

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

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24 Abstract:

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

45

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

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49 Introduction

50 Climate change is increasingly allowing many species to colonise previously limiting
51 environments at higher latitudes and elevations (Parmesan and Yohe 2003, Hickling et al.
52 2006, Chen et al. 2011). These novel environments are typically characterised by shorter
53 growing seasons, fewer resources and increased climate variation in comparison to ancestral
54 habitats. However, the rates at which populations are able to range shift into such
55 environments vary widely among species and taxa (Hickling et al. 2005, 2006). Ultimately,
56 such differences in rates of range shifting may contribute to the differential fate of species
57 under climate change, and may drive global biotic homogenisation as some species will be
58 able to keep pace with climate change via distributional changes, while other species lag
59 behind and face increasing risk of extinction (Thomas et al. 2004, Chen et al. 2011, Davey et
60 al. 2012, Dornelas et al. 2014). Developing a better understanding of the factors allowing
61 species to colonise limiting environments at higher latitudes and elevations is therefore of
62 high importance for developing conservation strategies for range shifting and non-range
63 shifting species, as well as for developing mitigation strategies for range shifting pests
64 (Cannon 1998, Perrings 2005), disease vectors (Lafferty 2009) and invasive species (Cannon
65 1998, Perrings 2005).

66

67 Studies geared towards understanding the future distributions of species have historically
68 relied on species distribution models, which match the current ecological fit of species to their
69 habitats to future environmental conditions (Elith et al. 2011, Pagel and Schurr 2012).
70 However, these studies have often fared poorly in predicting shifts in species geographic
71 ranges (Pearson and Dawson 2003), in part because these studies fail to incorporate species'

72 capacity for acclimation and adaptation to novel conditions. In recent years there has been a
73 shift from reliance on SDMs towards approaches that explicitly incorporate eco-evolutionary
74 processes such as biotic interactions, plasticity, and adaptive evolutionary change (Dormann
75 et al. 2012, Travis et al. 2013, Urban et al. 2016). Such mechanistic and process-based
76 modelling studies investigating the drivers of range shifts or invasion increasingly incorporate
77 information on dispersal abilities (Brooker et al. 2007, Poyry et al. 2009) and demographic
78 processes such as reproductive rates (Hastings et al. 2005, Huntley 2011, Angert et al. 2011,
79 Maclean and Beissinger 2017). These models have resulted in increased accuracy in
80 predictions of how species will respond to climate change (Barros et al. 2016, Santini et al.
81 2016, Urban et al. 2016), although recent work suggests that variation in these traits and
82 population characteristics, considered additively, do not adequately explain variation in range
83 shifting rates (Melbourne and Hastings, 2009).

84

85 However, developmental strategies as drivers of differential range shift success have received
86 much less attention. More particularly, the interdependencies of developmental strategy and
87 dispersal traits have remained relatively unexplored, despite the potentially high importance
88 of this trait interaction for accurate predictions of invasion spread or how species will respond
89 to climate change (Hassall et al. 2008, Van Pategem et al. 2016). For instance, shorter
90 developmental times have been shown to allow for greater numbers of dispersers within a
91 given year (Lenoir et al. 2008). However, developmental strategies also have implications for
92 morphology, with longer developmental times often associated with larger sizes (Angilletta
93 et al. 2004), especially for species with indeterminate growth (most ectotherms, plants, and
94 fungi). Larger body sizes in turn tend to be associated with increases in dispersal-related trait
95 values (Morrison and Hero 2003, Hassall et al. 2008). Species which take longer to reach

96 maturity are therefore potentially able to attain larger body sizes and more favourable
97 dispersal characteristics at the range limit (Hassall et al. 2008). Thus long development times
98 can also potentially increase rates of range expansion (Blanckenhorn and Demont 2004,
99 Hassall et al. 2008, Hassall 2013, Nylin and Sviird 2016), but via a different mechanism than
100 shorter generation times. Therefore, range shifts may be facilitated by either faster
101 development times (greater potential for demographic expansion), or longer development
102 times (larger body size and better dispersal ability at the range limit), but the conditions under
103 which each of these different developmental strategies may be favoured at the range limit
104 remains unexplored.

105

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

120 expense of longer generation times (and thus slower generational turnover and lower
121 dispersal frequency at the range front).

122

123

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

134

135

136 **Box 1: Motivational study**

137 We conducted an experiment to understand the costs associated with shifts in voltinism
138 (developmental duration) during a range shift. As species move polewards under climate
139 warming, they face a challenge of shorter growing seasons at high latitude, which limit
140 opportunities to acquire energy for growth and development. One possible strategy to
141 overcome this challenge for species exhibiting indeterminate growth is to prolong
142 developmental duration to encompass multiple seasons at high latitudes (Hassall 2013). This
143 strategy can help individuals maintain large body sizes, and thus favourable values for

144 dispersal characteristics which sustain the range shift. However, the flexible expression of
145 increased (multi-season) development times at high latitudes and elevations carries an a
146 number of costs arising from both extended generation times and also elevated mortality
147 risks. Developing over multiple seasons implies exposure to multiple bouts of harsh,
148 overwintering conditions, each episode of which can be costly and impose a strong survival
149 risk (Hahn and Denlinger 2007) as well as impose metabolic costs (Hahn and Denlinger 2007).
150 Overwintering in inhospitable, winter climates is often performed in a state of torpor,
151 hibernation, or diapause, which is initiated to preserve accumulated resources until the next
152 growing season (Blanckenhorn 1997, Xiao et al. 2006). While diapause is often essential for
153 survival in variable climates, it is also associated with high metabolic costs, including loss of
154 muscle mass, degradation of internal organs, and severe reductions in energy reserves (Hahn
155 and Denlinger 2007, Sadakiyo and Ishihara 2012). Under these conditions, benefits of large
156 body size and detrimental physiological costs of diapause on muscle quality may have
157 conflicting effects on the development of flight performance. Changes in the total duration of
158 diapause following colonisation of higher latitude habitats could therefore affect both
159 dispersal abilities and ultimately the propensity of a flexibly-developing species to continue
160 to successfully undergo range shifts during periods of climatic warming.

161

162 To assess the likelihood that increased overwintering time adds mortality stress to range
163 shifting species, mortality stress which may preferentially affect longer-lived organisms, we
164 experimentally decoupled voltinism (generation time) and diapause duration in the
165 laboratory, using the model system *Ischnura elegans* (Van der Linden 1820), a flexibly-
166 developing species which undergoes multi-year development at high latitudes and is rapidly
167 undergoing range shifts to higher latitudes in both the UK and Sweden (Hickling et al. 2005,

168 Lancaster et al. 2015). *Ischnura elegans* exhibits strong developmental effects on range shift-
169 related trait values of dispersal and fecundity, and also exhibits longer development times at
170 the expanding range margin than in the core of its range (Shama et al. 2011), which may
171 facilitate its rapid range shifts into harsher, poleward environments (Hickling et al. 2005).

172

173 To conduct our study, we collected 223 wild *Ischnura elegans* (Van der Linden 1820) damselfly
174 larvae from three sites in northeast Scotland while the larvae were still in a diapause state.
175 Individual size variation at capture corresponded to three age cohorts (1-, 2- and 3-year olds;
176 Figure 1 see SI for how these were assessed). Larvae were each randomly assigned to one of
177 two diapause treatments, short (i.e., maintained in diapause conditions for 33 days post
178 capture) and long (68 days post capture), with these treatments representing those
179 experienced by *I. elegans* under current environmental conditions (long treatment) and those
180 expected under a climate warming scenario (short treatment) (Thompson 1978, Hassell
181 2007). After diapause treatment, individuals were removed to ambient temperatures and
182 allowed to emerge as adults. Individuals of all three cohorts and both diapause treatments
183 emerged as adults, allowing us to disentangle the relative effects of these factors on adult
184 body size and flight performance (Figure S1). It is currently unknown whether 1- to 3-year old
185 larvae all emerge as adults during a single year in the wild, however our records of strong
186 adult density fluctuations over 4 years of observation at our study sites suggest that multiple
187 cohorts may emerge during warm summers, while cooler summers which are unsuitable for
188 breeding may prompt individuals to delay emergence (Fitt and Lancaster, unpublished data).

189

190 After emergence we assessed body size and flight endurance following Ducatez et al. (2013)
191 (see SI for full methodological details). Drivers of variation in larval post-diapause survival,

192 adult body size and flight endurance were assessed using a linear mixed model, including fixed
193 effects of diapause treatment, sex, size at collection and adult size (the latter included in for
194 models of endurance only), and random intercepts for individual and collection site. Analyses
195 were performed using the lme4 (Bates et al., 2015) and lmerTest (Kuznetsova et al., 2016)
196 packages for R v.3.2.3 (R Development Core Team 2012).

197

198 We found that diapause treatment had no effect on adult size or post-diapause survival (all
199 individuals survived during diapause treatments). However, our experimental manipulation
200 of developmental strategies demonstrated that longer developmental times (3-year strategy)
201 corresponds to increased adult size (mean difference of 3- vs. 2-year old adult body size =
202 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).
203 Body size is typically highly correlated with fecundity across invertebrates ($R^2= 70.1$ to 99.3 ,
204 Honěk, 1993), and high fecundity has previously been implicated as a driver of invasion and
205 colonisation potential (Borer et al. 2009; Kajita et al. 2010; Kroiss and HilleRisLambers 2015).
206 Furthermore, larger body size facilitated greater flight endurance in our motivational study
207 (effect of body size on endurance = 1.82 ± 0.57 , $t_{67}=3.38$, $p=0.001$; Figure 1c), where flight
208 endurance is an important dispersal-related trait (Grabow 1995; Berwaerts et al. 2002).
209 However, diapause did not affect post-diapause larval survival (effect of diapause on survival
210 = -0.26 ± 0.306 , $z=0.85$, $p=0.369$) or flight endurance (effect of diapause length on flight
211 endurance = -1.542 ± 1.696 , $t= -0.909$, $p= 0.366$). Thus, empirical results suggest that longer
212 development times may increase range shift potential via beneficial effects on dispersal
213 behaviours and reproductive rates. This motivational study also revealed that additional time
214 in diapause (i.e., under enhanced environmental stress) does not impose increased mortality
215 costs on range shifting species. Based on this motivational study, we therefore included

216 effects of developmental strategy on fecundity and dispersal related traits in our model, but
217 did not include changes in mortality costs associated with increased environmental stressors
218 often found at range limits. Stress-dependent mortality such as under prolonged bouts of
219 diapause, however, may be included in further extensions of our model.

220 **(end box 1)**

221

222

223

224 Methods

225 We took an individual-based modelling approach for developing general insights into the role
226 of development time on dispersal and population growth rates, and subsequently on rates of
227 range expansion under different environmental conditions, using the Rangeshifter v1.1
228 software package (Bocedi et al. 2014). Developmental strategies were fixed (i.e., did not
229 evolve), and were modelled separately for individuals with 1-year, 2-year, or 3-year
230 developmental times. We modelled females only. Individuals completed their developmental
231 process in their natal site. Once attaining the penultimate stage, they could then potentially
232 disperse, then enter their final (adult) stage and reproduce in either their natal site or in a
233 new site depending on whether dispersal had occurred (Figure 3). Dispersal was a stochastic
234 process, with distance being drawn as a random number from a negative exponential curve,
235 while dispersal decision was randomly drawn as a binomial function, with the probability to
236 disperse given as the emigration probability. Survival probability was set to be constant at 0.6
237 per year for the juvenile stage, and 1 for the dispersal/reproductive stages, resulting in a
238 greater cumulative mortality cost of longer juvenile developmental times. For models of the
239 2- and 3-year developmental strategies, populations were initialised to represent a balanced

240 age structure (e.g., for the 2-year strategy, the initial population consisted of 33% 0-year olds,
241 33% 1-year olds, and 33% 2-year olds). At model initialisation, 4250 individuals were seeded
242 across the first 10 rows of a 25 column x 1000 row, uniform gridded landscape. Range
243 expansion across the landscape was then allowed to occur for 100 years (33, 50 or 100
244 generations, depending on developmental strategy).

245

246 In each model, the traits of emigration probability (EP), mean of the dispersal kernel (DK), or
247 fecundity (F) were set to vary linearly with an abstract index of environmental quality, where
248 low values of environmental quality represent stressful conditions at the range limit, and high
249 values of environmental quality represent benign conditions typically found at lower latitudes
250 and elevations. Values of these traits were chosen to produce sufficiently general results
251 which apply to a range of species, with our empirical work (see results) forming the basis for
252 the differences between developmental strategies and their effects on traits. While
253 recognising that the relationships between traits and environmental variation will typically be
254 more complex than the modelled linear relationship, this abstraction provides a means for
255 gaining some general insights into responses to generally increasingly harsh conditions
256 towards the range expansion front. The assumption of linearity can be relaxed in later studies
257 and as greater empirical data become available to inform the modelling. Modelled variation
258 in development time affected the intercept of the relationship between the value of a trait
259 and environmental quality, but not the slope. Individuals with longer development had higher
260 fecundity, emigration probability, and dispersal distances than individuals with shorter
261 developmental times over all environmental conditions. This positive association between
262 development time and trait values is characteristic of most species with indeterminate
263 growth, such as ectotherms and plants, which are the same groups of species range shifting

264 most rapidly in response to climate change (Abrams et al. 1996; Blanckenhorn 1997;
265 Blanckenhorn and Demont 2004; Zeuss et al. 2016, Hickling et al. 2006). Effects of diapause
266 on flight performance were not modelled because our experimental results indicated that
267 these were negligible (see Box 1). To facilitate comparison of models, the 2-year
268 developmental strategy was used as a reference baseline (intercept and slope of the
269 relationship to environment were the same in each set of models), while the degree of
270 developmental dependence of each trait, and the effects of environmental stress on each
271 trait (i.e., the point along the underlying environmental gradient at which each range
272 expansion scenario as modelled), were allowed to vary among sets of models (Figure 2, see
273 Table S1 for full details of parameters). Environmental and developmental dependencies of
274 traits were always varied between rather than within model runs (i.e., populations did not
275 expand across an environmental gradient. Instead, range expansion rates were compared
276 among populations fixed at different positions along the underlying gradient).

277

278 Individual range shift models were modelled as a function of three parameters: emigration
279 probability (EP), mean of the dispersal kernel (DK), and fecundity (F). To assess model
280 sensitivity to these traits, we ran a sensitivity analysis with 1, 2, or all 3 parameters being
281 environmentally dependent in a fully factorial design. For this, the traits exhibiting
282 environmental dependence were modelled at 10 evenly-spaced intervals of environmental
283 stress levels (with trait values corresponding to those of table S1). For models in which only
284 1 or 2 traits varied with the environment, the non-environmentally dependent traits were
285 fixed over all environments, for the low (F=8.5, DK=290, EP=0.188), medium (F= 10.5, DK=
286 370, EP= 0.252) or high value (F=13, DK=470, EP=0.332). The results of the sensitivity analysis
287 are presented in Figures S2-S5, and highlight that the overall results of the study are

288 repeatable over a range of trait values and no single trait (F,DK or EP) has a disproportional
289 influence on the resulting patterns. This set of simulations was repeated for each
290 developmental strategy (1, 2, or 3-year maturation phase).

291

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

300

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

311 between each model under the scenario of moderate developmental and environmental
312 dependence of traits.

313

314 Data deposition

315

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

318

319 Results

320 When all three traits of emigration probability (EP), mean of the dispersal kernel (DK), and
321 fecundity (F) exhibited environmental variation, rates of range-shifting were always higher
322 under benign than under stressful conditions (Figure 4). In general, the 1-year strategy
323 showed the highest rate of range shifts under benign conditions (right side of panels in
324 Figure 4), However, under more stressful conditions such as might be expected towards a
325 poleward range margin, the developmental strategy that maximises the rate of range shifting
326 depended on the developmental effects on dispersal trait values. Where developmental
327 strategy had little effect on fecundities and dispersal traits (i.e., when trait values were more
328 canalised, or growth patterns were more determinate), the rate of range shifting decreased
329 with increasing development time, irrespective of the environment (Figure 4a). However,
330 when positive developmental effects on trait values traits were moderate to strong (Figure
331 4b,c), strategies with longer developmental times maintained higher rates of range shifting
332 than shorter-developing strategies when the environment became limiting (left side of
333 panels, Figure 4b,c).

334

335 Overall, 1-, 2- and 3-year strategies demonstrate different abilities to range shift quickly
336 enough to keep pace with climate change (Figure 5, Figure S6). Under a scenario of moderate
337 developmental impacts on trait values, and environmental dependencies of all three
338 dispersal-related traits, it can be seen that the strategy able to best keep pace with climate
339 change will depend on the rate of climate change. For example, if the climate is shifting at a
340 rate of 200 m/year (this value was chosen for theoretical illustration) then a 1-year strategy
341 will be able to range shift quickly enough to colonise a greater range of its potential
342 environments than a 2 or 3-year strategy. This is because, due to differential dispersal
343 limitation, 1-year strategy will be found closer to its theoretical new range limit, leaving only
344 the most limiting environments (to the left of the intersection marked "A" in Figure 5)
345 unoccupied during the dispersal lag phase of the range expansion. In contrast, 2- and 3- year
346 strategies will only be able to fill the more benign parts of their range (intersections "B" and
347 "C", Figure 5), and will therefore more strongly underfill the stressful, poleward parts of their
348 new range. This result arises because longer developmental times are costly in terms of
349 dispersal opportunities, thus the faster-developing species can out preform slower-
350 developing species at the fastest rates of range shifts. However, where the climate is shifting
351 at slower rates (e.g. 135 m/year, dashed line in Figure 5), the 2-year developmental strategy
352 is best able to maintain a high enough expansion rate to fill a more full range of its
353 fundamental niche, as its advantage gained in dispersal and fecundity traits outweigh the cost
354 in generation time under this slower rate of environmental change. From Figure 5 it can also
355 be seen that in general, 2- and 3-year strategies expand their ranges at greatest rates under
356 the most limiting of environments. Thus, selection on developmental strategy during range
357 shifts will depend on the acclimation or adaptive potential of species to persist in stressful

358 environments, in addition to the level of environmental stress experienced during the
359 expansion, and on the rate of expansion itself.

360

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

369

370 Discussion

371 We find that developmental strategies and effects of environmental stress have strong,
372 interactive influences on the rate at which a species can range shift. This strongly suggests
373 that intrinsic and environmental processes contributing to trait development and trade-offs
374 may influence biogeographic processes and species' responses to climate change. Our
375 modelling results indicate that simple increases in fecundity and dispersal traits associated
376 with longer development do not necessarily directly correspond to increased range expansion
377 rates. Under benign conditions (e.g., during rapid periods of warming; region to the right of
378 dashed lines in Figure 4) or adequate developmental compensation (Figure 4a), the
379 demographic costs of increased generation time outweigh the trait-based advantages of
380 extended development, such that the 1-year strategy exhibits fastest rates of range shifting
381 overall. However, when individuals experience more stressful environments, or increased

382 influence of developmental time on trait values, the 1-year strategy becomes increasingly
383 penalised by exhibiting a more restricted ability to develop adequate fecundities and
384 dispersal, and under these conditions the longer-developing individuals exhibit greater rates
385 of range shifting. Moreover, the results suggest that species or populations able to tolerate
386 more stressful conditions are also likely generally selected to have longer development times
387 in order to facilitate expansion into such conditions (left side of panels 4b,c, Figure 5), whereas
388 species lacking such stress tolerances also generally lack a need for strong developmental trait
389 dependencies.

390

391 The lowest rates of range shifting overall were observed in the 1-year old strategy under
392 stressful conditions, with high developmental dependence of trait values, suggesting that the
393 failure to undergo range shifts in the wild may commonly result from inadequate
394 developmental compensation under stress. For example, the frog *Rana temporaria*
395 demonstrates reduced developmental rates at the range limit and low phenological plasticity
396 under climate change (Walther et al. 2002, Laugen et al. 2003), and has also experienced rapid
397 range declines under climate change (D'Amen and Bombi 2009). Conversely, the greatest
398 rates of range shifting overall were observed in the 1-year strategies under benign conditions
399 and low developmental dependence of trait values, suggesting that species relatively
400 impervious to environmental stress, and with rapid compensatory growth and/or trait
401 independent (human-mediated) dispersal strategies, may exhibit the most dramatic range
402 shifts overall (e.g., rapid global spread of super-pests such as the Medfly (*Ceratitidis capitata*)
403 or Tiger mosquito (*Aedes albopictus*), which tolerate a wide range of environmental
404 conditions and have recently achieved global distributions from more limited ranges (Vera et
405 al.2002.; Benedict et al. 2008)).

406 Previous studies have investigated the independent roles of developmental rates, fecundity
407 and dispersal ability on range shift potential (Nuebert and Caswell, 2000; Clark, Lewis and
408 Horvath, 2001), and have validated the common wisdom that, all else being equal, rates of
409 range shifting can be facilitated by increased dispersal or fecundity traits, but inhibited by
410 longer development times. This study includes, for the first time, interactive effects of
411 developmental life history and dispersal/reproductive traits in the context of range shifts
412 under different environmental conditions, revealing that a longer development time can be
413 beneficial when it produces sufficiently positive effects on dispersal traits and fecundities, and
414 when the environment is stressful overall. This has important implications for how species
415 will maintain adequate populations and range sizes under climate change, considering that
416 interactions of developmental life history and dispersal/reproductive traits are common
417 across a wide range of species and taxa (Abrams et al. 1996, Blanckenhorn 1997,
418 Blanckenhorn and Demont 2004, Zeuss et al. 2016). Moreover, the rate of climate change
419 across the landscape (climate velocity, Loarie *et al.*, 2009) is often faster than a species' ability
420 to shift and occupy new habitats as they become available (this has been termed a 'dispersal
421 lag', Davis et al., 1986. Our results suggest that fast developing strategies are best able to
422 keep up under very rapid rates of climate change, but under more moderate rates of change,
423 species with longer development times and indeterminate growth are likely to outpace
424 species with short generation times (Figure 5). Therefore, the rate of environmental change
425 itself has strong effects on which is the 'winning' range shifting strategy.

426

427 Our model considers each strategy individually and does not directly compete the
428 developmental strategies against each other. However, we anticipate that the competitive
429 ability of each of these strategies may also have strong effects on the outcome. This is to be

430 expected because, under low rates of climate change (i.e., pre-industrially), longer
431 developmental strategies are expected to be found at the poleward range margin
432 (Intersection “A” in Figure 5). If climates start to change more rapidly, then a new (“faster”)
433 strategy will have to outcompete the previous (“slower”) strategy at the poleward margin in
434 order to maintain optimal range shift rates. However, the ability of individuals to plastically
435 switch between developmental strategies under environmental stress (Shama et al. 2011)
436 may reduce such delays, and preserve range-shift potential.

437

438 Selection on developmental strategies during range shifts may additionally result in the loss
439 of developmental strategy variation, either through a species becoming extinct, or a species
440 losing a specialised strategy at the range margin. For instance, under stable conditions, many
441 species demonstrate either shorter (Laugen et al. 2003) or longer (Hassall et al. 2008)
442 developmental strategies at their poleward range limits than in their range core, as a form of
443 local adaptation allowing these marginal populations to complete reproduction in limiting
444 environments. If there are strong evolutionary or physiological trade-offs between the
445 developmental strategies that best maintain survival under environmental stress, vs. the
446 strategies that maximise dispersal potential under developmental stress, this could also limit
447 the range shift potential of populations in stressful environments. Our model does not directly
448 explore this possibility, but we highlight it here as a fruitful avenue for further research. If
449 such strong trade-offs exist, range dynamics under changing climates may result in both
450 permanent reduction of a species’ geographic range and loss of variation in life history
451 strategies that maintain positive population growth rate at the most stressful portion of the
452 species’ range (in the context of the model, such losses may occur if strategies previously
453 found to occupy the space to the left of all intersections with the horizontal lines in Figure 5

454 will be lost under the respective rates of climate change). Loss of some developmental
455 strategies under this type of competition during range shifts may require range limit
456 developmental strategies to re-evolve in the post-expansion phase. The need to re-evolve
457 slow-moving, range margin specialists during periods of rapid climate change could inhibit the
458 rate of post-climate change range recovery, and place species at elevated risk of further
459 decline.

460

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

471

472 Conclusions

473 Previous studies linking range shifts to individual traits have often produced conflicting or
474 non-significant results (Comte *et al.* 2014, Angert *et al.*, 2011; Maclean & Beissinger, 2017).
475 This study demonstrates that differences in the strengths of developmental dependencies of
476 these traits, trade-offs among traits, rates of climate change, and the influence of
477 environmental stress may interact in complex ways to determine outcomes. This explains why

478 simple correlations among trait values and interspecific differences in rates of range shifting
479 remain difficult to detect, and more mechanistic models are needed. Considering a single trait
480 alone is unlikely to generate realistic predictions about the range shifting potential of a
481 species. Moreover, understanding how traits such as size and dispersal ability are shaped by
482 and interact with developmental strategy and environmental stressors is imperative to the
483 development of a more integrative understanding of a species' range shifting potential.

484

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486

487 Supplementary material (Appendix ECOG-03975 at <[www. ecography.org/appendix/ecog-](http://www.ecography.org/appendix/ecog-03975)
488 03975>). Appendix 1.

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

620

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

625

626 Figure 3. Demographic transitions modelled in the simulation study.

627

628 Figure 4. Modelled rates of range expansion that would be obtained by populations
629 exhibiting each of the three developmental strategies and living in a particular
630 environmental condition. Green line = 1-year developmental strategy, blue line = 2-year
631 developmental strategy, red line = 3-year strategy. Range shift rates are depicted when
632 developmental effects on trait values are a) low, b) medium and c) high.

633

634 Figure 5. Modelled rates of range expansion under moderate developmental dependence
635 and environmental dependence of all traits, where solid green line represents a one year
636 developmental strategy, solid blue line represents a two year developmental strategy and a
637 solid red line represents a three year strategy. Circles A, B and C represent the point at
638 which the environmental limitation determines each strategy's ability to keep pace with
639 climate change, when the velocity of climate change is $200 \text{ m} \cdot \text{y}^{-1}$ (black horizontal line), vs.
640 $135 \text{ m} \cdot \text{y}^{-1}$ (dashed horizontal line).

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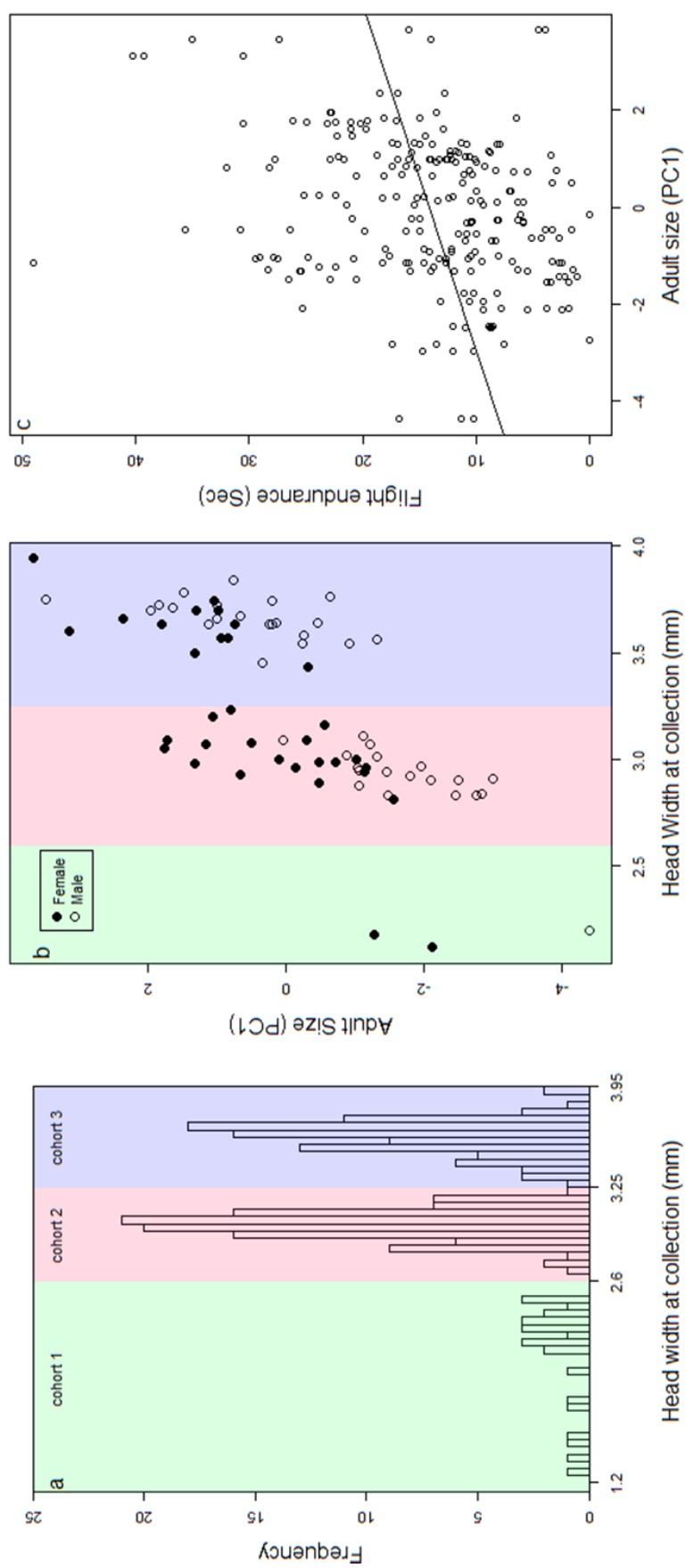
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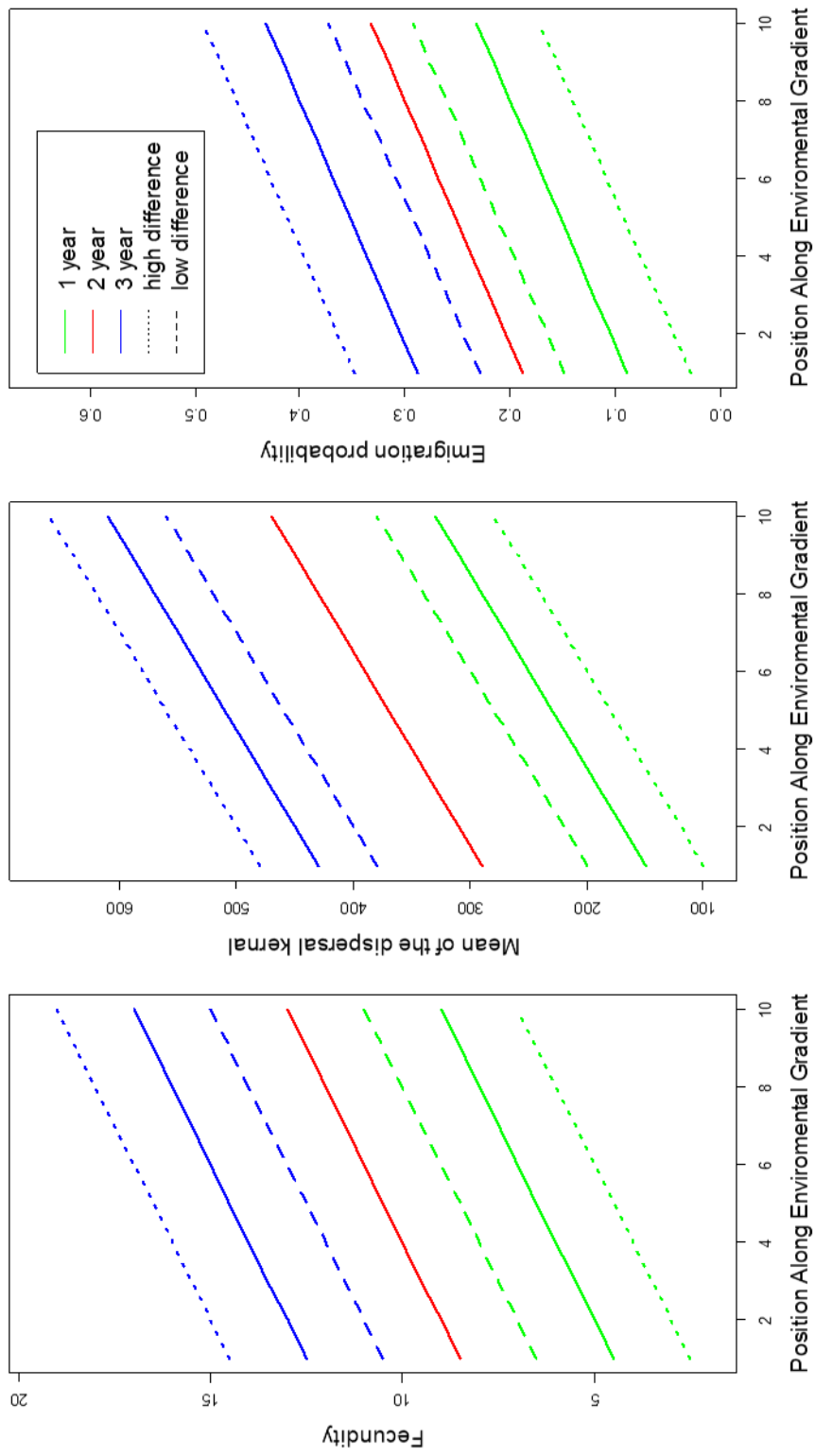
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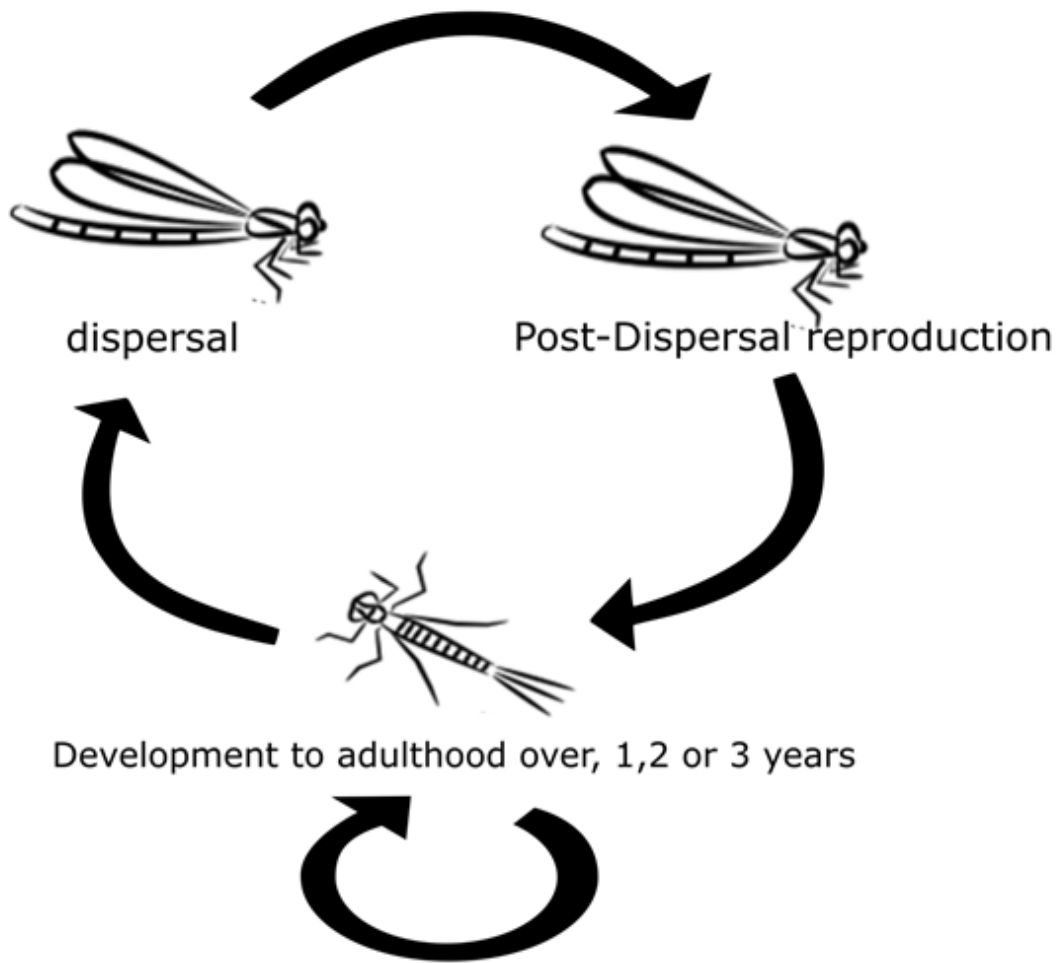
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Figure 2



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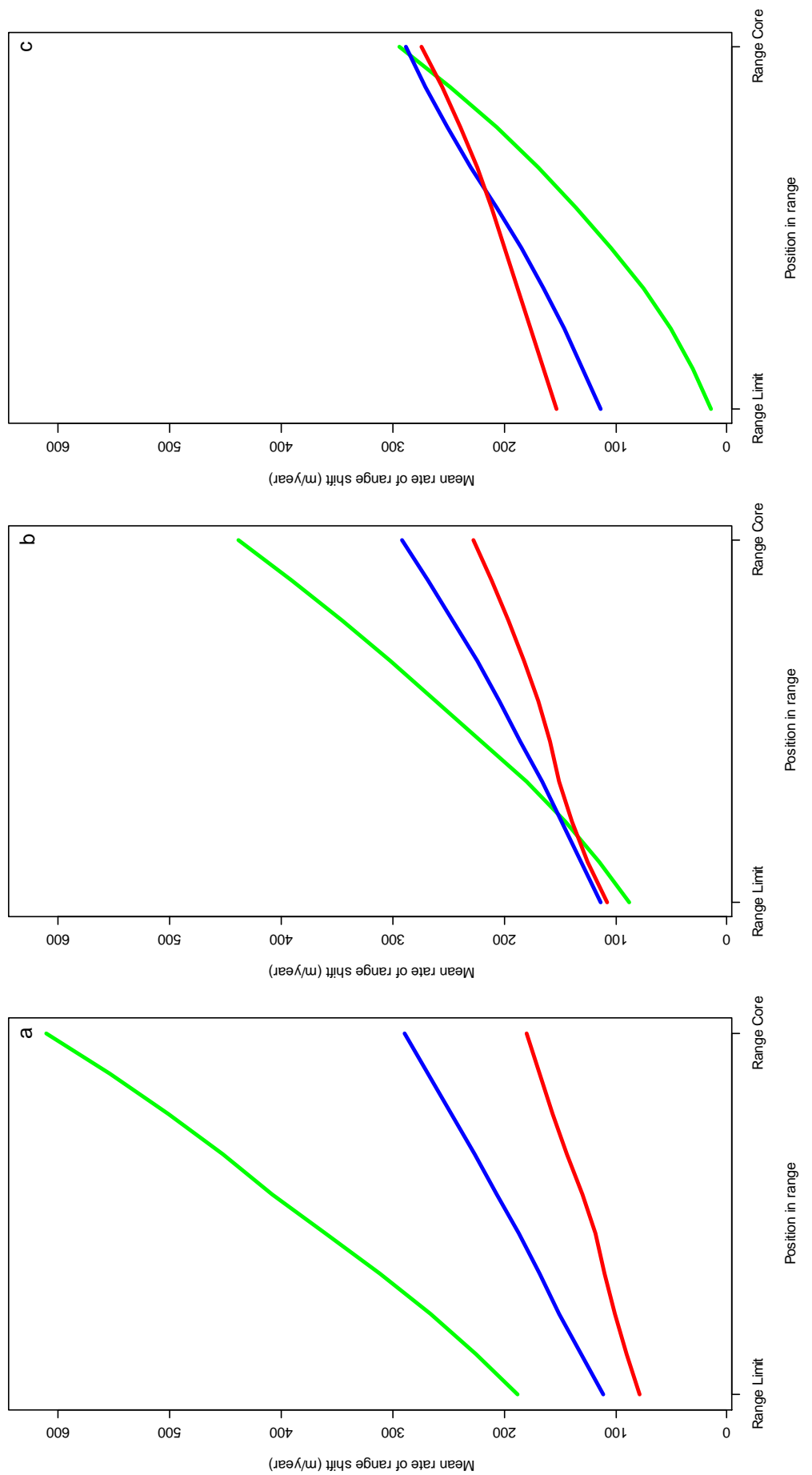
669 Figure 3.
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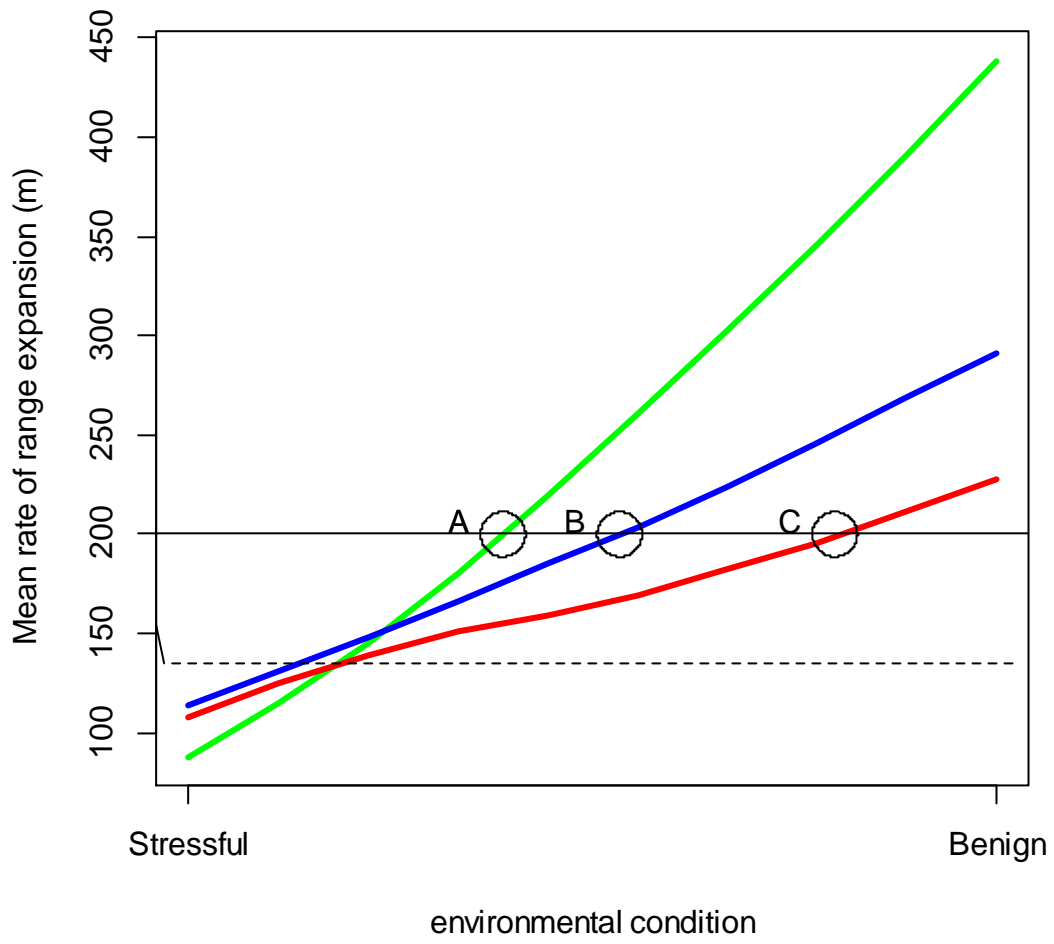
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690 Figure 4

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737 Figure 5.



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