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The fitness value of ecological information in a variable world

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Abstract

39 Information processing is increasingly recognized as a fundamental component of life in
40 variable environments, including the evolved use of environmental cues, biomolecular
41 networks, and social learning. Despite this, ecology lacks a quantitative framework for
42 understanding how population, community, and ecosystem dynamics depend on
43 information processing. Here, we review the rationale and evidence for 'fitness value of
44 information' (FVOI), and synthesize theoretical work in ecology, information theory and
45 probability behind this general mathematical framework. The FVOI quantifies how
46 species' *per capita* population growth rates can depend on the use of information in
47 their environment. FVOI is a breakthrough approach to linking information processing
48 and ecological and evolutionary outcomes in a changing environment, addressing
49 longstanding questions about how information mediates effects of environmental
50 change and species interactions.
51
52

Quantifying information in ecology

Biology is built upon information.From genetic architecture (Smith 1999; Goldenfeld & Woese 2007; Tkačik & Bialek 2016), to sub-cellular biomolecular networks (Tyson *et al.* 2002 ; Woods & Wilson 2013; Cai *et al.* 2018), to the countless examples of derived sensory apparatus in organisms, life is replete with mechanisms for detecting, processing, and storing information (Dangles *et al.* 2009). 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). Ecological studies account for the myriad ways in which organisms across all kingdoms of life respond to changing environments and use cues in their environment to find resources, refuges, and reproduce (Crespi 2001; Crone *et al.* 2009; Gil *et al.* 2018). However, accounting for the explicit role that information plays in population, community, and ecosystem dynamics remains a largely unexplored research frontier (O'Connor *et al.* 2019; Marleau *et al.* 2020).

Ecologists have long been interested in the ways that organisms detect and respond to cues in their environment, but recently information is increasingly acknowledged as a universal and essential component to life in fluctuating environments (Berhardt *et al.* 2020). Historically, information has been equated with a variety of cues including climatic shifts associated with seasonal change that drive phenology in growth, germination, reproduction, hibernation, and dormancy (Cohen 1966; Ellner 1997; Clauss & Venable 2000; Thackeray *et al.* 2016; Ten Brink *et al.* 2020). Information has also been studied in the form of social or chemical signals used to find food (Danchin *et al.* 2004; Magrath *et al.* 2015; Gil *et al.* 2018), shared between bacteria to monitor local densities (Crespi 2001), or transmitted between plants as volatile organic compounds triggered by defense against herbivor (De Moraes *et al.* 1998; Baldwin *et al.* 2006). While these important studies have guided scientific progress, taken collectively they create an idiosyncratic, system-specific perspective on information the precludes generalization across systems. Furthermore, they tend to lack a dynamical framing of information's role in populations, communities, and ecosystems.

A generalizable definition of information that captures the functional role of biological cues can be found in information theory (Goldenfeld & Woese 2007; Tkačik & Bialek 2016). In information theory, information is measured in relation to the uncertainty or "surprisal" of an event. Observing a less-probable (more surprising) event is more valuable precisely because there will be fewer opportunities to do so, meaning that an observer will be better-informed (about their environment) after a rare event, relative to having observed common events. To illustrate, 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 rain is absent on any day; low surprise indicates that little information has been gained by an observer who notes its absence. By comparison, learning that it has rained carries more

surprise, and thus conveys more information. Formally, surprisal of a single process is quantified as the log (1 / *probability* (*event*)) (related to the log-odds of an event) and this standardized unit of information forms the basis for information theoretic metrics including the Shannon Entropy (familiar to ecologists as the Shannon evenness). Surprisal extends naturally to consider the joint probability of two (or more) events occurring and leads to metrics of shared information such as the mutual information (MI). For example, temperature patterns often contain information about rain but this depends on the type of climate. If temperature is generally the same regardless of precipitation then knowing the temperature today is uninformative about the chance of rain (and vice versa). However, if a cold front precedes rain then the consequent temperature drop carries a great deal of information about the chance of rain.

Information theory demonstrates that information itself is measureable yet inherently free of value or meaning (Frank 2012). However, ecologists are typically more interested in the biological value of information without necessarily understanding its underlying role. What is necessary then are frameworks that link information with biological value and clarify how much ecological dynamics are driven by information versus the biological utility that organisms derive from it (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 the biological value of information can be measured via its effects on a population's fitness. Ecology and evolution share a universal measure of population-level fitness measured in terms of *per capita* population growth rates. The FVOI quantifies how information increases (or occasionally decreases) a population's fitness in varying environments by measuring 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 (Gould 1974; Stephens 1989; Donaldson-Matasci *et al.* 2010; Rivoire & Leibler 2011) (Figure 1). Because the formalism is built around *per capita* growth rates, the FVOI overlaps with models and other frameworks for analyzing stochastic population growth, including classic models of bet-hedging in annual plants (Gillespie 1974; Philippi & Seger 1989) and copepods (Hairston & Dillon 1990), and coexistence theory (Turelli 1978; Chesson & Warner 1981). However, by explicitly parsing the information content of per capita growth rates from other fitness components, the FVOI offers deeper insight into the dynamics of populations in fluctuating environments (Stephens 1989; Donaldson-Matasci *et al.* 2010; Rivoire & Leibler 2011).

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. The extent to which information use can increase fitness must account for concurrent costs and benefits associated with information detection and processing -- organisms bear metabolic costs to implementing and maintaining sensory machinery

134 (Koch 2004; Keller & Surette 2006; Nelson & MacIver 2006; Barth & Schmid 2013; Gil
135 *et al.* 2018) and cellular or biochemical networks for information (Laughlin *et al.* 1998;
136 Bruce *et al.* 2007; Bullmore & Sporns 2012; Crisp *et al.* 2016); although, in some cases
137 organisms may take advantage of biochemical pathways that are already in place
138 (Baldwin *et al.* 2006). On the other hand, information can have emergent benefits, as
139 when matching the phenology of life history events such as flowering and reproduction
140 with resources for growth compounds benefits through pollination success (Strauss
141 1997), herbivory avoidance (Schauber *et al.* 2002), or a reduction in interspecific
142 competition (Usinowicz *et al.* 2012). The FVOI inherently encompasses both costs and
143 benefits to using information because quantifyingthe overall net impact of these
144 processes is subsumed in rates of population change.
145   The goal of this paper is to develop the FVOI as a general framework that guides
146 ecological intuition about information's role in ecological dynamics; it is not our objective
147 to review information theory as others have (Goldenfeld & Woese 2007; Tkačik & Bialek
148 2016) and we only define specific concepts as they become relevant to in-depth
149 understanding of FVOI. In the first section **Measuring the fitness value of information**
150 we present an intuitive heuristic derivation of FVOI for general ecological audiences and
151 review the mathematical framework first presented by Donaldson-Matasci *et al.* (2010)
152 both in the text and in more detail in Box 1 and describe how FVOI can be measured
153 both in theory and in empirical settings. In the section **Parsing information's**
154 **contributions to fitness** we briefly review the historical development of information-
155 based population models in ecology in order to illustrate core principles of FVOI, point
156 out where the theory can inform empirical applications, and demonstrate a novel
157 extension to competitive communities. Finally, in **Biological examples of**
158 **information's value** we reviewstudies where organisms make fitness-related decisions
159 (behavioral and developmental) in response to environmental cues (biotic and abiotic);
160 beyond simply reviewing the literature, our goal in this section is to highlight the
161 potential for FVOI to facilitate novel, testable ecological hypotheses in particular
162 systems (Marleau *et al.* 2020), and help unify our understanding of anthropogenic
163 impacts on the information content of environmental cues (McMahon *et al.* 2017; Barton
164 *et al.* 2018). A major strength of the FVOI is that it can link these disparate bodies of
165 work through fundamental principles; in a variable and uncertain world organisms
166 constantly face decisions (or, developmental junctures) which can ultimately have
167 population-level consequences on the long-term persistence of their species, and
168 average fitness outcomes improve when populations of organisms make informed
169 decisions.
170

Measuring the fitness value of information

172   Evidence that information has fitness value seems unequivocal when considering
173 the countless adaptations found in species to detect, process, and produce cues and

174 signals. An integrated measure of the fitness value of information can be made by

175 measuring population growth rates with the benefits, costs, and community context

176 embedded in population dynamics (Cover & Thomas 2006; Donaldson-Matasci *et al.*

177 2010; Rivoire & Leibler 2011). Here we present a heuristic derivation of the FVOI for

178 ecology that synthesizes studies which have derived this relationship from fundamental

179 mathematical, information-theoretic principles to understand evolutionary dynamics

180 (Box 1) (Donaldson-Matasci *et al.* 2010; Rivoire & Leibler 2011).

181   Fitness can be given a concrete, mathematical, definition. Ecologists (Turelli

182 1978; Chesson 1994; Ellner *et al.* 2016) and evolutionary biologists (Haldane & Jayakar

183 1963; Cohen 1966; Ellner 1987) measure fitness using *per capita* population growth

184 rates: fitness is the expected value (average) of the logarithm of *per capita* population

185 growth rates (Frank 2016). Ecologists commonly model population growth with discrete-

186 time models of the form

187

188 $$N_i(t+1) = \lambda_i(t) N_i(t). \tag{1}$$

189

190 Here, $\lambda_i(t)$ is the *per capita* growth rate of population *i*, which is itself usually a function of

191 demographic parameters including survival and fecundity (e.g., Box 2). This indexing

192 may refer to a species, a phenotype, or a strategy depending on the study and its

193 context, but what is consistent is that all individuals within population *i* have an identical

194 response. A population's expected long-term growth rate ρ_i is the geometric mean of the

195 *per capita* growth rate:

196

197 $$\rho_i = E\left[\log \lambda_i(t)\right]. \tag{2}$$

198

199 The *E*[ ] signifies the expectation over many realizations of the term in brackets and is

200 defined for both discrete- and continuous-time models. The continuous-time analogue is

201 $d N_i/dt = G_i(t) N_i(t)$ and $G_i(t) = \rho_i$ is the log-growth rate.

202   In theory, ρ_i can be calculated for any specification of $\lambda_i(t)$, meaning it is

203 applicable to any population. By measuring ρ under different models or

204 parameterizations of $\lambda_i(t)$, biologists have used it to compare how different processes or

205 environmental conditions impact the fitness of populations. For example, the theory of

206 coexistence in fluctuating environments (Turelli 1978; Chesson 1994) is effectively

207 based on an underlying comparison of two versions of ρ_i, one with and one without a

208 varying environment; their difference measures how much population *per capita* growth

209 rates depend on environmental variation (Usinowicz 2015; Shoemaker & Melbourne

210 2016; Barabás *et al.* 2018). In evolutionary theory, ρ_i provides a measure of the fittest

211 strategy or adaptation when compared across different phenotypes in a population

212 (Cohen 1966; Ellner 1997).

213   The FVOI framework is based on comparing ρ_i under different assumptions of

214 information availability, usage, and cost. This assumes of course that $\lambda_i(t)$ can be

215 calculated with and without information components. Stated pseudo-mathematically

216 (see Box 1 for full mathematical derivation), the fitness value of information is measured

217 as the difference between $\rho(informed)$ and $\rho(uninformed)$:

218

219 $$\Delta \rho_i = \rho_i(informed) - \rho_i(uninformed) \tag{3}$$

220

221 Application of $\Delta\rho_i$ to some simple models of population growth has shown that at least

222 two key information-based mechanisms (*sensu* 'coexistence mechanism') contribute to

223 fitness (Donaldson-Matasci *et al.* 2010; Rivoire & Leibler 2011). The first mechanism

224 defines the maximum fitness benefit that could be obtained by perfectly detecting and

225 utilizing a cue. It is equivalent to the information-theoretic correlation between

226 environmental variation and the potential cue (a particular pattern that precedes

227 variation), known as the mutual information (MI) (Figure 1). The MI measures how much

228 information about the availability of a good (or bad) environmental condition is

229 potentially available to a population, and is thus proportionate to the maximum potential

230 fitness value of information (in a cue) (Donaldson-Matasci *et al.* 2010; Rivoire & Leibler

231 2011). The MI is generally positive and can be zero when the cue and the environment

232 are independent.

233   The other important component in the FVOI identified thus far in theory estimates

234 the fitness consequences when a population's response to patterns of environmental

235 variation does not utilize all of the available information (the MI). Quantitatively, this

236 difference is equivalent to the Kullback-Leibler (KL) divergence (D_{KL}), which is a

237 statistical distance (but not a true distance metric) between two probability distributions;

238 biologically, it measures how much the population's distribution of responses to the

239 environment (across individual organisms' internal models of the environment) differs

240 from the real probability distribution that describes environmental fluctuations (Box 1,

241 Figure 1C,D)). If detection of and response to the environment perfectly anticipate

242 patterns of environmental variation then the KL divergence is zero and the population

243 can fully utilize the information present (in the cue) (i.e., the MI).

244 One important result from the FVOI is that the MI between a cue and future

245 environmental conditions defines an upper limit for how much a source of information

246 can improve fitness (Donaldson-Matasci *et al.* 2010; Rivoire & Leibler 2011). This result

247 is useful because it confirms intuition that uninformative cues should not be expected to

248 contribute to fitness. Furthermore, the significance of MI as a bound on fitness benefit

249 provides justification for using MI as a simple metric to identify cues with potential

250 fitness value.

251

Parsing information's contributions to fitness

253   In practice, $\Delta\rho_i$ can be applied to quantify the fitness value of information

254 whenever *per capita* population growth rates can be quantified in fluctuating
255 environments. Measurements of ρ_i(*informed*) are commonly made in studies of
256 population persistence and coexistence in fluctuating environments, whether it is
257 through direct experimental meaurements (e.g. Grainger et al. 2019), parameterization
258 of mathematical models with observational data (e.g. Adler et al. 2006; Usinowicz et al.
259 2017), or a combination of the two. Measuring ρ_i(*uninformed*) may require novel
260 approaches, for example experiments that break the correlations between cues and
261 population fitness, and to our knowledge have never been performed. However, the
262 utility of the underlying mathematical framework for the FVOI and its different
263 expressions (Box 1; Donaldson-Matasci *et al.* 2010; Rivoire & Leibler 2011) is that it
264 provides other options to accommodate a variety of ecological data. In particular,
265 whenever ρ_i(*informed*) is measured in conjunction with the environment and potentially
266 informative cues (which may themselves be embedded in the environmental data), then
267 it should be possible to quantify $\Delta\rho_i$ by instead calculating the MI and KL divergences.
268   In this section, we illustrate how these lines of evidence are used to estimate
269 FVOI by reviewing the theoretical literature that has explored FVOI in single-species
270 population models. We review a classic motivating system in ecology (dormancy and
271 germination in annual plants) where the idea of informed resource allocation links
272 ecology to probability theory's concept of betting. We also review how the simplest
273 mathematical models of dynamics that link ecology and classic betting problems have
274 provided tremendous insight into natural dynamics, but much still stands to be gained
275 by extending analysis to more complex models which include dormancy, density
276 dependence, and interspecific competition. Details of all simulations presented in this
277 section can be found in the Supporting Information, and code and data files found at
278 https://github.com/jusinowicz/fvoi.git .
279

Betting on success: timing of seed germination in annual plants

281   A classic motivating example for understanding the FVOI is the timing of
282 germination of annual plants in fluctuating environments. Environmental conditions that
283 directly affect germination and reproductive success differ each generation, bounded
284 within a distribution of possible sets of conditions. Each generation, dormant seeds
285 within the population can germinate or remain dormant, and if they germinate the
286 resulting adult plant will produce new seeds, the number of which will reflect the
287 suitability of the environment. Ecologists have drawn on classic mathematical models of
288 betting from probability theory to model the dynamics of populations in this system
289 (Cohen 1966; Ellner 1997), and extended them to more complex community
290 interactions between zooplankton (Cáceres 1997), fish (Chesson & Warner 1981; Secor
291 2007), trees (Usinowicz *et al.* 2017), and viruses (Stumpf *et al.* 2002). A population is
292 treated as a bettor who has some amount of capital (seeds) to gamble on event
293 outcomes (environment conditions); the role of the bettor is to decide when and how
294 much to gamble on each event (the conditions each year). The betting analogy also

295 shows the value of information more intuitively; in general, knowledge of likely outcomes
296 allows a bettor to increase earnings by allowing them to make informed bets. However,
297 these previous applications have only quantified population-level consequence of
298 observed demographic patterns without seeking a deeper understanding of the role of
299 information in driving *per capita* growth rates.

300 Drawing the connection between betting in probability theory and population
301 dynamics of organisms in fluctuating environments requires some assumptions. In this
302 example, the ecological equivalent of an 'event' is a multivariate space of environmental
303 conditions, denoted E (Box 1), that are relevant to the organism's biology, e.g.,
304 moisture, temperature, and nutrient availability. An 'event outcome,' denoted e (Box 1),
305 is any particular combination of these conditions (visualized as a point that falls
306 somewhere in the multivariate space). It is common (but not necessary) to model
307 discrete events because gambling has discrete outcomes; a particular number is drawn,
308 or a particular horse wins a race. When analyzing ecological data, it may be possible to
309 fit continuous distributions to a discrete sampling space, but in many cases it may be
310 preferable to work with the observed distribution of samples to construct the (non-
311 parametric) distribution of environmental states.

312 Betting examples that motivate theory often refer to a bettor with decision-making
313 ability. This bettor has an internal model of probabilities that it uses to make betting
314 decisions (denoted by $x_{i,}(e)$ in Box 1). In reality, a bettor's internal model is just a device
315 to illustrate a mathematical concept and should not be taken too literally; in the
316 mathematical representation of dynamics, the internal model is encapsulated by a
317 function of a random variable $x_{i,}(e)$, whose underlying probability distribution dictates the
318 proportion of its resources to bet on each event (e.g. Box 1). Extending the analogy of
319 internal models to ecological dynamics does lead to interesting biological questions.
320 Organisms, or even populations, may have the ability to learn and improve decisions by
321 learning the odds in a way that is more similar to a bettor that learns probabilities. In
322 other cases, "decisions" are actually hard-wired life history transitions that are initiated
323 by a particular stimulus or cue. For example, the "decision" of a seed to germinate is not
324 behavioral, but is driven by a biochemical reaction initiated at the seed's surface that
325 generates a cascade of internal changes. The "internal model" is actually the
326 population-level manifestation of these decisions because the allocation of resources to
327 reproduction in each generation is a population-level phenomenon. Thus in making
328 analogies to probability theory, we are actually treating the population as a bettor whose
329 internal model is really a distribution of individual-level decisions made across all
330 individuals. In our notation, ρ_i is the rate at which a bettor accumulates wealth or a
331 population accumulates new individuals (i.e. *per capita* growth).

332 A naive bettor (or population) is uninformed about the distribution of possible
333 outcomes or states. The internal model of this population (bettor) may take various
334 forms, depending on the context, but one common representation is a uniform
335 distribution over states (outcomes) because without further knowledge the best that a

336 bettor can do is assume that each state is considered to be equally likely. This important
337 baseline appears in numerous information contexts, from Bayesian statistics
338 (uninformed priors) to maximum entropy (maxent) in information theory studies; a
339 uniform distribution of probabilities produces the maximum value of the Shannon
340 entropy (Cover & Thomas 2006). In the FVOI, the maximum entropy case can similarly
341 be used to establish a baseline of *per capita* growth rates because it is the best that a
342 population can do when it is entirely uninformed about future environmental states.
343 However, this does not mean that other distributions might be more biologically
344 appropriate in other contexts and the framework works regardless of this choice.
345 Furthermore, we do not expect uniformity to occur for real populations and emphasize
346 that this is a mathematical device which simplifies and standardizes analyses.
347 Formally, we denote the uninformed *per capita* growth rate as $\rho_i(uninformed) = \rho_i(x_i (E$
348 $\sim U(0,1))) = \rho_i(E\sim U)$ in this specific case, where $x_i(E)$ is the proportion that a
349 population gambles on each environmental state according to its internal model, $U(0,1)$
350 denotes the uniform distribution over the interval 0 to 1, and $\rho_i(E\sim U)$ is a shorthand that
351 we use to indicate the uninformed population (see Box 1 for notation).
352   In many cases, a population (bettor) may actually have some information about
353 the distribution of odds of possible states (outcomes), which we denote formally as $\rho_i(x_i$
354 $(E)) = \rho_i(E)$ simply to indicate that some distribution of probabilities is being used as an
355 internal model for allocation of resources (bets). A bettor might learn something about
356 the distribution of expected outcomes, for example by knowing how often each horse in
357 a race has won in past races. In a population, the information may also exist as learned
358 associations (Aplin *et al.* 2015; Gil *et al.* 2018), but it can also appear as a phenotypic
359 distribution that has evolved in response to historical temporal patterns in environmental
360 conditions (Kussell & Leibler 2005; Donaldson-Matasci *et al.* 2008; Frank 2012). In
361 either case, the optimal allocation strategy for reproductive effort under minimal
362 information (*i.e.*, knowing only the odds of events based on the assumption that past
363 distribution of occurrences predicts future odds) is the same, and the solution is for a
364 population to divide reproduction among expected events (environmental states) in
365 proportion to their odds of occurring. This is referred to as the Kelly criterion or Kelly
366 betting (Cover & Thomas 2006), and was derived to explain the best strategy for an
367 individual bettor that must allocate bets optimally to maximize winnings across many
368 horse races (Kelly 1956; Cover & Thomas 2006). The Kelly betting strategy is fairly
369 robust because it is independent of the underlying mechanism (cognitive or
370 evolutionary) (Box 1); thus even without predictive information about future states
371 provided by a cue (i.e., the conditional probability of environment, given a cue (3)) an
372 optimal long-term strategy exists for timing reproduction. The Kelly criterion is also the
373 choice of uninformed baseline used orginally by Donaldson-Matsci (2010) in their
374 original development of the framework.
375   If organisms in a population are able to detect information which can be used to
376 predict future events, then allocation (betting) strategies exist that are even more

377 efficient than classic Kelly betting. For example, if our imaginary plant populations are
378 attempting to germinate in an arid environment like the one discussed briefly in the
379 introduction, and reproductive success is maximized when germination is timed
380 coincident with optimal amounts of water each season, we can explore strategies when
381 populations are able to respond to environmental cues that signify future water
382 availability. In Box 1, the distribution of all cue states is C, and each realization as c. If
383 the amount of moisture today is a cue that is predictive of the amount of rain in the
384 future, then there is high MI between the cues C of moisture and the states E of rain
385 which can be exploited. The MI is itself driven by the conditional probability of seeing a
386 certain amount of rain in the future given current moisture levels (written formally as p_i
387 $(E|C)$), which may be a more familiar notation. As a probability, $p_i(E|C)$ ranges between
388 0 and 1, 0 indicates total independence of these two events, and 1 indicates that the
389 current cue is perfectly predictive. The corresponding *per-capita* growth rate is $\rho_i(x_i (E|$
390 $C)) = \rho_i(E|C)$.
391 　　　The additional fitness gain that is possible when information is available (e.g., MI
392 > 0) can be substantial (Box 1; Donaldson-Matasci et al. 2010). The optimal strategy
393 with informative cues is a conditional version of the Kelly criterion (Cover & Thomas
394 2006), where bets (allocations) are made in proportion to the conditional probabilities
395 (3). As long as the information is reliable (i.e., the conditional probability distribution has
396 less variation around the true state than the uninformed marginal distribution) then the
397 payout will always be better and $\Delta \rho_i$ will increase (Box 1; Figure 2A. The FVOI ($\Delta \rho_i$) is
398 the difference between these two growth trajectories, estimated as the comparison of
399 the rates of population increase over time (Figure 2C). Note from Figure 2C that the
400 FVOI and MI are equivalent in that scenario, showing that populations have fully utilized
401 the information in the cue and maximized the FVOI.
402 　　　In the real world, populations rarely invest all of their resources into *per capita*
403 growth and instead retain resources across reproductive events. This strategy, known
404 as bet-hedging (Gillespie 1974; Philippi & Seger 1989), is ubiquitous (Clauss & Venable
405 2000; Stephens *et al.* 2002; Childs *et al.* 2010; Tielbörger *et al.* 2012; Furness *et al.*
406 2015). It is evident wherever there is some form of "storage", whether it is in long-lived
407 adults such as in perennial plants (Adler *et al.* 2006; Usinowicz *et al.* 2012) or adult fish
408 (Secor 2007), or in propagules such as a seed (Sears & Chesson 2007; Jose M. Facelli
409 *et al.* 2008) or eggs (Cáceres 1997) that can remain dormant for long periods. Bet-
410 hedging is optimal when odds are "subfair," the mathematical term for a set of outcomes
411 where the sum over the reciprocals of the odds of each outcome is greater than 1
412 (sum(1/odds) >1)(see Cover & Thomas 2006 or Ellner 1997 for details). Basic
413 organismal physiology tends to constrain organisms such that there will be some
414 conditions under which reproduction rates approach 0, likewise making the odds of
415 reproductive success 0. Brief consideration of the equation for subfair odds above leads
416 to the observation that we should probably never expect nature to be fair; even one
417 outcome with odds approaching zero will lead to very large or even infinite sums.

418 Because nature is not fair, bet-hedging should be the norm.

419   Information improves fitness for bet-hedging populations in variable

420 environments (Box 1: Donaldson-Matasci *et al.* 2010). As with model 1 (Figure 2A), the

421 *per capita* growth rate for a bet-hedging population is higher when individuals use a cue

422 to time reproduction to align with favorable conditions (Figure 2B). *Per capita* growth

423 rate in the bet-hedging population is lower, however, because dormancy introduces

424 constraints on the FVOI. Dormancy represents increased phenotype specialization

425 when individuals of a certain phenotype are increasingly specialized to emerge in

426 response to specific cues. This physiological trade-off between generality and

427 specialization can prevent a population from fully exploiting the information in a cue (see

428 Box 2). The fitness cost of a physiological constraint like dormancy can be measured

429 by parsing the FVOI, which we have done numerically in Figure 2C-D. In the first

430 scenario, the FVOI is equivalent to the MI (Figure 2C) revealing that the

431 population/organism are able to perfectly use the MI in the environment. In the second

432 case, the FVOI measured by the difference in slopes is no longer equivalent to the MI

433 (Figure 2D). Note that this difference between $\Delta\rho_i$ and MI is the KL divergence, which

434 measures the information a population fails to use.

435   The theory reviewed here creates a general foundation that could be used to

436 unite phenomena from phenology, to behavior, to intraspecific diversity. Some of these

437 predictions and assumptions remain to be tested. For example, in the context of these

438 dynamics almost any information use has the potential to increases a population's

439 fitness, and certainly the use of cues to anticipate environmental conditions is

440 ubiquitous in real organisms. Likewise, the mathematical conditions that make

441 information advantageous (i.e., variable environments with sub-fair odds) are probably

442 the rule in nature. A primary point of contention in the annual plant systems, where bet-

443 hedging has been the most well-studied, has been whether the conditions that make a

444 cue informative actually exist (Venable & Lawlor 1980; Clauss & Venable 2000). To our

445 knowledge, no attempts have been made to measure the MI between the environmental

446 conditions which benefit annual plant reproduction and cues that seeds use to

447 germinate. This may not be surprising, however, since demography and phenology

448 have perhaps not been considered in the context of a formal information-based

449 framework before. It also remains unknown how often and to what extent biological

450 constraints (including dormancy) might reduce the FVOI to a point where there is no net

451 fitness value. Finally, many of the insights garnered here are based on theory that has

452 dealt with single-species populations without even conspecific interactions (such as

453 intraspecific competition). The handful of studies that consider the fitness value of social

454 information point to a complex landscape of fitness tradeoffs that can be dependent on

455 several factors, but tend to reflect a general potential for information to improves

456 fitness(Gil et al. 2017, Gil et al. 2019, Hein and Martin 2020).

457

458 ***Information's contributions to fitness in communities and community dynamics***

459   Given the importance of information to population dynamics and trajectories in
460   scenarios that consider only the population and its environment, we expect that
461   information use and the fitness advantages it confers may be an important dimension of
462   fitness in communities. In the single-species models studied to date only a direct
463   influence of information on fitness has been analyzed (Donaldson-Matasci *et al.* 2010;
464   Rivoire & Leibler 2011), and these models do not account for the density- and
465   frequency-dependent feedbacks that drive biodiversity (Adler *et al.* 2007; Hart *et al.*
466   2017; Usinowicz *et al.* 2017; Letten *et al.* 2018). Probability theory has also not probed
467   models with feedback dynamics that would be informative in the context of communities
468   and multiple interacting populations. A handful of models explore the fitness value of
469   information in the context of social information, but their relationip to the body of theory
470   behind the FVOI remains unresolved (Gil et al. 2017, Gil et al. 2019, Hein and Martin
471   2020).
472

How do species interactions mediate the fitness value of information?

474   Here we extend two classic ecological models of population dynamics in
475   fluctuating environments, to which we have added the potential for information-driven
476   dynamics (Box 2). The first of these is a novel extension of the lottery model (Chesson
477   & Warner 1981) where species compete based on the proportion of offspring that
478   emerge each generation (e.g., germinating proportions of seeds) which varies
479   randomly. We introduce the potential for information to be used in the emergence
480   process according to an early season cue that predicts whether environmental
481   conditions are favorable in a given year (high MI between early and later season
482   conditions). This is implemented by making the proportion of emerging individuals a
483   function of the conditional probability of seeing a favorable environment given a cue (
484   $p(E|C)$). In this form, the lottery model with information is an extension of the simple
485   single-species models used in Donaldson-Matsci et al (2010), and an information-
486   driven, extension of the lineage of bet-hedging models (Ellner 1997; Hairston et al.
487   1995) with competition added. An overview of this model for two species is given in Box
488   2, and the different competitive dynamics when germination is conditioned on a cue or
489   not, are given in Figure 3.
490   Information use benefits species that are competing for a shared, fluctuating
491   resource, as evidenced by comparing population growth rates with and without the use
492   of an environmental cue in Figure 3. For a single resource environment, at a particular
493   level of overlapping interspecific resource use (i.e., niche overlap), the ability to use
494   information about temporal patterns in the environment has clear and quantifiable
495   fitness benefits. It follows to ask, does the FVOI depend on the niche overlap of
496   competitors? In order to answer this question, we simulated the model across different
497   levels of resource use overlap (keeping species' average reproduction rates equivalent
498   to one another) and applied $\Delta\rho_i$ to measure changes in the FVOI across scenarios. It is
499   clear from the results in Figure 4A that increasing niche overlap through increases in

500 species' shared environmental preferences leads to a decrease in FVOI. This means
501 that high interspecific similarity in resource and environmental needs also decreases the
502 opportunity for species to avoid competition through information about patterns of
503 variation in those resources.
504   We can also ask, how does information influence coexistence? We can address
505 this question by applying $\Delta\rho_i$ to the model simulated over the same range of resource
506 overlap scenarios and calculating the niche differences (note that species were given
507 equivalent fitness) from the two different sets of low-density growth rates, $\rho_i(E|C)$ and ρ_i
508 ($E{\sim}U$) following previous methods (Carroll *et al.* 2011; Grainger *et al.* 2019). The
509 magnitude of niche partitioning with $\rho_i(E{\sim}U)$ at any particular level of resource overlap
510 reveals the potential for resource partitioning alone to promote coexistence, while the
511 difference in niche partitioning between $\rho_i(E|C)$ and $\rho_i(E{\sim}U)$ reveals the extent of niche
512 differentiation that is purely information based. Information can promote coexistence by
513 further decreasing niche overlap and this effect can be distinguished from purely
514 resource driven niche partitioning (Figure 4B). Information promotes niche partitioning in
515 this model by increasing each species' ability to target reproductive effort in its preferred
516 resource environments. As a result heterospecific individuals will encounter each other
517 less frequently and conspecific interactions will increase, decreasing interspecific
518 competition relative to intraspecific competion. Since broader niche differences facilitate
519 coexistence and the maintenance of biodiversity, our results also show that information
520 can therefore play a role in the maintenance of biodiversity in natural communities.
521 These results reinforce the few other studies where (social) information was found to
522 have tremendous potential to qualitative change competitive outcomes from exclusion
523 to coexistence (Gil et al. 2017; Gil et al. 2019). However, these studies also highlight a
524 complex, context-dependent suite of possible outcomes for information-driven
525 dynamics, including Allee affects and reversals of coexistence (Gil et al. 2019).
526

Fitness value of Social Information

528   Information exists in the environment in the patterns and behaviors of other
529 organisms, in addition to patterns in the environment as we have considered so far (Gil
530 et al 2018). When organisms detect physiological, chemical, or behavioral responses in
531 other individuals these cues are called social information. We also investigated the
532 FVOI in a model of social information based on classic Lotka-Volterra dynamics (Box 2)
533 (Gil *et al.* 2018). This version of the model includes an additional density-dependent
534 term with interaction rates that determine the value of social information passed
535 between con- and heterospecifics. We illustrate the different competitive dynamics with
536 and without social information in Figure 5. The main takeaway from this model is that
537 information again increases the rate at which a population recovers from low density. It
538 does not impact the equilibrium density; it is likely possible that other model
539 formulations could influence equilibrium density and this remains to be explored. The
540 simplicity of this model makes it straightforward to assess analytically, and serves as a

541 simple proof-of-concept because applying $\Delta\rho_i$ to the model in Box 2 recovers the term
542 $B_i(N_i...N_n)$ (Box 2) included by Gil et. al to represent information dynamics. This means
543 that the FVOI is equivalent to the value of social information in this example, and shows
544 more broadly how different types of ecological information can be nested and compared
545 within the more general FVOI framework.
546

Biological examples of information's value

548 All populations must contend with fluctuating environments, and most temporal
549 patterns of variation contain information that can be used to inform predictions about
550 likely future conditions (Pennekamp *et al.* 2019). By using information in the
551 environment, organisms stand a better chance of tracking beneficial conditions and
552 avoiding detrimental ones. Information is present in cues when they correspond to
553 patterns of environmental variation, and information is useful when it is predictive of
554 conditions that promote or inhibit species' growth or reproduction, and when that
555 information is detectable to the organisms. Species have evolved or learned responses
556 to specific cues, which signal behavioral decisions or life history responses. Although
557 the majority of our review has considered environmental cues to this point, cues may
558 also come in the form of social information from con- or heterospecifics that help avoid
559 predation, or improve the likelihood of finding resources or mates. A vast number of
560 studies enumerate examples of this ecological information without explicitly connecting
561 cue responses to population or community dynamics. Here, we discuss how ecological
562 information, in the form of abiotic and biotic cues, mediates fitness via two primary
563 pathways: 1) environmental information, when demographic rates change in response
564 to a unidirectional flow of information from environment to organism and 2) social
565 information, when population densities change in response to exchanges of information
566 between con- or heterospecific individuals.
567 Environmental information includes cues that trigger shifts in demographic rates,
568 often through life-history changes. In these situations, demographic responses are
569 independent of population densities. In a mathematical model, demographic responses
570 would be represented by a changing parameter value such as fecundity, germination or
571 survival rate (Box 2). Some of the most well-studied examples of environmental
572 information with demographic consequences include cues for the timing of dormancy
573 and emergence in plants (Thackeray *et al.* 2016; Montgomery *et al.* 2020), animals
574 (Koštál *et al.* 2017; Wilsterman *et al.* 2021), and bacteria (Jones & Lennon 2010). Plants
575 that experience seasonally harsh conditions often have dormancy strategies where
576 regrowth and germination (Tielbörger *et al.* 2012; Commander *et al.* 2017) respond to
577 cues associated with the onset of more favorable conditions (Box 2). In some cases
578 environmental information is produced by the presence or activities of other organisms.
579 Terrestrial and aquatic invertebrates are known to switch between phases of
580 parthenogenesis with rapidly hatching eggs and sexual reproduction with long-lived

581 diapausing eggs, and this switch can occur in response to a combination of cues
582 including temperature, photoperiod, and predation (Hairston & Dillon 1990; Hairston Jr
583 & Kearns 1995). Many larval amphibians switch growth and development strategies
584 along with behavior when predators are detected (Relyea 2003).
585   Environmental information can influence density- and frequency-dependent
586 population processes (Box 2). The seasonal timing of reproduction in many organisms
587 can lead to density and frequency dependent population dynamics via competition
588 (Chesson & Warner 1981; Usinowicz *et al.* 2012; Godoy & Levine 2014), predation
589 (Barbraud & Weimerskirch 2003; Tyson & Lutscher 2016), and mutualisms (Moeller
590 2004; Devaux & Lande 2009; Fabina *et al.* 2010). For example, when the seeds of
591 desert annual plants germinate in response to moisture and photoperiod, there will
592 naturally be competition for limited resources (Pake & Venable 1995; Alexander &
593 Levine 2019). This can lead to high intraspecific competition since conspecifics are
594 more likely to respond to similar cues; if intraspecific competition is high on average
595 relative to interspecific competition then population growth rates will be negatively
596 frequency dependent and coexistence is possible. This is the essence of the frequency-
597 dependent mechanism known as the storage effect, which has been documented in
598 numerous organisms in addition to annual plants (Cáceres 1997; Angert *et al.* 2009;
599 Ellner *et al.* 2016; Usinowicz *et al.* 2017).
600   Social information is based on cues that are passed between organisms as an
601 interaction or feedback. The production of and response to social informationare
602 typically linked through density-dependent feedbacks in population dynamics, for
603 example when conspecific attraction increases fitness by increasing reproduction rates
604 (Bever & Simms 2000; Schmidt *et al.* 2015), resource acquisition (Berryman *et al.* 1985;
605 Sultan 2000; Williams *et al.* 2000), or predator avoidance (Costerton *et al.* 1995; De
606 Moraes *et al.* 1998; Gil *et al.* 2019). Positive density-dependent feedbacks emerge
607 when social cues increase in magnitude or value with increasing population density
608 (Box 2). Negative density-dependent feedbacks can result when social information
609 repulses con- or heterospecifics (Durrett & Levin 1997; Chivers & Smith 1998).
610 Spatially explicit feedbacks lead to heterogeneous distributions of populations that can
611 lead to some of the complex phenomena and non-intuitive outcomes that have been
612 studied in the context of coexistence and predator avoidance (Huffaker 1958; Levin
613 1992; Bolker *et al.* 2003; Snyder 2006).
614   Social information is also shared between species. This can produce density-
615 dependent feedbacks driven by interspecific interactions with major implications for
616 community dynamics This is well documented in animals that hunt and scavenge
617 (Jackson *et al.* 2009; Kane & Kendall 2017) in association with other species, such as
618 mixed species foraging flocks of birds (Goodale et al 2020). For some animals such as
619 vultures, population growth relies on the positive density-dependence of these
620 associations to such a large degree that the collapse of certain predator populations has
621 brought a concurrent decline in vulture populations because of the loss of social

622 information around resources (Kane & Kendall 2017).

623

FVOI in inducible defenses

625 Among the best-known examples of organisms using information in fluctuating
626 environments to trigger life-history changes that improve fitness is in the context of
627 inducible defenses (Harvell 1992). Inducible defenses are morphological, behavioral or
628 phenotypic changes that occur in response to the detection of a cue indicating that a
629 predator or herbivore is nearby. In the context of our framework, inducible defenses
630 constitute a response to demographic information, even though cues are often biotic in
631 origin. It is well established that this use of information by prey can play a major role in
632 community structure and dynamics (Werner & Peacor 2003; Peacor & Werner 2004). In
633 an environment with irregular predation risk, there is a clear fitness value to detecting
634 cues that signal imminent predation. Intuitively, there is high MI between cues such as
635 chemical signals of predators or predation events and the presence of a predator, and it
636 has also been shown that environmental patterns such as temperature changes can
637 serve as cues for inducible defenses when their MI with predation pressure is high
638 (Miehls *et al.* 2013). The fitness benefit of detecting and acting on the information is also
639 high in these scenarios - it is survival by avoiding predation. The cost of not acting on
640 this information is also potentially high if it means mortality of individuals. The FVOI
641 provides a framework that makes the unique influence of inducible defenses on
642 dynamics comparable to other species interactions.
643 Despite a large body of research on the existence of inducible defense, there are
644 surprisingly few empirical tests of the fitness value of information in this context.
645 *Daphnia spp.* and their inducible defensive behavior of spine growth and diurnal
646 migration provides one example (Hammill *et al.* 2008). As we outline above, a
647 quantification of FVOI requires estimating the MI between cue and risk, as well as
648 fitness (here, population growth rate) in conditions with and without the predator. Most
649 inducible defense experiments include treatments that expose organisms to cues and
650 controls (no cue), but rarely also to the third factor: the predator, in a treatment that
651 allows predation. Perhaps the only experimental demonstration of FVOI in relation to
652 inducible defenses in animals (Boeing & Ramcharan 2010) exposed *Daphnia pulex*
653 clones to a control (no predation) and a predation treatment using planktivorous fish in
654 an *in situ* lake experiment, and the two experimental clones different in one important
655 way: one clone could detect the predator cues and initiate migratory behavior, while the
656 other clone could not detect the information about the predator. Population growth rates
657 of the *Daphnia* were higher in the clone that used information about predators, clearly
658 demonstrating FVOI.

659

The fitness value of information in a changing world

661 A growing literature addresses the roles of demographic and social information in
662 mediating anthropogenic impacts on natural communities. The fitness value of

663 information depends on its reliability, yet environmental cues and social information are
664 increasingly disrupted by anthropogenic change (Salmon *et al.* 1995; Inouye *et al.* 2000;
665 Cotton 2003; Longcore & Rich 2004). In the worst case, anthropogenic change leads to
666 misinformative cues that become "ecological traps," when organisms continue to follow
667 a formerly beneficial behavior that has become maladaptive (Schlaepfer *et al.* 2002;
668 Robertson *et al.* 2013). The FVOI provides a framework that can link seemingly
669 disparate studies seeking to understand and address anthropogenic impacts on natural
670 communities that emerge from anthropogenic disruptions to information-driven
671 dynamics. Then, $\Delta\rho_i$ provides a metric that can be applied to test hypotheses about and
672 quantify impacts on the reliability of key ecological information under global change.
673   Anthropogenic change can disrupt environmental information by altering patterns
674 of variability in the environment, and can even create misinformation. Climate change
675 has altered major patterns of climate variation, especially in the timing of seasonal
676 transitions. Reliable climate cues are an important component of ecological information
677 and research has shown that organisms across taxa shift phenology in response, often
678 to their detriment if the historical temporal relationship between the climate cue and the
679 needed resource supply have changed. For example, migratory bird species have
680 shifted the timing of both short and long distance migrations in response to changing
681 spring and autumn temperatures (Jenni & Kéry 2003; Horton *et al.* 2020), which has
682 been suggested to reduce fitness when the timing no longer coincides with the
683 availability of habitat or food (Cotton 2003). Climate cues that signal the end of
684 dormancy have become misinformative for some mammals, resulting in movement or
685 emergence that is mistimed with food availability (Inouye *et al.* 2000; Post &
686 Forchhammer 2008; Bronson 2009). Nearly all primary producers depend on seasonal
687 climate fluctuations as cues to time biomass production and reproduction; sometimes
688 these shifts boost single-species' by preempting access to resources (Alexander &
689 Levine 2019), but at the community scale such shifts are almost always detrimental due
690 to mismatches with environmental states (Suttle *et al.* 2007) or important mutualisms
691 (Hegland *et al.* 2009).
692   Urbanization has greatly increased the amount of noise and light in the
693 environment, creating events that are interpreted as cues but in fact have no relation or
694 even an opposite relationship with resource availability or risk. Night time light pollution
695 is misinformative for many phenotypes that have evolved to use phases of the moon as
696 cues for life history transitions (for example, sea turtles, fish and corals) or signals to
697 guide movement as they attempt to find mates, avoid predators, or locate habitat
698 (Salmon *et al.* 1995; Longcore & Rich 2004). Nocturnal insects can become disoriented
699 by artificial lights and are often more susceptible to predation (Acharya & Fenton 2011;
700 Firebaugh & Haynes 2019), and there is mounting evidence that polarized glass
701 surfaces that are increasingly common in windows and photovoltaics have increased
702 predation rates on insects disoriented by light reflection in the daytime (Horváth *et al.*
703 2009).

704   Social information is also disrupted by anthropogenic change. Noise pollution
705 tends to mask or dampen important auditory cues (Barber *et al.* 2010). Birds and
706 primates have been shown to change vocalization in response to chronic noise
707 exposure (Brumm *et al.* 2004; Patricelli & Blickley 2006). Noisy landscape features such
708 as roadways and population fitness are often cited as reducing the fitness of certain
709 vertebrate species (Barber *et al.* 2010), and experiments have found strong evidence
710 that noise-pollution can reduce population densities strongly enough to have cascading
711 trophic effects because organisms reduce foraging times (McMahon *et al.* 2017; Barton
712 *et al.* 2018). Furthermore, recent studies show that the rapid timescale of social
713 interactions means that disrupting social information can have very swift impacts on
714 demographic processes and hasten population collapse (Gil et al. 2020).
715

Concluding Remarks

717   Ecological information is a critical resource that promotes the fitness of
718 organisms in fluctuating environments. Yet the fitness value of information has
719 remained largely understudied in population and community dynamics. Environmental
720 information and social information are two ubiquitous categories of ecological
721 information that can critically determine species' fitness by guiding life-history decisions,
722 creating density-dependent feedbacks, and determining the nature of biotic interactions
723 in diverse communities. By adapting simple mathematical models of population
724 dynamics it is straightforward to demonstrate how important environmental cues and
725 social information (Box 2) can potentially be for promoting species coexistence (Fig 3-
726 5).
727   An important extension of $\Delta\rho_i$ is interpreting how ecological information mediates
728 anthropogenic impacts on fitness. While many studies have demonstrated that
729 ecological information is changed by anthropogenic activity, and in some cases shown
730 that individual or group behavior changes in response, none have quantified these
731 changes in terms of mutual information and estimated the impacts of these changes on
732 an organism's fitness. This is a necessary step to understand and predict the full range
733 of anthropogenic impacts on species persistence in a changing world. By giving the
734 fitness value of information a precise definition and providing an accompanying
735 mathematical framework we hope to facilitate a more complete understanding of
736 anthropogenic impacts on species' fitness.
737   We have presented a mathematical framework based on the comparison
738 between *per capita* population growth rates with and without information that provides a
739 formalized measure of the fitness value of information. The fitness value of information,
740 as measured by $\Delta\rho_i$, can parse *per capita* growth into components that show the
741 potential value of information, and how much fitness value is lost because a population
742 fails to anticipate its environment. Because these mechanisms mediate fitness through
743 universal features of population dynamics they are generalizable and comparable

744 across different systems. The FVOI framework is general and could be used to quantify

745 and compare FVOI across a broad range of ecological systems and contexts by relating

746 cue production and detection to population and community dynamics, and ultimately the

747 maintenance of biodiversity in changing environments.

748

749

750 (Boxes are 750 words, no figures)

751

752 Box 1. The fitness value of information and information theory

753 The framework for the fitness value of information can be used to derive an expression

754 that shows explicitly how information increases fitness (Donaldson-Matasci et al. 2010;

755 Rivoire & Leibler 2011). Consider a simple multiplicative growth process like that in eq

756 (1) in the main text. Assume that the environment is represented by the random variable

757 E and has some distribution of states e each with probability $p(e)$ of occurring

758 (temperature example in Figure 1). Also assume that a population i can produce

759 offspring in each environment e at rate $r_{i,e}$ and the probability of doing so is $x_i(e)$. This

760 combination of payoff $r_{i,e}$ and probability $x_i(e)$ is analogous to an environment-specific

761 phenotype defined as $\varphi_{i,e} = r_{i,e}\, x(e)$ (Donaldson-Matasci et al. 2010): in our simple

762 conceptualization of annual plant dynamics (section **Parsing information's**

763 **contributions to fitness**), $x_i(e)$ are the germination rates and $r_{i,e}$ are the *per-capita*

764 fitness in environment e for corresponding $x_i(e)$. The population's expected growth rate

765 i.e. eq (2) is now the expectation over $\lambda_i(\varphi_{i,e},\, e) = r_{i,e}x_i(e)$: that is, we shift from an

766 expectation over time to an expectation over possible environments

767 $$\rho_i = E\big[\log \lambda_i(\varphi_e, e)\big] = \sum_e p(e)\log r_{i,e} x(e).$$ (B1.1)

768

769 The latter part of the equation is the definition of an expected value.

770

771 When populations are uninformed then $x_i(e)$ may take on one of several statistical

772 distributions to represent a lack information. For example, in our simulations in the main

773 text we use the uniform distribution and $x_i(e) \sim U(0,1)$; here, we leave this unspecified to

774 follow the original derivation of the FVOI (Donaldson-Matsci et al. 2010). When

775 populations use information then we write this as a conditional probability $x_i(e)(e|c)$ with

776 $r_{i,e}$, defining the conditional phenotype $\varphi_{i,e|c}$. This simple model provides a foundational

777 understanding of $\Delta\rho_i$ that can be extended and generalized. In probability theory, it is

778 the starting place to derive optimality theorems like the Kelly criterion (Cover & Thomas

779 2006). ρ_i has been plotted for the model with $x_i(e \sim U)$ and $x_i(e|c)$ in Figure 2. Applying eq

780 (3) to this model

781 $$\Delta\rho_i = E\big[\log \lambda_i(\varphi_{i,e|c}, e|c)\big] - E\big[\log \lambda_i(\varphi_{i,e}, e)\big] =$$

782 $$\sum_c p(c)\sum_e p(e|c)\log\left[r_{i,e}x_i(e|c)\right]-\sum_e p(e)\log\left[r_{i,e}x_i(e)\right] \qquad \text{(B1.2)}$$

783 The summations and new probability terms ($p(e)$, $p(c)$, and $p(e|c)$) emerge from the

784 expectation. This can be simplifed by factoring $r_{i,e}$ from log-products and using the fact

785 that $\sum_c p(e|c)=p(e)$ to ultimately remove $r_{i,e}$

786 $$\Delta\rho_i=\sum_c p(c)\sum_e p(e|c)\log x_i(e|c)-\sum_e p(e)\log x_i(e) \qquad \text{(B1.3)}$$

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

788 $$\sum_e p(e)\log x_i(e)=\sum_e p(e)\log x_i(e)+\sum_e p(e)\log p(e)-\sum_e p(e)\log p(e)= \qquad \text{(B1.4)}$$

789 $$H(E)-D_{KL}(p(e)\|x_i(e))$$

790 The expression $H(E)=\sum_e p(e)\log p(e)$ is the Shannon entropy of the environment. The

791 first and last terms combined give $\sum_e p(e)\log p(e)-\sum_e p(e)\log x_i(e)=D_{KL}(p(e)\|x_i(e))$,

792 the Kullback-Liebler (KL) divergence between the two distributions $p(e)$ and $x_i(e)$. $H(E)$

793 describes the "information entropy" or the inherent unpredictability of the environment;

794 lower values mean that the environment is more predictable ($H(E) = 0$ in a constant

795 environment). The KL divergence quantifies how different $x_i(e)$ is from $p(e)$; when $x_i(e)$

796 = $p(e)$ the divergence is 0. In the current context it indicates how close a population has

797 come to adopting the optimal strategy.

798

799 The analogous terms exist for the conditional probabilities: the first part of eq (B1.2),

800 and (B1.3) lead to $H(E|C)$ and $D_{KL}(p(e|c) \| x_i(e|c))$, the analogous conditional versions of

801 the entropy and KL divergence. Each of these terms have similar conceptual

802 interpretations as well. These combine to give the general expression

803 $$\Delta\rho_i=H(E)-H(E|C)-D_{KL}(p(e)\|x_i(e))-D_{KL}(p(e|c)\|x_i(e|c)) = \qquad \text{(B1.4)}$$

804 $$I(E;C)-D_{KL}(p(e)\|x_i(e))-D_{KL}(p(e|c)\|x_i(e|c))$$

805

806 We have used the definition of mutual information (MI) to replace the entropies. The MI

807 measures much information is gained by a sequence with knowledge of another

808 sequence (Cover & Thomas 2006). Here, $I(E;C)$ quantifies the gain in information about

809 the environment from the cue (Figure 2C). If populations have optimal strategies then x_i

810 (e) = $p(e)$, $x_i(e|c) = p(e|c)$ and $D_{KL}(p(e) \| x_i(e)) = D_{KL}(p(e|c) \| x_i(e|c)) = 0$ and

811

812 $$\Delta\rho_i=H(E)-H(E|C)=I(E;C) \qquad \text{(B1.5)}$$

813

814 That is, the maximum FVOI is the MI between cue and environment. This upper bound

815 on MI (i.e. $\Delta\rho \le I(E;C)$) has been rigorously demonstrated (Donaldson-Matasci et al.

816 2010; Rivoire & Leibler 2011).

817

818 Box 2. Community dynamics models with information

819 Here we present two mathematical models of community dynamics that are influenced
820 by the availability of information. The first model is an example of demographic
821 information response, created by extending a classic stochastic model of dormancy to
822 include the potential for emergence in response to environmental cues; in the
823 community context, a new version of the lottery model is recovered. We then review a
824 deterministic model of social information response developed as an extension of classic
825 Lotka-Volterra competitive dynamics to include information-driven feedbacks.
826

1. Competition with fluctuating environmental cues

828 Environmental conditions can vary substantially, often outside the range of what
829 organisms can tolerate for survival or reproduction. In such conditions, persistence
830 requires that life history events align with favorable conditions, while also allowing
831 organisms to weather unfavorable conditions, sometimes across multiple generations.
832 For example, desert annual plants have long lived dormant seeds that survive many
833 generations. Under appropriate conditions seeds germinate, grow, and become adults
834 that produce new seeds within a single season. A common models for this kind of
835 population dynamic is the stochastic difference equation (Cohen 1966; Ellner 1997)
836

837 $$N_i(t+1) = \left[g_i F_i(t, R_i \dots R_n N_n) + (1 - g_i) s_i \right] N_i(t) \tag{B2.1}$$

838

839 Where s_i is the survival of seeds in the seedbank, g_i is the percentage of l seeds
840 germinating, F_i is total per-capita reproduction in year t that incorporates a species' own
841 reproductive rate R_i and possibly competitors $R_j N_j$, The reproductive fitness F_i is a
842 random variable with an underlying distribution. A common form of F_i with competition is
843

844 $$F_i(t, R_i \dots R_n N_n) = \frac{R_i}{\sum_{j=1}^{n} R_j N_j} \tag{B2.2}$$

845

846 This is the lottery model, where species "win" resources in proportion to their total
847 reproductive output each generation (Chesson & Warner 1981; Ellner 1987) (we refer to
848 the competition-independent model with $F_i = R_i(t)$ as the dormancy model).
849

850 To incorporate information use, allow g_i to vary in time: define $g_i(E(t))$ for germination as
851 a function of a varying environment (we subsequently drop the t from notation). When
852 organisms perfectly detect and immediately act on information about the environment,
853 then they germinate in ideal proportions to match the fitness benefits of the
854 environment. We use conditional probabilities $g_i(E|C)$ to capture how well an organism
855 detects and responds to the cue C. When organisms are unable to detect the
856 environment (or a delayed response prevents it from syncing), then g_i varies uniformly

857   between 0 and 1. An example realization of these dynamics is given in Figure 2.
858

2. Competition with social information feedbacks

860   The Lotka-Volterra competition model can be adapted to allow species to use social
861   information to reduce mortality rates, e.g. by avoiding predation. Density of individuals
862   (either conspecifics or heterospecifics) reduces mortality from predation (Gil et al.
863   2019).

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

865   The N_i are species densities, r_i are intrinsic growth rates, α_{ij} are inter- ($i \neq j$) and
866   intraspecific ($i = j$) competition coefficients, and $B_i(N_i \dots N_n)$, denotes the mortality rate.
867   Classically, $B_i(N_i \dots N_n)$ is constant and corresponds with any process that reduces
868   survival. Motivated by a biological example where increasing densities of individuals
869   might promote survival by a reduction in predation via shared alarm calls or other
870   behaviors, Gil et al. (2019) adapted $B_i(N_i \dots N_n)$ to incorporate an effect of social
871   information by defining $B_i(N_i \dots N_n)$ with negative exponential functions, such that mortality
872   rates decrease as conspecific density increases.
873

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

875

876   Here, b_{ij} are interaction coefficients which describe the rates at which hetero- or
877   conspecific densities produce usable information. The $p_{s,i}$ define a proportionate effect
878   of social information, and $p_{m,i}$ a minimum effect. When there is no social information b_{ij}=
879   0 and (4) reduces to a constant: $B_i(N_i \dots N_n) = p_{s,i} + p_{m,i}$. A comparison of the growth rates
880   and equilibrium dynamics of the model with and without information for two competing
881   species is plotted in Figure 4.
882
883

884 Figures
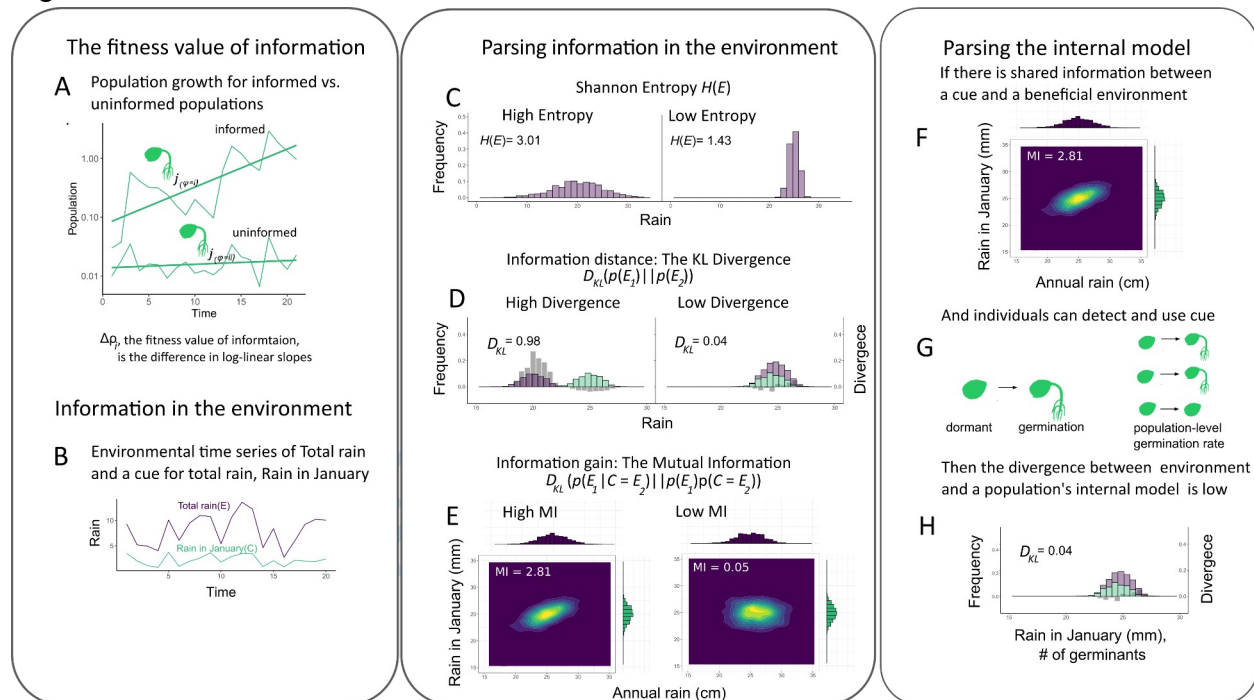
885 Figure 1. Conceptual layout of the fitness value of information (FVOI): see Box 1 for
886 more details. (A) Populations recover from low density more quickly when information is
887 present and they have an internal model of the frequency of favorable environments.
888 The FVOI ($\Delta\rho_i$) is measured as the difference between informed and uninformed
889 population (log) growth rates. (B) Patterns of environmental variation may serve as a
890 cue for favorable environments, as when the amount of early-season precipitation (e.g.
891 in January) signals the total amount of rain that will fall during the growing season. (C-E)
892 The FVOI framework parses the information in the environment using information-
893 theoretic metrics, using frequency distributions of environmental patterns. (C) The
894 Shannon Entropy measures the "surprisal" of a single variable. (D) The Kullback-Leibler
895 (KL) divergence provides a measure of how different two variables are in their
896 distribution (a statistical distance); bin-by-bin differences in the two variables are
897 pictured as dark gray bars. (E) Information gained by one variable from observing a
898 different variable is measured by the mutual information (MI). Surface plots show the
899 join probability distribution of two variables, whose individual (marginal) probabilities are
900 shown along the edges. (F-H) The FVOI parses the population's internal model using
901 the same information theoretic metrics. (F) Populations can exploit MI between two
902 variables by treating one variable as a cue. (G) In this example, high MI produces a
903 reliable cue used by seeds of an annual plant species to initiate germination. (H) How
904 efficiently a population uses this information can be measured by comparing the
905 population-level proportion of germinants in each environment against the actual
906 distribution of environments. Then, $\Delta\rho_i$ is the difference between the MI (F) and the KL
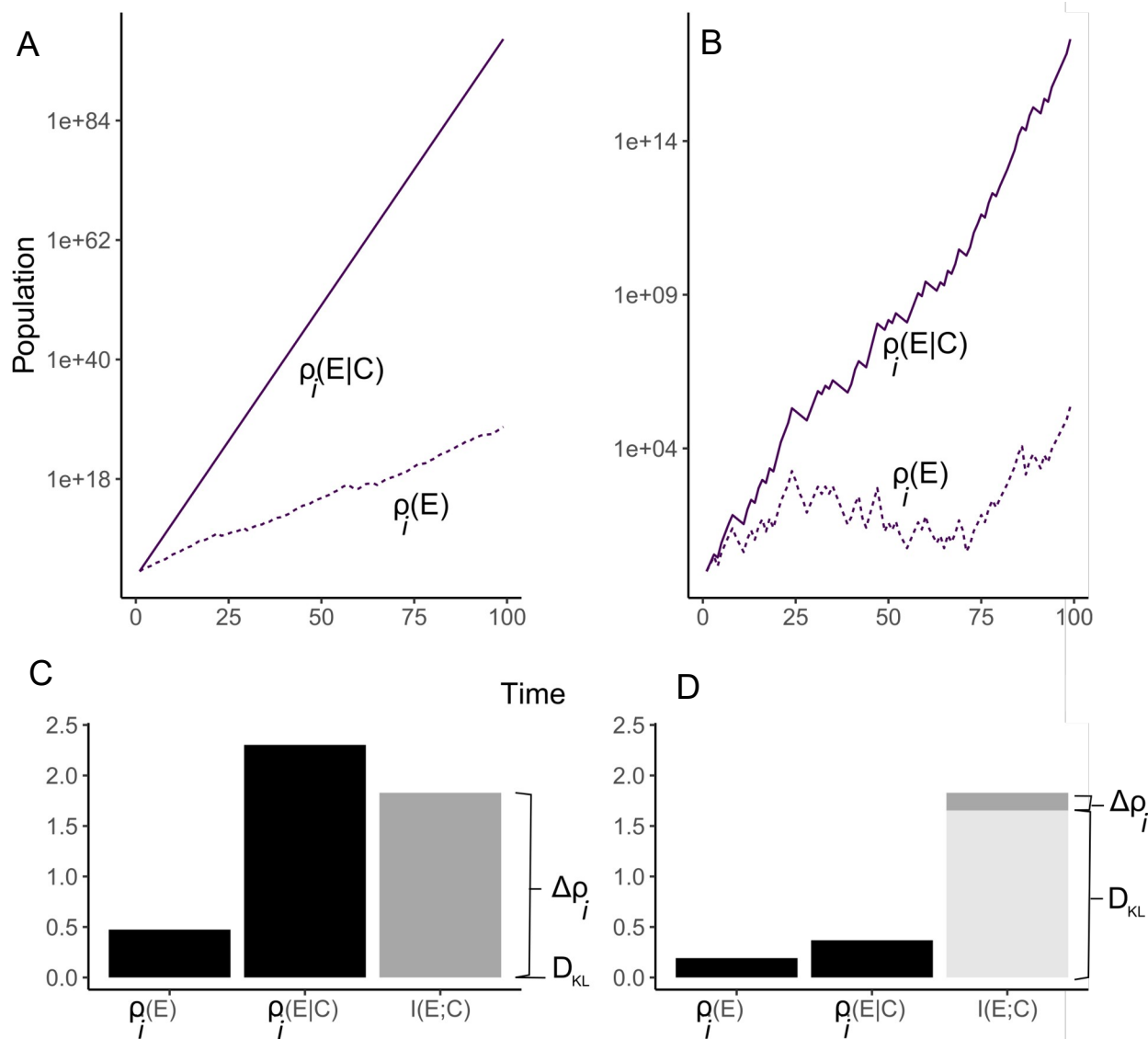907 divergence of environment and internal model (H).

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 $\rho_i(E)$, versus when it uses an environmental cue for information $\rho_i(E|C)$ (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 $\rho_i(E)$ and $\rho_i(E|C)$ are shown in C and D for each model. The fitness value of information is measured by the difference between the two slopes $\Delta\rho_i$. 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.
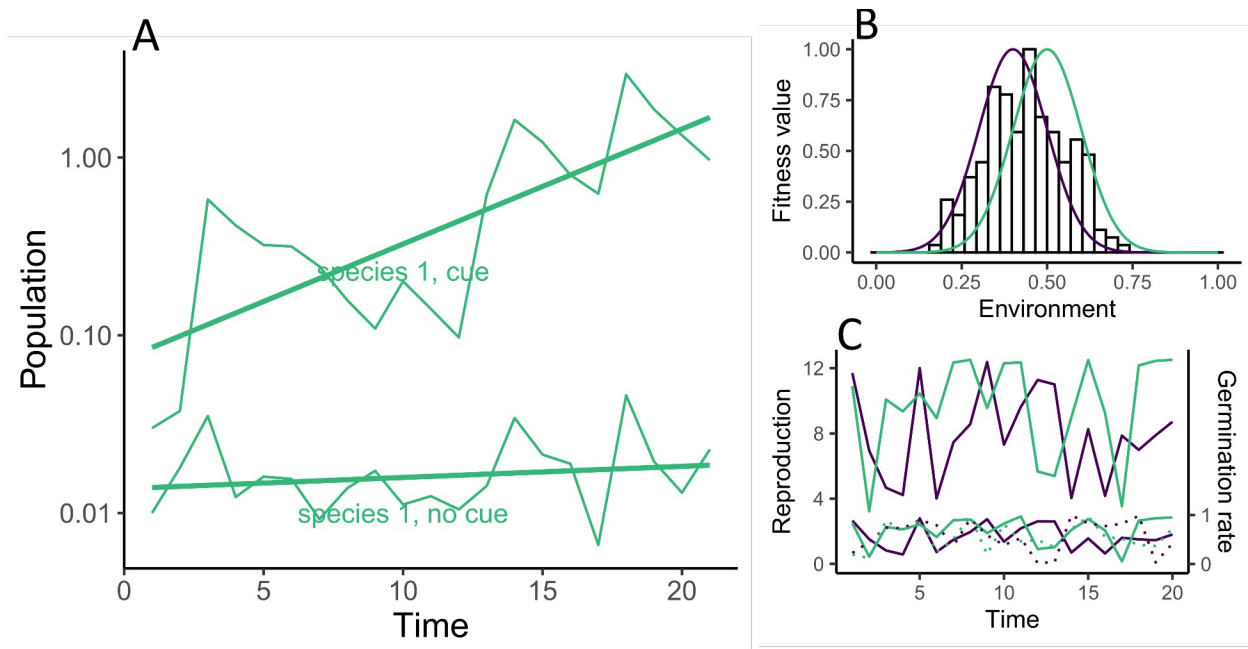
922
923 Figure 3. The dynamics of the lottery model (A) for a population of species 1 (shown in
924 green) in the presence of a competitor (not pictured in A, in purple) with and without the
925 ability to detect an environmental cue that helps it predict favorable environmental
926 conditions for germination (see Box 2 for model description). (B) The environment is
927 simulated by taking draws from a normal distribution to set the conditions for each time
928 step, without autocorrelation ($\mu = 0.5$ and $\sigma = 0.1$, B). Each species (green and purple
929 lines) has a different optimum environment modeled as Gaussian curves so that
930 reproductive fitness decays with the distance of an environmental state from the
931 optimum. (C) The varying environmental state, reproduction, and germination rates are
932 simulated as a time series. When germiation is informed (because $\rho_i(E|C)$ is high) then
933 germination rates match closely to the reproduction rates in that year, as seen in the
934 solid germination lines. When germination is not informed then there is no correlation
935 between germination rates and reproduction; this is seen by comparing the dotted
936 germination lines to the reproduction rates.   See the Supporting Information for
937 simulation code.
938
939

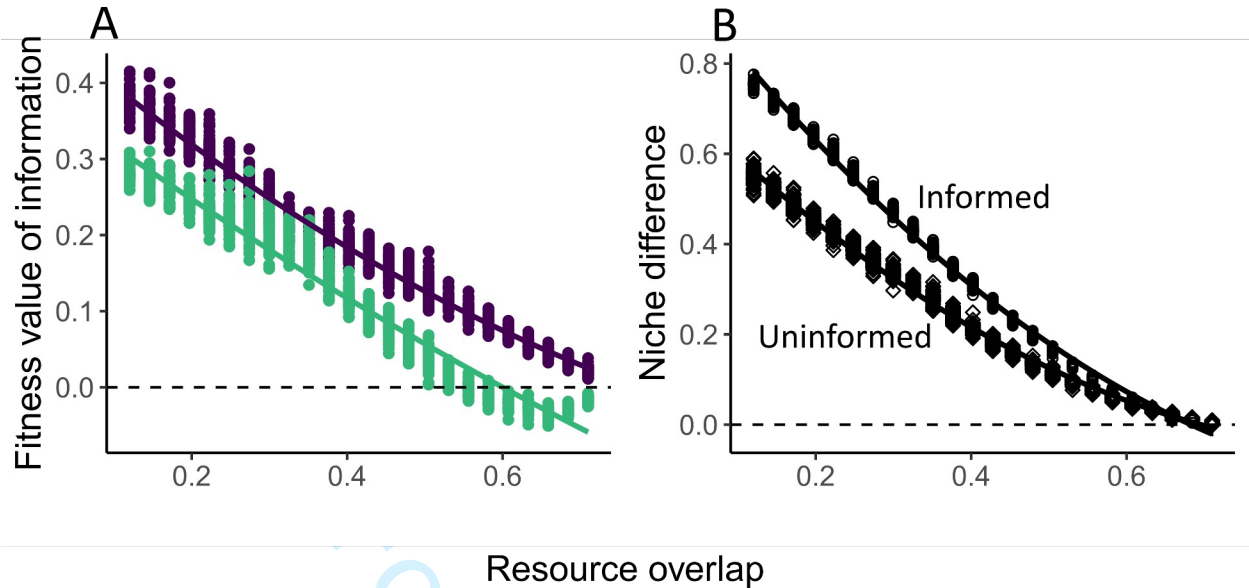26   ,26

Figure 4. The change in the fitness value of information for two species (one green, 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 $\Delta\rho_i$ for each species decreases when competition for resources increases. (B) The niche difference between the two species when both species use information, or when both species are uninformed (i.e. $\rho_i(E|C)$ and $\rho_i(E)$) as labelled. A niche difference of 1 corresponds with 100% differentiation.
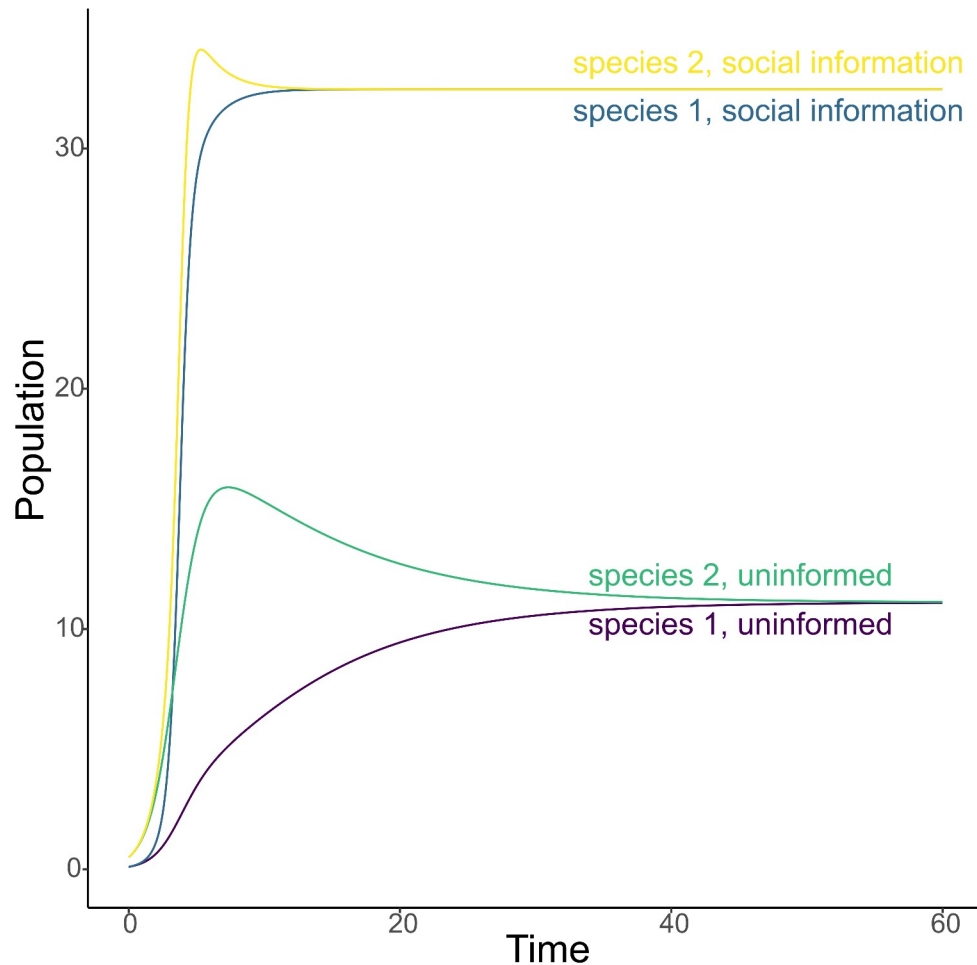
Figure 5. The population dynamics of the competition model with social information, with (upper lines) and without (lower lines) social information.

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