Developmental plasticity in deep time: a window to population ecological inference

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Abstract. —Developmental plasticity, where traits change state in response to environmental cues, is well-studied in modern populations. It is also suspected to play a role in macroevolutionary dynamics, but due to a lack of long-term records the frequency of plasticity-led evolution in deep time remains unknown. Populations are dynamic entities, yet their representation in the fossil record is a static snapshot of often isolated individuals. Here, we apply for the first time contemporary integral projection models (IPMs) to fossil data to link individual development with expected population variation. IPMs describe the effects of individual growth in discrete steps on long-term population dynamics. We parameterize the models using modern and fossil data of the planktonic foraminifer *Trilobatus sacculifer*. Foraminifera grow by adding chambers in discrete stages and die at reproduction, making them excellent case studies for IPMs. Our results predict that somatic growth rates have almost twice as much influence on population dynamics than survival and more than eight times more influence than reproduction, suggesting that selection would primarily target somatic growth as the major determinant of fitness. As numerous palaeobiological systems record growth rate increments in single genetic individuals, and imaging technologies are increasingly available, our results open up the possibility of evidence-based inference of developmental plasticity spanning macroevolutionary dynamics. Given the centrality of ecology in palaeobiological thinking, our model is one approach to help bridge eco-evolutionary scales while directing attention towards the most relevant life-history traits to measure.

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Introduction

The existence of plastic traits, where one genotype can produce multiple phenotypes depending on external cues (e.g. temperature-dependent sex ratios in reptiles (Sarre et al. 2004), nutrition-determined caste assignment in female honey bees (Slater et al. 2020)), is ubiquitous. Development of a phenotype best suited to the prevailing environment increases an individual's chances of survival and enables individuals within a population to adapt rapidly to changing environmental conditions within a generation, rather than having to wait for the spread of favourable mutations (West-Eberhard 2003). Especially when faced with regular change and/or extreme events, plastic traits in individuals can increase chances of population survival (Baldwin 1896; Chevin and Lande 2009; Richter-Boix et al. 2006; Simpson 1953). Plastic traits potentially also enhance species survival over longer time scales. However, the effects of developmental plasticity on macroevolutionary processes and the emergence of new species have long been ignored (Pfennig 2021; Pfennig et al. 2010; West-Eberhard 2003, 2008), largely due to a lack of fossil records with the necessary fine scale environmental resolution to identify what plasticity uses as a cue.

West-Eberhard (2003) argued that plastic traits can influence both phenotype and genotype frequency in a population through a process called genetic assimilation. A new environmental cue will cause a plastic trait to be expressed in a novel way, and if this new phenotype has a positive effect on fitness, it will likely be selected for, increasing the frequency of both the phenotypic and genetic components (West-Eberhard 2003, 2005). Plasticity is typically studied through single genotypes, either by examining amongst-individual variation within families or clones or by taking repeated measurements on the same individual exposed to different

environments. The second of these routes is amenable to study in the fossil record (Lister 2021) and our focus here. Modelling studies suggest that moderate plasticity, with plastic traits that are reasonably well, but not perfectly, adjusted are most likely to drive evolutionary innovation: suboptimal adaptation provides the opportunity to move to a new space on the adaptive landscape and can encourage the evolution of better adapted traits (DeWitt et al. 1998; Ghalambor et al. 2015; Murren et al. 2015; Price et al. 2003). Many studies have since recognised the potential evolutionary implications of developmental plasticity (e.g. Beldade et al. 2011; Moczek et al. 2011; Pfennig et al. 2010; Pigliucci et al. 2006) and increasingly recognise it as a central aspect of evolution, rather than an occasional 'add-on' (Laland et al. 2015; Moczek 2015). As a result, several authors have proposed to expand the Modern Synthesis, which merged Darwinian natural selection and Mendelian inheritance and therefore focusses mainly on mutation-driven change, into an Extended Evolutionary Synthesis (e.g. Laland et al. 2015; Pigliucci 2007; Pigliucci and Müller 2010). However, the need for an extended synthesis is still a topic of lively debate (e.g. Dickins and Rahman 2012; Futuyma 2017; Lu and Bourrat 2018). Opponents argue that no conceptual change is necessary to incorporate developmental processes into the existing synthesis (Futuyma 2017; Lu and Bourrat 2018) as the structure and content of the extended synthesis are still incomplete (Buskell 2019; Fábregas-Tejeda and Vergara-Silva 2018). In the case of evolutionary developmental biology, this is largely due to a lack of empirical data (Futuyma 2017; Levis and Pfennig 2016, 2020). To decide if, and if so, how much, the Modern Synthesis needs to be adjusted with regards to developmental plasticity, we must first know the frequency with which long-term plasticity-led evolution occurs in nature (Kovaka 2019).

Most studies investigating the effects of developmental plasticity on evolution focus on extant populations. Laboratory studies on live individuals can determine the full range of responses to external cues as well as provide insights in the effects of plasticity over several generations (e.g. Waddington 1953). Field studies of wild populations provide evidence of genetic accommodation and adaptation by comparing reaction norms in closely related species (Schlichting and Wund 2014) and many such studies have found signs of plasticity-led evolution. Work on spadefoot toads, for example, has shown that a novel diet released cryptic variation that resembled the derived feeding mechanism of its descendant (Ledon-Rettig et al. 2010), suggesting that developmental plasticity helped the descendant species adapt to a new diet.

However, there are several major drawbacks to studying the drivers of evolution using only extant populations. Over 99% of all species that ever lived are now extinct (Stearns and Stearns 1999). Modern species provide no direct information on past evolutionary transitions, and therefore excluding extinct species will make it impossible to assess the frequency of plasticity-led evolution in the past and its relative importance in the winners and losers of historical ecological interactions (Quental and Marshall 2010). Fossils contain information on both macroevolutionary transitions and microevolutionary change, allowing morphological evolution to be quantified through time and across plausible ancestor-descendant pairs rather than an ancestor-proxy of the descendant's closest living relative (Love et al. 2021). The lack of contemporaneous environmental and morphological data in ancestral forms makes it harder to find direct evidence for plasticity-led evolution (Kovaka 2019). In systems that ally strong phylogenetic understanding with high stratigraphic and environmental resolution, evolutionary

change can be studied through speciation intervals and post-speciation divergence (Lazarus 2011; Pearson and Ezard 2014).

Analysing variation in somatic development of single genetic individuals is a particularly promising avenue for research into plasticity in the fossil record (Lister 2021). Growth rates can be reconstructed from fossils when ontogeny is preserved in the skeleton, such as from lines of arrested growth in amphibians and reptiles. Several studies have indeed found evidence for plasticity in growth rates in dinosaurs (Sander and Klein 2005) and extinct amphibians (Gee et al. 2020; Sanchez et al. 2010). However, patterns in highly variable traits can only be detected with large sample sizes (Gee et al. 2020), which are rare in the vertebrate fossil record. As the fossil record contains no genetic information, and it is impossible to determine clonal reaction norms of extinct species by laboratory studies, the effects of environmentally dependent variation in somatic growth are still not well understood in deep time (e.g. Moss et al. 2016).

Ideally, we would bring the past and present together by using techniques that span the two communities. The combination of somatic growth, senescent declines, reproductive windows and trade-offs between survival and fertility add fundamental biodemographic aspects critical to ecological dynamics. Here, we leverage one such approach with these capabilities – an integral projection model (Easterling et al. 2000) – to investigate the potential for such models to provide insight given the alternative temporal dimensions of palaeobiological data. By embedding somatic growth and development centrally within the model assumptions (not all individuals are equally likely to reproduce nor to survive at each developmental stage (Caswell 2001)), we can better match an inferred historical population with an age-profile closer to living populations

rather than relying on the biased assemblage preserved in the sediment. Our conclusions chart a path to identify the most biodemographically relevant life-history traits to measure when investigating evolutionary ecology in deep time.

The model

Integral projection models (IPMs) are drawn from population ecology to describe the dynamics of populations whose demography is regulated by a continuous trait, such as size, that grows in discrete intervals (Easterling et al. 2000; Ellner et al. 2016). The continuous trait impacts demographic probabilities of survival and reproduction. For example, larger individuals might have a different risk of mortality than smaller ones, or might reproduce more successfully than smaller individuals, all else being equal. The outputs from the model track an individual's journey through life. The use of such structured population models therefore has the fundamental advantage over unstructured models in that individuals do not need to be assumed as equally influential in determining the ecological dynamics.

The fundamental building block of an IPM is the kernel (eq. 1). The kernel is a function that aggregates the chances of survival, growth and reproduction of individuals into an efficient mathematical expression to project the population dynamics into the future. Different kernels can take on simpler or more complex forms depending on the intended demographic model; Rees et al. (2014) provide step-by-step general instructions for implementing IPMs and further descriptions of adaptions for particular life-history scenarios. Since their origination, increasingly complex demographic scenarios have been envisaged and represented by increasingly complex birth and death models (Ellner and Rees 2006). We adapt one of the more straightforward

147 scenarios from Ellner and Rees (2006) to study the relative importance of births, deaths and
148 development on the evolution of the focal life history.
149
150 The kernel is used to project the population forward in time – the population at a point in time
151 can be described by the sum of the demographic contributions from all individuals alive at the
152 preceding time step:
153 $$n(z_{t+1}, t+1) = \int_U^L K(z_{t+1}, z_t) n(z_t, t)\, dz \quad (1)$$
154
155 Here n is a vector that describes the population given a continuous structuring trait z_t (here: size)
156 at time t. U and L represent minimum and maximum size, respectively. K is the kernel
157 representing all possible transitions from size z_t to size z_{t+1}, which can be more fully written as
158 $K(z_t, z_{t+1}) = P(z_t, z_{t+1}) + F(z_t, z_{t+1})$ where P represents survival and F represents fertility.
159 Both P and F can be further split into constituent components: P is size-dependent survival from
160 time t to $t+1$ and contemporaneous progression (here: growth) from size z_t to z_{t+1}; F
161 represents the probability of reproducing as a function of z and potentially the number of
162 offspring. $K(z_t, z_{t+1})$ therefore is built from the key building blocks that track an individual's
163 journey through a life cycle characteristic of the species.
164
165 Having established an integrable IPM, we then use eigendecomposition to probe the structure of
166 $K(z_t, z_{t+1})$ and distill out key features of the population dynamics and life-history evolution
167 (Ellner et al. 2016). By analysing the IPM kernel, we can quantify the relative importance of the
168 different demographic processes and their impact on mean population fitness. We do this in two
169 principal ways. Firstly, we use the right and left eigenvectors associated with the dominant

eigenvalue to study, respectively, the population structure and reproductive value of each size class. By decomposing *K* into these two eigenvectors, we establish a simpler representation of the essential behaviour of the system to estimate the proportion of individuals in each size class (the population structure) and the mean fecundity of the individuals that survived to each stage (the reproductive value). Both of these quantities are deeply relevant to project the population dynamics and the selective effects on individuals at different life stages (Taylor 1990), but are challenging to study in the fossil record. Secondly, we use elasticity analysis. Elasticities quantify the relative influence of each demographic rate on a demographic parameter of interest (Caswell 2007), in this case the projected population growth (λ_1), and thus mean population fitness, at equilibrium in a deterministic environment. A parameter with a higher elasticity is more influential in determining λ_1. Given the link between population growth and mean population fitness, elasticities are proportional to selection gradients. Elasticities are comparable relative to one another within a particular IPM, such that a rate with twice the elasticity is twice as important in determining population growth and assumed to be proportional to a selection pressure that is twice as strong. Elasticities of lower-level parameters can also be summed to get the overall influence of mortality, fertility and somatic growth on the evolution of the life-history. Taken together, these outputs of $K(z_t, z_{t+1})$ thus provide insight into the population ecology and evolutionary pressures experienced by extinct organisms during their life.

An Integral Projection Model for Trilobatus sacculifer. —Here we implement an IPM to the planktonic foraminifer *Trilobatus sacculifer* (Brady 1877; Spezzaferri et al. 2015). Planktonic foraminifera have a life history that is ideally suited to representation as an IPM: they grow in discrete stages (chambers, see Fig. 1 and Caromel et al. (2016)) deposited rapidly every two to

three days and die after reproduction (Hemleben et al. 1989). After death, shells settle on the sea floor where their entire ontogeny is preserved in the sediment, resulting in a rich fossil record that reaches back to the Jurassic (Kendall et al. 2020). Plankton net and sediment trap studies allow linking the developmental history and environmental records (Bijma et al. 1990; Bijma and Hemleben 1994; Mikis et al. 2019).

We take survivorship and probability of reproduction data from laboratory culture experiments by Bijma and Hemleben (1994) and the growth from one stage to the next from Schmidt et al. (2013)'s X-ray computed tomography reconstruction of the developmental history. The chance of survival per size class from Bijma and Hemleben (1994) is converted to chance of survival per ontogenetic step (i.e. addition of a chamber) by taking the n^{th} root of survival per size class, with n the number of ontogenetic steps per size class (Schmidt et al. 2013). Using the empirical size, survivorship and probability reproduction data we determine the remaining parameters of demographic equations (eq. 2-4) commonly used in population ecology (e.g. Ellner and Guckenheimer 2006; Ellner and Rees 2006). We parameterise the smooth expressions describing the demographic rates of survival, reproduction and growth as a function of size using nonlinear least-squares regression in the R environment for statistical and graphical computing (version 4.0.2, R Core Team 2020). Our fully annotated and executable R script, from data entry through nls fitting and IPM implementation (based on an appendix to Ellner and Rees (2006)), is in Supplementary Code 1.

The model for survivorship takes the form

$$s_1 x + s_2 e^{s_3 x} \quad (2)$$

The model for the probability of reproduction takes a logistic form

$$f_1 \Big/ (1 + e^{f_2(x - f_3)}) \quad (3)$$

The model for somatic growth from one stage (chamber) to the next is described by a mean change (eq. 4a) and the standard deviation around it (eq. 4b)

$$\mu_x = g_1 x \quad (4a)$$

$$\sigma_x = g_2 e^{2 g_3 \mu_x} \quad (4b)$$

Here *x* represents size, and μ_x and σ_x represent the mean and standard deviation of the size change from one stage to the next. All other parameters are obtained through non-linear least squares regression. Table 1 provides the numeric values obtained through nls() and verbal explanations for the interpretation of each parameter. Through equations (2-4), we can parameterise all demographic rates necessary for $K(z_t, z_{t+1})$ except for the rate of recruitment to the breeding population, which, following previous practise, we set to ensure that the long-run growth rate of the population in a deterministic environment was 1.01 (Rees and Rose 2002). Figure 2 shows the statistical fits to the raw data from Bijma and Hemleben (1994) and Schmidt et al. (2013) based on the parameters listed in Table 1. This approach allows us to study the composition of the projected population as would have existed, but is not necessarily preserved in deep time, and the relative contribution of each size class to the next generation.

Results

The assumed functional forms (eq. 2-4) provide acceptable fits to the empirical data (Fig. 2), increasing confidence that an IPM based on these inferred relationships captures the core aspects of the life history of *T. sacculifer*. $K(z_t, z_{t+1})$ and its constituent eigenvectors (Fig. 3) make a

number of key life-history predictions. Most planktonic foraminifera within a single generation will be the youngest individuals (note the darkest colours in the IPM kernel are in the top right corner, which represents the transition from adults to the earliest, one-chambered stage of life (proloculus) through successful reproduction (Fig. 3A) and the peak in the stable stage distribution that gives the relative numbers of individuals per generation at each size (Fig. 3B). However, the largest rates of mortality are also from those youngest individuals at the beginning of the main developmental track (note the darkest colours in the IPM kernel in the top right, but how the main developmental track from top left to bottom right is a lighter grey, Fig. 3A). The most important individuals for the persistence of the population are the small numbers that reach reproductive maturity (note the reproductive value projection in Fig. 3B), which are those that have the best chance of preservation in the sediment.

Somatic growth rate, g_1, is the major influence on λ_1 (Fig. 4). Summing across the lower-level parameters used in each of the four main demographic rates suggests that somatic growth rate is almost twice as important as survival, eight times more important than whether the individual probably reproduced, and three-and-a-half times more important than recruitment to the breeding population, in determining the population ecology. This implies that selection should target somatic growth because it is the major determinant of mean fitness in these plankton as well as other exponentially growing and size-regulated organisms well-described by this semelparous life-history. Therefore, the major signal we need to extract to best understand this population ecology is, reassuringly, something accessible to palaeobiological study as it is preserved in a diversity of organisms and sedimentary settings.

Figure 5 demonstrates the "what if" power of these models – the mean growth rate assumed is well-described statistically (Fig. 2) but does not fully enable comprehensive studies of variation during an individual's growth. By looping across a range of possible parameter values for the standard deviation in somatic growth increments, g_2, and the expansion of variation amongst specimens in later life stages, g_3, as exemplified by the "sac-like" final chamber of *T. sacculifer* compared to its ancestor species *Trilobatus trilobus*, we observe that increasing both parameters would increase λ_1 (Fig. 5). Specifically, fitness is highest at highest growth rate variation among, as well as within specimens. The relationship between g_2 and g_3 is not consistent: when g_2 is small, small increases in g_2 rapidly increase λ_1, but the change to population mean fitness is more evenly balanced between g_2 and g_3 when these parameters are larger and thus developmental plasticity is greater. Figure 5 predicts that, all else being equal, selection should seek to increase developmental plasticity (fitness is highest in the top right corner of Fig. 5). This, and the importance of growth on fitness imply that plasticity in growth is an ecologically meaningful metric of developmental plasticity that can be studied in deep time.

Discussion

Studies of growth rate variation through time can provide new information on the effects of developmental plasticity on long-term evolutionary change. While the fossil record holds an enviable record of temporal change at the largest scales, sufficiently quantifying fine-scale variation within an individual's journey through life, or amongst individuals within populations, is typically far less accessible given taphonomic challenges. Our integral projection model predicts that a focus on individual (somatic) growth for organisms with a semelparous lifestyle can yield biologically relevant traits expected to be under the strongest selection pressure (Fig.

4). The model helps to determine the palaeoecological population context (Fig. 5) that is deeply relevant yet often absent in deep time, even for the most well-studied and charismatic species (e.g. Marshall et al. 2021).

Outputs from models such as the IPM we present can shape new directions in inferring relevant ecological and evolutionary processes in deep time. Planktonic foraminifera are ideally suited in this regard through their abundant preservation in sea floor sediments (e.g. Fenton et al. 2021; Fraass et al. 2015; Hemleben et al. 1989), existence of a species-level phylogeny for all Cenozoic macroperforate planktonic foraminifera (Aze et al. 2011) and the capacity to extract tied morphological and environmental signals from the same specimens (Kearns et al. 2021). Predictions based on this group have broader utility due to the generality of logarithmic spires in nature (McGhee 2007) and the common preservation of ontogenetic information via morphology in organisms as diverse as bivalves (Moss et al. 2016), trilobites (Whittington 1957), fish (Trueman et al. 2016), trees (Falcon-Lang 2015) and dinosaurs (Sanchez et al. 2010; Sander and Klein 2005).

Isolating developmental or phenotypic plasticity in the fossil record is challenging as it is typically unclear whether an observed morphological pattern arose through plasticity or genetic mutation. Strong evidence for trait plasticity is provided when a single genetic individual or clonal system shows changes in trait expression throughout its life (Lister 2021). Under stable environmental conditions, expression of life-history traits with the highest influence on population growth were traditionally expected to be resistant to environmental change (Hilde et al. 2020; but see McDonald et al. 2017). In our IPM, evolution should promote developmental

plasticity because higher levels of variation in growth increments increase mean population fitness (Fig. 5). More generally, selection can favour phenotypic plasticity when a non-linear positive relationship between the vital rate and environment leads to increased population growth (Koons et al. 2009). That we do not see unfettered increases in plasticity is due, in part, to morphological constraints limiting evolutionary divergence (Goswami et al. 2014). Devoting more energy to measuring trait (co)variability amongst further morphological traits promises to be instructive in tracking expected evolutionary changes (Haber 2016; Hunt 2007; Puttick et al. 2014; Renaud et al. 2006) particularly the viability of certain trait combinations (Raup 1967). Mutation-driven change is predicted to alter the mean trait expression, without a simultaneous change in variation among individuals. As soon as the environment changes and different traits are expressed plastically, variation amongst individuals increases and there is more raw material for rapid diversification (Küttner et al. 2014; Ledon-Rettig et al. 2010; Masel 2005; Moczek 2008; Suzuki and Nijhout 2006; Vanadzina and Schmidt 2021; Zheng et al. 2019).

Given a sufficiently highly resolved temporal fossil sequence, initial stasis followed by increased variation during environmental instability can be strong evidence of evolution driven by developmental plasticity (Jackson 2020). A handful of studies has previously focused on variation in the fossil record as evidence of developmental plasticity, but none provided data of change in this plasticity through time. For example, Anton and Kuzawa (2017) show differences in body size variation in *Homo erectus* populations migrating to subtropical and temperate areas, while Schoch (2014) interpreted high variation among populations from different environmental settings as a fossil reaction norm, but both studies dealt with individual snapshot populations so variation could not be studied through time. We do not see unfettered increases in developmental

plasticity in *T. sacculifer* under different laboratory conditions, nor departures from logarithmic spires (Bé 1980; Bé et al. 1981). This implies a strong morphological constraint on plasticity in this species that regulates growth and thus maintains one-step deviations in growth rates in the lighter grey areas of Figure 5. When these constraints are relaxed, plasticity is expected to increase. Changing variation through time is stronger evidence for plasticity-led evolution than variation within a single population (Jackson 2020) and could be coupled with data on single genetic individuals or clonal systems (Lister 2021) as well as environmental context. Focussing on groups with enviable stratigraphic records (Lazarus 1994; Lazarus 2011) is one promising route to studying greater population context on temporally replicated samples.

Levis and Pfennig (2016) propose that a release of cryptic genetic variation following environmental change is an indicator of plasticity-led evolution in extant populations. The challenge is in contextualising developmentally sensitive variation into variance within-individuals, among-individuals and among-populations. Levis and Pfennig (2016) described four criteria to provide evidence of plasticity-led evolution in extant populations: (1) an environmentally induced target trait, (2) release of cryptic variation in a derived environment, (3) change in regulation and/or form in the target trait following environmental change and (4) adaptive refinement of the target trait in the derived lineage. Jackson (2020) described how criterion (2) could be observed in a very high-resolution fossil record, but extracting (4) will, even in the presence of a proxy for every individual's microenvironment, rely on model-based inference via statistical tracking of intraspecific variability alongside an independent metric of environmental change. The most promising systems to examine would be a population adapting

353 to a new environmental optimum (Hunt et al. 2008) as an indication of an altered adaptive
354 landscape (Arnold et al. 2001; Simpson 1953).
355
356 Genes can, given sufficient time, combine in many ways to form the same trait (Moczek et al.
357 2011; Pfennig et al. 2010). Following a release of cryptic variation, further evidence that
358 plasticity successfully led to innovation and speciation can be found through ancestor-descendant
359 comparisons that implement the approaches outlined above. A change in form of the target trait
360 in the derived lineage compared to the ancestor would suggest genetic accommodation (Levis
361 and Pfennig 2016). Traits showing subsequent adaptive refinement in the descendant lineage are
362 a particularly strong indicator of successful plasticity-led evolution (Levis and Pfennig 2016).
363 Direct inference of ecologically informative trait evolution in a phylogenetic context is available
364 in highly resolved systems where environmental data can also be resolved on a sub-individual
365 basis (Sadekov et al. 2009). Under divergent selection, it is more important to understand the
366 contemporaneous environmental context than always to seek to isolate a particular genetic
367 mechanism (Nosil 2012; Schluter 2000). This context can be observed in the fossil record of, for
368 example, foraminifera (Aze et al. 2011) and bryozoans (Liow et al. 2019) by comparing ancestor
369 and descendant trait distributions before, during and after speciation as a response to biotic and
370 abiotic ecological and environmental change. Growth traits are readily quantifiable and testable
371 in trait based ecosystem models (Grigoratou et al. 2021) that investigate the coevolution of life
372 and the planet and alter the longer-term environmental context.
373
374 As growth rate is the largest determinant of fitness in our model (Fig. 4), adaptive evolution in
375 growth rates is expected to increase the descendant's population size, and all else being equal,

provide a competitive advantage over the ancestor species or ecological competitors. The use of modelling frameworks such as the IPMs here focus attention beyond counts and towards ecological significance (Ezard et al. 2016). Focussing on traits such as growth rate increase our ability to make ecologically relevant inferences and build a more comprehensive picture of the palaeoecological context when these species were evolving millions of years ago.

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Figures

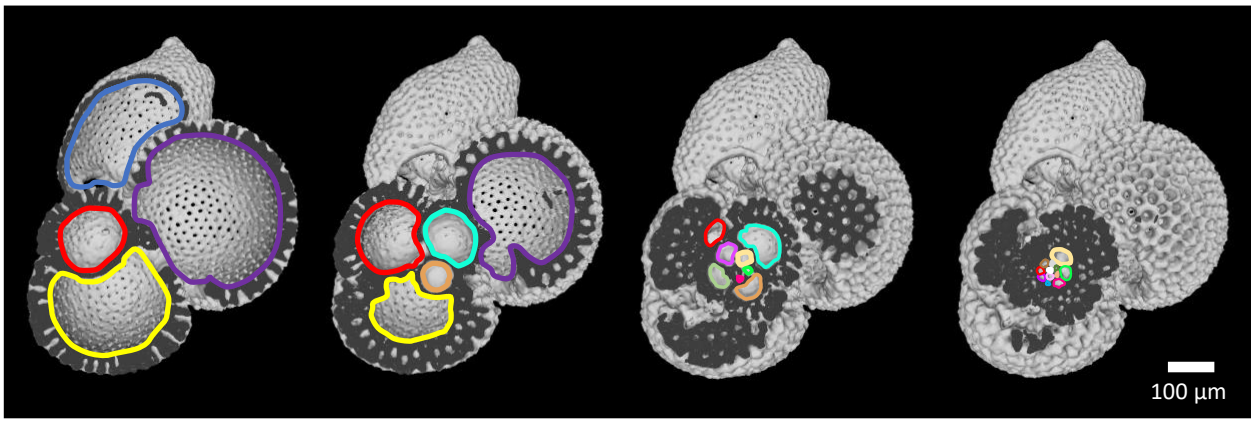

Figure 1: *Trilobatus sacculifer* internal structure. Every coloured chamber represents a single step in the ontogeny.

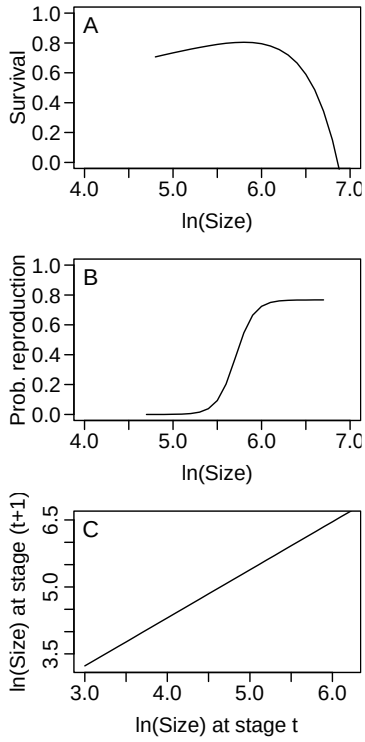

Figure 2: Survival (A), probability of reproduction (B) and size at stage $t + 1$ (C) data and model results from statistical fits to the relationships that feed into the integral projection model kernel. See Table 1 for coefficients.

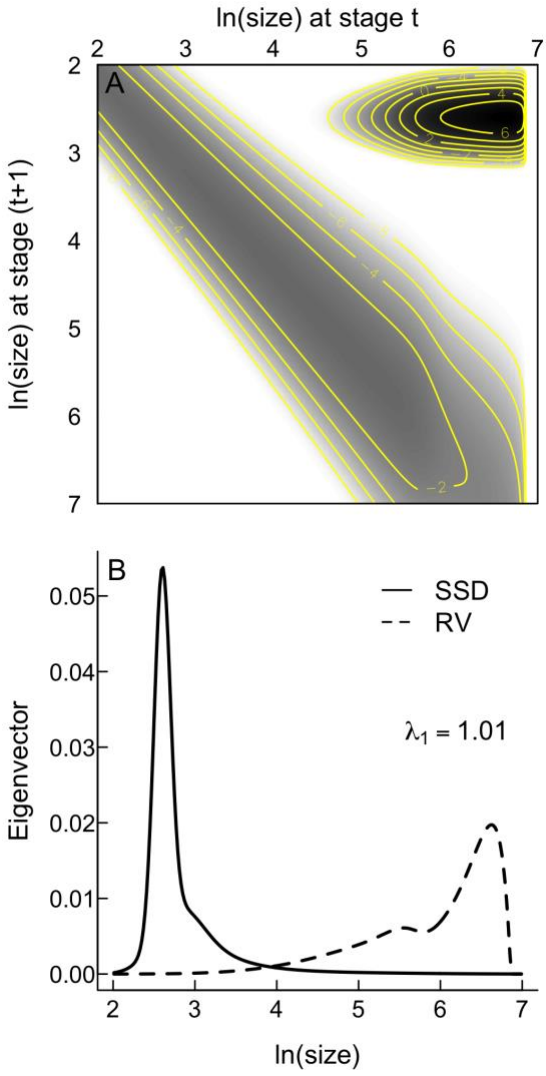

Figure 3: Matrix visualisation of the integral projection model kernel (A) and the right and left eigenvectors corresponding to the stable stage distribution (SSD) and reproductive value (RV), respectively (B). White cells in (A) are not accessed by the projected life-cycle; greys and blacks indicate the proportions (on a ln-scale) of individuals across the life-cycle in each stage. The main developmental track is the grey band from top-left to bottom right as individuals grow through successive discrete stages. The almost-black peak in the top right corner represents

fertility – the transition from the largest stages (at one end of life) to the smallest stages in the next generation. Isolines represent values of the kernel K.

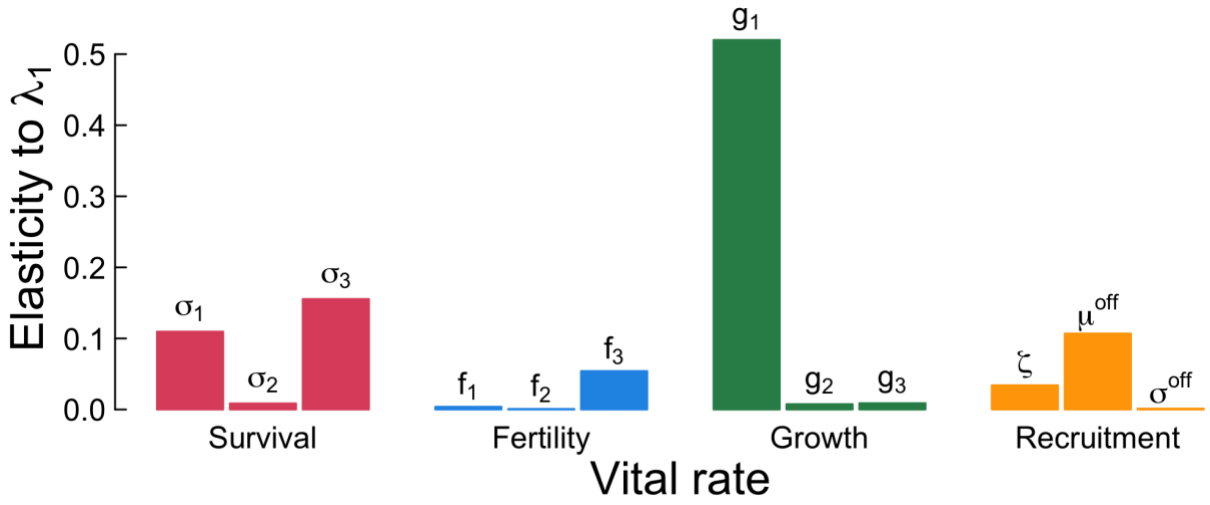

Figure 4: Elasticity represents the influence of each parameter on the long-run population growth rate in a deterministic environment λ_1. The three bars within each colour indicate lower-level parameters in the order of Table 1 as used to define the aggregated demographic rates.

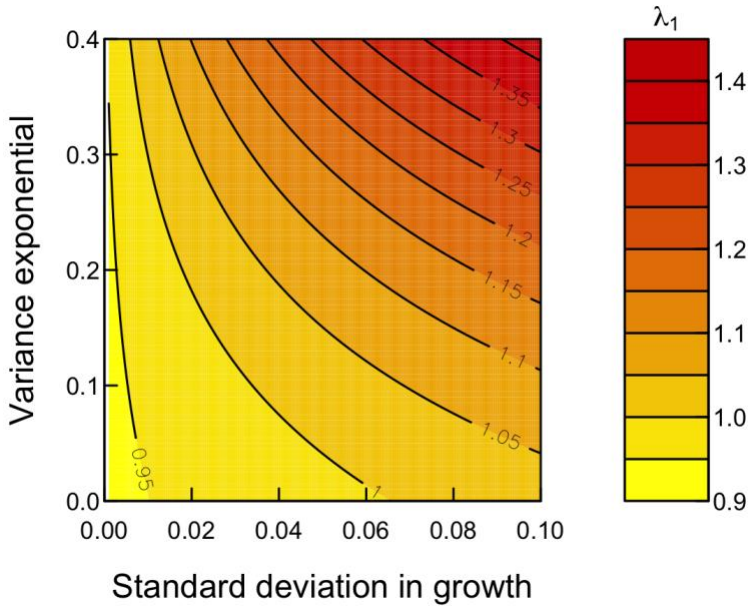

Figure 5: Increasing the extent of developmental plasticity by increasing g_2 , the standard deviation in growth, and g_3, the variance exponential, would be adaptive in the sense of increasing λ_1. The black contours represent different projections for λ_1 holding ζ as listed in Table 1.

662 Table 1. Fitted values to parameters stated in the vital rate expressions (equations 2-4) with
663 descriptions of their interpretation.
664

Symbol	Value	Description
s_1	0.16	Linear increase in survival probability
s_2	-3.2e-07	Scaling of the exponential term s_3
s_3	2.18	Non-linear rate of increase in mortality with age (senescence)
f_1	0.77	Asymptotic probability of reproduction
f_2	9.63	Rate of increase in the probability of reproduction
f_3	5.71	Sigmoidal midpoint during the transition from zero to asymptotic probability of reproduction
g_1	1.0768	Growth rate from one chamber to the next
g_2	0.0238	Standard deviation in one-step growth rate
g_3	0.185	Variance exponential in growth
ζ	0.013	Recruitment rate to the population. Set to ensure λ_1= 1.01 (except in Figure 5), where λ_1 represents population growth rate in a deterministic environment.
μ^{off}	2.6	Mean size of offspring (ln-scale, equivalent to 13.5 μm)
σ^{off}	0.1	Standard deviation in size of offspring (ln-scale, equivalent to an approximate 95% confidence interval of initial stage size of (11.0, 16.5) μm

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