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2 Running title: The fitness value of information

3 Authors: Jacob Usinowicz^{1,2} and Mary I. O'Connor^{1,2}

4
5 **Affiliations:**

6 1. *Department of Zoology, University of British Columbia, Vancouver, Canada*

7 email: usinowic@zoology.ubc.ca

8 2. *Biodiversity Research Centre, University of British Columbia, Vancouver, Canada*

9 email: oconnor@zoology.ubc.ca

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34 **Corresponding author:**

35 Jacob Usinowicz

36 Department of Zoology

37 4200-6270 University Boulevard

38 Vancouver, BC V6T 1Z4

Abstract (max 120)

Information processing is increasingly recognized as a fundamental component of life in variable environments, including the evolved use of environmental cues, biomolecular networks, and social learning. Despite this, ecology lacks a quantitative framework for understanding how population, community, and ecosystem dynamics depend on information processing. Here, we review the rationale and evidence for 'fitness value of information' (FVOI), and synthesize theoretical work in ecology, information theory and probability behind this general mathematical framework. The FVOI quantifies how species' *per capita* population growth rates can depend on the use of information in their environment. FVOI is a breakthrough approach to linking information processing and ecological and evolutionary outcomes in a changing environment, addressing longstanding questions about how information mediates effects of environmental change and species interactions.

Quantifying information in ecology

Biology is built upon information. The genetic architecture of life is an information storage and transcription scheme for constructing proteins (Smith 1999; Goldenfeld & Woese 2007; Tkačik & Bialek 2016). Sub-cellular biomolecular networks process and respond to information in order to maintain homeostasis (Woods & Wilson 2013), divide (Cai *et al.* 2018), and perform many tasks (Tyson *et al.* 2002). Countless examples of derived sensory apparatus exist that allow cells and organisms to transmit, process, and store information about their environment (Dangles *et al.* 2009). Organisms across all kingdoms of life respond to changing environments and act to improve resource acquisition, defense against consumption and reproduction rates (Crespi 2001; Crone *et al.* 2009; Gil *et al.* 2018). Natural selection itself is an information process, where changing gene frequencies encode population-level information about the fitness consequences of the environment (Smith 1999; Frank 2012). Despite the essential nature of information processing in the persistence of biological systems in dynamic environments ecological studies rarely acknowledge the important roles that information can play in population, community, and ecosystem dynamics (O'Connor *et al.* 2019; Marleau *et al.* 2020).

Although information is fundamental to life in variable environments (Bernhardt *et al.* 2020), our understanding of information's role in ecological dynamics has been limited by an idiosyncratic approach to defining information and relating it to biological processes. In ecological science, information is typically equated with patterns in the environment that are predictable enough to serve as cues corresponding with high chances of finding resources, mates, or refuges. Examples include animals that use social or chemical signals to find food (Danchin *et al.* 2004; Magrath *et al.* 2015; Gil *et al.* 2018), bacteria using chemical exudates to monitor local densities (Crespi 2001), plants using volatiles produced by neighbors to stimulate their own preemptive production of herbivory defense compounds (De Moraes *et al.* 1998; Baldwin *et al.* 2006), and organisms using seasonal environmental patterns to time phenology including growth, germination, reproduction, hibernation, and dormancy (Cohen 1966; Ellner 1997; Clauss & Venable 2000; Thackeray *et al.* 2016; Ten Brink *et al.* 2020); these examples are complimented by a growing literature that identifies the cost for misinterpreting cues as anthropogenic activities disrupt environmental regimes and historically stable relationships between events (McNamara *et al.* 2011; Horton *et al.* 2020). Yet, ecology lacks a common definition of information that would allow comparison and generalization across different systems where information is used, or a framework to measure the consequences of using (or not using) different sources of information.

An environmental or social cue contains information by being predictive of future conditions. This idea has been formalized with information theory (IT) (Goldenfeld & Woese 2007; Tkačik & Bialek 2016). In IT, information is measured in relation to the

“surprisal” of an event: less-probable (more surprising) events have higher information value (quantified as the $\log(1 / \text{probability}(\text{event}))$) to encapsulate the idea that an observer is better-informed after learning that a rare event has occurred. For example, consider a generally hot, arid environment where rain occurs only within a short rainy season. The chance of experiencing rain on any particular day is low, so it is unsurprising to learn that it will not rain today; low surprise indicates that little information has been gained by an observer about the weather. Learning that it will rain carries more surprise, and thus conveys more information. IT can also be used to measure how much information temperature conveys about rain in this example using the mutual information (MI) between temporal patterns of rain and temperature. If temperature is generally constant regardless of precipitation, then knowing the temperature today is uninformative about the chance of rain (and vice versa) and the MI is zero. However, if rain is triggered by the arrival of a cold front then the consequent temperature drop on that day carries a great deal of information about the chance of rain and the MI is high.

Even though IT provides useful metrics of information, its potential to answer ecological questions has remained limited because it does not account for information’s biological meaning or value (Frank 2012). The mathematical framework for the fitness value of information (FVOI) (Donaldson-Matasci *et al.* 2010; Rivoire & Leibler 2011) is a key innovation developed to bridge information theory with biological concepts of species’ fitness. The core insight of this theory is that information takes on biological value when its use affects a population’s fitness. In other words, the use of information can increase - and occasionally decrease - a population’s fitness in a varying environment compared to another population in the same environment that does not use information. Operationalizing this insight presents many challenges because the extent to which information can increase fitness must account for concurrent costs and benefits associated with information detection and processing -- even the copying, erasure, and storage of information are physical operations with thermodynamic costs (Leff & Rex 2014; Parrondo *et al.* 2015; Kempes *et al.* 2017). More tangibly, organisms bear metabolic costs to implementing and maintaining sensory machinery (Koch 2004; Keller & Surette 2006; Nelson & MacIver 2006; Barth & Schmid 2013; Gil *et al.* 2018) and cellular or biochemical networks for information (Laughlin *et al.* 1998; Bruce *et al.* 2007; Bullmore & Sporns 2012; Crisp *et al.* 2016); although, in some cases organisms may take advantage of biochemical pathways that are already in place (Baldwin *et al.* 2006). On the other hand, information can have emergent benefits, as when matching the phenology of life history events such as flowering and reproduction with resources for growth compounds benefits through pollination success (Strauss 1997), herbivory avoidance (Schauber *et al.* 2002), or a reduction in interspecific competition (Usinowicz *et al.* 2012). Quantifying the fitness value of information should encompass both costs and benefits to using information.

A major advantage of the FVOI framework is that it simplifies the accounting of

costs and benefits of information use because it shifts focus from the organismal to the population level. Ecology and evolution share a universal measure of population-level fitness measured in terms of *per capita* population growth rates. The FVOI can be measured based on changes in *per capita* population growth rates; if information improves an organism's ability to consume resources, locate mates, or survive then *per capita* growth rates increase relative to when information is absent in otherwise identical environments (Gould 1974; Stephens 1989; Donaldson-Matasci *et al.* 2010; Rivoire & Leibler 2011)(Figure 1). This approach has been applied to theoretical models of populations in varying environments to show when individuals in a population use environmental cues to time life history transitions with resource pulses, population fitness increases in a varying environment beyond what could be attained purely from average resource levels over time (Stephens 1989; Donaldson-Matasci *et al.* 2010; Rivoire & Leibler 2011). One important result from the FVOI is that the MI between a cue and future environmental conditions defines an upper limit for how much a source of information can improve fitness (Donaldson-Matasci *et al.* 2010; Rivoire & Leibler 2011). This result is useful because it confirms intuition that uninformative cues should not be expected to contribute to fitness and provides justification for using MI as a simple metric to identify cues with potential fitness value.

The goal of this review is to highlight the FVOI as a general framework that guides ecological intuition about information's role in ecological dynamics; it is not our objective to review IT as others have (Goldenfeld & Woese 2007; Tkačik & Bialek 2016) and we only define specific concepts as they become relevant to in-depth understanding of FVOI. We first present an intuitive heuristic derivation of FVOI following Donaldson-Matasci *et al.* (2010) for general ecological audiences and describe how FVOI can be measured both in theory and in empirical settings. We use two sets of theoretical models to illustrate core principles of FVOI spanning predator prey systems and competition in variable environments. By then surveying studies where organisms make fitness-related decisions (behavioral and developmental) in response to environmental cues (biotic and abiotic), we highlight the potential for FVOI to facilitate novel, testable ecological hypotheses (Marleau *et al.* 2020), and further our understanding of anthropogenic impacts on the information content of environmental cues (McMahon *et al.* 2017; Barton *et al.* 2018). A major strength of the FVOI is that it can link these disparate bodies of work through fundamental principles; in a variable and uncertain world organisms constantly face decisions (or, developmental junctures) which can ultimately have population-level impacts on the long-term persistence of their species, and that average fitness outcomes improve when populations of organisms make informed decisions.

Measuring the fitness value of information

Evidence that information has fitness value seems unequivocal when considering

the countless adaptations found in species to detect, process, and produce cues and signals. An integrated measure of the fitness value of information can be made by measuring population growth rates with the benefits, costs, and community context embedded in population dynamics (Cover & Thomas 2006; Donaldson-Matasci *et al.* 2010; Rivoire & Leibler 2011). Here we present a heuristic derivation of the FVOI for ecology that synthesizes studies which have derived this relationship from fundamental mathematical, information-theoretic principles to understand evolutionary dynamics (Box 1) (Donaldson-Matasci *et al.* 2010; Rivoire & Leibler 2011).

Fitness can be given a concrete, mathematical, definition. Ecologists (Turelli 1978; Chesson 1994; Ellner *et al.* 2016) and evolutionary biologists (Haldane & Jayakar 1963; Cohen 1966; Ellner 1987) measure fitness using *per capita* population growth rates: fitness is the expected value (average) of the logarithm of *per capita* population growth rates (Frank 2016). Ecologists commonly model population growth with discrete-time models of the form

$$N_i(t+1) = \lambda_i(t) N_i(t). \quad (1)$$

Here, $\lambda_i(t)$ is the species-specific *per capita* growth rate, which is itself usually a function of demographic parameters including survival and fecundity (e.g., Box 2). A population's expected long-term growth rate ρ is

$$\rho = E[\log \lambda_i(t)]. \quad (2)$$

The $E[\]$ signifies the expectation over many realizations of the term in brackets and is defined for both discrete- and continuous-time models. The continuous-time analogue is $dN_i/dt = G_i(t) N_i(t)$ and $G_i(t) = \rho$ is the log-growth rate.

In theory, ρ can be calculated for any specification of $\lambda_i(t)$, meaning it is applicable to any population. By measuring ρ under different models or parameterizations of $\lambda_i(t)$, biologists have used it to compare how different processes or environmental conditions impact the fitness of populations. For example, the theory of coexistence in fluctuating environments (Turelli 1978; Chesson 1994) is effectively based on an underlying comparison of two versions of ρ , one with and one without a varying environment; their difference measures how much population *per capita* growth rates depend on environmental variation (Usinowicz 2015; Shoemaker & Melbourne 2016; Barabás *et al.* 2018). In evolutionary theory, ρ provides a measure of the fittest strategy or adaptation when compared across different phenotypes in a population (Cohen 1966; Ellner 1997).

The FVOI framework is based on comparing ρ under different assumptions of information availability, usage, and cost. This assumes of course that $\lambda_i(t)$ can be calculated with and without information components. Stated pseudo-mathematically

(see Box 1 for full mathematical derivation), the fitness value of information is measured as the difference between $\rho(\text{information})$ and $\rho(\text{without information})$:

$$\Delta\rho = \rho(\text{information}) - \rho(\text{without information}) \quad (3)$$

Application of $\Delta\rho$ to some simple models of population growth has shown that at least two key information-based mechanisms (*sensu* ‘coexistence mechanism’) contribute to fitness (Donaldson-Matasci *et al.* 2010; Rivoire & Leibler 2011). The first mechanism defines the maximum fitness benefit that could be obtained by perfectly detecting and utilizing a cue. It is equivalent to the information-theoretic correlation between environmental variation and the potential cue (a particular pattern that precedes variation), known as the mutual information (MI) (Figure 1). The MI measures how much information about the availability of a good (or bad) environmental condition is potentially available to a population, and is thus proportionate to the maximum potential fitness value of information (in a cue) (Donaldson-Matasci *et al.* 2010; Rivoire & Leibler 2011). The MI is generally positive and can be zero when the cue and the environment are uncorrelated.

The other important component in the FVOI identified thus far in theory estimates the fitness consequences when a population’s response to patterns of environmental variation fails to utilize all of the available information (the MI). Quantitatively, this difference is equivalent to the Kullback-Leibler (KL) divergence (D_{KL}), which is a “probability distance” between two probability distributions; biologically, it measures how much the population’s distribution of responses to the environment (across individual organisms’ internal models of the environment) differs from the real probability distribution that describes environmental fluctuations (Box 1, Figure 1C,D)). If detection of and response to the environment perfectly anticipate patterns of environmental variation then the KL divergence is zero and the population can fully utilize the information present (in the cue) (i.e., the MI).

Parsing information’s contributions to fitness

In practice, $\Delta\rho$ can be applied to quantify the fitness value of information whenever *per capita* population growth rates can be quantified across the range of environmental conditions experienced by a population. Donaldson-Matasci *et al.* (2010) illustrate how $\Delta\rho$ effectively requires three key ingredients: 1) the distribution of *per capita* growth rates $\lambda_i(t)$ across environmental states, 2) the probability of experiencing each environmental state, and 3) the probability of experiencing each environmental state given a cue, be it environmental or social, formally expressed as a conditional probability. From (1) and (2) it is possible to calculate $\rho(\text{without information})$ and (1) and (3) combine for $\rho(\text{information})$. With each of these sets of observations, one can estimate the FVOI and potentially gain insight into the role of information-driven

adaptations or strategies in population and community dynamics. In this section, we illustrate how these lines of evidence are used to estimate FVOI by reviewing the theoretical literature that has explored FVOI in single-species population models. Details of all simulations presented in this section can be found in the Supporting Information, and code and data files found at <https://github.com/jusinowicz/fvoi.git>.

Betting on success: timing of seed germination in annual plants

A classic motivating example for understanding the FVOI is the timing of germination of annual plants in fluctuating environments. Environmental conditions that directly affect germination and reproductive success differ each generation, bounded within a distribution of possible sets of conditions. Each generation, dormant seeds within the population can germinate or remain dormant, and if they germinate the resulting adult plant will produce new seeds, the number of which will reflect the suitability of the environment. To understand whether and how plants use environmental cues to optimally time germination, ecologists have drawn on classic mathematical models of betting from probability theory to model the dynamics of populations in this system (Cohen 1966; Ellner 1997), an approach which has since been applied to organisms across myriad taxa including zooplankton (Cáceres 1997), fish (Secor 2007), trees (Usinowicz *et al.* 2017), and viruses (Stumpf *et al.* 2002). A population is treated as a bettor who has some amount of capital (seeds) to gamble on event outcomes (environment conditions); the role of the bettor is to decide when and how much to gamble on each event (the conditions each year). The betting analogy also shows the value of information more intuitively; in general, knowledge of likely outcomes allows a bettor to increase earnings by allowing them to make informed bets.

Drawing the connection between betting in probability theory and population dynamics of organisms in fluctuating environments requires some assumptions. In this example, the ecological equivalent of an ‘event’ is a multivariate space of environmental conditions that are relevant to the organism’s biology, e.g., moisture, temperature, and nutrient availability. An ‘event outcome’ is a combination of these conditions (visualized as a point that falls somewhere in the multivariate space). It is common (but not necessary) to model discrete events because gambling has discrete outcomes; a particular number is drawn, or a particular horse wins a race. When analyzing ecological data, it may be possible to fit continuous distributions to a discrete sampling space, but in many cases it may be preferable to work with the observed distribution of samples to construct the (non-parametric) distribution of environmental states.

Betting examples that motivate theory often refer to a bettor with decision-making ability. This bettor has an internal model of probabilities that it uses to make betting decisions. In reality, a bettor’s internal model is just a device to illustrate a mathematical concept and should not be taken too literally; in the mathematical representation of dynamics, the internal model is encapsulated by a function of a random variable, whose underlying probability distribution dictates the amount that is bet on the outcome of each

event (e.g. Box 1). Extending the analogy of internal models to ecological dynamics does lead to interesting biological questions. Organisms, or even populations, may have the ability to learn and improve decisions by learning the odds in a way that is more similar to a bettor that learns probabilities. In other cases, “decisions” are actually hard-wired life history transitions that are initiated by a particular stimulus or cue. For example, the “decision” of a seed to germinate is not behavioral, but is driven by a biochemical reaction initiated at the seed’s surface that generates a cascade of internal changes. But the “internal model” is actually the population-level manifestation of these decisions because the allocation of resources to reproduction in each generation is a population-level phenomenon. Thus in making analogies to probability theory, we are actually treating the population as a bettor whose internal model is really a distribution of individual-level decisions made across all individuals.

A naive bettor (or population) has zero information about the distribution of possible outcomes or states. The internal model of this population (bettor) is a uniform distribution over states (outcomes) because each state is considered to be equally likely. This important baseline is referred to as maximum entropy (maxent) in IT studies, because a uniform distribution of probabilities produces the maximum value of the Shannon entropy (Cover & Thomas 2006). In the FVOI, the maximum entropy case similarly establishes the baseline of *per capita* growth rates when we assume that populations are entirely uninformed about future environmental states. Formally, we denote the uninformed *per capita* growth rate as $\rho(\text{without information}) = \rho(x(E \sim U(0,1))) = \rho(E \sim U)$, where $x(E)$ is the rate at which a population gambles on each environmental state according to its internal model, $U(0,1)$ denotes the uniform distribution over the interval 0 to 1, and $\rho(E \sim U)$ is a shorthand that we use for the uninformed population.

In many cases, a population (bettor) may actually have some information about the distribution of odds of possible states (outcomes), which we denote formally as $\rho(x(E)) = \rho(E)$ simply to indicate that some distribution of probabilities is being used as an internal model for allocation of resources (bets). A bettor might learn something about the distribution of expected outcomes, for example by knowing how often each horse in a race has won in past races. In a population, the information may also exist as learned associations (Aplin *et al.* 2015; Gil *et al.* 2018), but it can also appear as a phenotypic distribution that has evolved in response to historical temporal patterns in environmental conditions (Kussell & Leibler 2005; Donaldson-Matasci *et al.* 2008; Frank 2012). In either case, the optimal allocation strategy for reproductive effort under minimal information (*i.e.*, knowing only the odds of events based on the assumption that past distribution of occurrences predicts future odds) is the same, and the solution is for a population to divide reproduction among expected events (environmental states) in proportion to their odds of occurring. This is referred to as the Kelly criterion or Kelly betting (Cover & Thomas 2006), and was derived to explain the best strategy for an individual bettor that must allocate bets optimally to maximize winnings across many

horse races (Kelly 1956; Cover & Thomas 2006). The Kelly betting strategy is fairly robust because it is independent of the underlying mechanism (cognitive or evolutionary) (Box 1); thus even without predictive information about future states provided by a cue (i.e., the conditional probability of environment, given a cue (3)) an optimal long-term strategy exists for timing reproduction.

If organisms in a population are able to detect information (e.g., MI) which can be used to predict future events, then allocation (betting) strategies exist that are even more efficient than classic Kelly betting. For example, if our imaginary plant populations are attempting to germinate in an arid environment like the one discussed briefly in the introduction, and reproductive success is maximized when germination is timed coincident with optimal amounts of water each season, we can explore strategies when populations are able to respond to environmental cues that signify future water availability. If the amount of moisture today is predictive of the amount of rain in the future, then there is high MI between the cue of moisture and the state of rain which can be exploited. In terms of the underlying probabilities, the conditional probability of seeing a certain amount of rain in the future given current moisture levels (written formally as $p(E|C)$) can range between 0 and 1: 0 indicates total independence of these two events, and 1 indicates that the current cue is perfectly predictive of a corresponding future event. The corresponding *per-capita* growth rate is $\rho(x(E|C)) = \rho(E|C)$.

The additional fitness gain that is possible when information is available (e.g., MI > 0) can be substantial (Box 1; Donaldson-Matasci et al. 2010). The optimal strategy with informative cues is a conditional version of the Kelly criterion (Cover & Thomas 2006), where bets (allocations) are made in proportion to the conditional probabilities (3). As long as the information is reliable (i.e., the conditional probability distribution has less variation around the true state than the uninformed marginal distribution) then the payout will always be better and $\Delta\rho$ will increase (Box 1; Figure 2A. The FVOI ($\Delta\rho$) is the difference between these two growth trajectories, estimated as the comparison of the rates of population increase over time (Figure 2C). Note from Figure 2C that the FVOI and MI are equivalent in that scenario, showing that populations have fully utilized the information in the cue and maximized the FVOI.

In the real world, populations rarely invest all of their resources into *per capita* growth and instead retain resources across reproductive events. This strategy, known as bet-hedging (Gillespie 1974; Philippi & Seger 1989), is ubiquitous (Clauss & Venable 2000; Stephens et al. 2002; Childs et al. 2010; Tielbörger et al. 2012; Furness et al. 2015). It is evident wherever there is some form of “storage”, whether it is in long-lived adults such as in perennial plants (Adler et al. 2006; Usinowicz et al. 2012) or adult fish (Secor 2007), or in propagules such as a seed (Sears & Chesson 2007; Jose M. Facelli et al. 2008) or eggs (Cáceres 1997) that can remain dormant for long periods. Bet-hedging is optimal when odds are “subfair,” the mathematical term for a set of outcomes where the sum over the reciprocals of the odds of each outcome is greater than 1

($\sum(1/\text{odds}) > 1$)(see Cover & Thomas 2006 or Ellner 1997 for details). Basic organismal physiology tends to constrain organisms such that there will be some conditions under which reproduction rates approaches 0: the odds of reproduction success when environmental states that drastically reduce or even preclude reproduction likewise approach 0. Brief consideration of the equation for subfair odds above leads to the observation that we should probably never expect nature to be fair; even one outcome with odds approaching zero will lead to very large or even infinite sums. Because nature is not fair, bet-hedging should be the norm.

Information improves fitness for bet-hedging populations in variable environments (Box 1: Donaldson-Matasci *et al.* 2010). As with model 1 (Fig 2A), the *per capita* growth rate for a bet-hedging population is higher when individuals use a cue to time reproduction to align with favorable conditions (Fig 2B). *Per capita* growth rate in the bet-hedging population is lower, however, because dormancy introduces constraints on the FVOI. Dormancy represents increased phenotype specialization when individuals of a certain phenotype are increasingly specialized to emerge in response to specific cues. This physiological trade-off between generality and specialization can prevent a population from fully exploiting the information in a cue (see Box 2). The fitness cost of a physiological constraint like dormancy can be measured by parsing the FVOI, which we have done numerically in Fig 2C-D. In the first scenario, the FVOI is equivalent to the MI (figure 2C) revealing that the population/organism are able to perfectly use the MI in the environment. In the second case, the FVOI measured by the difference in slopes is no longer equivalent to the MI (Figure 2D). Note that this difference between $\Delta\rho$ and MI is the KL divergence, which measures the information a population fails to use.

The applicability of these theoretical insights to real populations remains an open question. On the one hand, they suggest that almost any information use increases a population's fitness, and certainly the use of cues to anticipate environmental conditions is ubiquitous in real organisms. Likewise, the mathematical conditions that make information advantageous (i.e., variable environments with sub-fair odds) are probably the rule in nature. A primary point of contention in the annual plant systems, where bet-hedging has been the most well-studied, has been whether the conditions that make a cue informative actually exist (Venable & Lawlor 1980; Clauss & Venable 2000). To our knowledge, no attempts have been made to measure the MI between the environmental conditions which benefit annual plant reproduction and cues that seeds use to anticipate them. It also remains unknown how often and to what extent biological constraints (including dormancy) might reduce the FVOI to a point where there is no net fitness value. Finally, these models have been restricted to single-species populations and the role of species interactions in the FVOI remains unexplored, even theoretically.

Information's contributions to fitness in communities and community dynamics

Given the importance of information to population dynamics and trajectories in

scenarios that consider only the population and its environment, we expect that information use and the fitness advantages it confers may be an important dimension in fitness in communities. In the single-species models studied to date only a direct influence of information on fitness has been analyzed (Donaldson-Matasci *et al.* 2010; Rivoire & Leibler 2011), and these models do not account for the density- and frequency-dependent feedbacks that drive biodiversity (Adler *et al.* 2007; Hart *et al.* 2017; Usinowicz *et al.* 2017; Letten *et al.* 2018). Probability theory has also not probed models with feedback dynamics that would be informative in the context of communities and multiple interacting populations. Thus it remains an open question even in theory, *How do species interactions mediate the fitness value of information?*

To begin exploring this question, we present novel extensions of two classic ecological models of population dynamics in fluctuating environments to which we have added the potential for information-driven dynamics (Box 2). The first of these builds from the classic lottery model (Chesson & Warner 1981) where the proportion of offspring that emerge each generation (e.g., germinating proportions of seeds) may be fixed or may vary randomly. We introduce the potential for information to be used in the emergence process according to an early season cue that predicts whether environmental conditions are favorable in a given year (high MI with early season conditions and later season conditions). Technically, this is implemented by making the proportion of emerging individuals a function of the conditional probability of seeing a favorable environment given a cue ($p(E|C)$). An overview of this model for two species is given in Box 2, and the different competitive dynamics when germination is conditioned on a cue or not, are given in Figure 3.

Information use benefits species that are competing for a shared, fluctuating resource, as evidenced by comparing population growth rates with and without the use of an environmental cue in Figure 3. For a single resource environment, at a particular level of overlapping interspecific resource use (i.e., niche overlap), the ability to use information about temporal patterns in the environment has clear and quantifiable fitness benefits. It follows to ask, does the FVOI depend on the niche overlap of competitors? In order to answer this question, we simulated the model across different levels of resource use overlap (keeping species' average reproduction rates equivalent to one another) and applied $\Delta\rho$ to measure changes in the FVOI across scenarios. It is clear from the results in Figure 4A that increasing niche overlap through increases in species' shared environmental preferences leads to a decrease in FVOI. This means that high interspecific similarity in resource and environmental needs also decreases the opportunity for species to avoid competition through information about patterns of variation in those resources.

We can also ask, how does information influence coexistence? We can address this question by applying $\Delta\rho$ to the model simulated over the same range of resource overlap scenarios and calculating the niche differences (note that species were given equivalent fitness) from the two different sets of low-density growth rates, $\rho(E|C)$ and

$\rho(U)$ following previous methods (Carroll *et al.* 2011; Grainger *et al.* 2019). The magnitude of niche partitioning with $\rho(U)$ at any particular level of resource overlap reveals the potential for resource partitioning alone to promote coexistence, while the difference in niche partitioning between $\rho(E|C)$ and $\rho(U)$ reveals the extent of niche differentiation that is purely information based. Information can promote coexistence by further decreasing niche overlap and that this is an effect that can be distinguished from purely resource driven niche partitioning (Figure 4B). Since broader niche differences facilitate coexistence and the maintenance of biodiversity, our results also show that information can therefore play a role in the maintenance of biodiversity in natural communities.

Fitness value of Social Information

Information exists in the environment in the patterns and behaviors of other organisms, in addition to patterns in the environment as we have considered so far (Gil *et al.* 2018). We also investigated the FVOI in a model of social information based on classic Lotka-Volterra dynamics (Box 2) (Gil *et al.* 2018). This version of the model includes an additional density-dependent term with interaction rates that determine the value of social information passed between con- and heterospecifics. We illustrate the different competitive dynamics with and without social information in Figure 4. The simplicity of this model makes it straightforward to assess analytically, and serves as a simple proof-of-concept because applying $\Delta\rho$ to the model in Box 2 recovers the term $B_i(N_i \dots N_n)$ (Box 2) included by Gil *et al.* to represent information dynamics. This means that the FVOI is equivalent to the value of social information in this example, and shows more broadly how different types of ecological information can be nested and compared within the more general FVOI framework.

Biological examples of information's value

All populations must contend with fluctuating environments, and most temporal patterns of variation contain information that can be used to inform predictions about likely future conditions (Pennekamp *et al.* 2019). By using information in the environment, organisms stand a better chance of tracking beneficial conditions and avoiding detrimental ones. Information is present in cues when they correspond to patterns of environmental variation, and information is useful when it is predictive of conditions that promote or inhibit species' growth or reproduction, and when that information is detectable to the organisms. Species have evolved or learned responses to specific cues, which signal behavioral decisions or life history responses. Although the majority of our review has considered environmental cues to this point, cues may also come in the form of social information from con- or heterospecifics that help avoid predation, or improve the likelihood of finding resources or mates. A vast number of studies enumerate examples of this ecological information without explicitly connecting

cue responses to population or community dynamics. Here, we discuss how ecological information, in the form of abiotic and biotic cues, mediates fitness via two primary pathways: 1) environmental information, when demographic rates change in response to a unidirectional flow of information from environment to organism and 2) social information, when population densities change in response to exchanges of information between con- or heterospecific individuals.

Demographic information includes cues that trigger shifts in demographic rates, often through life-history changes. Demographic responses are independent of population densities. In a mathematical model, demographic responses would be represented by a changing parameter value such as fecundity, germination or survival rate (Box 2). Some of the most well-studied examples of demographic information include cues for the timing of dormancy and emergence in plants (Thackeray *et al.* 2016; Montgomery *et al.* 2020), animals (Košťál *et al.* 2017; Wilsterman *et al.* 2021), and bacteria (Jones & Lennon 2010). Plants that experience seasonally harsh conditions often have dormancy strategies where regrowth and germination (Tielbörger *et al.* 2012; Commander *et al.* 2017) respond to cues associated with the onset of more favorable conditions (Box 2). In some cases demographic information is produced by the presence or activities of other organisms. Terrestrial and aquatic invertebrates are known to switch between phases of parthenogenesis with rapidly hatching eggs and sexual reproduction with long-lived diapausing eggs, and this switch can occur in response to a combination of cues including temperature, photoperiod, and predation (Hairston & Dillon 1990; Hairston Jr & Kearns 1995). Many larval amphibians switch growth and development strategies along with behavior when predators are detected (Relyea 2003).

Demographic information can influence density- and frequency-dependent population processes (Box 2). The seasonal timing of reproduction in many organisms can lead to density and frequency dependent population dynamics via competition (Chesson & Warner 1981; Usinowicz *et al.* 2012; Godoy & Levine 2014), predation (Barbraud & Weimerskirch 2003; Tyson & Lutscher 2016), and mutualisms (Moeller 2004; Devaux & Lande 2009; Fabina *et al.* 2010). For example, when the seeds of desert annual plants germinate in response to moisture and photoperiod, there will naturally be competition for limited resources (Pake & Venable 1995; Alexander & Levine 2019). This can lead to high intraspecific competition since conspecifics are more likely to respond to similar cues; if intraspecific competition is high on average relative to interspecific competition then population growth rates will be negatively frequency dependent and coexistence is possible. This is the essence of the frequency-dependent mechanism known as the storage effect, which has been documented in numerous organisms in addition to annual plants (Cáceres 1997; Angert *et al.* 2009; Ellner *et al.* 2016; Usinowicz *et al.* 2017).

Social information is based on cues that are passed between organisms as an interaction or feedback. It is typified by density-dependent population dynamics, for

example when conspecific attraction increases fitness by increasing reproduction rates (Bever & Simms 2000; Schmidt *et al.* 2015), resource acquisition (Berryman *et al.* 1985; Sultan 2000; Williams *et al.* 2000), or predator avoidance (Costerton *et al.* 1995; De Moraes *et al.* 1998; Gil *et al.* 2019). Positive density-dependent feedbacks emerge when social cues increase in magnitude or value with increasing population density (Box 2). Negative density-dependent feedbacks can result when social information repulses con- or heterospecifics (Durrett & Levin 1997; Chivers & Smith 1998). Spatially explicit feedbacks lead to heterogeneous distributions of populations that can lead to some of the complex phenomena and non-intuitive outcomes that have been studied in the context of coexistence and predator avoidance (Huffaker 1958; Levin 1992; Bolker *et al.* 2003; Snyder 2006).

Social information is also shared between species. This can produce density-dependent feedbacks driven by interspecific interactions with major implications for community dynamics. This is well documented in animals that hunt and scavenge (Jackson *et al.* 2009; Kane & Kendall 2017) in association with other species, such as mixed species foraging flocks of birds (many have refs). For some animals such as vultures, population growth relies on the positive density-dependence of these associations to such a large degree that the collapse of certain predator populations has brought a concurrent decline in vulture populations because of the loss of social information around resources (Kane & Kendall 2017).

FVOI in inducible defenses

Among the best known examples of organisms using information in fluctuating environments to trigger life-history changes that improve fitness is in the context of inducible defenses (Harvell 1992). Inducible defenses are morphological, behavioral or phenotypic changes that occur in response to the detection of a cue indicating that a predator or herbivore is nearby. In the context of our framework, inducible defenses constitute a response to demographic information, even though cues are often biotic in origin. It is well established that this use of information by prey can play a major role in community structure and dynamics (Werner & Peacor 2003; Peacor & Werner 2004). In an environment with irregular predation risk, there is a clear fitness value to detecting cues that signal imminent predation. Intuitively, there is high MI between cues such as chemical signals of predators or predation events and the presence of a predator, and it has also been shown that environmental patterns such as temperature changes can serve as cues for inducible defenses when their MI with predation pressure is high (Miehl *et al.* 2013). The fitness benefit of detecting and acting on the information is also high in these scenarios - it is survival by avoiding predation. The cost of not acting on this information is also potentially high if it means mortality of individuals. The FVOI provides a framework that makes the unique influence of inducible defenses on dynamics comparable to other species interactions.

Despite a large body of research on the existence of inducible defense, there are

surprisingly few empirical tests of the fitness value of information in this context. *Daphnia spp.* and their inducible defensive behavior of spine growth and diurnal migration provides one example (Hammill *et al.* 2008). As we outline above, a quantification of FVOI requires estimating the MI between cue and risk, as well as fitness (here, population growth rate) in conditions with and without the predator. Most inducible defense experiments include treatments that expose organisms to cues and controls (no cue), but rarely also to the third factor: the predator, in a treatment that allows predation. Perhaps the only experimental demonstration of FVOI in relation to inducible defenses in animals (Boeing & Ramcharan 2010) exposed *Daphnia pulex* clones to a control (no predation) and a predation treatment using planktivorous fish in an *in situ* lake experiment, and the two experimental clones different in one important way: one clone could detect the predator cues and initiate migratory behavior, while the other clone could not detect the information about the predator. Population growth rates of the *Daphnia* were higher in the clone that used information about predators, clearly demonstrating FVOI.

The fitness value of information in a changing world

A growing literature addresses the roles of demographic and social information in mediating anthropogenic impacts on natural communities. The fitness value of information depends on its reliability, yet environmental cues and social information are increasingly disrupted by anthropogenic change (Salmon *et al.* 1995; Inouye *et al.* 2000; Cotton 2003; Longcore & Rich 2004). In the worst case, anthropogenic change leads to misinformative cues that become “ecological traps,” when organisms continue to follow a formerly beneficial behavior that has become maladaptive (Schlaepfer *et al.* 2002; Robertson *et al.* 2013). The FVOI provides a framework that can link seemingly disparate studies seeking to understand and address anthropogenic impacts on natural communities that emerge from anthropogenic disruptions to information-driven dynamics. Then, $\Delta\rho$ provides a metric that can be applied to test hypotheses about and quantify impacts on the reliability of key ecological information under global change.

Anthropogenic change can disrupt demographic information by altering environmental cues, and can even create misinformation. Climate change has altered major patterns of climate variation, especially in the timing of seasonal transitions. Reliable climate cues are an important component of ecological information and research has shown that organisms across taxa shift phenology in response, often to their detriment if the historical temporal relationship between the climate cue and the needed resource supply have changed. For example, migratory bird species have shifted the timing of both short and long distance migrations in response to changing spring and autumn temperatures (Jenni & Kéry 2003; Horton *et al.* 2020), which has been suggested to reduce fitness when the timing no longer coincides with the availability of habitat or food (Cotton 2003). Climate cues that signal the end of dormancy have become misinformative for some mammals, resulting in movement or

emergence that is mistimed with food availability (Inouye *et al.* 2000; Post & Forchhammer 2008; Bronson 2009). Nearly all primary producers depend on seasonal climate fluctuations as cues to time biomass production and reproduction; sometimes these shifts boost single-species' by preempting access to resources (Alexander & Levine 2019), but at the community scale such shifts are almost always detrimental due to mismatches with environmental states (Suttle *et al.* 2007) or important mutualisms (Hegland *et al.* 2009).

Urbanization has greatly increased the amount of noise and light in the environment, creating events that are interpreted as cues but in fact have no relation or even an opposite relationship with resource availability or risk. Night time light pollution is misinformative for many phenotypes that have evolved to use phases of the moon as cues for life history transitions (for example, sea turtles, fish and corals) or signals to guide movement as they attempt to find mates, avoid predators, or locate habitat (Salmon *et al.* 1995; Longcore & Rich 2004). Nocturnal insects can become disoriented by artificial lights and are often more susceptible to predation (Acharya & Fenton 2011; Firebaugh & Haynes 2019), and there is mounting evidence that polarized glass surfaces that are increasingly common in windows and photovoltaics have increased predation rates on insects disoriented by light reflection in the daytime (Horváth *et al.* 2009).

Social information is also disrupted by anthropogenic change. Noise pollution tends to mask or dampen important auditory cues (Barber *et al.* 2010). Birds and primates have been shown to change vocalization in response to chronic noise exposure (Brumm *et al.* 2004; Patricelli & Blickley 2006). Noisy landscape features such as roadways and population density are often cited as reducing the fitness of certain vertebrate species (Barber *et al.* 2010), and experiments have found strong evidence that noise-pollution can reduce population densities strongly enough to have cascading trophic effects because organisms reduce foraging times (McMahon *et al.* 2017; Barton *et al.* 2018).

Concluding Remarks

Ecological information is a critical resource that promotes the fitness of organisms in fluctuating environments. Yet the fitness value of information has remained largely understudied in population and community dynamics. Demographic information and social information are two ubiquitous categories of ecological information that can critically determine species' fitness by guiding life-history decisions, creating density-dependent feedbacks, and determining the nature of biotic interactions in diverse communities. By adapting simple mathematical models of population dynamics it is straightforward to demonstrate how important environmental cues and social information (Box 2) can potentially be for promoting species coexistence (Fig 3-5).

An important extension of $\Delta\rho$ is interpreting how ecological information mediates anthropogenic impacts on fitness. While many studies have demonstrated that ecological information is changed by anthropogenic activity, and in some cases shown that individual or group behavior changes in response, none have quantified these changes in terms of mutual information and estimated the impacts of these changes on an organism's fitness. This is a necessary step to understand and predict the full range of anthropogenic impacts on species persistence in a changing world. By giving the fitness value of information a precise definition and providing an accompanying mathematical framework we hope to facilitate a more complete understanding of anthropogenic impacts on species' fitness.

We have presented a mathematical framework based on the comparison between *per capita* population growth rates with and without information that provides a formalized measure of the fitness value of information. The fitness value of information, as measured by $\Delta\rho$, can parse *per capita* growth into components that show the potential value of information, and how much fitness value is lost because a population fails to anticipate its environment. Because these mechanisms mediate fitness through universal features of population dynamics they are generalizable and comparable across different systems. The FVOI framework is general and could be used to quantify and compare FVOI across a broad range of ecological systems and contexts by relating cue production and detection to population and community dynamics, and ultimately the maintenance of biodiversity in changing environments.

(Boxes are 750 words, no figures)

Box 1. The fitness value of information and information theory

The framework for the fitness value of information can be used to derive an expression that shows explicitly how information increases fitness (Donaldson-Matasci et al. 2010; Rivoire & Leibler 2011). Consider a simple multiplicative growth process like that in eq (1) in the main text. Assume that the distribution of environmental states is known and $p(e)$ is the probability of any environment occurring. Also assume that a population produces offspring in each environment at rate r_e with known probability $x(e)$: Donaldson-Matasci et al. (2010) equate this combination of payoff and probability in each environment to phenotypes, $\varphi_e = r_e x(e)$. The population's expected growth rate is analogous to eq (2), except now the expectation is of $\lambda_i(\varphi_e, e) = r_e x(e)$ and is taken over environmental realizations instead of over time

$$\rho = E[\log \lambda_i(\varphi_e, e)] = \sum_e p(e) \log r_e x(e). \quad (\text{B1.1})$$

The latter part of the equation comes from the definition of an expected value.

701

702 When populations use no information, then all $x(e)$ are equally likely such that
 703 $x(e) \sim U(0,1)$ (i.e. the uniform distribution over the interval 0,1). If populations use
 704 information then $x(e)$ is a conditional probability $x(e|c)$ with r_e , defining the conditional
 705 phenotype $\varphi_{e|c}$. This simple model provides a foundational understanding of $\Delta\rho$ that
 706 can be extended and generalized. In probability theory, it is the starting place to derive
 707 optimality theorems like the Kelly criterion (Cover & Thomas 2006). ρ has been plotted
 708 for the model with $x(e \sim U)$ and $x(e|c)$ in Figure 2. Applying eq (3) to this model

$$709 \Delta\rho = E[\log \lambda_i(\varphi_{e|c}, e|c)] - E[\log \lambda_i(\varphi_e \sim U, e)] =$$

$$710 \sum_c p(c) \sum_e p(e|c) \log[r_e x(e|c)] - \sum_e p(e) \log[r_e x(e \sim U)] \quad (B1.2)$$

711 The summations and new probability terms ($p(e)$, $p(c)$, and $p(e|c)$) emerge from the
 712 expectation. This can be simplified by factoring r_e from log-products and using the fact
 713 that $\sum_c p(e|c) = p(e)$ to ultimately remove r_e

$$714 \Delta\rho = \sum_c p(c) \sum_e p(e|c) \log x(e|c) - \sum_e p(e) \log x(e \sim U) \quad (B1.3)$$

715 These terms can be parsed to reveal the role of information. In the second term,

$$716 \sum_e p(e) \log x(e \sim U) = \sum_e p(e) \log x(e \sim U) + \sum_e p(e) \log p(e) - \sum_e p(e) \log p(e) = \quad (B1.4)$$

$$717 H(E) - D_{KL}(p(e) \| x(e \sim U))$$

718 The expression $H(E) = \sum_e p(e) \log p(e)$ is the Shannon entropy of the environment. The
 719 first and last terms combine to define $D_{KL}(p(e) \| x(e))$, the Kullback-Liebler (KL)
 720 divergence between the two distributions $p(e)$ and $x(e)$. $H(E)$ describes the “information
 721 entropy” or the inherent unpredictability of the environment; lower values mean that the
 722 environment is more predictable ($H(E) = 0$ in a constant environment). The KL
 723 divergence quantifies how different $x(e)$ is from $p(e)$; when $x(e) = p(e)$ the divergence is
 724 0. In the current context it indicates how close a population has come to adopting the
 725 optimal strategy.

726

727 The analogous terms exist for the conditional probabilities: the first part of eq (B1.2),
 728 and (B1.3) lead to $H(E|C)$ and $D_{KL}(p(e|c) \| x(e|c))$, the analogous conditional versions of
 729 the entropy and KL divergence. Each of these terms have similar conceptual
 730 interpretations as well. These combine to give the general expression

$$731 \Delta\rho = H(E) - H(E|C) - D_{KL}(p(e) \| x(e)) - D_{KL}(p(e|c) \| x(e|c)) = \quad (B1.4)$$

$$732 I(E; C) - D_{KL}(p(e) \| x(e)) - D_{KL}(p(e|c) \| x(e|c))$$

733

734 We have used the definition of mutual information (MI) to replace the entropies. The MI
 735 measures much information is gained by a sequence with knowledge of another
 736 sequence (Cover & Thomas 2006). Here, $I(E; C)$ quantifies the gain in information about
 737 the environment from the cue (Figure 2C). If populations have optimal strategies then
 738 $x(e) = p(e)$, $x(e|c) = p(e|c)$ and $D_{KL}(p(e) \| x(e)) = D_{KL}(p(e|c) \| x(e|c)) = 0$ and

$$\Delta\rho = H(E) - H(E|C) = I(E;C) \quad (\text{B1.5})$$

That is, the maximum FVOI is the MI between cue and environment. This upper bound on MI (i.e. $\Delta\rho \leq I(E;C)$) has been rigorously demonstrated (Donaldson-Matasci et al. 2010; Rivoire & Leibler 2011).

Box 2. Community dynamics models with information

Here we present two mathematical models of community dynamics that are influenced by the availability of information. The first model is an example of demographic information response, created by extending a classic stochastic model of dormancy to include the potential for emergence in response to environmental cues; in the community context, a new version of the lottery model is recovered. We then review a deterministic model of social information response developed as an extension of classic Lotka-Volterra competitive dynamics to include information-driven feedbacks.

1. Competition with fluctuating environmental cues

Environmental conditions can vary substantially, often outside the range of what organisms can tolerate for survival or reproduction. In such conditions, persistence requires that life history events align with favorable conditions, while also allowing organisms to weather unfavorable conditions, sometimes across multiple generations. For example, desert annual plants have long lived dormant seeds that survive many generations. Under appropriate conditions seeds germinate, grow, and become adults that produce new seeds within a single season. A common model for this kind of population dynamic is the stochastic difference equation (Cohen 1966; Ellner 1997)

$$N_i(t+1) = [g_i F_i(t, R_i \dots R_n N_n) + (1 - g_i) s_i] N_i(t) \quad (\text{B2.1})$$

Where s_i is the survival of seeds in the seedbank, g_i is the percentage of i seeds germinating, F_i is total per-capita reproduction in year t that incorporates a species' own reproductive rate R_i and possibly competitors $R_j N_j$. The reproductive fitness F_i is a random variable with an underlying distribution. A common form of F_i with competition is

$$F_i(t, R_i \dots R_n N_n) = \frac{R_i}{\sum_{j=1}^n R_j N_j} \quad (\text{B2.2})$$

This is the lottery model, where species “win” resources in proportion to their total reproductive output each generation (Chesson & Warner 1981; Ellner 1987) (we refer to the competition-independent model with $F_i = R_i(t)$ as the dormancy model).

To incorporate information use, allow g_i to vary in time: define $g_i(E(t))$ for germination as a function of a varying environment (we subsequently drop the t from notation). When organisms perfectly detect and immediately act on information about the environment, then they germinate in ideal proportions to match the fitness benefits of the environment. We use conditional probabilities $g_i(E|C)$ to capture how well an organism detects and responds to the cue C . When organisms are unable to detect the environment (or a delayed response prevents it from syncing), then g_i varies uniformly between 0 and 1. An example realization of these dynamics is given in Figure 2.

2. Competition with social information feedbacks

The Lotka-Volterra competition model can be adapted to allow species to use social information to reduce mortality rates, e.g. by avoiding predation. Density of individuals (either conspecifics or heterospecifics) reduces mortality from predation (Gil et al. 2019).

$$\frac{d N_i}{dt} = \left[r_i \left(1 - \sum_{j=1}^n \alpha_{ij} N_j - B_i(N_1 \dots N_n) \right) \right]_{N_i} \quad (\text{B2.3})$$

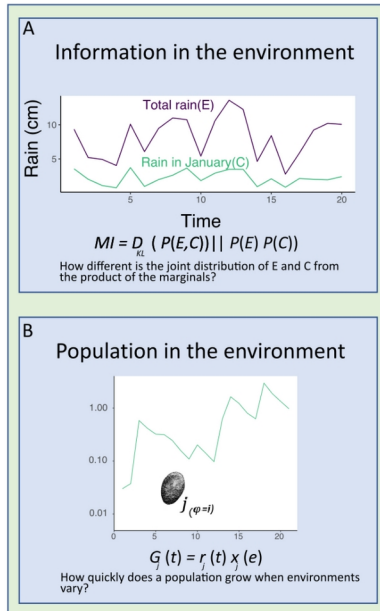
The N_i are species densities, r_i are intrinsic growth rates, α_{ij} are inter- ($i \neq j$) and intraspecific ($i = j$) competition coefficients, and $B_i(N_1 \dots N_n)$, denotes the mortality rate. Classically, $B_i(N_1 \dots N_n)$ is constant and corresponds with any process that reduces survival. Motivated by a biological example where increasing densities of individuals might promote survival by a reduction in predation via shared alarm calls or other behaviors, Gil et al. (2019) adapted $B_i(N_1 \dots N_n)$ to incorporate an effect of social information by defining $B_i(N_1 \dots N_n)$ with negative exponential functions, such that mortality rates decrease as conspecific density increases.

$$B_i(N_1 \dots N_n) = p_{s,i} e^{-\sum_{j=1}^n b_{ij} N_j} + p_{m,i} \quad (\text{B2.4})$$

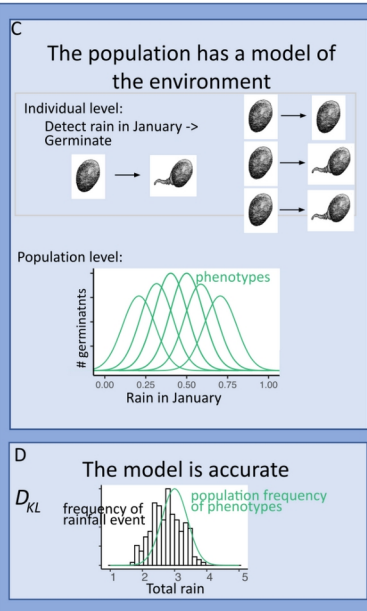
Here, b_{ij} are interaction coefficients which describe the rates at which hetero- or conspecific densities produce usable information. The $p_{s,i}$ define a proportionate effect of social information, and $p_{m,i}$ a minimum effect. When there is no social information $b_{ij} = 0$ and (4) reduces to a constant: $B_i(N_1 \dots N_n) = p_{s,i} + p_{m,i}$. A comparison of the growth rates and equilibrium dynamics of the model with and without information for two competing species is plotted in Figure 4.

Figures

1. Given:



2. And, if:



3. Then, there is fitness value to information:

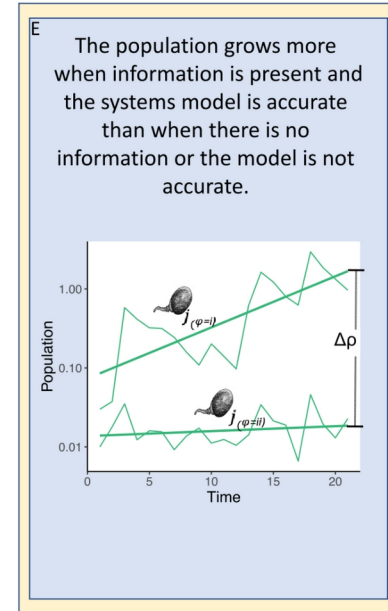
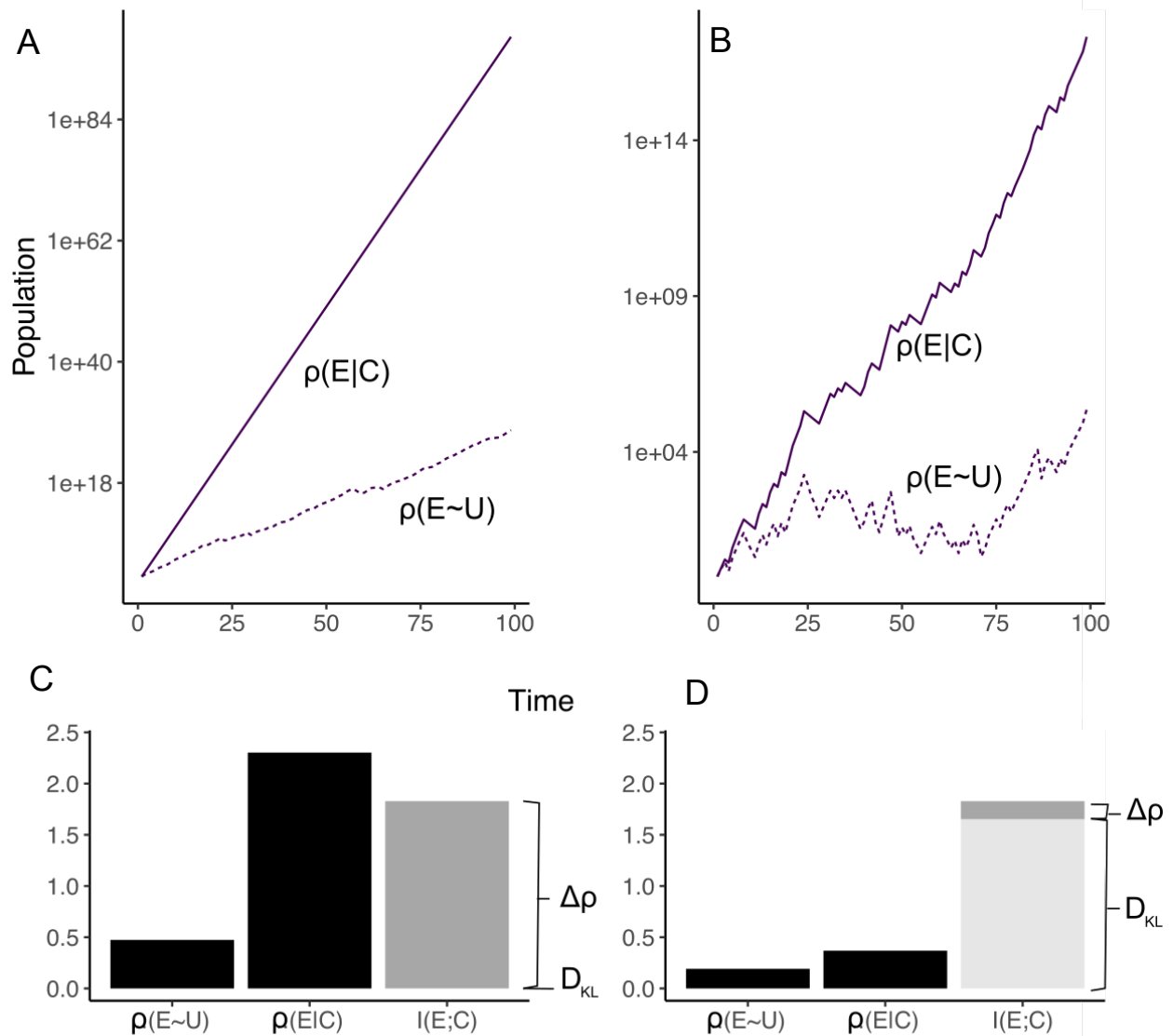


Figure 1. Conceptual layout of the fitness value of information (FVOI). Estimating FVOI requires (A) time-series observations of two environmental variables, here hypothetical temporal trends of rain in January and total annual rain, where rain in January serves as a cue for total rain during the growing season. The fitness value of this cue is equal to the mutual information (MI) between the two time series (labeled “C” for cue and “E” for environment). Estimating FVOI also requires observations of (B) population dynamics in a variable environment, where *per capita* growth rates vary according to the favorability of conditions in a generation (a year, for this hypothetical annual plant). (C) A population’s varying response may correspond with underlying differences amongst individuals or phenotypes to detect and/or respond to an available cue: for example, different seed phenotypes that respond physiological to different levels of rain in January (in other examples, the response could be behavioral). (D) A population will capitalize on information (MI, panel A) to the extent that it has an accurate “internal model” of how cues correspond with desired environments. This is measured formally with the Kullback-Leibler divergence (D_{KL}) between the actual probability of seeing an environmental state (here, histogram of the magnitude of total rainfall) and the population’s internal representation of this histogram (here, the frequency of phenotypes corresponds with each environmental state’s likelihood). (E) The FVOI ($\Delta \rho$) is the difference in log per-capita growth rates between a population that is able to utilize a cue, and one that does not.



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Figure 2. Population growth for two life history models: a multiplicative model (A) and a dormancy model (B) when the probability of a strategy or phenotype does not use information $\rho(E \sim U)$, versus when it uses an environmental cue for information $\rho(E|C)$ (see text and model details in box 1). To illustrate the relative contributions of $I(E;C)$ and each population to the FVOI, values of the slopes $\rho(U)$ and $\rho(E|C)$ are shown in C and D for each model. The fitness value of information is measured by the difference between the two slopes $\Delta\rho$. The mutual information $I(E;C)$ between the environment and the cue defines the maximum potential contribution of a cue to fitness, while the KL Divergence (D_{KL}) quantifies the extent to which a population fails to benefit from an informative cue; the stacked bars in C and D illustrate that the FVOI is the difference between $I(E;C)$ and D_{KL} . See the Supporting Information for simulation details.

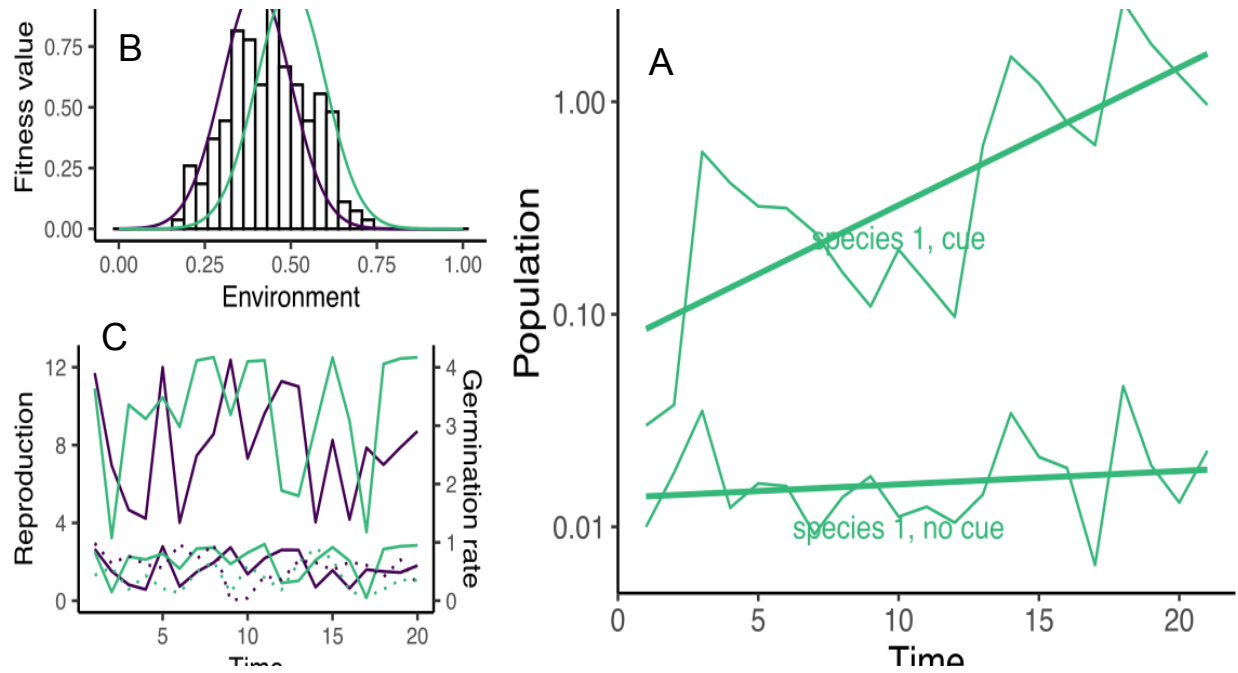
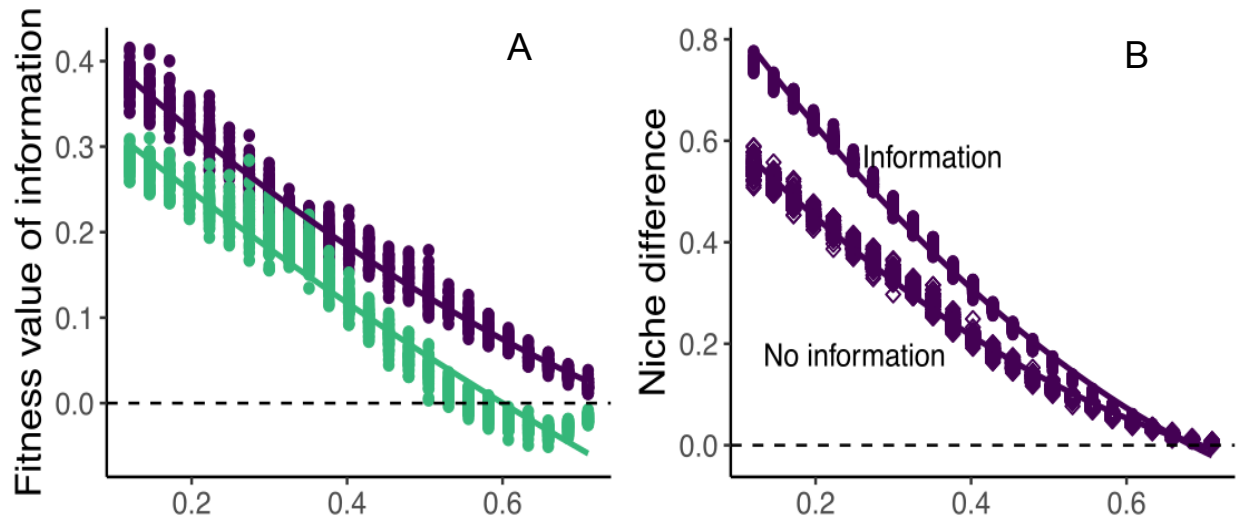


Figure 3. The dynamics of the lottery model (A) for a population with and without the ability to detect an environmental cue in a varying environment. The environment is simulated by taking draws from a normal distribution to set the conditions for each time step, without autocorrelation ($\mu = 0.5$ and $\sigma = 0.1$, B). Each species has a different optimum environment, shown as the two Gaussian curves (B): fitness decays with the distance of an environmental state from the optimum. (C) The varying environmental state, fitness, and germination rate are simulated as a time series. Germination is simulated in two ways: when populations use an informative cue (i.e. $\rho(E|C)$), the distribution of germination rates is highly correlated with the fitness series (solid lines - compare green solid line trajectories for reproduction rate and germination rate); when species cannot use information, germination is a random uniform distribution that is uncorrelated with fitness (i.e. $\rho(U)$; dotted lines). See the Supporting Information for simulation details.



Resource overlap

Figure 4. The change in the fitness value of information for two species (one blue, one purple) competing for fluctuating resources. Competition increases with more resource overlap because species will reproduce more often under similar conditions and limit the growth of the other. (A) The fitness value of information $\Delta\rho$ decreases when competition for resources increases. (B) The niche difference between species in the presence and absence of information (i.e. $\rho(E|C)$ and $\rho(U)$) as labelled. A niche difference of 1 corresponds with 100% differentiation.

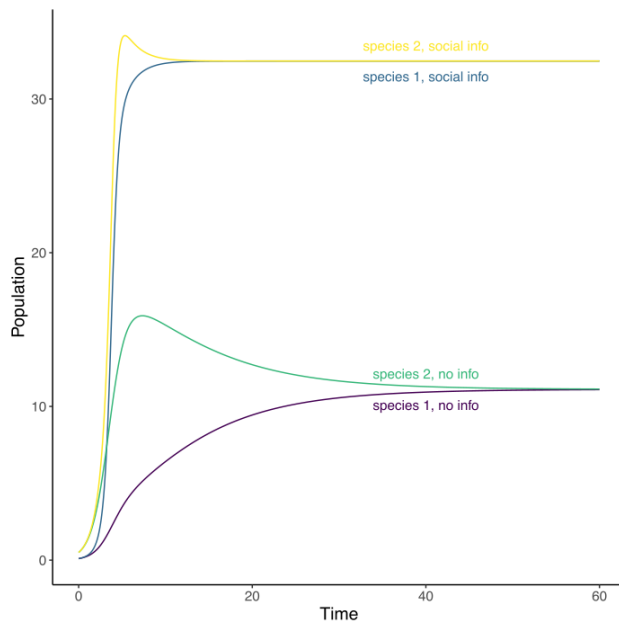


Figure 5. The population dynamics of the competition model with social information, with (upper lines) and without (lower lines) social information.

Bibliography

- Acharya, L. & Fenton, M.B. (2011). Bat attacks and moth defensive behaviour around street lights. *Can. J. Zool.*
- Adler, P.B., HilleRisLambers, J., Kyriakidis, P.C., Guan, Q. & Levine, J.M. (2006). Climate variability has a stabilizing effect on the coexistence of prairie grasses. *Proc. Natl. Acad. Sci.*, 103, 12793–12798.
- Adler, P.B., HilleRisLambers, J. & Levine, J.M. (2007). A niche for neutrality. *Ecol. Lett.*, 10, 95–104.
- Alexander, J.M. & Levine, J.M. (2019). Earlier phenology of a nonnative plant increases impacts on native competitors. *Proc. Natl. Acad. Sci.*, 116, 6199–6204.
- Angert, A.L., Huxman, T.E., Chesson, P. & Venable, D.L. (2009). Functional tradeoffs determine species coexistence via the storage effect. *Proc. Natl. Acad. Sci.*, 106, 11641–11645.
- Aplin, L.M., Farine, D.R., Morand-Ferron, J., Cockburn, A., Thornton, A. & Sheldon, B.C. (2015). Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature*, 518, 538–541.
- Baldwin, I.T., Halitschke, R., Paschold, A., Von Dahl, C.C. & Preston, C.A. (2006). Volatile signaling in plant-plant interactions: "talking trees" in the genomics era. *science*, 311, 812–815.
- Barabás, G., D'Andrea, R. & Stump, S.M. (2018). Chesson's coexistence theory. *Ecol. Monogr.*, 88, 277–303.
- Barber, J.R., Crooks, K.R. & Fristrup, K.M. (2010). The costs of chronic noise exposure for terrestrial organisms. *Trends Ecol. Evol.*, 25, 180–189.
- Barbraud, C. & Weimerskirch, H. (2003). Climate and density shape population dynamics of a marine top predator. *Proc. R. Soc. Lond. B Biol. Sci.*, 270, 2111–2116.
- Barth, F.G. & Schmid, A. (2013). *Ecology of sensing*. Springer Science & Business Media.
- Barton, B.T., Hodge, M.E., Speights, C.J., Autrey, A.M., Lashley, M.A. & Klink, V.P. (2018). Testing the AC/DC hypothesis: Rock and roll is noise pollution and weakens a trophic cascade. *Ecol. Evol.*, 8, 7649–7656.
- Bernhardt, J.R., O'Connor, M.I., Sunday, J.M. & Gonzalez, A. (2020). Life in fluctuating environments. *Philos. Trans. R. Soc. B*, 375, 20190454.
- Berryman, A.A., Dennis, B., Raffa, K.F. & Stenseth, N.C. (1985). Evolution of optimal group attack, with particular reference to bark beetles (Coleoptera: Scolytidae). *Ecology*, 66, 898–903.
- Bever, J.D. & Simms, E.L. (2000). Evolution of nitrogen fixation in spatially structured populations of *Rhizobium*. *Heredity*, 85, 366–372.
- Boeing, W.J. & Ramcharan, C.W. (2010). Inducible defences are a stabilizing factor for predator and prey populations: a field experiment. *Freshw. Biol.*, 55, 2332–2338.
- Bolker, B.M., Pacala, S.W. & Neuhauser, C. (2003). Spatial dynamics in model plant communities: What do we really know? *Am. Nat.*, 162, 135–148.
- Bronson, F.H. (2009). Climate change and seasonal reproduction in mammals. *Philos. Trans. R. Soc. B Biol. Sci.*, 364, 3331–3340.
- Bruce, T.J., Matthes, M.C., Napier, J.A. & Pickett, J.A. (2007). Stressful "memories" of plants: evidence and possible mechanisms. *Plant Sci.*, 173, 603–608.
- Brumm, H., Voss, K., Köllmer, I. & Todt, D. (2004). Acoustic communication in noise: regulation of call characteristics in a New World monkey. *J. Exp. Biol.*, 207, 443–448.
- Bullmore, E. & Sporns, O. (2012). The economy of brain network organization. *Nat. Rev. Neurosci.*, 13, 336–349.
- Cáceres, C.E. (1997). Temporal variation, dormancy, and coexistence: A field test of the storage effect. *Proc. Natl. Acad. Sci. U. S. A.*, 94, 9171–9175.

930 Cai, Y., Hossain, M.J., Hériché, J.-K., Politi, A.Z., Walther, N., Koch, B., *et al.* (2018).
 931 Experimental and computational framework for a dynamic protein atlas of human cell
 932 division. *Nature*, 561, 411–415.
 933 Carroll, I.T., Cardinale, B.J. & Nisbet, R.M. (2011). Niche and fitness differences relate the
 934 maintenance of diversity to ecosystem function. *Ecology*, 92, 1157–1165.
 935 Chesson, P. (1994). Multispecies Competition in Variable Environments. *Theor. Popul. Biol.*, 45,
 936 227–276.
 937 Chesson, P.L. & Warner, R.R. (1981). Environmental variability promotes coexistence in lottery
 938 competitive systems. *Am. Nat.*, 117, 923.
 939 Childs, D.Z., Metcalf, C.J.E. & Rees, M. (2010). Evolutionary bet-hedging in the real world:
 940 empirical evidence and challenges revealed by plants. *Proc. R. Soc. B Biol. Sci.*, 277,
 941 3055–3064.
 942 Chivers, D.P. & Smith, R.J.F. (1998). Chemical alarm signalling in aquatic predator-prey
 943 systems: a review and prospectus. *Ecoscience*, 5, 338–352.
 944 Clauss, M.J. & Venable, D.L. (2000). Seed Germination in Desert Annuals: An Empirical Test of
 945 Adaptive Bet Hedging. *Am. Nat.*, 155, 168–186.
 946 Cohen, D. (1966). Optimizing reproduction in a randomly varying environment. *J. Theor. Biol.*,
 947 12, 119–129.
 948 Commander, L.E., Golos, P.J., Miller, B.P. & Merritt, D.J. (2017). Seed germination traits of
 949 desert perennials. *Plant Ecol.*, 218, 1077–1091.
 950 Costerton, J.W., Lewandowski, Z., Caldwell, D.E., Korber, D.R. & Lappin-Scott, H.M. (1995).
 951 Microbial biofilms. *Annu. Rev. Microbiol.*, 49, 711–745.
 952 Cotton, P.A. (2003). Avian migration phenology and global climate change. *Proc. Natl. Acad.*
 953 *Sci.*, 100, 12219–12222.
 954 Cover, T.M. & Thomas, J.A. (2006). *Elements of Information Theory*. John Wiley & Sons.
 955 Crespi, B.J. (2001). The evolution of social behavior in microorganisms. *Trends Ecol. Evol.*, 16,
 956 178–183.
 957 Crisp, P.A., Ganguly, D., Eichten, S.R., Borevitz, J.O. & Pogson, B.J. (2016). Reconsidering
 958 plant memory: Intersections between stress recovery, RNA turnover, and epigenetics.
 959 *Sci. Adv.*, 2, e1501340.
 960 Crone, E.E., Miller, E. & Sala, A. (2009). How do plants know when other plants are flowering?
 961 Resource depletion, pollen limitation and mast-seeding in a perennial wildflower. *Ecol.*
 962 *Lett.*, 12, 1119–1126.
 963 Danchin, E., Giraldeau, L.-A., Valone, T.J. & Wagner, R.H. (2004). Public information: from nosy
 964 neighbors to cultural evolution. *Science*, 305, 487–491.
 965 Dangles, O., Irschick, <? break?> Duncan, Chittka, <? break?> Lars & Casas, <? break?>
 966 Jérôme. (2009). Variability in sensory ecology: expanding the bridge between physiology
 967 and evolutionary biology. *Q. Rev. Biol.*, 84, 51–74.
 968 De Moraes, C.M., Lewis, W.J., Paré, P.W., Alborn, H.T. & Tumlinson, J.H. (1998). Herbivore-
 969 infested plants selectively attract parasitoids. *Nature*, 393, 570–573.
 970 Devaux, C. & Lande, R. (2009). Displacement of flowering phenologies among plant species by
 971 competition for generalist pollinators. *J. Evol. Biol.*, 22, 1460–1470.
 972 Donaldson-Matasci, M.C., Bergstrom, C.T. & Lachmann, M. (2010). The fitness value of
 973 information. *Oikos*, 119, 219–230.
 974 Donaldson-Matasci, M.C., Lachmann, M. & Bergstrom, C.T. (2008). Phenotypic diversity as an
 975 adaptation to environmental uncertainty. *Evol. Ecol. Res.*, 10, 493–515.
 976 Durrett, R. & Levin, S. (1997). Allelopathy in spatially distributed populations. *J. Theor. Biol.*,
 977 185, 165–171.
 978 Ellner, S. (1987). Alternate plant life history strategies and coexistence in randomly varying
 979 environments. *Vegetatio*, 69, 199–208.
 980 Ellner, S.P. (1997). You bet your life: life-history strategies in fluctuating environments. *Case*

981 *Stud. Math. Model. Ecol. Physiol. Cell Biol.*, 3–24.

982 Ellner, S.P., Snyder, R.E. & Adler, P.B. (2016). How to quantify the temporal storage effect
 983 using simulations instead of math. *Ecol. Lett.*

984 Fabina, N.S., Abbott, K.C. & Gilman, R.T. (2010). Sensitivity of plant–pollinator–herbivore
 985 communities to changes in phenology. *Ecol. Model.*, 221, 453–458.

986 Firebaugh, A. & Haynes, K.J. (2019). Light pollution may create demographic traps for nocturnal
 987 insects. *Basic Appl. Ecol.*, 34, 118–125.

988 Frank, S.A. (2012). Natural selection. V. How to read the fundamental equations of evolutionary
 989 change in terms of information theory. *J. Evol. Biol.*, 25, 2377–2396.

990 Frank, S.A. (2016). The invariances of power law size distributions. *F1000Research*, 5.

991 Furness, A.I., Lee, K. & Reznick, D.N. (2015). Adaptation in a variable environment: Phenotypic
 992 plasticity and bet-hedging during egg diapause and hatching in an annual killifish.
 993 *Evolution*, 69, 1461–1475.

994 Gil, M.A., Baskett, M.L. & Schreiber, S.J. (2019). Social information drives ecological outcomes
 995 among competing species. *Ecology*, 100, e02835.

996 Gil, M.A., Hein, A.M., Spiegel, O., Baskett, M.L. & Sih, A. (2018). Social information links
 997 individual behavior to population and community dynamics. *Trends Ecol. Evol.*, 33, 535–
 998 548.

999 Gillespie, J.H. (1974). Natural selection for within-generation variance in offspring number.
 1000 *Genetics*, 76, 601–606.

1001 Godoy, O. & Levine, J.M. (2014). Phenology effects on invasion success: insights from coupling
 1002 field experiments to coexistence theory. *Ecology*, 95, 726–736.

1003 Goldenfeld, N. & Woese, C. (2007). Biology’s next revolution. *Q-Bio*0702015.

1004 Gould, J.P. (1974). Risk, stochastic preference, and the value of information. *J. Econ. Theory*, 8,
 1005 64–84.

1006 Grainger, T.N., Levine, J.M. & Gilbert, B. (2019). The Invasion Criterion: A Common Currency
 1007 for Ecological Research. *Trends Ecol. Evol.*, 34, 925–935.

1008 Hairston Jr, N.G. & Kearns, C.M. (1995). The interaction of photoperiod and temperature in
 1009 diapause timing: a copepod example. *Biol. Bull.*, 189, 42–48.

1010 Hairston, N.G. & Dillon, T.A. (1990). Fluctuating selection and response in a population of
 1011 freshwater copepods. *Evolution*, 44, 1796–1805.

1012 Haldane, J.B.S. & Jayakar, S.D. (1963). Polymorphism due to selection of varying direction. *J.*
 1013 *Genet.*, 58, 237–242.

1014 Hammill, E., Rogers, A. & Beckerman, A.P. (2008). Costs, benefits and the evolution of
 1015 inducible defences: a case study with *Daphnia pulex*. *J. Evol. Biol.*, 21, 705–715.

1016 Hart, S.P., Usinowicz, J. & Levine, J.M. (2017). The spatial scales of species coexistence. *Nat.*
 1017 *Ecol. Evol.*, 1, 1066.

1018 Harvell, C.D. (1992). Inducible defenses and allocation shifts in a marine bryozoan. *Ecology*, 73,
 1019 1567–1576.

1020 Hegland, S.J., Nielsen, A., Lázaro, A., Bjerknes, A.-L. & Totland, Ø. (2009). How does climate
 1021 warming affect plant-pollinator interactions? *Ecol. Lett.*, 12, 184–195.

1022 Horton, K.G., La Sorte, F.A., Sheldon, D., Lin, T.-Y., Winner, K., Bernstein, G., *et al.* (2020).
 1023 Phenology of nocturnal avian migration has shifted at the continental scale. *Nat. Clim.*
 1024 *Change*, 10, 63–68.

1025 Horváth, G., Kriska, G., Malik, P. & Robertson, B. (2009). Polarized light pollution: a new kind of
 1026 ecological photopollution. *Front. Ecol. Environ.*, 7, 317–325.

1027 Huffaker, C. (1958). Experimental studies on predation: dispersion factors and predator-prey
 1028 oscillations. *Hilgardia*, 27, 343–383.

1029 Inouye, D.W., Barr, B., Armitage, K.B. & Inouye, B.D. (2000). Climate change is affecting
 1030 altitudinal migrants and hibernating species. *Proc. Natl. Acad. Sci.*, 97, 1630–1633.

1031 Jackson, S.T., Betancourt, J.L., Booth, R.K. & Gray, S.T. (2009). Ecology and the ratchet of

1032 events: climate variability, niche dimensions, and species distributions. *Proc. Natl. Acad.*
 1033 *Sci.*, pnas-0901644106.
 1034 Jenni, L. & Kéry, M. (2003). Timing of autumn bird migration under climate change: advances in
 1035 long-distance migrants, delays in short-distance migrants. *Proc. R. Soc. Lond. B Biol.*
 1036 *Sci.*, 270, 1467–1471.
 1037 Jones, S.E. & Lennon, J.T. (2010). Dormancy contributes to the maintenance of microbial
 1038 diversity. *Proc. Natl. Acad. Sci.*
 1039 Jose M. Facelli, Peter Chesson & Nicola Barnes. (2008). *DIFFERENCES IN SEED BIOLOGY*
 1040 *OF ANNUAL PLANTS IN ARID LANDS: A KEY INGREDIENT OF THE STORAGE*
 1041 *EFFECT*. Available at: <http://www.esajournals.org/doi/abs/10.1890/05-0304>. Last
 1042 accessed 8 July 2009.
 1043 Kane, A. & Kendall, C.J. (2017). Understanding how mammalian scavengers use information
 1044 from avian scavengers: cue from above. *J. Anim. Ecol.*, 86, 837–846.
 1045 Keller, L. & Surette, M.G. (2006). Communication in bacteria: an ecological and evolutionary
 1046 perspective. *Nat. Rev. Microbiol.*, 4, 249–258.
 1047 Kelly, J.L. (1956). A new interpretation of information rate. *Bell Syst. Tech. J.*, 35, 917–926.
 1048 Kempes, C.P., Wolpert, D., Cohen, Z. & Pérez-Mercader, J. (2017). The thermodynamic
 1049 efficiency of computations made in cells across the range of life. *Phil Trans R Soc A*,
 1050 375, 20160343.
 1051 Koch, K. (2004). Sucrose metabolism: regulatory mechanisms and pivotal roles in sugar
 1052 sensing and plant development. *Curr. Opin. Plant Biol.*, 7, 235–246.
 1053 Košťál, V., Štětina, T., Poupardin, R., Korbelová, J. & Bruce, A.W. (2017). Conceptual
 1054 framework of the eco-physiological phases of insect diapause development justified by
 1055 transcriptomic profiling. *Proc. Natl. Acad. Sci.*, 114, 8532–8537.
 1056 Kussell, E. & Leibler, S. (2005). Phenotypic diversity, population growth, and information in
 1057 fluctuating environments. *Science*, 309, 2075–2078.
 1058 Laughlin, S.B., van Steveninck, R.R. de R. & Anderson, J.C. (1998). The metabolic cost of
 1059 neural information. *Nat. Neurosci.*, 1, 36–41.
 1060 Leff, H.S. & Rex, A.F. (2014). *Maxwell's demon: entropy, information, computing*. Princeton
 1061 University Press.
 1062 Letten, A.D., Dhimi, M.K., Ke, P.-J. & Fukami, T. (2018). Species coexistence through
 1063 simultaneous fluctuation-dependent mechanisms. *Proc. Natl. Acad. Sci.*, 201801846.
 1064 Levin, S.A. (1992). The problem of pattern and scale in ecology: the Robert H. MacArthur award
 1065 lecture. *Ecology*, 73, 1943–1967.
 1066 Longcore, T. & Rich, C. (2004). Ecological light pollution. *Front. Ecol. Environ.*, 2, 191–198.
 1067 Magrath, R.D., Haff, T.M., Fallow, P.M. & Radford, A.N. (2015). Eavesdropping on
 1068 heterospecific alarm calls: from mechanisms to consequences. *Biol. Rev.*, 90, 560–586.
 1069 Marleau, J.N., Peller, T., Guichard, F. & Gonzalez, A. (2020). Converting Ecological Currencies:
 1070 Energy, Material, and Information Flows. *Trends Ecol. Evol.*
 1071 McMahon, T.A., Rohr, J.R. & Bernal, X.E. (2017). Light and noise pollution interact to disrupt
 1072 interspecific interactions. *Ecology*, 98, 1290–1299.
 1073 McNamara, J.M., Barta, Z., Klaassen, M. & Bauer, S. (2011). Cues and the optimal timing of
 1074 activities under environmental changes. *Ecol. Lett.*, 14, 1183–1190.
 1075 Miehl, A.L., McAdam, A.G., Bourdeau, P.E. & Peacor, S.D. (2013). Plastic response to a proxy
 1076 cue of predation risk when direct cues are unreliable. *Ecology*, 94, 2237–2248.
 1077 Moeller, D.A. (2004). Facilitative interactions among plants via shared pollinators. *Ecology*, 85,
 1078 3289–3301.
 1079 Montgomery, R.A., Rice, K.E., Stefanski, A., Rich, R.L. & Reich, P.B. (2020). Phenological
 1080 responses of temperate and boreal trees to warming depend on ambient spring
 1081 temperatures, leaf habit, and geographic range. *Proc. Natl. Acad. Sci.*, 117, 10397–
 1082 10405.

1083 Nelson, M.E. & MacIver, M.A. (2006). Sensory acquisition in active sensing systems. *J. Comp.*
1084 *Physiol. A*, 192, 573–586.

1085 O'Connor, M.I., Pennell, M.W., Altermatt, F., Matthews, B., Melián, C.J. & Gonzalez, A. (2019).
1086 Principles of Ecology Revisited: Integrating Information and Ecological Theories for a
1087 More Unified Science. *Front. Ecol. Evol.*, 7.

1088 Pake, C.E. & Venable, D.L. (1995). Is Coexistence of Sonoran Desert Annuals Mediated by
1089 Temporal Variability Reproductive Success. *Ecology*, 76, 246–261.

1090 Parrondo, J.M., Horowitz, J.M. & Sagawa, T. (2015). Thermodynamics of information. *Nat.*
1091 *Phys.*, 11, 131–139.

1092 Patricelli, G.L. & Blickley, J.L. (2006). Avian communication in urban noise: causes and
1093 consequences of vocal adjustment. *The Auk*, 123, 639–649.

1094 Peacor, S.D. & Werner, E.E. (2004). How dependent are species-pair interaction strengths on
1095 other species in the food web? *Ecology*, 85, 2754–2763.

1096 Pennekamp, F., Iles, A.C., Garland, J., Brennan, G., Brose, U., Gaedke, U., *et al.* (2019). The
1097 intrinsic predictability of ecological time series and its potential to guide forecasting. *Ecol.*
1098 *Monogr.*, 89, e01359.

1099 Philippi, T. & Seger, J. (1989). Hedging one's evolutionary bets, revisited. *Trends Ecol. Evol.*, 4,
1100 41–44.

1101 Post, E. & Forchhammer, M.C. (2008). Climate change reduces reproductive success of an
1102 Arctic herbivore through trophic mismatch. *Philos. Trans. R. Soc. B Biol. Sci.*, 363,
1103 2367–2373.

1104 Relyea, R.A. (2003). Predators come and predators go: the reversibility of predator-induced
1105 traits. *Ecology*, 84, 1840–1848.

1106 Rivoire, O. & Leibler, S. (2011). The value of information for populations in varying
1107 environments. *J. Stat. Phys.*, 142, 1124–1166.

1108 Robertson, B.A., Rehage, J.S. & Sih, A. (2013). Ecological novelty and the emergence of
1109 evolutionary traps. *Trends Ecol. Evol.*, 28, 552–560.

1110 Salmon, M., Tolbert, M.G., Painter, D.P., Goff, M. & Reiners, R. (1995). Behavior of Loggerhead
1111 Sea Turtles on an Urban Beach. II. Hatchling Orientation. *J. Herpetol.*, 29, 568–576.

1112 Schaubert, E.M., Kelly, D., Turchin, P., Simon, C., Lee, W.G., Allen, R.B., *et al.* (2002). Masting
1113 by Eighteen New Zealand Plant Species: The Role of Temperature as a Synchronizing
1114 Cue. *Ecology*, 83, 1214–1225.

1115 Schlaepfer, M.A., Runge, M.C. & Sherman, P.W. (2002). Ecological and evolutionary traps.
1116 *Trends Ecol. Evol.*, 17, 474–480.

1117 Schmidt, K.A., Johansson, J. & Betts, M.G. (2015). Information-mediated Allee effects in
1118 breeding habitat selection. *Am. Nat.*, 186, E162–E171.

1119 Sears, A.L. & Chesson, P. (2007). New methods for quantifying the spatial storage effect: an
1120 illustration with desert annuals. *Ecology*, 88, 2240–2247.

1121 Secor, D.H. (2007). The year-class phenomenon and the storage effect in marine fishes. *J. Sea*
1122 *Res.*, 57, 91–103.

1123 Shoemaker, L.G. & Melbourne, B.A. (2016). Linking metacommunity paradigms to spatial
1124 coexistence mechanisms. *Ecology*, 97, 2436–2446.

1125 Smith, J.M. (1999). The idea of information in biology. *Q. Rev. Biol.*, 74, 395–400.

1126 Snyder, R.E. (2006). Multiple risk reduction mechanisms: can dormancy substitute for
1127 dispersal? *Ecol. Lett.*, 9, 1106–1114.

1128 Stephens, D.W. (1989). Variance and the value of information. *Am. Nat.*, 134, 128–140.

1129 Stephens, P.A., Frey-roos, F., Arnold, W. & Sutherland, W.J. (2002). Model complexity and
1130 population predictions. The alpine marmot as a case study. *J. Anim. Ecol.*, 71, 343–361.

1131 Strauss, S.Y. (1997). Floral Characters Link Herbivores, Pollinators, and Plant Fitness. *Ecology*,
1132 78, 1640–1645.

1133 Stumpf, M.P., Laidlaw, Z. & Jansen, V.A. (2002). Herpes viruses hedge their bets. *Proc. Natl.*

1134 *Acad. Sci.*, 99, 15234–15237.

1135 Sultan, S.E. (2000). Phenotypic plasticity for plant development, function and life history. *Trends*

1136 *Plant Sci.*, 5, 537–542.

1137 Suttle, K.B., Thomsen, M.A. & Power, M.E. (2007). Species interactions reverse grassland

1138 responses to changing climate. *science*, 315, 640–642.

1139 Ten Brink, H., Gremer, J.R. & Kokko, H. (2020). Optimal germination timing in unpredictable

1140 environments: the importance of dormancy for both among-and within-season variation.

1141 *Ecol. Lett.*, 23, 620–630.

1142 Thackeray, S.J., Henrys, P.A., Hemming, D., Bell, J.R., Botham, M.S., Burthe, S., *et al.* (2016).

1143 Phenological sensitivity to climate across taxa and trophic levels. *Nature*, 535, 241–245.

1144 Tielbörger, K., Petru\uu, M. & Lampei, C. (2012). Bet-hedging germination in annual plants: a

1145 sound empirical test of the theoretical foundations. *Oikos*, 121, 1860–1868.

1146 Tkačik, G. & Bialek, W. (2016). Information processing in living systems. *Annu. Rev. Condens.*

1147 *Matter Phys.*, 7, 89–117.

1148 Turelli, M. (1978). Does environmental variability limit niche overlap? *Proc. Natl. Acad. Sci.*, 75,

1149 5085–5089.

1150 Tyson, J.J., Csikasz-Nagy, A. & Novak, B. (2002). The dynamics of cell cycle regulation.

1151 *Bioessays*, 24, 1095–1109.

1152 Tyson, R. & Lutscher, F. (2016). Seasonally varying predation behavior and climate shifts are

1153 predicted to affect predator-prey cycles. *Am. Nat.*, 188, 539–553.

1154 Usinowicz, J. (2015). Limited Dispersal Drives Clustering and Reduces Coexistence by the

1155 Storage Effect. *Am. Nat.*, 186, 634–648.

1156 Usinowicz, J., Chang-Yang, C.-H., Chen, Y.-Y., Clark, J.S., Fletcher, C., Garwood, N.C., *et al.*

1157 (2017). Temporal coexistence mechanisms contribute to the latitudinal gradient in forest

1158 diversity. *Nature*, 550, 105–108.

1159 Usinowicz, J., Wright, S.J. & Ives, A.R. (2012). Coexistence in tropical forests through

1160 asynchronous variation in annual seed production. *Ecology*, 93, 2073–2084.

1161 Venable, D.L. & Lawlor, L. (1980). Delayed germination and dispersal in desert annuals: escape

1162 in space and time. *Oecologia*, 46, 272–282.

1163 Werner, E.E. & Peacor, S.D. (2003). A review of trait-mediated indirect interactions in ecological

1164 communities. *Ecology*, 84, 1083–1100.

1165 Williams, P., Camara, M., Hardman, A., Swift, S., Milton, D., Hope, V.J., *et al.* (2000). Quorum

1166 sensing and the population-dependent control of virulence. *Philos. Trans. R. Soc. Lond.*

1167 *B. Biol. Sci.*, 355, 667–680.

1168 Wilsterman, K., Ballinger, M.A. & Williams, C.M. (2021). A unifying, eco-physiological framework

1169 for animal dormancy. *Funct. Ecol.*, 35, 11–31.

1170 Woods, H.A. & Wilson, J.K. (2013). An information hypothesis for the evolution of homeostasis.

1171 *Trends Ecol. Evol.*, 28, 283–289.