How well can body size represent effects of the environment on demographic rates? Disentangling correlated explanatory variables

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Abstract: 1. Demographic rates are shaped by the interaction of past and current environments that individuals in a population experience. Past environments shape individual states via selection and plasticity, and fitness-related traits (e.g. individual size) are commonly used in demographic analyses to represent the effect of past environments on demographic rates. 2. We quantified how well the size of individuals captures the effects of a population's past and current environments on demographic rates in a well-studied experimental system of soil mites. We decomposed these interrelated sources of variation with a novel method of multiple regression that is useful for understanding nonlinear relationships between responses and multicollinear explanatory variables. We graphically present the results using area-proportional Venn diagrams. Our novel method was developed by combining existing methods and expanding upon them. 3. We showed that the strength of size as a proxy for the past environment varied widely among vital rates. For instance, in this organism with an income breeding life history, the environment had more effect on reproduction than individual size, but with substantial overlap indicating that size encompassed some of the effects of the past environment on fecundity. 4. This demonstrates that the strength of size as a proxy for the past environment can vary widely among life-history processes within a species, and this variation should be taken into consideration in trait-based demographic or individual-based approaches that focus on phenotypic traits as state variables. Furthermore, the strength of a proxy will depend on what state variable(s) and what demographic rate is being examined; that is, different measures of body size (e.g. length, volume, mass, fat stores) will be better or worse proxies for various life-history processes.

1 **How well can body size represent effects of the environment**

2 **on demographic rates? Disentangling correlated explanatory**

3 **variables**

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18 **Summary**

19 1. Demographic rates are shaped by the interaction of past and current environments

20 　 that individuals in a population experience. Past environments shape individual

21 　 states via selection and plasticity, and fitness-related traits (e.g., individual size)

22   are commonly used in demographic analyses to represent the effect of past

23   environments on demographic rates.

24   2. We quantified how well the size of individuals captures the effects of a

25   population's past and current environments on demographic rates in a well-

26   studied experimental system of soil mites. We decomposed these interrelated

27   sources of variation with a novel method of multiple regression that is useful for

28   understanding nonlinear relationships between responses and multicollinear

29   explanatory variables. We graphically present the results using area-

30   proportional Venn diagrams. Our novel method was developed by combining

31   existing methods and expanding upon them.

32   3. We showed that the strength of size as a proxy for the past environment varied

33   widely among vital rates. For instance, in this organism with an income

34   breeding life-history, the environment had more effect on reproduction than

35   individual size, but with substantial overlap indicating that size encompassed

36   some of the effects of the past environment on fecundity.

37   4. This demonstrates that the strength of size as a proxy for the past environment can

38   vary widely among life-history processes within a species, and this variation

39   should be taken into consideration in trait-based demographic or individual-

40   based approaches that focus on phenotypic traits as state variables. Furthermore,

41   the strength of a proxy will depend on what state variable(s) and what

42   demographic rate is being examined; i.e., different measures of body size (e.g.,

43   length, volume, mass, fat stores) will be better or worse proxies for various life-

44   history processes.

45

Introduction

The past and current environments experienced by individuals shape their

demographic rates, and these effects can be partially captured in individual state

variables such as body condition, mass, and size (Easterling, Ellner & Dixon 2000;

Caswell 2001; Benton, Plaistow & Coulson 2006). For many species, size-at-age,

body-mass-index, or fat reserves are influenced by food availability and relate to

patterns of resource acquisition and storage (Kooijman 2000). Size can be a good

proxy for an individual's general state including developmental stage, resource

acquisition and stores, and the outcomes of competitive interactions (Peters 1986).

Past experiences shape an individual's current state, and current state interacts with

the current environment to determine the individual fate (i.e., survival, growth, and

reproduction). An individual's full multifaceted state includes its genotype,

phenotype, epigenetics, energy reserves and many other variables that can be difficult

to measure. Recent research on trait-based demography has highlighted the power of

including easy to measure state variables such as individual size in demographic

models including matrix and integral projection models (IPMs) (Easterling *et al.*

2000; Caswell 2001; Ozgul *et al.* 2009; 2010) and agent-based models (Grimm *et al.*

2006). However, how much of the past and current environmental effects on

demographic rates are captured by individual size and how much variation is left to be

explained has not been explored as thoroughly and directly as we aim to here.

The dynamics of state variables and demographic rates are shaped by

selection, phenotypic plasticity, and parental effects (Ozgul *et al.* 2010; Coulson *et al.*

71 2011; Benton 2011; Ozgul *et al.* 2012). In many cases, much of the cumulative effects

72 of the past and current environments on demographic rates are integrated into an

73 individual's size (or condition), but not all (Festa-Bianchet, Gaillard & Jorgenson

74 1998; Ozgul *et al.* 2010; DeLong, Hanley & Vasseur 2014). For example, in bighorn

75 sheep, which are considered to be capital breeders, body mass reflects the amount of

76 stored resources available for reproductive effort. Yet, a positive effect of body mass

77 on female reproductive success was only evident at high population densities, a biotic

78 component of the current environment resulting from conditions in the past

79 environment (Festa-Bianchet et al. 1998).

80   Such cases of weak or context-dependent relationships between an

81 individual's state and demographic rates can arise from differences in the sensitivity

82 of life-history traits to past and current environments (Le Galliard et al. 2010;

83 Beckerman et al. 2003; Taborsky 2006). Such differences can be due to the fact that

84 selection, plasticity, and parental effects do not affect traits equally (Benton *et al.*

85 2006). In addition, context-dependent associations between traits can arise from

86 changes in life-history trade-offs in response to environmental variation that affect

87 patterns of covariation between life-history traits throughout time (e.g., Plaistow et al.

88 2006; Plaistow and Benton 2009). These examples highlight the complex array of

89 potentially interacting mechanisms shaping life-history and population dynamics and

90 the importance of investigating how much of this variation can be summarized into

91 one easily observable, individual condition-index such as body size (Beckerman *et al.*

92 2002; Benton *et al.* 2006; Evans *et al.* 2013).

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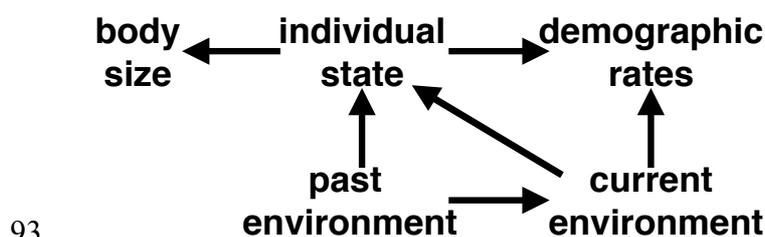
94   **Fig. 1. Influence diagram.** Arrows indicate the influence of demographic

95   components on each other. Past environments influence the current environment by

96   shaping the demographic structure and population density. Past environments

97   influence individual states via natural selection, plasticity, and maternal effects. We

98   observe part of an individual's multifaceted state via its body size. In the soil mite

99   model system, past environments include those an individual has experienced, but

100   also those experienced by maternal, grand maternal and great-grand-maternal

101   generations (Plaistow, Lapsley & Benton 2006).

102

103   In this study, we used an extensive laboratory experiment to characterize how

104   demographic rates changed through time in populations experiencing drastically

105   different environments. Our model organism, *Sancassania berlesei* (a soil mite), has a

106   life-history that plastically responds to food availability and population density, and

107   exhibits maternal effects (Benton, Lapsley & Beckerman 2001; Benton, St Clair &

108   Plaistow 2008; Ozgul *et al.* 2012). This experiment enabled us to quantify the

109   influence of individual body size, current environment, and past environment on

110   demographic rates.

111   Favorable past and current environments lead to better individual states and

112   thus enhanced demographic rates, but a favorable past environment increases

113   population density and can thus reduce the quality of the current environment. The

114   interdependencies of body size, current environment, and past environment (Fig. 1)

115   cause multicollinearity (i.e., correlation) among explanatory variables in regression

116   models that makes it difficult to disentangle the effects (Graham 2003). To

117   disentangle the influence of body size, the current environment, and the past

118   environment, we have used a novel procedure based on the practice of fitting all

possible subsets of these multicollinear explanatory variables (Chevan & Sutherland 1991; Graham 2003; Murtaugh 2009). We modeled potentially nonlinear effects of these explanatory variables on demographic rates using splines (Dahlgren, Garcia & Ehrlén 2011). We teased apart the overlap in explanatory power by comparing the proportion of deviance explained (a generalization of r^2, Wood 2006) from models with all subsets of explanatory variables. Overlap in explanatory power is a result of multicollinearity among the explanatory variables, caused by the interdependencies described above. This method is novel because it disentangles multicollinearity in nonlinear splines in a way previously used for linear models (Ip 2001). Also, this paper is the first to plot the results of this decomposition using area-proportional Venn diagrams which are visually intuitive (Micallef & Rodgers 2014). Our goal was to quantify how well the past and current environmental effects on demographic rates were represented by body size, and how much variation was left to be explained.

In the past, researchers have attempted traditional time series decomposition of measured phenotypes in *Sancassania berlesei* and how they change over time (Benton *et al.* 2005) but this is complex because the importance of the past environments vary over time in a way that is itself context dependent (Beckerman *et al.* 2003; Plaistow *et al.* 2006; 2007). So standard linear time series models are not informative. Our new method of decomposing the variability in demographic rates is therefore valuable as it can highlight the importance of processes that we know to be sensitive to conditions in complex ways. Most importantly, it challenges one major assumption underlying recently popular trait-based demographic models: that a focal state variable such as body size captures the effects of past and current environments on the individual's performance, and acts as a memory mechanism to project the individual performance to future time steps. By using a well-studied system we can benchmark the

144 performance of the new technique. If the technique produces results that match our

145 detailed understanding of this model system, we can have confidence that it has utility

146 for studying systems where the background knowledge is lower.

147 In the following text, we first describe our methods including the experiment

148 for our soil mite case study and then statistical analyses including hypothesis testing

149 and variance decomposition. Then we present results from the case study and divide

150 our discussion into a soil mite specific discussion and a discussion of the general

151 applicability of our method for both demographic and general ecological studies.

Materials and methods

Experimental Methods

154 The goal of our experiment was to observe how population dynamics and

155 individual demographic rates change in response to vastly different environments that

156 should induce selection, plasticity, and maternal effects.

157 Populations of soil mites were raised in 22 mm diameter tubes for nine weeks

158 in four environments: one constant (control) and three varying (famine, declining, and

159 fluctuating). Famine and fluctuating populations experienced abrupt changes in their

160 food (Fig. 2). The experimental timespan is approximately two times the generation

161 time of soil mites maintained in food conditions similar to our control treatment

162 (Ozgul *et al.* 2012; Cameron *et al.* 2013). Treatments differed in the amount of food

163 provided and subsequently, population densities naturally varied accordingly (Fig. 2).

164 All populations experienced a constant food environment prior to the experiment until

165 population dynamics and stage structure stabilized. The life stages are as follows (in

166 order): egg, larva, protonymph, tritonymph, and adult (male or female).

167 There were two replicate sampling populations and five replicate counting

168 populations per treatment. The counting populations were censused twice per week to

169 monitor population density and stage structure. There were twenty-eight populations

170 total; more replicates were not possible due to the work required for censusing the

171 counting populations. Twice per week per sampling population, five adult males and

172 five adult females were sampled and placed in five mixed-sex tubes for a period of 24

173 hours; also three individuals from each juvenile stage (larva, protonymph, tritonymph)

174 were placed in three mixed-stage tubes for a period of 24 hours. Sampling was done

175 several hours after feeding. Sampled individuals were photographed before and after

176 the 24-hour period in which the following responses were monitored: survival

177 (binary), final body length (mm), stage transition (binary), reproduction (binary and

178 egg counts). After the 24-hour monitoring period, surviving individuals were put back

179 in the sampling populations. Eggs were not put back because of the time required to

180 move eggs 0.18 mm in diameter. See appendix S1 for more experimental details.
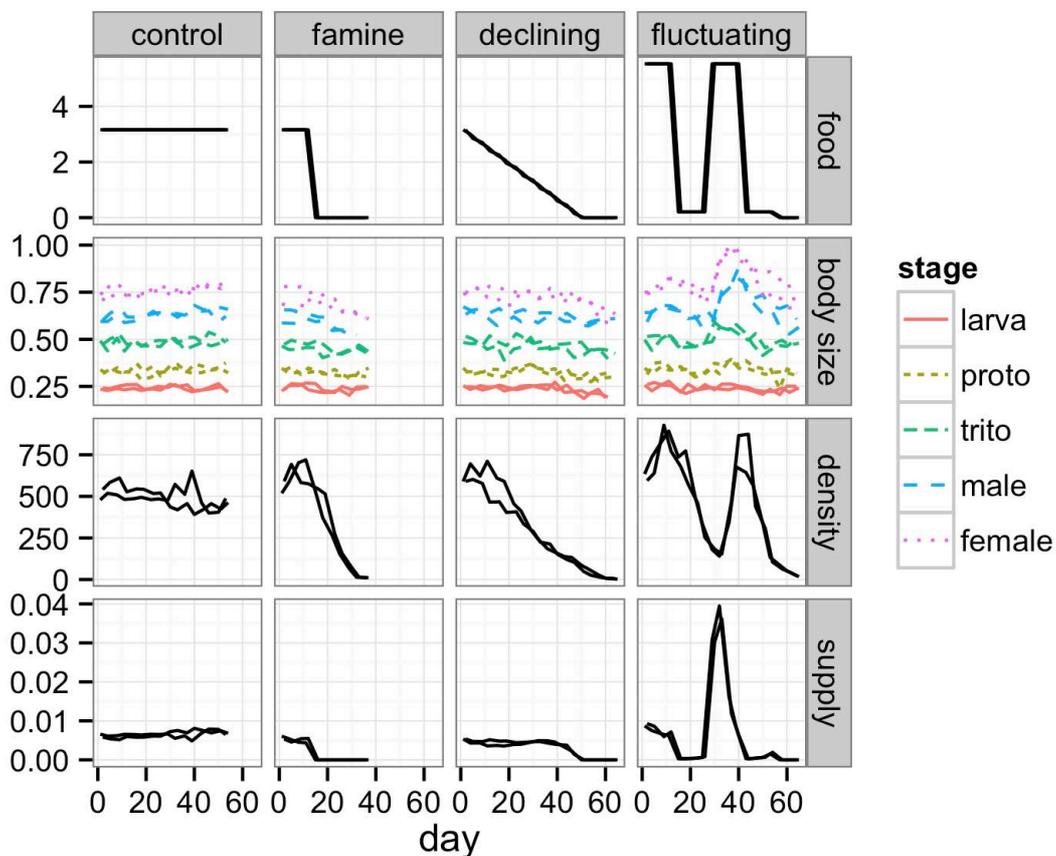
181

182   **Fig. 2. Experimental environments and demographic covariates.** Each column is a

183   different experimental treatment with two populations per treatment each represented

184   by a line. Each row represents a different covariate: food provided (in mg), naturally

185   varying average individual body size at start of monitoring (length in mm), population

186   density weighted by the average body size in each stage (i.e., total body length per

187   tube), and food supply (food divided by density, i.e., mg food per mm body length).

188   The number of individuals per density unit is equal to the inverse of the stage-specific

189   average length: approximately 4.3 larvae, 3.1 protonymphs, 2.2 tritonymphs, 1.6

190   males, or 1.4 females, but this varies throughout the experiment as body sizes vary.

191

192   *Statistical Methods*

193   The goals of our statistical analyses were to determine which demographic

194   responses (i.e., life-history processes) depended on starting body size, current

195   environment, and past environment; then to determine the power of these explanatory

196   variables and how much power overlapped due to multicollinearity.

197   We quantified evidence of the influence of starting body size, current

198   environment, and past environment on demographic responses using generalized

199   additive mixed models (GAMMs). We used GAMMs because demographic responses

200   potentially have nonlinear dependence on starting body size (Anderson *et al.* 2008;

201   Dahlgren *et al.* 2011; Ozgul *et al.* 2012; Cameron *et al.* 2013) and we expected

202   responses to change nonlinearly during the experiment in response to the

203   environment. Generalized additive models (GAMs) are convenient because they do

204   not require that one makes assumptions about the shape of the nonlinear relationships.

205   They are generalized linear models that represent the nonlinear relationship using

206   smooth functions of covariates (Wood 2006). GAMMs are GAMs with random

207 effects in addition to fixed effects, which we use here to account for repeated

208 measures of populations.

209   Demographic responses of interest were measured after 24 hours for mites

210 sampled from the population (see Experimental Methods). Responses included final

211 body size (length in mm), initiation of transition from one developmental stage to the

212 next (binary), reproduction by females (binary), fecundity (number of eggs laid given

213 reproduction), egg size (in mm, average within female), and survival. In trait-based

214 demography, it is common to model the growth process as an individual's size at the

215 end of a time step dependent on its size at the start of the time step, so we follow that

216 standard and use "final body size" and "growth" interchangeably.

217   Explanatory variables of interest included starting life-history stage (the stage

218 of an individual at the start of a 24-hour monitoring period), starting body size,

219 current environment, and past environment; see the following three paragraphs for

220 further descriptions of starting body size, current environment, and past environment

221 (Fig. 1). For clarity, we consistently refer to these four components as "explanatory

222 variables". Alternatively, we use "covariates" to refer to the observed variables

223 included in the smooth functions that make up these explanatory variables.

224   The explanatory variable "body size" (i.e., starting body size) was a smooth

225 function of an individual's observed body size at the start of the 24-hour monitoring

226 period. Throughout this text, all discussions of the explanatory power of body size are

227 referring to this starting body size explanatory variable.

228   The explanatory variable "current environment" was a two-dimensional

229 smooth function of the most recent estimate of (i.e., within the past 24 hours)

230 population density and food supply (used here to mean food given divided by density;

231 density and food supply are further described below). Two-dimensional smooth

232   functions allow for nonlinear effects of the covariates and their interaction. The fit of

233   a two-dimensional smooth function results in a three-dimensional nonlinear surface,

234   the height (i.e., third dimension) of which represents how the response variable

235   changes with the covariates. We assumed that the current environment experienced by

236   an individual is an interaction between the population density and the available food.

237   Population density (per tube) was calculated as the number of individuals in a given

238   stage times the average body size in that stage, summed across all stages, except eggs,

239   to account for asymmetric competition. See appendix S2 for details of our density

240   calculations. Food supply (food given divided by density, i.e., mg food per mm body

241   length) was used as a covariate (as part of the current environment smooth function)

242   instead of absolute food because preliminary analyses indicated that it was a better

243   predictor of all demographic responses.

244   The explanatory variable "past environment" was a treatment intercept and a

245   smooth function of the day of each treatment. When specifying a smooth function of a

246   continuous variable by a categorical variable in a GAM (as in our past environment

247   by treatment), it is usually necessary to include a separate intercept for that categorical

248   variable. Our treatment intercepts are parameterized in the standard way with the

249   control treatment as a baseline and other treatments as contrasts. The smooth

250   functions of time are not tied to any informative covariates and can take any nonlinear

251   shapes that are smooth through time and thus account for cumulative changes in

252   demographic responses that arise through selection, plasticity, or parental effects. This

253   flexibility can incorporate the cumulative effects of the environment up to the moment

254   a demographic response is observed which encompasses much of what we call the

255   "current environment" i.e., the most recently estimated population density and food

256   supply. Thus, effects of the environment before this "current environment" should be

257 evident in explanatory power from the "past environment" that does not overlap that

258 of the "current environment". The "past environment" spline was defined in such a

259 flexible way so that, in a full model with all explanatory variables, it can pick up any

260 population level patterns not explained by individual body size, population density, or

261 food supply. This implies that, given two individuals of the same body size in the

262 same current environment in different treatments or different times in the same

263 treatment, we assume that any differences in their demographic rates are caused by

264 differences in their past environments. It is possible that there are aspects of the

265 current environment that differ, but are not incorporated into our current environment

266 spline. So this interpretation of the residual patterns is not strong evidence but a

267 means of generating hypotheses that could be tested with further experiments that are

268 more mechanistic.

269   For example, the full GAMM fit to egg counts (fecundity) contained a smooth

270 function of starting body size, a treatment intercept, a smooth function of the day for

271 each treatment, a two-dimensional smooth function of the population density and food

272 supply, and a random effect of population. The hypothesis represented by this model

273 is that an individual's fecundity depends on its current access to food and the body

274 size of that focal individual (which determines its competitive ability). However, the

275 allocation strategy of individuals in some treatments or time points of treatments may

276 differ from individuals of similar size in similar current environments due to differing

277 past environmental experiences. These differences due to past environmental

278 experiences should appear in the non-overlapping explanatory power of the past

279 environment spline.

280   To be clear, as part of the GAM fitting procedure, the smooth functions

281 described above took on different nonlinear shapes (thin-plate regression splines) for

282   each model just as coefficients would differ among linear models. Variation in a

283   demographic response can be explained by one explanatory variable in one model and

284   a different explanatory variable in a different model that contains a different set of

285   variables. This is the same issue that occurs when estimating coefficients in linear

286   multiple regression with correlated explanatory variables (Chevan & Sutherland 1991;

287   Graham 2003). Multicollinearity hinders the interpretability of the coefficients and

288   smooth functions (Mitchell-Olds & Shaw 1987).

289   For each demographic response separately, we fit the full GAMM containing

290   all explanatory variables described above. We applied Wald-type tests to the full

291   GAMM (Wood 2013b); these are p-values indicating the strength of evidence against

292   the null hypothesis that explanatory variables have no influence. We also examined all

293   submodels of the full GAMM using information theory and results were similar to the

294   Wald-type tests; the details including R code can be found in appendix S3.

295   For demographic responses whose supported explanatory variables contained

296   starting body size, current environment, or past environment we calculated the

297   explanatory power of each of these and their overlap. We focused on these

298   explanatory variables because they were relevant to all responses whereas life-history

299   stage only applies to some responses and may not apply to all species. Unlike models

300   that tested for effects, to simplify the interpretation of explanatory power, these

301   contained no random effect. It is possible to expand this method to apply to mixed

302   models, but this is beyond the scope of this paper (Nakagawa & Schielzeth 2012).

303   We fit GAMs with all subsets of the supported explanatory variables. We calculated

304   the overlap in explanatory power as the difference from what the explanatory power

305   of a model with multiple variables would be if it were additive relative to single

306   variable models. The non-overlapping explanatory power is the increase in

307 explanatory power when adding a variable to a model that already contains other

308 variables. These calculations have been previously described for variance partitioning

309 in linear models (Chevan & Sutherland 1991; Ip 2001; Grömping 2007).

310   Other statistical methods exist for dealing with multicollinearity, but they do

311 not address our interest in interpreting both the overlapping and non-overlapping

312 portions of explanatory power to get insight into the demographic processes that lead

313 to multicollinearity (Graham 2003). Principal components analysis takes many

314 predictors and summarizes them into just a few, but we wanted to look at all of the

315 predictors and their relationship with body size. Residual and sequential regression

316 require that you assume some hierarchy among the explanatory variables, but we

317 wanted to see if body size was more important, not assume it. Structural equation

318 modeling and path analysis can not handle relationships as flexibly as GAMs and we

319 wanted our method to be able to pick up minor nonlinearities in the time series

320 (Brandt, Kelava & Klein 2014). For these reasons, we have expanded upon existing

321 methods and combined existing tools in new ways to produce a new method for

322 examining multicollinear predictors that have nonlinear relationships with the

323 response variable.

324   All GAMMs were fit in R using gamm4 with lme4 and GAMs were fit using

325 mgcv (Wood 2013a; Bates *et al.* 2013; Wood & Scheipl 2013). For smooth functions,

326 we used penalized thin-plate regression splines that tend to give the best mean squared

327 error (Wood 2003; 2013a). All continuous covariates except day were standardized to

328 have mean zero and unit variance. We allowed smooth functions of starting body size,

329 current environment, and past environment to have a maximum of five, ten, and ten

330 knots respectively. Five knots for the effect of starting body size were previously

331 discussed by (Dahlgren et al. 2011). Because current environment was a two-

332 dimensional spline, we assumed it might need more knots. Examination of the

333 responses (Fig. 3) suggested that they might be more flexible through time (i.e., past

334 environment). The mgcv package automatically reduces the flexibility of splines

335 based on maximum likelihood using the Laplace approximation. All models used

336 typical distributions and link functions for the responses as follows: final body size

337 was Gaussian (identity link); stage transition was binomial (logit link); reproduction

338 was binomial (logit link); non-zero fecundity minus one was Poisson (log link);

339 survival was binomial (logit link).

340

Results

342   In each experimental environment, demographic responses varied through

343 time and with some consistency between the two replicate populations (Fig. 3). Wald-

344 type tests applied to the full model indicated that starting body size and the current

345 environment had effects on most demographic rates (Table 1). Development and

346 reproductive rates were higher for individuals with larger body sizes and in

347 environments with higher food supply (appendix S5). Higher density decreased

348 growth and reproductive rates, but had a positive effect on transition probability with

349 marginal significance (Table 1 and appendix S5). While controlling for the effects of

350 body size and the current environment, declining and fluctuating environments also

351 caused temporal patterns for some demographic rates (Table 1 and appendix S5).

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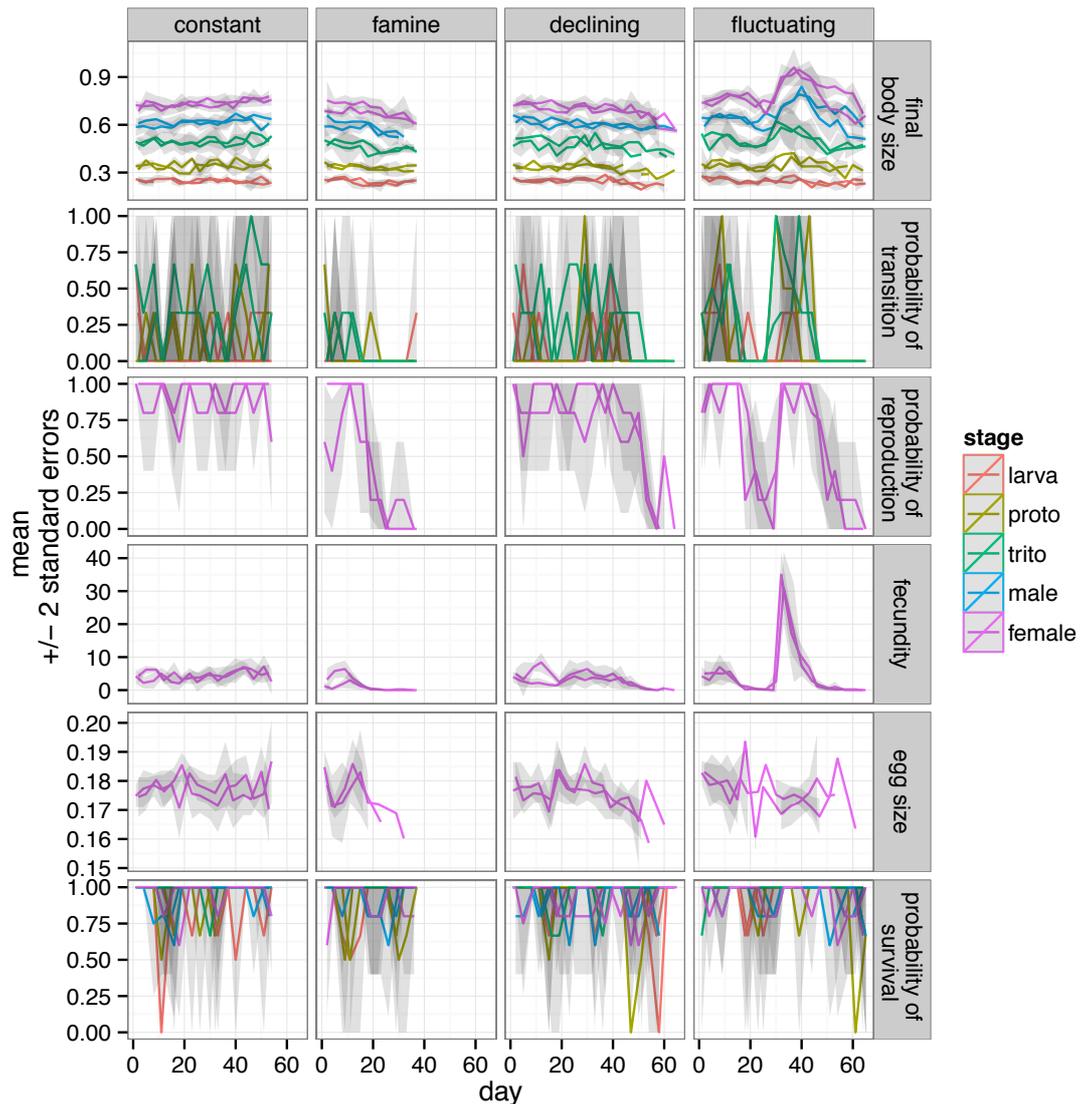
Fig. 3. Observed life-history processes.

Each column represents an experimental treatment. Each row represents a life-history process observed over a 24 hour monitoring period: final body size at the end of monitoring (length in mm), probability of initiating transition from one developmental stage to the next, probability of reproduction (given female), fecundity (number of eggs laid given reproduction), egg size (in mm, average within female), and survival. Lines represent the mean of individuals sampled from a population on a given day (a subset of the population: 5 from each adult stage and 3 from each juvenile stage). Grey ribbons represent +/- 2 standard errors. Standard errors are missing for egg size

362   on days when only one female was sampled. Observations in the famine populations

363   ended when all individuals died. The control populations persisted to the end, but

364   observations ended. 'Proto' refers to protonymph and 'trito' to tritonymph.

365

Table 1: Wald-type tests (to test the null hypothesis that the smooth function was not different from 0) applied to all smooth functions in the full GAMMs. The control intercept was used as the baseline for treatment contrasts and was always non-zero (***). The growth model containing stage gave a convergence warning, so we omitted it (see appendix S3 for details). 'NA' indicates that stage was not included in a model to distinguish this case from non-significance. 'Proto' refers to protonymph and 'trito' to tritonymph.

'.' $p<0.1$, '*' $p<0.05$, '**' $p<0.01$, '***' $p<0.001$

	Stage	Body size	Current environment	Past environment smooth functions (and intercept in parentheses)			
				Control	Famine	Declining	Fluctuating
Growth	NA	***	***				* (.)
Transition	***(proto) ***(trito)	***	.			.	** (***)
Reproduction	NA	***	***		(*)	**	(***)
Fecundity	NA	***	***			**(**)	(.)
Egg Size	NA				(.)	*	*
Survival	*(trito)						

376 *Power of supported explanatory variables*

377 The best explanatory variable of growth and stage transition was body size (Fig. 4).

378 Both reproductive rates depended more on the environment than on female body size

379 (Fig. 3). Body size encompassed almost all of the explanatory power of the current

380 and past environments for growth (0.99); 0.27 and 0.26 respectively for stage

381 transition; 0.39 and 0.34 respectively for reproduction; and 0.47 and .48 for fecundity

382 (numbers are proportion of explanatory power overlapping). See Appendix S4 for

383 explanatory power calculations. As is common for variance decompositions, some

384 shares came out slightly negative so we rounded these to zero for graphing in Fig. 4

385 (Hamilton 1987; Ip 2001); these were an order of magnitude smaller than the portions

386 we interpret (Growth: se=-0.001; Transition: se=-0.007, sh=-0.005). This indicates

387 that one variable was masking a tiny amount of the explanatory power of another

388 variable (Hamilton 1987). This omission is why the subareas do not perfectly add up.

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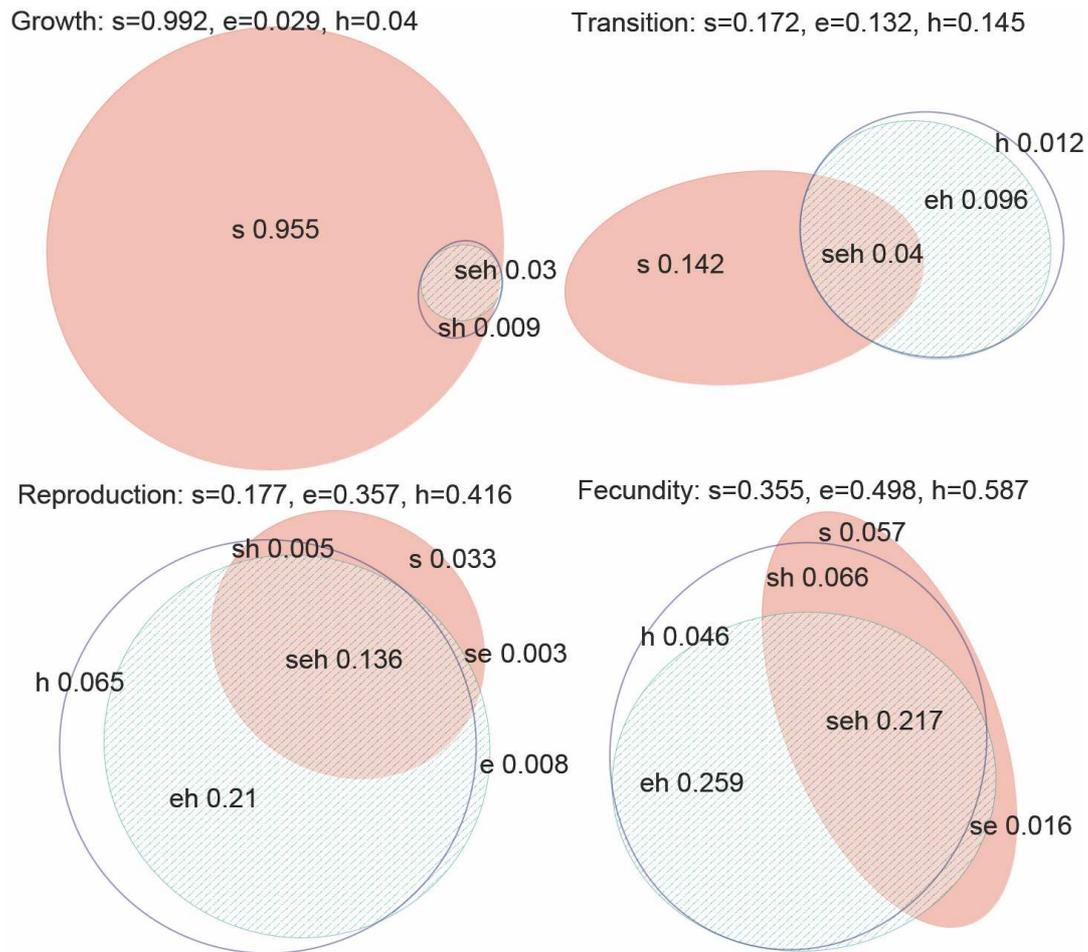
Fig. 4. Overlapping explanatory power of starting body size (s), current environment (e), and past environment (h). Each panel contains an area-proportional Venn diagram (Micallef & Rodgers 2014) of explanatory power for a demographic response: final body size after 24 hours (Growth), probability of initiating stage transition (Transition), probability of reproducing (Reproduction), and Fecundity. Areas of the ellipses within a panel represent the proportion of null deviance explained by models with one of the explanatory variables. Subareas, designated with letters and quantities, represent explanatory power attributable to one, two, or three of the explanatory variables due to interdependence of the variables. Labels of zero areas were omitted. The total explanatory power of a component is the sum of the subareas, noted at the top of each panel. See Appendix S4 for calculations.

Discussion

Predicting life-history and population responses to changing environments has long been the focus of population ecologists (e.g., Williams 1966). Trait-based demographic models have highlighted the strength of including state variables such as body size to understand and predict population dynamics (Easterling et al. 2000; Caswell 2001; Ozgul et al. 2010). However, these models rely on the assumption that chosen state variables are a good proxy of the effects of the environment on demographic rates. Here, we challenged this assumption by investigating how well body size represented the integrated effects of environmental sequences by quantifying the dependence of demographic responses on individual body size, current environment, and past environment in a well-studied soil mite experimental system. To do so, we used a quantitative method for decomposing the effects of multicollinear explanatory variables, extended to allow for nonlinear relationships and graphically presented using area-proportional Venn diagrams.

The past environment explanatory variable was designed to pick up population level patterns after controlling for the effects of body size and the current environment. This should include delayed effects from past environments experienced by individuals and their mothers. Although not all of these splines were significantly different from zero, examining the patterns is useful for generating hypotheses to be investigated with more detailed data and more mechanistic models. Here, we demonstrate this with the soil mite model system because many mechanisms are already known.

We found that the total explanatory power of body size and the amount of environmental effects encompassed by body size strongly varies among demographic responses. Although this general result is already known, we demonstrate that the

428   strength of our method lies in its flexibility, making it easily applicable to data limited

429   situations, which are common in ecology. It is a useful tool to identify patterns and

430   test for the ability of state variables to encompass environmental effects on

431   demographic and life-history responses that can later be explored with more

432   mechanistic experiments.

433

434   ***The case of soil mite populations in drastically different environments***

435   Developmental rates depended more on body size than past or current

436   environments, and reproductive rates were more strongly affected by the

437   environments than by body size. For final body size (i.e., growth), the effect of the

438   environment was almost fully encompassed by starting body size, while for other

439   demographic responses, body size only accounted for a quarter to half of the

440   environmental explanatory power. These results demonstrate that demographic

441   responses differed in their sensitivity to the environment and the proportion of

442   environmental effects transmitted through an individual's body size (e.g., Ozgul et al.

443   2012; Ozgul et al. 2010).

444   We expected to find significant effects of the past environment on

445   developmental rates because previous work demonstrated that soil mites can exhibit

446   strong delayed life-history effects in response to densities and food regimes

447   (Beckerman et al. 2003; Plaistow et al. 2006; Cameron et al. 2013). However, in our

448   experiment, these effects were almost completely overlapped by the current

449   environment. Previous experiments, that found effects of past environments on

450   development rates utilized very different food levels (high *vs* low food for individuals,

451   or stochastically varying food with high frequency for populations) (Beckerman et al.

452   2003; Plaistow et al. 2006; Cameron et al. 2013). In the current experiment, on a daily

453   basis, food and population density was strongly autocorrelated, meaning that current

454   and previous environments were on average similar across the experiments. Under

455   these conditions, the impact of current conditions on developmental rates was very

456   strong. One exception was in the fluctuating environment where, after controlling for

457   the effects of body size and the current environment, developmental rates declined

458   over time (supplementary Fig. S1). This could be due to delayed density dependence

459   driven by the high densities during the first 3 weeks of the experiments in response to

460   the first peak of food availability (Beckerman et al 2003, Benton et al 2005). Cohorts

461   of juveniles born under high densities grow and develop slowly and can only recruit

462   when competition for food is very low (Benton et al 2005). In the fluctuating

463   treatment, competition for food was very low at the beginning of the second peak of

464   food availability, when density was low, leading to a peak of fecundity and generating

465   a new cohort of juveniles born under even higher densities.

466   As expected, our results indicate that females adjusted their reproductive effort

467   according to their environment more than their current body condition (Fig. 4).

468   Reproduction increased with food availability, which was especially evident in the

469   fluctuating environment where a ten-fold rise in reproduction coincided with a spike

470   in food supply (Figs 2 and 3). For both reproductive rates, the explanatory power of

471   the environment not encompassed by body size was substantial (Fig. 4). Under these

472   experimental conditions, female soil mites were on the income breeding end of the

473   income to capital breeding life-history continuum, relying more on current income

474   than on stored resources for reproduction (Stearns 1989). However, we know that

475   under conditions where food differs radically between different parts of the life-

476   history, females raised in low food environments are lower quality and when given

477   excess food as adults are much less fecund than females raised in high food

478 environments (Beckerman, Benton et al. 2003). It is possible that the duration of our

479 fluctuating food experiment was not long enough to observe the effects of this.

480   We hypothesized in Fig. 1 that the past environment can affect demography

481 via the individual's state. We can observe this as an overlap between the explanatory

482 power of body size and the past environment. Interestingly, fecundity showed

483 substantial overlap between these two components. So a portion of the effects of the

484 past environment experienced by a female and her ancestors (effects we know exist in

485 this model organism) were integrated into body size.

486   After accounting for the effects of body size and current environment, the

487 gradually declining environment further reduced both reproductive rates. Also, the

488 past environment had 6% non-overlapping explanatory power. Together, these results

489 support previous findings that females adjust their reproduction through a

490 combination of evolutionary, plastic, and maternal effects in addition to their current

491 environment and condition (e.g., Plaistow et al. 2007; Benton and Plaistow 2008,

492 Cameron et al 2013).

493 ***Unexplained demographic rates in the soil mite case study***

494   Observed daily survival of individuals was independent of environments and

495 body size and may have been artificially high due to reduced density dependent

496 effects during the 24h of sampling. Maternal effects on egg size were not observed in

497 this experiment, but effects may have been transmitted through unobserved pathways

498 such as epigenetics (Youngson & Whitelaw 2008) or nutrient investment (Benton et

499 al. 2008). Transition rates only responded to the environment with marginal

500 significance. Although our experimental design did not allow for collection of further

501 data, the estimation of some of the vital rates can be improved by increasing the

502 sample sizes in future experiments (Fig. 3).

503

504   ***General applicability***

505   The soil mite *S. berlesei* is an attractive model system because much is known

506   about the potential interplay between current and past environments in determining

507   phenotypic variation (Beckerman *et al.* 2003; Plaistow *et al.* 2006; 2007); yet a

508   critical conclusion from the detailed work on individuals under controlled conditions

509   is that the interaction between current and past environments to determine the

510   phenotype is itself highly plastic. The purpose of this investigation was not to develop

511   a mechanistic understanding of an already well-studied system. Instead, this new

512   variance decomposition method is useful because it is a way of generating an overall

513   picture across a range of environments, of the average interplay between historical

514   and current drivers of phenotypic dynamics.

515   More generally, this method is useful for examining the shared and unique

516   contributions in multiple regression beyond demographic studies, including linear and

517   generalized linear regression. Researchers often wonder which explanatory variables

518   have the greatest influence on their responses – a complicated issue when there is

519   multicollinearity among explanatory variables (Graham 2003). The method described

520   by Ip (2001) and used here for intuitively visualizing the shared explanatory power

521   and interdependence of variables has not yet been adopted by the ecological literature.

522   Here we have expanded upon this method by applying it to nonlinear regression using

523   GAMs rather than linear regression and presenting the results using area-proportional

524   Venn diagrams (Micallef & Rodgers 2014). We propose this method as a technique

525   complementary to those discussed by Graham (2003), including principal components

526   regression, structural equation modeling, and residual and sequential regression.

527   Future work could extend this method further to include confidence intervals

528   estimated by bootstrapping.

529   In demographic studies, there are more mechanistic ways of quantifying the

530   effects of the environment and individual states on life-history processes and

531   population dynamics than our method. More mechanistic methods will lead to

532   stronger inference and the ability to make predictions. These include physiologically

533   structured population models which characterize individuals based on multiple

534   physiological traits such as their size, age, stage, and energy reserves (de Roos 1997).

535   They also include mechanisms such as the consumption and digestion of resources.

536   These models require either data detailed enough to parameterize or *a priori*

537   assumptions about the underlying physiological mechanisms. As is the case in most

538   experimental and wildlife population studies, we did not have such detailed data

539   available in this study. However, our non-mechanistic model has the strength of being

540   flexible enough to apply in these data-limited situations and will be useful for

541   identifying patterns and generating hypotheses that can later be explored with more

542   mechanistic models and experiments with more detailed data collection.

543   The demographic method presented here can be applied to any dataset in

544   which an individual state variable, individual fates, and relevant environmental

545   covariates are available for a population in a variable environment, including data

546   from wild plant and animal populations e.g., St John's wort (Buckley, Briese & Rees

547   2003); Soay sheep (Ozgul et al. 2009); yellow-bellied marmots (Ozgul et al. 2010).

548   When sufficient data are available to develop mechanistic demographic models, the

549   assumption that the state variables chosen are good proxies of the environmental

550   effects on phenotypic traits should be tested. If, as in our study, the state variables

551   only encompass a small portion of the effect of the environment, then additional

552 environmental variables may need to be measured and included as predictors. Several

553 IPMs (e.g. Ozgul et al 2012, Coulson 2011) and physiologically structured population

554 models (e.g., Persson & de Roos 2006; Le Bourlot, Tully & Claessen 2014) accounted

555 for current environmental effects on life history and demography. Also these types of

556 models can implicitly account for delayed life-history effects because the past

557 environment can affect the current state of individuals and thus their life-history

558 trajectory (de Roos et al. 2003). However, an explicit consideration of the past

559 environment on demographic responses is so far missing, mainly due to the difficulty

560 of mechanistically modeling delayed life-history effects such as delayed density

561 dependence (Beckerman *et al.* 2003), and this is one of the main challenges left to be

562 achieved to improve the predictions of mechanistic demographic models.

563 Overall, body size and environmental variation are simply variables that were

564 convenient for answering the bigger question of how good is an easily observable,

565 individual state variable as a proxy for the nutritional effects of environments in a

566 population model. A comparative study using the approach presented here could offer

567 further refinement of our understanding of what kinds of organisms (e.g., capital vs.

568 income breeders) and patterns of environmental variations (e.g., magnitude and

569 temporal frequency of variation relative to generation time) are most likely to be

570 associated with a complex and limited ability of a single individual state variable to

571 predict demographic rates.

572 **Data Accessibility**

575

576 **Acknowledgements**

582

Supporting Information

584 The following Supporting Information is available for this article online

585 Appendix S1: Details of Lab Experiments

586 Appendix S2: Density Calculations

587 Appendix S3: Model Selection and Full GAMM (R Code with Output)

588 Appendix S4: Decomposing Explanatory Power and Drawing Euler Diagrams (R

589 Code with Output)

590 Appendix S5: Full GAM Fits and Splines (R Code with Output)

591 Figure S1: Effects of Past Environment

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