

# Evolution of individual variation in a competitive trait: a theoretical analysis

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## Abstract

When competitive traits are costly, negative frequency dependence can maintain genetic variance. Most theoretical studies examining this problem assume binary polymorphisms, yet most trait variation in wild populations is continuous. We propose that continuous trait variation can result from continuous variation in resource quality and that, specifically, the shape of the resource distribution determines trait maintenance. We used an individual-based model to test which conditions favour the stable maintenance of variation and which cause temporal fluctuations in trait values. This approach, inspired by contrasting outcomes of previous studies regarding variance and fluctuations in trait values, clearly showed a decisive role played by the shape of resource distributions. Under extreme conditions, e.g., the absence of resource variation or with very scarce resources for weak competitors, traits evolved to a single non-competitive or highly competitive strategy, respectively. Most other distributions led to strong temporal fluctuations on trait values or the maintenance of stable, standing variation. Our results thus explain the contradicting outcomes of previous theoretical studies and, at the same time, provide hypotheses to explain the maintenance of genetic variation and individual differences. We suggest ways to empirically test the proposed effects of resource variation on trait maintenance.

**Keywords:** maintenance of variation, standing variation, negative frequency dependence, individual-based model, resource distribution, temporal fluctuations

## Introduction

High values for evolvability and heritability have frequently been found for traits that are supposedly under strong selection (e.g., Houle, 1992; Merilä & Sheldon, 2000). This is surprising, as selection should tend to erode standing genetic variation according to Fisher's fundamental theorem (Grafen, 2015). There are several theoretical explanations for such findings. Temporal or spatial fluctuations in selection could maintain genetic variation in populations, as traits that are under positive selection in some environments can be selected against in other environments (Radwan et al., 2016; Reinhold, 2001; Svardal et al., 2015). Another widely discussed possibility is the presence of negative frequency-dependent selection, meaning that the direction of selection changes from positive to negative with increasing frequencies of phenotypes (Trotter & Spencer, 2007). Negative frequency-dependent selection has been suggested to explain the evolution of variation in resistance to parasites or diseases. Bacteria and parasites tend to be better adapted to more frequent genotypes and thus selection can favour rarer host genotypes (Hamilton & Zuk, 1982). Another source of negative frequency-dependent selection may be competition for resources. Theoretical examinations of the evolution of costly investments into competition have shown that negative frequency-dependent selection can lead to the maintenance of genetic variation under many

environmental conditions (Baldauf et al., 2014; Kikuchi & Reinhold, 2021; Wolf et al., 2007, 2008). However, we do not know what characterizes environments that favour variation, especially when traits vary continuously.

The vast majority of theoretical studies on frequency-dependent selection and its role in maintaining genetic variation assume a small, discrete number of genotypes. Often, only two or three alleles are assumed to produce a limited number of phenotypes (Broom et al., 2018; Christie et al., 2018; Harris et al., 2008; McElreath & Strimling, 2006; Sinervo & Lively, 1996; Wolf et al., 2007, 2008). These simple models of negative frequency-dependent selection are nevertheless very helpful in giving criteria for the maintenance or erosion of genetic variation, e.g., in small populations, under inbreeding, with temporal or spatial fluctuations in selection, or when overdominance in fitness is present. However, with these simplified models, it is very hard to give quantitative predictions of genetic or phenotypic variation that can be maintained and how this depends on environmental conditions. A few studies have allowed a continuum of phenotypes to occur simultaneously in populations. In one of these, Baldauf et al. (2014) used individual-based simulations to show that dynamic fluctuations in the value of traits frequently occur when individuals with costly competitive traits compete for resources that vary in quality. Here, “costly” means that

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resources that could otherwise be utilized for offspring production are invested into competitive ability. In most of their analyses, Baldauf et al. (2014) assumed that there were only two types of resources: good resources that were rare and poor resources that were unlimited. Under these conditions, recurring fluctuations in mean trait values occurred. These fluctuations were caused by an initial arms race in the development of competitive traits resulting in extreme trait values, which subsequently allowed the invasion of less competitive trait values. In contrast to Baldauf et al. (2014), another study showed that under broad and realistic conditions of costly competition, temporally stable polymorphisms of many genotypes were often maintained (Kikuchi & Reinhold, 2021). Even though there are many similarities between these two approaches, the differences in the stability of the outcomes are striking. Baldauf et al. (2014) obtained dynamic fluctuations in mean trait value assuming binary or uniform distributions of resource quality. In contrast, Kikuchi and Reinhold (2021) observed stable polymorphisms when they assumed resource quality to be distributed like the right half of a normal distribution. However, Kikuchi and Reinhold (2021) also observed temporal fluctuations under uniform resource distributions. This leads to the hypothesis that resource distributions have a large influence on the evolution of costly competitive adaptations.

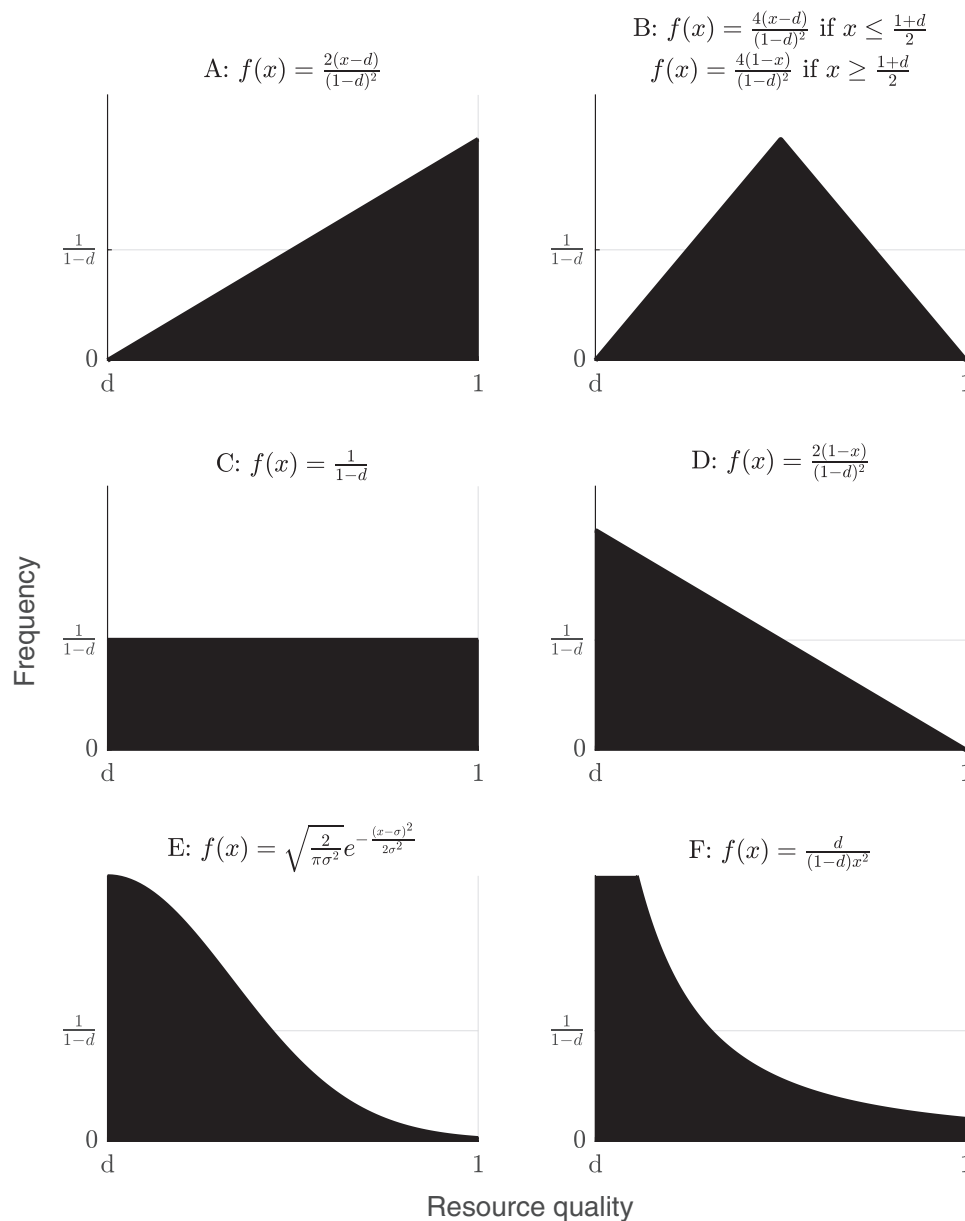
In this study, we provide a resolution of the two contrasting outcomes from Baldauf et al. (2014) and Kikuchi and Reinhold (2021). We examine the role that the shape of resource distributions plays in the evolution of costly investments into competition and temporal trait stability. Similar to Baldauf et al. (2014), we examine the evolution of costly competitive traits in a large asexually reproducing population but use several different resource distributions to examine under which conditions temporally stable or fluctuating polymorphisms are produced. Our main aim is to test whether the fluctuating trait values observed by Baldauf et al. (2014) and the stable maintenance of large trait variance observed by Kikuchi and Reinhold (2021) rely on the specific conditions assumed in their models or are likely to occur under a wide array of resource distributions, i.e., ecological conditions.

## Methods

We used an individual-based model to test the evolutionary dynamics of a costly competitive trait that determines the quality of resources an individual obtains. We denote the trait by  $c \geq 0$ , where  $c = 0$  corresponds to no investment into competitive traits, and higher  $c$  values signify higher energetic investments. To facilitate direct comparison, we assumed the same trade-off between competitive traits and reproduction as Baldauf et al. (2014). That is, we assumed that any individual that attains a resource of quality  $r$ , can only invest a proportion of  $1 - c$  into reproduction because the remaining resources are required to develop and maintain their competitive ability. Note that we impose no upper bound on the trait value  $c$  and, in principle, allow  $c \geq 1$  to occur through mutation (see below). In such cases, we assume that no energy can be allocated for reproduction, which immediately leads to selection of  $c < 1$ . Moreover, we show below that  $c = 1 - d$ , where  $d$  denotes the ratio of the resource quality that can be obtained without investment into competitiveness ( $c = 0$ ) to the quality of the best available resources, forms a natural upper bound for the competitive trait.

We used a fixed population size of  $N = 10,000$  individuals and model simulations were conducted as follows. In the first generation, we always started our simulations by randomly choosing a value of  $c_i$ ,  $i = 1, \dots, N$  on the interval  $[0, 1]$  for each individual. For each individual and each generation, we varied the value of  $c_i$  by adding random values from a normal distribution with zero mean and SD of 0.01 to find the “expressed” value  $\hat{c}_i$ , so that there were slight deviations from the “genetic” value of  $c_i$ . This is similar to the approach of Baldauf et al. (2014) and smoothens the curve of the relationship between genotype and fitness. It can be interpreted as the effect of developmental noise, mimicking chance effects on the phenotype when individuals with very similar genetic traits compete. For every generation,  $N$  resources were drawn randomly from the chosen distribution (see Figure 1 for the expressions of the probability density functions). We assumed that the individual that expressed the most competitive trait  $\hat{c}_i$  obtained the best available resource (which we normalized to be of quality  $r = 1$ ) and so on, such that the individual with the lowest value of  $\hat{c}_i$  obtained the least valuable resource with quality  $r = d$ , where the ratio between the worst and best resource ( $d$ ) was a model input parameter. We chose the reproductive fitness of each individual ( $W_i$ ) to be the product of the resource quality obtained ( $r_i = r(\hat{c}_i)$ ), and the proportion of resources not invested into the competitive trait ( $1 - c_i$ ), i.e.,  $W_i = r_i(1 - c_i)$ . We assumed asexual reproduction. Using these fitness values, we chose  $N$  offspring using a draw with replacement so that individuals were expected to reproduce in proportion to their fitness. That is, for each of the  $N$  draws, the probability to draw an offspring of parent  $i$  was  $W_i / \sum W_j$ . For the offspring, we assumed like Baldauf et al. (2014), a mutation rate of 0.01 for the genetic value of  $c$  (i.e., 1% of the offspring mutated), and a normally distributed effect of the mutation with zero mean SD 0.1. If mutations led to  $c$  values smaller than 0, we set them to 0 (i.e., there was a lower bound for  $c$  that represented no development of any competitive traits).

To represent various types of resource distributions, we used four simplistic linear relationships (A–D) and two non-linear ones (E and F), and without loss of generality assumed that the best resources have quality 1 and the worst resources have quality  $d$ , with  $d$  varying from 0 to 1 (see Figure 1). We ordered the distributions according to an increase in the availability of low-quality resources from A to F. The distribution with the lowest frequency of poor-quality resources assumed a linear increase in the availability of resources between  $d$  and 1 (distribution A). To allow a comparison with mid-centred unimodal distributions, we used distribution B, where resources with value  $(1 + d)/2$  have twice the frequency compared to a uniform distribution and resource values towards  $d$  and 1 linearly approach frequencies of 0 (see Figure 1). We also used the uniform distribution (distribution C). Distribution D is a linear distribution with more poor resources than good ones, where resource abundance decreases linearly from resources with quality  $d$  that have an abundance of twice the level of the uniform distribution C, to resources of quality 1 that have an abundance of 0 (and thus constitutes a mirror image of distribution A). As we (Kikuchi & Reinhold, 2021) did not observe trait fluctuations in a model similar to the one by Baldauf et al. (2014) when using the right half of a normal distribution, we also used such a distribution (distribution E), defining it to be the right half of a normal distribution with mean  $d$  and SD of  $(1 - d)/3$ , and truncating it at  $+3SD$  to avoid resource values above unity (Figure 1). Finally, we used a power law (distribution F) because



**Figure 1.** Depiction and description of the resource distributions used in our simulations. The resource values are given on the x-axis ( $d \leq r \leq 1$ ), and the relative probability densities are given on the y-axis. Equations for the probability density are superimposed within each panel. (A) Linear increasing. (B) Linear mid-centred.  $d \leq r \leq \frac{d+1}{2} < r \leq 1$  (C) Uniform distribution. (D) Linear decreasing. (E) Truncated right half of normal distribution. (F) Power law distribution.

we can analytically show (see [Appendix](#)) that it leads to a uniform distribution of the competitive trait value.

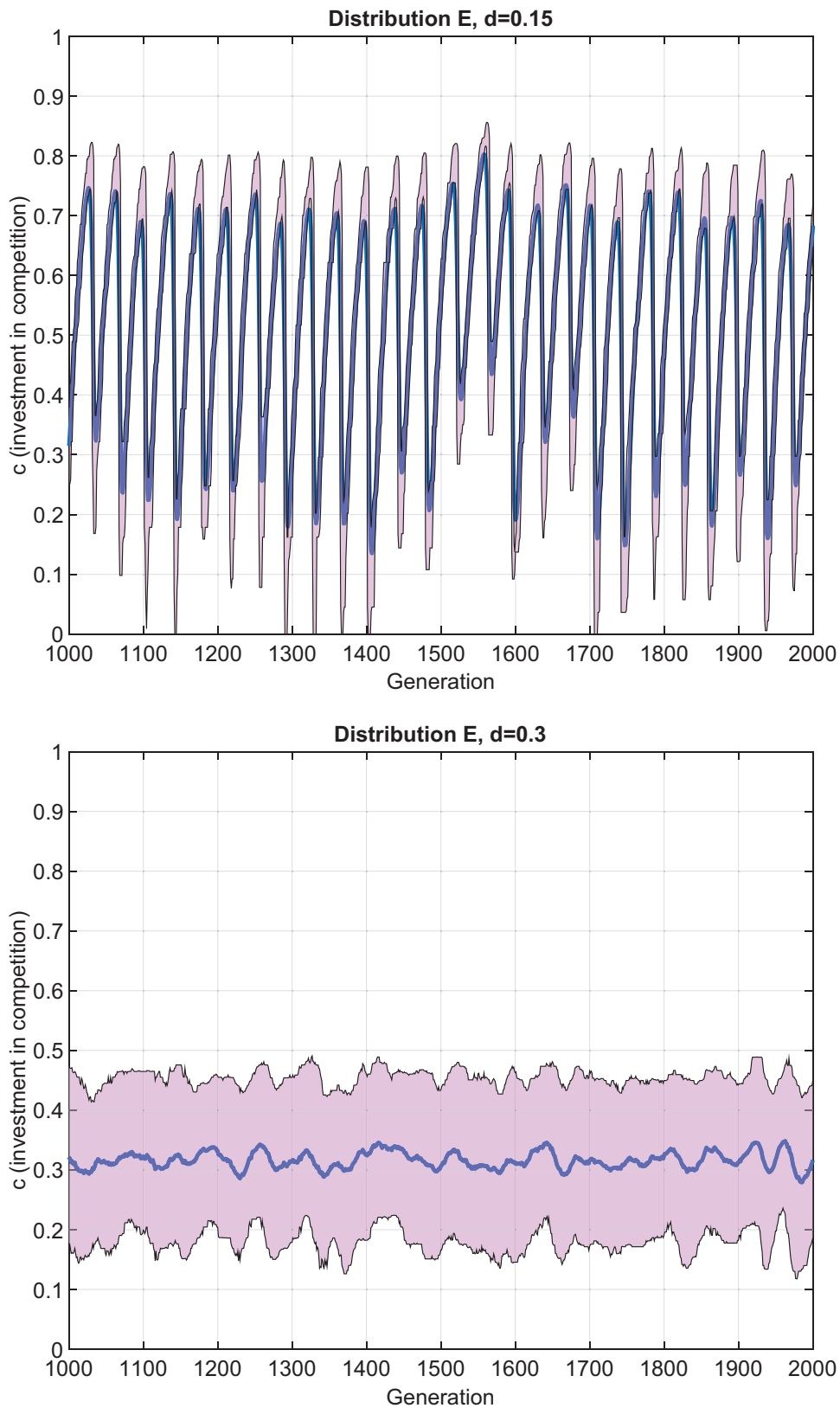
## Results

### Resource distributions affect evolutionary dynamics

We first performed test simulations of our individual-based model in which individuals with high competitiveness obtain higher quality resources but convert a lower percentage of resources into offspring. In these test simulations, we varied the ratio between the best and worst resource ( $d$ ) for a number of different resource distributions and investigated the evolutionary dynamics over time. Across all simulations, we observed one of two possible types of time dynamics: stable mean investment into competitiveness with large individual

variation across the population, or oscillations in the mean competitiveness with little individual variation ([Figure 2](#)). For all resource distributions considered (except the power law distribution F; see below for more details of this special case), large differences between high- and low-quality resources (low  $d$ ) led to oscillatory mean competitiveness with low individual variability, while low differences between high- and low-quality resources (high  $d$ ) led to stable mean competitiveness with high individual variability.

Motivated by these test simulations, we performed a comprehensive parameter scan, changing the ratio between the worst and best resource ( $d$ ) for each resource distribution to elucidate the different evolutionary dynamics in more detail. We recorded the population mean value of  $c$  and the SD of the distribution of trait values at generation 1,000, and the minimum and maximum mean value of  $c$  between generations



**Figure 2.** Exemplary results of simulations for the distribution E. For (A), the value of  $d$  was set to 0.15, and in (B), it was set at 0.4. Depicted are the temporal variation of the average  $c$  values (solid blue curve) as well as the interquartile range (rose-shaded area) as an estimate for the extent of standing genetic variation.

1,000 and 2,000. Given that random processes in our model induce differences between independent simulations of the model with the same parameters, we performed 100

independent model simulations for each  $d$  value and resource distribution. We report the mean of all recorded quantities across the 100 model runs. We report the results obtained

from this comprehensive simulation programme in the following paragraphs.

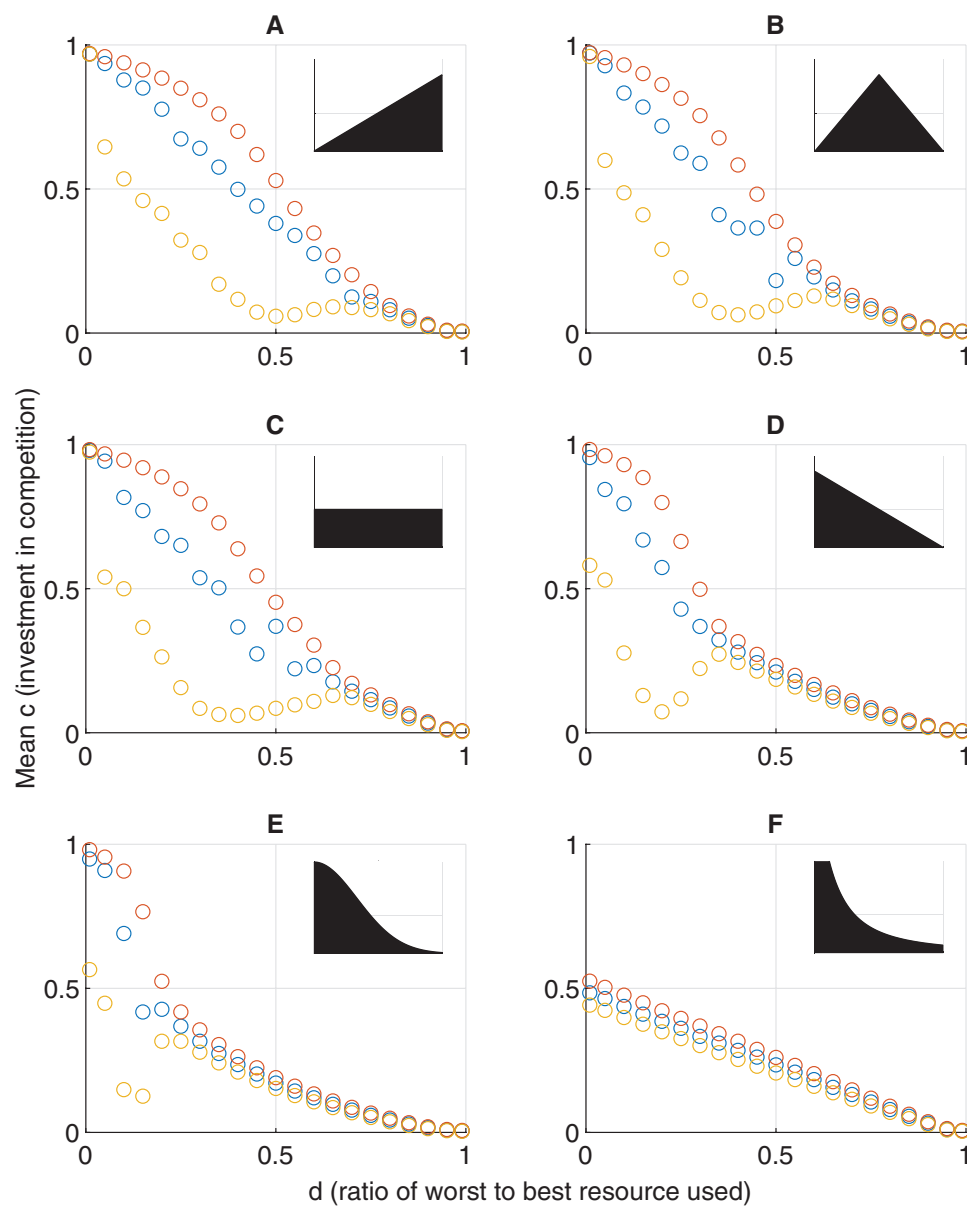
### Evolution of average investment into competition

The mean trait value  $c$  observed at generation 1,000 is strongly influenced by the value of  $d$  and the shape of the resource distribution (Figure 3). Simulations with  $d = 0.01$  resulted in an evolutionary stable value of  $c$  between 0.94 and 0.99 for all resource distributions considered, except the power law distribution (F). For resource distribution F, we observed markedly lower values of  $c$ , around 0.5 (see Appendix for an explanation of why this fits the expectation). As expected, the simulations with  $d = 1$ , i.e., in the absence of resource variation,  $c$  always evolved towards 0. Its value only remained slightly above 0 due to a mutation–selection

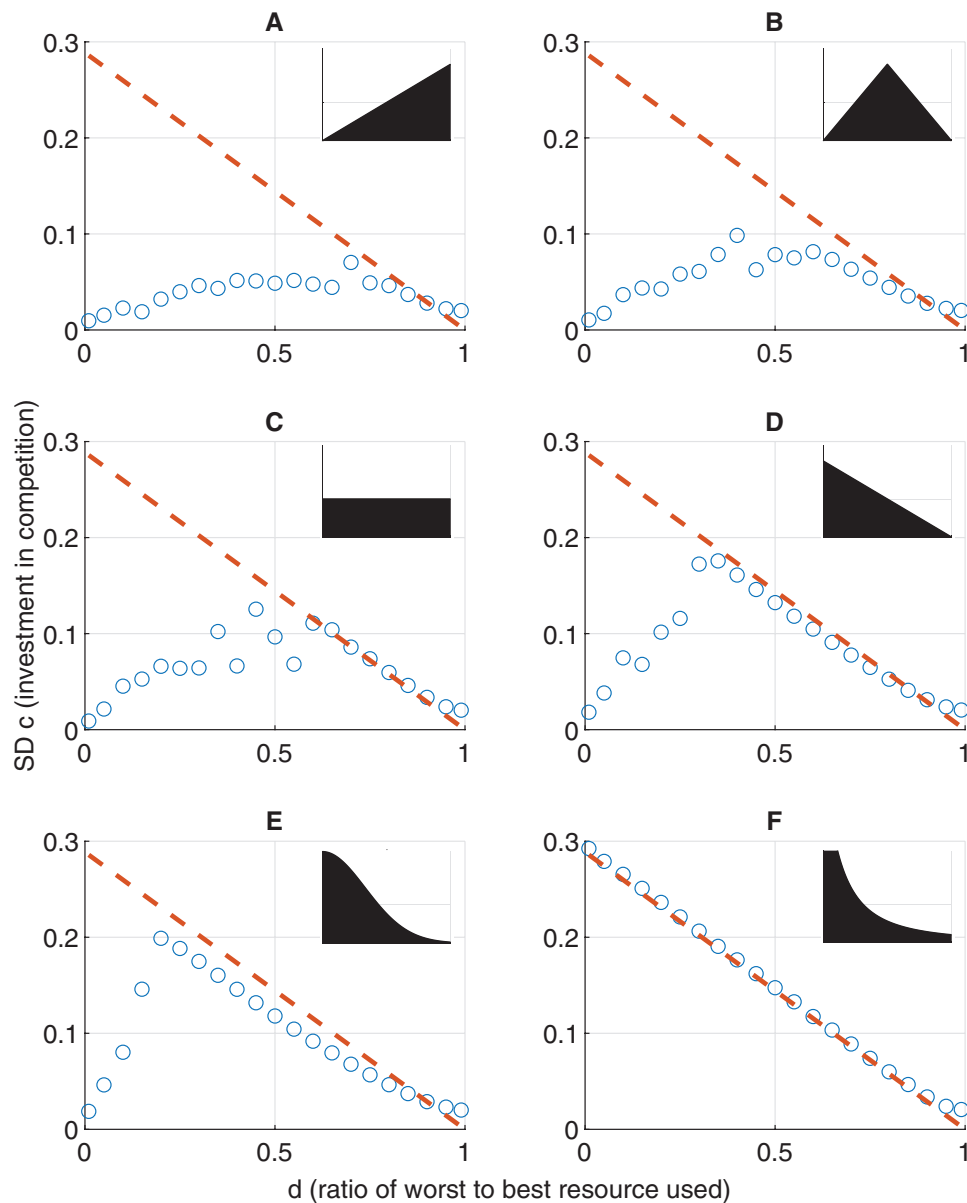
balance. At intermediate values of  $d$ , there are noteworthy differences among the distributions in the mean value of  $c$ . For intermediate values of  $d$ , and the linear resource distributions with few low-quality resources (distributions A–C), the observed mean values of  $c$ , at generation 1,000, decreased approximately proportional to  $1 - d$  (see Figure 3). For two of the resource distributions with a majority of low-quality resources (distributions D and E), mean  $c$  initially decreased more steeply with increasing  $d$ . For the resource distribution based on a power law (distribution F), mean  $c$  decreased linearly and was always very close to  $(1 - d)/2$  (see Appendix).

### Occurrence of strong temporal fluctuations

For intermediate values of  $d$ , all resource distributions except the power-law distribution (distribution F) regularly resulted in strong temporal fluctuations of the mean competitive trait



**Figure 3.** Summary of simulation results dependent on the assumed resource distributions A–F and  $d$ , the assumed ratio between the worst and the best resource. Depicted are the mean values of the competitive trait  $c$ , at generation 1,000 (blue dots), as well as the range of temporal fluctuations given as the average minimum (yellow dots) and the average maximum (orange dots) between generations 1,000 and 2,000. Large vertical differences between red and yellow dots indicate strong temporal variations. All averages are calculated from 100 independent repetitions.



**Figure 4.** Summary of simulation results dependent on the assumed resource distributions A–F and  $d$ , the assumed ratio between the worst and the best resource. Depicted are as an estimate of the extent of maintained genetic variation, the average standard deviations of the competitive trait  $c$ , at generation 1,000, calculated from 100 independent replicates (blue circles). The red dashed lines indicate the maximum expected standard deviation  $SD = \frac{1-d}{\sqrt{12}}$ .

between generations 1,000 and 2,000, as can be seen by the large range between the average minimum and the average maximum for this interval (Figure 3). Such strong and quick temporal fluctuations occurred for these distributions with values of  $d$  clearly larger than 0 and up to a certain value of  $d$ . Above this threshold, the strong temporal fluctuations disappeared (see Figure 2 for an example on both sides of this threshold value). The threshold was negatively correlated with the proportion of low-quality resources, and thus decreased from distribution A to distribution E. However, such strong temporal fluctuations were absent for resource distribution F, in agreement with our analytical prediction (Appendix).

#### Maintenance of standing genetic variation of competitive trait

Some maintenance of standing genetic variation in competitive trait values was evident in all our simulations (see

Figure 4). Very low standing variation, likely caused by mutation–selection balance, only occurred when  $d$  was assumed to be close to 1 or 0. The amount of standing variation was high for all distributions whenever strong temporal fluctuations were absent. Under these conditions, the standing variation approached the expected maximal value, given the assumption that all competitive trait values  $c \leq 1 - d$  are present in equal frequencies (with such a uniform distribution of trait values, the SD of the variation in genetic traits is  $SD = (1 - d)/\sqrt{12}$ ). Higher trait values are not expected to persist, as the fitness of the trait with low competitiveness would be at least  $d$ , and thus higher than the fitness of any individual investing more into competitiveness than  $1 - d$ . The standing variation in competitive traits was observed to be almost exactly this value for resources distributed according to the power-law distribution F for all  $d$  values and for  $d$  values above the threshold between fluctuating and

temporally stable outcomes for the other distributions. Thus, standing genetic variation was only comparatively high when strong temporal fluctuations were absent.

A closer look reveals some finer details in which the results differ between the various distributions. For a large range of  $d$  values, the distributions that contain many poor resources and few good resources, i.e., distributions D–F, show larger standing variation in  $c$  values at generation 1,000, but lower temporal variation in mean  $c$  values compared to distributions A–C. This is most evident for intermediate values of  $d$ . This means that distributions with few very good resources resulted in the maintenance of much standing variation in the competitive trait for many  $d$  values. This variability appeared to be almost stationary. On the other hand, the resource distributions with larger proportions of good resources resulted in strong temporal variation and comparatively low standing variation in the competitive trait (at least at any particular time point) for a broader range of  $d$  values.

### The special case of the power-law distribution

Distribution F led to results that were divergent from the other distributions. The distribution of trait values was, for all  $d$ -values smaller than 1, approximately uniform, as suggested by the analytical result (see [Appendix](#)) mentioned earlier. In addition, quick and strong temporal fluctuations in  $c$ , which were typical for the other resource distributions, did not occur for any  $d$  values. The mean  $c$  value for this resource distribution was always very close to the predicted value of  $d/2$ , as expected when all  $c$  values below  $1 - d$  occur with approximately equal frequencies.

## Discussion

As expected, our simulations show that larger variation in resource values, i.e., assuming small values of  $d$ , generally resulted in the evolution of larger investments into the competitive trait  $c$ . We found that the shape of the resource distribution was also important, in addition to the value of  $d$ , confirming our hypothesis. Only some resource distributions led to strong temporal variation in the mean value of the competitive trait. At least under some  $d$  values, all resource distributions led to the maintenance of standing genetic variation in the competitive trait, though the extent of the maintained variation differed strongly between resource distributions. In the following paragraphs, we will discuss how the variation in the mean value of  $c$ , in the occurrence of temporal fluctuations and in the maintenance of standing variation, can be explained.

The ratio between the worst and the best resource available, i.e., the value of  $d$ , primarily determined how much individuals invested on average into the competitive trait. For three vastly different linear distributions (A–C), the average mean trait values we observed were very similar but depended strongly on  $d$ . In all these cases, the observed average competitive trait  $c$  was close to the assumed value of  $1 - d$ , i.e., the diagonal in the figures, but mean traits tended to be slightly below this value. When good resources were rare, and poor resources were frequent (distributions D and E), mean  $c$  was similar to that observed under distributions A–C for low values of  $d$ , but mean  $c$  decreased more steeply at higher values of  $d$ . At least for those distributions that include a decent share of high-quality resources, the ratio between the worst and the best resource seems to predict

quite well how much individuals evolve to invest on average into the competition. This statement is also valid for distribution F, but the relationship is a different one for this distribution, as the average values we observed were closer to  $(1 - d)/2$ . This result exactly matches our prediction, as this average value is expected for a uniform distribution of trait values between 0 and  $1 - d$ .

Even though the results vary depending on the resource distribution, our study predicts that the ratio between the worst and the best resource available is approximately linearly related to the average investment into competition, when competition is costly and when traits can be expected to vary continuously. This is a novel finding, as, to the best of our knowledge, no other studies have previously addressed this question.

Most resource distributions (A–E) did not lead to a stable mean competitive trait but led to some fluctuations in the mean competitive trait value over time, if  $d$  was larger than 0 and sufficiently smaller than 1. Thus, under some specific conditions, temporal fluctuations in  $c$  could be observed. In these cases, adaptive evolution causes cycles of arms races where increasingly higher values of  $c$  are favoured, but only to a certain point, after which much less competitive mutants can invade. This creates an “engine” that maintains temporal variability in  $c$ . Strong temporal trait fluctuations resulting from selection as reported by [Baldauf et al. \(2014\)](#) are thus not restricted to the very idealized resource distributions used in that study. However, in our study, strong temporal fluctuations were also absent under many conditions. Strong temporal fluctuations were absent for resource distribution F (independent of the chosen  $d$ ), as well as for all other examined distributions (A–E) if sufficiently large values of  $d$  were assumed. In these cases, individuals with low competitive traits on average achieved similar fitness, than those individuals that invested more into competitive traits, leading to an absence of arms races.

Some maintenance of standing genetic variation in competitive trait values was evident in all our simulations, but overall, it was highest when resource distribution F was assumed, and also when poor resources were common (distributions C–E), given that  $d$  was high enough to prevent strong temporal fluctuations (see [Figure 4](#)). When the variation maintained was very low, it was likely caused by mutation–selection balance. This occurred either when  $d$  was approaching 1, leading to the evolution of non-competitive trait values, or when weak competitors gained very few resources, leading to an arms race for strongly competitive traits. Our results thus show that costly competition can maintain ample continuous genetic and phenotypic variation under diverse resource distributions. This finding likely depends on the assumption that more competitive individuals can use a smaller proportion of the gained resources for reproduction. A similar individual-based model by [Netz et al. \(2023\)](#) assumed a one-time fixed cost increasing with competitiveness predicted, alternatively, the erosion of individual variability.

Our findings provide a potential explanation for the continuous variation observed, e.g., in studies examining individual differences or personality traits ([Vukasović & Bratko, 2015](#)). They can contribute to explain the surprisingly high values of heritability frequently observed for traits under strong selection ([Lynch & Walsh, 1998](#)), and they provide a sufficient condition for the existence of individualized niches ([Krüger et al., 2012](#); [Trappes et al., 2022](#)).

Our results show that the striking differences in the outcome of two otherwise comparable models (Baldauf et al., 2014; Kikuchi & Reinhold, 2021) likely can be explained by differences in assumptions about resource distributions. For some distributions, we observed strong temporal fluctuations in the competitive trait for a broad interval of  $d$  values; for others, such fluctuations could only be observed for a limited range of  $d$  values or could not be observed at all. In line with our results, strong temporal fluctuations are expected for uniform distributions as reported by Baldauf et al. (2014) for  $d = 0.11$  and  $d = 0.67$  and not expected for distribution E and  $d \geq 0.25$ , as used by Kikuchi and Reinhold (2021).

It is also important to consider the limitations of our modelling approach. Most significantly, we employed a model of asexual reproduction. In our model, single individuals reproduced, and trait values of offspring were determined by those of their single parents, up to mutations. We did not consider sexual reproduction processes and associated dynamics that can be affected by competitiveness, such as mate choice (Baldauf et al., 2014). However, we note that modelling of evolution that explicitly considers combinations of gametes and other associated dynamics also has a rich legacy in theoretical studies of evolution (Brown & Thomson, 2018; DeAngelis & Mooij, 2005). Testing if, or to what extent, the results in this article carry over to sexually reproducing organisms is therefore an important aspect of future work. A different important direction of future modelling efforts could be the relaxation of our assumption that the most competitive individual always attains the highest quality resource and so on. This strict hierarchy is a suitable description if individuals can compete with all others independent of location or distance in between. For example, this is the case in well-mixed populations or systems in which competitive interactions occur over long spatial scales. However, it is not applicable to systems in which competitive (and other) interactions are underpinned by population structure (Perc et al., 2013) such as microbial biofilms (Eigentler et al., 2022) or self-organized vegetation (Gandhi et al., 2019).

It might seem difficult to relate the results of our model to empirical data, e.g., because the distribution of resources in empirical systems is difficult to measure and to generalize due to the high number of niche dimensions a species may utilize (e.g., Clark et al., 2010). However, the obtained data fit very well with our knowledge about variation of extravagant traits used in intense intrasexual fighting where losers in competition obtain very few mating opportunities. In line with the evolution of extravagant fighting abilities and highly skewed reproductive success as observed in sea elephants or stag beetles, our model would predict high investment into these competitive traits, as competitors with non-competitive traits in these systems are likely to obtain very low fitness. As we observed the maintenance of large trait variation when exceptionally good resources are comparatively rare so that weak competitors can obtain a share, we predict that larger genetic variance can be maintained. One prediction of our model would be that continuously varying phenotypes produced through costly investment can achieve similar fitness values. Future empirical studies should test whether this is the case and whether the genetic variation maintained in competitive traits and the average trait size depend on the resource distributions

present. Critically, our model also predicts that such equal fitness among phenotypes will disappear under resource distributions with greater disparity between good and poor resources, or when good resources become more common. Such resources could, e.g., be represented by territories and their quality or area, groups of mating partners over which the other sex fights, or specific spots on a mating lek. When a new habitat is colonized, and population density is low, most individuals likely can achieve some high-quality resources, equivalent to a comparatively high value of  $d$ . Under such conditions, our model would predict less investment into competition together with some maintenance of genetic variation.

We conclude that depending on the resource distribution, dynamic fluctuations of trait values can but need not occur regularly with costly competition. Such instability has been predicted to often occur in evolutionary games (McGill & Brown, 2007) but was absent in our models for resource distribution F and for distributions A–E if  $d$  was sufficiently large. Under these conditions, large-scale continuous genetic variation is maintained by negative frequency-dependent selection. Stable high investments in competitive traits only developed if weak competitors obtained relatively little fitness. Stable low investment into competitive traits only evolved when very little variation in resource values was present. Our results thus suggest explanations for the maintenance of continuous phenotypic variation and the occurrence of temporal fluctuations when individuals compete with costly traits.

## Data availability

Modelling code and data have been published in a GitHub repository, and an image at the time of submission has been achieved through Zenodo (Reinhold et al., 2023).

## Author contributions

Klaus Reinhold (Conceptualization [Lead], Formal analysis [Equal], Investigation [Equal], Methodology [Lead], Project administration [Lead], Writing—original draft [Lead], Writing—review & editing [Equal]), Lukas Eigentler (Data curation [Lead], Formal analysis [Equal], Validation [Equal], Visualization [Equal], Writing—review & editing [Equal]), and David Kikuchi (Formal analysis [Equal], Investigation [Equal], Visualization [Equal], Writing—review & editing [Equal])

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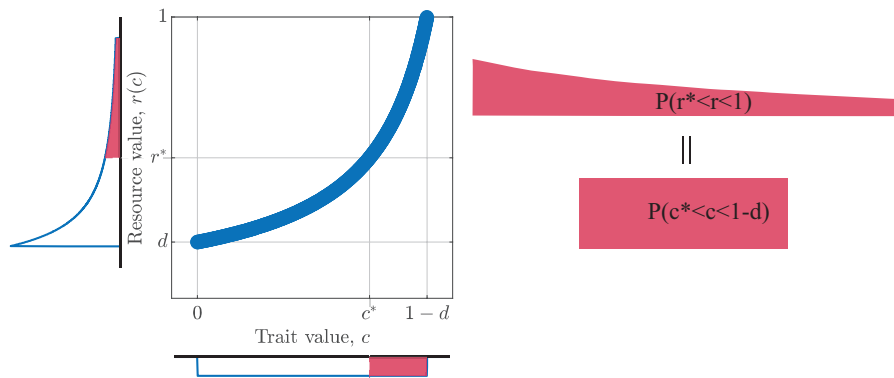
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## Conflicts of interest

None declared.



**Figure A1.** This sketch visualizes the relationship between trait values and assigned resource values if all individuals attain identical fitness  $(1 - c)r(c) = d$ . The distribution plot next to the y-axis shows the resource distribution (F). The area of the shaded region is the relative abundance of individuals that attain resource values higher than  $r^*$ . As our analysis shows, this equals the area shaded in the distribution plot for the trait value below the x-axis, which indicates the relative abundance of individuals with investment into competition higher than  $c^*$  only if the trait distribution is uniform.

## Appendix

### Distribution F leads to uniform trait distributions

In this section of Appendix, we show analytically that for a large number of individuals, the power law resource distribution (F) leads to a stable trait distribution that is uniform, i.e., a distribution in which all trait values  $0 \leq c \leq 1 - d$  occur with the same frequency.

For this, note that the probability density function of resource distribution F is  $g(r) = \frac{d}{(1-d)r^2}$ . Therefore, its cumulative distribution function is  $G(r) = \frac{r-d}{(1-d)r}$ . We look for a trait distribution that is stable. In this context, stable corresponds to a setting in which every single individual attains the same fitness, that is the quantity  $(1 - c)r(c)$  is constant for all  $0 \leq c \leq 1 - d$ . Since individuals with no investment into competitiveness ( $c = 0$ ) obtain a resource of quality  $r(0) = d$ , we obtain that  $(1 - c)r(c) = d$  for all individuals with  $0 \leq c \leq 1 - d$ . Rearranging this equality gives  $c = \frac{r(c)-d}{r(c)}$ .

Due to the hierarchical assignment of resource values  $r(c)$  in response to the trait values  $c$  present in the population, we can relate the resource distribution with the stable trait distribution through

$$P(r^* < r < 1) = P(c^* < c < 1 - d),$$

$$\text{with } d < r^* < 1, \quad c^* = \frac{r^* - d}{r^*}.$$

That is, for any resource value  $d < r^* < 1$ , the number of individuals that obtain higher resource values equals the number of individuals with investment into competition larger than  $c^* = \frac{r^* - d}{r^*}$  (Figure A1).

This enables us to obtain the cumulative distribution function of the stable trait distribution through

$$\begin{aligned} P(0 < c < c^*) &= 1 - P(c^* < c < 1 - d) \\ &= 1 - P(r^* < r < 1) \\ &= 1 - (1 - P(d < r < r^*)) = G(r^*) \\ &= \frac{r^* - d}{(1-d)r^*} = \frac{1 - \frac{d}{r^*}}{1-d} = \frac{c^*}{1-d}. \end{aligned}$$

This is the cumulative distribution function of the uniform distribution on  $0 \leq c \leq 1 - d$ . Thus, the power law resource distribution F leads to a uniform trait distribution.

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