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Temporal fluctuations in the environment and intra-specific polymorphism: a model simulating the flowering phenology of gorse (*Ulex europaeus*)

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Abstract

The onset and conservation of genetic polymorphism is a major question in evolutionary ecology. The influence of temporal fluctuations in the environment was invoked by early theorists such as J.B.S. Haldane and S. Jayakar in a controversial article published in, 1963, but their frequently cited model has almost never been used with empirical evidence. In this paper, we present a simulation model inspired by the biology of common gorse (*Ulex europaeus*), a species which shows polymorphism of flowering phenology: long flowering plants produce flowers from winter to spring and short flowering plants only flower in the spring. The early fruits of the former run the risk of frost, but largely escape seed predation, while those of the latter escape the risk of frost but are subject to a strong risk of seed predation. These two selection pressures vary unpredictably from year to year, making this flowering phenotype a good candidate to test Haldane and Jayakar's model. Assuming that both flowering types are determined by a single major locus, we devise a simulation model firstly in a diploid form, and secondly by taking into account the hexaploid characteristic of gorse. Our results show that the combination of the two selective pressures acting on gorse flowering phenology can lead to fitness values meeting the Haldane and Jayakar's conditions on geometric and arithmetic means, and to long term maintenance of polymorphism. In addition, the values of the parameters allowing polymorphism persistence and the relative proportions obtained are in agreement with values observed in natural populations. We also show that hexaploidy strongly increases the range of parameters in which polymorphism is self sustaining. These results are discussed in the context of climatic change, where increases of both mean temperature and its variance are predicted.

Keywords

Temporal fluctuations, polymorphism, reproductive phenology, polyploidy, *Ulex europaeus*

1. Introduction

Understanding the maintenance of genetic polymorphism against the erosion by selection is a long standing challenge, and remains nowadays a puzzling subject. Indeed, according to Fisher's fundamental theorem, natural selection tends to fix the alleles with the highest fitness, and should thus produce monomorphic populations (Fisher, 1930). Since it was formulated, this prediction has been considered to be in disagreement with the evidence that polymorphism is widespread in nature (Wright, 1930, Haldane, 1930). Solving this apparent contradiction thus became an important evolutionary and ecological challenge. One of the first mechanisms invoked to explain the maintenance of polymorphism by natural selection was overdominance (Dobzhansky, 1970), but such genetic determinism is too rare to explain the high level of polymorphism observed in natural populations. Frequency-dependant selection is a more common mechanism, since it was demonstrated to be associated to selection linked with pathogens, predators, resource utilization, self incompatibility and behaviour (Maynard-Smith, 1998). However, this mechanism is by no means general. Another cause, often cited and debated, is the spatial and temporal fluctuation of selective pressures. There is much evidence of polymorphism maintained by spatial heterogeneity (reviewed in Hedrick, 1986, 2006), but the influence of fluctuations in time are more debatable (Kimura, 1954, Gillespie, 1972, Karlin and Liberman, 1975, Hartl and Cook, 1974). Indeed, under temporal fluctuation of selective pressures, the outcome of fitness over time is its geometric mean (which increases as the variance decreases), so that the phenotype with the highest geometric mean fitness (i.e. the one with the lowest variance) should increase in frequency and become fixed. The first model predicting maintenance of polymorphism with temporal variation despite this effect was devised by Dempster (1955). However, Dempster's model assumes that the geometric mean fitness of the heterozygote exceeds that of both homozygotes, which is just an effect of overdominance. In fact, most models predict that temporal variations may help to maintain polymorphism, but only if coupled with another mechanism. This mechanism can be spatial variation, as in metapopulation models (e.g. Ronce and Olivieri, 1997, Hanski, 1998, Hui and Li, 2003), and especially frequency-dependent selection (e.g. Calsbeek et al., 2009). Other models predict phenotypic variability, such as bet-hedging strategies or mixed ESS, but not genetic variability (e.g. Satake et al., 2001). Furthermore, the unpredictability of temporal fluctuation increases the likelihood of the preservation of genetic variation (Frank and Slatkin, 1990, Roff, 2002, Yi and Dean, 2013).

The only model that predicts maintenance of genetic polymorphism as the strict effect of temporal variations was proposed in, 1963 by J.B.S. Haldane and S. Jayakar, referred to hereafter as H&J. According to their model, to maintain binary polymorphism, one phenotype must be recessively determined, and the arithmetic mean of its relative fitness to the dominant one over time must be greater than one, while the relative geometric mean must be lower than one. This means that most of the time, the recessive genotype has better fitness, but which is

more variable over time than the dominant one. There were two criticisms of the model. Firstly, mathematicians argued that Haldane and Jayakar's conclusions were not fully exact (Cornette, 1981), but actually this work only demonstrates rigorous limitations, that do not falsify the general conclusions. Secondly, the precise conditions defined by H&J's model were considered to be so restrictive that the likelihood of their occurrence in nature was probably very low (Gillespie, 1972). Furthermore, these conditions were found for a phenotype determined by a single locus and only two alleles, under strict dominance. All these considerations led classical population geneticists to consider that frequency-dependence was the main explanation of polymorphism and that temporal fluctuations of the environment played nearly no role in its maintenance (e.g. Lachance, 2008).

On the other hand, temporal fluctuations, especially in climatic conditions, are attracting more and more attention, and the debate may be taken up again (e.g. Burroughs, 2007, Jackson et al., 2009, Bozinovic, F. et al., 2011, Estay et al., 2014). Lachance (2008) found an interesting index to detect selection in random environments, based on the ratio of the geometric means of homozygote fitness and the geometric mean of the heterozygote one. This finding led him to reconsider H&J's conclusions and to emphasize the importance of geometric means in evolutionary genetics. Recently, Yi and Dean (2013) have strongly advocated the role of fluctuating temporal conditions of selection in the maintenance of biological diversity. They extended the analysis by geometric means to a chemostat model, and found surprisingly large conditions of coexistences. The importance of geometric fitness provides theoretical support for the results of the H&J model, but despite its fame, the model has received almost no empirical or experimental support. To fit the conditions of the model, the two phenotypes have to differ both in their fitness mean and variance, which implies that one phenotype is more risk-prone and the other is more risk-averse. To our knowledge, only two cases that seemed to fit these requirements were studied. Rispe *et al.* (1998) in the case of coexistence between parthenogenetic and sexual aphids, and Tomiuk *et al.* (2004) who investigated the coexistence of diapausing and non diapausing clones in insects. Both produced a model close to H&J's, but they considered the clones i.e. genetically isolated phenotypes, and do not consider explicitly the relationship between geometric and arithmetic means.

Here, we propose to study another case where two phenotypes differ in both their fitness mean and variance: the flowering phenology of the shrub *Ulex europaeus* L. (the common gorse) (Tarayre et al., 2007). In this species, two flowering types coexist in natural populations: short-flowering individuals that flower massively in spring, and long-flowering individuals that flower from autumn to spring. These two flowering types were considered to be two different strategies that reduce seed predation (Atlan et al., 2010). Indeed, the main seed predator of this species, the weevil *Exapion ulicis*, may attack up to 90% of seed pods (Davies, 1928, Barat et al., 2007), but lays eggs only in spring (Hill et al., 1991, Barat et al., 2007). Short flowering plants flower only in spring, so that all their fruits are exposed to seed predation. As a consequence, the reproductive output of short flowering plants is directly linked to the temporal fluctuation of seed predation, which appears to be highly variable depending on the year (Tarayre et al., 2007, Barrat et al., 2007). Short flowering plants are

thus expected to have high inter-annual variation and a low geometric mean of their fitness. In contrast, by flowering in winter, the long-flowering plants partly escape seed predators in time. However, flowering in winter results in being exposed to risks induced by weather, in particular the risk of fruit freezing. Fruits of long-flowering plants spread their risk of failure between freezing in winter and seed predation in spring, and can be considered as bet-hedgers that reduce their temporal variation of fitness (Ripa et al., 2010), resulting in an increased geometric mean. The differences between the two phenotypes were demonstrated to be genetically based and the study of offspring in an experimental garden suggested that the long-flowering phenotype was dominant (Atlan et al., 2010), as required by H&J's model for the phenotype with the highest geometric mean. The flowering polymorphism of gorse thus seems to be a good candidate for polymorphism maintained by the H&J model. However, the species is hexaploid, and an exact fit with H&J's model cannot be expected. On the other hand, extending the model to polyploid determinism may increase its generality.

Our goal was thus to explore a model inspired by the empirical data of flowering phenology of gorse to test whether selection linked with variation in risk spreading can support the theoretical conditions of the H&J model. To do so, we assume that both phenotypes are determined by a single major locus, and are exposed to only two selective pressures, frost in winter and seed predation in spring. We devised the model firstly in a diploid form, and secondly in a hexaploid form. We aimed to answer the following questions: 1/ Can the fitnesses of the two flowering phenotypes satisfy the conditions of the H&J model, and if so, does this explain their coexistence? 2/ Is the range of parameters that allow the coexistence of the two phenotypes compatible with observations in natural populations? 3/ Does the hexaploid nature of gorse facilitate the maintenance of polymorphism?

2. The model

2.1. Fitness of phenotypes

The parameters of the model are inspired by the biology of gorse (Figure 1). We consider that the two phenotypes, short and long flowering plants, produce a similar number of flowers (Tarayre et al., 2007). Short-flowering plants concentrate their blooming in spring, and are only subject to the risk of parasitism (here seed predation). Long-flowering plants flower from autumn to spring, so that they partly escape parasitism, but are subject to frost risk. The whole flower stock can be split in two fractions, whose proportions are denoted Q_f for the fraction exposed to the frost risk, and Q_p for the fraction exposed to the risk of parasitism. The proportion of seed lost due to frost is f . The seed lost due to parasitism is p_s for short flowering plants, and p_l for the Q_p fraction of long-flowering plants exposed to parasitism. We assume that $p_s < p_l$ because short-flowering plants appeared to be less sensitive to parasitism than the exposed fraction of long-flowering plants (Tarayre et al., 2007, Atlan et al., 2010).

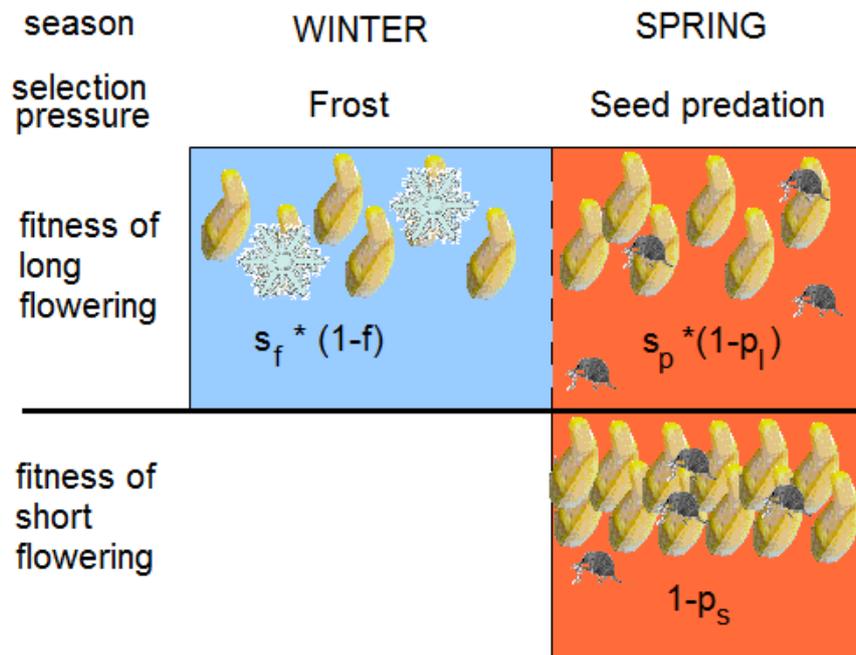


Figure 1. Correspondence between the biological model and the parameters of the model. Long flowering plants flower in both winter and spring. Their winter fraction Q_f is subject to frost risk: f , and their spring fraction Q_p is subject to seed predation risk: p_l . Short flowering plants produce all their flowers in spring and they are all subject to seed predation risk: p_s . Since short flowering plants are less sensitive to seed predation in spring than long flowering plants, $p_s < p_l$, which is represented by the relation $p_s = Sp_l$ with $S < 1$.

The ratio p_s / p_l is noted S , a parameter that represents the relative sensitivity of short compared to long flowering plants. Since $p_s < p_l$, parameter S is bounded in the range $[0,1]$. The resistance of short flowering plants increases as S decreases.

Writing the fitness of both phenotypes is then straightforward:

$$\text{Short flowering: } W_s = 1 - p_s = 1 - Sp_l$$

$$\text{Long flowering: } W_l = Q_f(1-f) + Q_p(1-p_l)$$

Their long term arithmetic and geometric means can be compared to H&J's conditions (the dominant phenotype has higher geometric and lower arithmetic mean fitness than the recessive phenotype). Indeed, H&J's model defined neither the distribution nor the cause of the variations of fitness, but only general condition on their geometric and arithmetic means, over generations. Furthermore, since these conditions applied to phenotypes and not to genotypes, they can be tested whatever the underlying genetic determinism with absolute dominance.

Environment fluctuation is simulated by considering f and p_l as two random variables. They are basically mortality rates, and thus bounded within the interval $[0,1]$. This range leads to the attribution of Beta distributions which have the advantage of giving means bounded in the interval $[0,1]$, together with a large set of relations between mean and variance (referred to hereafter as μ and σ^2). The variance is however bounded in an interval that depends on the mean, $[0, \sigma_{\max}^2]$, with $\sigma_{\max}^2 = \mu(1-\mu)$. To explore the range of mean and standard deviation of the distribution from the parameters a, b of Beta distributions, we used the following transformations:

$$a = [\mu^2(1-\mu)^2 - \mu\sigma^2] / \sigma^2$$

$$b = [\mu(1-\mu)^2 - \sigma^2] (1-\mu) / \sigma^2$$

As a consequence, W_s is distributed as a generalized Beta distribution of parameters a and b bounds $[(1-S),1]$, and W_l is distributed as the sum of two generalized Beta variable, the first of parameters bounds $[0, Q_f]$, the second of parameters bounds $[0, Q_p]$. Thus the relative fitness so obtained is the sum of two quotient variables, which bounds extend from zero to infinity. Although difficult, thus, some closed formal expressions are probably accessible and will be considered in a further study, but a lot of useful conclusions may be obtained from the simulations that we present here.

2.2. Reproduction and selection.

We assume that the two phenotypes arise from a diallelic locus, where "A" is the dominant allele and "a" the recessive allele, and that the proportions of allele "A" and "a" are p and $q=1-p$. We will consider that "A" determines the long-flowering phenotype and "a" the short-flowering phenotype, with strict dominance of allele "A" (a single allele "A" is enough to determine the long flowering phenotype). This determinism is compatible with empirical data obtained in an experimental garden (Atlan et al., 2010).

Crosses are supposed to occur in panmixy, so that after reproduction, the genotypic frequencies reach the Hardy-Weinberg proportions:

$$\begin{aligned}P_{AA} &= p^2 \\P_{Aa} &= 2pq \\P_{aa} &= q^2\end{aligned}$$

After selection, the frequencies of each genotype become:

$$\begin{aligned}P'_{AA} &= \frac{p^2W_l}{W_T} \\P'_{Aa} &= 2\frac{pqW_l}{W_T} \\P'_{aa} &= \frac{q^2W_s}{W_T}\end{aligned}$$

with

$$W_T = p^2W_l + 2pqW_l + q^2W_s$$

And the allelic frequencies at next generation are:

$$\begin{aligned}p' &= P'_{AA} + \frac{P'_{Aa}}{2} \\q' &= \frac{P'_{Aa}}{2} + P'_{aa}\end{aligned}$$

The process is reiterated for a large number of generations, taking the new allelic frequencies as new starting point for the next generation. For the polyploid scheme, see Appendix A.

2.3. Values of the parameters

The parameter calibration was based on data collected during the monitoring performed by Anne Atlan and Michèle Tarayre in natural gorse populations in Brittany (Western France) from, 2001 to, 2007 (partly described in Tarayre et al., 2007) and in an experimental garden (Atlan et al., 2010). The values used initially were those that were in agreement with these observations, and then a wider range of values was explored to test the sensitivity of the model to the parameters.

- For long-flowering phenotypes, the fraction exposed to the risk of parasitism, and the fraction exposed to frost risk were considered to be equal: $Q_f = Q_p = 0.5$, since pod production did not differ significantly between winter and spring (Tarayre et al., 2007).
- The seed predation risk of long flowering plants p_l was assumed to follow a Beta distribution (1,1) that corresponds to a mean of 0.50 and a standard deviance of 0.29. These values were in the range observed in the natural populations (the mean of 5 populations over 4 years varied from of 0.45 to 0.66 and the standard deviance varied from 0.07 to 0.31).

- S , the ratio p_s/p_l was first fixed at 0.7. This value was in the range observed in natural populations, where it varied depending on the year and on the population between 0.48 and 0.86.
- The frost risk f cannot be calibrated from observations, because the temporal variability of this parameter had not been measured. A rough estimation supposed that about, 20% of the pods could be lost and that this proportion was highly variable depending on the year (Taraure et al., 2007). The mean and variance of this parameter was therefore not fixed and the responses to its variation were simulated.

2.4. Simulations

The population was considered as infinite, and only allelic proportions were generated. Each run consisted of 1000 generations, i.e. 1000 iterations of the two steps: panmictic reassortment then selection. In each set of runs, the parameters Q_f (hence $Q_p=1-Q_f$) and S were fixed, while the risk of seed failure due to frost f and parasitism p_l (hence $p_s=Sp_l$) were drawn randomly at each generation in Beta distributions. In each run, the persistence of polymorphism was assessed, as well as compliance with H&J's conditions. The polymorphism was considered to be maintained if none of the two alleles fell below 0.05 in proportion after 1000 generations. H&J's conditions were considered to be satisfied if the fitness of the dominant phenotype (long flowering) had a higher geometric mean and a lower arithmetic mean than the fitness of the recessive phenotype (short flowering).

A first type of simulations focused on the mean-variance of parameter f that allow polymorphism persistence and the H&J's conditions for given values of the other parameters calibrated from empirical data (see §2.3). The space of parameters for $\mu(f)$ and $\sigma(f)$ were explored by first determining the broad limits of allelic frequencies allowing polymorphism, then by simulating once all possible values around this area, by steps of 0.01. For each tested value of $\mu(f)$ and $\sigma(f)$, the geometric and arithmetic means of the fitnesses W_L and W_S were calculated after 1000 generations, and the H&J's conditions were tested. The persistence of polymorphism (none of the two allele frequencies should fall below 0.05 after 1000 generations) was tested with the initial frequencies of allele "A" taken at random between 0.05 and 0.95. The areas of H&J's conditions and polymorphism maintenance correspond to the parameter space where at least 90% of the simulations satisfy these requirements.

A second type of simulations explored all possible combinations of $\mu(f)$, $\sigma(f)$, $\mu(p_l)$ and $\sigma(p_l)$ by steps of 0.02. These represented more than 360,000 combinations, each tested once, with initial frequencies of allele "A" of 0.5. The results on 4 dimensional grids were not easy to visualise, so we tried some methods to reduce them to three dimensions. One of the more enlightening methods was to replace the couple of means of distributions $\mu(f)$ and $\mu(p_l)$ by their ratio $\mu(f)/\mu(p_l)$ on the vertical axis, and to keep their two standard deviations as the two axes of the bottom plan.

3. Results

3.1. Maintenance of polymorphism in diploid simulations

In a first set of simulations (Figure 2), all parameters were attributed with values inspired from empirical distributions (see §2.3), and the tested variables were the means and standard deviations of the frost risk, $\mu(f)$ and $\sigma(f)$. We observe that a persistence of polymorphism is possible, but in a relatively narrow range of values for $\mu(f)$, between 0.1 and 0.23. The range of values of $\sigma(f)$ allowing polymorphism is larger and depends on $\mu(f)$: if we follow the area of polymorphism persistence in the figure from right to left, we observe that variance decreases when mean increases on a parabolic shaped curve. The area of H&J's has a similar shape, but only partly intercepts the area of polymorphism persistence. In some cases the H&J's conditions are satisfied, but no persistent polymorphism was detected (blue area in Figure 2). This might be explained by the fact that we consider that the polymorphism is lost when one of the alleles falls below 0.05, while H&J designated no threshold limit. Figure 3A shows one of these cases: the two alleles are effectively maintained in the sense of the H&J model, but one of the alleles falls below 0.05 before 1000 generations. We also reveal cases when the H&J's conditions are not satisfied, but persistent polymorphism is detected (yellow area in Figure 2).

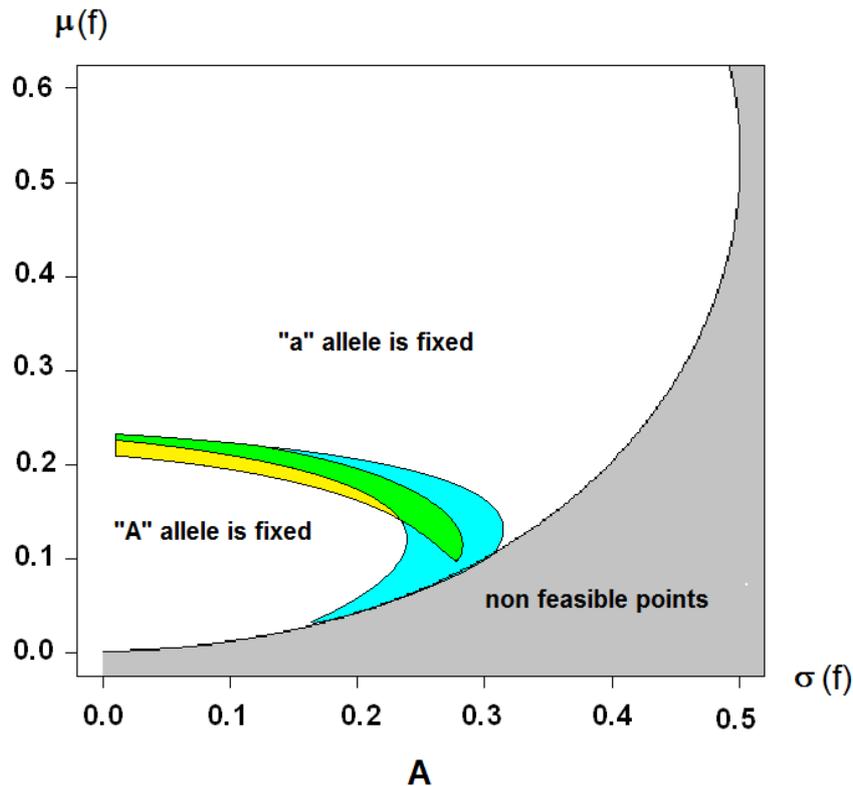


Figure 2: Outcome of the model under a given distribution of seed predation in the diploid case.

x axis and y axis: standard deviation and mean of f , the risk of seed failure due to frost.

Yellow area: polymorphism persistence. Blue area: H&J's conditions. Green area: intersection. Values of the other parameters: $Q=0.5$, $S=0.7$, $\mu(p_i)=0.5$, $\sigma(p_i)=0.29$.

This arises from the fact that the polymorphism is maintained if the two alleles are still present after 1000 generations, while H&J's conclusions hold for an infinite length of time. Figure 3B illustrates one such case, where very slow fixation of the A allele is not reached before 1000 generations. Cases where H&J's conditions are satisfied together with detection of persistent polymorphism (green area in Figure 2) are illustrated in Figure 3C.

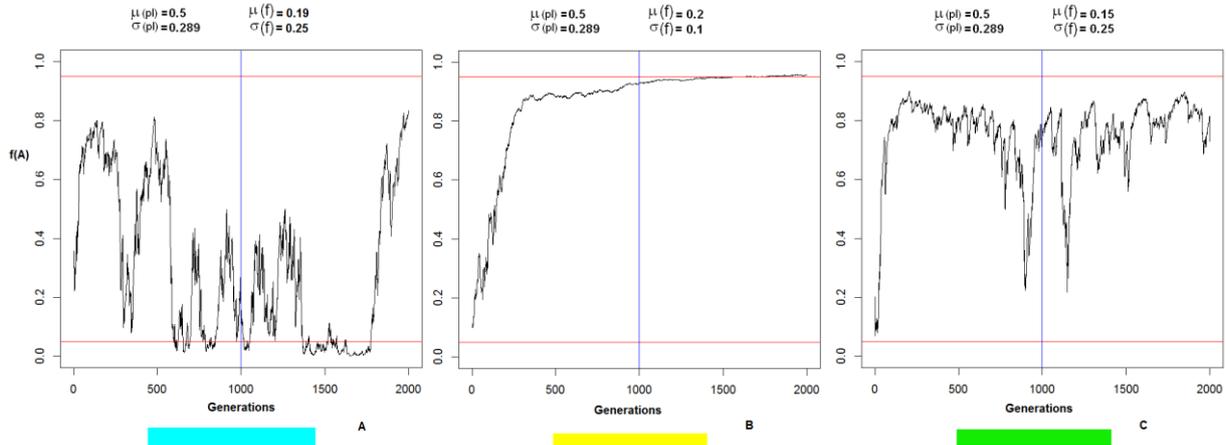


Figure 3: Typical series of allele A frequencies in the three types of areas defined in Figure 1. Fig. 3A: H&J's conditions (blue area in Fig. 1). Fig. 3B: polymorphism persistence (yellow area in Fig. 1). Fig. 3C: intersection (green area in Fig. 1). Red lines: limits of frequency corresponding to our definition of polymorphism persistence (0,05 and 0,95); blue line: 1000 generations.

3.2. Overview of the whole parameter space of the risks of seed predation and frost in diploid simulations

Figure 4 represents the three dimensional graph obtained when all possible combinations of $\mu(f)$, $\sigma(f)$, $\mu(p_1)$, $\sigma(p_1)$ were tested (with values of the fixed parameters equal to those of Figure 1 and an initial frequency of allele "A" fixed at 0.5). The scatterplot is limited by construction to a maximum of 0.5 for the two standard deviations (the maximum possible standard deviation for a Beta variable). However, two other limits appear as a result of simulations: all the combinations allowing polymorphism are below the plane $\mu(f)/\mu(p_1) = 1$ (horizontal plane on Figure 4). It signifies the coexistence of the two types, implying that the risk of seed failure due to frost must be lower than the risk of seed predation. Another limit concerns $\sigma(f)$, that must stay below 0.34 (horizontal plane on Figure 3). It signifies that coexistence cannot be obtained if variance of frost risk is too high. Within these constraints, polymorphism can be obtained for a large range of parameter combinations.

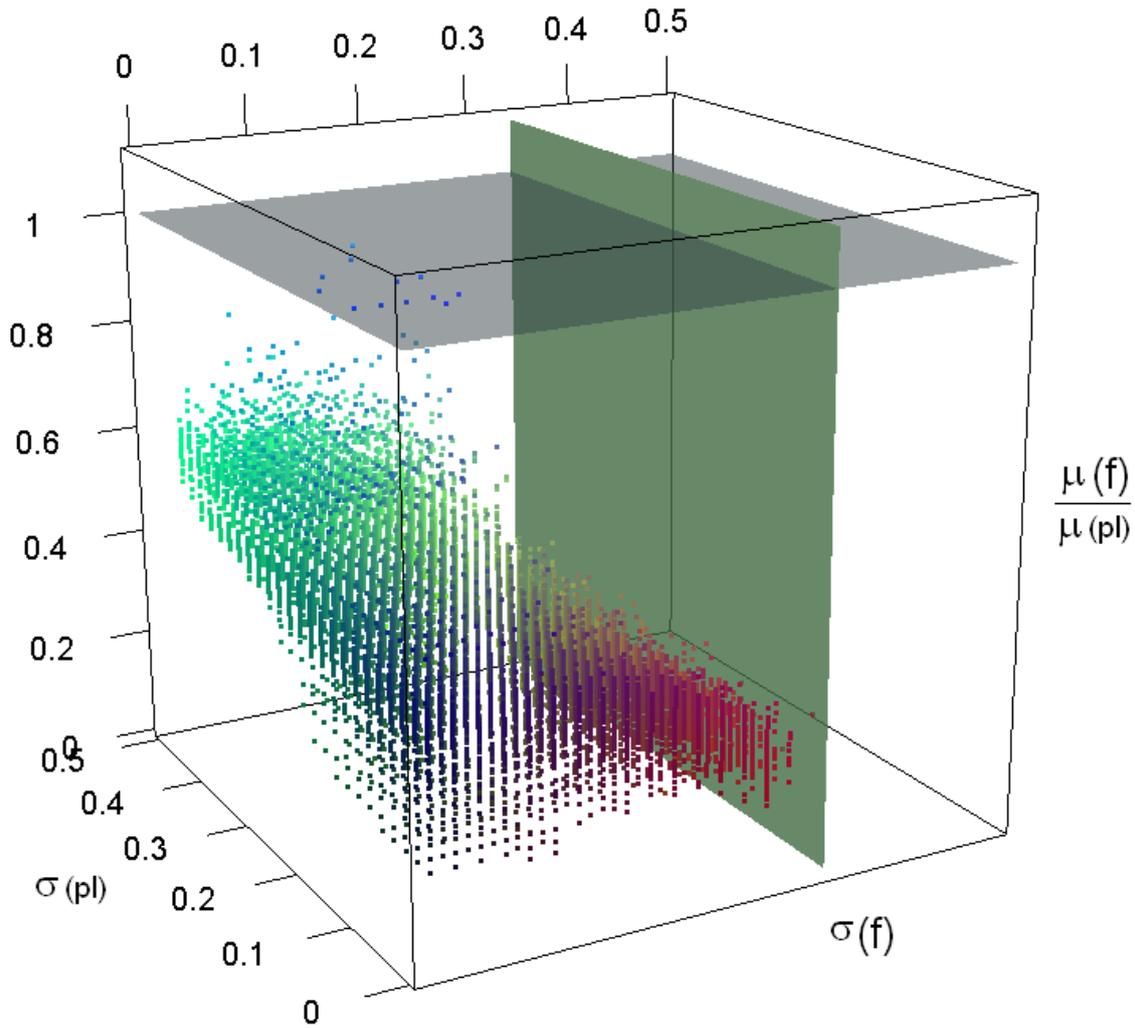


Figure 4: Risk distributions allowing polymorphism persistence.

Floor axis: standard deviance of frost risk: f (front), and of seed predation risk: p_i (depth).
Vertical axis: ratio $\mu(f)/\mu(p_i)$.

Each point plotted represents a simulation where polymorphism was maintained; colours are only used to strengthen the distinction between these points. No polymorphism maintenance was observed above the the two planes represented.

Horizontal plane, on top: $\mu(f)/\mu(p_i) = 1$. Vertical plane: $\sigma(f)=0.34$.

Values of the other parameters: $Q_f=0.5$, $S=0.7$

3.3. Sensitivity to fixed parameters in diploid simulations

Figure 5 illustrates the consequences of a variation of Q_f , the fraction of the long flowering plants which is sensitive to winter frost and S , the factor measuring the relative sensitivity to seed predation of short flowering plants compared to the fraction Q_p of long flowering plants exposed to seed predation.

The central simulation (Figure 5B) gives the reference calibrated from empirical data, with the same parameters values as Figure 1. The increase of Q_f (Figure 5A) results in a very small modification of the range of standard deviation of f likely to preserve polymorphism: the standard deviation limit remains around 0.3 although a little greater than in the reference.

The consequences on the mean are greater, but the area of the parameters allowing coexistence does not change much. The biological interpretation is that, when the fraction susceptible to frost increases (reducing the fraction exposed to seed predation), the mean frost risk must increase too.

The increase of S (Figure 5C) has consequences on the range of both mean and standard deviance of f , that have to increase to preserve polymorphism. These modifications are also correctly predicted by the H&J model. The biological interpretation is that, when the susceptibility of short flowering plants to parasitism increases (that disadvantages short flowering plants), both mean and variance of frost risk (that disadvantages long flowering plants) must increase to preserve the polymorphism.

3.4. Comparison between diploid and hexaploid simulations

Figure 6 presents the same simulations as Figure 5 but in the hexaploid case. Figure 6B shows that, when values of all parameters but $\mu(f)$, $\sigma(f)$ were fixed to those calibrated by empirical data, the area of polymorphism persistence is much larger than in the similar diploid case (Figure 5B). This is especially true for the transitory polymorphism zone (yellow zone). Conversely to the diploid simulations, this yellow zone includes all of the area below the H&J zone, which means that there is no absolute minimum for $\mu(f)$ allowing polymorphism, and that the allele A cannot be fixed.

When all possible combinations of $\mu(f)$, $\sigma(f)$, $\mu(p_1)$ and $\sigma(p_1)$ were tested with the same fixed parameters, results were very similar to the diploid case (Figure 3), with an upper limit of $\mu(f)/\mu(p_1)$ at 1, and an upper limit for $\sigma(f)$ at 0.36. The only difference was that, as can be expected from Figure 6B, the set of parameters allowing polymorphism was larger, especially for low values of $\mu(f)$ (data not shown).

The effects of an increase of S or f (Figures 6A and 6C) are qualitatively similar in the hexaploid and in the diploid case, but in the latter, the area of the parameter space allowing coexistence enlarges more clearly, moderately when Q_f increases, but noticeably when S increases. The role of polyploidy in protecting polymorphism is even more efficient as these two parameters increase.

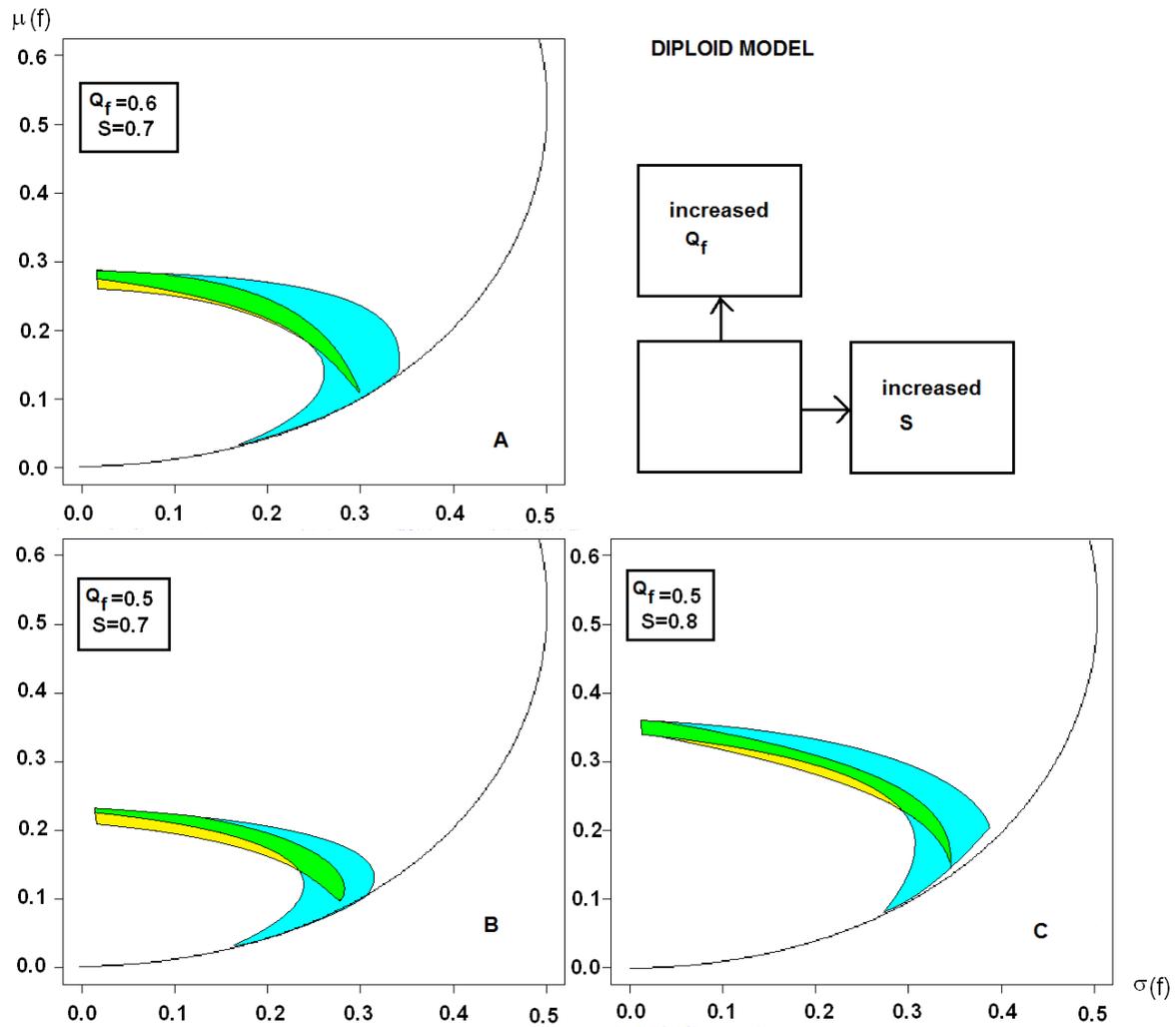


Figure 5: Sensitivity of the model to the parameters and S in the diploid case.

5A: central simulation (same as Fig. 1); 5B: increased Q_f ; 5C: increased S .

x axis and y axis: standard deviation and mean of f , the risk of seed failure due to frost.

Yellow area: polymorphism persistence. Blue area: H&J's conditions. Green area: intersection. Above the coloured zone, allele "a" is fixed; below this zone, allele "A" is fixed.

Values of the other parameters: $\mu(p_i)=0.5$, $\sigma(p_i)=0.29$.

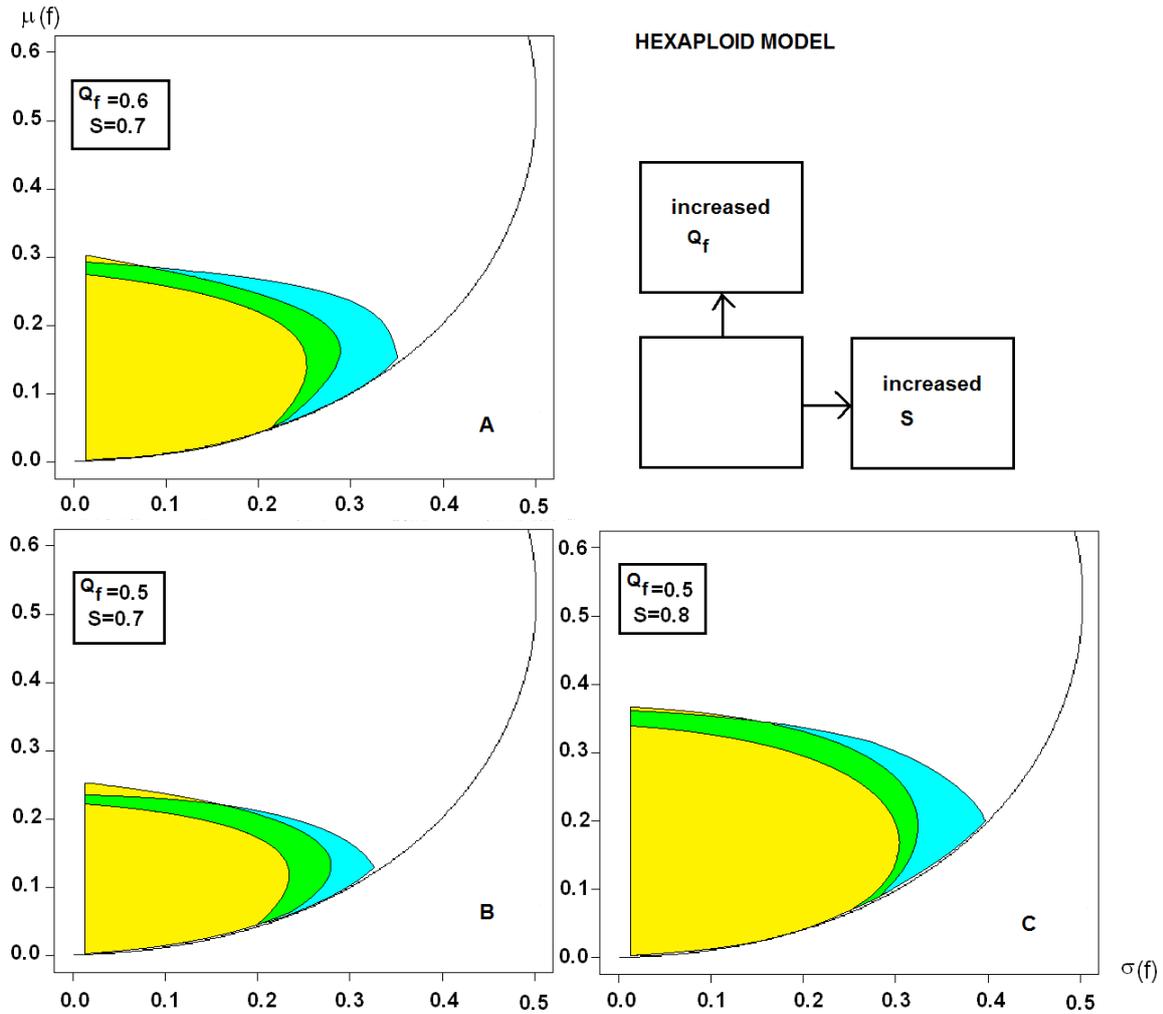


Figure 6: Sensitivity of the model to the parameters and S in the hexaploid case.

6A: central simulation; 6B: increased Q_f ; 6C: increased S .

x axis and y axis: standard deviation and mean of f , the risk of seed failure due to frost.

Yellow area: polymorphism persistence. Blue area: H&J's conditions. Green area: intersection. Above the coloured zone, allele "a" is fixed; below this zone, allele "A" is fixed.

Values of the other parameters: $\mu(p_i) = 0.5$, $\sigma(p_i) = 0.29$.

4. DISCUSSION

The model based on the example of *U. europaeus* suggests three major conclusions: firstly that a combination of two unpredictable selective pressures can lead to mean fitness satisfying the conditions of Haldane and Jayakar's model; secondly, that genetic polymorphism can be maintained by temporal fluctuations of the environment; and thirdly, that a hexaploid determinism substantially enlarges the range of conditions under which polymorphism resists.

4.1 H&J's conditions and the maintenance of polymorphism

The required conditions of the H&J's model for polymorphism maintenance are that the dominant phenotype has higher geometric means and lower arithmetic mean fitness than the recessive phenotype. We found that some combinations involved in the temporal fluctuation of seed failure in *U. europaeus* can satisfy this requirement, and they provide one of the first examples corresponding to a concrete biological situation. The system that we described has the particularity of combining two selective pressures based upon two independent risks. Obtaining the combination of geometric and arithmetic means required by the H&J model may be easier when considering a combination of selective pressures than when considering only one. Facing several risks is not specific to the flowering phenology of gorse, so the H&J's conditions may be more common than previously thought.

For a given the distribution of seed predation risk calibrated from empirical data, we found that mean and variance combinations of frost risk that satisfy to the H&J's conditions are bounded in a narrow area. In addition, they do not fully overlap the ranges of combinations allowing polymorphism persistence. This arises from the fact that our definition of persistence is different from that of H&J's model. Firstly, we consider that the polymorphism is lost when one of the alleles falls below 0.05 before 1000 generations, while H&J defined no threshold limit. Thus, the H&J model can predict maintenance of polymorphism at the expense of periods where one allele falls below infinitesimal values, whereas we do not consider this as persistent polymorphism. Our definition is more restrictive, but also more realistic, since values below 0.05 are very likely to lead to extinction in finite populations. Secondly, we consider that polymorphism is maintained if the two alleles are still present after 1000 generations, even if it is transitory polymorphism, while H&J's conclusions hold for an infinite length of time. On that point, our definition is less restrictive, but again more realistic, since gorse is a pioneer species, and its populations persist for much shorter periods than a thousand generations. The polymorphism is however more stable when parameters values are close to H&J's conditions.

The area of the parameter space where polymorphism is maintained is substantially enlarged in the hexaploid case, especially for transient polymorphism. The extension mainly concerns frost risk, which can fall to nearly zero, without fixing the long flowering phenotype. This suggests that genome redundancy associated with a high level of dominance protects the recessive alleles efficiently against the hazards of fluctuating selection. This is a novel characteristic of plant polyploidy. Many evolutionary consequences of polyploidy have been cited in the past (Otto, 2010, Parisod, 2012), but as far as we know, an increase in the likelihood of genetic polymorphism maintenance has not been mentioned.

4.2 Parameters influencing the maintenance of polymorphism

When all possible values for the mean and variance of frost and seed predation risks were explored, maintenance of polymorphism was possible for a large range of parameter combinations. There are however some clear limits. Firstly, in most cases, polymorphism can be maintained only below a given threshold of variance, both for frost risk and for seed predation risk. This confirms that variance plays a key role in polymorphism maintenance, as already suggested by previous studies (e.g. Lachance, 2008, Yi and Dean, 2013). Secondly, the mean frost risk must be lower than the mean seed predation risk, unless long flowering alleles are eliminated. The two risks are not equivalent, because seed predation risk is common to both of the phenotypes, while frost risk is specific to the long flowering one. Long flowering plants can compensate for their disadvantage in facing frost risk by escaping seed predation in time only if failure due to frost is lower than failure due to seed predation.

The maintenance of polymorphism is also dependent on two fixed characteristics of the phenotypes, the proportion of flowers exposed to frost in winter, and the relative sensitivity of short flowering plants to seed predation in spring. An advantage conferred by one of this parameter to long flowering plants has to be compensated by an increase of their frost risk. This confirms that escaping seed predation in time on the one hand, and relative insensitivity to seed predation on the other hand, can be viewed as two alternative evolutionary strategies. In the hexaploid case, short flowering strategy can be maintained whatever the mean and variance of seed predation risk while long flowering strategy can be maintained only if frost risk is not too high, neither in mean, nor in variance. In this way, long flowering appears as a risk-averse strategy, and short flowering as risk-prone (Caraco, 1981, 1988, Kačelnik, 1984). Such a coexistence of two strategies has been described previously, e.g. for seed germination (Philippi, 1993), parthenogenesis and sexuality (Rispe et al., 1998), timing of reproduction (Satake et al., 2001) or diapause (Tomiuk et al., 2004) but they correspond to phenotypic dimorphism known as bet-hedging (Gillespie, 1974), mixed ESS (Maynard-Smith, 1982), or clonal diversity, and not to the genetic polymorphism described here.

4.3. Agreement with the observations made in the wild.

Our results agree with observations made in the wild. Indeed, all parameters except for frost were calibrated using data from a monitoring programme of natural populations in Brittany (Western France), maintenance of polymorphism occurs within a mean range of seed failure due to frost between 0 and 30%, which is compatible with our observations. In this range of parameters, the outcome of the model predicts that populations should exhibit: 1/ a high and stochastic variability of the frequency of the two alleles, and 2/ on average, a lower frequency of long flowering alleles. This is in agreement with the observations made in natural populations, which show very high variability of the frequency of long flowering plants among populations. Tarayre et al., (2007) monitored 16 populations in Brittany and the frequency of long flowering plants varied from 0 to 78%, with a mean of 22% and a mode of 15%. Furthermore, the hexaploid model predicts that the short flowering type can be fixed (especially above a threshold of frost risk), but not the long flowering type. This again is in

agreement with observations in the wild, since populations containing only short flowering plants have sometimes been observed (Tarayre et al., 2007, Delarue et al., 2014), while populations with only long flowering plants have never been described. Indeed, long flowering plants can be maintained only if frost risk is moderate, without too many fluctuations and above all, not reaching high values. This is the case in Brittany, which is characterized by a mild oceanic climate and more generally in the native range of gorse. It is thus likely that the polymorphism of flowering phenology observed in native populations of gorse, and more specifically in Brittany, is maintained by the temporal variations of the selective pressures induced by frost and seed predation.

A more realistic model could include drift (finite populations), overlapping selection, or partial homogamy. The effect of drift was partly taken into account by considering a threshold of allele frequency of 5%. Partial homogamy should restrict the range of parameters allowing polymorphism, but this may be compensated for by overlapping generations, that facilitate the maintenance of polymorphism (e.g. Ellner and Sasaki, 1991). However, the aim was not to simulate the situation of gorse precisely, but to test whether a combination of two random selective pressures could allow polymorphism maintenance.

4.4. Conclusion

The framework designed by Haldane and Jayakar more than fifty years ago still appears relevant, despite the criticism it has received. We observed that various mechanisms made it possible to broaden its validity, including the combination of risks and the genetic protection offered by polyploidy. This result suggests that maintenance of genetic polymorphism by temporal fluctuations of the environment may be much more common than previously envisaged.

Most studies on the effect of variation in environmental conditions explored changes in the mean of biotic and abiotic selective pressures, rather than changes in their variance (Root et al., 2003, Tittensor et al., 2010); although some of them did consider the consequences of extreme events (e.g. Jentsch et al., 2007). Furthermore, these studies were mainly concerned with the maintenance or disappearance of the ecological niches of species, and consequently with inter-specific diversity (Walther, 2010, McMahon et al., 2011). Yet, in a context of global changes, not only the mean, but also the variance of environmental conditions are expected to change, and these changes may impact not only inter-specific diversity, but also intra-specific diversity. Our study shows that the variance of environmental conditions can be as important as their mean when considering the preservation of the intra-specific diversity. It also confirms that including the impact of the variance of environmental selective pressures is necessary to gain a better understanding and to improve predictions, of the evolution of intra-specific diversity in the context of global change.

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Appendix A: reproduction and selection in the hexaploid case

At generation 0, the proportions of allele A and a are p and $q=1-p$. We assume that breeding is panmictic, and that each of the six chromosomes of a hexaploid gamete segregates independently. The four possible gametes, AAA, AAa, Aaa, aaa are expected in proportions, p^3 , $3p^2q$, $3pq^2$ and q^3 respectively, and these proportions are the terms of the development of the binome $p + q$ raised to power 3. These gametes lead to generation 1, where genotypic frequencies are the terms of binome $p + q$ raised to power 6. For commodity, in the following text we will use, a chemical-like notation, in which each genotype is defined by two letters, A and a , followed by a subscript indicating the number of alleles of the respective types in it. The seven resulting genotypes are therefore referred as: A_6 , A_5a , A_4a_2 , A_3a_3 , A_2a_4 , A_1a_5 , a_6 . Their relative proportions before selection are respectively:

$$P_{A_6} = p^6, P_{A_5a} = 6p^5q, P_{A_4a_2} = 15p^4q^2, P_{A_3a_3} = 20p^3q^3, P_{A_2a_4} = 15p^2q^4, P_{A_1a_5} = 6pq^5, P_{a_6} = q^6$$

The associated fitness of each of the seven types must then be defined. Under the hypothesis of strict dominance, the first six types determine the long flowering phenotype, and their fitness is W_l , and the seventh type has a short flowering phenotype with a fitness W_s . The total fitness is W_T . Taking the equations into account, gives:

$$W_T = W_l(p^6 + 6p^5q + 15p^4q^2 + 20p^3q^3 + 15p^2q^4 + 6pq^5) + W_s q^6$$

The frequencies after selection are therefore:

$$\begin{aligned} P_{A_6} &= p^6 \frac{W_l}{W_T} \\ P_{A_5a} &= 6p^5q \frac{W_l}{W_T} \\ P_{A_4a_2} &= 15p^4q^2 \frac{W_l}{W_T} \\ P_{A_3a_3} &= 20p^3q^3 \frac{W_l}{W_T} \\ P_{A_2a_4} &= 15p^2q^4 \frac{W_l}{W_T} \\ P_{A_1a_5} &= 6pq^5 \frac{W_l}{W_T} \\ P_{a_6} &= q^6 \frac{W_s}{W_T} \end{aligned}$$