Voltinism and resilience to climate-induced phenological mismatch

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Abstract

Changes in the seasonal timing of recurring biological events are considered to be a major component of the global "fingerprint" of climate change. One effect of these changes is that ecologically important seasonal species interactions could become desynchronised as a result of these shifts (i.e. phenological mismatching), leading to reductions in fitness for some or all of the organisms concerned. One important, but unresolved, issue is the extent to which variations in voltinism (the number of generations a population of a species produces per year) may serve to exacerbate, or confer resilience to, the effects of seasonal shifts. Univoltine organisms (those with one generation per year) will always suffer the deleterious consequences of phenological mismatch, whereas multivoltine species are likely to experience at least some relief from these negative effects in generations that occur later in the season. Conversely, univoltine species will experience continual selection to adapt to changing seasonality, whereas multivoltine species will experience reduced or no selection during those generations that occur later in the season. Here, we present a new theoretical model to explore the population consequences of scenarios of changing seasonality and varying voltinism in clonal species. We find that organisms that undergo multiple generations per year show greater resilience to phenological mismatching in the spring and adapt better to changing seasonality, because of the recovery of population size and genetic diversity after each spring mismatching event. These results have clear implications for management and conservation of populations that are threatened by the effects of mismatch.

Keywords

Introduction

Climate change is already having detectable ecological impacts globally (IPCC 2014), including movements in species range boundaries, changes in community and population size structure, and altered patterns of seasonal activity. Changes in the seasonal timing of recurring biological events, such as breeding and migration, (phenological changes) have been a particularly pronounced, with many spring and summer life-history events, for a wide range of taxa, occurring earlier in the year than historically. Estimated mean rates of change of 2.3 to 5.1 days per decade (Parmesan and Yohe 2003; Root et al. 2003; Thackeray et al. 2010) belie considerable among-species variation, which has resulted in concerns that seasonal ecological relationships may be disrupted, with negative consequences for the fitness and population trends of interacting species (Visser and Both 2005). For example, recruitment success in an intensively studied freshwater fish population is partially dependent upon the seasonal synchrony between larval fish hatching and peaks in zooplankton prey populations (Ohlberger et al. 2014), while the individual fitness of insectivorous birds declines when breeding is desynchronized from seasonal caterpillar peaks (Reed et al. 2013). Notably, in both cases, the population-level consequences of phenological desynchronisation are strongly dependent upon demographic processes.

A species' response to phenological mismatch will be determined by the exact nature of the mismatch in question, by the degree of phenotypic plasticity in response to changes in spring and summer events, and by the ability of the species in question to evolve in response to changes in the timing of the important events in their life history. This has been quantified for the common frog (*Rana temporaria*), in the UK (Phillimore et al. 2010). Using current climate change predictions for the UK, Phillimore et al. calculated that for most populations of *R. temporaria* to retain current levels of adaptation they would have to advance their date of first spawning by somewhere between 20 and 40 days by the middle of the second half of the century. It was estimated that phenotypic plasticity, in this case, could only give a maximum advance of between 5 and 9 days. If the remainder is not made up by evolution towards new optimal spawning dates, then *R. temporaria* populations in the UK are predicted to experience a general decline in fitness from phenological mismatch.

One aspect of a species' biology which is likely to have a strong effect on its evolutionary response to phenological mismatch, but which has not previously been considered, is the number of generations the species completes within each year – its voltinism. Consider a univoltine species, with only a single generation every year. As the timing of spring events changes, between-species differences in rates of phenological change may desynchronise consumer-resource interactions at the population level. Variation in the phenological phenotype within the consumer population will allow well adapted (i.e. the most optimally timed) survivors to produce proportionally more of the offspring that form subsequent generations the next year – in other words, there will be selection for those members of the population who are better adapted to the new timing of events, and as new mutants or individuals with new gene combinations that enable better matching to events arise they too will be selected. This selection will be recurring because every generation will be exposed to the effects of phenological mismatch.

Now consider a multivoltine species with several generations every year. As with the univoltine species, phenological mismatch in the spring will mean that the most optimally timed survivors of the spring cohort will be selected for, but these multivoltine organisms will produce offspring that form subsequent generations within the same growing season, leading to several potential differences in adaptation rates between uni- and multivoltine organisms. Firstly, it is likely that these subsequent generations within the same season will experience reduced or no selection regarding the timing of life history events associated with spring dormancy breaking or migration, and this could slow the rate of adaptation because selection will be intermittent, allowing less well adapted genotypes to increase in frequency during the second and subsequent generations, either because of drift or because they have some other fitness advantage. Secondly, if the population does not experience the effects of phenological mismatch in generations other than the first of the season, then reproduction in the second and subsequent generations will allow population-level recovery from the effects of spring mismatching, which is not an option for univoltine organisms. Population recovery during the season means that severe effects of phenological mismatch will be less likely to cause extinction, and the larger size of the population could lead to an increased rate of adaptation (Lanfear et al. 2014) because there will be more individuals present, making a larger target for mutation and the generation of novel gene combinations. This will enhance genetic variation within the population and potentially boost population variation in the phenological phenotype, increasing the probability that some

individuals will be well adapted to the seasonal timing of resources at the start of the following growing season. There will also, of course, be a higher probability that some individuals will be less well adapted which could, under some circumstances, counteract the potential beneficial effect of increased genetic variance. Finally, under "normal" directional selection a multivoltine population would be expected to adapt more quickly than a univoltine one because there are more generations per unit time (Thomas et al. 2010; Bromham 2011). As with population size, this will lead to more novel mutations and gene combinations arising and therefore potentially more individuals within a population who are able to match their phenology to a changed environment.

It is difficult, therefore, to predict how voltinism will affect long-term responses to phenological mismatching. On the one hand, selection on univoltine organisms will act on every generation, whereas multivoltine organisms are likely only to experience selection on spring life-history events intermittently with selection being relaxed in the second and subsequent generations each year, potentially reducing the speed by which a population adapts to phenological mismatch. On the other hand, multivoltine organisms will experience population level recovery from the effects of phenological mismatch in the second and subsequent generations and have more generations per unit time, both of which will potentially allow more genetic variation to arise, enabling adaptation to changing environments. How these conflicting pressures will ultimately affect population survival and adaptation in the face of phenological mismatch is not currently known.

Here, we present a theoretical model which, for the first time, attempts to capture the relationship between shifts in the timing of spring resource peaks and effects upon the population trajectories of consumers which differ in their patterns of voltinism. As an eco-evo model (Moya-Laraño et al. 2014) which allows population sizes to vary as well as gene frequencies the model allows us to test whether, all else being equal, multivoltine species will have a greater or a lesser ability to survive and adapt to phenological mismatching with spring resource peaks [*sensu* the match-mismatch hypothesis, (Cushing 1990)].

Model description

The model is of a clonally reproducing organism that has its emergence date determined genetically. We model spring as occurring on a specific date which is the optimal emergence date for the population in the model. As this date becomes earlier it is assumed that organisms with an emergence date which is no longer synchronised to the start of spring suffer a fitness reduction as a consequence of phenological mismatch with some aspect of their environment. The model organism can have more than one generation per year, but only the first generation is subjected to the fitness consequences of a mismatch between its emergence date and the actual date of spring, so if the species is univoltine then every generation experiences the effects of phenological mismatch due to the optimal date of spring emergence changing, if bivoltine then the generations alternate between experiencing the effects of phenological mismatch and reproducing normally, if trivoltine then one generation experiences the effects of phenological mismatch and the subsequent two generations reproduce normally, and so on.

The population of organisms is modelled as a set of sub-populations ("strains") which differ according to the day when they emerge in spring. This date is assumed to be genetically determined and if the optimal date of spring is different from the emergence date for that strain, then the individuals in that particular strain suffer a fitness reduction according to the fitness function described below.

Setup

The simulation starts with fifty initial strains. Each one has a population size assigned to it, drawn at random from a normal distribution with mean of K/50, where K is the environmental carrying capacity, and standard deviation 10 and rounded to the nearest integer. Each strain then has an emergence day assigned to it (drawn from a normal distribution with mean 90 and sd 3 and rounded to the nearest integer again). If more than one strain gets the same emergence day their population sizes are added together.

Changes in the date of Spring over time

The model is run for fifty years with the day of year of spring set to a value of 90 (i.e. 31st March). This is to allow the population to reach a near-equilibrium with a structure determined

by selection and with the amount of variation in emergence date being set by a process which is essentially mutation-selection balance. Following this initial period the optimal date of spring emergence is allowed to change and to become earlier, with the rate depending on a parameter called *spring.change* in the model code: if 0.2 then it changes by one day every 5 years, if 0.1 then one day every 10 years and so on. The model is run for 100 years with the date of spring changing for a total run of 150 years.

Fitness function

In the model, emergence dates and the date of spring are all expressed as a number between 1 (1st January) and 110 (20th April). The fitness consequences of a mismatch between spring date and emergence date are modelled using a truncated parabola; a quadratic function of the degree of mismatch between the strain in question and the actual date of spring, and with values less than zero set to zero, with a parameter *s* which controls the shape of the function (equation 3 below). Small values of *s* correspond to a situation where the emergence date has to be close to the date of spring for the strain in question to reproduce, and large values give a wider distribution. The function is symmetrical which is not likely to be particularly realistic but in practice we have little knowledge of what the actual shape such functions is likely to be (Miller-Rushing et al. 2010). .

Calculating the population in generation *t*

The population size for each strain in generation *t* is calculated as the population size in generation *t-1* multiplied by the reproductive rate adjusted by how close the total population size (all strains) is to the carrying capacity and with an amount of stochastic noise added. If it is the first generation of the year this is also multiplied by the value from the appropriate fitness function. The population size of strain *i* at time *t* is therefore:

$$N_{i,t} = N_{i,t-1} * (B * D * P_i + Z_i) \qquad (1)$$

Where

B is the reproductive rate in the absence of competition etc.

D is the density dependence term calculated as

$$D = 1 - \frac{N_{total} * (1 - B^{-1})}{K} \qquad (2)$$

P_i is the fitness cost for strain i of phenological mismatch, calculated as

$$P_i = -s * (emergence\ date_i - Spring\ date)^2 + 1 \qquad (3)$$

with negative values of P_i set to zero, and Z_i is stochastic noise, drawn from a normal distribution with mean equal to zero and standard deviation 0.1 (initial analyses indicated that model outcomes were not very sensitive to the amount of stochastic noise).

If the model is run for a multivoltine organism then for generations which are not the first generation of the year the population size of strain i is calculated as above but with the P parameter missing, so

$$N_{i,t} = N_{i,t-1} * B * D + Z_i. \qquad (4)$$

All population sizes are rounded off to the nearest integer.

Mutation

An important aspect of the model is that new strains with different phenologies are able to arise. In the model we refer to this as "mutation" but in reality this would occur via both mutation and novel gene combinations arising via processes such as recombination. Each generation each new individual has a probability of mutating. An individual who mutates will have a new emergence date which is a rounded number drawn from a random distribution with mean equal to that individuals original emergence date and standard deviation equal to 2. We present results here from simulations using "mutation" rates of 0.01 and 0.001. These are obviously much higher than, for example, mutation rates per base pair per generation in normal, stable genomes which are generally estimated to be between around 1 per 10^8 and 1 per 10^{10} base pairs (Baer et al. 2007) but we use these higher numbers because emergence in spring is likely to be controlled by a number of genes, giving a mutational target of the order of 10^5 to 10^6 base pairs. Furthermore, because of the way they are calculated the majority of "mutations" will be the same as, or very close to, the original value so these rates seem reasonable to us. Using lower mutation rates increases extinction rates generally in the model but does not change the qualitative patterns observed.

Model variant 1: effects of phenological mismatch acting on more than one generation

In the model as described above, the effects of phenological mismatch are only experienced by the first generation each year. It is possible that when the organism in question is multivoltine phenological mismatch in spring could have effects on later generations as well, either directly because of continuing mismatch between organism and environment or indirectly if, for example, parental investment in a second generation is reduced because of reduced condition of the first generation arising from their own phenological mismatch. To test whether this might change the behaviour of the model a new variant was analysed in which the negative effects of phenological mismatch in spring are carried over to the second and any subsequent generations in a diminishing manner, so for an organism with four generations in a year the second generation experiences ½ of the fitness reduction of the first generation, the third generation $^1/_3$ of the reduction and the fourth generation ¼.

Model variant 2: stochastic variation in the date of spring

In the model as implemented above the date of spring is a deterministic and entirely predictable value. This does not, of course, reflect reality particularly well because there are stochastic effects acting every year which cause the date of spring to vary unpredictably. To investigate the effect of random fluctuations of this date on the effects of phenological mismatch, a further variant of the model was analysed in which the date of spring fluctuated according to a normally distributed random number with mean zero and standard deviation of zero (no random change), one or two in addition to the directional change specified in the model.

Coding and Simulation

The model was coded in R v. 3.1.2 (R Core Team 2013) and the full code is available in the online supplementary material (Online resource 1). Following initial exploratory analysis simulations were run on a PC running Ubuntu Linux v.14.04 with an Intel Core i7 3770 3.4GHz processor. Parallel simulations on multiple cores were enabled using the Snowfall package (Knaus 2013).

Results

Diversity of outcomes

The typical behaviour of the model is that while the date of spring is constant the number of strains will reach a fairly constant number (essentially being maintained by mutation-selection balance). When the date of spring starts to get earlier there are several possible outcomes. Firstly, the population can go extinct, either immediately or after a period when a few mutant strains are able to briefly invade (figure 1). Extinction occurs due to a "vortex of doom" whereby the changing spring date leads to phenological mismatch for the dominant strain in the population, thus reducing the reproductive output of the population and reducing the overall population size. This then means that fewer new strains which might be better matched to the new spring date arise, so the population becomes increasingly poorly matched to the changing date of spring and eventually becomes extinct. This can be seen in the declining diversity of the population (figure 1C) and in the increasing mismatch between the mean emergence date and the actual day of spring (figure 1B).

The alternative to extinction is that the population can persist. As the date of spring gets earlier, new strains which emerge closer to the optimal date arise and become common, while less well adapted strains become extinct. This can be manifested as new strains sweeping through the population at regular time intervals, leading to regular or semi-regular cycles in the population after spring has started to change (figure 2), or it can be a noisier process without regular cycles being seen in the population (figure 3). In all cases, however, the population is reduced to a smaller size than before, because the continual movement of the date of spring means that the population is never as well adapted as it was when spring stayed constant: note how the mean emergence date tracks the date of spring but is always some time later.

Univoltine populations

Under reasonable assumptions about the rate of change of spring, simulated univoltine populations are prone to extinction, especially when the carrying capacity is small, birth rate is low and when fitness declines rapidly with phenological mismatch (Online resource 2, figure 1). When change is reasonably rapid, so that the date of spring advances by one day every two

years, almost all populations are extinct after 100 years of change unless the carrying capacity, the birth rate and the mutation rate are all high and fitness is not too closely linked to phenological mismatch. Conversely, when the rate of change is one day every 10 years most populations are able to survive and extinction only occurs in small populations when fitness declines rapidly with phenological mismatch.

Uni- versus multivoltine populations

Voltinism has a profound effect on the probability of extinction, which is much lower for multivoltine populations. This appears to be due to the two factors discussed in the introduction: the effect of one or more generation of respite from the fitness consequences of phenological mismatch allowing the populations to increase between periods when they are negatively affected by the changing date of spring, and larger population size and extra generations allowing for more mutation, leading to a greater diversity of strains in the population. Together these mean that even though selection is only acting intermittently on these populations, multivoltine populations are better able to adapt and considerably less likely to become extinct than are univoltine ones. Figure 4 shows how extinction risk varies with voltinism and population size when the rate of change of the date of spring is roughly one day per 3 years, which is a reasonable approximation to the current rate of change (Parmesan and Yohe 2003; Root et al. 2003; Thackeray et al. 2010). As the number of generations per year increases, so the risk of extinction declines and smaller and smaller populations are able to persist – so while even the largest univoltine populations simulated are likely to go extinct except under the least harsh conditions, populations with several generations per year avoid this except when the carrying capacity of the environment is particularly low.

Figure 5 shows how extinction risk varies for populations with varying degrees of voltinism when the rate of change of the date of spring is also allowed to vary. It is again clear from this that univoltine populations are much more vulnerable than populations with several generations per season, with high risks of extinction for univoltine populations over many values of the rate of change in the timing of spring, unless other conditions are benign. Even when the effect of phenological mismatch is minimized, the population birth rate is high and the rate of appearance of new genetic variants is high univoltine populations can still go extinct when the date of spring is changing rapidly, whereas multivoltine populations are much more resilient.

Size of surviving populations.

When a population survives the reduced fitness experienced by most or all individuals in the population that arises from phenological mismatch means that the population densities are reduced to below the carrying capacity (Online resource 2, figure 2), with the extent of the reduction being (as with extinction) determined by factors such as birth rate, the degree by which phenological mismatch reduces fitness and the rate at which the date of spring is changing. One important message from this analysis is that even when the probability of extinction is low the population in question can still experience a considerable reduction in size, as can be seen clearly in the top left panel.

Fitness costs from mismatch carried over to later generations

Allowing the fitness costs from phenological mismatch to affect the second and subsequent generations in each year of multivoltine organisms had little qualitative effect, although it did increase the probability of extinction somewhat (Online resource 2, figure 3).

Effect of stochastic variation in the date of spring

The qualitative results from the model were unchanged by including an element of randomness in the date of spring each year, but overall adding this stochastic element led to an increased probability of extinction (Online resource 2, figure 4). This increased probability of extinction was caused by occasional values for the date of spring which were far from the previous value and which caused severe declines in fitness because of high phenological mismatch. One notable pattern is that when stochasticity was high and the effect of phenological mismatch was strong this could lead to populations which would otherwise be very robust to changes in the date of spring becoming extinct (bottom right hand panel of the figure).

Discussion

This model represents the first attempt to develop mechanistic insight into the relationship between voltinism and response to climate change, with particular regard to the importance of adaptation to phenological mismatch. The basic outputs are similar to those which have been

found for other models of adaptation under sustained environmental change: the trait in question evolves in response to change but lags behind its optimal value, unless the rate of change is too high at which point the population is unable to persist and becomes extinct (Lynch and Lande 1993; Visser 2008; Chevin et al. 2010). Whether extinction occurs is dependent not only on the rate of environmental change but also on factors such as the maximum size of the population under selection, the rate at which new variants arise and the birth rate.

In the introduction we posed the question of whether multivoltine populations were more or less likely to adapt in response to phenological mismatch. Univoltine populations experience selection every generation so might adapt faster, but multivoltine populations have periods of recovery from the effects of mismatch which might lead to better survival. The answer from this model is clear – assuming that only the first generation of each season is affected by phenological mismatch, multivoltine populations or species appear to be considerably more resilient to the negative consequences arising from desynchronisation, and are much better able to adapt to changing dates of spring despite only experiencing intermittent selection. This result holds when the negative consequences of mismatch also affect subsequent generations in a year but with reduced impact – obviously if the impact were the same for every generation then voltinism would make little difference. These findings have obvious relevance to conservation and management of species which might be threatened by phenological mismatch: univoltine species are likely to pay a much higher price and so should be prioritized above similar multivoltine species.

The model described here is an eco-evolutionary model and represents a rather different approach to understanding the effects of continual directional selection from more "traditional" quantitative genetics models (e.g. (Lynch and Lande 1993; Burger and Lynch 1995; Chevin et al. 2010), and for the sake of simplicity a great deal of genetic realism has been left out. Many organisms facing selection from phenological mismatch will of course be sexually reproducing diploid organisms rather than the clonal organisms modelled here, and it is possible that incorporating a more realistic genetic architecture would alter the results presented here, especially given that phenology is likely to be a fairly complex and polygenic trait itself. Nonetheless, as noted above our results mostly conform with those from previous, more genetically based models, which lends a degree of support to our conclusions.

One aspect by which our results differ from those of previous models is in our finding that narrower fitness functions (high values for the effect of mismatch leading to a narrow function with more serious fitness consequences for mismatched organisms) lead to a greater risk of extinction. Quantitative genetics models such as those analysed by Lynch and Lande (1993) have found either that the width of the fitness function is independent of the likelihood of extinction (for large asexual populations) or is negatively related to the risk of extinction (finite sexual populations). Because our results are arrived at by simulation rather than analytically it is difficult to be certain about why this is the case, but we tentatively suggest that it is probably a consequence of the strongly stochastic nature of our model, coupled with the fact that the fitness function is based on phenotypes and an environmental variable expressed as whole numbers. This means that in our model a narrow fitness function can lead to significant reductions in fitness even for organisms that are close to the optimum, and this coupled with the strong chance that when a population is small there will be no individuals in a population that are at the optimal value could lead to an increased risk of extinction. This link between stochasticity, the shape of the fitness function and probability of extinction is supported by the results shown in figure 4 of Online resource 2: note the apparent interaction between stochasticity (in this case in the date of spring) and the width of the fitness function leading to extinction in almost every case in the bottom right hand panel, as noted in the results section.

In addition to genetic effects, it is important to remember that phenology can show considerable phenotypic plasticity, which can act under some circumstances to buffer effects of environmental change. For species with considerable plasticity in their phenology, therefore, it is likely that the effects of changes in the date of spring would be mitigated to some extent and that the risks of extinction would be less severe (Chevin et al. 2010). Some populations could also be plastic in their voltinism, which could influence the eco-evolutionary dynamics of systems such as the one modelled here strongly. Nonetheless, as environmental change continues so phenotypic plasticity can become exhausted and as discussed in the introduction it is likely that even strongly plastic species will be adversely affected by continual directional change in the environment (Phillimore et al. 2010: see also Deputié et al. 2015).

Research to date has focused on mechanisms by which climatic change can affect the timing of recurring seasonal events (phenological effects), and fundamentally alter overall patterns of

seasonal activity via effects upon voltinism. Specifically, recent process-based and empirical modelling of insect population dynamics has suggested that the number of generations completed within each growing season may change as a result of both the earlier initiation of seasonal growth and activity in warmer springs, and more rapid growth and development during warmer growing seasons. Such changes have great socio-economic implications, as climate-induced increases in voltinism may allow larger populations of potentially damaging agricultural pests to develop during warm growing seasons (Altermatt 2010).

The present eco-evolutionary model extends our understanding of the relationship between phenology, climate change and voltinism and shows hypothetical scenarios in which voltinism not only responds to climatic change, but also mediates the sensitivity of populations of organisms to climate-induced phenological mismatching. In this sense, the results are broadly analogous with recent findings that "internal" population attributes, such as abundance and age structure, can influence population sensitivity to "external" ecological influences such as mismatching (Reed et al. 2013a; Ohlberger et al. 2014). Notwithstanding the necessary simplifications that we have made to the genetic architecture of our simulated population, we believe that our model isolates demographic and ecological processes that are potentially relevant to a range of taxa that are multivoltine. These include insects and aquatic microcrustacea such as cladocerans and copepods. In nature, the multiple generations produced by such taxa may be temporally distinct or strongly overlapping.

The purpose of the present study is to highlight a novel mechanism that can mediate the impacts of phenological change upon the survival and reproduction of wild populations. This model is, by necessity, a simplified abstraction of the complex interacting pressures and drivers influencing natural populations, but is proposed as a hypothesis to be confronted and tested with empirical data. The model incorporates a realistic estimate of change in the timing of ecological spring-time, and could be further developed to increase ecological realism by building in process representation to capture the immigration of genotypes with different voltinisms from outside the local simulated population, and local adaptation of voltinism in response to changes in the timing of spring i.e. simulated strains shifting from uni- to bivoltine dynamics, as has been observed in insect populations.

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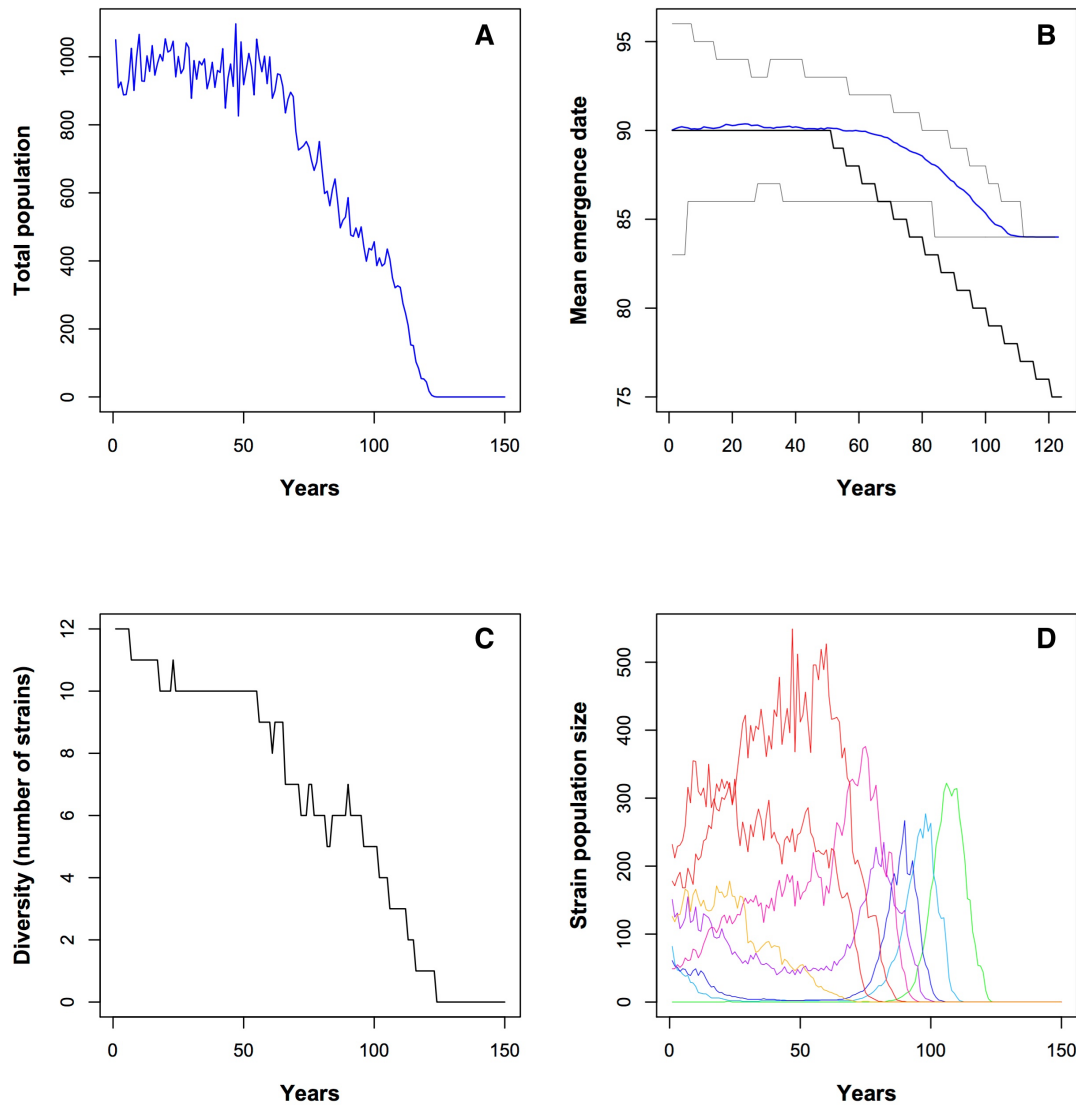
Fig 1 Univoltine population being driven to extinction by phenological mismatch as the date of spring changes. The simulation was run for the first 50 years with a constant spring date and then for 100 years with the date of spring advancing by one day every five years. A = Total population over time, B = mean emergence date (blue) plotted against the "actual" date of spring (black), narrow lines indicate maximum and minimum emergence dates, C = Diversity of the population over time and D = Population size for each strain in the overall population. Note how the number of strains in the population reaches an apparent equilibrium at 10 during the first fifty years and then steadily declines once the date of Spring begins to change. Note that for panel D the colour palette repeats every 10 strains so if colours are reappearing it doesn't mean a strain has been resurrected. Values for this simulation: Environmental carrying capacity = 1000, rate of change of the date of spring =0.2, meaning that the date of spring advances by one day every five years on average, birth rate = 2, probability of an individual mutating = 0.001, parameter determining the fitness cost of phenological mismatch = 0.01
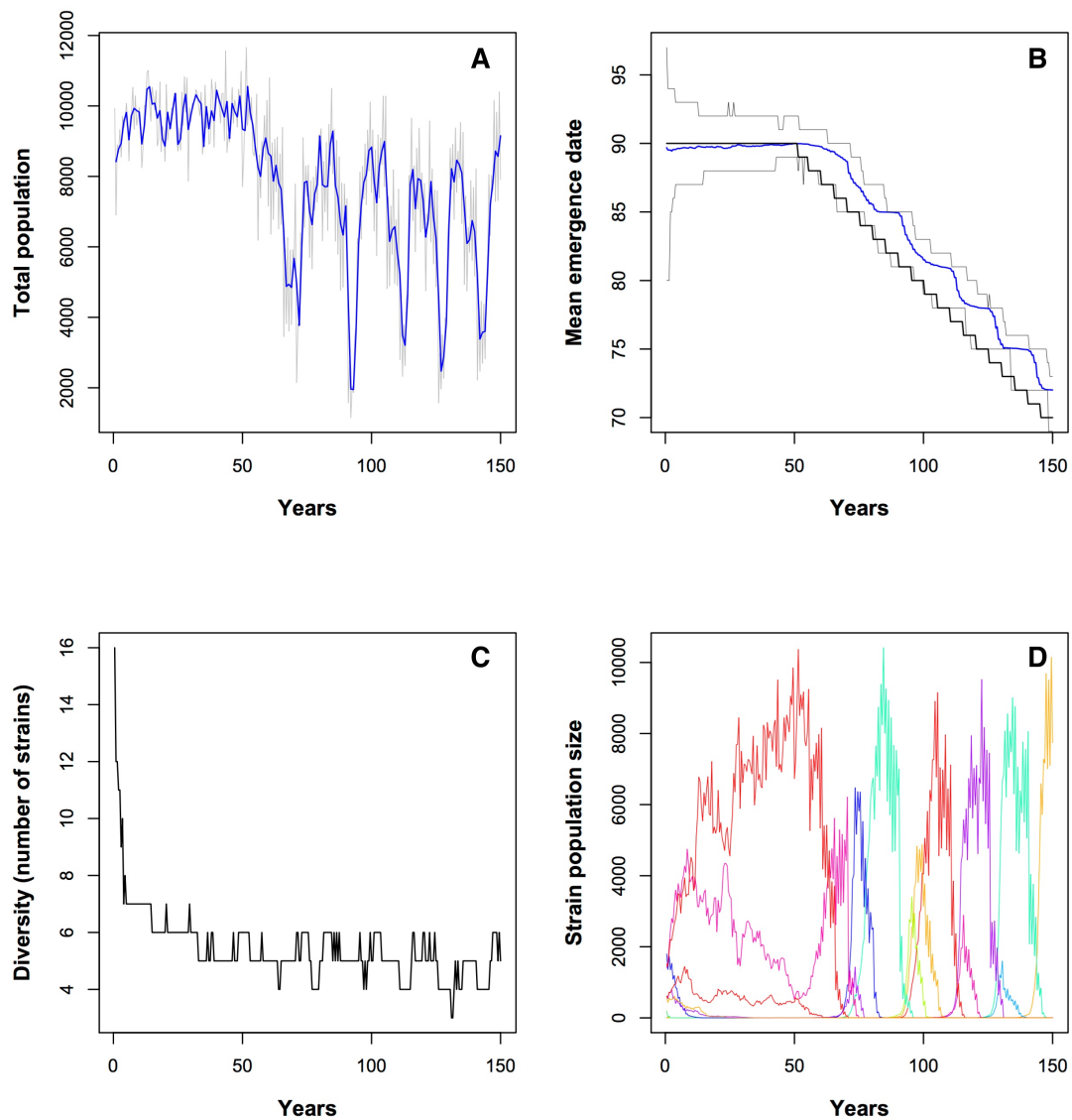
Fig 2 Bivoltine population persisting with apparent cycles. A = Total population over time, B = mean emergence date (blue) plotted against the "actual" date of spring (black), narrow lines indicate maximum and minimum emergence dates, C = Diversity of the population over time and D = Population size for each strain in the overall population. Parameter values are as for figure 1 except the environmental carrying capacity = 10,000, the parameter relating fitness to phenological mismatch = 0.05, the probability of mutation = 0.0001 and the degree of voltinism = 2. Grey lines in panel A indicate population size per generation whereas the blue line indicates mean population size per year
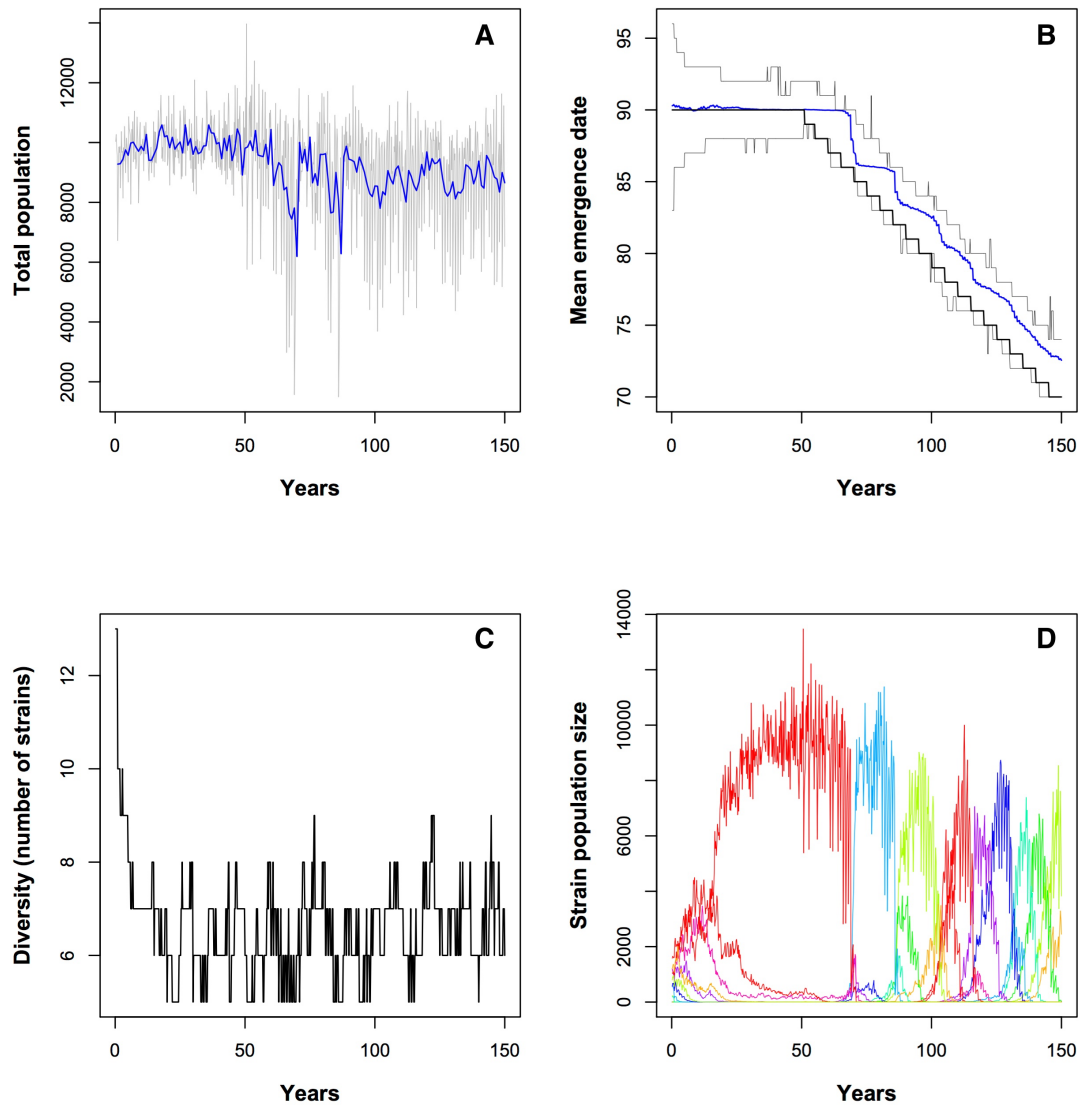
Fig 3 Pentavoltine population persisting with less obvious cycles. A = Total population over time, B = mean emergence date (blue) plotted against the "actual" date of spring (black), narrow lines indicate maximum and minimum emergence dates, C = Diversity of the population over time and D = Population size for each strain in the overall population. All parameter values are as for figure 2 but this is now a pentavoltine simulation. Note that the mean population size after the spring date starts to change is not reduced as much as it is for the bivoltine example
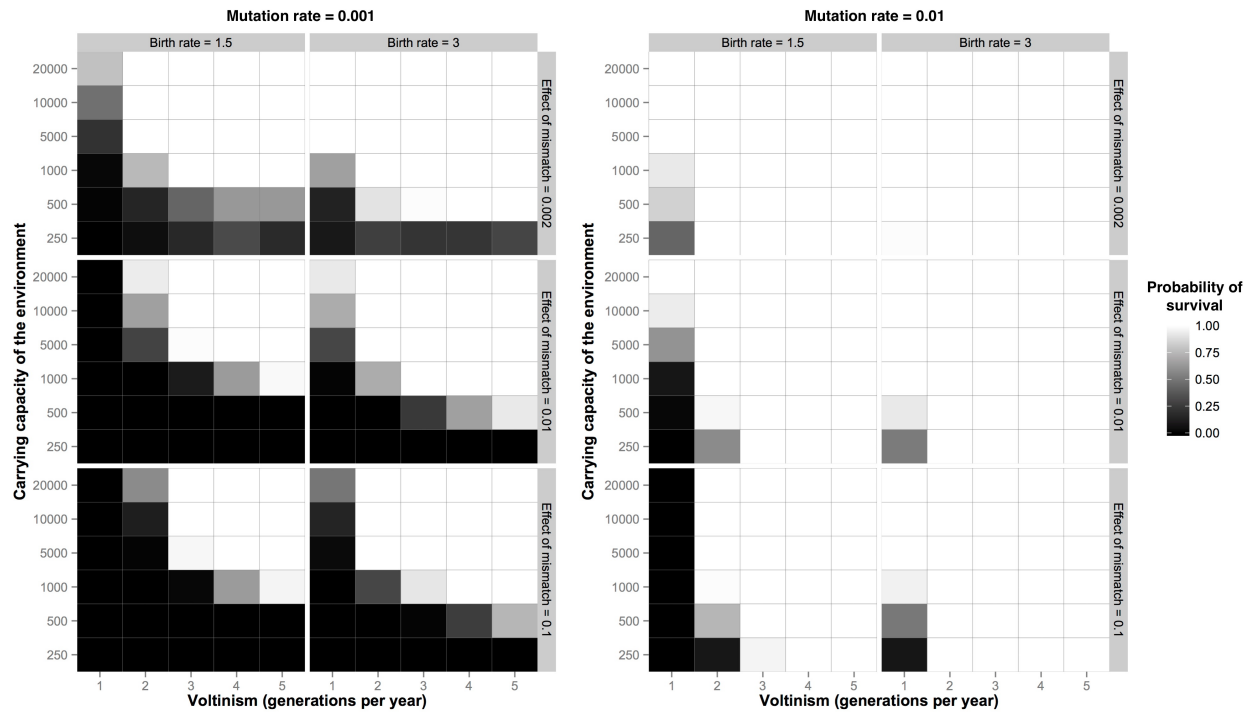
Fig 4 Probability of extinction for populations ranging from univoltine to pentavoltine. In all cases the parameter determining the rate of change of the date of spring was set to 0.3, meaning that on average the date of spring advances by one day every 3.33 years. For each plot the x-axis indicates the degree of voltinism and the y-axis is the environmental carrying capacity for that population. Black squares indicate 100% extinction and white squares 100% survival. The left hand panel shows results for a mutation rate of 0.001 and the right hand one for a mutation rate of 0.01. Left hand columns show results for a low birthrate (1.5 per generation) and right hand columns a higher one (3 per generation). Rows correspond to three values for the parameter relating mismatch to fitness, with the top row having the weakest relationship between mismatch and fitness and the bottom row the strongest. Data based on 100 simulations for each parameter combination
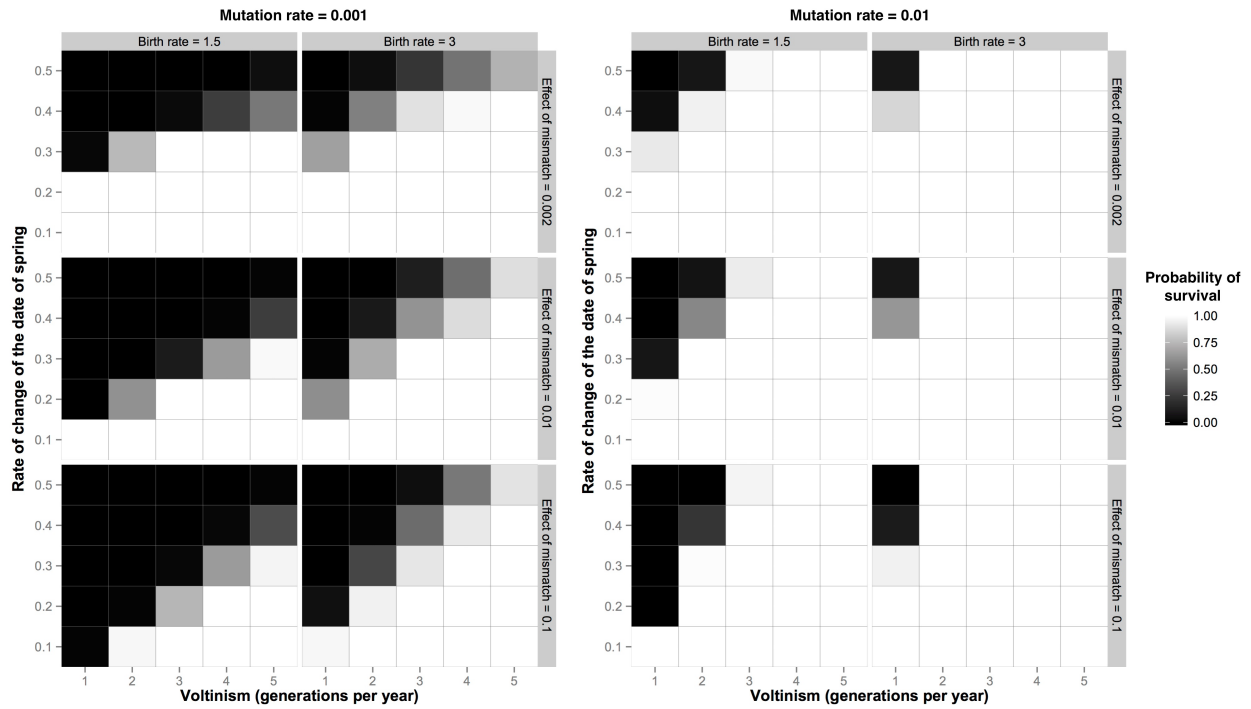
Fig 5 Probability of extinction for populations ranging from univoltine to pentavoltine across the range of rates of change of the date of spring. In all cases the carrying capacity of the environment was set at 1000. For each plot the x-axis indicates the degree of voltinism and the y-axis is the rate of change of the date of spring, with a value of 0.1 indicating that the date of spring advances by one day every 10 years and a value of 0.5 indicating a rate of advance of one day every two years. Black squares indicate 100% extinction and white squares 100% survival. The left hand panel shows results for a mutation rate of 0.001 and the right hand one for a mutation rate of 0.01. Left hand columns show results for a low birthrate (1.5 per generation) and right hand columns a higher one (3 per generation). Rows correspond to three values for the parameter relating mismatch to fitness, with the top row having the weakest relationship between mismatch and fitness and the bottom row the strongest. Data based on 100 simulations for each parameter combination