Adaptational lags during periods of environmental change

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Abstract

Effects of climate change can be handled by means of mitigation and adaptation. In the biological sciences, adaptations are evolved solutions of engineering problems where organisms need to match an ecological challenge. Based on Adaptive Dynamics theory, a definition is proposed of adapted states and adaptational lags which is applicable during periods with environmental change of any speed and to any character. Adaptation can thus be studied even when it emerges from complex eco-evolutionary processes and targets for adaptation are not defined or known a priori. The approach is exemplified with a model for delayed germination (germination probability) in an annual plant, which is the classic life history example for adaptation to uncertain environments. Plasticity and maternal effects are added to the model to investigate lags in these modes of trait determination which are often presumed to be adaptive. In the example, adaptational lags are not converging to an equilibrium and change sign. For the model version with plasticity and maternal effect weights, the presence of a lag in these trait components can temporarily change the direction of selection on the genotypic weight. Adaptational lag is related to the establishment probability of mutants in the model example. It could therefore have practical relevance. A first general classification is proposed of model structures that include both adaptive control and evolutionary adaptation.

Introduction

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

Adaptation is a term in biology which predates the development of evolutionary biology (Amundson 1996). The term specifies that the engineering problem of matching organisms to an existing ecological challenge has been solved for the traits that are adapted. Natural selection and evolutionary responses are seen as the main problem solvers in this respect and by means of strategic compromises or a trait development responding to cues, adaptation can be to a range of variable environments (Levins 1968). However, in the context of human climate change responses, "adaptation" has become reframed over the years from this eco-evolutionary meaning applicable to any organism into a policy response (Schipper 2006), from describing a dynamics of autonomously evolving systems into a concept more in line with human adaptive systems control towards a given target (Tyukin 2011). This trend makes it increasingly difficult to integrate and predict effects of autonomous evolutionary adaptation and of (policy) control in biological systems. A revised or re-clarified notion of evolutionary adaptation to climate change could address this and might facilitate the integration of evolutionary adaptation and system control into forecasts.

The consensus is that most organisms currently respond to climate change with phenotypic plasticity (Gienapp & Merilä 2018), developmental changes in response to altered environmental cues that are often believed to be adaptive (Merilä & Hendry 2014). The alternative considered, evolution by changes in genotype frequencies, requires the presence of heritable genetic variation for the involved traits and therefore most studies looking for ongoing adaptation in natural systems focused on demonstrating evolutionary phenotypic responses by means of changes in gene frequencies (Gienapp & Merilä 2018). However, such responses don't need to point in the direction where adaptation would be fastest or even where phenotypic changes are adaptive (Leimar 2009, Teplitsky et al. 2014). Additional evidence is required to support and demonstrate adaptation to a particular target phenotype or that a plastic response observed is adaptive. In addition, the target of adaptation can move over time. This has usually been modeled by making the target an explicit time-dependent parameter (Lynch et al 1991), i.e., as if the target is known. We can certainly define and model targets in our policies, but these might not align with how the considered system or system components we try to control will evolve and adapt autonomously during climate change. There is a need to investigate what the targets of biological adaptation are during climate change, whether evolving organisms approach them and how far we are removed from them, for situations where they are not pre-defined or controlled but emerge from eco-evolutionary processes, affected or not by policy control.

Using a classical model for delayed germination in annual plants with a seed bank (Cohen 1966, Ellner 1997), I propose and exemplify an analysis of evolutionary adaptation and adaptational lags during environmental change. Note that this is an exercise involving a single projection of population states into the future, and many projections of evolution. Essential to the proposal is that most of the concepts applied were already developed in so-

called Adaptive Dynamics approximations (Metz et al. 1996, Geritz et al. 1998) also known as evolutionary invasion analysis (Otto & Day 2007).

Model specification

The simplest incarnation of a well-known model for the demography of an annual plant (Cohen 1966, Bulmer 1984) tracks densities (number per unit of area) of individual seeds of a single genotype in a seed bank across years, each time censused right after seed production. With N_t the number of seeds at the end of the season in year t and assuming large population sizes such that demographic stochasticity can be ignored, the number of seeds one year later is

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

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

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

This is one of the simplest and best-known structured population models (during the growing season seeds and plants are simultaneously present). It is the prime example used to demonstrate that adaptation is not always towards the fastest life history with the largest number of offspring (Stearns 2000). It is easily modified to allow for the occurrence of many genotypes in a population. We can then use simple forward simulations to investigate how selection gradually changes population composition among genotypes with different phenotypic traits. A common idea is that adapted states emerge when genotype frequencies equilibrate, for example by fixation. However, evolutionary invasion analysis (Adaptive Dynamics, Metz et al. 1996, Geritz et al. 1998, Methods) finds adapted states differently and also considers genotypes not yet present in a population. It assumes that we first need to determine which genotypes can invade so-called resident populations (established, stationary). More importantly, we must determine which resident population compositions can evolve by means of a trait substitution sequence fueled by mutations. The most interesting ones are those with the property that once their state attained, they cannot be invaded by genotypes with similar germination phenotypes. Hence, they have a stability in a longer-term evolutionary sense and are considered to be adapted to the ecological circumstances. In order to determine these states, invasion fitness (Metz et al. 1992) is used to assess resident population states. Here we assume that only a single resident phenotype determines the population feedback on the success of rare genotypes, and that the process characterising the resident state and the fluctuations in demographic parameters is stochastic, stationary and ergodic (Rand et al. 1994, Ferrière & Gatto 1995, Ripa & Dieckmann 2013) such that the precise starting point t becomes irrelevant. For a single resident genotype with the germination trait value p as above, and a rare mutant genotype with a different germination probability p', invasion fitness equals

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

This expression assumes clonal inheritance and that the number of seeds recruited varies between years, even for the same amount of seeds germinated. $N_t(p)$ is the number of seeds in the seed bank at time *t* with the resident genotype having phenotype *p*. By extension, when survival in the seed bank is also allowed to be time-dependent, we get the invasion fitness

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

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

In order to find adapted states, we proceed as follows. Ellner (1997) contains an insightful presentation of results that depend on a partial derivative used to determine whether a germination probability below one can invade. It is $\frac{\partial}{\partial p'}\rho(p',p)\Big|_{p'=p=1}$ (Eqn. 3a). When this quantity is positive, it is adaptive to always germinate. When it is negative, we can expect adapted states with a germination probability below one, i.e. the establishment of a seed bank where a fraction of the seeds remain more than one season. A crucial insight in evolutionary ecology was that such probabilities can only be adaptive when life history parameters fluctuate and long-term fitness is appropriately used as the quantity to determine adaptation. In these cases, we need to locate the intermediate germination probability values that are so-called evolutionarily singular points (represented here as p^*, Geritz et al. 1998). For resident populations with a single genotype, these are defined by the condition that the fitness

derivative $\frac{\partial}{\partial p'}\rho(p',p)\Big|_{p'=p}$ (Eqn. 3b) locally vanishes, i.e. there is no directional selection driving away from such a germination probability p^*. Local second-order partial derivatives determine further requirements for adapted states: they need to be convergence stable, hence reachable, and non-invasible (see Methods). When these adapted states consist of a single genotype, they are called CSS (Continuously Stable Strategy, Eshel 1983).

Continuation

If we assume that years can be good with probability q and otherwise bad, that the total recruitment to the seed bank equals K per unit of area in a good year and k in a bad year, then (Eqn. 3a) can be worked out. This is an exercise in Elmer (1997) which I don't want to spoil, but the result is summarized in Figure one. For environments with fluctuations between good and bad years that occur according a Bernoulli distribution with probability q, it is advantageous to delay germination when recruitment parameters K and k of good and bad years differ very much, when survival in the seed bank s is high and when probability q is intermediate (Fig.1). Now arises the question what this tells us on adaptation when the environment changes in a non-stationary manner, for example when s and q gradually change between years. A first line of attack could be to assume "continuation" (Kuznetsov 2004), namely that the population will always be able to attain the adapted state very rapidly and that gradual environmental changes provoke gradually changing population states that are each predicted well by the adapted state for the environment of that year (Fig. 1). Essential is that the state of the environment in a specific year is given by the four parameters s, q, K and k and not just s and the seeds recruited in that specific year. Three examples of continuation

trajectories are given in Fig.1. The first two are for gradual changes in survival and the probability that years are good. In such scenarios, it can be first adaptive to have a seed bank when survival in the seed bank is still high, and when survival has decreased a lot, to always germinate. The opposite route can also be adaptive: first always germinate, but when good years occur less often and survival gradually decreases, it can become adaptive to develop a seed bank. If recruitment parameters gradually change as well, differences between good and bad years could first become smaller and subsequently larger again. This scenario is elaborated below. However, Fig. 1 already shows that in such cases having a seed bank can first be adaptive, then it can become adaptive to always germinate, followed by a second period where a smaller germination probability is adaptive. With the continuation assumption, populations are expected to then actually show this pattern.

Adaptational lag

However, it is a strong assumption to make that populations would be well adapted all the time. For systems that evolve, but where genotypes are not necessarily at an adapted state all the time, we can determine how far each individual in the population is from a predicted adapted state. For an individual with a genotypically determined germination probability p and an adapted state at time t which is p_t^* this adaptational lag is $p_t^* - p$. It is positive when the adapted state is a larger germination probability than the one for this individual, negative when it is smaller. The average adaptational lag in a population then is the average of this quantity over the distribution of genotypes present at a given census point. Even with high levels of standing additive genetic variation, non-zero average lags are predicted to occur when adapted states are boundary values and genetic variation remains present due to

mutation pressure or segregation, when distributions of mutational effects or standing variation are otherwise asymmetric, when selection fluctuates over time and when organisms have complex life histories inherently generating lags in selection responses.

From now on, think of good and bad years as referring to initially warm and cool years (Figure 2), such that q is the probability of a warm year, K is the total recruitment in a warm year, k in a cold year. To explore potential time trajectories of adaptational lags, a scenario is investigated where the probability q that a year has recruitment K gradually changes. At the same time, and mimicking an effect where all years become gradually warmer, K and k change in values over time (as for the example Fig.1C). When warm years become too hot, K will decrease. At the same time, cold years gradually improve such that k increases. Survival probability in the egg bank gradually decreases as well due to gradually increasing soil temperatures. This is a scenario with an intermittent period where an egg bank is not adaptive (Figure two). I simulated a population of selfing annual plants with a substantial mutation rate per individual (0.01 per individual, Methods) and determined the adapted state for each year in the scenario (Figure two). The lag remains substantial even with continual input of new mutational variation. The adaptational lag can change sign (Fig. 2). It is not the case that populations equilibrate at a constant lag distance from the CSS. Instead, as the CSS can be on a trait boundary or move towards it or not, the lag can change sign. Mutational pressure on the germination probability near the boundary where $p = 1$, makes it that the seed bank is never completely gone, even when that would be adaptive. This opposes the idea that increased genetic heritable variation will inherently lead to improved adaptation.

Phenotypic plasticity and parental effects

I extended the ways in which evolving strategies can respond to climate change by adding extra relevant components of trait determination. Germination could depend on an environmental cue perceived by an embryo (phenotypic plasticity) or by the mother plant (a parental effect). The reaction norm specification becomes as follows (Eqn. 4)

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

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

Germination probability $p_t$now depends in a non-linear manner specified by an inverse-logit function on the genotypic component of an individual g, on an environmental cue E_t and on a maternal cue M stored by that individual. The maternal and the environmental cues are weighed by specific factors, b and m respectively. These factors and the genotypic component g evolve by mutations and selection. For the maternal effect, it is assumed that it is a marker left by a mother on an offspring individual, that it can have two states and that it is fixed and stored by the individual in the same state for the rest of its life. I assume that only part of the individuals are responsive to a cue for a good year or get the right cue from their parent. In the simulations presented, 70% of individuals respond to a warm year (warm year $E_t = 1$, cool year $E_t = 0$). In a warm year, 70% of individuals get the maternal cue $M = 1$, the others get $M = 0$. In a cool year, 70% of individuals get $M = 0$, the others $M = 1$. Because of the probit transformation, trait values g, b, m can range from minus to plus infinity, while the individual germination probabilities are constrained between zero and one. Note that each individual has five state variables, of which three are evolving and adapting via mutations

and selection. What is also important is that the seed bank now contains individuals in different states, namely those that carry markers $M = 0$ and the others that carry $M = 1$.

If we repeat the environmental scenario of Fig. 2 and determine adapted CSS states per year for the three trait components, then adapted states for the plasticity weight are generally extreme (Figure 3A), while for the genotypic value a pattern similar to Fig. 2 is observed, but with a shorter time interval where bet-hedging is not adaptive. The adaptive maternal effect weight is often opposite in sign to the plasticity. In fact, in part of the time interval where bet-hedging is not adaptive, all three traits jointly have their maximum values as adapted states. The eco-evolutionary dynamics of the simulated population shows a rather different pattern (Fig. 3B): the maximum average genotypic value g in the simulation is only reached when bet-hedging is already adaptive again. Note that the genotypic value g slightly increase further in the second time interval where bet-hedging is adaptive, even when its adaptational lag has already changed sign. The plasticity weight also evolves for part of the years in a direction opposite where the adapted state is for these years. However, the adapted states might not be entirely representative for directions of selective pressures in populations with standing heritable variation. When adapted states are not determined by means of trait substitution sequences but approximated by simulated evolution over an extended period in the environment characteristic for a year, the mutational pressures near trait boundaries and standing amounts of variation have effects on the outcome (Fig. 3D). Approximate adapted states on the trait boundaries are much less observed, and when a trait such as g has not evolved to the boundary, the parental effect for example seems to converge to a different value as well. This demonstrates that approximating adapted states by evolutionary simulation with a continual input of a lot of genetic variation, is imprecise. On the other hand, it remains the case that the population trajectory of an average trait value sometimes changes

in a direction opposite of the state where the evolutionary process simulated for that year converges to in the long-term.

Multivariate lags

When individual phenotypes depend on several underlying components, we can calculate adaptational lags in different ways. It is straightforward to represent lags by vectors in a multivariate trait space, but there is no obvious standardization of each axis to make different traits comparable. Alternatively, we can focus on the germination phenotypes and substitute the evolving components of individuals in the actual population (g, b, m) by the values at the adapted state (g^*, b^*, m^*), leaving the non-evolving state variables of the individual untouched (E_t and M). The adaptational lag then becomes

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

Note that lags can cause genetic conflicts: selective pressures on heritable phenotype components evidenced by speeds of trait change, change in dependence on the magnitude of the lag in others. Lags in the model version with evolving genotypic values, plasticity and parental effects can show non-trivial trajectories (Figure 3E), with overshoots around an adapted state and lag trajectories resembling cycles. Adaptational lag averages in the population can be calculated for warm and cool years, and this shows (Fig. 3F) that in the

first half of the simulation, lags are smallest in warm years, and in the second half in cool years.

Responsiveness to selection and establishment probabilities

It remains to be shown that knowledge of the adaptational lag has predictive value. As a measure of turnover indicating how fast a population can respond to selection, I calculated per year which fraction of the seed bank at the end of the reproductive season was recruited in that same year. Figure four shows that it relates well to the average germination probability in a population (Fig. 4A), but that the dependence on the adaptational lag is complex and gives the lag little predictive value of this fraction (Fig. 4B). Peischl and Kirkpatrick (2012) found that establishment probabilities of populations in arbitrarily changing environments depend on the time pattern of fluctuations. However, the per capita number of offspring of a strategy in the first year has the largest weight on the outcome. When the log per capita number of offspring of germinated seeds is estimated, this relates poorly to the average germination probability in the population (Fig. 4C), but it does better to the adaptational lag (Fig. 4D). A lowess regression with a restricted span of the smoother shows a peak near zero adaptational lag. This means that establishment probabilities of mutations, for example, relate more to the adaptational lag than to the average germination probability in a population. When mutants appear with effects in the juvenile or adult stage that are slightly advantageous, they have to overcome a bigger disadvantage to get established when the adaptational lag in the population is not zero. Adaptational lag can thus be seen in this case as a measure of adaptability. From Fig. 3F we see that the lag is smallest in the cooler years near the end of the simulation. Upon inspection, it turns out that the lag is smallest and the newly

recruited fraction in the seed bank largest when the total number of recruits per year is largest. This is, however, only the case because phenotypic plasticity is included in the determination of germination probability. Strategies can then exploit the good years to outcompete other strategies more easily by always germinating and don't need to adapt with a compromise between good and bad years.

Discussion

Evolutionary invasion analysis was used as an evolutionary genetic algorithm, to determine adapted states during a period of environmental change. Together with the results of an eco-evolutionary simulation, these adapted states determined adaptational lags. This exercise was repeated in a model for delayed germination in an annual plant, assuming two different possible trait determination mechanisms. In principle, the key elements of the approach proposed by means of this example can be carried out for any ecological system where the dependence of demography on environmental state is specified, and where phenotypic trait determination is known or assumed to work in a particular way. Previous eco-evolutionary modeling studies considered adaptation to climate change in different ways. Johansson (2008) investigated evolutionary responses to a moving resource distribution and showed lags for one-, two- and three species systems exploiting the resource distribution. However, these were calculated with respect to the resource with the largest carrying capacity. Johansson and Jonzén (2012) were the first to consider frequency-dependence within species in their determination of adapted states for bird arrival date. Botero et al. (2015) investigated environmental changes that demanded restructuring of phenotype determination, but did not work out any adaptational lags in the trait components.

Adaptive Dynamics studies have distinguished various types of adapted states, of which Figure five gives a non-exhaustive overview. Next to adapted states with single genotypes, with plasticity or not, outcomes such as adaptive protected polymorphisms can occur (Geritz et al. 1998). In other studies, evolutionary suicide occurred (Gyllenberg & Parvinen 2001), where the adapted state is extinction. For one environmental setting, multiple adapted states can co-occur such that adaptational lags become multivariate. In particular for polymorphic adapted states, it needs to be worked out how to calculate adaptational lags best. The adaptive phenotypes in an adapted polymorphism are co-determined by the genetic architecture such that it needs to be accounted for in the model and the lag calculations. Outcomes that are not represented in Fig. 5 are coevolutionary adapted states of several species (Débarre et al. 2014) and adapted states that are cyclic (Dercole and Rinaldi 2008), with a non-equilibrium attractor of the adaptive dynamics.

The adaptational lag corresponds to an intuitive notion of "fitness" where it corresponds to the precision of the match between organisms and phenotypes demanded by their environments. It needs to be noted that here, adaptation is not interpreted in the myopic sense where adaptation only occurs if every single demographic trait or phenotypic trait minimizes a difference from a target (Cotto et al. 2019). Adaptation is rather seen in the sense of Levins (1967) where strategies weigh different options they encounter and achieve the best compromise in the face of their constraints.

From the simulation results, it turned out that adaptational lags can be partial predictors of the invasion success of mutants in other life history traits than germination. If we therefore develop our understanding of adaptational lags further, it could be of use in conservation biology and agro-ecology as partial measures of adaptability. For extant populations, would it be possible estimate lag and adapted state? In the current environment, selection optima can be estimated from data, and the changes in optima over successive years can be tracked or

projected. In models with pre-defined adapted states, the difference between population average of a trait and its adapted state is a commonly used measure of the lag (Kopp and Matuszewski 2015) and in the vicinity of the adapted state, it can be determined from slope and curvature of fitness surfaces (Estes and Arnold 2007). As a first approximation, we could use this as a proxy for the adaptational lag or the estimated optima from estimated fitness landscapes as adapted states. However, additional modeling and data analysis should be carried out alongside such estimation to determine whether the approximation is warranted.

It was found that lags can't be removed for boundary adaptive strategies if any phenotypic variance remains present. This result is similar to the variance lag load in population genetics, but arises near trait space boundaries. If we extend this idea to human socio-economic evolution and if we assume that strategies aiming for zero carbon dioxide emission are boundary strategies, then the conclusion must be that they will never be reached as long as heritable variation or non-heritable variation in our population remains. Beckage et al. (2018) modelled the feedback between human behaviour and projected climate change. Nudging the perceived risk of climate change was proposed as a mitigation policy response, but whether behavioural responses will be adaptive was not considered. In evolutionary ecology, cue perception and associated response plasticity are often studied as adaptations and even if we refuse to see our own adaptation as an evolutionary response, it might be useful to try to determine the adapted states of what we aim to implement.

Human-earth system feedbacks remain largely unexplored (Calvin and Bond-Lamberty 2018) and adaptation seems not considered in that context yet. Adaptive control by us and evolutionary adaptation of all species we wish to consider can be modeled jointly in different ways. First of all, we can consider adaptive control as part of the environmental change, as an external driver of population and evolutionary dynamics. This seems warranted for evolution and adaptation of species which will experience our control, but adaptive control is not

specifically geared towards them. Second, an already defined adaptive control strategy can depend on the state of one or several populations. The adaptive control becomes part of the eco-evolutionary feedback of these populations. Adapted states then become responses to an environmental challenge which includes our adaptive control, as planned and carried out. Adaptational lags therefore partially depend on the adaptive control. A third possibility is modeling an integrated system, which includes our species as a non-evolving entity but where our adaptive control can depend on our own population state. Projected adapted states and adaptational lags then also project our population state and the associated control strategies in each calculation. A last possibility is an integrated system where our species and the others included can all adapt by evolutionary dynamics. It can then be chosen to allow our adaptive control to be part of the traits that evolve by mutations. It can be a strategy involving non-genetic inheritance or a strategy without any heritability. The adaptation pathways framework proposed by Wise et al. (2014) seems to fit within the last two approaches.

In the human adaptation context, clear metrics of adaptation in comparison to mitigation seem to lack (Michaelowa and Stadelmann 2018). It might be advantageous to distinguish policy targets and metrics of achieving those, from metrics of evolutionary adaptation derived according to one of the frameworks above. There can be cases where states that adaptive control aims to achieve and adapted states of evolutionary adaptation are the same. In particular, so-called optimization principles (Gyllenberg and Service 2011) where a combination of traits or a scalar function of the environments engendered by populations become maximized by adaptation seem first candidates for that.

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Methods

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

Simulation code for R which was used to study this model is available on request. I simulated populations of selfing plants according the model described. For the simulation with genotypically determined germination probabilities, trait values were binned from zero to one

in steps of 0.2. For the simulations with plasticity and maternal effects, trait values were discretized at integer values from -5 to +5 for each trait *g*, *b*, *m*. The mutation rate was always set at 0.01 per individual. Mutant individuals were uniformly distributed over all bins adjacent to their ancestral trait value and within the range of trait values allowed. The initial state of the population was in each simulation a uniform distribution over all trait values, with densities summing up to value one half in the simpler simulation and one when plasticity and maternal effects were included. For the evolutionary invasion analysis, evolutionary trait substitution sequences were simulated with trait step sizes of 0.1 and with steps in all traits simultaneously in the direction of positive invasion fitness.

Figures

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

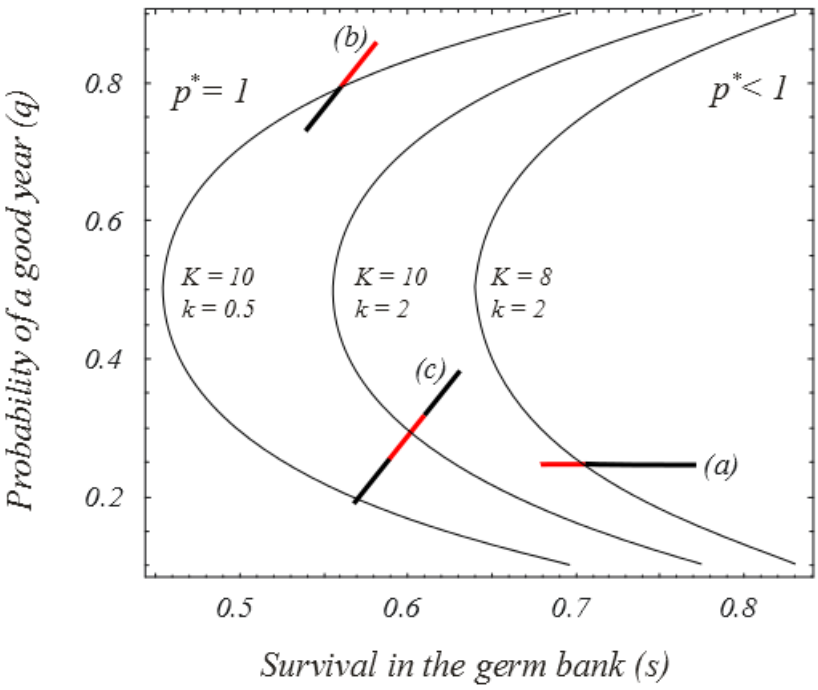

Figure two. Adaptational lags for a single evolving trait. Left. A scenario of gradual change in the four parameters characterising the environment per year. As in the example (c) of Fig.1, the difference between recruitment parameters *K* (warm year) and *k* (cool year) first gradually decreases, then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

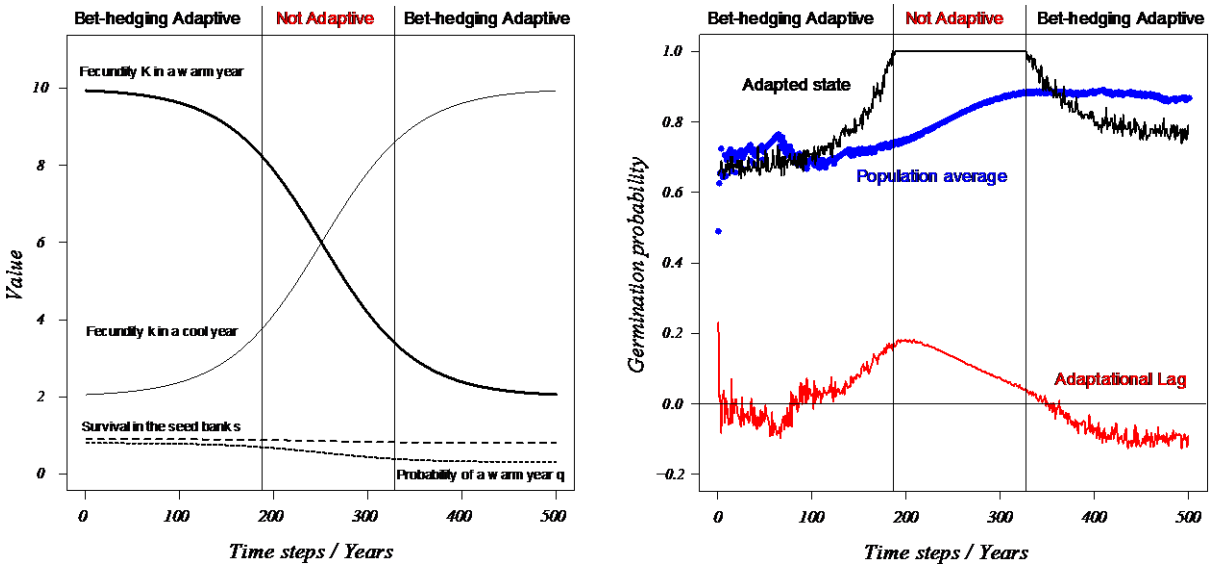

Figure three: Adapted states and adaptational lags for a model version with multiple components of trait determination. The same environmental change scenario as in figure two is simulated. (A) Adapted states of the three trait components. The genotypic component is drawn in black, the plasticity weight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

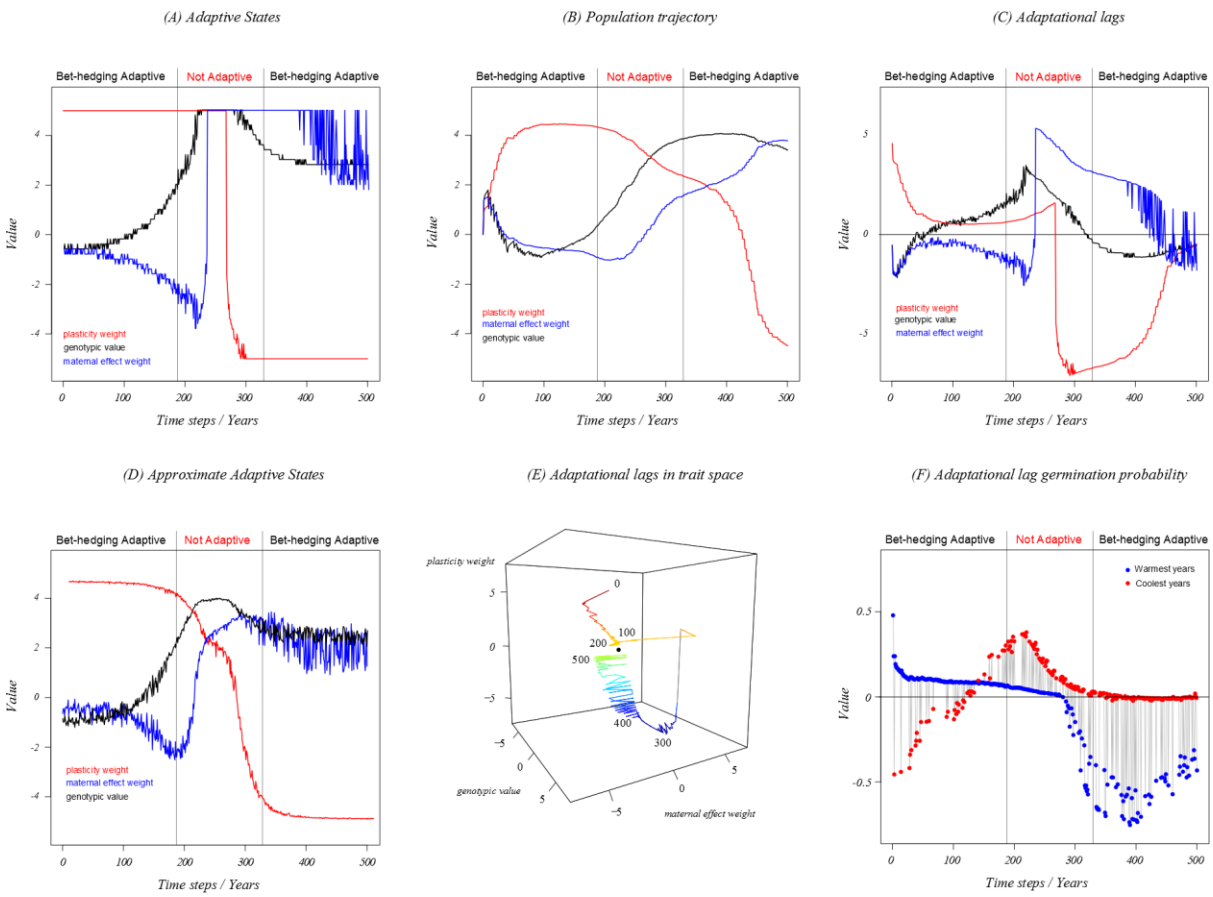

Figure four. Relationships between demographic statistics and adaptational lag. For the model version with plasticity and maternal effects, I calculated per year the fraction of the seed bank that was recruited within that year. This statistic is indicative of how fast a population might respond as a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

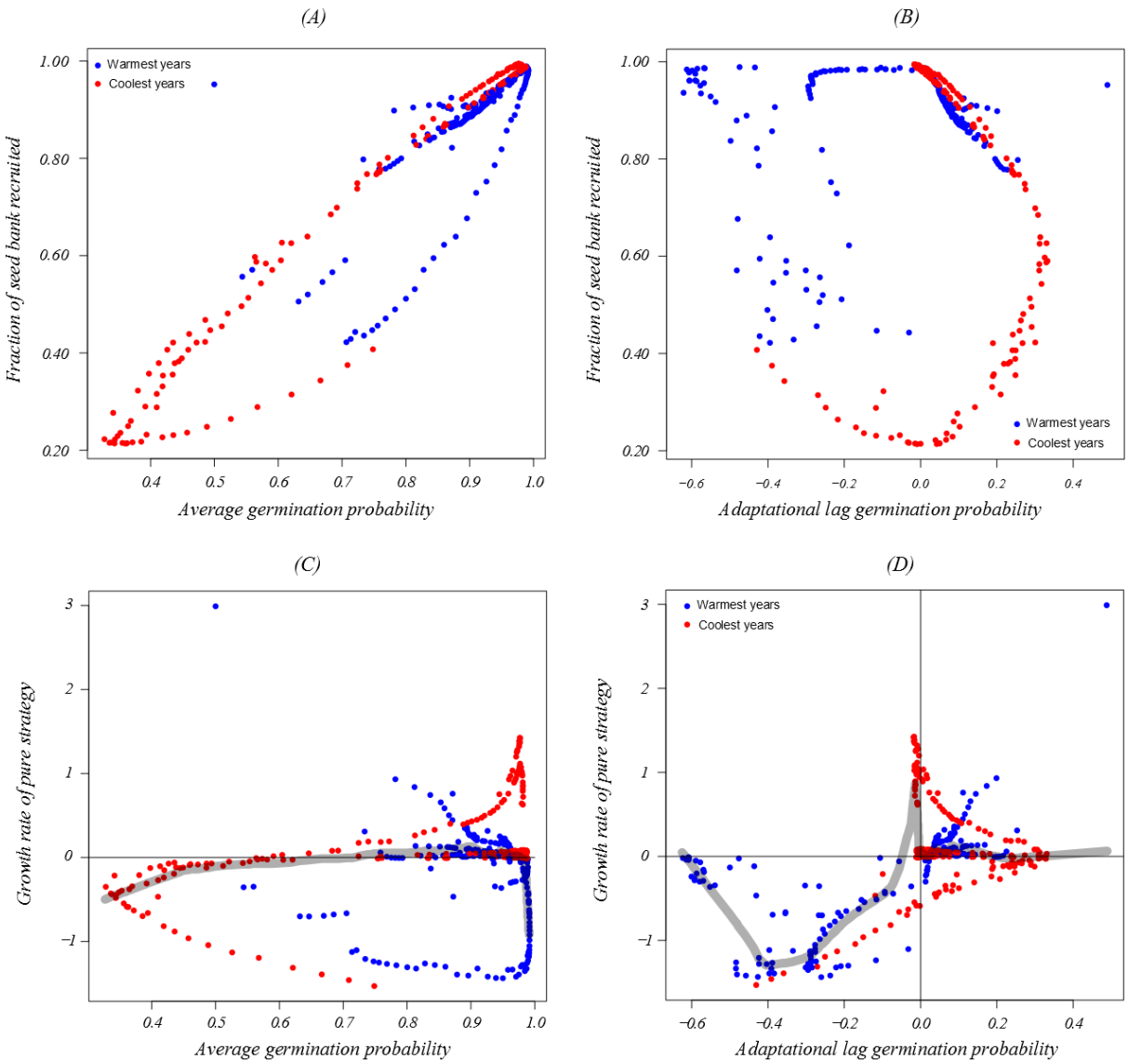
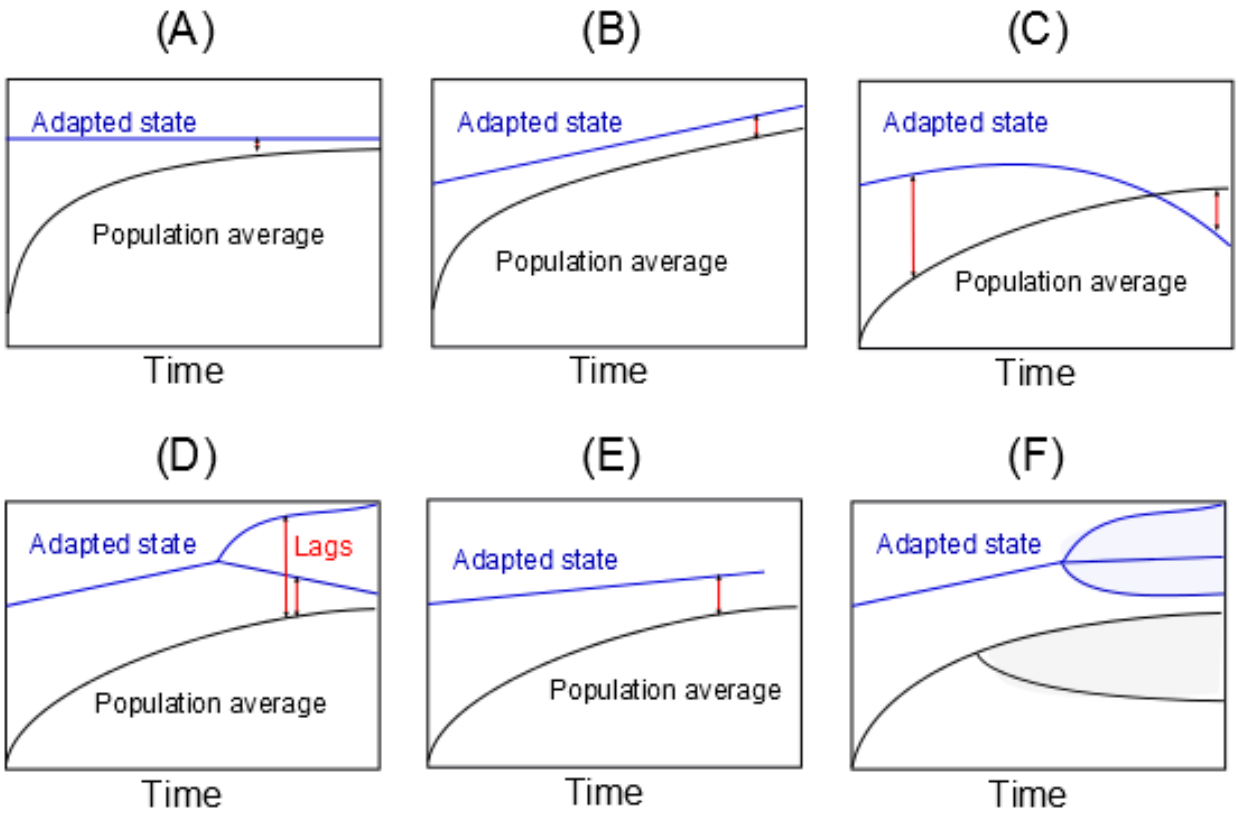
Figure five. A provisory overview of possible adaptational lag patterns. The y-axis represents a scalar trait, the x-axis time. (A) The population approaches an adapted state. (B) There is convergence to an equilibrium adaptational lag. The population lags with respect to the adapted state at a fixed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