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17

18

19

20 **Abstract**

21 Recognition of the importance of intraspecific variation in ecological processes
22 has been growing, but empirical studies and models of global change have only
23 begun to address this issue in detail. This review discusses sources and patterns
24 of intraspecific trait variation and their consequences for understanding how
25 ecological processes and patterns will respond to global change. We examine
26 how current ecological models and theories incorporate intraspecific variation,
27 review existing data sources that could help parameterize models that account
28 for intraspecific variation in global change predictions, and discuss new data that
29 may be needed. We provide guidelines on when it is most important to consider
30 intraspecific variation, such as when trait variation is heritable or when non-
31 linear relationships are involved. We also highlight benefits and limitations of
32 different model types, and argue that many common modeling approaches such
33 as matrix population models or global dynamic vegetation models would allow a
34 stronger consideration of intraspecific trait variation if the necessary data were
35 available. We recommend that existing data needs to be made more accessible,
36 and in some case new experiments are needed to disentangle causes of variation.
37

38

39 **Introduction**

40 Recently, many authors have stressed the importance of moving towards
41 more mechanistic models to be able to describe the response of species and
42 ecosystems to global change (Kearney & Porter, 2009; Chevin *et al.*, 2010;
43 Pereira *et al.*, 2010; Schurr *et al.*, 2012). Current mechanistic and process-based
44 models are typically based on species-level traits and properties or even on
45 functional types, but some models are beginning to account for the fact that
46 species' traits are neither static nor homogenous in space or time (Bolnick *et al.*,
47 2011; Violle *et al.*, 2014). For instance, many species exhibit trait differences
48 between populations, frequently taking the form of geographic clines that
49 correspond to environmental gradients (Aitken & Whitlock, 2013), and
50 important phenotypic differences also exist between individuals within
51 populations, and even within sex, age, or size classes (Bolnick *et al.*, 2011;
52 Richardson *et al.*, 2014). Such intraspecific variation can strongly influence
53 ecological processes and the conclusions drawn from models thereof (Boyce,
54 1977; Kendall & Fox, 2002; Grear & Elderd, 2008; Kearney *et al.*, 2009; Kramer *et*
55 *al.*, 2010; Schindler *et al.*, 2010; Oney *et al.*, 2013). Understanding and
56 incorporating variation in traits is therefore important for basic science, for
57 making predictions about global change impacts, and for managing species
58 affected by global change.

59 In this review, we address the following questions:

- 60 1. What are the sources and patterns of intraspecific trait variation?
- 61 2. When will intraspecific variation be crucial for ecological responses to
62 environmental change?

- 63 3. How do existing models attempt to address trait variation, and have their
64 capabilities to do so been fully utilized?
- 65 4. Are there useful data sources that have been overlooked, or new data that
66 must be collected?

67

68 We will define “traits” broadly, as including phenotypic characters (e.g.
69 coat color), behavioral or growth characteristics (e.g. fast vs. slow growth rate),
70 or individual-level demographic rates (e.g. expected number of offspring).

71

72 **Sources and patterns of trait variation**

73 Sources

74 Intraspecific trait variation may be due to **heritable differences**
75 **between individuals**, or it may be due to **phenotypic plasticity in trait values**
76 **across varying environmental conditions**. Understanding which of these
77 sources is responsible for trait variability is crucial for predicting global change
78 responses. If differences in trait values within a population are due to genetic
79 differences they will be heritable, and therefore population-level means will be
80 subject to change through natural selection over generational timescales.
81 Plasticity, on the other hand, enables immediate adjustment of phenotypic traits,
82 which can buffer a population against rapid environmental change. Plasticity
83 tends to slow adaptive evolution in the short term by weakening selective
84 pressures, but by preserving population size and genetic diversity may provide
85 potential for evolutionary responses in the long run (Crispo, 2008). The degree
86 of plasticity exhibited in a trait is typically subject to genetic control and can
87 therefore also evolve. Stable conditions, for instance, can select against plasticity

88 if it is costly (Crispo, 2008). See also Gomez-Mestre & Jovani (2013), who
89 developed a simple heuristic model to illustrate the potential interactions
90 between plasticity and adaptation.

91 **Epigenetic differences**, which affect gene expression but not the
92 underlying genetic code, can contribute to both categories. They contribute to
93 plastic responses, but some can also be heritable over intermediate timespans
94 (~1-5 generations). For instance, differential DNA methylation in plants can
95 affect traits such as flowering-time or drought tolerance, and their heritability
96 (Fieldes & Amyot, 1999; Zhang *et al.*, 2013). Such heritable epigenetic variation
97 may aid population adaptation to global change, but not all epigenetic effects are
98 adaptive: Rats exposed to pesticides show negative fitness effects over at least 3
99 generations, likely due to methylation changes (Manikkam *et al.*, 2012). Broadly
100 speaking, any phenotypic effect not due to genetics might be said to be
101 epigenetic. However, as discussed above, “plasticity” refers to non-heritable
102 changes in phenotype due to environmental variation (Scheiner & Goodnight,
103 1984), while the epigenetic effects that have received the most research
104 attention are heritable (Richards, 2011). As the molecular basis of phenotypic
105 plasticity becomes better understood, we may need to develop new terms
106 distinguishing epigenetic mechanism with short-term vs. long-term effects.

107 Disentangling these different sources of trait variation is often challenging
108 (Gienapp *et al.*, 2008). Plasticity can lead to trait variation between populations
109 even when they are genetically highly similar (Crispo, 2008). Common garden
110 experiments or pedigree studies are needed to distinguish plastic and heritable
111 variation (Wilson *et al.*, 2010; Aitken & Whitlock, 2013; Blanquart *et al.*, 2013),

112 though distinguishing heritable genetic and epigenetic effects presents further
113 challenges (Richards, 2011).

114 Moreover, which sources of variation are most important in real
115 ecological systems is still poorly understood. In recent years, more researchers
116 have begun to consider the consequences of genetic variation and evolutionary
117 adaptation in studies of global change responses (Moran & Alexander, 2014), but
118 epigenetic mechanisms and maternal effects are still rarely addressed (Bossdorf
119 *et al.*, 2008). For most species, the cause of observed trait variation remains
120 unknown.

121 When genetic and plastic effects on trait values are disentangled for
122 current global change responses, the contribution of plasticity has been larger in
123 many systems (Hoffmann & Sgro, 2011), but this likely reflects the relatively
124 short timespans involved. Heritability for traits strongly related to fitness (eg.
125 fecundity) is generally lower than for behavioral or morphological traits, but
126 significant heritability (and therefore potential for responses to selection) often
127 exists even in these traits (Mousseau & Roff, 1987). Where heritable changes
128 have been observed in response to global change, it is generally in species with
129 short generation times, high fecundity, and/or large population sizes – the types
130 of species one would expect to exhibit more rapid evolutionary change (Moran &
131 Alexander, 2014).

132

133 Patterns

134 Within a population or geographic area, trait variation can be **structured**
135 (varying in a consistent or predictable way) or **unstructured** (random) with
136 respect to space, time, or kinship. For instance, variation due to sex differences

137 in mammals and birds would usually be considered unstructured, because
138 stochastic processes typically determine sex, as would variation due to annual
139 fluctuations in an environmental variable around a stable mean. Persistent
140 differences between individuals in space or time (in behavior, growth rate etc.)
141 are structured variation. Such differences may either be due to heritable
142 differences, or to persistent environmental differences that cause plastic
143 responses. Natural history data can be useful in determining whether variation
144 is likely to be structured (Kendall & Fox, 2002). This can be important – for
145 example, misattributing structured variation to demographic stochasticity can
146 lead to overestimation of extinction probabilities (Fox & Kendall, 2002).

147 Structured variation in traits across populations or large geographic areas
148 can often be related to environmental gradients (Figure 1) or to geographic
149 structure. If the variation is heritable and dispersal is very low, lack of genetic
150 variation may inhibit adaptation to changing conditions; if dispersal is extremely
151 high, the movement of alleles between heterogeneous environments may
152 counteract local selective pressures (Aitken & Whitlock, 2013). If differences are
153 due adaptive plasticity (trait changes that increase fitness in the new
154 environment), it will facilitate gene flow by reducing the costs of dispersal,
155 whereas maladaptive plasticity (eg. smaller size or lower fecundity when
156 stressed) will do the opposite (Crispo, 2008).

157

158 **Influences of intraspecific variation on ecological processes**

159 One way that ecological processes can be affected by trait variation is due
160 to non-linearity in the relationship between the variable trait and the response of
161 interest, which is expressed by a mathematical relationship called **Jensen's**

162 **inequality** (Ruel & Ayres, 1999; Bolnick *et al.*, 2011). This states that when the
163 relationship between a random variable x and a response variable y is non-
164 linear, the expectation for y differs depending on whether we use the mean of x ,
165 or the whole distribution. Specifically, if the relationship $y = f(x)$ is concave-up,
166 then $E[y] > f(E[x])$ and if it is concave-down (convex), then $E[y] < f(E[x])$. To give
167 an example: seeds produced per unit pollen declines with increasing pollen
168 deposition; when pollen deposition varies, the average seeds per flower is lower
169 than predicted based on the average pollen deposited per flower (Richards *et al.*,
170 2009). Similarly, genetic variation in host insects that leads to variation in
171 number of eggs per seed can stabilize host-parasitoid population dynamics via
172 Jensen's inequality (Imura *et al.*, 2003).

173 Biology is rife with non-linear relationships (Benton *et al.*, 2006), and
174 therefore there are many situations where using the trait mean in a process does
175 not lead to the same result as using the whole trait distribution. This can be
176 particularly important in predicting population growth and viability. For
177 instance, unstructured variation in survival probabilities or offspring number
178 between years typically reduces the long-term average growth rate in population
179 models (Boyce, 1977), which increases the extinction probability in small
180 populations (Kendall & Fox, 2002). The form of the non-linear relationship
181 determines how variation affects the responses. If a matrix model is constructed
182 with even age/size bins, survival for the individuals within the bin will be
183 estimated well for a linear type II survival curve, but for a type III curve with
184 high juvenile mortality the survival of the younger classes will be
185 underestimated, and for a type I curve with late mortality the survival of older

186 classes will be overestimated. This, in turn, leads to under- or over-estimation of
187 population growth, respectively (Gear & Elderd, 2008).

188 The type of variation most frequently included in population models is
189 **demographic stochasticity**, which refers to variation in population growth
190 rates resulting from random variation in survival or reproduction (Bolnick *et al.*,
191 2011). This process is most important in small populations, because as
192 population size increases the mean survival or reproduction in a given year will
193 approach the true population mean. Genetic drift resulting from demographic
194 stochasticity can lead to random evolutionary changes in traits.

195 Intraspecific variation can also have positive effects on population growth
196 or stability. The **portfolio effect**, for example, arises when intraspecific or
197 interspecific variation reduce the variability of population growth or an
198 ecosystem service in a temporally variable environment (Bolnick *et al.*, 2011).
199 For instance, Schindler *et al.* (2010) estimated that asynchrony between local
200 populations and variation within cohorts of Bristol Bay salmon led to 2.2-fold
201 lower variability in annual returns than if the population were homogeneous.
202 Intraspecific variation (in the form of trait diversity) can also positively affect
203 average productivity. This can be due to **sampling effects**, whereby the larger
204 the number of species or genotypes included the more likely it is that one with
205 high productivity will be present (similar to the portfolio effect, but in a spatial
206 context), or to **complementarity effects**, whereby species or genotypes use
207 resources differently and thus reduce competition. For example, ecological
208 experiments (Crutsinger *et al.*, 2006) and restoration studies (Bischoff *et al.*,
209 2010) suggest that intraspecific genetic variation (more maternal families or
210 clones) in plants will often increase primary productivity (eg. 50% increase in

211 NPP in 12-genotype vs. 1-genotype plantings of *Solidago altissima*) and reduce
212 variation in establishment success. Genetic differences in environmental
213 responses or resource use, cohort or microsite effects, and sub-population effects
214 are all examples of structured variation, though unstructured variation could
215 potentially contribute to these stabilizing or productivity-enhancing effects.

216

217 Besides having implications for population- or species-level responses to
218 global change, intraspecific variation may also affect species interactions and
219 community and ecosystem responses. There has been a renewed effort in recent
220 years to link species traits to environmental responses and ecosystem processes
221 (Lavorel & Garnier, 2002), and the need to understand the role of species
222 interactions in global change responses has become increasingly well recognized
223 (Gilman *et al.*, 2010). Variation between individuals in environmental responses,
224 diet, etc. broadens the species niche for the species as a whole (though
225 population- and individual-level tolerances may be narrow), and broadens the
226 range of effects a species may have on its environment, including on other
227 species. Through heritable or plastic effects, global change drivers have the
228 potential to alter species trait means distributions in ways that affect species
229 interactions.

230 The amount of heritable variation in traits may be particularly important
231 for species interactions. Overall, intraspecific genetic diversity in parameters
232 affecting species interactions (eg. prey choice) tends to increase the number of
233 connections and decrease interaction strength, which in turn tends to increase
234 the stability of the network by dampening population oscillations and reducing
235 the probability of cascading extinctions when a member of the community is lost

236 (Fridley & Grime, 2010; Bolnick *et al.*, 2011; Wolf & Weissing, 2012). Similarly,
237 mathematical models have shown that heritable variation in prey preference
238 within a predator population can alleviate apparent competition between prey
239 species and affect the dynamics of predator and prey populations (Schreiber *et*
240 *al.*, 2011) and higher levels of heritable variation in both predator and prey can
241 lead to more stable dynamics (Saloniemi, 1993). The emerging sub-field of
242 community genetics has demonstrated that genetic variation in a “foundation
243 species” (e.g. in phytochemistry of a common plant) can have cascading effects
244 on the abundance and community composition of soil and leaf arthropods,
245 nutrient cycling, and even higher trophic levels (Crutsinger *et al.*, 2006; Whitham
246 *et al.*, 2008). For instance, *Populus* genotypes in a common garden experiment
247 explained more than 70% of microbial community composition and 78% of the
248 variation in microbial biomass (Schweitzer *et al.*, 2008). The amount of variation
249 in plastic responses to global change factors, including shifts in timing and body
250 size, could also affect species interactions. For instance, if a plant and a
251 pollinator shift their phenology different amounts in response to climate change,
252 this could result in a mismatch in timing that may negatively affect one or both
253 populations (Gilman *et al.*, 2010) – but if either population exhibits variation in
254 the extent of the shift, this mismatch would be alleviated.

255 Evolutionary processes not only can alter trait means and variability
256 (Figure 2D), but in some cases can affect population dynamics directly. In ‘**hard**
257 **selection**’, there is a threshold that individuals must pass in order to survive or
258 reproduce (e.g., surviving a minimum temperature) independent of population
259 size. The removal of individuals that do not pass the threshold can have a strong
260 impact on population size and persistence (Saccheri & Hanski, 2006). If a

261 population is exposed to altered environmental conditions, hard selection can
262 reduce its maximum population growth rate below replacement levels. If the
263 population evolves a higher intrinsic rate of population increase (r_{\max}) in the new
264 environment before it goes extinct, then it can increase again; this is called
265 **evolutionary rescue** (Kinnison & Hairston Jr., 2007; Aitken & Whitlock, 2013).
266 In '**soft selection**', the strength of selection is frequency and/or density
267 dependent (e.g. the largest 20% of individuals survive), and thus selection may
268 not directly affect population size – though it can affect population cycles if, for
269 example, the competing genotypes have reproductive rates that respond
270 differently to their own density (Saccheri & Hanski, 2006). For colonizing
271 populations, small evolutionary increases in r_{\max} in the first few generations can
272 increase the probability of establishment by enabling super-exponential
273 population growth (Kinnison & Hairston Jr., 2007). This seems to have occurred
274 in some invasive species. For instance, invasive populations of salmon in New
275 Zealand accumulated changes in a variety of traits over 26 generations that more
276 than doubled survival and fecundity relative to non-local genotypes (Kinnison &
277 Hairston Jr., 2007).

278 **Shifts in the mean trait value of a population** may change the selective
279 environment experienced by co-occurring species, resulting in **eco-evolutionary**
280 **interactions** (Post & Palkovacs, 2009). Such eco-evolutionary interactions can
281 alter competitive and trophic dynamics. Several notable examples come from
282 cases of introduced species or biological control. Lankau and Strauss (2007)
283 found that genetic variation in *Brassica nigra*'s production of sinigrin, an
284 allelopathic chemical, promoted community diversity, and vice versa. High-
285 sinigrin plants did well in heterospecific (newly-invaded) but not conspecific

286 neighborhoods, causing low-sinigrin plants to tend to increase in areas
287 dominated by *B. nigra*, finally enabling other species to re-invade low-sinigrin
288 patches of *B. nigra* where there was a 1.5 to 8-fold increase in seedling density
289 compared to high-sinigrin patches. In communities invaded by the related
290 *Allaria petiolata*, some resident species also exhibit evolution of increased
291 tolerance to sinigrin, exhibiting up to a 2.8-fold difference in response to
292 competition (Lankau, 2012).

293 Starting in the 1960's, many models have examined the effect of evolution
294 on the dynamics of two-species systems and have found that evolution can either
295 stabilize or destabilize interactions (Fussman *et al.*, 2007; Hartig *et al.*, 2014).
296 However, the ecological assumptions in these models tend to be relatively simple
297 and there has been limited work on multi-species systems (Fussman *et al.*,
298 2007). One of the best documented empirical examples is that of myxoma virus
299 and rabbits in Australia: the virus was introduced as a biological control but, as
300 has been observed in other host-parasite systems, evolution led to both reduced
301 virulence of the virus and reduced susceptibility of the host (Fussman *et al.*,
302 2007), dampening oscillations and making population crashes less likely.

303

304 **Dispersal** is a further crucial component for understanding the effects of
305 trait variability on global change responses within species and communities, as it
306 **affects both the probability of range shifts and population expansion as**
307 **well as the potential for evolution** (Aitken *et al.*, 2008; Kubisch *et al.*, 2014).

308 The interaction between dispersal and evolution, coupled with interspecific
309 interactions, will likely determine the extent to which species respond to climate

310 change via either range shifts or local adaptation (Brooker *et al.*, 2007; Aitken *et*
311 *al.*, 2008; Atkins & Travis, 2010; Bocedi *et al.*, 2013).

312 Dispersal ability is a trait that can evolve and exhibit plasticity itself
313 (Ronce, 2007). Variation in dispersal affects population spread rates. Dispersers
314 are likely to be a non-random subset of the population in terms of their behavior
315 (Wolf & Weissing, 2012), size, or other traits (Nathan *et al.*, 2011). This may
316 result in important structured variation between new and old populations, and
317 can result in selection on dispersal traits (Shine *et al.*, 2011). Such increases in
318 dispersal ability have been documented in the invasive cane toad and invasive
319 plants, as well as in insects undergoing climate-linked range expansions, and can
320 accelerate range shifts (Shine *et al.*, 2011). Conversely, if most dispersers have
321 low survival due to unsuitability of the matrix between habitat patches, or if poor
322 dispersers are left behind, selection or trait sorting can favor reduced dispersal
323 ability (Shine *et al.*, 2011; Travis *et al.*, 2012; Moran & Alexander, 2014).
324 However, these changes in dispersal traits may be transitory on a population
325 scale, as dispersal ability can trade off with other traits (Travis *et al.*, 2012), such
326 as competitive ability, that are more important in high-density populations.

327 Besides evolving itself, dispersal ability strongly affects the amount of
328 local genetic variation in populations. This local variation tends to increase the
329 speed of evolutionary responses because alleles advantageous in new
330 environment may already be present at moderate frequencies (Barrett &
331 Schluter, 2007; Wolf & Weissing, 2012). Because species that have small or
332 highly fragmented populations and low genetic diversity may have limited
333 potential for adaptation to changing future conditions, managers are increasingly
334 considering “genetic restoration” or assisted movement to boost local genetic

335 diversity (Hoffmann & Sgro, 2011; Aitken & Whitlock, 2013). The direction of
336 gene flow also matters: gene flow from historically warmer areas and between
337 areas of similar historical climate may increase the probability that alleles
338 advantageous under climate change will be present; gene flow from the range
339 center toward the trailing edge, however, is likely to be unfavorable (Moran &
340 Alexander, 2014).

341

342 **Modeling approaches and current applications incorporating intraspecific** 343 **variation**

344 *Population models*

345 Three common approaches for modeling trait variability in local
346 populations are matrix models (MM), integral projection models (IPMs), and
347 individual-based models (IBMs). All three can incorporate unstructured
348 variation by adding stochastic effects to account for “random” environmental
349 variation or demographic stochasticity. All can also include population-
350 ecological relationships such as density dependence. They differ more strongly
351 in their ability to include structured variation. All approaches can be
352 incorporated into landscape- or range-wide models, as discussed in the next
353 section.

354 **Matrix models** are an extension of classical population models – instead
355 of modeling one population with uniform trait values they divide a population
356 into several age or size classes, each of which is uniform in its trait values. A
357 transition matrix represents fecundity, mortality and the transition between
358 classes. The obvious limitation of these models is that they neglect variation in
359 demographic rates within classes (Boyce, 1977). Particularly if there is size-

360 dependent growth or growth correlations within classes (2B), this can lead to
361 errors in prediction (Pfister & Stevens, 2003). Careful use of natural history to
362 define age or stage divisions (Figure 2A) will reduce, but may not eliminate, this
363 problem (Gear & Elderd, 2008).

364 Matrix models can include structured variation in phenotypic traits, even
365 heritable variation, but only if the traits are discrete, and the mode of inheritance
366 simple. For instance, Kruger and Lindstrom (2001) divided buzzards into three
367 color morphs which differed in reproductive success. In stage-based models, the
368 distribution of ages within a stage or variation in the length of time an individual
369 occupies a stage can affect dynamics, especially transient dynamics (de Valpine
370 *et al.*, 2014).

371 **Integral projection models (IPMs)** can be viewed as an extension of
372 matrix models, where differences within a population are modeled by
373 continuous distributions instead of discrete classes (Ellner & Rees, 2007).
374 Compared to matrix models, this makes it easier to incorporate multiple
375 differences between individuals, such as differences within a size or age class
376 (Zuidema *et al.*, 2010; de Valpine *et al.*, 2014).

377 Heritability can be included in more complex IPMs by introducing a
378 distribution of trait values within an age class, and making this distribution in
379 offspring traits dependent on parental traits (Coulson *et al.*, 2010). Changes in
380 the environment (Hoffmann & Merila, 1999) and in the amount of genetic
381 variation in a population due to immigration, selection, or bottlenecks (Bryant *et*
382 *al.*, 1986; van Straalen & Timmermans, 2002; Lavergne & Molofsky, 2007) can
383 affect heritability. Model projections based on a fixed heritability estimate
384 should therefore only be applied over short time periods. While cumulative

385 effects (such as survival effects of past reproduction) are typically not included
386 in an IPM, age-class models can identify differences in individual growth rates
387 because fast growing individuals will be unusually large for their age. For
388 instance, Jansen et al. (2012) found that in a tropical understory palm growth
389 differences between individuals persisted over a lifetime and that fast growers
390 had a 1.8-fold greater contribution to population growth. IPMs can also be used
391 to explore trait evolution using an evolutionarily stable strategy (ESS) approach,
392 though this does not account for transitory dynamics (Ellner & Rees, 2007).

393 **Individual-based models (IBMs)**, as the name suggests, model a
394 population by describing each individual separately, using state variables such as
395 age, size, location, genotype, and fecundity (Grimm & Railsback, 2005). This
396 allows tracking cumulative changes over the lifecycle of each individual (e.g.
397 increasing size or reproductive history), as well as any conceivable variation
398 between individuals, including genetic variation in environmental responses.
399 Besides evolution, they can also incorporate spatial heterogeneity and individual
400 movement (DeAngelis & Mooij, 2005; Dytham *et al.*, 2014).

401 There are a number of additional advantages associated with an
402 individual-based approach. Like real populations, IBMs have a discrete number
403 of individuals rather than a continuous value, making them naturally suitable for
404 capturing effects of demographic stochasticity in small populations, as well as for
405 simulating spatial dynamics within a population. Also, they allow one to
406 explicitly model allelic frequency and diversity, avoiding the problem of
407 assuming constant heritability. For instance, Kuparinen *et al.* (2010) simulated
408 the evolution of growing-season timing in *Pinus* and *Betula*, using a simple multi-

409 locus model of bud-burst and bud-set date, over 100 years of climate change, and
410 found that a higher adult mortality rate reduced evolutionary lags.

411 Due to these advantages, and supported by growing computing power
412 which makes it possible to simulate large numbers of individuals, IBMs have
413 become increasingly popular. A common application is individual-based forest
414 gap models that project the influence of environmental factors on productivity
415 and species composition (Smith *et al.*, 2001). Individual-based models are also
416 used for fisheries models and for population viability analysis (DeAngelis &
417 Mooij, 2005; Frank *et al.*, 2011). Comparing IBMs with different levels of detail
418 to data from real systems can help to identify which types of variation are most
419 important in these systems (DeAngelis & Mooij, 2005; Benton, 2012). IBM
420 simulations can also be used to test when the simplifying assumptions of other
421 model classes are likely to lead to problems (Pfister & Stevens, 2003).

422

423 *Modelling landscape- or range-scale dynamics*

424 In many global change applications, the focus is not so much on
425 describing the change in local populations, but rather on capturing spatial
426 structure and large-scale dynamics. For this purpose, two approaches exist that
427 allow including trait variability. The first consists of using known spatial
428 extensions of the above-described process-based population models. The second
429 is to extend widely used statistical approaches such as correlative species-
430 distribution models to include trait variability. We cover both options in this
431 section, as well as the application of these concepts in dynamic vegetation
432 models.

433

434 **Metapopulation or metacommunity models** are extensions of non-
435 spatial population models that describe spatial structure through assuming a
436 number of connected local populations (Ovaskainen & Hanski, 2004). Within
437 each local population (patch), population dynamics may be modeled using any of
438 the approaches previously described. For example, the CD FISH model, a
439 simulator incorporating population genetics, demography, and stream
440 connectivity, has shown how landscape-level connectivity in stream systems can
441 constrain population vulnerability to environmental change in salmonid species
442 (Landguth *et al.*, 2014). Spatial Integral Projection Models (SIPMs) combine
443 IPMs with models of dispersal to predict spread across a landscape (Jongejans *et*
444 *al.*, 2011), which can be useful in understanding the spread of invasive species or
445 native species under climate change. In principle, this approach allows one to
446 naturally scale-up the effects of intra-specific variation within and between
447 populations to examine its impact on larger scales. In practice, the
448 computational demands of this approach often limit the size of the landscape
449 that can be simulated.

450

451 **Species distribution models (SDMs)** aim to predict the occurrence
452 probability of a species given environmental variables and therefore the limits
453 and size of its geographic range. The simplest and still most common approach
454 is to correlate presences (and absences if available) with environmental
455 variables. Various criticisms have been against **correlative SDMs**, mostly
456 relating to the fact that the realized niche (where the species does occur) can
457 differ from the fundamental niche (where it could occur) for a number of
458 reasons, including disequilibrium with the environment, biotic interactions, and

459 dispersal and source-sink dynamics (Guisan & Thuiller, 2005). Still, correlative
460 SDMs are widely used because they make use of the museum or herbarium
461 records and climate data that are easily available (Moran & Alexander, 2014).

462 Due to the challenges of using correlative SDMs to predict range
463 dynamics, particularly in the presence of biotic interactions, intraspecific
464 variability and evolutionary potential, there has been a steady movement
465 towards including more processes in these models (Dormann *et al.*, 2012). For
466 example, **physiological SDMs** make use of knowledge about physiological limits
467 (Porter *et al.*, 2002; Buckley, 2008; Rödder *et al.*, 2009; Buckley *et al.*, 2011) and
468 behavior (Kearney *et al.*, 2009). While most physiological SDMs to date have
469 been applied to ectothermic organisms or plants, known relationships of body
470 size to metabolic rate and/or heat exchange (Yarbrough, 1971) could be more
471 widely applied to birds or mammals as well. **Hybrid SDMs** add a dispersal
472 model on top of a classical SDM (De Cáceres & Brotons, 2012)(Marion *et al.*,
473 2012), while **Dynamic Range Models** include both explicit population dynamics
474 and dispersal (Schurr *et al.*, 2012). SDMs can also be “stacked” to examine effects
475 of environmental changes on biodiversity, either assuming that species
476 distributions are independent (Guisan & Rahbeck 2010) or interacting (Clark *et*
477 *al.*, 2013).

478 In all such extensions of classical SDMs, intraspecific differences can be
479 included in principle, but such applications are still rare. When intraspecific
480 differences are included, the most common approach is to describe **differences**
481 **in the environmental response of subpopulations** by fitting separate SDMs to
482 each subpopulation across a species’ range. This has mainly been done in trees,
483 for which good provenance (common garden) study data are often available

484 (Savolainen *et al.*, 2007). An example is the Phenofit model, which predicts tree
485 presence based on the link between phenology and reproductive success, can
486 allow different populations different responses (Chuine & Beaubien, 2001).
487 Incorporating intraspecific population variation in that way can alter predictions
488 of global change responses, making them either more (Valladares *et al.*, 2014) or
489 less (Garzon *et al.*, 2011) severe. For instance, incorporating population-level
490 differences in *Pinus contorta* yielded similar results to a species-level model for
491 current distribution, but the models incorporating genetic diversity projected
492 less than half as much range loss even without migration (Oney *et al.*, 2013).
493 Ideally, such studies will be based on or complemented by data confirming
494 genetic differences in environmental responses, as apparent differences between
495 subpopulations could also be caused by biotic interactions or other non-genetic
496 factors.

497

498 There are multiple examples in the recent literature of metapopulation or
499 SDM models being used to investigate the potential impact of evolution on global
500 change responses. For instance, using sequentially updated SDMs, Urban *et al.*
501 (2007) showed that the maximum annual temperature of areas occupied by the
502 invasive cane toad (*Chaunus [Bufo] marinus*) had increased from 1975 to 2005,
503 interpreted by the authors as niche expansion into increasingly extreme habitats.
504 Models can also identify when such adaptation could alter dynamics. Kearney *et*
505 *al.* (2009) developed a mechanistic niche model incorporating a quantitative
506 genetic model to investigate whether evolution of egg desiccation resistance in
507 the dengue mosquito *Aedes aegypti* might enable it to expand its range, and
508 found that it would take 17.4% less time to reach Darwin under climate change

509 with a heritability 0.5 vs. 0.15. Similarly, a dynamic vegetation model developed
510 by Kramer *et al.* (2010) to explore climate change responses in European beech
511 incorporated a quantitative genetic submodel for budburst and stomatal
512 conductance, and found that adaptive changes could occur at the leading and
513 trailing edge over just 2-3 generations. Interactions between landscape features,
514 the evolution of dispersal traits, and spread rates can also be investigated with
515 IBMs (Travis *et al.*, 2012).

516 An important caveat is that most models that aim to project the effects of
517 evolutions, with a few exceptions (Kramer *et al.*, 2010), have not been
518 systematically validated, for example by reproducing the current pattern of local
519 adaptation. We suggest that results should therefore not be interpreted as
520 predictions, but rather as indicators that suggest a potential impact of evolution
521 on environmental responses. It is also unclear how well the true genetic
522 structure of ecologically important traits are approximated by the assumptions
523 made in particular models (e.g. ten two-allele loci), and it is increasingly
524 recognized that models of species presence or persistence need to take into
525 account phenotypic plasticity (Chevin *et al.*, 2010; Valladares *et al.*, 2014).

526

527 **Dynamic global vegetation models (DGVMs)** are individual- or
528 population-based population models that have a focus on predicting the
529 composition and dynamics of the vegetation by describing physiological
530 processes such as photosynthesis and water uptake, biotic interactions, and
531 disturbances. In principle, the structure of these models is well suited to assess
532 the effects of intraspecific variability in those processes. However, due to data
533 limitations and computational constraints, most DGVMs currently still describe

534 vegetation dynamics and community interactions in terms of broad functional
535 types that summarize a potentially large group of similar species. Hence,
536 potential for improvement exists regarding the representation of interspecific as
537 well as intraspecific trait differences(Hartig *et al.*, 2012).

538 In recent years, various studies have considered options to include trait
539 variability in DGVMs. One approach is motivated by the observation that
540 environmental drivers explain 52% of global variation in traits (van Bodegom *et al.*,
541 2014). Allowing traits to vary within PFTs following observed trait-climate
542 relationships can therefore improve the match of predicted to observed
543 vegetation types (Verheijen *et al.*, 2013). Similarly, Stahl (2014) demonstrated
544 that a few easily-measured species-level traits could help predict environmental
545 range limits in trees, which could impose useful constraints on a DGVM. Rödder
546 *et al.* (2009) found that including physiological limits in an SDM for slider turtles
547 enabled better prediction of their invasive range; including similar limits on
548 vegetation types could provide similar benefits in DGVMs. Trait variation could
549 also be assumed to arise from a large potential for plasticity (Nicotra *et al.*, 2010)
550 or genetic variation (Kramer *et al.*, 2010; Valladares *et al.*, 2014). Adaptive
551 global dynamic vegetation models construct communities of trait combinations
552 by filtering those traits that are most competitive and able to coexist in a given
553 environment (Scheiter *et al.*, 2013).

554

555 To conclude the review of the state-of-the-art in the field of modelling
556 trait variability: all commonly used population model types could accommodate
557 trait variability to a much greater degree than is the current practice. When trait
558 variability is included, conclusions can be substantially altered. The inclusion of

559 trait variability has been limited by computational and data constraints. The
560 former constraint is easing as computers become more powerful, the latter will
561 be discussed in the next section. Finally, we emphasize that no one modeling
562 approach is ideal for all situations, but that model choice rather depends on how
563 the model will be used and whether there is sufficient data and/or
564 understanding of process to parameterize and justify a more complex model.

565

566 **Data and methods for parameterizing models that include trait variation**
567 **and trait evolution**

568 Recent advances in modeling techniques (see above) provide increasing
569 flexibility to ecologists and evolutionary biologists to model and understand the
570 consequences of trait variation. However, they also highlight the need for
571 gathering new data that allows more direct estimates of structured and
572 unstructured trait variation, and the need of making existing data better
573 available to researchers.

574 *Data sources*

575 Especially at the local scale, useful data for estimating variation in
576 important traits or demographic rates often already exist. For example, data on
577 phenotype, growth, fecundity, and survival are typically collected at the
578 individual level (Clark *et al.*, 2011), enabling one to construct trait distributions.
579 If multiple measurements are available for each individual, structured variation
580 (e.g. individuals that consistently grow faster or slower) can be distinguished
581 from unstructured variation. Such longitudinal data can also be used to
582 disentangle plastic versus evolutionary responses to global change, using
583 approaches such as the ‘animal model’ (Gienapp *et al.*, 2008) – especially if family

584 relationships are also known. For instance, phenotypic plasticity in red squirrels
585 accounted for 62% of an 18-day advance in average birth date, while 13% was
586 attributable to evolutionary change (Berteaux *et al.*, 2004).

587 However, data are rarely synthesized in this manner, and instead are
588 usually aggregated for analysis – for instance, into species-level means and
589 variances (Clark *et al.*, 2011). Unless the original data are included as an
590 appendix, it is usually impossible to obtain the individual-level measurements
591 from the published literature, which greatly complicates meta-analysis and
592 means that information can easily be lost. Fortunately, journals and funding
593 agencies have been encouraging or, more recently, requiring researchers to
594 archive data in a more accessible format. Trait databases are currently being
595 constructed for many taxa. Plants seem to be better represented than animals
596 (but see the linked trait databases at <http://scales.ckff.si/scaletool/>). The TRY
597 database, for instance, contains 5.6 million trait entries for 100,000 plant species
598 around the world, and preliminary analyses showed that up to 40% of overall
599 variation in a trait can be intraspecific (Kattge *et al.*, 2011). Such data can be
600 used to better define plant functional types, and to give an idea of the range of
601 values a trait may take within a species, though for many species it is as yet too
602 patchy to, for example, compare trait distributions between multiple populations
603 of a species.

604 Large-scale observational networks can also provide useful data. Again,
605 this kind of data tends to be more abundant for plants than for animals. For
606 instance, Forest Inventory and Analysis (FIA) censuses have tracked tree sizes
607 and identities in plots across the United States for decades, and such data can be
608 used to examine variation in global change responses between life stages, species

609 types, or regions, or to parameterize individual-based forest models (Canham *et*
610 *al.*, 2006; Bell *et al.*, 2014). The new National Ecological Observatory Network
611 (NEON), now coming online, while not explicitly geared to investigate
612 intraspecific variation, will be collecting data such as size and reproductive
613 status for select species, phenology, soil microbial metagenomes, as well as
614 detailed measurements of the physical environment (Keller, 2010). Data on
615 plants' plastic phenological responses to climate can be obtained from both
616 observation networks (eg. <https://www.usanpn.org/>) and meta-databases.

617 However, to fully investigate the role of intraspecific variation in species'
618 environmental responses, new data specifically collected for this purpose are
619 needed. In addition to the need for accessible trait-variation data for a broader
620 range of species, some research questions, such as those relating to the role of
621 evolution in global change responses, require specialized experiments or
622 observations. For instance, while provenance study data can be useful for
623 understanding tree responses to climate, these studies rarely included very long-
624 distance transfers, or populations from or test sites at the environmental limits
625 (Leites *et al.*, 2012). Another important consideration is that covariation in traits
626 can be important for population and eco-evolutionary dynamics, so sampling
627 schemes should be designed to make calculation of covariances possible - long-
628 term demographic data are particularly valuable (Saether & Bakke, 2000).

629 Theoretical models can suggest where it is important to consider
630 variation, and therefore where more data is required. For instance, key factors
631 affecting the potential rate of evolutionary change, and therefore the probability
632 of extinction or persistence in a population facing environmental change, include
633 demographic properties of populations (e.g. generation time and maximum

634 population growth rate), the strength of selection, and the available genetic and
635 environmental variance in the key traits (Chevin *et al.*, 2010). They can also
636 suggest when the costs of selection might lead to extinction (Burger & Lynch,
637 1995). Gienapp *et al.* (2013) provide a good example of applying such models to
638 real populations. Another key area in which more data is needed to understand
639 global change responses is range shifts, as it is unknown in most cases whether
640 species ranges are currently limited by abiotic factors, biotic interactions,
641 dispersal, or lack of genetic variation (Sexton *et al.*, 2009).

642 Distinguishing genetic (or epigenetic) variation from plastic responses to
643 the environment tends to require either detailed, long-term observational data
644 that enables one to build a pedigree (Wilson *et al.*, 2010) or common-garden
645 experiments in which different genotypes are reared in one or more common
646 environments (Blanquart *et al.*, 2013). Unlike the incidental individual-level data
647 discussed above, which may be able to generally distinguish structured vs.
648 unstructured variation, these types of studies are usually specifically designed to
649 investigate the genetic components of intraspecific variation. They are thus
650 extremely valuable for understanding how and when to include genetic variation
651 in models of environmental responses. However, because of high cost in time
652 and money, these studies are rarer than short-term observational trait
653 measurements, and have similar issues of accessibility if the data have not been
654 archived.

655 If we could better identify the genetic basis of the trait(s) of interest,
656 extrapolating heritabilities outside of tested environments would become more
657 feasible. Genome-wide association studies (GWAS), usually making use of single-
658 nucleotide polymorphisms (SNPs) are becoming more widely used as a means of

659 identifying candidate genes for particular traits of interest. SNP variation can be
660 correlated either with variation in phenotype (e.g. water use efficiency), or with
661 variation in environment (e.g. climatic water deficit) (Neale & Kremer, 2011).
662 Results are usually qualitatively consistent with other approaches. However,
663 the amount of variation explained is typically lower than the total heritability
664 because rare variants unique to local families are often missed, multiple
665 functional alleles may exist, and linkage disequilibrium and epistasis may
666 interfere with the analysis (Brachi *et al.*, 2011). Some of the missing heritability
667 may also be attributable to epigenetic variation (Bossdorf *et al.*, 2008). A range-
668 wide sample will have low power to detect significant associations with
669 phenotype if adaptive alleles are locally common but globally rare, so sampling
670 must be structured to account for this (Brachi *et al.*, 2011). Methods for
671 incorporating realistic functional genetic submodels into models of species'
672 responses to global change are still in the early stages of development.

673 Neutral genetic variation (e.g. microsatellites), while not always closely
674 correlated with functional variation (Holderegger *et al.*, 2006), is useful for
675 estimating the degree of gene flow between populations, hybridization, or
676 dispersal ability (Aldrich *et al.*, 2003; Ashley, 2010; Moran & Clark, 2012).
677 Dispersal ability and population connectivity can also be estimated based on
678 physical traits in systems for which there are good mechanistic models, such as
679 wind dispersal of seeds (Kuparinen, 2006), via inverse modeling of observations
680 of dispersed individuals (Jones & Muller-Landau, 2008), or through tracking of
681 tagged individuals. Regardless of the method, it is advisable to take into account
682 intraspecific variation – for instance, considering that adult trees may vary in
683 seed production.

684

685 A further challenge connected to data on trait variability is statistical
686 analysis and the connection of these data to models. Many of the data types we
687 have discussed above should probably be treated with hierarchical statistical
688 models that allow including underlying dependencies between traits as well as
689 spatial, taxonomic and phylogenetic structure in the data. Such multilevel
690 models describe how individual responses vary according to the context, help
691 avoid over-fitting because they don't use independent "individual" parameters,
692 and enable the proper propagation of uncertainty from parameters to
693 predictions (Clark, 2003). If vital rate calculations are based on capture-
694 recapture methods, it may also be important to account for size- or stage-effects
695 on capture or detection probabilities (Punt *et al.*, 2006).

696 For process-based models such as IPMs, DRMs (Dynamic Range Models),
697 or DGVMs, data can be used in two ways: one can use statistical approaches to
698 infer individual parameters or subsets of the model parameters first, and then
699 use the process-based model to calculate the consequences of those parameter
700 estimates. An alternative is to infer model parameters inversely for the entire
701 model simultaneously, using the raw observations. For DRMs and SDMs, for
702 example, this is often still possible in a hierarchical Bayesian approach (Bykova
703 *et al.*, 2012; Marion *et al.*, 2012). For more complex models such as DGVMs, it
704 may become necessary to resort to simulation-based inference methods to
705 calibrate model parameters (Hartig *et al.*, 2011). Bayesian approaches allow
706 mixing parameter estimates from independent analysis and from calibration,
707 which allows a flexible mix of both approaches (Hartig *et al.*, 2012).

708

709 Conclusions

710 *When variation matters*

711 Generally, intraspecific variation is likely to be important for
712 understanding responses to global change a) for phenotypic traits that affect
713 demography, b) when the relationship of interest is a non-linear function of the
714 trait (Jensen's inequality), c) in small populations, where demographic
715 stochasticity can cause mean demographic rates or phenotypic traits to fluctuate,
716 d) when variation in the trait of interest is structured (because structured
717 variation cannot be accounted for merely by adding stochasticity to a model),
718 and e) if the timescale of interest spans multiple generations, and the trait is
719 likely to be under directional selection (e.g. drought tolerance in a warming
720 environment).

721 Mechanistic models can be helpful in identifying which traits or
722 demographic rates have the largest effect on a process of interest, and where
723 variation might be most important. For instance, Nathan et al. (2011) found that
724 for wind-dispersed trees, the plant traits most important for migration rate
725 tended to be 1) age at maturity, 2) post-dispersal survival, 3) seed terminal
726 velocity, 4) fecundity, 5) tree height, and 6) time between seed crops.

727 Conversely, natural history data can suggest what traits should be allowed to
728 vary in models: in *Pinus sylvestris*, for instance, there is little variation in seed
729 wing loading because seed mass and wing size are correlated, but isolated trees
730 have more seeds than those in dense populations (Debain *et al.*, 2003).

731 *Incorporating variation in global change models*

732 Although models differ in their ability to include trait variation, it seems
733 from our analysis that the opportunity for including and analyzing trait

734 variability hasn't been fully explored or exploited in any of the modeling
735 approaches we considered. The main reason seems the lack of data and
736 computational restrictions. As both limitations should ease in the coming years,
737 we hope that these capabilities will become more widely used.

738 *Data needs for the future*

739 Computational limits can be expected to improve without active effort of
740 the ecological community, but the limits on data will not. Existing data collected
741 at the individual level should be more frequently used to investigate intraspecific
742 variation. The growing availability of databases and data archives mean that
743 future meta-analyses and models will be able to rely less heavily on published
744 trait statistics and therefore will be able to address variation more accurately.
745 However, for distinguishing causes of structured variation that may have
746 different effects (e.g. genetic vs. environmental) more specialized experiments
747 are required. Data from these variation-focused studies also needs to be made
748 more widely available.

749 Summary

750 Intraspecific variation has been gaining attention in ecological theory. Empirical
751 studies quantify and classify variation in real populations, while developments in
752 modeling techniques enable the effects of variation to be assessed in more
753 sophisticated ways. Successfully integrating theoretical insights with these new
754 data and modeling techniques will be crucial for making robust predictions of
755 species responses to global change.

756

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761

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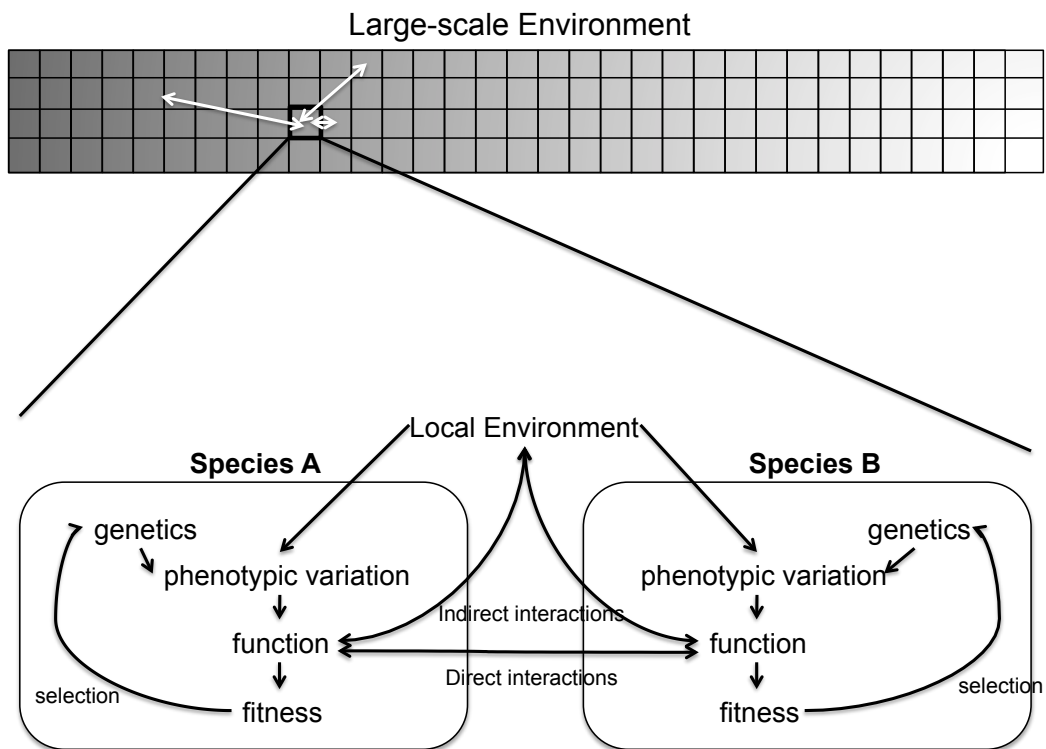
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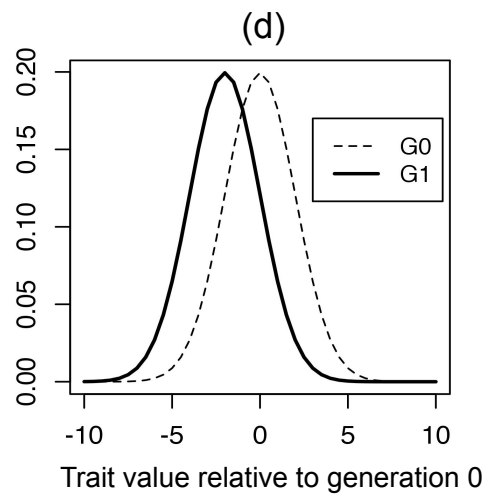
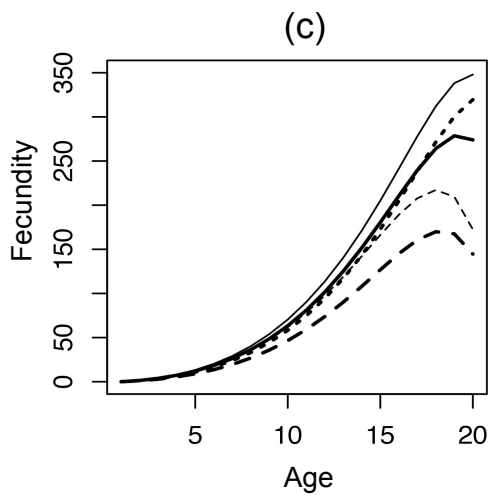
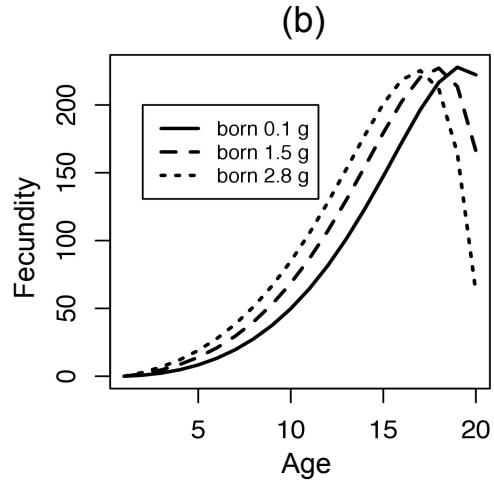
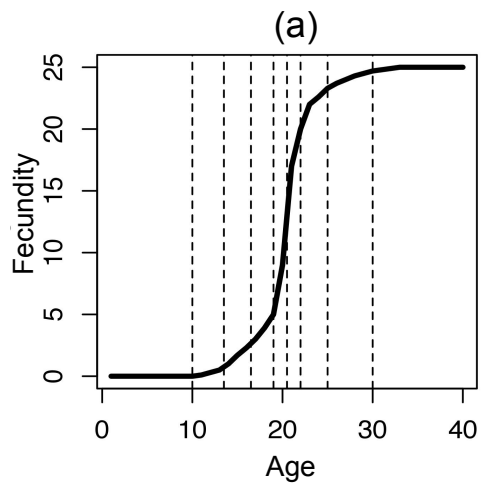
1118 Figure Captions

1119 **Figure 1:** At the landscape scale (top), trait variation is shaped by large-scale
1120 environmental gradients. Within local sites (bottom), phenotypic variation in
1121 each species is shaped by genetic variation and by plastic responses to the local
1122 biotic and abiotic environment. This variation affects species interactions with
1123 one another and with the environment, ultimately impacting individual fitness.

1124 Differences in fitness feed back to affect genetic variation. Local genetic
 1125 variation is also affected by dispersal between populations (white arrows at top).
 1126 **Figure 2:** A) Variation in a trait deriving from developmental processes (e.g.
 1127 changes in offspring number with size or age) can be accounted for – for
 1128 example, by defining age/size classes to minimize intra-class variation (dashed
 1129 lines). However, variation in natural populations is not so simple. B) If growth
 1130 rate and offspring number both depend on current size, then small differences in
 1131 initial size can cause the relationship between age and fecundity to vary between
 1132 individuals. In this example, larger individuals grow faster. C) Even without
 1133 such growth correlations, individuals can differ in the relationship between the
 1134 predictor and response variables, affecting the shape of the function. D) If such
 1135 differences are heritable, then trait distributions and the population processes
 1136 that depend on them may change over time.



1137
 1138 **Figure 1**



1139