



HAL
open science

Adaptational lags during periods of environmental change

Tom JM Van Dooren

► **To cite this version:**

| Tom JM Van Dooren. Adaptational lags during periods of environmental change. 2022. hal-03852217

HAL Id: hal-03852217

<https://hal.science/hal-03852217>

Preprint submitted on 14 Nov 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17

Adaptational lags during periods of environmental change

Tom J. M. Van Dooren

CNRS - UMR 7618 Institute of Ecology and Environmental Sciences (iEES) Paris, Sorbonne

University, Case 237, 4 place Jussieu, 75005 Paris, France

tvdooren@gmail.com

Version: November 18, 2021

Keywords: Adaptation, adaptive control, climate change, evolutionary ecology, maladaptation, invasion analysis, pest management.

Word Count: 200 (Abstract), 6360 (Main text)

Figures: 7; Tables: 0; Text Boxes: 0

References: 89

18 **Abstract**

19 Effects of climate change can be handled by means of mitigation and adaptation. In the
20 biological sciences, adaptations are solutions which evolved when organisms needed to
21 match an ecological challenge. Based on Adaptive Dynamics theory, a definition is proposed
22 of adapted states and adaptational lags applicable during periods with environmental change
23 of any speed. Adaptation can thus be studied when it emerges from complex eco-evolutionary
24 processes or when targets for adaptation are not defined a priori. The approach is exemplified
25 with a model for delayed germination in an annual plant. Plasticity and maternal effects are
26 often presumed to be adaptive and added to the model to investigate lags in these modes of
27 trait determination. Adaptational lags can change sign and to understand their dynamics,
28 effects of trait space boundaries and characteristics of years with large numbers of recruits
29 had to be considered. Adaptational lags can be crucial elements of adaptive control strategies
30 for managed ecosystems. To demonstrate their practical relevance, examples from pest
31 management show that evolutionary adaptation has been used to infer targets of control.
32 Adaptational lags then serve as measures of the distance to the control target and become
33 integral elements of strategies for adaptive pest population management.

34

35 Introduction

36

37 Climate change generates massive challenges to our societies. Other species will show a
38 range of responses to environmental change (Newman et al. 2011), and these can be to our
39 own advantage or not. Initially, human policy to deal with climate change mostly focused on
40 mitigating our interactions with the environment (Schipper 2006), by reducing the speed and
41 magnitude of change or by dampening the effects of environmental changes. However,
42 awareness has increased that human adaptation is necessary, merits attention and that it
43 interacts with mitigation (Kane & Shogren 2000).

44 In biology, adaptation is a term which predates the development of evolutionary biology
45 (Amundson 1996). It is not equivalent to the presence of an evolutionary response. Walsh and
46 Lynch (2018) for example, a reference work on selection and evolutionary responses, hardly
47 use the term and equate "adaptive" to "beneficial". Fisher (1930) stated that adaptation
48 concerns assessing the conformity of an organismal phenotype to an adapted phenotype
49 determined from an imagined comparison of several potential environments and phenotypes.
50 In this view, adaptation is not merely a description of an actual evolutionary process, but an
51 investigation of the conformity of phenotypes with predictions obtained from considering a
52 wider range of environments and phenotypes. Adaptation is believed to be important for the
53 survival of populations, but more recent modelling also found the opposite: evolutionary
54 suicide can occur when populations adapt (Gyllenberg & Parvinen 2001). Above all,
55 assuming adaptation helps formulating and testing hypotheses. When we assume perfect
56 adaptation to arrive at sharp predictions, this leads to hypotheses which are generally
57 falsifiable.

58 In the context of human climate change responses, "adaptation" has become reframed over
59 the years from the eco-evolutionary meaning applicable to any organism into a policy
60 response (Schipper 2006); from describing a dynamics of (autonomously) evolving systems
61 into a concept more in line with human adaptive systems control towards a given target
62 (Tyukin 2011). This trend complicates the integration of evolutionary adaptation by
63 biological systems into adaptation policies. A revised or re-clarified notion of evolutionary
64 adaptation to climate change could address this.

65 The consensus is that most organisms currently respond to climate change with phenotypic
66 plasticity (Gienapp & Merilä 2018), i.e., developmental changes that are often believed to be
67 adaptive in response to altered environmental conditions (Merilä & Hendry 2014). The
68 alternative which is usually considered, evolution and adaptation by changes in genotype
69 frequencies, requires the presence of heritable genetic variation for the involved traits.
70 Therefore, most studies looking for ongoing adaptation in natural systems focused on
71 demonstrating that phenotypic responses were due to changes in gene frequencies (Gienapp
72 & Merilä 2018). However, evolutionary responses don't need to move systematically in the
73 direction where we expect that adaptation would be fastest or even where phenotypic changes
74 are adaptive (Leimar 2009, Teplitsky et al. 2014). On top of that, the target of adaptation can
75 move over time. This has usually been modelled by making the target an explicit time-
76 dependent parameter (Lynch et al 1991), i.e., as if the changes in the target of adaptation are
77 highly predictable or known. For situations where the targets of adaptation need to emerge
78 from a study of eco-evolutionary processes across environments and phenotypes, it is unclear
79 how to predict them precisely or how to capture their time patterns during climate change
80 with a simple function.

81

82 Below, I propose a strategy to determine adaptations during climate change. Essential to the
83 proposal is that most of the concepts applied were already developed in so-called Adaptive
84 Dynamics approximations (Metz et al. 1996, Geritz et al. 1998) also known as evolutionary
85 invasion analysis (Otto & Day 2007). A classical model for delayed germination in annual
86 plants with a seed bank (Cohen 1966, Ellner 1997) is used as an example of an analysis of
87 evolutionary adaptation and adaptational lags during environmental change. I then attempt to
88 characterize the combination of evolutionary adaptation and adaptive control and give
89 examples of managed ecosystems where predictions of evolutionary adaptation are relevant
90 for their control and where adaptational lags are measures of the distance from the control
91 target.

92

93 A general approach to determine adaptations during environmental change

94

95 Organisms adapt to a range or set of situations encountered, hence adaptation always
96 accounts for environmental variability (Fisher 1930, Levins 1968). When adapted states are
97 determined, it is often assumed that these variable environments don't show any lasting trends
98 over time and occur with fixed probabilities. The time series of the variables describing them
99 are then stationary (Tuljapurkar 1986, Metz et al. 1992, Coulson 2020). On the other hand,
100 projections of environmental variables in periods of climate change involve systematically
101 changing temperature and rainfall averages (Collins et al. 2013). We describe these
102 environmental changes as time-dependent changes in the parameters of probability
103 distributions of environmental variables (Figure 1A). These parameters determine how the
104 mean and dispersion of environmental variables change over time. We usually assume that
105 they change gradually within the same probability distribution family. The actual

106 environmental history observed will thus be a realization from a stochastic process with time-
107 dependent parameters (Fig. 1B). Each probability distribution per time point, say year, is
108 specified by a set of parameter values and this distribution of environmental states represents
109 a collection of situations to which organisms can adapt. For each given set of parameter
110 values of the environment, we can therefore determine what the adaptative phenotypes are
111 (Fig. 1C). The result for a period of environmental change is then a time series of adapted
112 stated determined using a time series of parameters of the distributions of environmental
113 variables (Fig. 1C). Adapted states can be determined using Adaptive Dynamics
114 approximations (Metz et al. 1996, see also Abrams 2005, Methods Supplement), which
115 assume separated ecological and evolutionary timescales and simple genetics in order to
116 focus the analysis on the relationship between ecological environments and phenotypes
117 (Dieckmann 1997). Adaptive Dynamics approximations have been used to generate new
118 hypotheses, to predict evolutionary outcomes driven by ecological interactions (Dieckmann
119 1997) and to develop management strategies, for example for the management of epidemics
120 during climate change (Sabelis and Metz 2002). For evolving populations where genotypes
121 are not necessarily at an adapted state all the time, we can determine how far each individual
122 in the population is from a predicted adapted state at each given point in time (Fig. 1D). For
123 example, for an individual with a scalar phenotypic trait x and an adapted phenotypic state at
124 time t which is x_t^* , the adaptational lag is $x_t^* - x$.

125

126 Adaptational lags in delayed germination

127

128 Several aspects of the determination of adaptational lags can be illustrated using a well-
129 known model for the demography of an annual plant (Cohen 1966, Bulmer 1984). This model

130 tracks densities (number per unit of area) of individual seeds of a single genotype in a seed
131 bank across years, each time censused right after seed production. With N_t the number of
132 seeds at the end of the season in year t and assuming large population sizes such that
133 demographic stochasticity can be ignored, the number of seeds one year later is

134

$$135 \quad N_{t+1} = (pf_t(pN_t) + (1 - p)s)N_t \quad (\text{Eqn. 1})$$

136

137 with p their probability of germination, s the survival probability in the seed bank across one
138 year and f_t the per capita number of seeds contributed to the seed bank by a germinated seed
139 in year t . The number of seeds recruited is stochastic and density-dependent. It depends on
140 the total number germinated pN_t . Across successive years the population grows in a
141 multiplicative manner. The population density $N_{t+\tau}$ after an interval of τ years is:

142

$$143 \quad N_{t+\tau} = \prod_{i=t}^{t+\tau-1} (pf_i(pN_i) + (1 - p)s) N_t \quad (\text{Eqn. 2a})$$

144

145 This is one of the simplest and best-known structured population models (during the growing
146 season ungerminated seeds and plants are simultaneously present). It is the prime example
147 used to demonstrate that adaptation is not always towards the fastest life history with the
148 largest number of offspring (Stearns 2000).

149 This model is easily modified to allow for the occurrence of many genotypes in a population.
150 We can then use simple forward simulations to investigate how selection gradually changes
151 population composition among genotypes with different phenotypic traits. A common idea is
152 that adapted states emerge when genotype frequencies equilibrate, for example by fixation of

153 one genotype among several already present in a population. However, evolutionary invasion
154 analysis (Adaptive Dynamics, Metz et al. 1996, Geritz et al. 1998, Methods Supplement)
155 finds adapted states differently and also considers genotypes not yet present in a population.
156 It values resistance to invasion and we therefore need to determine which genotypes can
157 invade so-called resident populations (established populations, with stationary fluctuations or
158 equilibria in their densities). More importantly, we must determine which resident population
159 compositions (1) can evolve by means of a trait substitution sequence fuelled by mutations
160 and (2) additionally have the property that once their state attained, they cannot be invaded by
161 genotypes with similar germination phenotypes. Hence, they can persist in a longer-term
162 evolutionary sense and are considered to be adapted to the ecological circumstances. In order
163 to determine these states, invasion fitness (Metz et al. 1992) is used to assess the evolutionary
164 stability (convergence stability and invasibility, see Methods Supplement) of resident
165 population states. Here we assume that only a single resident phenotype affects the success of
166 rare genotypes, and that the process characterising the resident state and the fluctuations in
167 demographic parameters is stochastic, stationary and ergodic (Rand et al. 1994, Ferrière &
168 Gatto 1995, Ripa & Dieckmann 2013) such that the precise starting point t becomes
169 irrelevant. For a single resident genotype with the germination trait value p as above, and a
170 rare mutant genotype with a different germination probability p' , invasion fitness equals

171

$$172 \quad \rho(p', p) = \lim_{\tau \rightarrow \infty} \frac{1}{\tau} \ln \left(\prod_{t=1}^{\tau} (p' f_t(p N_t(p)) + (1 - p') s) \right) \quad (\text{Eqn. 2b})$$

173

174 This expression assumes clonal inheritance and that the number of seeds recruited varies
175 between years, even for an identical amount of germinated seeds. $N_t(p)$ is the number of
176 seeds in the seed bank at time t , with the resident genotype having phenotype p . By

177 extension, when survival in the seed bank is also allowed to be time-dependent, we get the
178 invasion fitness

179

$$180 \quad \rho(p', p) = \lim_{\tau \rightarrow \infty} \frac{1}{\tau} \ln \left(\prod_{t=1}^{\tau} (p' f_t(p N_t(p)) + (1 - p') s_t) \right) \quad (\text{Eqn. 2c})$$

181

182 Invasion fitness is directly related to the establishment probability of a new strategy in a given
183 stationary environment with a resident population already present (Haldane 1927, Ripa &
184 Dieckmann 2013).

185 Ellner (1997) contains an insightful presentation of results which exploit a partial derivative
186 used to determine whether delayed germination, i.e., a germination probability below one, can

187 invade. This derivative is $\left. \frac{\partial}{\partial p'} \rho(p', p) \right|_{p'=p=1}$ (Eqn. 3a). From its sign we know whether selection

188 favours mutant germination probabilities smaller than the resident germination probability,

189 which is equal to one. When it is positive, mutant germination probabilities below one are

190 disfavoured and it is adaptive to always germinate. When it is negative, we can expect adapted

191 states with a germination probability below one, i.e., the establishment of a seed bank where

192 seeds remain one or several seasons. A crucial insight in evolutionary ecology was that such

193 probabilities can only be adaptive when life history parameters fluctuate. In these cases, we

194 need to determine the intermediate germination probability values that are so-called

195 evolutionarily singular points (ESS, Geritz et al. 1998, represented here as p^*). For resident

196 populations with a single genotype, these are defined by the condition that the fitness derivative

197 $\left. \frac{\partial}{\partial p'} \rho(p', p) \right|_{p'=p}$ (Eqn. 3b) locally vanishes. There is no directional selection driving traits away

198 from an ESS germination probability p^* . Local second-order partial derivatives determine

199 further requirements for adapted states: they need to be convergence stable, hence reachable,

200 and non-invasible (see Methods). When adapted states consist of a single genotype, they are

201 called CSS (Continuously Stable Strategy, Eshel 1983). There is no analytical expression for
202 the adaptations p^* . Their dependence on environmental parameters needs to be determined from
203 numerical analysis.

204

205 **Continuation.** If we assume that years can be good with probability q and otherwise bad, that
206 the total recruitment to the seed bank equals K per unit of area in a good year and k in a bad
207 year, then (Eqn. 3a) can be worked out. This is an exercise in Elmer (1997) which I don't want
208 to spoil, but the result is summarized in Figure two. For environments with fluctuations
209 between good and bad years that occur according a Bernoulli distribution with probability q , it
210 is adaptive to delay germination when recruitment parameters K and k of good and bad years
211 differ sufficiently, when survival in the seed bank s is high and when probability q is
212 intermediate (Fig. 2). Now arises the question what this tells us on adaptation when the
213 environment changes in a non-stationary manner, for example when s and q would gradually
214 change between years. A first line of attack could be to assume "continuation" (Kuznetsov
215 2004), namely that the population will always be able to attain the adapted state very rapidly
216 and that gradual environmental changes provoke gradually changing population states that are
217 each predicted well by the adapted state for the environment of that year (e.g., Ferrière &
218 Legendre 2013). For the example model here, the state of the environment in a specific year is
219 given by the four parameters s , q , K and k . Three examples of continuation trajectories are
220 given in Fig. 2. The first two are for gradual changes in survival and the probability that years
221 are good, with contrasting patterns. It can be first adaptive to have a seed bank when survival
222 in the seed bank is still high, and when survival has decreased, to always germinate. The
223 opposite route can also be adaptive: first always germinate, but when good years occur less
224 often and survival gradually decreases, it can become adaptive to develop a seed bank. If
225 recruitment parameters gradually change as well, differences between good and bad years

226 could first become smaller and subsequently larger again. This scenario is elaborated below.
227 However, Fig. 2 already shows that in such cases having a seed bank can first be adaptive, then
228 it can become adaptive to always germinate, followed by a second period where delayed
229 germination is adaptive.

230

231 **Adaptational lag.** However, it is a strong assumption to make that populations would be well
232 adapted all the time when the environment changes. For an individual with a genotypically
233 determined germination probability p and an adapted state at time t which is p_t^* the adaptational
234 lag equals the difference $p_t^* - p$. It is positive when the adapted state is a larger germination
235 probability than the one for this individual, negative when it is smaller. The average
236 adaptational lag in a population is the average of this quantity among the individuals present at
237 a given census point. Even with high levels of standing additive genetic variation, non-zero
238 average lags are predicted to occur when adapted states are boundary values and genetic
239 variation remains present due to mutation pressure or segregation. In other cases, average
240 adaptational lags are immediately generated when distributions of standing variation are
241 asymmetric around an adapted state, when selection fluctuates over time or when organisms
242 have complex life histories inherently generating lags in selection responses.

243

244 From now on, think of good and bad years as referring to initially warm and cool years
245 (Figure 3), such that q is the probability of a warm year, K is the total recruitment in a warm
246 year and k in a cold year. To explore potential time trajectories of adaptational lags, we
247 investigate a scenario where the probability q of a relatively warm year gradually changes. At
248 the same time, and mimicking an effect where all years become gradually warmer, K and k
249 change in values over time (as in example C in Fig.2). When warm years become hot, K will

250 decrease. At the same time, cold years gradually improve such that recruitment k increases.
251 Survival probability in the seed bank gradually decreases, for example due to gradually
252 increasing soil temperatures (Ooij 2012). This scenario has an intermittent period where an
253 egg bank is not adaptive (Fig. 3). I determined the adapted state for each year in the scenario
254 and simulated a population of selfing annual plants with a substantial mutation rate per
255 individual (0.01 per individual, Methods, Fig. 3). The lag remains substantial even with this
256 large continual input of new mutational variation. It is not the case that the population
257 equilibrates at a constant lag distance from the CSS adaptive state as in many other models
258 (Kopp and Matuszewski 2015). While the CSS moves towards a boundary trait value,
259 remains there and subsequently moves away from it, the adaptational lag changes sign (Fig.
260 3). Mutational pressure on the germination probability near $p = 1$, makes it that the seed bank
261 never completely disappears, even when that would be adaptive. This opposes the idea that
262 increased amounts of heritable genetic variation will inherently lead to improved adaptation.

263

264 **Phenotypic plasticity and parental effects.** Additional relevant components of trait
265 determination were added to this model, by allowing germination to depend on an
266 environmental cue perceived by a plant embryo (phenotypic plasticity) or by the mother plant
267 (a parental effect). Botero et al. (2015) already investigated environmental changes that
268 demanded restructuring of phenotype determination, but did not work out any adaptational
269 lags. For the annual plant example, the reaction norm specification becomes as follows (Eqn.
270 4):

271

$$272 \quad p_t(g, b, m, M) = \text{invlogit}(g + bE_t + mM) \quad (\text{Eqn. 4})$$

273

274 where invlogit denotes the inverse-logit function, $\text{invlogit}(x) = e^x / (1 + e^x)$.

275 Germination probability p_t now depends in a non-linear manner on a genotypic component of
276 an individual g , on an environmental cue E_t and on a maternal cue M stored by that
277 individual. The maternal and the environmental cues are weighed by specific factors, b and m
278 respectively. These factors and the genotypic component g can evolve by mutations and
279 selection. For the maternal cue, it is assumed that it is a marker left by a mother on an
280 offspring individual, that it can have two states and that it is fixed and stored by the
281 individual in the same state for the rest of its life. I assume that only part of the individuals
282 are responsive to a cue for a good year or get the right cue from their parent. In the
283 simulations presented, 70% of individuals respond to a warm year (warm year $E_t = 1$, cool
284 year $E_t = 0$). In a warm year, 70% of individuals get the maternal cue $M = 1$, the others get M
285 $= 0$. In a cool year, 70% of individuals get $M = 0$, the others $M = 1$. Because of the inverse-
286 logit transformation, trait values g , b , m can range from minus to plus infinity, while the
287 individual germination probabilities remain constrained between zero and one. Note that each
288 individual has five state variables, of which three are evolving and adapting via mutations
289 and selection. What is also important is that with maternal effects, the seed bank contains
290 individuals in different states, namely those that carry maternal cue $M = 0$ and the others
291 carrying $M = 1$.

292 If we rerun the environmental scenario of Fig. 3 and determine the adapted CSS states per
293 year for the three trait components, then adapted states for the plasticity weight are generally
294 extreme (Figure 4A), while a pattern similar to Fig. 3 is observed for the genotypic value,
295 with a shorter time interval where bet-hedging is not adaptive. The adaptive maternal effect
296 weight is often opposite in sign to the plasticity weight. In fact, in part of the time interval

297 where bet-hedging is not adaptive, all three traits jointly have their adapted states at
298 maximum values. The eco-evolutionary dynamics of the simulated population shows a rather
299 different pattern (Fig. 4B): the maximum average genotypic value g in the simulation is only
300 reached when bet-hedging is already adaptive again. Note that the genotypic value g slightly
301 increases further in the second time interval where bet-hedging is adaptive, even when its
302 adaptational lag has already changed sign. The plasticity weight also evolves for part of the
303 years in a direction opposite from where the adapted state is for these years. When adapted
304 states are not determined by means of trait substitution sequences but approximated by
305 simulated evolution in the environment characteristic for a year, the mutational pressures near
306 trait boundaries and standing amounts of variation have effects on the outcome (Fig. 4D).
307 Approximate adapted states on trait space boundaries are much less observed than in Fig. 4A,
308 and when a trait such as g has not evolved to the boundary, the parental effect for example
309 seems to converge to a different value as well. This demonstrates that approximating adapted
310 states by evolutionary simulations with a continual input of a lot of genetic variation is
311 imprecise.

312

313 **Multivariate lags?** When individual phenotypes depend on several underlying component
314 traits, we can calculate adaptational lags in different ways. It is straightforward to represent
315 lags by vectors in a multivariate trait space, but there is no obvious standardization of each
316 axis to make different trait components directly comparable. As Fisher (1930) focused on
317 organismal individual phenotypes, we can focus on the germination phenotypes and
318 substitute the evolving components of individuals in the actual population (g, b, m) by the
319 values at the adapted state (g^*, b^*, m^*), leaving the non-evolving state variables of each
320 individual untouched (E_t and M). The adaptational lag of an individual then becomes

321

$$322 \quad \text{invlogit}(g^* + b^*E_t + m^*M) - \text{invlogit}(g + bE_t + mM) \quad (\text{Eqn. 5})$$

323

324 Note that a study of lags could provide evidence of genetic conflicts: selective pressures on
325 heritable phenotype components evidenced by speeds of trait change, can change in
326 dependence on the magnitude of the lag in others. Next to that, the average lags in the more
327 elaborate model version with evolving genotypic values, plasticity and parental effects show
328 non-trivial trajectories (Fig. 4E), with overshoots around an adapted state and average lag
329 trajectories resembling those of a stable focus in other dynamical systems (Kuznetsov 2004).

330 Adaptational lag averages in the population can be calculated for warm and cool years
331 separately, and this demonstrates (Fig. 4F) that in the first half of the simulation, lags become
332 smallest in warm years, when these occur more often than cool years. In the second half, the
333 lags become smallest in cool years. This suggests that evolution reduces adaptational lags in
334 the most common environments fastest.

335

336 **Responsiveness to selection and establishment probabilities.** The average adaptational lag
337 can be useful as a measure of the lag in other population statistics. For example, many
338 evolutionary models find the maximum population density at the adaptive state and the
339 adaptational lag then represents the distance from that situation. In the model example it is
340 less obvious what the practical relevance of the lag might be and this requires further
341 exploration. Such a simple exploration was carried out for the model version with plasticity
342 and maternal effects.

343 As a measure of turnover indicating how fast a population can respond to selection on
344 juvenile and adult traits, I calculated per year which fraction of the seed bank at the end of the
345 reproductive season was recruited in that same year. Figure four shows that it relates well to
346 the average germination probability in a population (Fig. 5A), but that the dependence on the
347 adaptational lag is complex and gives the lag little predictive value for this measure of
348 responsiveness to selection (Fig. 5B). Peischl and Kirkpatrick (2012) found that
349 establishment probabilities of populations in arbitrarily changing environments depend on the
350 time pattern of fluctuations and that the per capita number of offspring of a new strategy in its
351 first year has the largest weight on the outcome. When the log per capita number of offspring
352 of germinated seeds is estimated, this relates poorly to the average germination probability in
353 the population (Fig. 5C), while the adaptational lag predicts it to some extent. A lowess
354 regression with a restricted span of the smoother shows a peak near zero adaptational lag
355 (Fig. 5D). When mutants appear with effects in the juvenile or adult stage that are slightly
356 advantageous, they will have larger probabilities to get established when the adaptational lag
357 for germination probability in the population is near zero. This adaptational lag can thus be
358 seen as a measure of general adaptability. In Fig. 4F we observed that the lag was smallest in
359 the cooler years near the end of the simulation. Upon inspection, it turns out that the lag is
360 smallest when the total number of recruits per year is largest. This requires, however,
361 phenotypic plasticity of the germination probability. Plastic strategies can exploit the good
362 years to outcompete other strategies more easily by germinating with probability one and
363 don't need to implement a compromise between good and bad years because of lack of
364 information.

365

366 Evolutionary Adaptation and Adaptive Control

367

368 There have been repeated calls for an increased use of control theory in ecology, where the
369 most successful applications thus far were in agriculture (Loehle 2006). The objective of
370 control theory is to develop control actions (a "controller") for dynamical systems such that
371 their outputs follow a desired pattern. Several notions of adaptive control exist (Tyukin
372 2011), while there is no mention of adaptive control in the review by Loehle (2006) on
373 control theory in ecology. According Walters and Hilborn (1978), adaptive control refers to
374 situations where the best control action of a dynamical system must be established through
375 sequential reassessment of system states and dynamic relationships. This generally requires
376 tuning the controller (Tyukin 2011) in dependence on the state of the environment and the
377 responses of the system. In addition, adaptive control often uses a model-based reference
378 response (MRAC, model reference adaptive control, Frank 2018), and this model can also be
379 updated as part of the tuning or when new knowledge becomes available. MRAC can involve
380 actions with the intention of improving knowledge on the system. Such actions can trade-off
381 or conflict with adaptively managing other targets (Walters & Hilborn 1978) and make
382 adaptive management or control more prone to implementation failure (Allen & Gunderson
383 2011). The implementation of adaptive control is generally challenging (Anderson &
384 Dehghani 2008). It needs to be determined how concepts of evolutionary adaptation and
385 adaptational lags during climate change relate to adaptive control as defined in control theory
386 and in the context of adaptive management of population dynamical systems.

387 Next to its relevance for the adaptive management of populations, control theory has been
388 used to derive predictions from modelling for phenotypic traits which can vary continually
389 over time (Frank 2019) and are thus examples of phenotypic plasticity or flexible phenotypes.
390 This line of research can be used to illustrate the principles of adaptive control and to situate
391 it relative to evolutionary adaptation, by gradually incrementing the complexity of a series of

392 trait determination models, where the apparent phenotypic traits are examples of system
393 outputs. A simple partitioning of the contributions of genetic and an environmental input is a
394 common representation of the determination of phenotypes (Fig. 6A&B). The environmental
395 input generates predictable phenotypic consequences in the presence of phenotypic plasticity.
396 There is no control of phenotypes here towards a specific target because all inputs are
397 assumed to have additive and linear effects. Models of phenotypic switches do invoke a sort
398 of controller (Fig. 6B, Leimar et al. 2006), which is usually a non-linear function of an
399 underlying liability. Models of phenotypic plasticity which explicitly assume a controller of
400 plasticity or flexibility exist (Fig.6C, Frank 2019), and classical dynamical models of energy
401 allocation can be interpreted in this manner too (Perrin & Sibly 1993). These controls do not
402 have the recurrent tuning by environment and system states characterizing adaptive control.
403 They can assume that the controller is the result of evolutionary adaptation (Frank 2019) but
404 the control in itself can be non-adaptive in the sense of control theory (compare Fig. 6C with
405 Fig. 6D). On the other hand, experimental studies on the control of gaits or bipedal movement
406 envisage elements of adaptive control in locomotor control: Lam et al. (2006) for example
407 explicitly mention that the nervous system uses an internal model for the control of
408 locomotion.

409 Adaptive control could use a model of evolutionary adaptation (Fig. 6E) to generate a model
410 reference and target of control (Fig. 6F). This would integrate evolutionary adaptation and
411 adaptive control, with the adaptational lag providing the distance from the control target or
412 becoming the quantity to control. This raises the question what an adaptive controller will
413 look like in this case and how to assure that it operates safely without divergence from the
414 target or a general crash of an ecological system. Much remains to be developed. However,
415 there are examples where evolutionary modelling of managed ecosystems led to proposals to
416 control adaptational lags.

417

418 Adaptive pest and crop management

419

420 Studies which considered coevolutionary principles in the adaptive management programs of
421 plant diseases in agriculture, tend to focus on minimizing evolution (Zhan et al. 2015).

422 Pathogens at adapted states are generally undesirable in agricultural practises when properties
423 of the agro-ecology lead to the evolutionary minimization of plant resources available to
424 competing pathogens (Lion & Metz 2018), hence maximization of yield losses. Adaptational
425 lags should then be kept maximal or control should be towards increasing diversifying and
426 disruptive selection weakening selection and imposing trade-offs (Zhan et al. 2015).

427 Précigout et al. (2020), for example, studied adaptation of the latent period of a plant
428 pathogen to plant traits which depend on fertilization levels. The analysis demonstrated that
429 adaptive pathogen states minimize the amount of healthy leaf canopy, and that it is therefore
430 desirable to maximize the adaptational lag. Preventing adaptation can occur by reducing
431 selection gradients through generally limiting pathogen growth rates (Carolan et al. 2017).

432 Bargués-Ribera and Gokhale (2020) present an example optimizing cumulative yield in
433 dependence on rotation schemes between cash and cover crops. We also start considering the
434 maintenance of pathogen diversity as a useful strategy, if this limits the evolution of pathogen
435 virulence and reduces average pathogen reproduction per host by increasing host diversity
436 (Dutta et al. 2021). However, if adaptation favours a polymorphism of coexisting strains each
437 specializing on a different host plant, avoiding such adaptive genetic polymorphisms can be
438 crucial in heterogeneous landscapes (Précigout 2018). Alternatively, also in plant crops cases
439 are imaginable where adaptational lags need to be maximized, when plant stages are

440 harvested which occur at their lowest densities in adapted states, for example due to
441 asymmetric competition.

442 It seems easier to imagine examples where adaptational lags in crops should be minimized.
443 Loeuille et al. (2013) use adaptive dynamics modelling to predict consequences of different
444 agricultural practises and landscape designs, presenting an example where adaptation by
445 plants minimizes nutrient loss, therefore maximizes sustainability of the ecosystem.
446 Adaptation of plants is desirable from this point of view, and adaptive management should
447 aim to minimize the adaptational lag in plants even if this does not necessarily occur by
448 natural selection. van den Bosch et al. (2007) were to my knowledge the first to demonstrate
449 that predictions of adapted states have relevance in agricultural systems and made a point of
450 general relevance: the control strategy should be chosen depending on whether adapted states
451 imply increased or reduced crop damage. van den Bosch et al. (2007) modelled the adaptation
452 of virus strains in response to different disease control strategies and assumed that control
453 would lead to zero adaptational lag. Sanitation by roguing came out as a control strategy
454 where virus evolution leads to more favourable adaptive states, because these reduce virus
455 titre in comparison to virus adaptation to other control strategies.

456 Among prospects for future research in modelling plant virus epidemiology, Jeger et al.
457 (2018) pointed to the importance of environmental change, of considering evolution but did
458 not propose to integrate both. In the studies above, the target of control was identified, but it
459 remained unclear whether that control in itself would need to occur in an adaptive manner.
460 These studies all assumed that adaptation occurs in a period without environmental change. I
461 conjecture that when environments change gradually and unpredictably to some extent, most
462 control will need to become adaptive.

463

464 Discussion

465

466 The term "adaptation" links a cluster of concepts which each are at the core of a subject in
467 climate change research. In this paper, *adaptational lag* is introduced in the context of
468 evolutionary adaptation and its integration into adaptive control theory is proposed. Other
469 related concepts, such as adaptability and adaptive capacity are only minimally discussed
470 here (Nelson et al. 2007, Bateson 2017, Siders 2018, Angeler et al. 2019).

471

472 Moving optimum models (Kopp & Matuszewski 2015) generally assume that the adaptive
473 states are optimal phenotypes which follow a prescribed and linear pattern of change. With
474 more involved life histories and selection on different life history components it is known that
475 generally and even without environmental change, fitness is largest for a compromise
476 phenotype which is in many cases not equal to any of the phenotypes maximizing individual
477 life history components (Cotto et al. 2019). Adaptation in complex life histories should be
478 seen in the sense of Levins (1968) where strategies weigh different options they encounter
479 and achieve the best compromise in the face of their constraints. For example, the
480 compromise phenotype of Cotto et al. (2019, their Eqn. 9) then is the adaptive state. When
481 the genetic variance-covariance at the adaptive state would be restricted to what is maintained
482 by selection in the long run, when not assuming linear environmental change in the adapted
483 state or that the adaptational lag equilibrates at a fixed distance from the compromise
484 phenotype, their method would approach the proposal here. Johansson and Jonzén (2012)
485 were the first to consider frequency-dependence within species in their determination of
486 adapted states for bird arrival date. They determined adaptive states but did not consider
487 adaptational lags. Gienapp et al. (2013) inserted adapted states determined for a different

488 model of bird breeding dates as the optimal phenotypes in a standard quantitative genetic
489 model from which adaptational lags were determined. Their study can thus be interpreted as
490 the first where the current approach was implemented.

491 In principle, the approach to determine adaptational lags based on Adaptive Dynamics can be
492 carried out for any ecological system where the dependencies of demography on
493 environmental state (including feedbacks of population state) are specified and where
494 phenotypic trait determination is known or assumed to work in a particular way such that an
495 evolutionary model can be constructed. In the example of the evolution of germination
496 probability in an annual plant, the adapted states were germination probabilities which
497 depended on the scenario of environmental change. Adaptive Dynamics studies have
498 distinguished various types of adapted states, of which Figure seven gives a non-exhaustive
499 overview. Next to adapted states with single genotypes, with plasticity or not, outcomes such
500 as adaptive genetic polymorphisms can occur (Geritz et al. 1998). For these adapted states, it
501 remains to be worked out how to calculate adaptational lags best, but it has already been
502 proposed that in some cases, maladaptation should be the target here (Précigout 2018).

503 Johansson (2008) determined lags for one-, two- and three species systems exploiting a
504 resource distribution. These were calculated with respect to the evolutionarily repelling trait
505 matching the resource with the largest carrying capacity, which is opposite the definition of
506 adaptational lag used here based on attracting adapted states. Evolutionary suicide is another
507 possible outcome of adaptation (Gyllenberg & Parvinen 2001), where the adapted state is
508 extinction. Next to the existence of these qualitatively different outcomes, multiple adapted
509 states can co-occur for one environmental setting such that adaptational lags become
510 multivalued. Further outcomes which are not represented in Fig. 7 are coevolutionary adapted
511 states of several species (Débarre et al. 2014), relevant in the agro-ecological context of

512 plants and pests, and adapted states which are cyclic (Dercole & Rinaldi 2008), with a non-
513 equilibrium attractor of the adaptive dynamics.

514 It was found that adaptational lags can't be removed for boundary adaptive strategies if any
515 non-adaptive genotypic variance remains present, and in general, extreme strategies face a
516 variance load (Lande & Shannon 1996) with any individual phenotypic variance present. If
517 we extend this idea to human socio-economic evolution, climate adaptation strategies which
518 are extreme and therefore boundary strategies, will never be reached as long as variation in
519 our population remains. Beckage et al. (2018) modelled the feedback between human
520 behaviour and projected climate change. Nudging the perceived risk of climate change was
521 proposed as a mitigation policy response, but whether behavioural responses will be adaptive
522 was not considered. In evolutionary ecology, cue perception and associated response
523 plasticity are often studied as adaptations and even if we refuse to compare our own
524 adaptation to an evolutionary response, it might be useful to try to determine the adapted
525 states of what we aim to implement. Despite the differences between evolutionary adaptation
526 and adaptive control, they can be modelled jointly. In the adaptation policy context, clear
527 metrics of adaptation in comparison to mitigation seem to lack (Michaelowa & Stadelmann
528 2018). Using an adaptive control perspective in adaptation policies naturally leads to relevant
529 metrics: they are the distances to the model reference which the controller assesses and uses
530 for its updates. The examples of control and evolutionary adaptation in agro-ecologies can be
531 used to model and determine strategies for adaptive management during environmental
532 change and can lead to strategies for developing appropriate controllers.

533 From the simulation results, it turned out that adaptational lags might be partial predictors of
534 the invasion success of mutants in other life history traits than germination. If we develop our
535 understanding of adaptational lags further, it could be of use in conservation biology and
536 agro-ecology as partial measures of adaptability. For extant populations, would it be possible

537 to estimate adaptational lag and adaptive state approximately with limited modelling? In
538 models with pre-defined adaptive states, the difference between the population average of a
539 trait and its adaptive state is a commonly used measure of the lag (Kopp & Matuszewski
540 2015) and in the vicinity of the adapted state, it can be determined from slope and curvature
541 of fitness surfaces (Estes & Arnold 2007). In the current environment, selection optima can
542 be estimated using data on the dependency of the number of offspring on phenotype, and the
543 changes in optima over successive years can be tracked or projected. As a first
544 approximation, we could use these as proxies. However, additional modelling and data
545 analysis should be carried out alongside such estimation to determine whether the
546 approximation is warranted and remains useful during environmental change. In other words,
547 we should implement an adaptive control strategy.

548

549 Acknowledgements. This manuscript has taken years to develop due to my own
550 environmental changes, and has been adapted a few times. It has benefited from discussions
551 with Marcel Visser, Luis Chevin and Marc Girondot and from numerous invitations for
552 seminars where I could gauge my ideas on an audience.

553

554 References

- 555 Abrams, PA (2005) Adaptive Dynamics' vs. 'adaptive dynamics. *J. evol. Biol.* 18: 1162-1165.
- 556 Allen, CR, Gunderson, LH (2011) Pathology and failure in the design and implementation of
557 adaptive management. *J Environ Manage.* 92: 1379-84.
- 558 Amundson, R (1996) Historical development of the concept of adaptation. In: Adaptation,
559 eds. Rose, MR, Lauder, GV. Academic Press, New York, pp. 11-54.
- 560 Anderson, B, Dehghani, A (2008) Challenges of adaptive control-past, permanent and future.
561 *Annu. Rev. Control.* 32: 123-135.
- 562 Angeler, DG, Fried-Petersen, H, Allen, CR, Garmestani, A, Twidwell, D, Birgé, HE *et al.*
563 (2019) Adaptive capacity in ecosystems. *Adv Ecol Res.* 60: 1-24.
- 564 Bargués-Ribera, M, Gokhale, CS (2020) Eco-evolutionary agriculture: Host-pathogen
565 dynamics in crop rotations. *PLoS Comput. Biol.* 16: e1007546
- 566 Bateson, P (2017) Adaptability and evolution. *Interface Focus.* 7: 20160126.
- 567 Beckage, B, Gross, LJ, Lacasse, K, Carr, E, Metcalf, SS, Winter, JM *et al.* (2018) Linking
568 models of human behaviour and climate alters projected climate change. *Nat. Clim. Change*
569 8: 79.
- 570 Botero, CA, Weissing, FJ, Wright, J, Rubenstein DR (2015) Evolutionary tipping points in
571 the capacity to adapt to environmental change. *Proc. Natl. Acad. Sci. U.S.A.* 112: 184-189.
- 572 Bulmer, MG (1984) Delayed germination of seeds: Cohen's model revisited. *Theor. Pop.*
573 *Biol.* 26: 367-377.

- 574 Carolan, K, Helps, J, van den Berg, F, Bain, R, Paveley, N, van den Bosch, F (2017)
575 Extending the durability of cultivar resistance by limiting epidemic growth rates. *Proc. Royal*
576 *Soc. B* 284: 20170828.
- 577 Champagnat, N, Ferrière, R, Ben Arous, R (2001) The canonical equation of adaptive
578 dynamics: a mathematical view. *Selection* 2: 73-84.
- 579 Cleveland, WS (1981) LOWESS: A program for smoothing scatterplots by robust locally
580 weighted regression. *Am. Stat.* 35, 54.
- 581 Cohen, D (1966) Optimizing reproduction in a randomly varying environment. *J. Theor.*
582 *Biol.* 12: 110-129.
- 583 Collins, MR, Knutti, J, Arblaster, J-L, Dufresne, T, Fichet, P, Friedlingstein, X, *et al.*
584 (2013) Long-term climate change: Projections, commitments and irreversibility. In: *Climate*
585 *Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth*
586 *Assessment Report of the Intergovernmental Panel on Climate Change.* Eds. Stocker, TF,
587 Qin, D, Plattner, G-K, Tignor, M, Allen, SK, Doschung, J, Nauels, A, Xia, Y, Bex, V,
588 Midgley PM. Cambridge University Press, pp. 1029-1136.
- 589 Cotto, O, Sandell, L, Chevin, LM, Ronce, O (2019) Maladaptive shifts in life history in a
590 changing environment. *Am. Nat.* 194: 558-573.
- 591 Coulson, T (2020) Equilibrium, the new dirty word of ecology. Authorea. Available at
592 <https://doi.org/10.1111/ele.13629>.
- 593 Débarre, F, Nuismer, SL, Doebeli, M (2014) Multidimensional (co) evolutionary stability.
594 *Am. Nat.* 184: 158-171.

- 595 **Dercole, F, Rinaldi, S (2008)** Analysis of Evolutionary Processes: The Adaptive Dynamics
596 Approach and its Applications. Princeton University Press, Princeton New Jersey.
- 597 **Dieckmann, U (1997)** Can adaptive dynamics invade? *Trends Ecol Evol.* 12:128-31.
- 598 **Dieckmann, U, Law, R (1996)** The dynamical theory of coevolution: a derivation from
599 stochastic ecological processes. *J Math Biol.* 34: 579-612.
- 600 **Dutta, A, Croll, D, McDonald, BA, Barrett, LG (2021)** Maintenance of variation in virulence
601 and reproduction in populations of an agricultural plant pathogen. *Evol. Appl.* 14: 335-47.
- 602 **Ellner, S (1997)** You bet your life: life-history strategies in fluctuating environments. In:
603 Case Studies in Mathematical Modeling: Ecology, Physiology, and Cell Biology. Eds.
604 Othmer, HG, Adler, FR, Lewis, MA, Dallon, JC. Prentice-Hall, New Jersey, pp. 3-24.
- 605 **Eshel, I (1983)** Evolutionary and continuous stability, *J. theor. Biol.* 103: 99–111.
- 606 **Estes, S, Arnold, SJ (2007)** Resolving the paradox of stasis: models with stabilizing selection
607 explain evolutionary divergence on all timescales. *Am. Nat.* 169: 227-44.
- 608 **Ferrière, R, Gatto, M (1995)** Lyapunov exponents and the mathematics of invasion in
609 oscillatory or chaotic populations. *Theor. Pop. Biol.* 48: 126-171.
- 610 **Ferrière R, Legendre S (2013)** Eco-evolutionary feedbacks, adaptive dynamics and
611 evolutionary rescue theory. *Phil. Trans R Soc B* 368:20120081.
- 612 **Fisher, RA (1930).** The Genetical Theory of Natural Selection. Clarendon Press, Oxford.
- 613 **Frank, SA (2018)** Control Theory Tutorial: Basic Concepts Illustrated by Software Examples.
614 Springer, Cham, Switzerland.

- 615 **Frank SA** (2019) Evolutionary design of regulatory control. I. A robust control theory
616 analysis of tradeoffs. *J. Theor. Biol.* 463: 121-137
- 617 **Geritz, SAH, Meszéna, G, Metz, JAJ** (1998) Evolutionarily singular strategies and the
618 adaptive growth and branching of the evolutionary tree. *Evol. Ecol.* 12:35-57.
- 619 **Gienapp, P, Merilä, J** (2018) Evolutionary responses to climate change. In: Encyclopedia of
620 the Anthropocene, eds. DellaSalla, D, Goldstein, M. Elsevier, Oxford, pp. 51-59.
- 621 **Gienapp, P, Lof, M, Reed, TE, McNamara, J, Verhulst, S, Visser, ME** (2013) Predicting
622 demographically sustainable rates of adaptation: Can great tit breeding time keep pace with
623 climate change? *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 368: 20120289.
- 624 **Gyllenberg, M, Parvinen, K** (2001) Necessary and sufficient conditions for evolutionary
625 suicide. *Bull. Math. Biol.* 63: 981–993.
- 626 **Haldane, JBS** (1927) A mathematical theory of natural and artificial selection, Part V:
627 selection and mutation. *Math. Proc. Camb. Philos. Soc.* 23: 838-844.
- 628 **Johansson, J** (2008) Evolutionary responses to environmental changes: how does competition
629 affect adaptation? *Evolution* 62: 421-435.
- 630 **Johansson, J, Jonzén, N** (2012) Game theory sheds new light on ecological responses to
631 current climate change when phenology is historically mismatched. *Ecol. Lett.* 15: 881-888.
- 632 **Jeger, MJ, Madden, LV, van den Bosch, F** (2018) Plant virus epidemiology: applications and
633 prospects for mathematical modeling and analysis to improve understanding and disease
634 control. *Plant Dis.* 102: 837-854.

- 635 **Kane, S, Shogren, JF (2000)** Linking adaptation and mitigation in climate change policy. In:
636 Societal Adaptation to Climate Variability and Change. Eds. Kane, SM, Yohe, GW. Springer,
637 Dordrecht, pp. 75-102.
- 638 **Kopp, M, Matuszewski, S (2014)** Rapid evolution of quantitative traits: theoretical
639 perspectives. *Evol. Appl.* 7: 169-91.
- 640 **Kuznetsov, YA (2004)** Elements of Applied Bifurcation Theory (Vol. 112), Third Edition.
641 Springer Science & Business Media, New York.
- 642 **Lam T, Anderschitz M, Dietz V. (2006)** Contribution of feedback and feedforward strategies
643 to locomotor adaptations. *J Neurophysiol.* 95: 766-73.
- 644 **Lande, R, Shannon, S (1996)** The role of genetic variation in adaptation and population
645 persistence in a changing environment. *Evolution* 50: 434-437.
- 646 **Leimar, O (2009)** Multidimensional convergence stability. *Evol. Ecol. Res.* 11: 191-208.
- 647 **Leimar, O, Hammerstein, P, Van Dooren, TJM (2006)** A new perspective on developmental
648 plasticity and the principles of adaptive morph determination. *Am Nat.* 167: 367-76.
- 649 **Levins, R (1968)** Evolution in Changing Environments. Some Theoretical Explorations.
650 Princeton University Press, Princeton New Jersey.
- 651 **Lion S, Metz JAJ. (2018)** Beyond R0 maximisation: on pathogen evolution and
652 environmental dimensions. *Trends Ecol Evol.* 33: 458-473.
- 653 **Loehle, C (2006)** Control theory and the management of ecosystems. *J. Appl. Ecol.* 957-966.
- 654 **Loeuille, N, Barot, S, Georgelin, E, Kylafis, G, Lavigne, C (2013).** Eco-evolutionary
655 dynamics of agricultural networks: implications for sustainable management. *Adv. Ecol. Res*
656 49: 339-435.

- 657 **Lynch, M, Gabriel, W, Wood, AM (1991)** Adaptive and demographic responses of plankton
658 populations to environmental change. *Limnol. Oceanogr.* 36: 1301-1312.
- 659 **Merilä, J, Hendry, AP (2014)** Climate change, adaptation, and phenotypic plasticity: the
660 problem and the evidence. *Evol. Appl.* 7: 1-14.
- 661 **Metz, JAJ, Nisbet, RM, Geritz, SAH (1992)** How should we define ‘fitness’ for general
662 ecological scenarios? *Trends Ecol. Evol.* 7: 198-202.
- 663 **Metz, JAJ, Geritz, SAH, Meszner, G, Jacobs, FJA, van Heerwaarden, JS (1996)** Adaptive
664 dynamics: A geometrical study of the consequences of nearly faithful reproduction. In:
665 Stochastic and Spatial Structures of Dynamical Systems. Eds. Van Strien, SJ, Verduyn Lunel,
666 SM. North-Holland, Amsterdam, pp. 183-231.
- 667 **Michaelowa, A, Stadelmann, M (2018)** Development of universal metrics for adaptation
668 effectiveness. In: Adaptation metrics: perspectives on measuring, aggregating and comparing
669 adaptation results. Eds. Christiansen, L, Martinez, G, Naswa, P. UNEP DTU Partnership,
670 Copenhagen, pp. 63-72.
- 671
672 **Nelson, DR, Adger, WN, Brown, K (2007)** Adaptation to environmental change:
673 contributions of a resilience framework. *Annu. Rev. Environ. Resour.* 21: 32:395-419.
- 674 **Newman, JA, Anand, M, Henry, HAL, Hunt, S, Gedalof, Z (2011)** Climate change biology.
675 CABI, Cambridge, MA.
- 676 **Ooi, M (2012).** Seed bank persistence and climate change. *Seed Science Res.* 22: S53-S60.
- 677 **Otto, SP, Day, T (2007)** Evolutionary invasion analysis. In: A Biologist’s Guide to
678 Mathematical Modeling in Ecology and Evolution. Princeton University Press, New Jersey,
679 pp. 454-502.

680

681 **Peischl, S, Kirkpatrick, M (2012)** Establishment of new mutations in changing environments.

682 *Genetics* 191: 895-906.

683 **Perrin, N, Sibly, RM (1993)** Dynamic models of energy allocation and investment. *Annu.*

684 *Rev. Ecol. Evol. Syst.* 24: 379-410.

685 **Précigout, PA. (2018)** Epidemiology and evolution of fungal foliar pathogens in the face of

686 changes in crop fertilization : application of evolutionary-ecological theory to crop

687 epidemiology. PhD thesis Université Sorbonne Paris Cité. Available at: [https://tel.archives-](https://tel.archives-ouvertes.fr/tel-02333571)

688 [ouvertes.fr/tel-02333571](https://tel.archives-ouvertes.fr/tel-02333571)

689 **Précigout PA, Robert C, Claessen D (2020)** Adaptation of biotrophic leaf pathogens to

690 fertilization-mediated changes in plant traits: a comparison of the optimization principle to

691 invasion fitness. *Phytopathology* 110: 1039-1048.

692 **Rand, DA, Wilson, HB, McGlade, JM (1994)** Dynamics and evolution: evolutionarily stable

693 attractors, invasion exponents and phenotype dynamics. *Phil. Trans. R. Soc. B* 343: 261-283.

694 **Ripa, J, Dieckmann, U (2013)** Mutant invasions and adaptive dynamics in variable

695 environments. *Evolution* 67: 1279-1290.

696 **Sabelis, MW, Metz, JAJ (2002)** Taking stock: relating theory to experiment. In: Adaptive

697 Dynamics of Infectious Diseases: in Pursuit of Virulence Management. Eds. Dieckmann, U,

698 Metz, JAJ, Sabelis, MW, Sigmund, K. Cambridge Series in Adaptive Dynamics, Cambridge

699 University Press, Cambridge UK.

700 **Schipper, ELF (2006)** Conceptual history of adaptation in the UNFCCC process. *Rev. Eur.*

701 *Comp. Int. Environ. Law* 15: 82-92.

- 702 Siders, AR (2019) Adaptive capacity to climate change: A synthesis of concepts, methods,
703 and findings in a fragmented field. *Wiley Interdiscip. Rev. Clim. Change* 10: e573.
- 704 Stearns, SC (2000) Life history evolution: successes, limitations, and prospects.
705 *Naturwissenschaften* 87: 476-486.
- 706 Teplitsky, C, Tarka, M, Møller, AP, Nakagawa, S, Balbontín, J, Burke, TA, *et al.* (2014)
707 Assessing multivariate constraints to evolution across ten long-term avian studies. *Plos One*
708 *E* 9: e90444.
- 709 Tuljapurkar, S (1986) Demography in stochastic environments. II. Growth and convergence
710 rates. *J Math Biol.* 24: 569-81.
- 711 Tyukin, I (2011) Adaptation in dynamical systems. Cambridge University Press, New York.
- 712 van den Bosch, F, Jeger, MJ, Gilligan, CA (2007) Disease control and its selection for
713 damaging plant virus strains in vegetatively propagated staple food crops; a theoretical
714 assessment. *Proc Biol Sci.* 274: 11-18.
- 715 Van Dooren, TJM (2000) The evolutionary dynamics of direct phenotypic overdominance:
716 emergence possible, loss probable. *Evolution* 54: 1899-1914.
- 717 Van Dooren, TJM (2006) Protected polymorphism and evolutionary stability in pleiotropic
718 models with trait-specific dominance. *Evolution* 60: 1991-2003.
- 719 Walsh, B, Lynch, M (2018) Evolution and selection of quantitative traits. Oxford University
720 Press, Oxford.
- 721 Walters, CJ, Hilborn, R (1978) Ecological optimization and adaptive management. *Annu.*
722 *Rev. Ecol. Evol. Syst.* 9: 157-188

723 **Zhan J, Thrall PH, Papaïx J, Xie L, Burdon JJ (2015) Playing on a pathogen's weakness:**
724 **using evolution to guide sustainable plant disease control strategies. *Annu Rev Phytopathol.***
725 **53: 19-43.**
726

727 Methods

728

729 Adaptive Dynamics approximations describe evolutionary processes where it is assumed that
730 characters exist which are faithfully replicated in offspring (Metz et al. 1996), except for rare
731 mutational changes. Additionally, mutations are often assumed to have small effects at the
732 individual phenotypic level (Dieckmann and Law 1996, Champagnat et al. 2002).
733 Characteristic is that evolving populations can feed back onto selective pressures through the
734 selective environments they create. However, it is assumed that external environmental
735 fluctuations that act as input are stationary (Ripa and Dieckmann 2003, Geritz et al. 1998)
736 and that the rarity of mutational changes makes the so-called resident environments stationary
737 too. Based on all these assumptions, a deterministic dynamic system can be defined, referred
738 to as the canonical equation of AD (Dieckmann and Law 1996). Not assuming small
739 mutations implies that evolutionary trait substitution sequences are studied (Champagnat et
740 al. 2002) where in each substitution a resident genotype is replaced by a mutant with positive
741 invasion fitness. Convergence and stability of singular points is then based on geometric
742 arguments, not directly deriving from a deterministic dynamical system. Evolutionarily
743 singular points (candidate adapted states) can be CSS endpoints of trait substitution
744 sequences or the canonical equation of Adaptive Dynamics when conditions on second order
745 partial derivatives of invasion fitness confirm convergence stability and non-invasibility
746 (Geritz et al. 1998). CSS's and their properties are relatively independent of genetic makeup
747 when adapted states contain one phenotype (Van Dooren 2006). Systematic phenotypic
748 advantages for heterozygotes are not expected for most smooth genotype-phenotype maps
749 (Van Dooren 2000).

750 Simulation code for R used to study the germination probability model is available on
751 request. I simulated populations of selfing plants according the model described in the main
752 text. For the simulation with genotypically determined germination probabilities, trait values
753 were discretized from zero to one in steps of 0.02. The initial state of the population was a
754 uniform distribution of individuals over all trait values, with densities summing up to value
755 one half. The mutation probability was set at 0.1 per individual and mutants occupied trait
756 bins adjacent to their parental trait value. To determine adapted states for this model version
757 with genotypic germination probabilities only, evolutionary trait substitution sequences were
758 simulated with trait step sizes of 0.1 starting from germination probability one and trait
759 boundaries at values 0.1 and one. For the forward simulations with plasticity and maternal
760 effects, trait values were discretized at integer values from -5 to +5 for each trait g , b , m
761 resulting in 1331 trait combinations which occurred. The mutation rate was set at 0.1 per
762 individual. Mutant individuals were uniformly distributed over all bins adjacent to their
763 parental trait combination and within the range of trait values allowed. The initial state of the
764 population was in each forward simulation a uniform distribution over all trait combinations,
765 with densities summing up to value one. For the evolutionary invasion analysis used to
766 determine adapted states, evolutionary trait substitution sequences were simulated with trait
767 step sizes of 0.1 and starting from zero trait values for g , b and m . At each substitution,
768 simultaneous trait changes were made in all traits with a direction of positive invasion fitness.
769 Trait boundaries were fixed at -5, 5 for each trait.

770

771 Figure Legends

772

773 Figure one. A general approach to determine adaptations and adaptational lags during periods
774 of environmental change. (A) Environmental change is described by gradual changes in
775 parameters of the probability distributions of environmental variables. (B) The actual
776 environmental history is a single realization of this time-dependent stochastic process. (C) For
777 each value or set of values of environmental parameters per time point, adapted states which
778 evolution could arrive at can be determined (blue). (D) An actual population shows
779 evolutionary responses depending on, inter alia, selection occurring at each point in time. At
780 each point in time, there will be a range of phenotypes present (grey band), and an average
781 phenotypic value across the population (black line). The difference between the phenotypic
782 trait value or traits composing an adapted state and the phenotype of an individual is the
783 adaptational lag. It therefore varies between individuals, and population statistics of this lag
784 can be calculated.

785 Figure two. Continuation of adaptations during environmental change. We can determine
786 which combinations of total recruitment in good (K) and bad years (k), survival in the seed
787 bank (s) and the probability that a year is good (q) lead to (CSS) adaptations where the
788 adaptive germination probability p^* is smaller than one. To the right of each curve labeled
789 with the corresponding recruitment parameters (recruitment boundary), adapted germination
790 probabilities for these combinations of s and q and the recruitment values specified on the
791 boundary are smaller than one, hence a seed bank adaptive. When the difference between K
792 and k increases, boundaries shift to the left and more combinations of s and q have a CSS p^*
793 < 1 . When environments change gradually, we can assume that parameter values (s , q , k , K)
794 change gradually between years and that evolution tracks the adapted germination probability
795 value specific to the environmental regime of each year. Three examples are given, with
796 adapted states where $p^* < 1$ in black, with $p^* = 1$ in red: (a) If survival in the seed bank is
797 decreasing, then it will become adaptive to always germinate. (b) Environmental change
798 decreases q and s such that it is first adaptive to always germinate, later it becomes adaptive
799 to develop a seed bank. (c) If recruitment parameters would gradually change as well, we can
800 imagine that differences between good and bad years become smaller and then larger again,
801 as in the scenario elaborated further in the main text.

802 Figure three. Adaptational lags for a single evolving trait. (A) A scenario of gradual change in
803 the four parameters characterising the environment per year. As in the example (C) of Fig.2,
804 the difference between recruitment parameters K (warm year) and k (cool year) first gradually
805 decreases, then increases again. It can be determined that there is a time window from years
806 188 to 329 where it is adaptive to germinate with probability $p^* = 1$. (B) Calculation of the
807 adaptational lag for the environmental change scenario in the left panel and a simulation of a
808 population of selfing individuals with a high mutation rate in the germination probability. Full
809 blue line: Adapted states determined using Adaptive Dynamics. Grey line: population
810 trajectory, average germination probability of the seeds in the seed bank. Red line: difference
811 between adapted states and population average.

812 Figure four: Adapted states and adaptational lags for a model version with multiple components
813 of trait determination. The same environmental change scenario as in Fig. 2 is simulated. (A)
814 Adapted states of the three trait components. The genotypic component is drawn in dark blue,
815 the plasticity weight in blue and the maternal effect weight in light blue (B) Population
816 trajectories of the averages of each trait component. (C) Average adaptational lag trajectories
817 per trait component. (D) Approximate adapted states determined by evolution with a large
818 supply of mutational variation in each stationary environment. (E) Average adaptational lag as
819 a three-dimensional trajectory. (F) Average adaptational lag calculated for the germination
820 probability as described by Eqn. 5. Points for warm and cool years are plotted in red and brown,
821 respectively.

822 Figure five. Relationships between demographic statistics and adaptational lag. For the
823 germination probability model with plasticity and maternal effects. (A) and (B) I calculated per
824 year the fraction of the seed bank that was recruited within that year. This statistic is indicative
825 of how fast a population might respond as a whole to selection during the juvenile and adult
826 stages. Panels (A) and (B) show the dependence on average germination probability and
827 adaptational lag (as in Fig. 3F), respectively. (C) and (D) The log per capita number of seeds
828 contributed by a juvenile plant (the growth rate of the pure strategy which always germinates),
829 is a component of the establishment probability of variants. Panel (C) shows its dependence on
830 average germination probability and (D) on the adaptational lag. Lowess regression fits
831 (Cleveland 1981) with a smoother span of 0.1 are added as wide grey lines in panels (C) and
832 (D).

833 Figure six. Adaptive control and adapted states. Left. Elaborating modes of trait determination
834 demonstrates that adaptive control shares characteristics with a particular mode of trait
835 determination. Right. Evolutionary adaptation and its integration within an adaptive controller.
836 (A) Phenotypic plasticity (B) Phenotypic switch (C) Plasticity with controller (D) Adaptive
837 control (E) Adaptive dynamics predicts adapted trait values for a trait determination process
838 using a demographic model with environmental feedbacks and mutational variation. (F) These
839 predictions can be used as a model reference in an adaptive control system.

840 Figure seven. A provisory overview of possible adaptational lag patterns driven by eco-
841 evolutionary dynamics. The y-axis represents a scalar phenotypic trait, the x-axis time. (A) The
842 population approaches an adapted state. (B) There is convergence to an equilibrium
843 adaptational lag. The population then lags with respect to the adapted state at a fixed distance.
844 (C) The adaptational lag changes sign. The population average trait shows inertia in adaptation,
845 the adaptational lag diverges again. (D) Multiple adapted states can co-occur for the
846 environment specific to one year. The lag then becomes a multi-valued function of time. (E)
847 Evolutionary suicide. The adapted state is extinction. (F) For a range of environmental states,
848 the adapted state is an adaptive polymorphism. The population can then also become
849 phenotypically polymorphic or not.

850

Figure one

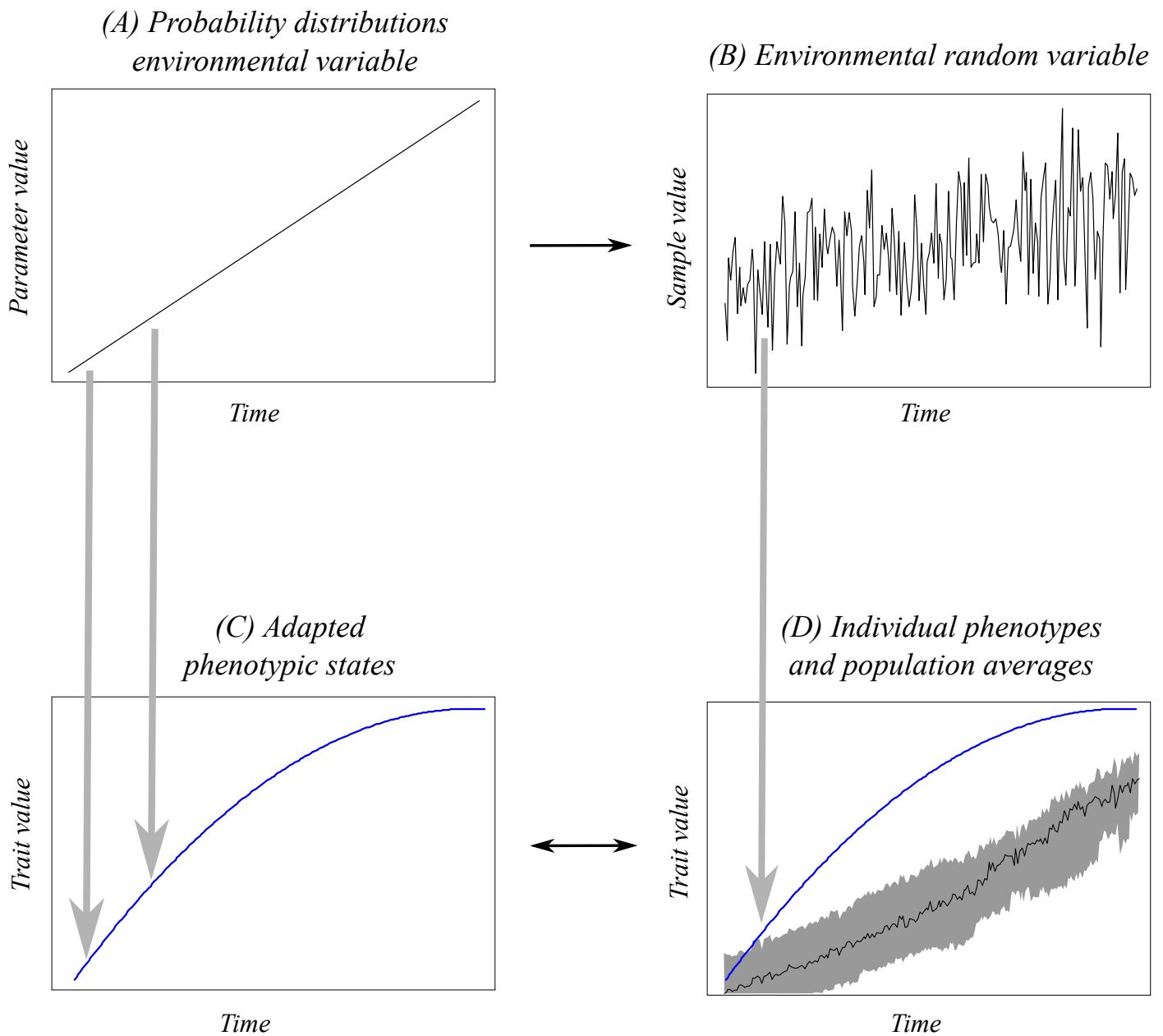


Figure two

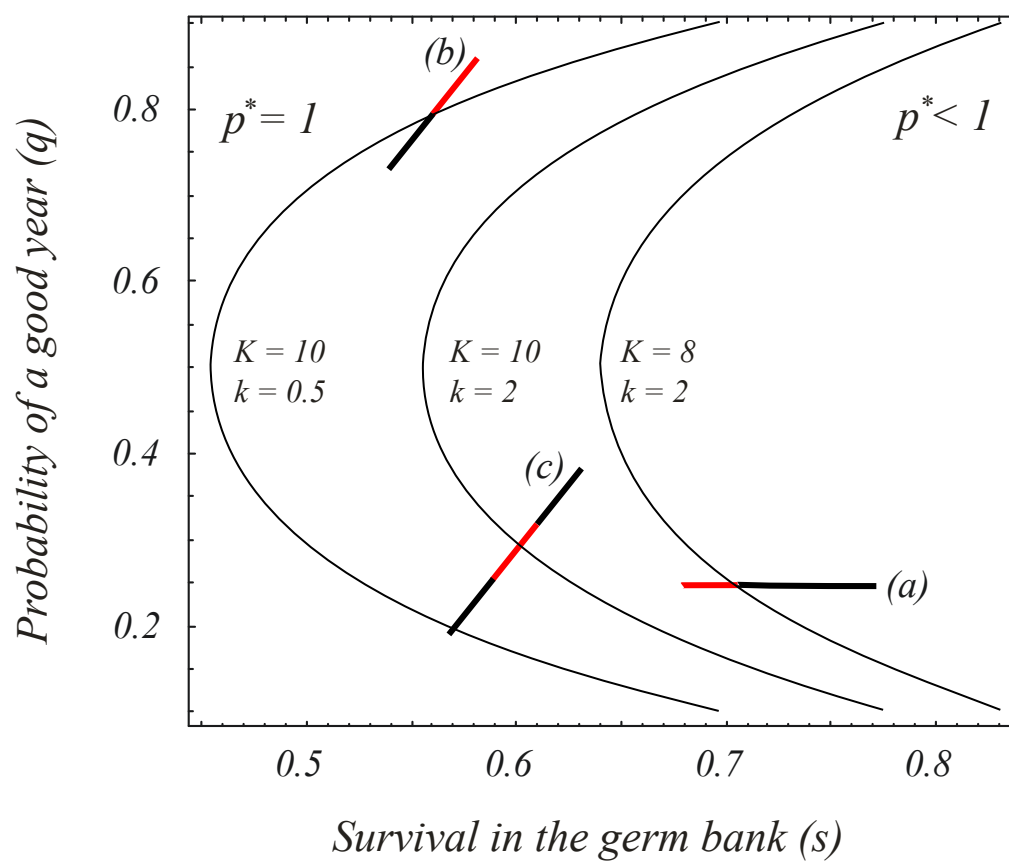
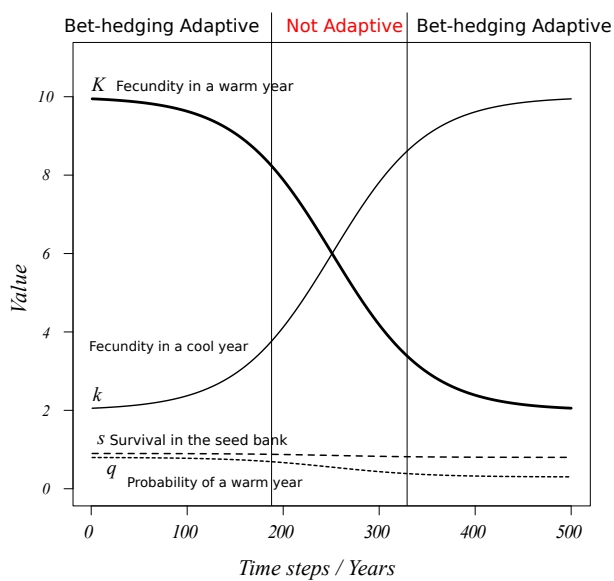


Figure three

(A) Environmental scenario



(B) Evolutionary changes and adapted states

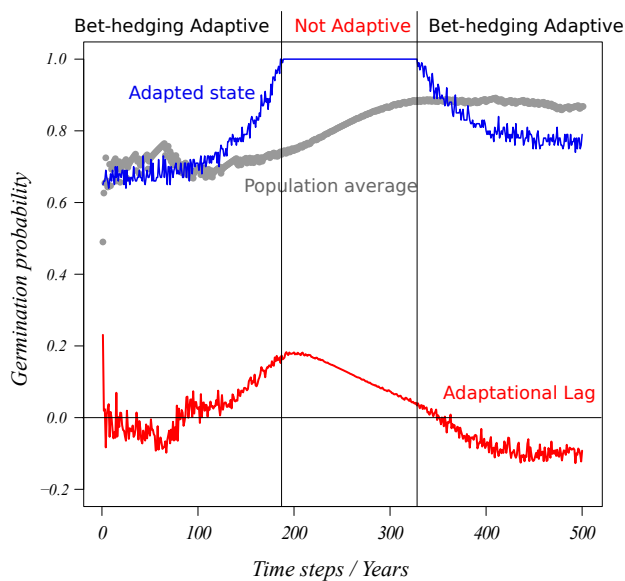
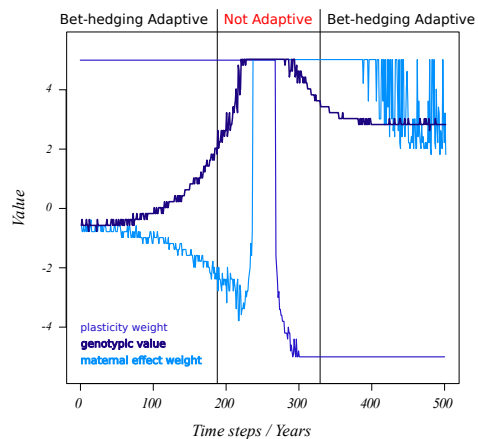
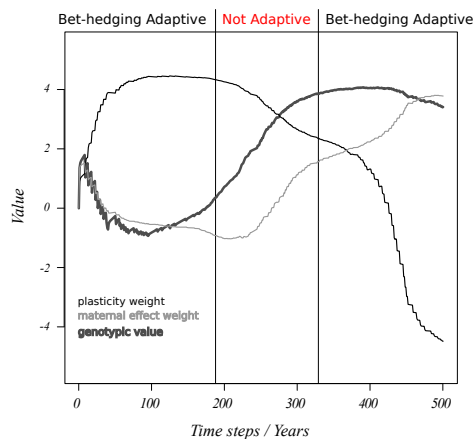


Figure four

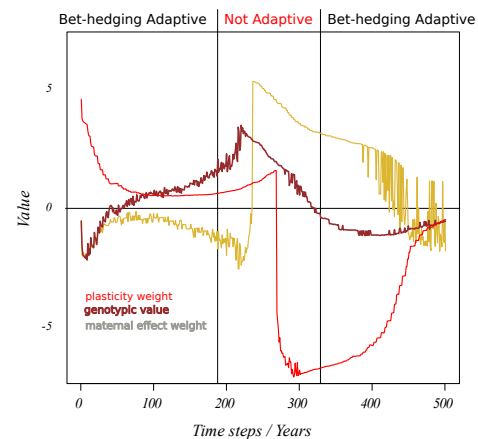
(A) Adapted States



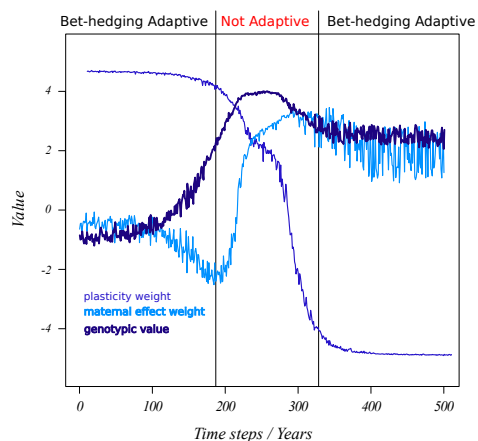
(B) Population trajectory



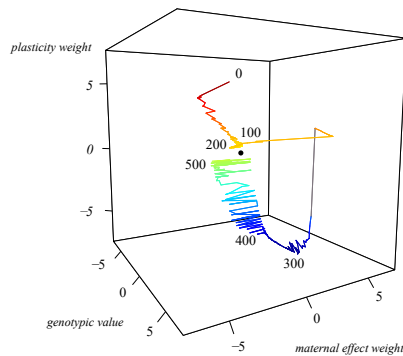
(C) Adaptational lags



(D) Approximate Adapted States



(E) Adaptational lags in trait space



(F) Adaptational lag germination probability

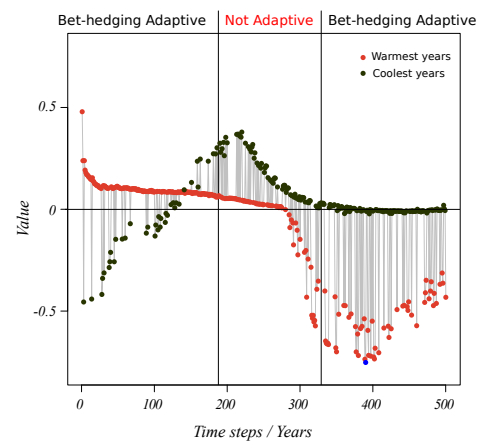


Figure five

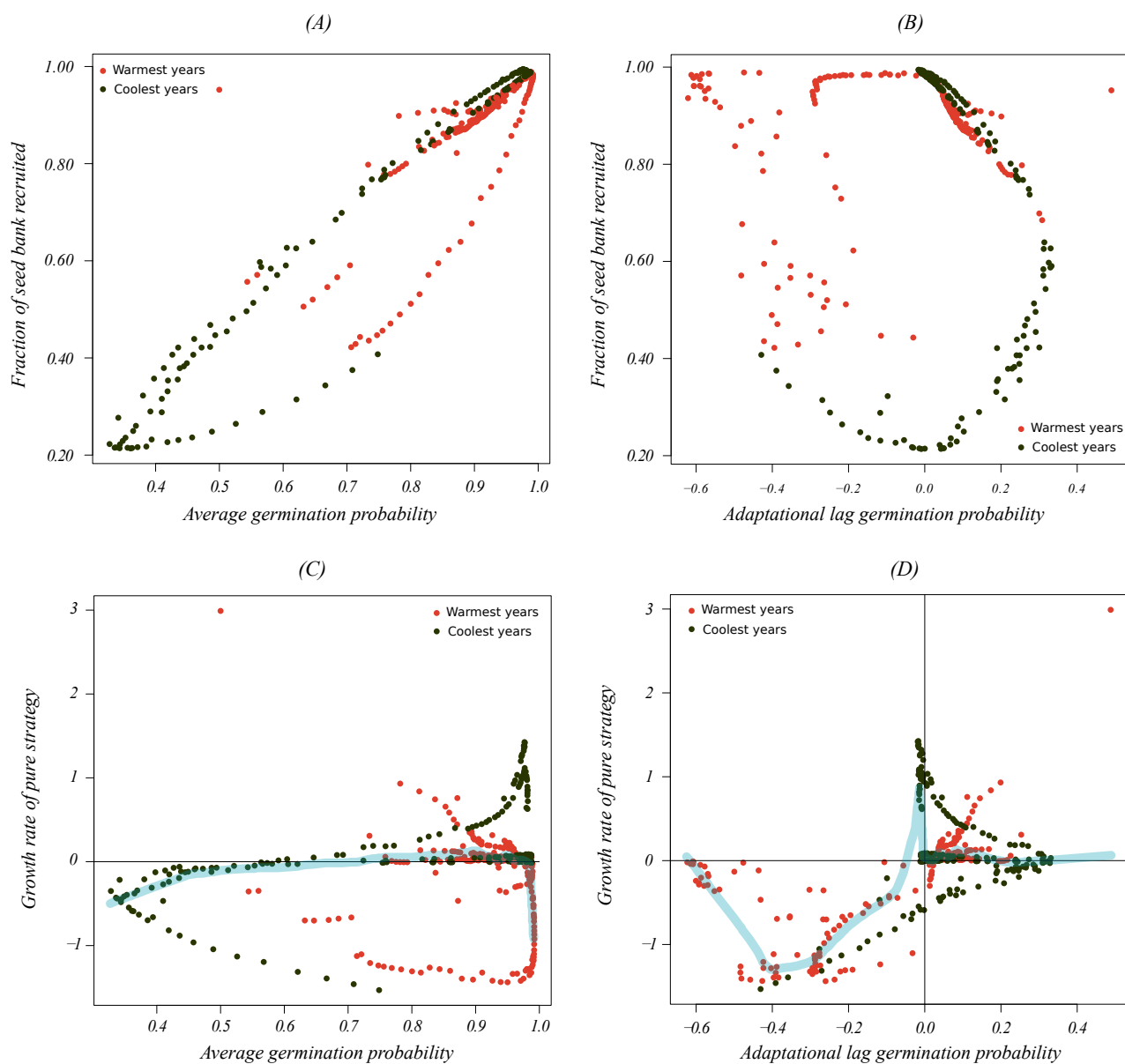


Figure six

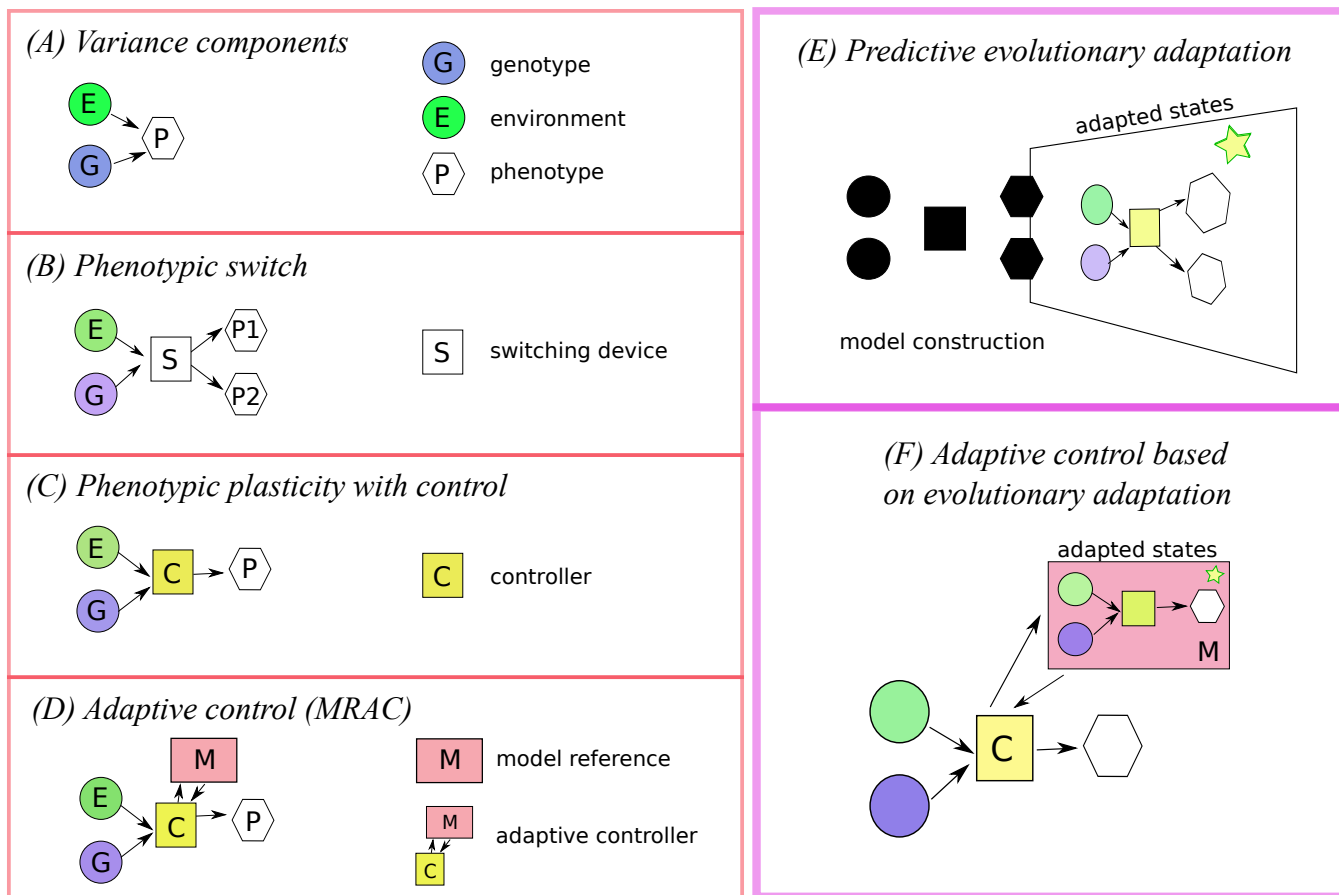


Figure seven

