Towards an interactive, process-based approach to understanding range shifts: developmental and environmental dependencies matter.

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Abstract:

Many species are undergoing distributional changes in response to climate change. However, wide variability in range shifting rates has been observed across taxa, and even among closely-related species. Attempts to link climate-mediated range shifts to traits has often produced weak or conflicting results. Here we investigate interactive effects of developmental processes and environmental stress on the expression of traits relevant to range shifts. We use an individual-based modelling approach to assess how different developmental strategies affect range shift rates under a range of environmental conditions. We find that under stressful conditions, such as at the margins of the species’ fundamental niche, investment in prolonged development leads to the greatest rates of range shifting, especially when longer time in development leads to of improved fecundity and dispersal-related traits. However, under benign conditions, and when traits are less developmentally plastic, shorter development times are preferred for rapid range shifts, because higher generational frequency increases the number of individual dispersal events occurring over time. Our results suggest that the ability of a species to range shift depends not only on their dispersal and colonisation characteristics but also how these characteristics interact with developmental strategies. Benefits of any trait always depended on the environmental and developmental sensitivity of life history trait combinations, and the environmental conditions under which the range shift takes place. Without considering environmental and developmental sources of variation in the expression of traits relevant to range shifts, there is little hope of developing a general understanding of intrinsic drivers of range shift potential.

Keywords: Voltinism, life history trade-offs, range shifting, invasions, climate velocity, evolutionary rescue, environmental stress, developmental life history strategies
Introduction

Climate change is increasingly allowing many species to colonise previously limiting environments at higher latitudes and elevations (Parmesan and Yohe 2003, Hickling et al. 2006, Chen et al. 2011). These novel environments are typically characterised by shorter growing seasons, fewer resources and increased climate variation in comparison to ancestral habitats. However, the rates at which populations are able to range shift into such environments vary widely among species and taxa (Hickling et al. 2005, 2006). Ultimately, such differences in rates of range shifting may contribute to the differential fate of species under climate change, and may drive global biotic homogenisation as some species will be able to keep pace with climate change via distributional changes, while other species lag behind and face increasing risk of extinction (Thomas et al. 2004, Chen et al. 2011, Davey et al. 2012, Dornelas et al. 2014). Developing a better understanding of the factors allowing species to colonise limiting environments at higher latitudes and elevations is therefore of high importance for developing conservation strategies for range shifting and non-range shifting species, as well as for developing mitigation strategies for range shifting pests (Cannon 1998, Perrings 2005), disease vectors (Lafferty 2009) and invasive species (Cannon 1998, Perrings 2005).

Studies geared towards understanding the future distributions of species have historically relied on species distribution models, which match the current ecological fit of species to their habitats to future environmental conditions (Elith et al. 2011, Pagel and Schurr 2012). However, these studies have often fared poorly in predicting shifts in species geographic ranges (Pearson and Dawson 2003), in part because these studies fail to incorporate species’
capacity for acclimation and adaptation to novel conditions. In recent years there has been a shift from reliance on SDMs towards approaches that explicitly incorporate eco-evolutionary processes such as biotic interactions, plasticity, and adaptive evolutionary change (Dormann et al. 2012, Travis et al. 2013, Urban et al. 2016). Such mechanistic and process-based modelling studies investigating the drivers of range shifts or invasion increasingly incorporate information on dispersal abilities (Brooker et al. 2007, Poyry et al. 2009) and demographic processes such as reproductive rates (Hastings et al. 2005, Huntley 2011, Angert et al. 2011, Maclean and Beissinger 2017). These models have resulted in increased accuracy in predictions of how species will respond to climate change (Barros et al. 2016, Santini et al. 2016, Urban et al. 2016), although recent work suggests that variation in these traits and population characteristics, considered additively, do not adequately explain variation in range shifting rates (Melbourne and Hastings, 2009).

However, developmental strategies as drivers of differential range shift success have received much less attention. More particularly, the interdependencies of developmental strategy and dispersal traits have remained relatively unexplored, despite the potentially high importance of this trait interaction for accurate predictions of invasion spread or how species will respond to climate change (Hassall et al. 2008, Van Pategem et al. 2016). For instance, shorter developmental times have been shown to allow for greater numbers of dispersers within a given year (Lenoir et al. 2008). However, developmental strategies also have implications for morphology, with longer developmental times often associated with larger sizes (Angilletta et al. 2004), especially for species with indeterminate growth (most ectotherms, plants, and fungi). Larger body sizes in turn tend to be associated with increases in dispersal-related trait values (Morrison and Hero 2003, Hassall et al. 2008). Species which take longer to reach
maturity are therefore potentially able to attain larger body sizes and more favourable dispersal characteristics at the range limit (Hassall et al. 2008). Thus long development times can also potentially increase rates of range expansion (Blanckenhorn and Demont 2004, Hassall et al. 2008, Hassall 2013, Nylin and Sviird 2016), but via a different mechanism than shorter generation times. Therefore, range shifts may be facilitated by either faster development times (greater potential for demographic expansion), or longer development times (larger body size and better dispersal ability at the range limit), but the conditions under which each of these different developmental strategies may be favoured at the range limit remains unexplored.

In addition to their putative role in driving range shifts to higher latitudes and elevations, developmental strategies are also impacted by the climate into which they migrate. Higher latitudes and elevations typically have shorter growing seasons and harsher winter conditions than more equatorial or low-elevation sites (Tucker et al. 2001), and these latitudinal gradients are often not ameliorated by warming. In response to shorter growing seasons, individuals may increase developmental rates in order to complete development in the same number of seasons as in the ancestral environment, but typically this comes at a cost of smaller body size at maturity (resulting in a reverse-Bergmann cline of smaller body sizes at higher latitudes in species with obligate development times; Nylin & Sviird, 2016; Sniegula et al., 2016). As an alternative response to shorter growing seasons, individuals may flexibly extend their total development time over greater numbers of growing seasons at higher latitudes and elevations (Morrison and Hero 2003, Hassall et al. 2008). Such a strategy is increasingly likely to allow species to maintain large body sizes (and therefore dispersal distance and fecundity) during a poleward or elevational range expansion, but with the added
expense of longer generation times (and thus slower generational turnover and lower
dispersal frequency at the range front).

In order to understand how environmental stress and development time interactively affect
dispersal abilities, we conducted a motivational study (box 1) and implemented proof-of-concept individual-based modelling to investigate how development strategy, generation
time and dispersal ability interactively affect range shifting rates. The goal of our experiment
and theoretical model was to generally explore the costs and benefits of different
developmental strategies for the ability of populations to sustain a range shift into
progressively harsher and more variable environments. This approach provides a focussed
and timely assessment of the potential mechanisms by which these life history syndromes
may facilitate or impede future biogeographic shifts and changes in community composition
in response to ongoing climate change at high latitudes (Fitt and Lancaster 2017).

Box 1: Motivational study

We conducted an experiment to understand the costs associated with shifts in voltinism
(developmental duration) during a range shift. As species move polewards under climate
warming, they face a challenge of shorter growing seasons at high latitude, which limit
opportunities to acquire energy for growth and development. One possible strategy to
overcome this challenge for species exhibiting indeterminate growth is to prolong
developmental duration to encompass multiple seasons at high latitudes (Hassall 2013). This
strategy can help individuals maintain large body sizes, and thus favourable values for
dispersal characteristics which sustain the range shift. However, the flexible expression of
increased (multi-season) development times at high latitudes and elevations carries an a
number of costs arising from both extended generation times and also elevated mortality
risks. Developing over multiple seasons implies exposure to multiple bouts of harsh,
overwintering conditions, each episode of which can be costly and impose a strong survival
risk (Hahn and Denlinger 2007) as well as impose metabolic costs (Hahn and Denlinger 2007).
Overwintering in inhospitable, winter climates is often performed in a state of torpor,
hibernation, or diapause, which is initiated to preserve accumulated resources until the next
growing season (Blanckenhorn 1997, Xiao et al. 2006). While diapause is often essential for
survival in variable climates, it is also associated with high metabolic costs, including loss of
muscle mass, degradation of internal organs, and severe reductions in energy reserves (Hahn
and Denlinger 2007, Sadakiyo and Ishihara 2012). Under these conditions, benefits of large
body size and detrimental physiological costs of diapause on muscle quality may have
conflicting effects on the development of flight performance. Changes in the total duration of
diapause following colonisation of higher latitude habitats could therefore affect both
dispersal abilities and ultimately the propensity of a flexibly-developing species to continue
to successfully undergo range shifts during periods of climatic warming.

To assess the likelihood that increased overwintering time adds mortality stress to range
shifting species, mortality stress which may preferentially affect longer-lived organisms, we
experimentally decoupled voltinism (generation time) and diapause duration in the
laboratory, using the model system *Ischnura elegans* (Van der Linden 1820), a flexibly-
developing species which undergoes multi-year development at high latitudes and is rapidly
undergoing range shifts to higher latitudes in both the UK and Sweden (Hickling et al. 2005,
Ischnura elegans exhibits strong developmental effects on range shift-related trait values of dispersal and fecundity, and also exhibits longer development times at the expanding range margin than in the core of its range (Shama et al. 2011), which may facilitate its rapid range shifts into harsher, poleward environments (Hickling et al. 2005).

To conduct our study, we collected 223 wild Ischnura elegans (Van der Linden 1820) damselfly larvae from three sites in northeast Scotland while the larvae were still in a diapause state. Individual size variation at capture corresponded to three age cohorts (1-, 2- and 3-year olds; Figure 1 see SI for how these were assessed). Larvae were each randomly assigned to one of two diapause treatments, short (i.e., maintained in diapause conditions for 33 days post capture) and long (68 days post capture), with these treatments representing those experienced by I. elegans under current environmental conditions (long treatment) and those expected under a climate warming scenario (short treatment) (Thompson 1978, Hassell 2007). After diapause treatment, individuals were removed to ambient temperatures and allowed to emerge as adults. Individuals of all three cohorts and both diapause treatments emerged as adults, allowing us to disentangle the relative effects of these factors on adult body size and flight performance (Figure S1). It is currently unknown whether 1- to 3-year old larvae all emerge as adults during a single year in the wild, however our records of strong adult density fluctuations over 4 years of observation at our study sites suggest that multiple cohorts may emerge during warm summers, while cooler summers which are unsuitable for breeding may prompt individuals to delay emergence (Fitt and Lancaster, unpublished data).

After emergence we assessed body size and flight endurance following Ducatez et al. (2013) (see SI for full methodological details). Drivers of variation in larval post-diapause survival,
adult body size and flight endurance were assessed using a linear mixed model, including fixed effects of diapause treatment, sex, size at collection and adult size (the latter included in for models of endurance only), and random intercepts for individual and collection site. Analyses were performed using the lme4 (Bates et al., 2015) and lmerTest (Kuznetsova et al., 2016) packages for R v.3.2.3 (R Development Core Team 2012).

We found that diapause treatment had no effect on adult size or post-diapause survival (all individuals survived during diapause treatments). However, our experimental manipulation of developmental strategies demonstrated that longer developmental times (3-year strategy) corresponds to increased adult size (mean difference of 3- vs. 2-year old adult body size = 1.86, \( t_{35}=6.2, P<0.001 \); 2- vs. 1-year old mean difference = 2.04, \( t_{48}=3.1, P=0.003 \); Figure 1b).

Body size is typically highly correlated with fecundity across invertebrates (R2= 70.1 to 99.3, Honěk, 1993), and high fecundity has previously been implicated as a driver of invasion and colonisation potential (Borer et al. 2009; Kajita et al. 2010; Kroiss and HilleRisLambers 2015). Furthermore, larger body size facilitated greater flight endurance in our motivational study (effect of body size on endurance =1.82±0.57, \( t_{67}=3.38, P=0.001 \); Figure 1c), where flight endurance is an important dispersal-related trait (Grabow 1995; Berwaerts et al. 2002). However, diapause did not affect post-diapause larval survival (effect of diapause on survival = -0.26±0.306, \( z=0.85, p=0.369 \)) or flight endurance (effect of diapause length on flight endurance = -1.542±1.696, \( t=-0.909, p=0.366 \)). Thus, empirical results suggest that longer development times may increase range shift potential via beneficial effects on dispersal behaviours and reproductive rates. This motivational study also revealed that additional time in diapause (i.e., under enhanced environmental stress) does not impose increased mortality costs on range shifting species. Based on this motivational study, we therefore included
effects of developmental strategy on fecundity and dispersal related traits in our model, but did not include changes in mortality costs associated with increased environmental stressors often found at range limits. Stress-dependent mortality such as under prolonged bouts of diapause, however, may be included in further extensions of our model.

(end box 1)

Methods

We took an individual-based modelling approach for developing general insights into the role of development time on dispersal and population growth rates, and subsequently on rates of range expansion under different environmental conditions, using the Rangeshifter v1.1 software package (Bocedi et al. 2014). Developmental strategies were fixed (i.e., did not evolve), and were modelled separately for individuals with 1-year, 2-year, or 3-year developmental times. We modelled females only. Individuals completed their developmental process in their natal site. Once attaining the penultimate stage, they could then potentially disperse, then enter their final (adult) stage and reproduce in either their natal site or in a new site depending on whether dispersal had occurred (Figure 3). Dispersal was a stochastic process, with distance being drawn as a random number from a negative exponential curve, while dispersal decision was randomly drawn as a binomial function, with the probability to disperse given as the emigration probability. Survival probability was set to be constant at 0.6 per year for the juvenile stage, and 1 for the dispersal/reproductive stages, resulting in a greater cumulative mortality cost of longer juvenile developmental times. For models of the 2- and 3-year developmental strategies, populations were initialised to represent a balanced
age structure (e.g., for the 2-year strategy, the initial population consisted of 33% 0-year olds, 33% 1-year olds, and 33% 2-year olds). At model initialisation, 4250 individuals were seeded across the first 10 rows of a 25 column x 1000 row, uniform gridded landscape. Range expansion across the landscape was then allowed to occur for 100 years (33, 50 or 100 generations, depending on developmental strategy).

In each model, the traits of emigration probability (EP), mean of the dispersal kernel (DK), or fecundity (F) were set to vary linearly with an abstract index of environmental quality, where low values of environmental quality represent stressful conditions at the range limit, and high values of environmental quality represent benign conditions typically found at lower latitudes and elevations. Values of these traits were chosen to produce sufficiently general results which apply to a range of species, with our empirical work (see results) forming the basis for the differences between developmental strategies and their effects on traits. While recognising that the relationships between traits and environmental variation will typically be more complex than the modelled linear relationship, this abstraction provides a means for gaining some general insights into responses to generally increasingly harsh conditions towards the range expansion front. The assumption of linearity can be relaxed in later studies and as greater empirical data become available to inform the modelling. Modelled variation in development time affected the intercept of the relationship between the value of a trait and environmental quality, but not the slope. Individuals with longer development had higher fecundity, emigration probability, and dispersal distances than individuals with shorter developmental times over all environmental conditions. This positive association between development time and trait values is characteristic of most species with indeterminate growth, such as ectotherms and plants, which are the same groups of species range shifting
most rapidly in response to climate change (Abrams et al. 1996; Blanckenhorn 1997; Blanckenhorn and Demont 2004; Zeuss et al. 2016, Hickling et al. 2006). Effects of diapause on flight performance were not modelled because our experimental results indicated that these were negligible (see Box 1). To facilitate comparison of models, the 2-year developmental strategy was used as a reference baseline (intercept and slope of the relationship to environment were the same in each set of models), while the degree of developmental dependence of each trait, and the effects of environmental stress on each trait (i.e., the point along the underlying environmental gradient at which each range expansion scenario as modelled), were allowed to vary among sets of models (Figure 2, see Table S1 for full details of parameters). Environmental and developmental dependencies of traits were always varied between rather than within model runs (i.e., populations did not expand across an environmental gradient. Instead, range expansion rates were compared among populations fixed at different positions along the underlying gradient).

Individual range shift models were modelled as a function of three parameters: emigration probability (EP), mean of the dispersal kernel (DK), and fecundity (F). To assess model sensitivity to these traits, we ran a sensitivity analysis with 1, 2, or all 3 parameters being environmentally dependent in a fully factorial design. For this, the traits exhibiting environmental dependence were modelled at 10 evenly-spaced intervals of environmental stress levels (with trait values corresponding to those of table S1). For models in which only 1 or 2 traits varied with the environment, the non-environmentally dependent traits were fixed over all environments, for the low (F=8.5, DK=290, EP=0.188), medium (F=10.5, DK=370, EP=0.252) or high value (F=13, DK=470, EP=0.332). The results of the sensitivity analysis are presented in Figures S2-S5, and highlight that the overall results of the study are
repeatable over a range of trait values and no single trait (F, DK or EP) has a disproportional influence on the resulting patterns. This set of simulations was repeated for each developmental strategy (1, 2, or 3-year maturation phase).

For models in which all three traits were environmentally dependent, we also adjusted the degree of developmental dependence of trait values. For this, the difference in trait value intercepts between the baseline 2 year strategy and the 1- and 3-year development strategies was increased or decreased for all three traits. Due to computational limitations and potential interpretability issues of overly-complex models, we did not vary the developmental dependence of each trait separately, and in all cases the degree of developmental dependence of three traits EP, DK and F changed simultaneously (see Table S1 for how these relate to baseline developmental dependencies as described in the paragraph above).

In each model, individuals were allowed to colonise the empty portion of the landscape, thus experiencing a range expansion, and no portion of the range was ever lost. To calculate the rate of range expansion, we first estimated the distance by which the range front had shifted in each model, by taking the difference in maximum cell occupancy between initialisation and completion of the simulation. Distances were then divided by the number of years (100) to calculate the rate of expansion, and to subsequently compare range shifting rates among developmental strategies, under different environmental conditions, and according to environmental and developmental dependencies of dispersal- and expansion-related trait values. For each set of parameters, the model was replicated 20 times. Variation in range shift rates between replicate models was minimal, with Figure S6 indicating the standard deviation...
between each model under the scenario of moderate developmental and environmental dependence of traits.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.4j867pv> (Fitt et al. 2018).

Results

When all three traits of emigration probability (EP), mean of the dispersal kernel (DK), and fecundity (F) exhibited environmental variation, rates of range-shifting were always higher under benign than under stressful conditions (Figure 4). In general, the 1-year strategy showed the highest rate of range shifts under benign conditions (right side of panels in Figure 4), However, under more stressful conditions such as might be expected towards a poleward range margin, the developmental strategy that maximises the rate of range shifting depended on the developmental effects on dispersal trait values. Where developmental strategy had little effect on fecundities and dispersal traits (i.e., when trait values were more canalised, or growth patterns were more determinate), the rate of range shifting decreased with increasing development time, irrespective of the environment (Figure 4a). However, when positive developmental effects on trait values traits were moderate to strong (Figure 4b,c), strategies with longer developmental times maintained higher rates of range shifting than shorter-developing strategies when the environment became limiting (left side of panels, Figure 4b,c).
Overall, 1-, 2- and 3-year strategies demonstrate different abilities to range shift quickly enough to keep pace with climate change (Figure 5, Figure S6). Under a scenario of moderate developmental impacts on trait values, and environmental dependencies of all three dispersal-related traits, it can be seen that the strategy able to best keep pace with climate change will depend on the rate of climate change. For example, if the climate is shifting at a rate of 200 m/year (this value was chosen for theoretical illustration) then a 1-year strategy will be able to range shift quickly enough to colonise a greater range of its potential environments than a 2 or 3-year strategy. This is because, due to differential dispersal limitation, 1-year strategy will be found closer to its theoretical new range limit, leaving only the most limiting environments (to the left of the intersection marked “A” in Figure 5) unoccupied during the dispersal lag phase of the range expansion. In contrast, 2- and 3- year strategies will only be able to fill the more benign parts of their range (intersections “B” and “C”, Figure 5), and will therefore more strongly underfill the stressful, poleward parts of their new range. This result arises because longer developmental times are costly in terms of dispersal opportunities, thus the faster-developing species can out preform slower-developing species at the fastest rates of range shifts. However, where the climate is shifting at slower rates (e.g. 135 m/year, dashed line in Figure 5), the 2-year developmental strategy is best able to maintain a high enough expansion rate to fill a more full range of its fundamental niche, as its advantage gained in dispersal and fecundity traits outweigh the cost in generation time under this slower rate of environmental change. From Figure 5 it can also be seen that in general, 2- and 3-year strategies expand their ranges at greatest rates under the most limiting of environments. Thus, selection on developmental strategy during range shifts will depend on the acclimation or adaptive potential of species to persist in stressful
environments, in addition to the level of environmental stress experienced during the expansion, and on the rate of expansion itself.

When only a single trait (EP, DK, or F) exhibits environmental dependence, longer development times consistently result in higher rates of range shifting at low values of the environmentally-invariant traits (i.e. when performance with respect to the non-variable traits was poor overall), but shorter developmental strategies became more advantageous for range shifting when the environmentally-invariant trait values were high (i.e. when the species expresses generally good performance over all environmental conditions) (Supplementary Figures S2-S6). This suggests that the strategy best for promoting range shifts also depends on the general overall fitness of the species.

Discussion

We find that developmental strategies and effects of environmental stress have strong, interactive influences on the rate at which a species can range shift. This strongly suggests that intrinsic and environmental processes contributing to trait development and trade-offs may influence biogeographic processes and species’ responses to climate change. Our modelling results indicate that simple increases in fecundity and dispersal traits associated with longer development do not necessarily directly correspond to increased range expansion rates. Under benign conditions (e.g., during rapid periods of warming; region to the right of dashed lines in Figure 4) or adequate developmental compensation (Figure 4a), the demographic costs of increased generation time outweigh the trait-based advantages of extended development, such that the 1-year strategy exhibits fastest rates of range shifting overall. However, when individuals experience more stressful environments, or increased
influence of developmental time on trait values, the 1-year strategy becomes increasingly penalised by exhibiting a more restricted ability to develop adequate fecundities and dispersal, and under these conditions the longer-developing individuals exhibit greater rates of range shifting. Moreover, the results suggest that species or populations able to tolerate more stressful conditions are also likely generally selected to have longer development times in order to facilitate expansion into such conditions (left side of panels 4b,c, Figure 5), whereas species lacking such stress tolerances also generally lack a need for strong developmental trait dependencies.

The lowest rates of range shifting overall were observed in the 1-year old strategy under stressful conditions, with high developmental dependence of trait values, suggesting that the failure to undergo range shifts in the wild may commonly result from inadequate developmental compensation under stress. For example, the frog *Rana temporaria* demonstrates reduced developmental rates at the range limit and low phenological plasticity under climate change (Walther et al. 2002, Laugen et al. 2003), and has also experienced rapid range declines under climate change (D’Amen and Bombi 2009). Conversely, the greatest rates of range shifting overall were observed in the 1-year strategies under benign conditions and low developmental dependence of trait values, suggesting that species relatively impervious to environmental stress, and with rapid compensatory growth and/or trait independent (human-mediated) dispersal strategies, may exhibit the most dramatic range shifts overall (e.g., rapid global spread of super-pests such as the Medfly (*Ceratitis capitata*) or Tiger mosquito (*Aedes albopictus*), which tolerate a wide range of environmental conditions and have recently achieved global distributions from more limited ranges (Vera et al. 2002.; Benedict et al. 2008)).
Previous studies have investigated the independent roles of developmental rates, fecundity and dispersal ability on range shift potential (Nuebert and Caswell, 2000; Clark, Lewis and Horvath, 2001), and have validated the common wisdom that, all else being equal, rates of range shifting can be facilitated by increased dispersal or fecundity traits, but inhibited by longer development times. This study includes, for the first time, interactive effects of developmental life history and dispersal/reproductive traits in the context of range shifts under different environmental conditions, revealing that a longer development time can be beneficial when it produces sufficiently positive effects on dispersal traits and fecundities, and when the environment is stressful overall. This has important implications for how species will maintain adequate populations and range sizes under climate change, considering that interactions of developmental life history and dispersal/reproductive traits are common across a wide range of species and taxa (Abrams et al. 1996, Blanckenhorn 1997, Blanckenhorn and Demont 2004, Zeuss et al. 2016). Moreover, the rate of climate change across the landscape (climate velocity, Loarie et al., 2009) is often faster than a species’ ability to shift and occupy new habitats as they become available (this has been termed a ‘dispersal lag’, Davis et al., 1986. Our results suggest that fast developing strategies are best able to keep up under very rapid rates of climate change, but under more moderate rates of change, species with longer development times and indeterminate growth are likely to outpace species with short generation times (Figure 5). Therefore, the rate of environmental change itself has strong effects on which is the ‘winning’ range shifting strategy.

Our model considers each strategy individually and does not directly compete the developmental strategies against each other. However, we anticipate that the competitive ability of each of these strategies may also have strong effects on the outcome. This is to be
expected because, under low rates of climate change (i.e., pre-industrially), longer
developmental strategies are expected to be found at the poleward range margin
(Intersection “A” in Figure 5). If climates start to change more rapidly, then a new (“faster”) strategy will have to outcompete the previous (“slower”) strategy at the poleward margin in order to maintain optimal range shift rates. However, the ability of individuals to plastically switch between developmental strategies under environmental stress (Shama et al. 2011) may reduce such delays, and preserve range-shift potential.

Selection on developmental strategies during range shifts may additionally result in the loss of developmental strategy variation, either through a species becoming extinct, or a species losing a specialised strategy at the range margin. For instance, under stable conditions, many species demonstrate either shorter (Laugen et al. 2003) or longer (Hassall et al. 2008) developmental strategies at their poleward range limits than in their range core, as a form of local adaptation allowing these marginal populations to complete reproduction in limiting environments. If there are strong evolutionary or physiological trade-offs between the developmental strategies that best maintain survival under environmental stress, vs. the strategies that maximise dispersal potential under developmental stress, this could also limit the range shift potential of populations in stressful environments. Our model does not directly explore this possibility, but we highlight it here as a fruitful avenue for further research. If such strong trade-offs exist, range dynamics under changing climates may result in both permanent reduction of a species’ geographic range and loss of variation in life history strategies that maintain positive population growth rate at the most stressful portion of the species’ range (in the context of the model, such losses may occur if strategies previously found to occupy the space to the left of all intersections with the horizontal lines in Figure 5
will be lost under the respective rates of climate change). Loss of some developmental strategies under this type of competition during range shifts may require range limit developmental strategies to re-evolve in the post-expansion phase. The need to re-evolve slow-moving, range margin specialists during periods of rapid climate change could inhibit the rate of post-climate change range recovery, and place species at elevated risk of further decline.

Our model tracks individual strategies over a range of uniform environmental conditions, facilitating direct comparisons of the expansion success of different strategies under different conditions. However, the success of each strategy may also be influenced by a) competition with other strategies in the same environment, b) environmental gradient functions, c) the ability to shift evolutionarily or plastically between alternative developmental strategies, and d) trade-offs with survivorship functions. Further work is needed to investigate how different developmental strategies may evolve over such environmental and competitive gradients. Furthermore, evolutionary constraints on fixed environmental cues for development (such as photoperiod, Xiao et al., 2006) may influence the ability of different developmental strategies to evolve.

Conclusions

Previous studies linking range shifts to individual traits have often produced conflicting or non-significant results (Comte et al. 2014, Angert et al., 2011; Maclean & Beissinger, 2017). This study demonstrates that differences in the strengths of developmental dependencies of these traits, trade-offs among traits, rates of climate change, and the influence of environmental stress may interact in complex ways to determine outcomes. This explains why
simple correlations among trait values and interspecific differences in rates of range shifting remain difficult to detect, and more mechanistic models are needed. Considering a single trait alone is unlikely to generate realistic predictions about the range shifting potential of a species. Moreover, understanding how traits such as size and dispersal ability are shaped by and interact with developmental strategy and environmental stressors is imperative to the development of a more integrative understanding of a species’ range shifting potential.

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Figure 1. Effects of larval cohort on body size and flight performance. a) Distribution of damselfly larvae size (head width) at collection, demonstrating the three cohorts represented in the population, where cohorts 1, 2 and 3 represent damselfly larvae approximately one year, two year and three years old at the time of collection. b) The effect of larval size at collection and sex on adult body size for all larvae emerging as adults in the year of the study, as indexed by the first PCA axis of 5 morphological measurements (PC1). Coloured shading indicates cohort (corresponding to Fig. 2a). c) Flight endurance of laboratory reared damselflies in relation to adult body size. Data points correspond to individual behavioural trials.

Figure 2. Modelled environmental and developmental dependence of trait values. Traits always were developmentally dependent, but the low high represents the degree of developmental dependence. Environmentally invariant traits (not depicted) were fixed at environmental values 1, 5, or 10.

Figure 3. Demographic transitions modelled in the simulation study.

Figure 4. Modelled rates of range expansion that would be obtained by populations exhibiting each of the three developmental strategies and living in a particular environmental condition. Green line = 1-year developmental strategy, blue line = 2-year developmental strategy, red line = 3-year strategy. Range shift rates are depicted when developmental effects on trait values are a) low, b) medium and c) high.
Figure 5. Modelled rates of range expansion under moderate developmental dependence and environmental dependence of all traits, where solid green line represents a one year developmental strategy, solid blue line represents a two year developmental strategy and a solid red line represents a three year strategy. Circles A, B and C represent the point at which the environmental limitation determines each strategy’s ability to keep pace with climate change, when the velocity of climate change is 200 m*yr\(^{-1}\) (black horizontal line), vs. 135 m*yr\(^{-1}\) (dashed horizontal line).
Figure 1.
Figure 2
Figure 3.

Dispersal → Post-Dispersal reproduction → Development to adulthood over 1, 2 or 3 years
Figure 4
Figure 5.

The graph illustrates the mean rate of range expansion (m) under different environmental conditions. The x-axis represents the environmental condition (Stressful and Benign), and the y-axis represents the mean rate of range expansion. Three categories, A, B, and C, are marked on the graph, indicating different levels of expansion under stressful conditions. The lines show a positive correlation between the environmental condition and the mean rate of range expansion, with more severe conditions leading to higher rates of expansion.