters α_{jk} ($k = \{1,2\}$) described by the function.

$$\alpha_{jk}(T) = \max\left[0, \alpha'_{jk} + \psi_{jk}(T-20)\right], \quad (3)$$

where α'_{jk} are competition coefficients measuring the proportional effect of N_k on the growth rate of species j at 20 C, and ψ_{jk} describe the change in the strength of competition with ambient temperature. We prevent the competition parameter from switching sign by setting the parameter to zero in instances where it would otherwise be negative. We use the logarithm of competitor density to describe each species' concave-up density-dependent growth responses. Instantaneous temperature-dependent turion investment, d_j, and germination, g_j, fractions were modelled as logistic functions of temperature using the equations.

$$d_j(T) = 1 - \frac{e^{T_{d,j}+T}}{1+e^{T_{d,j}+T}}, \quad (4)$$

and

$$g_j(T) = \frac{e^{T_{d,j}+T}}{10(1+e^{T_{d,j}+T})}, \quad (5)$$

where $T_{d,j}$ is the temperature at which turion production accounts for 50% of total new growth, and $T_{g,j}$ is the temperature at which 50% of turions or sunken vegetative fronds that have germinated after 10 days. For *L. minor*, we substitute temperature-dependent dormancy, $d(T)$, with a constant of 0.01%, representing sunken vegetative fronds that remain susceptible to mortality yet do not reproduce nor compete. Model parameters were empirically estimated from replicated growth and competition assays conducted in environmental chambers spanning a range of ambient temperatures from 3 C to 37 C (Fig. S3, Table S1), and had good predictive accuracy for both laboratory-measured growth rates ($R^2 \approx 0.8$, Fig. S4) and field-measured relative abundances (Fig. S5).

Mechanistic range prediction

We used 2.5 arcmin-resolution mean annual temperatures and temperature amplitudes (Hijmans *et al.*, 2005) to generate 10 years of sinusoidal temperature fluctuations for each grid cell. These approximations closely approximate observed lake surface temperatures, particularly over the range of temperatures during which duckweeds can grow and invade (Fig. S6) (Carrea and Merchant, 2019). Using these time series, we simulated the population dynamics of each species to monoculture equilibria, saving each day's *per capita* growth rate, $r_{res}(t)$ ($= [N_j + S_j]^{-1}[dN_j/dt + dS_j/dt]$). Here, the subscript 'res' indicates that the species is in its resident, monoculture state and so interspecific competition does not occur. After verifying $\bar{r}_{res}$ had reached its dynamic equilibrium (≈ 0), we saved the last year of equilibrial resident abundances. We used each grid cell's temperature and resident population time series to estimate the long-term average growth rates of an invading species $\bar{r}_{inv}$. We set resident densities N_k at equilibrium and conspecific densities N_j at one, then calculated $r_{inv}(t)$ at each time step t over the final year, time-averaging the resulting growth rates. We identified the set of cells where each species' long-term low-density growth rates as residents ($\bar{r}_{res}$) and invaders ($\bar{r}_{inv}$) were greater than zero. The former set are range predictions derived from the pure environmental response, while the latter set, which includes the effects of competition, are range predictions derived from the biotically determined realised niche. Coexistence is predicted where $\bar{r}_{inv} > 0$ for both species in their invasion states (Turelli, 1978). Note that while our model contains competition terms that would be considered proximate or phenomenological in a population dynamic model, we follow the standard practice of labelling such process-based models as *mechanistic* to contrast them with *correlative* niche modelling approaches (Kearney and Porter, 2009).

Statistical range prediction

Occurrence records of *S. polyrhiza* and *L. minor* used to fit our models were obtained from the Global Biodiversity Information Facility (*GBIF*) (dois: 10.15468/dl.wpisn8 and 10.15468/dl.2pixjr) and The Botanical Society of Britain & Ireland's (*BSBI*) geo-referenced database. We focused our analyses on three regions possessing an abundance of high-quality botanical records and encompassing our species' northern latitudinal range limits. These regions include the United Kingdom and Ireland, North America (Mexico, US and Canada), and Northern Continental Europe. Global records were accessed and downloaded from *GBIF* and *BSBI*, which were then quality filtered (Zizka *et al.*, 2019). Given the high density of occurrence records in our study regions, we made the assumption that the distribution of occurrence records reflected the true geographic distributions of our study species. We note that while high-latitude observations may have been missed due to a lack of sampling effort (particularly in Central Canada and NE Europe), the observed distributions

of points align closely with distributional accounts from the literature (Landolt, 1986).

We used the maximum entropy method (MaxEnt) to predict the distributions of *S. polyrhiza* and *L. minor* (Phillips *et al.*, 2006). Models were fit to spatially thinned occurrence records for each species in all three study regions, as well to the combined suite of point records across all study regions. Covariates included two sets of 2.5 arcmin bioclimatic variables. The first group of models, called MaxEnt12, used 11 temperature variables and one precipitation variable, while the second group, called MaxEnt2, include only mean temperature and annual temperature amplitude – the same two covariates used in our mechanistic models' predictions (Table S3). MaxEnt models were fit using fourfold cross validation across nested, geographically independent checkerboard-partitioned presence and random background points (Muscarella *et al.*, 2014) and across a range of regularisation parameters (Radosavljevic and Anderson, 2014). Best-fit models were selected based on relative AIC rankings (Burnham and Anderson, 2003), 10% omission rate metrics (Muscarella *et al.*, 2014), and by visual inspection of the results. Binary predictions of species' ranges were made by thresholding the predicted occurrence probabilities, p_{occ}, by 10% omission threshold, τ, to ensure at least 90% of location records are included within the range (Pearson *et al.*, 2007).

Evaluating and comparing model predictions

We compared the predictive success of competition-explicit and competition-free mechanistic models using the mutual information criterion, $I(\hat{Y}, Y)$ (Finn, 2007). This quantity measures the amount of information that a classifier prediction, $\hat{Y}$, reveals about its true classification, Y. Here, mutual information measures the agreement between 'true' presence/background points (Y) and our models' classifications of these points ($\hat{Y}$) by computing the difference between two entropies $I(\hat{Y}, Y) = H(Y) - H(Y|\hat{Y})$. We estimated mutual information for both classes of mechanistic models ($\bar{r}_{inv}$ and $\bar{r}_{res}$) across a gradient of presence/absence cutoffs corresponding to various growth rates ($\bar{r}$), with the expectation that the best-fitting model's mutual information will be maximised at or near the biologically meaningful presence/absence cutoff of $\bar{r} = 0$. To compare agreement between our statistical and mechanistic models, we used a beta regression with a logit link function (Ferrari and Cribari-Neto, 2004) to assess the relationship between predicted invasion or resident growth rates and MaxEnt occurrence probabilities. Here, a positive log-odds coefficient combined with a high coefficient of determination (R^2) signifies a close, positive correspondence between pairs of model outputs. Furthermore, the beta regression line should pass near to or through the point corresponding to $\bar{r} = 0$ and $p_{occ} = \tau$, signifying close agreement between the biologically motivated invasion threshold and the statistically motivated MaxEnt occurrence threshold. True poleward range limits for each species were estimated from occurrence records by calculating the 95% confidence intervals for each region's latitudinal maxima. These were estimated from 5000 nonparametric bootstrap samples of maximum values. Niche model estimates were regressed against latitude to identify x-intercepts and

their associated inverse 95% confidence intervals (Draper and Smith, 1998) corresponding to latitudes at which $\bar{r}_{inv}$ and $p_{occ} - \tau$ were zero (Fig. 3a).

Quantifying coexistence mechanisms

We estimated the contributions of various fluctuation-dependent and fluctuation-independent mechanisms on the coexistence of *S. polyrhiza* and *L. minor* (details in Supporing Information) (Ellner *et al.*, 2019). This method partitions differences between the long-term growth rate of an invading species, $\bar{r}_{j\backslash inv}$ and that of a resident, $\bar{r}_{k\backslash res}$, $(j \neq k)$ (which is approximately zero at equilibrium), using the equation.

$$\bar{r}_{j\backslash inv} \approx \Delta_j^* + \Delta_j' + \Delta_j^T + \Delta_j^{N_k} + \Delta_j^{(T\#N_k)} + \Delta_j^{(TN_k)}, \qquad (6)$$

where Δ_j^* is the fluctuation-free growth rate, Δ_j' is the contribution of fluctuation-driven change in mean competitor density, Δ_j^T is the contribution of relative nonlinearity in temperature-growth responses, $\Delta_j^{N_k}$ is the contribution of relative nonlinearity in responses to competitor densities, $\Delta_j^{(T\#N_k)}$ is the is the interaction between competitor density and temperature variability, and $\Delta_j^{(TN_k)}$ is the covariance between temperature and competition, which quantifies the temporal storage effect. These values were calculated across a two-dimensional grid of average annual temperatures and annual temperature amplitudes to identify the thermal regimes where particular coexistence-promoting mechanisms operate. We overlaid global observation records for each species on these grids to identify (1) the environmental states where coexistence was predicted to break down relative to the observed environmental distribution of each species, and (2) which coexistence mechanisms contributed most strongly to shaping these coexistence margins. Note that despite the spatial dimension of these partitions, they do not measure any purely spatial coexistence mechanisms such as fitness-density covariance (Chesson 2000b).

RESULTS

Accounting for interspecific competition improves poleward range limit estimates

Using a mechanistic niche model to predict long-term low-density growth rates of *S. polyrhiza* in the absence ($\bar{r}_{res}$) and presence ($\bar{r}_{inv}$) of interspecific competition, we found that range predictions made using $\bar{r}_{inv}$ closely matched the distribution of observation records, while predictions from competition-free models ($\bar{r}_{res}$) did not (Fig. 2). Based on the mutual information criterion, we found strong support for our competition models over competition-free models for predicting the observed distribution of *S. polyrhiza*, with mutual information peaks lying almost exactly at $\bar{r}_{inv} = 0$ for all three regions (Fig. S7). This was not the case for *L. minor* models, where mutual information for both invader and resident classifications peaked at approximately equal $\bar{r}_{res}$ cutoffs – all of which were greater than zero. This indicates that both competition-explicit and competition-free models for *L. minor*

performed similarly and had slight poleward bias in their range limit predictions, which was also evident after mapping the predictions (Fig. S8). There was also close correspondence between the observed latitudinal limits of *S. polyrhiza* from occurrence records and the competition model-predicted maximum latitude, as evidenced by the overlapping 95% confidence intervals between observed limits and predictions from our mechanistic invasion model ($\bar{r}_{inv}$) (Fig. 3b–d, Fig. S10 and Table S5).

Across all study regions, our mechanistic competition model performed as well as the best-fit statistical niche models in predicting latitudinal maxima, according to the models' overlapping 95% confidence intervals (Fig. 3b–d, Fig. S10 and Table S5). We encountered a significant, positive correspondence between statistical and mechanistic competition model outputs for both *S. polyrhiza* and *L. minor* (Figs S11 and S12), signifying broad agreement between these two different modelling approaches. Beta regression fits for *S. polyrhiza* passed near the points corresponding to $\bar{r} = 0$ and $p_{occ} = \tau$, demonstrating a good agreement between the two occurrence thresholds, while those fit to *L. minor* predictions were not close to this point, indicating disagreement between modeling frameworks possibly stemming from a positively biased growth rate estimate for this species. Although all models had high true positive rates, binomial omission tests indicated only MaxEnt models and mechanistic models with competition terms yielded predictions significantly better than random, while mechanistic models without competition terms terms did not (Table. S5).

Thermal fluctuations maintain the coexistence boundary of L. minor and S. polyrhiza

Our model-predicted invasion growth rates, $\bar{r}_{inv}$, are complex functions of interacting, nonlinear competition and environmental responses which – while useful for predicting coexistence – do not reveal the mechanisms underlying these outcomes. To quantify these coexistence mechanisms and investigate how they vary across species' distributions, we partitioned our species' invasion growth rates into a variety of additive terms reflecting the contributions of average and fluctuating temperatures and competitor densities (including their interactions) (eqn 6). Our predicted coexistence boundary (the isocline where $\bar{r}_{inv} = 0$) aligned very closely with the true distributional margin of each species' global occurrence records. For *S. polyrhiza*, this boundary is associated with a negative fluctuation-free growth rate Δ^*, offset by a positive response to temperature fluctuations, Δ^T (Fig. 4). The mechanisms operating near this boundary for *L. minor* are qualitatively similar, although the mean effects of temperature (Δ^*) are stronger relative to those of temperature fluctuations (Δ^T) (Fig. S13). In contrast, we found no evidence that relative nonlinearity in competition Δ^N nor the storage effect $\Delta^{(TN)}$ contribute to maintaining the coexistence boundary (Fig. 4). At the coexistence boundary, Δ^T contributed positively to both species' low-density growth rates while also reducing the growth rate differences that favour *L. minor* over *S. polyrhiza* (Fig. 5). In MCT terminology, Δ^T was primarily *stabilising* (helping both species invade) but also *equalising* (reducing fitness differences) across much of the coexistence boundary.

DISCUSSION

These results highlight the potential limiting effects of interspecific competition on species' poleward ranges. While the overall strength of interspecific competition declined with decreasing temperatures (all $\psi_{jk} > 0$), its negative *per capita* effects on *S. polyrhiza* growth rates outpaced reductions in its environmental response. This observation contradicts prevailing hypotheses concerning the general primacy of abiotic factors in structuring poleward range limits. While our data are consistent with the SIASH's expectation that the strength of competition declines in harsh environments, it challenges its prediction that the relative *importance* of competition should also decrease compared to abiotic factors. Accordingly, our results align with theoretical and empirical results showing that growth rates become increasingly sensitive to the effects of competition in suboptimal environments (Holt, 1985; Chesson and Huntly, 1997; Cunningham *et al.*, 2009; Violle *et al.*, 2010; Hart and Marshall, 2013; Napier *et al.*, 2016; Germain *et al.*, 2018).

Importantly, the range-limiting effect of competition was only observed for the subordinate competitor, *S. polyrhiza*, while the latitudinal limits of *L. minor* do not appear affected
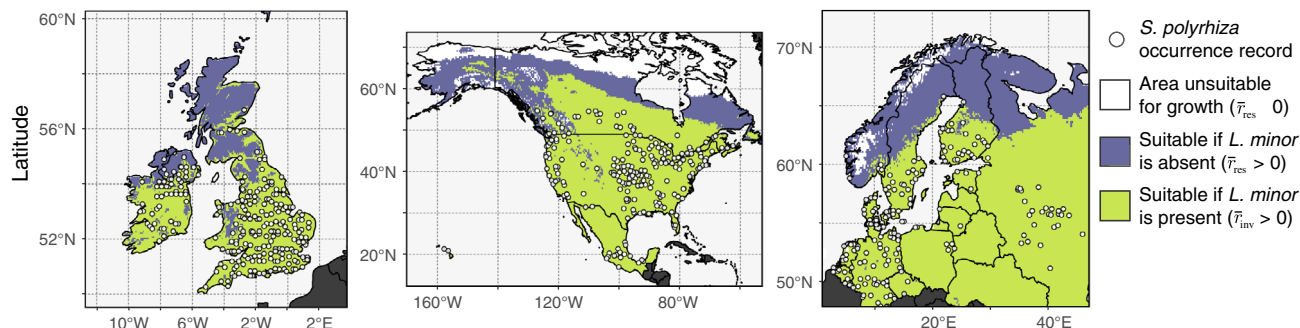

Figure 2 Range predictions for *S. polyrhiza* from the competition model (eqn1) projected across geographic space. Shading denotes areas of predicted population persistence where long-term low-density growth rates in the absence ($\bar{r}_{res}$) or presence ($\bar{r}_{inv}$) of resident competitor *L. minor* is greater than zero. Points denote spatially thinned occurrence records from *GBIF* and *BSBI* databases.
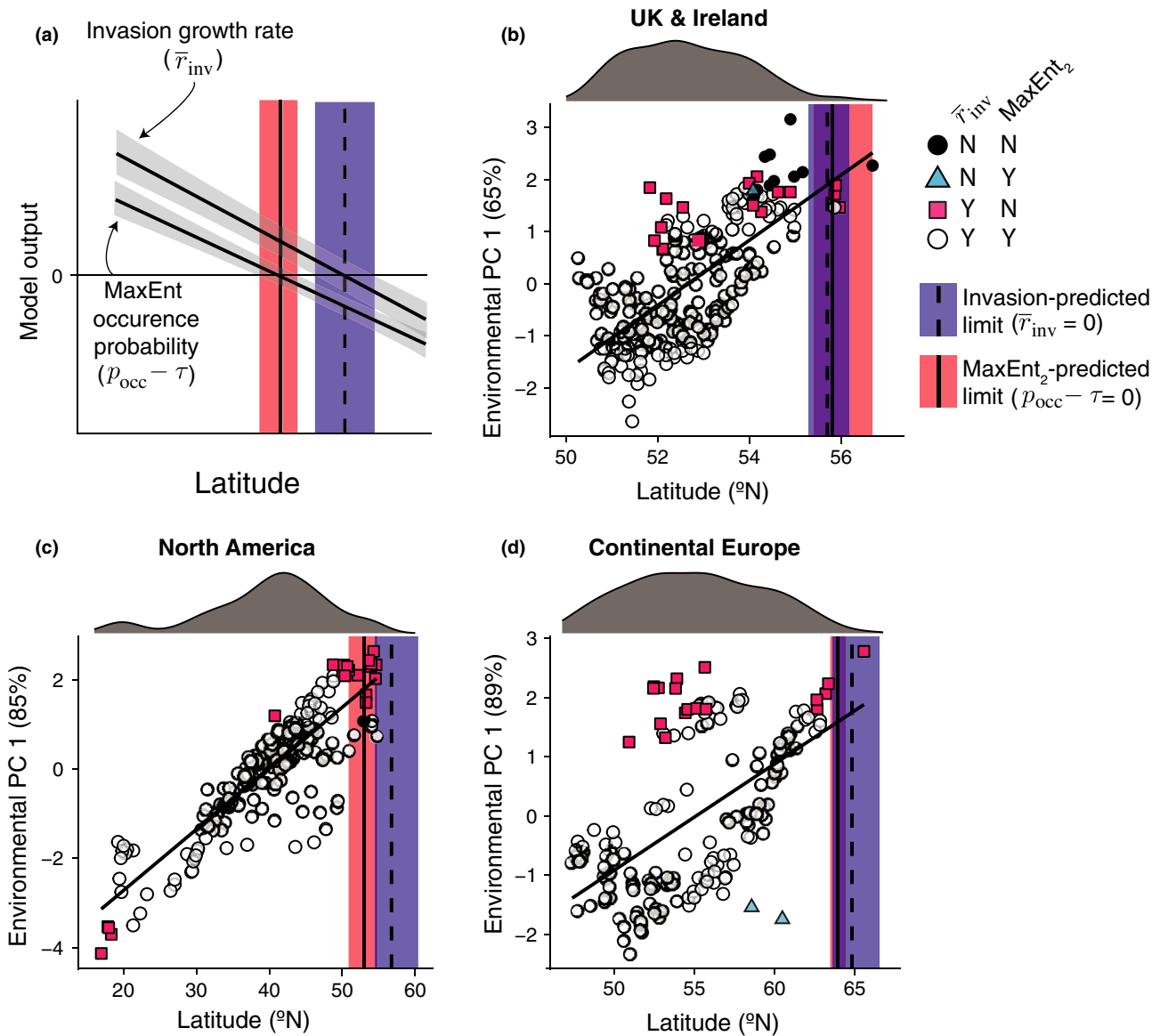
Figure 3 (a) Conceptual diagram of how range limits for *S. polyrhiza* are predicted from niche model outputs. Model outputs were regressed against latitude and their *x*-intercepts (± 95% CI) were used to determine the predicted latitudinal limits. For MaxEnt models, outputs were the probability of occurrence p_{occ} minus the 10% omission threshold value (τ). For mechanistic models, we use the predicted long-term invasion growth rate ($\bar{r}_{inv}$). (b-d) Latitudinal limit predictions for invasion model and 2-variable MaxEnt model. Points denote *S. polyrhiza* observation records, coloured by binary model classification results, and vertical lines show the estimated mean latitudinal limits (± 95% CI) for each model and region. Histograms above each plot show the latitudinal dispersion of occurrence records after spatial thinning.

by competition with *S. polyrhiza*. So, while it is possible for competition to set a species' latitudinal limits, it is by no means a general rule, and abiotic limits are likely important range determinants for many species (Hargreaves *et al.*, 2014). In particular, abiotic factors may set the range limits of species that do not experience strong regulation from resident competitors (or predators) in harsh environments. Some of these taxa, like *L. minor*, may have a competitive advantage at high latitudes and be the lone survivors of an otherwise speciose guild of competitors coexisting at lower latitudes.

The relationship between competition and environmental harshness is also predicted to depend on the ecological similarity of the competitors and the degree to which each is able

to ameliorate the effects of abiotic stress (Maestre *et al.*, 2009). Under this framework, duckweeds – with their high ecological similarity and inability to ameliorate thermal extremes – would not be predicted to show the typical stress gradient pattern of competition giving way to facilitation under increasing stress. In accordance with this framework, we anticipate our results to hold for pairs or guilds of ecologically similar competitors that coexist under favourable conditions, compete for resources, and do not ameliorate abiotic stressors through increased biomass. Many ecologically similar pairs of species show evidence of coexistence and could be candidates for further testing of these predictions (reviewed in Siepielski and McPeek, 2010; Adler *et al.*, 2018). Importantly,
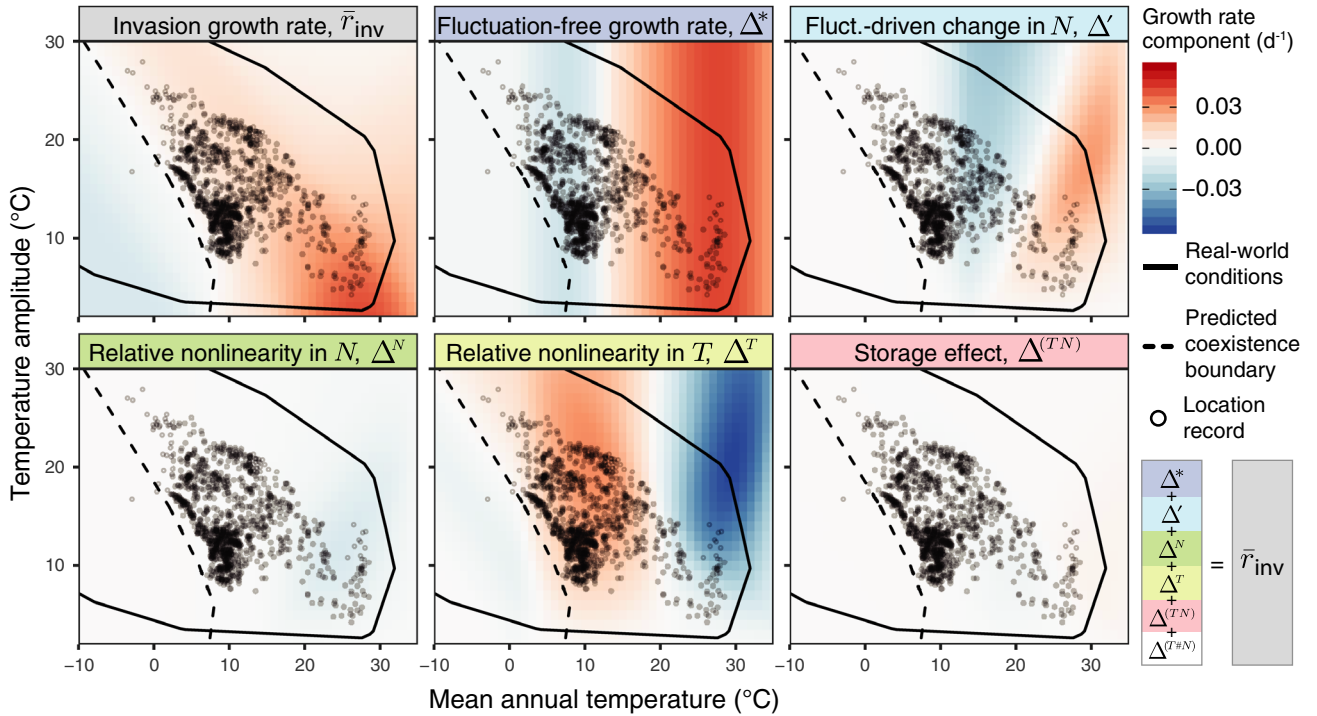
Figure 4 The upper-left panel displays the long-term invasion growth rate, $\bar{r}_{\text{inv}}$, of *S. polyrhiza*, as a function of annual temperature averages and amplitudes. The dashed line denotes the model-predicted coexistence boundary (where $\bar{r}_{\text{inv}} = 0$), and the solid line encompasses the temperature regimes that occur across Earth. Points represent global occurrence records for *S. polyrhiza* projected onto their local temperature axes. The remainder of the panels quantify the contributions of the partitioned coexistence mechanisms from eqn 6. Note the crucial role of relative nonlinearity in temperature responses, Δ^T, in maintaining coexistence near the boundary. The independent joint variation term $\Delta^{(T\#N)}$, which is approximately zero, is not plotted.
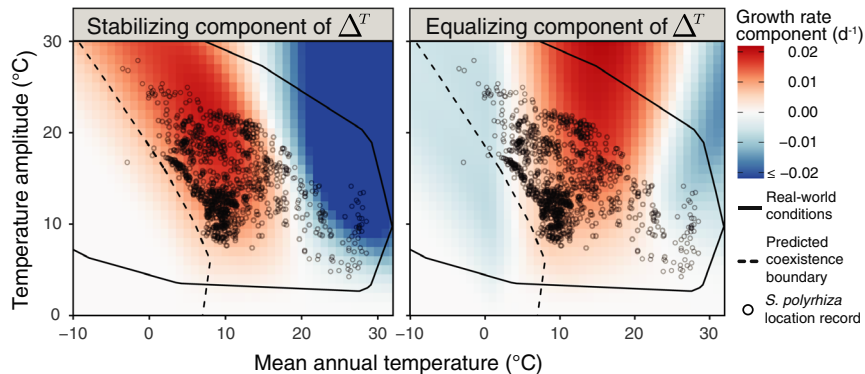

Figure 5 Stabilising and equalising components of Δ^T for *Spirodela polyrhiza*. Stabilisation in Δ^T occurs when relative nonlinearity in thermal responses facilitates both species' invasion growth rates, relative to mean effects, and is proportional to the ratio of intraspecific to interspecific competition. Equalisation in Δ^T occurs when relative nonlinearity in thermal responses reduces the difference in invasion growth rates, favouring the species with the lower growth rate. Stabilising components of Δ^T are the same for both species, while equalising components for *L. minor* are opposite those of *S. polyrhiza*. Points represent thinned global occurrence records for *S. polyrhiza*.

these studies are often performed in benign environments and do not investigate whether coexistence conditions (such as reciprocal invasion or stabilisation) break down under heightened environmental stress. To clarify these issues, we encourage future studies to experimentally quantify invasibility either across real geographical range boundaries or along natural abiotic gradients (such as elevation) reflecting conditions experienced at these boundaries. Invasibility studies could also be done over orthogonal environmental axes to identify whether

general classes of competitive and/or environmental factors predictably result in either abiotic limitation, facilitation or competitive exclusion with increased environmental stress.

Our mechanistic competition models performed well when tasked to predict the geographical ranges of *S. polyrhiza*. However, there were some instances of over-prediction in the N. America region, which may be due to either (1) poor model fit, (2) the inability of *S. polyrhiza* to successfully disperse to this area or (3) the lack of sufficient sampling effort

in these remote areas. Nonetheless, the overall predictions made using this population dynamic approach were similar to both observed duckweed distributions as well as those derived from statistical MaxEnt niche models, demonstrating how laboratory-measured species' environmental and biotic interactions can be useful for modelling species' distributions when reliable occurrence records are not available. In doing so, thermal responses could be supplemented with additional environmental factors such as precipitation and dissolved nutrient concentrations for improved accuracy. However, we concede that this approach may not be tractable for organisms whose reaction norms cannot be experimentally determined.

Our results also illustrate an important point concerning the utility of statistical niche models for estimating species' environmental responses: In areas where a species' intrinsic growth rate is regulated by a competitor, the pure environmental responses of the focal species cannot be statistically recovered with any degree of certainty. This is because environmental responses extracted from occurrence records can be confounded with the latent effects of biotic interactions, yet are modelled as pure environmental responses. While this issue has been recognised for some time (Pearson and Dawson, 2003; Kearney, 2006; Holt, 2020), it is commonly neglected when using statistical niche model outputs to project species ranges under climate change. And while newer multispecies niche models can begin to parse biotic and abiotic factors contributing to species' distributions (Pollock *et al.*, 2014), we remain unable to do so when a species' range is completely nested within that of its strongest competitors, as is the case for *S. polyrhiza* and probably many other organisms. Our mechanistic model predictions can also guide MaxEnt practitioners' selection of the binary occurrence threshold, τ. While τ is commonly a subjective choice based on capturing some proportion of occurrence records, a more biologically meaningful τ could be defined as the MaxEnt probability corresponding to an invasion growth rate, $\bar{r}_{inv}$, of zero.

Previous empirical studies in this experimental system encountered strong negative frequency-dependent (i.e. stabilising) effects on both species' low-density growth rates, but their underlying causes could not be determined (Armitage and Jones, 2019). Here, by fully partitioning these low-density growth rates into coexistence mechanisms, we were able to identify the important fluctuation-dependent components underlying coexistence. That global occurrence records for *S. polyrhiza* overwhelmingly occur in regions where mean temperature effects, Δ^*, are less than zero and relative nonlinearities in thermal responses, Δ^T, are greater than zero means that over much of the known global range of this species, temperature fluctuations, mediated through differences in competitors' nonlinear thermal responses, are critical for maintaining positive *per capita* growth rates and thereby coexistence. However, it is important to note that our dynamic models include only the effects of a single abiotic variable – temperature – and so the inclusion of additional growth factors (such as dissolved nutrients) may further clarify these results.

Studies in other systems have demonstrated the important roles of fluctuation-dependent coexistence mechanisms such as relative nonlinearity in competition (Δ^N) (Letten *et al.*, 2018) and the temporal storage effect ($\Delta^{(TN)}$) (Cáceres, 1997), which do not appear to promote coexistence in our study organisms. While a weak storage effect may be surprising, given the ability of *S. polyrhiza* to buffer population growth in the form of dormant turions, the competitive benefits of this effect are significantly dampened by the species' correlated environmental responses (Armitage and Jones, 2019). Likewise, the effects of relative nonlinearity in competition might be expected to occur under our concave-up competition functions, which intersect for invading *S. polyrhiza* at low *L. minor* densities. However, because our species share similar curvatures of this function over N_k and T, and because *L. minor* fluctuations occur over densities much greater than the point of curve intersection ($\approx 20 - 50$ individuals, depending on temperature), the relative nonlinearity effect is minimal. However, the role of relative nonlinearity in environmental responses (Δ^T) is one that, until recently, was not explicitly accounted for in MCT, yet is clearly important in cases where competitors' environmental responses are nonlinear and non-identical (Ellner *et al.*, 2019). The stabilising effects of Δ^T can only manifest when thermal fluctuations help an invader overcome growth disadvantages under mean conditions, and reflects the net benefit of reduced competition experienced when invading during the most optimal interval of a fluctuating environment. With this in mind, we suggest future studies of species' responses to global change quantify the separate effects of environmental fluctuations *per se* and those of mean conditions, as the former can easily negate or amplify the effects of the latter, even leading to reversals in competitive outcomes (Armitage and Jones, 2019). Our results further demonstrate the degree to which coexistence mechanisms can abruptly shift across environments (shown also in Usinowicz *et al.*, 2017), implying that locally measured coexistence mechanisms cannot be assumed uniform across a species' range.

Despite the concordance between the observed and model-predicted ranges, our mechanistic niche modelling approach is not without limitations. First, we did not account for the effects of pathogens or predators in our model and assumed their effects were negligible. While anecdotal evidence supports this assumption (Landolt and Kandeler, 1987), future studies are needed to quantify the differential effects of natural enemies on duckweed growth rates. Second, our focal species often occur in complex communities of plants and phytoplankton, and so our two-species model may underestimate the strength of interspecific regulation. Although small floating plants widely co-occur with our focal species at lower latitudes, they are absent or very rare near and above the poleward limit of *S. polyrhiza*. This presence of additional competitors at lower latitudes precludes the estimation of competition-limited equatorial limits of our species without additional data on other members of this guild. Submerged macrophytes, on the other hand, are very common at high latitudes, but in most cases do not appear to prevent duckweed from successfully invading (Scheffer *et al.*, 2003). Finally, while duckweed strains exhibit phenotypic variation in their competitive and environmental responses (Ziegler *et al.*, 2014; Hart *et al.*, 2019), our mechanistic niche models use mean values extracted from regression parameters. While identifying

how variation around these means affects geographical range predictions is beyond the scope of this study, our mechanistic model can be expanded to investigate these effects. These potential effects underlie the more general assumption that our laboratory-measured growth and competitive functions approximate the behaviour of duckweeds in natural systems. While additional mechanisms limiting duckweed growth and mortality occur in nature, we note that our recovered growth curves and density-dependence functions are quantitatively consistent with previous laboratory and outdoor mesocosm studies (McLay, 1974; Docauer, 1983; Driever *et al.*, 2005; Demirezen *et al.*, 2007; Hart *et al.*, 2019), and our model accurately predicts the relative abundances of duckweeds in local ponds when simulated using a real thermal time series (Fig. S5).

CONCLUSIONS

Our study responds to calls for a more mechanistic, population ecology-based integration of niche theory with biogeography (Pulliam, 2000; Holt, 2009, 2020; Wiens, 2011; Godsoe *et al.*, 2017). Using an experimentally parameterised dynamic competition model, we are among the first to demonstrate, contrary to prevailing expectations, that interspecific competition can plausibly explain a species' poleward range limit. We note, however, that this was only the case for our inferior competitor, *S. polyrhiza*, and the general extent to which competition influences species' range boundaries remains an open question. It is likely that the importance of competition and other biotic interactions for range delimitation depends on how these factors covary across abiotic environmental gradients and influence the abiotically determined fundamental niche (Fig. 1). Quantifying such interactions between biotic and abiotic factors will be a productive step towards understanding how and why communities and the coexistence mechanisms that maintain them vary over space (Godsoe *et al.*, 2017, 2018; Alexander *et al.*, 2018).

From a methodological perspective, our results showcase the utility of mechanistic niche models for accurate range prediction without the need for occurrence records. With appropriate data, this framework could be employed to predict the effects of novel competitors encountered by species during climate-driven range shifts or following (re)introductions. It may also be valuable for predicting the distributions of species having few or no occurrence records using *ex situ* measurements of their environmental responses. Looking forward, we contend that geographically partitioning mechanistic niche models into their constituent coexistence mechanisms can fundamentally enhance our understanding of how populations and communities vary over space, potentially leading to strategies for promoting species coexistence in restoration, conservation and relocation projects.

ACKNOWLEDGEMENTS

AUTHORSHIP

PEER REVIEW

DATA AVAILABILTY STATMENT

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