**Supporting Information**

Complementary Variety: when can cooperation in uncertain environments outperform competitive selection?

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## S1. Short primer on the Kullback-Leibler divergence.

The Kullback-Leibler divergence (also known as relative entropy), is a measure from information theory. Information theory is a branch of probability theory that defines information in terms of uncertainty and frames uncertainty in terms of probability theory. The less uncertainty, the more information and vice versa (for standard textbooks see MacKay 2003; Cover & Thomas 2006; for shorter overviews see Pierce, 1980; Stone, 2015).

For discrete probability distributions P and Q, the Kullback–Leibler divergence of Q from P is defined as . It is a nonsymmetrical, positive measure of the divergence between two probability distributions P and Q. In applications, P typically represents the ‘true’ distribution of data (observations), while Q typically represents a model (approximation of P). In information theory it measures the expected number of extra bits required to code samples from P using a code optimized for Q rather than the code optimized for P. Naturally, can also be used for joint distributions: .

A derivate of relative entropy is the mutual information, which is the joint if the estimator distribution Q is the distribution of the two random variables X and Y being independent. In other words, it is the divergence between the joint and its independent distribution: . This shows its similarity to the more familiar concept of covariance: . In information theoretic terms it represents the expected number of extra bits that must be transmitted to identify X and Y if they are coded using only their marginal distributions instead of the joint distribution (the amount of extra information contained in the joining).

The fundamental role of these three measures stems from the fact that are linked to the typical sets that appear when considering large numbers. For example, quantifies the probability that a population ends up with an updated population when originating from an original population . Imagine an ecosystem with two types of finches (long and short peaked) represented by a random variable distributed according to , with and . The law of large numbers tell us that with many observations the probability of observing long-peaked finches in this ecosystem is on average close to 1. But it might also be that at a certain count we observe (for example) of long-peaked and of short-peaked finches. What is the probability that this would happen? It is exponentially unlikely that this occurs with many observations on average (since such sequences are outside of the typical set). It would however be very likely if the real distribution were , with and . The probability that such largely deviated observations occur depends on the distance between both distributions, which is quantified by the Kullback-Leibler relative entropy. Sanov’s (1957) theorem tells us that this occurs on average number of times, each with probability . Getting rid of the logarithm in equation [34] from the main article, this results in an intuitive interpretation. Population fitness consists of the weighted geometric mean fitness of updated types, times the average probability of ending up with the updated population distribution when starting out with the original population distribution.

It is straightforward to expand all of the three foregoing measures to their conditional equivalents, which leads to the chain rule that essentially chains or unchains conditional nesting of probabilities. For example, equations [9] and [10] from the main article uses the chain rule for conditional (see Cover and Thomas, 2006):

Sometimes there is a confusing inconsistency in the literature with regard to the definition of conditional relative entropy. While the leading text book in information theory (Cover and Thomas, 2006) is implicit of the mention of the distribution , others are explicit about it (note that the right hand side of the following two equations is the same):

## S2. Derivation of fitness decomposition

The fitness decompositions that involve (equations [3] and [4]) can be derived in two basic steps. The first step consists in the fact that the expected value of a constant is a constant (in this case the constant is the logarithmic population fitness ). We expand with the expected value of the distribution of types:

Second, we expand with a reversed form of the replicator equation, , namely :

The joint entropy equation [4] considers the fact that population fitness over time periods, , can be represented as the weighted product of the population fitness of the environmental states.

Dividing by the number of periods provides the geometric mean of the population fitness per period: . The rest follows the equivalent of the two steps from above and expands with to reach equation [4] (note that as updating of the population does not change the distribution of the environment):

Note that the same derivation can also be executed by taking the expected value over the future updated population distribution in equation [S1]. In this case, equation [S1] would become:

and our decomposition would be:

This equivalently valid reformulation can in some cases be preferable. For example, it naturally lends itself to other existing explorations of bet-hedging, and is also intuitive for interpretative reasons: for optimal bet-hedging the reverse term becomes Shannon’s mutual information, , the mutual information between the environment and the updated population (see Hilbert, 2015; 2017). In words, and using the standard interpretation of the Kullback-Leibler divergence, if we look at it from the (average) updated population, we have to subtract the “inefficiency of encoding with the code optimized for the past generation”, since the actual population distribution is based on the updated future generation. Both are complementary ways of decomposing average population fitness:

This is leads back to the important results of Frank (2012) about .

## S3. Proofs

### S3.1 Complementary variety in terms of covariance

We start with the equivalence relation that underlines equation [5] from the main article:

The left hand side decomposes total population fitness from the initial period 0 to the final period T as the arithmetic mean of the long term fitness of each type (long term fitness as the product of the fitness in each period). The right hand side represents it as the product of the population fitness in each environmental state . If we let natural selection do its work, we start with an initial distribution and then let competitive selection decide which types increase and which decrease their share. Therefore, population fitness through competitive selection is: .

If we intervene in an uncertain environment, we do not know which environment will come up next, so the best we can do is to decide on a (hopefully pretty reasonable) population distribution and hold it constant (with more information about the environmental distribution we can fine tune this, and look for an optimal population distribution, in the sense of bet-hedging, see Supporting Information S4). This means that at each discrete period of reproduction we return to the same stable population distribution. This means that the population before updating in any environmental state looks the same (). Biology often does this by maintaining a stochastic phenotype switch on the genetic level, while in social evolution a portfolio manager might constantly intervene to keep a diversified portfolio. There is an ongoing cooperation, manifested through constant resource redistribution that benefits the total. The resulting long-term fitness is the weighted product of the population fitness in each environmental state. Population fitness through strategic cooperation: .

For our comparative purposes, we set the initial population distribution for the case of natural selection equal to the population distribution before average updating for the case of strategic intervention: . This makes it straightforward to compare both cases directly with each other.

We will now show the covariance relation of equation [2] from the main article. This can be shown for the special case in which we have only two environmental states (a covariance is designed to distinguish between two dimensions), while each of them appears the same number of times (:

The left hand side has the form , where the function consists of an exponentiation with a number larger than 1, namely . This function is convex. Jensen’s inequality says that for convex function the following relation holds (Jensen, 1906; Cover and Thomas, 2006): . This leads to a tightening of the inequality and to equation [5] from the main text:

For the case of a uniform environment, with , equation reduces to a variance, which is the case of the equation [1] from the main article:

A variance is always non-negative. Going backward from equation to shows that ‘strategic cooperation’ (holding shares constant) can at best equal competitive selection. This is the case when the shares are hold constant with all resources allocated at the fittest type.

### S3.2 Complementary variety in terms of relative entropies

We look at the population fitness from the initial to the final generation of the observational period in two different ways. The first measures the average selection over the entire period of observation (first versus last generation). The other decomposition measures the average force of selection per average updating measured at each period (the average fitness per period, multiplied with itself as often as there are periods T).

We then take the logarithm and express the left hand side in terms of equation [3] from the main article, and the right hand side in terms of equation [4] from the main article:

We use the first to represent (as competitive selection works its natural force during the entire period), and the second one to quantify strategic cooperation, , as intervention reorganizes the distribution at each step. The second reformulation allows us to recognize that we hold constant at each step.

Our comparative assumption of cancels the expected value term on both sides:

This leaves us with equation [7] from the main article:

or

Note that in our case . This stems from the fact the the environmental distribution does not change during average updating, and :

### S3.3 Benefit of fine-graining in time

As shown in Figure 8 of the main article, in both of our empirical cases, it turned out to be the case that distinguishing among more environmental states than population types decreased population fitness: the highest fitness increase was detected with as many types as states (a squared fitness matrix). Here we show that this is not necessarily always the case. We proof this by showing a case in which the identification of more environmental states than population types enables the population to increase its fitness.

The first case shows a squared fitness matrix with two population types and two environmental states (‘Space2\_Time2’). Bet-hedging optimization suggest that fitness can be optimized by maintaining a stable share of some 73 % of type A and 27 % of type B. The obtained average population fitness is .

Table SI1. Coarse-grained perception of two environmental states

|  |  |  |  |
| --- | --- | --- | --- |
| **Space2\_Time2** |  |  |  |
|  | 4 | 3 |  |
|  | 2 | 5 |  |
|  | | | |

The second case opens up environmental state and distinguishes among its two sub-states: and . Both appear with equal probability and together create the higher level fitness values from the previous aggregate matrix: and (being geometric means in time). These lower-level variations of the fitness landscape also existed in the previous case, just that Table SI1 assumes no intervention at this level, which results in these higher level averages.

Strategic cooperation can now also exploit this more fine-grained representation of the fitness landscape by redistributing resources at each one of the three different identified environmental states (not merely at the rhythm of two more coarse-grained states). In this case, bet-hedging optimization within environmental state leads to the same recommendation of maintaining a stable share of some 73 % of type A and 27 % of type B. This strategic intervention increases the average population fitness during state from to and total population fitness to , an fitness increase of compared to the more coarse-grained cooperation.

Table SI2. Fine-grained perception of three environmental states

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Space2\_Time3** | |  |  |  | |
|  |  | 2 | 4.5 |  |  |
|  | 8 | 2 |  |
|  | | 2 | 5 |  | |
|  | | | | | |

## S4. Short primer on bet-hedging and its implications.

In the words of Richard Levins, the central challenge of bet-hedging is to “establish a correspondence between the optimal structures of populations and species and the pattern of environmental heterogeneity in space and time” (Levins 1962). In biology, a genotypic bet-hedging strategy is often called ‘stochastic switching’ and refers to the fact that the genotype maintains a stochastic developmental switch that randomly produces one of several possible phenotypes in proportions that reflect environmental distributions (e.g. Cohen 1966; Kussel & Leibler 2005; Rivoire & Leibler 2011; Rivoire 2015). The resultant superior population fitness of the resulting bet-hedging strategy assures that this genotypic mechanism is maintained by natural selection. Behavioral bet-hedging that is executed among conscious beings consists of resource redistribution through intelligence with foresight. This implies that organisms learn environmental patterns and redistribute population shares accordingly. This application is in line with portfolio theory in financial economics (e.g. Latané, 1959; Algoet & Cover 1988; Blume & Easley 1993; Hens & Schenk-Hoppe 2005). We follow Kelly’s information theoretic approach (Kelly, 1956; for a overview see Cover & Thomas, 2006, Chapter 6) and its generalizations (Haccou & Iwasa 1995; Donaldson‐Matasci et al. 2008; 2010; Rivoire & Leibler 2011).

### S4.1 Bet-hedging in extremist and mixed fitness landscapes

The long term population growth rate can be calculated by multiplying the generational growth rates: .. If certain environmental states exhibit exactly the same fitness values, it is natural to group them into environmental states , which results in the product of fitness values in different environmental states with probability : . . Kelly (1956) worked with a diagonal fitness matrix with only one non-zero fitness value per environmental state and type (see the notation from Figures 1 and 4 from the main article). This simplifies long-term population fitness to the product of the diagonal fitness values:

Maximizing the long term growth rate is equivalent to maximizing the generational exponent of growth, which suggests taking the logarithm and divide by T:

Equation [S7] shows that the logarithmic time average of the population fitness consists of three components. The first sets the benchmark of optimal fitness and is the weighted average of the diagonal non-zero type fitness. In an uncertain environment, optimal fitness is reduced by the uncertainty of the environment, its entropy , and by the divergence between the population distribution and the distribution of the environment, measured by the relative Kullback-Leibler entropy . Both absolute entropy and relative entropy are non-negative measures. With perfect foresight of the next environmental state there is no environmental uncertainty and is minimized to zero. In this case it is most efficient to bet all population weight on the state corresponding to this non-zero fitness value. This also sets to zero and results in: . With remaining environmental uncertainty (), population fitness is optimized by minimizing , which is done through a one-to-one proportional bet-hedging strategy, where the population is distributed in the same proportions as the different environmental states ().

This classical result from Kelly (1956) provides the most important intuition of how information is linked to growth, but is restricted to the special case of a diagonal fitness matrix. More recently, the result has been expanded to any kind of mixed (non-diagonal) fitness matrix (see Haccou and Iwasa, 1995; Donaldson‐Matasci, et al., 2008; 2010; Rivoire and Leibler, 2011). This assumes a hypothetical world with one perfectly specialized type per environment (a hypothetical diagonal fitness matrix) and expresses any existing type fitness as a combination of those specialized fitness values over the different environmental states. The stochastic weighting matrix expresses the mixed growth landscape in which each environmental state has a specialized type. The values of are positive weights, . They are identified by summing up all fitness values of a certain type over all environmental states, , and looking for the corresponding specialized types would have to be weighted in a certain way to obtain the same aggregated fitness value: . In other words, this reformulation expresses a fitness value from a real-world mixed fitness matrix as a fraction of a hypothetical specialized fitness value: . Expressed in matrix algebra, for the binary case of two types and two environmental states (Figure 2 from the main text), this implies the following (note that the matrix is column stochastic, with columns summing up to 1)[[1]](#footnote-1):

Solving for these two unknown matrixes is straightforward and can almost always be done uniquely. This gives the mixed matrix in terms of a diagonal matrix and Kelly’s result tells to optimize diagonal matrixes through a one-to-one proportionality. This suggests that the mixed fitness matrix can be optimized by optimizing the diagonal matrix. Therefore, we optimize the diagonal matrix by weighing it with the vector of environmental weights and solve for the optimal distribution of the vector of types for the mixed matrix :

Solving for the optimal distribution of types results in a distorted proportionality between the distribution of the environment and the growth-optimal distribution of types. For example, for a binary environment with a distribution of with the following mixed fitness landscape, the optimal population distribution is :

It can also be that the optimal placement of weights on the population types would require or for some types. For example, for = , it turns out that one type would need to receive -10% and the other 110%.

This is of course not possible. The literature says that this constellation is “outside the region of bet-hedging” (Donaldson‐Matasci et al. 2008; 2010; Rivoire and Leibler 2011). The solution is not to place any weight on the type with the negative value, and all on the other one. For cases with more than two types, a similar logic holds in a successive order. Non-linear constrained optimization algorithms (such as Sequential Quadratic Programming, or Augmented Lagrangian Algorithm) suggest that the optimum can be found by neglecting some types, and optimizing among the remaining ones (for example, the optimum among 3 types can consist of neglecting one type and bet-hedging between the other two, or by neglecting two of them and placing all weight on only one single type).

### S4.2 The size of the region of bet-hedging

The size of the region of bet-hedging influences the likelihood that population growth can reach its theoretical optimum in a given fitness landscape. The following explores its size. For this we work with square fitness matrixes , which means that there are as many population types as environmental states. In line with equation [S8], the squared fitness matrix is set up in a way that the highest type-fitness per environmental state are in the diagonal. We show that the size of the region of bet-hedging in this case is defined by the determinant of the weighting matrix: (see S.4.1). This the weighting matrix corresponds to the diagonal setup of the fitness matrix (see [S8]), the determinant is larger if there is a large difference between the diagonal values (the highest type-fitness per state) and the less fit (with the extreme case being a pure diagonal matrix, such as in Kelly’s (1956) setup).

To show this we take inverses in both equations [S8] and [S9] (which is only defined for square matrixes, hence our assumption of this case):

Using the adjoint method for the inverse of the weighting matrix, , and defining as the row vector of row n of the adjoint of , equation [S10] says:

Bet-hedging is only possible among all types if for all . The fulfillment of this condition, requires that for all the bet-hedging region is governed by the size of the determinant of :

A fundamental result of linear algebra is that the determinant of a stochastic matrix (such as ) is between 0 and 1, with 0 if some of the rows or columns of the matrix are linearly dependent, and 1 if the matrix is a permutation matrix (exactly one entry with value 1 in each row and each column and 0s elsewhere, such as for an identity matrix). With this in mind equation [S5] says that if the weighting matrix is linearly dependent, bet-hedging among all types can never be realized. If it is a diagonal matrix, it is always possible.

If the weighting matrix is linearly dependent, so is the mixed fitness matrix . This can be seen by returning to equation [S8]. Multiplying the right hand side out and eliminating the hypothetical extremist fitness value through an elementary row operation (dividing each row by the nonzero scalar ) preserves linearity and shows the equivalence of both matrixes and in terms of their linear dependence:

Equation [S12] also shows that in the case that the weighting matrix is an identity matrix with exactly one entry of value 1 in the diagonal, the fitness matrix needs to be a diagonal matrix as well. This brings us back to Kelly’s special case of the diagonal fitness matrix, Equation [S11] reveals that in this and bet-hedging is always possible.

Additionally, we can rewrite the weighting matrix in terms of the mixed fitness matrix and the diagonal matrix . For example, for the binary case:

This implies that the size of depends on the superiority of the diagonal values (the ones that are larger and specialized for each environment) versus the other (non-specialized) values:

The larger the difference between the superior (specialized) and inferior (non-specialized) fitness values, the larger and the larger the region of bet-hedging.

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1. Note that Donaldson‐Matasci, et al. (2008, 2010) flip the weighting matrix, with rows summing up to 1. [↑](#footnote-ref-1)