

The fitness value of information

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Abstract

Biologists measure information in different ways. Neurobiologists and researchers in bioinformatics often measure information using information-theoretic measures such as Shannon's entropy or mutual information. Behavioral biologists and evolutionary ecologists more commonly use decision-theoretic measures, such the value of information, which assess the worth of information to a decision maker. Here we show that these two kinds of measures are intimately related in the context of biological evolution. We present a simple model of evolution in an uncertain environment, and calculate the increase in Darwinian fitness that is made possible by information about the environmental state. This fitness increase — the *fitness value of information* — is a composite of both Shannon's mutual information and the decision-theoretic value of information. Furthermore, we show that in certain cases the fitness value of responding to a cue is exactly equal to the mutual information between the cue and the environment. In general the Shannon entropy of the environment, which seemingly fails to take anything about organismal fitness into account, nonetheless imposes an upper bound on the fitness value of information.

1 Introduction

Living organisms acquire, store, process, and transmit information — and as such, information is a central organizing principle in biological systems at every

scale from the digital coding in DNA to the long-range calls of cetaceans [1]. While information-theoretic measures such as entropy and mutual information [2, 3, 4] have been embraced in neurobiology and bioinformatics, these measures are less commonly used in behavioral biology and evolutionary ecology.

The problem is that entropy and mutual information do not directly address information quality; they do not distinguish between relevant and irrelevant information. Thus decision theorists, economists, and behavioral biologists typically measure information by considering its value: its effect on expected payoff or expected fitness [5, 6, 7, 8, 9, 10].

Definition: The *value of information* associated with a cue or signal C is defined as the difference between the maximum expected payoff or fitness that a decision-maker can obtain by conditioning on C and the maximum expected payoff that could be obtained without conditioning on C .

The disconnect between entropy and mutual information on one hand and the value of information on the other has long puzzled biologists in general and the authors of this paper in particular. Entropy and mutual information appear to measure information quantity while reflecting nothing about fitness consequences; the value of information measures fitness consequences but has nothing to do with the actual length or information quantity of a message. But early work in population genetics [11, 12, 13, 14]¹ and recent analyses of evolution in fluctuating environments [17, 18] hint at a possible relation between information and fitness. What is this relation? Information theorists since Kelly [19] have observed that in special circumstances, information value and information-theoretic measures may be related. Here we argue that these special circumstances are exactly those about which biologists should be most concerned: the context of evolution by natural selection. We address the question “how much is information worth to living organisms?” and show that the answer turns out to be a striking amalgam of mutual information and the decision-theoretic value of information.

2 A basic model

As evolutionary biologists, how should we measure the cost of uncertainty² or the value of information? We want to know how the information affects fitness,

¹Indeed, Claude Shannon wrote a PhD thesis in population genetics before embarking on the work that launched the field of information theory [15, 16].

²Numerous studies in population ecology and genetics have shown that fitness and population growth in uncertain environments depend on the exact nature of the uncertainty; they depend both on the distribution of individual reproductive successes, and on the correlations in individual successes (reviewed in ref. [20]). One can capture this complexity by distinguishing between two types of uncertainty or risk [21]. *Idiosyncratic risk* is independent of that faced by other individuals, whereas *aggregate risk* is perfectly correlated among individuals. For example, predation imposes largely idiosyncratic risk on a herd of herbivores, whereas drought imposes largely aggregate risk. In this paper, we focus exclusively on aggregate risk. We will address mixed aggregate and idiosyncratic risk in a subsequent report.

so the natural measure of the worth of information is the following: The *fitness value of information*, G , is the greatest fitness decrement or cost that would be favored by natural selection in exchange for the ability to attain the information.

Like stockbrokers and habitual gamblers, biological organisms faced with uncertain conditions are selected to behave as if they are concerned with long-term growth rates. Thus the fitness value of information to biological organisms is best measured in terms of the consequences of this information on the long-term growth rates of organismal lineages. Maximizing long-term growth in such conditions is the same as maximizing the expected value of the logarithm of the growth rate in a single generation [22, 23] (as opposed to the expected value of the growth rate itself).

To illustrate these results and to develop an intuition about the value of information in biological systems, consider the following simple model of a population of annual organisms living in a variable environment³. The state of the environment in each year is an independent random variable Φ with two states ϕ_1 and ϕ_2 , that occur with probability p_1 , and $p_2 = 1 - p_1$ respectively. All individuals encounter exactly the same environment in a given year. At the beginning of its development, each organism makes an important developmental decision to adopt one of two alternative phenotypes: one suited to environment ϕ_1 , or one suited to ϕ_2 . The organism survives to reproduce only if its phenotype properly matches the demands of the current environment. The organism's fitness is given by the following matrix:

	Phenotype 1	Phenotype 2
Environment ϕ_1	w_1	0
Environment ϕ_2	0	w_2

What should these individuals do in the absence of information about the condition of the environment? In the short run, individuals maximize expected fitness by employing the highest-payoff phenotype only. This yields an expected single-generation fitness of $\max[p_1 w_1, p_2 w_2]$.

But in the long run, playing only one strategy will inevitably lead to a year with zero fitness and consequent extinction. Thus natural selection will favor not the short run maximization above, but rather a maximization of long-term fitness. These organisms will be selected to *hedge their bets* during development [24, 25], developing into phenotype 1 with some probability and phenotype 2 otherwise⁴. As we consider a larger and larger span of generations, natural selection is overwhelmingly likely [21] to favor the strategy that maximizes the growth rate for “typical sequences” [4], in which environment ϕ_1 occurs $N p_1$ times, and environment ϕ_2 occurs $N p_2$ times. For a genotype that develops with probability x into phenotype 1, the population growth over such

³In this section, we follow Cover and Thomas's (1991) presentation; these authors offer a parable about a habitual gambler who perpetually reinvests his entire winnings at the horse track. Their gambling story can be recast quite naturally as a model of organisms evolving by natural selection to match their physiologies to uncertain environmental conditions.

⁴Alternatively, organisms can hedge their bets via phenotypic switching, as with the bacterial persistence phenotype [26, 27, 18].

a sequence of N events will be $(w_1 x)^{Np_1} (w_2(1-x))^{Np_2}$ and will be maximized when $N(p_1 \log(w_1 x) + p_2 \log(w_2(1-x)))$ is maximized. This occurs when $p_1/x = p_2/(1-x)$ or when $x = p_1$. Thus for almost all sequences of environments, the strategy that develops into phenotype 1 with probability p_1 will maximize the growth rate and thus take over the population. For this strategy, the expected log growth rate will be $p_1 \log(w_1 p_1) + p_2 \log(w_2 p_2)$.

We have set up a simple biological model where uncertainty critically affects fitness. What is the fitness value of information here? Suppose that individuals are able to detect a cue that they can use to forecast the state of the environment with 100% accuracy. In this case the organism will use phenotype 1 in environment 1, and phenotype 2 in environment 2. What is the fitness value of [being able to obtain] this cue?

First, we can look at how the cue improves the short-run expected fitness. With the cue, individuals can always develop the appropriate phenotype for the environment, and obtain short-run expected fitness $p_1 w_1 + p_2 w_2$. Thus in the short run, the expected value of information is $p_1 w_1 + p_2 w_2 - \max[p_1 w_1, p_2 w_2] = \min[p_1 w_1, p_2 w_2]$. This is exactly the decision-theoretic value of information.

But natural selection will not maximize short run expected fitness; instead as discussed above it maximizes the expected log fitness. Without the cue, the expected log growth rate is $R_{\text{no inf}} = p_1 \log(p_1 w_1) + p_2 \log(p_2 w_2)$. With the cue it is $R_{\text{inf}} = p_1 \log w_1 + p_2 \log w_2$. The fitness value of information G is the difference between growth with and without the cue, $R_{\text{inf}} - R_{\text{no inf}}$; and this quantity is exactly the mutual information between the perfectly informative cue and the environment, $p_1 \log p_1 + p_2 \log p_2$. The payoffs w_i have dropped out. For this very simple example, the fitness value of information has nothing to do with the fitnesses w_1 and w_2 , but instead depends exclusively on the mutual information measure.

This result generalizes naturally to cues that are only partially informative [19, 4]. If the cue is a random variable C , the fitness value of information will be the mutual information $I(\Phi; C) = \sum_{\phi, c} p(\phi, c) \log \frac{p(\phi, c)}{p(\phi)p(c)}$ between the cue C and the state of the environment ϕ .

3 Two illustrative examples

Thus far we have been looking at a very special case in which the fitness of the organism is zero when the wrong phenotype is adopted. A more realistic model would allow the possibility of non-zero fitness even when the organism develops to the wrong phenotype.

Example 1

We start with a two-environment, two-phenotype example. Since the players have no control over the state of the environment, we can study the decision-theoretic behavior of the players without loss of generality using the following matrix where $1 > a \geq b$:

	Phenotype 1	Phenotype 2
Environment ϕ_1	1	b
Environment ϕ_2	a	1

If the organism invests x in phenotype 1 and $1 - x$ in phenotype 2, her expected log growth rate will be $p \log[x + a(1 - x)] + (1 - p) \log[bx + (1 - x)]$. In the absence of information about which environmental state is realized, the choice of $x^*(p)$ that maximizes expected log growth given the probability p of environment 1 is:

$$x^*(p) = \begin{cases} 0 & \text{for } p \leq \frac{a(1-b)}{1-ab} \\ \frac{p+a b(1-p)-a}{(1-a)(1-b)} & \text{for } \frac{a(1-b)}{1-ab} < p < \frac{1-b}{1-ab} \\ 1 & \text{for } \frac{1-b}{1-ab} \leq p \end{cases} \quad (1)$$

We see that the organism hedges bets only in a central region. Beyond that region, the optimal bet-hedging strategy would require the organism to produce one of the phenotypes with negative probability. This sort of investment may be feasible in a stock market or a horse race, but negative bets seem to lack a biological meaning. In biological situations, we do better to look at the constrained case where the organism must produce each phenotype with non-negative probability.

[Figure 1 about here]

If the organism responds to a cue C that gives the exact state of the environment, she will match her phenotype to the environment always, for an expected log growth rate of $\log(1) = 0$. The fitness value of information G is shown in figure 1. In the central region $\frac{a(1-b)}{1-ab} < p < \frac{1-b}{1-ab}$, the fitness value of information is equal to the mutual information $I(\Phi; C)$ between the (perfectly informative) cue C and the environment Φ , plus a linear function of the probability of each environment. Outside the range, when the optimal strategy invests in only one of the phenotypes, the value of the cue is $-p \log[a]$ or $-(1-p) \log[b]$. This is simply the decision-theoretic log value of information, i.e., the expected log of the value one would get if one took the decision-theoretic approach of maximizing fitness in one generation.

Example 2

To get a better intuition of how the fitness value of information relates to the evolutionarily optimal strategy in the absence of information, we move to the case of 3 environments that occur with probabilities p_1 , p_2 , and $p_3 = (1 - p_1 - p_2)$. While the principles generalize to larger numbers of environments and less-symmetric payoffs, three symmetric environments are far easier to represent graphically than are the more complicated alternatives. Thus we consider the following payoffs structure where $a > 1$:

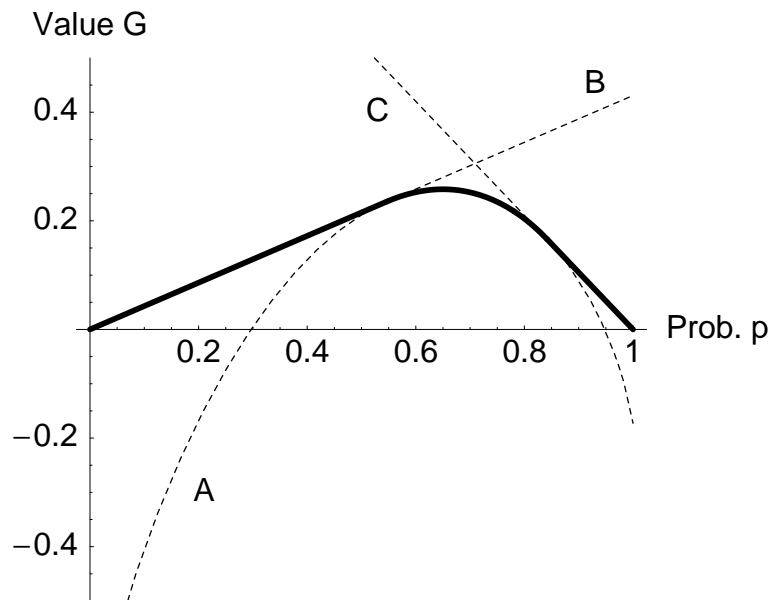


Figure 1: The fitness value of information (heavy solid curve) as a function of environmental probabilities p is a composite of three value functions: Curve (A) is the sum of mutual information between cue and environment and a linear function of the environmental probabilities: $-(p \log[p] + (1 - p) \log[1 - p]) - (\log[1 - ab] - (1 - p) \log[1 - a] - p \log[1 - b])$. Curves (B) and (C) are the linear functions $-p \log[a]$ and $-(1 - p) \log[b]$ respectively. Parameter values: $a = 0.65$, $b = 0.35$. Simple calculus reveals that the despite being composed of a linear component and a logarithmic component, the fitness value of information G is not only continuous but also once continuously differentiable.

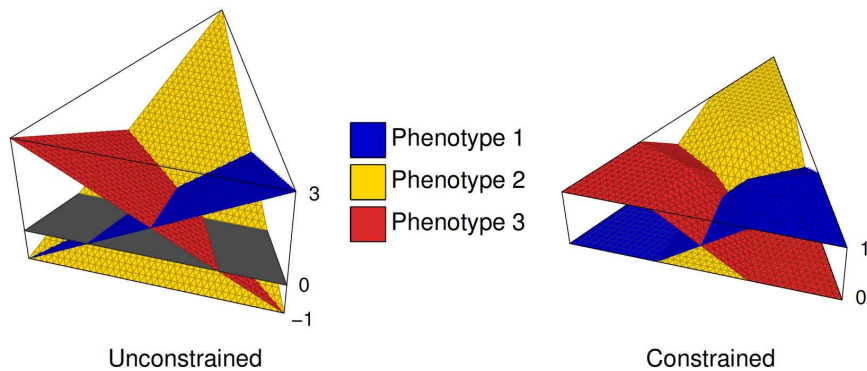


Figure 2: Fractional investment in each strategy in order to maximize long-term growth rate, as a function of the probabilities (p_1, p_2, p_3) of each environment, for example 2 with $a = 2$. Because of the constraint $p_1 + p_2 + p_3 = 1$, we can represent the space of all possible environment probabilities (p_1, p_2, p_3) as the two-dimensional simplex where one corner represents $(1, 0, 0)$, another $(0, 1, 0)$, and the third $(0, 0, 1)$. The height of the three surfaces at any point indicates the fractional investment in each strategy at that point. On the left, we have the unconstrained optimum, in which individuals may “bet against” certain phenotypes, investing negatively in them and putting the surplus into the other phenotypes. On the right is the constrained (and biological relevant) solution, in which the fraction invested in each phenotype must be non-negative.

	Phenotype 1	Phenotype 2	Phenotype 3
Env. ϕ_1	a	1	1
Env. ϕ_2	1	a	1
Env. ϕ_3	1	1	a

Using the approach sketched out above, we can compute the fractional investment x_1, x_2, x_3 in each strategy that maximizes long-term growth rate:

$$\begin{aligned}
 x_1 &= (p_1(1+a) - p_2 - p_3)/(a-1) \\
 x_2 &= (p_2(1+a) - p_1 - p_3)/(a-1) \\
 x_3 &= (p_3(1+a) - p_1 - p_2)/(a-1)
 \end{aligned}
 \tag{2}$$

[Figure 2 about here]

This optimal strategy is shown in the left panel of Figure 2. Here we have a curious sort of investment; the gray surface is the “invest zero” plane. When the colored surfaces drop below this, the player is effectively betting against those phenotypes by producing them with negative probability — which makes

no biological sense, as discussed above. Our solution is then only reasonable in the central region where all three bets are non-negative. This area, which we will call Region 1, is delimited by $p_i > 1/(2+a)$ for all $i = 1, 2, 3$. Outside of Region 1, we will have to compute optimal bets subject to constraints that no bet is negative. We do this below and illustrate the result in the right panel of Figure 2.

When one environment is sufficiently infrequent but the other two are common, an individual will invest in the phenotypes corresponding to the two common environments but not in the rare one. There are three such regions on the simplex, with boundaries given by the trio of inequalities $p_i < 1/(2+a)$, $p_j < p_k a$, and $p_k < p_j a$. In these three areas which collectively we call Region 2, optimal allocation is given by

$$\begin{aligned} x_i &= 0 \\ x_j &= (p_j a - p_k)/(a-1) \\ x_k &= (p_k a - p_j)/(a-1) \end{aligned} \tag{3}$$

Finally, when two environments are sufficiently rare, individuals will produce only the phenotype corresponding to the common environment. This occurs outside of the areas covered by Regions 1 and 2, in three corner areas which collectively we call Region 3.

Because of the different betting strategies in each region, the value of information in each region is computed by a different formula. We take these in turn. In Region 1, a cue indicating the state of the environment increases the expected log growth rate by

$$\log[a/(2+a)] - \sum p_i \log p_i = \log[a/(2+a)] + I(\Phi, C) \tag{4}$$

This is simply a constant plus the mutual information between the environment and the (perfectly informative) cue.

In Region 2, let l be the phenotype never adopted by the organism. Then the cue increases the expected growth rate by

$$\log a - \sum_{i \neq l} p_i \log p_i - (1-p_l) \log[(1+a)/(1-p_l)] \tag{5}$$

In Region 3, let l be the phenotype always adopted by the organism. The cue increases the expected log growth rate by

$$(1-p_l) \log a \tag{6}$$

This is simply the decision-theoretic log value of information, i.e., the log of the value one would get if one took the decision-theoretic approach of maximizing fitness in one generation.

Putting these all together, we get the surface shown in Figure 3.

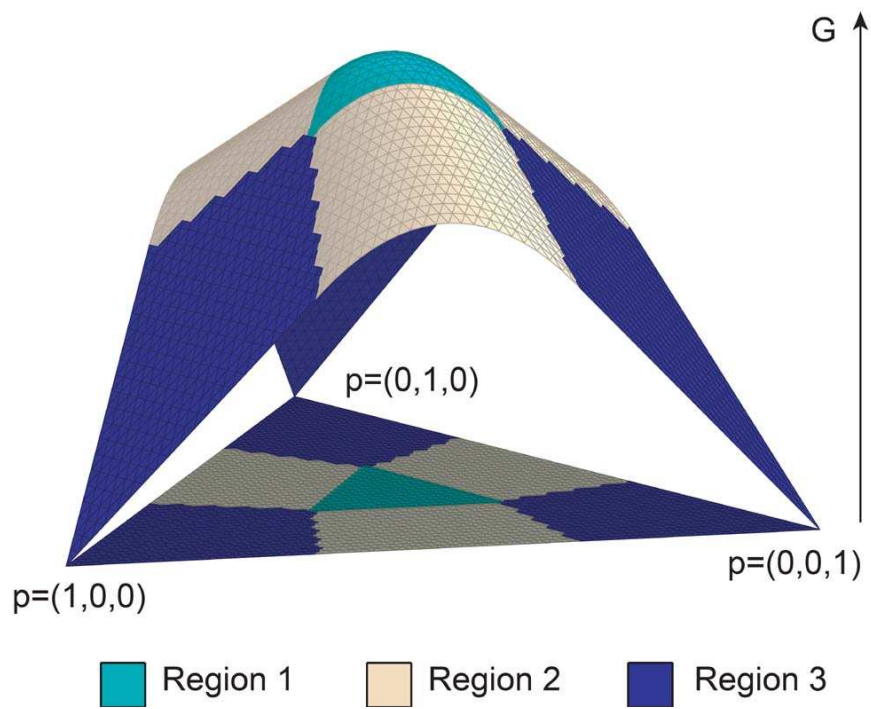


Figure 3: The fitness value of information G as a function of the probabilities that each environment occurs, for the symmetric three-environment scenario with $a = 2$, displayed on the simplex $p_1 + p_2 + p_3 = 1$.

[Figure 3 about here]

Surprisingly, this fitness value of information surface seamlessly sews together a region described by the mutual information (Region 1), a region described by the decision-theoretic value of information (Region 3), and an intermediate region (Region 2). Comparing the height of the surface and the gradients along the relevant edge and point boundaries, calculus reveals that this surface is again continuous and once continuously differentiable everywhere. The fitness value of information incorporates both the information-theoretic measure and the decision-theoretic value — and through the continuity of the corresponding regions, we also see a fundamental connection between these two measures.

4 Extending the model

Let us now assume that an organism has to make a developmental decision between n possible phenotypes, each of which is a best match to one of n environments. The environments ϕ_i occur with probabilities p_i and the fitness of phenotype j in environment i is w_{ij} .

How should an organism respond? To maximize short-run expected fitness, the organism should simply develop the phenotype with the highest expected fitness. Expected fitness then will be $E[w] = \max_j [\sum_i p_i w_{ij}]$.

What about long-term fitness? We can find a general form for the fitness value of information for those cases corresponding to Region 1 in the previous example, i.e., where the organism develops into all n phenotypes with positive probability. Let us look at a strategy that produces phenotype i with frequency $x_i > 0$. The organism will be selected to maximize the expected log growth rate R , so we want to find the strategy that maximizes the log growth rate $\sum_i p_i \log \sum_j w_{ij} x_j$ subject to the constraint that the fractional investments in the various phenotypes sum to one: $\sum_i x_i = 1$. The Lagrangian for this problem is

$$L(x_1, x_2, \dots, x_n, r) = \sum_i p_i \log \sum_j w_{ij} x_j - \lambda \left(\sum_i x_i - 1 \right) \quad (7)$$

Since the constraint function is a linear function, it immediately satisfies the constraint qualification that the partials of the constraint function at the constrained maximizer are not all zero. We maximize the Lagrangian by taking partial derivatives and setting to zero. The partials with respect to x_k yield a set of n equations:

$$\frac{\partial}{\partial x_k} \left[\sum_i p_i \log \sum_j w_{ij} x_j - \lambda \sum_i x_i \right] = 0 \quad (8)$$

Assuming that W (the matrix whose (i, j) entry is w_{ij}) is invertible, we can write $y_i = \sum_j w_{ij}x_j$, and $V = W^{-1}$, so that $x_j = \sum_i v_{ji}y_i$. Then we can solve

$$\frac{\partial}{\partial y_k} \left[\sum_i p_i \log \sum_j y_j - \lambda \sum_{ij} v_{ji} y_i \right] = 0 \quad (9)$$

for all k , which gives for all k :

$$\frac{p_k}{y_k} - \lambda \sum_j v_{jk} = 0 \quad (10)$$

Now we can solve for the constraint $\sum_i x_i = 1$, which gives $\lambda = 1$ and thus we have $y_k = p_k / \sum_j v_{jk}$. Though this solution for y_k always exists, and the corresponding x_i always satisfy the constraint $\sum_i x_i = 1$, a solution might contain negative x_i , which would not be biologically plausible. Thus the rest of the derivation will assume that we are in a region of parameter space in which the solution is indeed non-negative for all x_i . Substituting y_k into the equation for the log growth rate, to get the maximal log growth rate without the cue, gives

$$R_{\text{no inf}} = \sum_i p_i \log \left(\frac{p_i}{\sum_j v_{ji}} \right) = \sum_i p_i \log(p_i) - \sum_i p_i \log \left(\sum_j v_{ji} \right) \quad (11)$$

This expression is simply $-H(\Phi) + L(p)$, where $H(\Phi)$ is the entropy of the environment and L is a linear function of the probabilities of each environmental state.

We would now like to calculate the value of a cue. This will be the difference in the expected log growth rate between this optimal strategy, and the optimal strategy when a cue C is received.

First we consider a cue that reveals the exact environment. The organism will maximize fitness by matching phenotype to the known environment, yielding a log growth rate $R_{\text{inf}} = \sum_i p_i \log(w_{ii})$. Thus the value of this cue is

$$J = R_{\text{inf}} - R_{\text{no inf}} = - \sum_i p_i \log(p_i) + \sum_i p_i \log \left(w_{ii} \sum_j v_{ji} \right) \quad (12)$$

This is the mutual information between the (perfectly informative) cue and environment, $I(\Phi; C) = H(p) - 0$ plus a linear function of the probabilities p_i .

Next we assume that the cue does not reveal the exact state of the environment, but instead only contains partial information about the environment. Let the mutual information between the cue C and the environment be $I(\Phi; C)$. The strategy of the organism will depend on the cue. We can thus maximize growth rate for each cue separately using the conditional probabilities of all environments $\Pr(\phi|c)$, and the same argument we used above to calculate the optimal strategy. We used two assumptions there: first, that W is invertible, and this still holds, and second that in our solution all x_k are non-negative. We

now assume that this is true for the responses to all cues, and limit the domain of our solution correspondingly, as discussed below. We can then compute the maximal growth rate by averaging equation 11 over all cues, for a maximal growth rate of:

$$\begin{aligned}
 R_{\text{inf}} &= \sum_c \Pr(c) \sum_{\phi} \Pr(\phi|c) \log(\Pr(\phi|c)) - \sum_c \Pr(c) \sum_{\phi} \Pr(\phi|c) \log\left(\sum_j v_{ji}\right) \\
 &= \sum_c \sum_{\phi} \Pr(\phi, c) \log(\Pr(\phi|c)) - \sum_i p_i \log\left(\sum_j v_{ji}\right) \quad (13)
 \end{aligned}$$

This is $-H(\Phi|C) + L(p)$, where $H(\Phi|C)$ is the conditional entropy of the environment given the cue. The fitness value of information G conferred by the cue is the difference in the growth rates: $-H(\Phi|C) + L(p) + H(\Phi) - L(p) = I(\Phi; C)$. Thus G is simply the mutual information between the cue and the environment.

Note that the fitness difference will be exactly $I(\Phi; C)$ only when the organism produces all phenotypes with positive probability both with and without the cue. In our calculation we assumed that for all cues, all x_i are positive. If the environmental probabilities are such that the organism hedges in the absence of a cue, then if the cue conveys sufficiently little information, the organism will also do best to hedge after receiving the signal as well, albeit with different fractions going into each phenotype. The reason is that for each particular signal c , we get a solution using conditional probabilities $\Pr(\phi|c)$ instead of the original probabilities $\Pr(\phi)$. If all the $\Pr(\phi|c)$ are sufficiently close to $\Pr(\phi)$, they will fulfill the same requirements that $\Pr(\phi)$ fulfills, and thus there will be a solution with positive x_i for each signal. In all such cases, the fitness gained from a signal will be exactly the mutual information between the signal and the environment. When we are outside this range, the gain from a signal will be lower relative to the mutual information, and can even be 0. For example, if without the signal no bet-hedging occurs, and all signals convey so little information that no decision is changed, then the gain in growth rate resulting from the signal will be 0.

5 Bounding the fitness value of information

We can also show that the fitness value of information is bounded above by the mutual information between cue and environment. Compare the expected log growth rate of individuals of two types. Type A individuals receive a cue C with possible values $c_1, c_2, c_3, \dots, c_n$ drawn from a distribution with probability function $\Pr(C)$ and entropy $H(C)$. Each individual then maximizes expected log growth rate by following some investment strategy $s(c)$ that sets how to invest in the various phenotypes, given the receipt of cue c .

Type B individuals do not receive this cue. Instead, they follow the betting strategy $r = \sum_c \Pr(c)s(c)$, thereby employing a probability-matching mixture of the various $s(c)$ strategies used by Type A individuals.

Represent the fitness of an individual using strategy $s(y)$ when the cue was c by $w(s(y)|c)$. The expected log growth rate for Type A individuals is then

$$R_A = \sum_c \Pr(c) \log[w(s(c)|c)]. \quad (14)$$

The expected log growth rate for Type B individuals is

$$R_B = \sum_c \Pr(c) \log \left[\sum_{c'} \Pr(c') w(s(c')|c) \right]. \quad (15)$$

Since fitnesses are non-negative, the $w(s(c')|c)$ terms in the summation above must be at least zero even for $c' \neq c$, and therefore $\sum_{c'} \Pr(c') w(s(c')|c) \geq \Pr(c) w(s(c)|c)$. Since log is a monotone function, this implies $\log \left[\sum_{c'} \Pr(c') w(s(c')|c) \right] \geq \log \left[\Pr(c) w(s(c)|c) \right]$. Thus:

$$\begin{aligned} R_B &\geq \sum_c \Pr(c) \log[\Pr(c) w(s(c)|c)] \\ &= \sum_c \Pr(c) \log[w(s(c)|c)] + \sum_c \Pr(c) \log \Pr(c) \\ &= R_A - H(C). \end{aligned} \quad (16)$$

Since a growth rate of at least R_B can be attained without information, the fitness value of information is therefore bounded by $G \leq R_A - R_B < H(C) = I(\Phi, C)$. Thus the fitness value of information is at most equal to the mutual information between a perfectly informative cue and the environment, *irrespective of the actual fitness payoffs w* . As before, this result can be generalized to partially informative cues [4].

6 Discussion

In this paper we have shown that two measures of information, the information-theoretic mutual information and the decision-theoretic value of information, are united into a single measure when one looks at the strategies that natural selection will favor, namely those that maximize the long term growth rate of biological organisms. Furthermore, we have shown that under conditions in which bet-hedging is advantageous, and with cues that convey little information, the fitness value of information associated with those cues is exactly the mutual information between the cue and the environment. Finally, we have shown that the fitness value of an informative cue is bounded above by the mutual information between that cue and the environment, and in some cases is equal to exactly this value. These results establish a close relationship between biological fitness and information-theoretic measures such as entropy or mutual information.

But why does this relation exist? To answer that question, we should take a closer look at the concept of information: information is the reduction of uncertainty, where uncertainty measures the number of states a system might be in. Thus mutual information between the world and a cue is the fold reduction in uncertainty about the world after the cue is received. For example, if a system could be in any of six equiprobable states, and a cue serves to narrow the realm of possibility to just three of these, the cue provides a twofold reduction in uncertainty. For reasons of convenience, information is measured as the logarithm of the fold reduction in uncertainty — this ensures that the measure is additive, so that for example we can add the information received by two successive cues to calculate the total information gained [28, 29, 3].

Thus while information concepts are often thought to be linked with the famous sum $\sum p \log(p)$, the fundamental concept is not a particular mathematical formula. Rather, it is the notion that information measures the fold reduction in uncertainty about the possible states of the world.

With this view, it is easy to see why information bears a close relation to biological fitness: For simplicity, consider an extreme example in which individuals survive only if their phenotype matches the environment exactly, and suppose that there are ten possible environments that occur with equal probability. In the absence of any cue about the environment, the best the organism can do is randomly choose one of the ten possible phenotypes with equal probability. Only one tenth of the individuals will then survive, since only a tenth will match the environment with their phenotype. If a cue conveys 1 bit of information and thus reduces the uncertainty about the environment twofold, the environment can be only in one of five possible states. The organism will now choose randomly one of five possible phenotypes, and now a fifth of the population will survive — a twofold increase in fitness, or a gain of 1 bit in the log of the growth rate.

What happens when the environments are not equiprobable? In this case we can understand the connection between information and fitness by looking to long sequences of environments and the theory of typical sequences. The theory tells us that almost surely one of the “typical sequences” — those sequences in which the environments occur in their expected frequencies — will occur [4]. Moreover, all typical sequences occur with equal probability. Thus a lineage is selected to divide its members equally among all typical sequences. Since any one mistake in phenotype is lethal, only a fraction of these lineages, those that have just the right sequence, will survive. The number of typical sequences in this case is exactly $2^{NH(\Phi)}$ where N is the number of generations in the sequence and $H(\Phi)$ is the entropy of the environment. Correspondingly, the fraction of surviving lineages will be $2^{-NH(\Phi)}$. If a cue C is received that reduces the uncertainty of the environments by $I(\Phi; C)$, then the fraction of surviving lineages can be increased by exactly $2^{NI(\Phi; C)}$. This is analogous to the situation in communication: if we need to encode a string of symbols that are not equiprobable, we turn to a long sequence of such symbols. Our code then needs only to be efficient for representing typical sequences of symbols, and those typical sequences occur with equal probability. The number of such sequences is

2^{NH} , where N is the length and H is the entropy of the symbols. If the message recipient also obtains side information related to the message itself, then the mutual information $I(\text{message}; \text{side information})$ measures the reduction in the number of possible messages that need to be encoded by the transmitter. This number of messages is reduced by exactly $2^{NI(\text{message}; \text{side information})}$ -fold by the presence of the side information.

We can now see why the concept of information is the same across different disciplines. In biology, fitness refers to the fold increase in the number of surviving lineages. In communication theory, information refers to the fold increase in the number of messages to encode. In physics, entropy refers to the fold increase in the number of possible states in phase space.

Finally, our results also suggest that information theory will be useful in studying the evolution of communication. Even before knowing what a biological signal means, how it is used, or what the fitness structure of the environment may be, we have shown that one can place an upper bound on the fitness consequences of responding to that signal, simply by measuring the information content of the signalling channel.

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References

- [1] John Maynard Smith. The idea of information in biology. *Quarterly Review of Biology*, 74(4):395–400, 1999.
- [2] N. Wiener. *Cybernetics*. John Wiley and Sons, New York, 1948.
- [3] C. E. Shannon. A mathematical theory of communication. *Bell Systems Technical Journal*, 27:379–423; 623–656, 1948.
- [4] T. M. Cover and J. A. Thomas. *Elements of Information Theory*. John Wiley and Sons, New York, 1991.
- [5] L. J. Savage. *The Foundations of Statistics*. Wiley, New York, 1954.
- [6] I. J. Good. On the principle of total evidence. *British Journal for the Philosophy of Science*, 17:319–321, 1966.
- [7] J. P. Gould. Risk, stochastic preference, and the value of information. *Journal of Economic Theory*, 8:64–84, 1974.
- [8] D. W. Stephens and J. R. Krebs. *Foraging Theory*. Princeton University Press, Princeton, 1986.
- [9] D. W. Stephens. Variance and the value of information. *American Naturalist*, 134(1):128–140, 1989.
- [10] F. P. Ramsey. Weight or value of knowledge. *The British Journal for the Philosophy of Science*, 41:1–4, 1990). Published posthumously from personal notes.
- [11] J. B. S. Haldane. The cost of natural selection. *Journal of Genetics*, 55:511–524, 1957.
- [12] M. Kimura. Natural selection as the process of accumulation of genetic information in adaptive evolution. *Genetical Research*, 2:127–140, 1961.
- [13] J. Felsenstein. Macroevolution in a model ecosystem. *American Naturalist*, 112:177–195, 1978.

- [14] L. Demetrius. Statistical mechanics and population biology. *Journal of Statistical Physics*, 30:709 – 753, 1983.
- [15] C. E. Shannon. An algebra for theoretical genetics. In N. J. A. Sloane and A. D. Wyner, editors, *Claude Shannon: Collected Papers*. John Wiley and Sons, 1940. Ph.D dissertation, Massachusetts Institute of Technology.
- [16] J. F. Crow. Shannon’s brief foray into genetics. *Genetics*, 159:915–917, 2001.
- [17] C. T. Bergstrom and M. Lachmann. Shannon information and biological fitness. In *IEEE Information Theory Workshop 2004*, pages 50–54. IEEE, Oct. 2004.
- [18] E. Kussell and S. Leibler. Phenotypic diversity, population growth, and information in fluctuating environments. *Science*, 309:2075–2078, 2005.
- [19] J. L. Kelly. A new interpretation of information rate. *Bell Systems Technical Journal*, 35:917–926, 1956.
- [20] J. Yoshimura and V. A. A. Jansen. Evolution and population dynamics in stochastic environments. *Res. Popul. Ecol.*, 38(2):165–182, 1996.
- [21] A. J. Robson, C. T. Bergstrom, and J. K. Pritchard. Risky business: Sexual and asexual reproduction in variable environments. *Journal of Theoretical Biology*, 197:541–556, 1999.
- [22] D. Cohen. Optimizing reproduction in a randomly varying environment. *Journal of Theoretical Biology*, 12:119–129, 1966.
- [23] R. C. Lewontin and D. Cohen. On population growth in a randomly varying environment. *Proceedings of the National Academy of the Sciences*, 62:1056–1060, 1969.
- [24] W. S. Cooper and R. H. Kaplan. Adaptive “coin-flipping”; a decision-theoretic examination of natural selection for random individual variation. *Journal of Theoretical Biology*, 94(94):135–151, 1982.
- [25] Seger and Brockmann. What is bet-hedging? *Oxford Surverys in Evolutionary Biology*, 4:182–211, 1987.
- [26] M. Lachmann and E. Jablonka. The inheritance of phenotypes: an adaptation to fluctuating environments. *Journal of Theoretical Biology*, 81:1–9, 1996.
- [27] E. Kussell, R. Kishony, N. Q. Balaban, and S. Leibler. Bacterial persistence: A model of survival in changing environments. *Genetics*, 169:1807–1814, 2005.
- [28] H. Nyquist. Certain factors affecting telegraph speed. *Bell Systems Technical Journal*, pages 324–346, 1924.

- [29] R. V. Hartley. Transmission of information. *Bell Systems Technical Journal*, 7:535–563, 1928.