

1 **Rapid evolution slows extinctions in food webs**

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14 Online Appendix A: Effects of species richness

15 Online Appendix B: Results from ‘standing variation only’ regime

16 Online Appendix C: Cost of trait variation

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24 **Abstract**

25 Historically, evolutionary changes have been thought to act on much longer time scales than ecological
26 dynamics. However, a recent body of research has demonstrated that evolution that is rapid enough to
27 dramatically affect ecological dynamics can lead to feedbacks between ecological and evolutionary
28 processes. Thus, to understand the stability of ecological communities, we must also consider
29 evolutionary change in the component species. Here, we use individual-based simulations of a
30 quantitative genetic eco-evolutionary model to describe how trait evolution influences the stability of
31 ecological communities. On short time scales, faster evolutionary rates decreased the probability of
32 species extinctions as populations at low densities were rescued via trait evolution. However, on longer
33 time scales, evolutionary had little effect on the number of extinctions. The extent of short-term
34 evolutionary rescue depended on the source of trait variation; populations with variation generated
35 through mutation experienced more rescue events and were less prone to extinction, relative to
36 populations with only standing trait variation. Trait evolution leading to more rescued populations
37 increased the stability of the community on timescales relevant to conservation. Our work highlights
38 the importance of intraspecific trait variation and the evolutionary mechanisms maintaining this
39 variation for community ecology, as well as management of declining populations in a community
40 context.

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45 **Introduction**

46 While ecology and evolutionary biology each play central roles in our understanding of patterns of
47 biological diversity, many ideas in these fields have developed independently. The time scales at which
48 ecological processes and trait evolution operate have long been thought to be distinct, with ecological
49 changes occurring over significantly shorter periods than evolutionary changes. However, recent work
50 has made great strides in understanding how the conflation of these timescales affects both ecological
51 and evolutionary dynamics. Rapid, contemporary evolution can affect ecological processes, such as
52 population dynamics (e.g., Hairston et al. 2005; Turcotte et al. 2011), species interactions (e.g., Post
53 and Palkovacs 2009; terHorst et al. 2010; Schreiber et al. 2011; Vasseur et al. 2011; Becks et al. 2012;
54 Hiltunen et al. 2014; Patel & Schreiber 2015), community assembly (Pantel et al. 2015), and
55 ecosystem function (Bassar et al. 2010; Miner et al. 2012; terHorst et al. 2014). In addition to our
56 understanding of ecological processes, rapid evolution can have important conservation implications,
57 as it may lead to evolutionary rescue, whereby a population is able to rebound from low population
58 sizes following a change in the environment through changes in genotype frequencies (Lynch and
59 Lande 1993; Gomulkiewicz and Holt 1995; Gonzalez et al. 2013; Carlson et al. 2014; Orr and
60 Unckless 2014).

61 Rapid evolution and evolutionary rescue require intraspecific trait variation to provide the opportunity
62 for evolution to occur within populations (Bolnick et al. 2011). In a closed population, the amount of
63 variation subject to selection at any given time is a result of the standing genetic variation, with
64 additional mutational input over time (Hermisson and Pennings 2005; Orr and Unckless 2014). If
65 evolutionary change is dependent on waiting for rare mutations to arise, then it may be less likely to
66 affect ecological outcomes over shorter time scales. In contrast, evolution can act on standing trait
67 variation immediately. As such, many experimental eco-evolutionary studies have focused on trait

68 evolution on standing variation (e.g., Hendry and Kinnison 1999; Reznick and Ghalambor 2001). Trait
69 variation may also have ecological effects independent of evolutionary change, as more variable
70 interactions can significantly alter the mean strength and outcomes of ecological interactions (Bolnick
71 et al. 2011).

72 Consumer-resource interactions are a fundamentally important interaction in ecology, as they dictate
73 energy flow through ecosystems (Begon et al. 2006; Estes et al. 2011). In natural communities, species
74 are embedded in multispecies food webs of consumer-resource interactions (McCann 2011). These
75 interactions can be complex and lead to both direct and indirect effects due to regularly observed
76 phenomena such as omnivory (Pimm and Lawton 1978; Kratina et al. 2012) and intraguild predation
77 (Polis et al. 1989; Arim and Marquet, 2004). The combination of these direct and indirect effects are
78 important ecologically (Strauss 1991; Wootton 1994; Miller and terHorst 2012), but can also have
79 important evolutionary consequences (Miller and Travis 1996; Walsh and Reznick 2008; Walsh 2013;
80 Patel and Schreiber 2015; terHorst 2010; terHorst et al. 2015), resulting in complex evolutionary
81 dynamics in multispecies communities.

82 How the complexity that arises from multiple species interactions affects the stability of those
83 communities has been the subject of debate in ecology for decades (Pimm 1991; McCann 2000). The
84 thought that diversity should stabilize communities, proposed by early ecologists (MacArthur 1955;
85 Elton 1958) was challenged by May (1974), who demonstrated mathematically that increases in
86 diversity result in a decreased likelihood of local stability in randomly interacting communities.
87 Analogous stability criteria have since been described for a variety of more realistic ecological
88 interaction structures (Allesina and Tang 2012). Ecologists have also investigated how trait variation
89 and evolution affect ecological stability. Kondoh (2003) found that predators who behaviorally alter
90 their foraging patterns to match an optimal niche increase species diversity and stabilize communities.

91 This result echoes the early ideas that more diverse communities can be buffered through prey
92 switching (MacArthur 1955; Elton 1958).

93 Here, we move beyond plastic changes in traits, such as behavioral modification, to investigate
94 whether rapid trait evolution can have similar stabilizing effects in diverse ecological communities. We
95 are particularly interested in whether rapid trait evolution can confer stability to communities through
96 evolutionary rescue. While previous discussions of evolutionary rescue have focused on shifts in the
97 abiotic environment (e.g., Bell 2013), we are interested in scenarios where populations can be
98 evolutionarily rescued following changes in the community composition (Kovach-Orr and Fussman
99 2013; Yamamichi and Miner 2015). For example, prey that are driven to low densities by predators
100 may recover because of ecological feedbacks that lead to predator-prey oscillations. Alternatively, prey
101 populations may adapt in response to strong selection by predation pressure, and the surviving resistant
102 genotypes increase the prey population size.

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104 We built a stochastic, individual-based simulation model to study how the ecological and evolutionary
105 effects of intraspecific trait variation influence stability in food web communities. We found that trait
106 evolution stabilized these food web communities by slowing the rate of species extinctions on short
107 time scales. On longer time scales, however, trait evolution had a less pronounced effect on the number
108 of extinctions. A key mechanism underlying this increase in this transient increase persistence is
109 population rescue via trait evolution. We did not find strong effects of species richness on the
110 evolutionary effect on food web stability. Further, we found that this evolutionary stabilizing effect on
111 communities relied predominantly upon the novel generation of genetic variation through mutation,
112 rather than selection on preexisting standing variation.

113 **Models and Methods**

114 *The Eco-evolutionary model*

115 To study whether trait evolution confers stability to food web communities, we developed and
116 simulated the dynamics of a stochastic, individual-based eco-evolutionary quantitative genetics model.
117 The model consists of N_B basal species and N_C consumer species. Basal species are autotrophs (i.e., do
118 not need to consume other individuals in order to reproduce), and are assumed to have no intraspecific
119 trait variation, and thus do not evolve in our model. Consumer species, on the other hand, have
120 intraspecific trait variation, and can evolve over time. These species are omnivorous (i.e., can
121 potentially eat both basal and other consumer species), however, cannibalistic interactions are
122 forbidden. Inclusion of cannibalism is beyond the scope of our current study, but we recognize it's
123 potential importance for ecological communities (Fox 1975; Rudolf 2007). While only consumer
124 species are able to evolve in our model, both consumer and basal species exhibit ecological dynamics,
125 and can go extinct.

126 The per-capita birth rate of the i -th basal species is $b(1-R_i/S)$ where b is the maximal per-capita birth
127 rate, R_i is the density of the basal species, and S is the maximal number of occupiable sites available to
128 species i . In the absence of predation, the per-capita death rates of all basal species are a constant d .

129 The attack rate of a consumer individual on a heterospecific individual depends on the trait values of
130 the interacting individuals (Nuismer and Doebeli 2004; Nuismer et al. 2005; Schreiber et al. 2011;
131 Patel and Schreiber 2015). That is, an individual with trait value y attacks an individual with trait value
132 x at the following rate $a(y,x)$:

$$\alpha e^{-\frac{(y-\theta-x)^2}{2\tau^2}}$$

133 where α is the maximum possible attack rate, θ is the optimal difference in trait values that maximizes
134 the attack rate, and τ determines the degree of specialization of the predator (i.e., diet breadth) (fig.
135 1A).

136 To describe the per-capita mortality rates due to consumption and the consumer birth rates, let
137 $y_{i1}, y_{i2}, \dots, y_{iC_i}$ be the trait values of C_i individuals of consumer species i . Then the per-capita mortality
138 rate due to consumption for an individual of consumer species i with trait y is

$$M_i^C(y) = \sum_{\substack{j=1 \\ j \neq i}}^{N_C} \sum_{k=1}^{C_j} a(y, y_{jk}).$$

139 The per-capita mortality rate of an individual of basal species i is:

$$M_i^B = \sum_{j=1}^{N_C} \sum_{k=1}^{C_j} a(x_i, y_{jk})$$

140 where x_i is the trait value for all individuals of basal species i . The birth rate of an individual consumer
141 of species i with trait y is proportional to its consumption rate:

$$B_i(y) = e \sum_{j=1}^{N_R} a(x_j, y) R_j + e \sum_{\substack{j=1 \\ j \neq i}}^{N_C} \sum_{k=1}^{C_j} a(y_{jk}, y)$$

142 where the proportionality constant e corresponds to the conversion efficiency of a consumer. The first
143 term of this sum corresponds to the consumption of basal species, while the second term corresponds
144 to the consumption of heterospecific consumers. When a consumer individual reproduces, it
145 randomly mates with another conspecific individual. The trait value of the offspring is normally

146 distributed around the mean of its parental trait values with mutational variance σ^2 (Slatkin 1970;
147 Lynch & Walsh 1998) (fig. 1B). With higher σ values, populations evolutionarily explore trait space
148 more rapidly.

149 The model corresponds to a continuous-time Markov chain (Norris 1998) where individuals are
150 updated at the previously described rates. That is, over a sufficiently small time interval Δt , the
151 probability of an individual of consumer species i with trait value y giving birth is (approximately)
152 $B_i(y)\Delta t$ and the probability of this individual dying is (approximately) $d\Delta t + M_i^C(y)\Delta t$. The
153 probability of an individual of basal species i giving birth is (approximately) $b(1 - R_i/K)\Delta t$ while the
154 probability of this individual dying is (approximately) $d\Delta t + M_i^R\Delta t$. The limit as Δt goes to zero
155 determines the continuous-time Markov chain. As doing exact simulations with Gillespie's algorithm
156 (Gillespie 1977) is computationally expensive, we use the tau-leaping approach (Cao et al. 2005, 2006)
157 in which one performs simultaneous independent updates for sufficiently small Δt . This method has
158 been proven to approximate the distributional dynamics of the exact simulations (Anderson et al.
159 2011).

160 *Methods*

161 We ran continuous-time, stochastic, individual-based simulations of communities following the model
162 described above. In these simulations, we tracked changes in both population densities and mean trait
163 values through time. We varied the amount of trait variation in the communities to assess the effect of
164 rapid evolution in consumers. Finally, we ran alternative sets of simulations where trait variation is
165 either generated solely through mutation or solely through pre-existing standing variation. In all cases,
166 basal species trait values were fixed through time.

167 *Treatments and replication.* For both trait variation regimes, we simulated eco-evolutionary dynamics

168 of 500 communities with $N_T=20$ (10 consumer and 10 basal species). In all cases, basal species had
169 birth rates $b = 0.25$ and death rates $d = 0.1$, with population carrying capacities of 200 individuals.
170 Consumer attack rate parameters were held constant for all consumer species: $\alpha = 0.001$, $\tau = 0.1$, and θ
171 $= 1$. Consumer species converted consumed prey with efficiency $e = 0.75$ and died at rate $\delta = 0.01$.
172 Each simulation ran for 10,000 time steps. We scaled these time steps to the life expectancy for a
173 typical individual of a basal species, as $(1/d\Delta t)$, resulting in approximately 250 basal species
174 generations per simulation. For each full set of σ^2 values $[0,1.5]$, the initial trait values for all species
175 were independent draws from a uniform distribution on the interval $[0,5]$. We tracked ecological
176 (changes in population densities) and evolutionary (changes in trait values) dynamics for each species
177 in the community (fig. 2). While we primarily focused on communities with total initial richness of N_T
178 $= 20$, we also simulated communities with total species richness ranging over $N_T = \{4, 6, 10, 20\}$ (all
179 with equal numbers of basal N_B and consumer species N_C) and σ^2 in $[0,1.5]$, with 50 replicates for each
180 treatment combination. Each community had initial trait values for the species (both basal and
181 consumer) drawn randomly from a uniform distribution on the interval $[0,5]$. We found little effect of
182 species richness on extinction probability, and no significant interaction with the effects of evolution.
183 These additional results are presented in Appendix A.

184 *Trait variation regimes.* To explore the effect of trait variation σ^2 on community dynamics, we
185 imposed two distinct regimes that determined how trait variation was generated. In the ‘standing
186 variation’ regime, we introduced standing trait variation σ^2 at the beginning of each simulation, and no
187 subsequent trait variation was generated through mutation (i.e., the trait of all offspring is the midpoint
188 of their parental traits). In the ‘mutation only’ regime, we initiated simulations with no initial trait
189 variation, but mutations contributed to trait variation through time. In this ‘mutation only’ regime, all
190 intraspecific trait variation arises via mutation over the course of the simulations. Comparison between

191 these trait variation regimes allows us to determine whether lineage sorting of standing variation or
192 continual mutation and selection contributes more to evolutionary effects on community dynamics
193 (Appendix B).

194 *Extinctions and species persistence.* For both consumer and basal species, we measured stability
195 through species persistence, i.e., the fraction of species persisting throughout the simulations. We
196 measured both the rate of species losses as well as the total number of extinctions at the end of the
197 simulations. The simulation data allowed us not only to determine the number of species extinctions in
198 each community (extent of extinction), but also the timing of these extinction events (dynamics and
199 rate of extinctions). We then compared how trait evolution affects the extent and rate of species
200 extinction by looking at extinction patterns as a function of the mutational variance or initial standing
201 variation (σ^2). We defined the extent of extinction as the proportion of species at the beginning of the
202 simulation that go extinct by the end of the simulation. To quantify the rate of extinction, we calculated
203 the accumulation of extinction events through time and the average time for a community to
204 experience 50% of its eventual extinction events.

205 *Population rescues.* To quantify the effect of trait evolution on consumer population rescues, we
206 counted the number of times a population crossed a threshold density L (fig. 3). Each of these
207 categories (i.e., number of threshold crossings) has a distinct biological interpretation. If a population
208 never crossed the threshold, it means that the population persisted for the entire simulation while never
209 falling to low densities. ('Low' is defined by the threshold density). If a population crossed the
210 threshold density only once, we found that in our simulations the population always went extinct by
211 the end of our simulations. Two crossings of the threshold density indicated that the population fell to
212 low density, but was subsequently rescued and continued to persist to the end of the simulation. This
213 scenario captures the iconic U-shaped population trajectory of evolutionary rescue (Gomulkiewicz and

214 Holt 1995). Three crossings indicated a population was rescued, but then suffered subsequent
215 extinction. More crossings (> 3) indicated multiple rescues from repeated low density, either with
216 eventual persistence (an even number of crossings) or extinction (an odd numbers of crossings). We
217 used a threshold density of $L = 25$ individuals, approximately 10% of typical peak population densities.
218 We calculated the number of threshold crossings from smoothed population trajectory data to ignore
219 small, random changes in population densities using the ‘filter’ function in R. While we quantified the
220 number of threshold crossings, our presentation focuses on the number of rescues (the floor of half of
221 the number of threshold crossings), the biologically more relevant quantity. For each rescue event,
222 then, the population can either persist or subsequently go extinct.

223 *Dynamics of trait variation.* We examined the dynamics of trait variation with two methods. First, we
224 quantified the standard deviation of population trait values for all populations through time for both the
225 mutation only and standing variation regimes. This approach gave a general picture of differences in
226 how trait variation was generated and maintained in the simulated communities. Second, we
227 investigated whether the patterns of intraspecific trait variation correlated with population rescues. To
228 do so, we measured trait variation in populations at the times at which they crossed the low density
229 threshold L . That is, at the time when a population crossed L , we measured the standard deviation in its
230 trait values. All simulations and subsequent data analyses were written and performed in R (R Core
231 Development Team 2014).

232 **Results**

233 *Extinction and persistence*

234 The parameter controlling the rate of trait evolution (σ^2) influenced the dynamics of population
235 extinctions from communities by changing both the rate and extent of species losses (fig. 4). Increasing

236 σ^2 resulted in slowing of the consumer extinction rates (fig. 4B,E). We also tracked the basal
237 extinctions over our simulation (fig. 4A,D). We found that at low σ^2 values, basal extinctions are the
238 highest, with no extinctions occurring at $\sigma^2 > 0.5$. At low σ^2 values (0.1 - 0.2), consumer populations
239 drove basal species extinct, and had the potential to evolve to utilize new basal species, resulting in the
240 continued accumulation of basal extinctions at these low levels of mutational variance (fig. 4B). This
241 decrease in basal extinctions at higher values of σ^2 can be attributed to the decreasing ability of a
242 population to efficiently exploit the basal species when consumer populations have more variable trait
243 values. As σ^2 increases, the average attack rate of each consumer individual decreases (fig. C1). This
244 decrease can be interpreted as a cost of trait variation (Schreiber et al. 2011).

245 As a result, we see that the number of basal species extinctions peaks at low values of σ^2 (0.1), then
246 quickly falls to zero as σ^2 increases (fig. 4D). In contrast, the extent of consumer extinctions is
247 relatively constant with respect to σ^2 (fig. 4E). Figure 4D and 4E show the shifting relationship
248 between σ^2 and the number of extinctions over time. The bottom and top curves in each panel represent
249 the extent of extinction at early and late time points, respectively in the simulations, across a range of
250 σ^2 values. For consumer species, we show that the effect of σ^2 on the extent of extinctions becomes less
251 negative over time (fig. 4E). However, for basal species extinctions continue to accumulate at lower
252 values of σ^2 , leading to extinction peaks at these values of σ^2 (fig. 4D). This peak at $\sigma^2 = 0.1$
253 corresponds to the slight increase in the number of consumer extinctions, and is reflected in the
254 dynamics of total community extinction (fig. 4F).

255 *Population rescues*

256 For any given number of rescues, populations can either persist or eventually go extinct. We found that
257 the number of populations that undergo rescue (2+ crossings) increases with σ^2 , while the number of

258 populations that directly go extinct (one threshold crossing) or persist at high density without falling to
259 low density (zero threshold crossings) decreases with σ^2 (fig. 5A).

260 *Trait variation regimes*

261 In simulations in which trait variation is generated via mutations, the proportion of populations that
262 were rescued one or multiple times increased with σ^2 (fig. 5A). By contrast, in simulations with only
263 standing variation, the proportion of populations that were rescued once increased with σ^2 , but the
264 proportion of multiple rescues (which is close to zero) was relatively unaffected by σ^2 (fig. 5B).

265 Trait variation due to mutations or standing genetic variation differentially affected the proportion of
266 populations that persisted without falling to low density (zero threshold crossings) (fig. 5). With
267 mutational input, the proportion of these persisting populations decreased rapidly at low values of σ^2 ,
268 and then slightly increased at high values of σ^2 . With standing variation only, the proportion of these
269 persisting populations decreased in a linear fashion with increasing σ^2 .

270 *Exhaustion of genetic variation*

271 Mutations generated trait variation throughout the simulations as long as populations persisted, while
272 trait variation was exhausted quickly when initial standing variation was the only source of trait
273 variation (fig. 6A). Mutations generated trait variation to the same level of variation that existed at the
274 beginning of the standing variation regime within 100 time steps (~2.5 basal species generations) at the
275 beginning of the simulations. However, mutations continually renewed this variation, whereas without
276 mutations, the variation was rapidly lost.

277 At times of crossing the threshold density, the standard deviation of trait values was significantly
278 higher for the mutation only regime (fig. 6B). In particular, at the time of secondary rescue events (4+

279 threshold crossings), the trait variation in the standing variation only regime fell to virtually zero (fig.
280 6C). By contrast, the standard deviations in trait values for the ‘mutation only’ regime were
281 approximately equal for all secondary threshold crossings, with slightly lower values at the first
282 crossing. This suggests that before the first threshold crossing, at which point the population is
283 decreasing, mutations had not generated as much variation as later in the simulation. Indeed, with
284 standing variation, the mean time to the first rescue event was significantly lower than the mutation
285 only regime (Mann-Whitney U test, $p < 0.0001$; fig. B1).

286

287 **Discussion**

288 Using individual-based, stochastic simulations of an eco-evolutionary model, we found that rapid trait
289 evolution increases persistence by slowing the rate of species extinctions. The slower pace of
290 extinctions found with increased mutational variance (i.e., evolutionary potential) is a result of
291 evolutionary rescues from low population densities. While the rate of evolution – controlled by the
292 mutational variance parameter σ^2 – does not have a major effect on the number of eventual consumer
293 extinctions in the long term, increased evolution substantially decreases the rate of extinctions on
294 shorter time scales.

295 In the absence of evolution, extinctions occur very rapidly until the community reaches a stable state
296 (fig. 4). If species in a community are unable to evolve, the initial community trait structure will
297 determine which species go extinct. For instance, if the trait values of the initial community result in
298 very low attack rates by a consumer species (no or few prey individuals available), then that population
299 will starve and go extinct. Likewise, a consumer near the optimum on a basal species can rapidly drive
300 the basal species extinct through consumption. This overexploitation can subsequently lead to the

301 consumer species' extinction.

302 At low values of σ^2 , consumers are able to evolve to overexploit basal species and drive them extinct.
303 This overexploitation does not occur at higher mutational variances because the consumer attack rates
304 are spread out among more basal species, allowing each population to maintain growth despite some
305 consumption. Because there is no trait variation in basal species, increasing trait variation in consumer
306 populations means that more consumer individuals are further away from the optimal trait difference
307 from basal species (θ), thereby lowering average attack rates, and generating a fitness load on
308 consumers (fig. C1). The consumers driving basal species extinct leads to an increase in subsequent
309 consumer extinctions, resulting in a slight peak in the extent of consumer extinctions at $\sigma^2 = 0.1$ (fig.
310 4E).

311 With trait variation, consumer species are able to evolve to consume new species if they drive one
312 extinct. This can particularly be seen in basal species (fig. 4A), where the accumulation of extinctions
313 reaches an approximate equilibrium quickly, while with trait variation, basal extinctions continue to
314 accumulate. An analogous, but less pronounced, pattern is seen in the accumulation of consumer
315 extinctions (fig. 4B). However, as sigma values increase further, the load of trait variation suppresses
316 the ability of consumers to drive prey species extinct (either basal or other consumers). This conclusion
317 is further supported in the 'standing variation only' model, in which there is no mutational input, and
318 therefore across all values of σ^2 , the curves for extinction accumulation level off more quickly (fig.
319 B1). In the case of standing variation only, however, the load of trait variation vanishes because the
320 variation is quickly lost (fig. 6).

321 Our results illustrate two ways that intraspecific trait variation can affect ecological communities. First,
322 trait variation provides an opportunity for evolutionary change. We show that with inputs of trait

323 variation through time, populations are able to avoid extinction through evolutionary change, leading
324 to increased persistence. Second, beyond the opportunity for selection, trait variation can alter
325 ecological interactions strengths, as exemplified by the reduced consumer attack rates at higher values
326 of σ^2 (fig. C1). Our simulations show how these two consequences of intraspecific trait variation can
327 jointly affect community dynamics. This is most clearly demonstrated by the contrast in the number of
328 basal species extinctions at low and high values of mutational variance (fig. 4A,D). These basal
329 extinctions can then affect subsequent extinctions in the community. Populations with the same
330 population trait means can have starkly different interaction strengths, reflecting the fitness load of
331 increased σ^2 (fig. C1; Schreiber et al. 2011). In nature, there is natural variation in many traits
332 measured across taxonomic systems and environments (Lynch and Walsh 1998; Bolnick et al. 2011),
333 and as such, ecologists should consider how trait variation affects species interactions within
334 communities for more realistic predictions for outcomes of species interactions.

335 Introducing mutation and evolution into our simulations has different effects on species extinctions
336 over short and long time scales. On shorter time scales, increasing σ^2 stabilizes communities by
337 slowing extinctions, but has diminishing effect over longer time scales. This difference among time
338 scales of the effect of increasing σ^2 is best illustrated in figure 4F, where the early negative relationship
339 flattens over time. This suggests that early evolutionary and extinction dynamics result in a community
340 structure that is relatively stable in the long term.

341 Extinction and evolution can alter the ecological connectedness in these communities, resulting in
342 novel relationships among community members. In an individual-based population genetic model of
343 predator-prey communities, Yamaguchi et al. (2011) also found that evolution could affect the number
344 of extinctions in communities. In their two-trophic level system, they found that the effects of
345 evolution on extinctions were dependent on the connectivity and genetic architecture. Evolution

346 allowed consumers to change their prey use (i.e., gain or loss of trophic links), which could increase
347 extinctions through altered competitive exclusion dynamics or decrease extinction via escape from
348 competition among predators (Yamaguchi et al. 2011). We also found that evolutionary losses and
349 gains of trophic links affected extinction dynamics, through overexploitation of prey species and
350 evolutionary rescue of declining consumer populations. However, unlike their model, our communities
351 were not strictly two trophic levels. In our model, because consumers can both evolve and eat each
352 other, dynamics of trophic interaction losses and gains are complex. Interestingly, Yamaguchi et al.
353 found that the specifics of the predator's genetic system dictated whether the loss or gain of trophic
354 links affected stability. Assessing the effects of variable genetic systems in our system is a compelling
355 topic for future study (Schreiber et al. 2016).

356

357 *Mechanisms of rescue*

358 Our method of quantifying rescue events as the number of threshold-crossings (fig. 4) does not provide
359 direct information for the mechanisms underlying the rescue events. In the most intuitive rescue
360 scenario, a focal population can be rescued from low density if the trait values of that focal species
361 change such that some individuals are able to survive and reproduce (e.g., evolve to utilize a new prey
362 resource). However, the mechanism of rescue may be indirect. For instance, a competing species could
363 go extinct, or trait evolution in other community members could indirectly allow the focal species to
364 rebound (e.g., Yamamichi and Miner 2015).

365 More simply, the multiple rescue events we found at higher σ^2 values could arise from ecological
366 dynamics in which predators abundances respond to prey abundances and vice versa, such as in
367 predator-prey cycles. In such cases, the density of the 'rescued' consumer population would dip below

368 the threshold density and recover as the basal species recover. However, the difference between the
369 ‘mutation only’ and ‘standing variation’ regimes suggest that this is not the case. If multiple population
370 rescues were driven by ecological dynamics, we would expect those dynamics to continue regardless
371 of the regime of trait variation. In other words, if rescue events were driven purely by these ecological
372 oscillations, we would not expect to see population rescues stop after the exhaustion of genetic
373 variation in the standing variation regime (fig. 5). Comparison of the relationship between number of
374 rescues and σ^2 across the trait variation regimes supports that trait evolution is leading to the rescue
375 events. This suggests that if populations are unable to continue to generate this intraspecific trait
376 variation, they may soon face extinction risk, as they will not be able to be rescued from subsequent
377 declines in density (fig. 6).

378 *Implications for conservation*

379 We find that evolution can substantially slow the rate of extinctions on short time scales, but that it
380 only modestly alters the extent of species loss from communities over longer periods of time. The short
381 time scales over which we observe these strong effects are on the order of ~ 10 basal species
382 generations, and thus relevant for most conservation efforts. The slowed extinction rate we found could
383 provide critical time necessary for secondary ecological or environmental processes to act. In
384 particular, this transient increase in persistence could be important when considering a broader
385 landscape perspective (Thompson 2005). In this study, we have only simulated eco-evolutionary
386 dynamics in a single focal community. We did not examine any effects of immigration or emigration
387 among communities. When considering broader meta-community dynamics (Holyoak et al. 2005;
388 Urban et al. 2008), the increased persistence through evolutionary rescue could have important effects
389 on the maintenance of diversity at a larger scale. The slowed rate of extinction allows for more
390 opportunity for rescue via immigration (Mouquet and Loreau 2002, 2003; Urban et al. 2008). Further,

391 our model ignores other complexities that can alter eco-evolutionary outcomes, such as facilitative
392 interactions (Bruno et al. 2003) and spatiotemporal environmental variation (e.g., Levins 1968;
393 Mouquet and Loreau 2003).

394 Even with only standing genetic variation, we find that intraspecific trait variation is critical for
395 evolutionary rescue of declining populations in the short term. In fact, evolutionary rescues occur
396 significantly faster with standing variation (as opposed to waiting for relevant trait variation to
397 accumulate through mutation) (fig. B2). This points to the maintenance of genetic variation in species
398 of concern as an important aspect of conservation strategy (beyond the maintenance of variation for
399 inbreeding avoidance). This suggests that in species with relatively slow generation times – and
400 therefore reduced opportunity for rapid evolution on ecological timescales -- populations of these
401 species with low variation may need input of variation if they are to be rescued through evolutionary
402 mechanisms (Sgro et al. 2011; van Oppen et al. 2015; Whiteley et al. 2015).

403 *Future directions*

404 Relaxing several assumptions of the current work opens compelling avenues for future research. We
405 studied an abstract trait that governs ecological interactions among species in a food web community.
406 Future work should seek to assign more explicit biological identity to the trait values. For instance, we
407 could treat our trait values as body size, a variable trait that has been shown to determine feeding
408 relationships across a wide breath of taxa and communities (Brose et al. 2006). However, with more
409 explicit assignment of functional traits comes the attendant model complexities that would have to be
410 addressed, such as trait dependent demographic parameters (i.e., rates of metabolism, birth, and death;
411 Brose et al. 2006; Brose 2010).

412 Genetic rescue, as opposed to evolutionary rescue, can occur in declining populations by increasing

413 fitness through the demographic contribution of immigrants. While such input of genetic variation can
414 facilitate declining populations (van Oppen et al. 2015; Whiteley et al. 2015), this will depend on the
415 genetic composition of the immigrants. In particular, when there is evolution in a focal/local
416 community, if the immigrants are arriving from a source community where the selection pressures are
417 not parallel to the local community, the effect of immigrants may have a variety of effects. It is
418 possible that they could allow the population to recover (if the immigrating genetic variants facilitate
419 response); alternatively, if the immigrants are phenotypically more ancestral, this could have the
420 opposite effect of genetic rescue in which the immigrants constrain the evolutionary change, thereby
421 increasing the likelihood of extinction. Further, immigration of basal species individuals could
422 potentially stabilize consumer species that otherwise overexploit the basal species. Such studies of eco-
423 evolutionary meta-community dynamics are compelling avenues for research (Urban et al. 2008; De
424 Meester et al. 2016; Wittmann and Fukami 2016).

425 **Conclusion**

426 We provide evidence that intraspecific trait variation and evolution significantly stabilize diverse
427 ecological food web communities. Our eco-evolutionary simulations revealed that, on short time
428 scales, the decreased extinction risk is a result of trait variation that allows species that have fallen to
429 low density to be rescued via evolutionary changes. These results contribute to our understanding of
430 how rapid evolution can generate patterns in ecological community dynamics that do not occur in the
431 absence of intraspecific variation. Moreover, the slowing of species losses from diverse communities
432 occurs on timescales relevant to conservation and management concerns, further stressing the value of
433 evaluating concurrent ecological and evolutionary processes. Our results support the calls for
434 accounting for intraspecific trait variation found in natural populations, and the resultant capacity for
435 trait variation and rapid evolution to affect important ecological phenomena.

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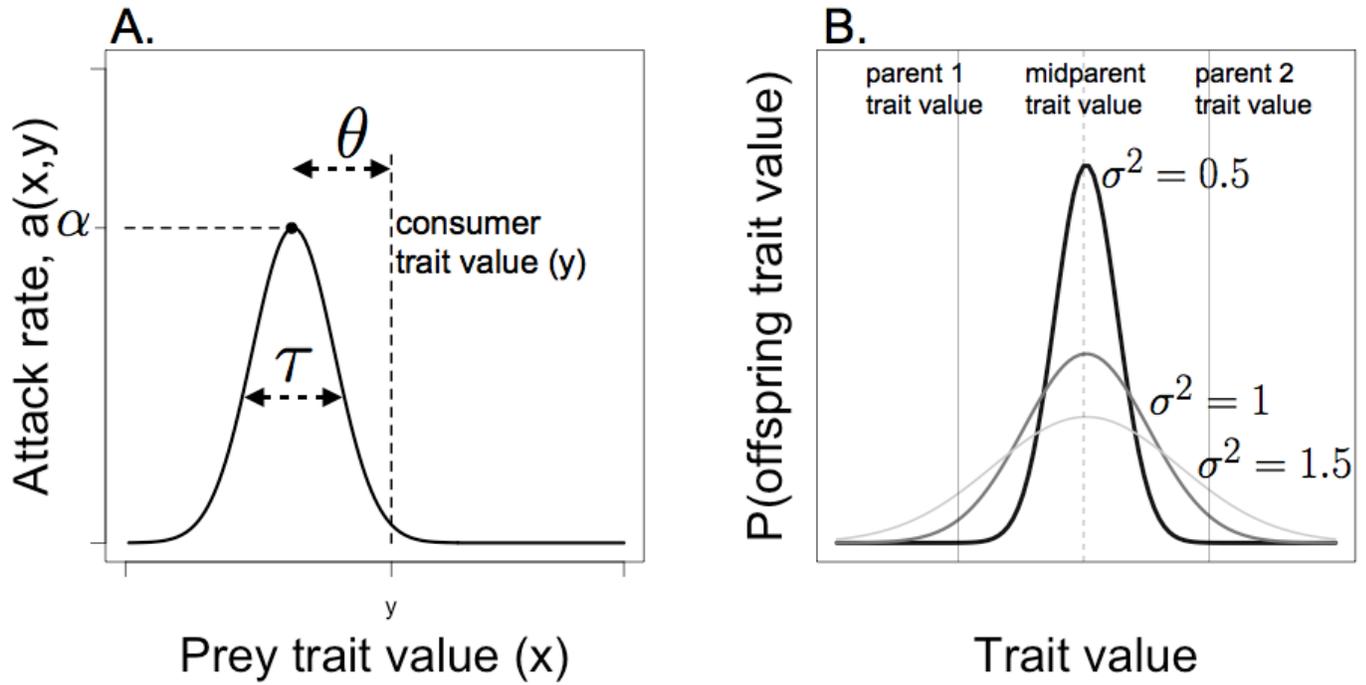
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624 **Figure 1:** Attack rate and reproduction. (A) Attack rate function. (B) Trait values of consumer
625 offspring are given by the deviation from the midparent mean trait value determined by the mutational
626 variance σ^2 .

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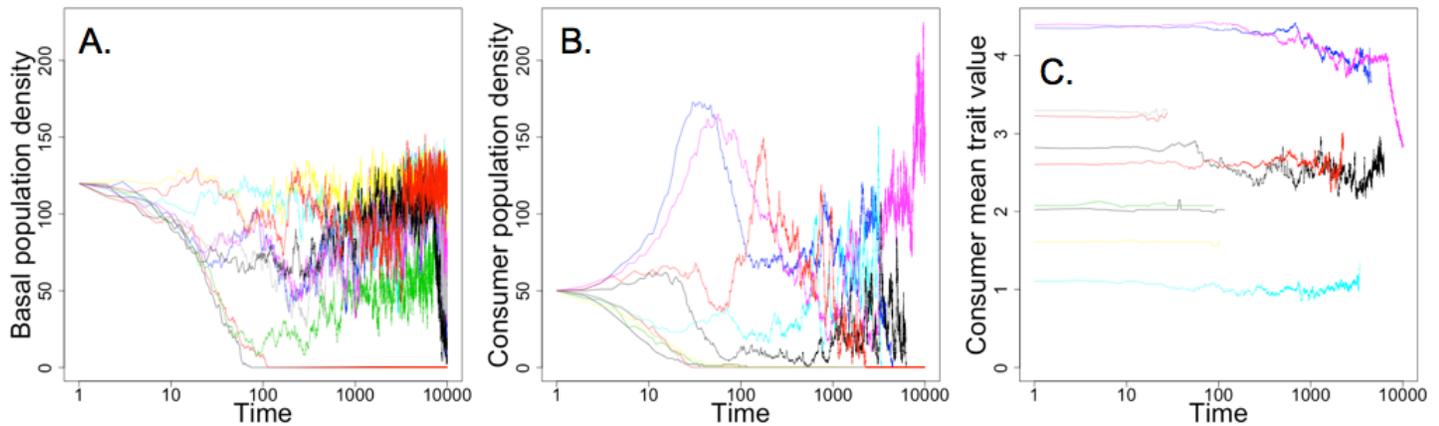
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638 **Figure 2:** Representative ecological and evolutionary dynamics. (A) Ecological dynamics of basal
639 species. (B) Ecological dynamics of consumer species. (C) Consumer trait evolution dynamics. Each
640 curve shows dynamics for one consumer species. For the simulation shown, $\sigma^2 = 0.2$. Note that time
641 (x-axis) is on a log-scale.

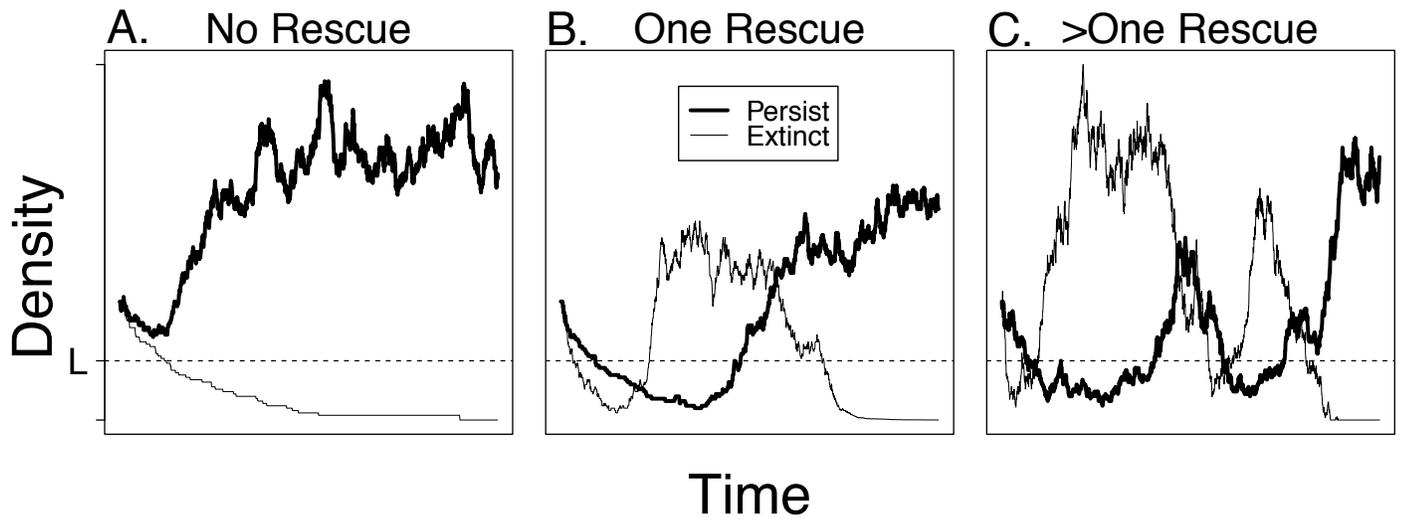
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656 **Figure 3:** Classification of population rescues. Dashed line at L shows the low density threshold for
657 population rescue. Each panel shows a classification of population rescues, with either eventual
658 persistence (dark line) or extinction (light line). (A) No rescues. (B) One rescue. (C) More than one
659 rescue.

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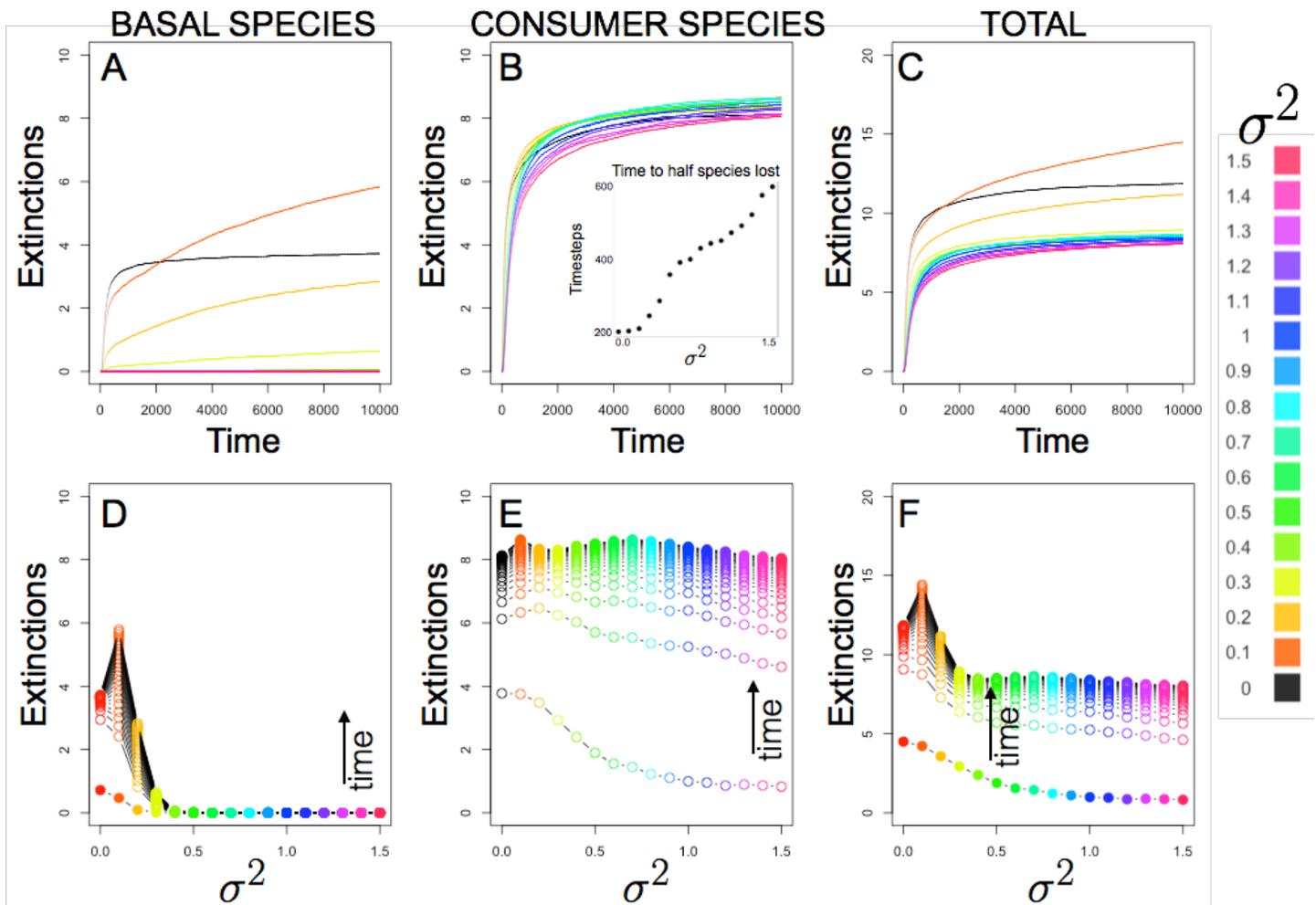


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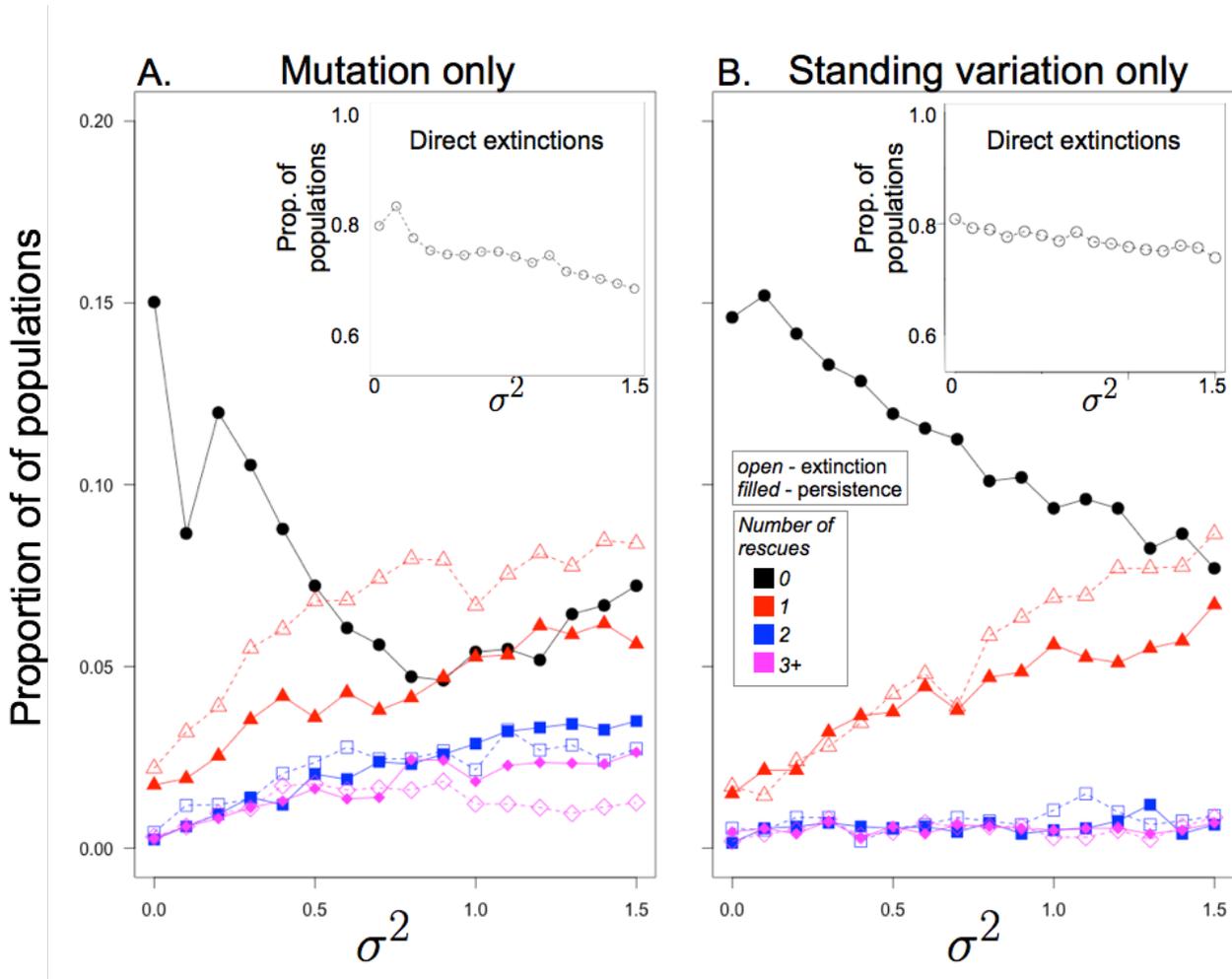
673 **Figure 4:** Extinction dynamics. (A-C) Each curve represents the accumulation of extinctions over time
674 for different values of the mutational variance σ^2 . (D-F) The relationship between basal (B), consumer
675 (C), or species (D) extinctions and σ^2 at different points in time. The uppermost curves in (B)-(D) show
676 the mean number of extinctions at the end of our simulation runs. In all panels, colors represent
677 different values of σ^2 .

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683 **Figure 5:** Evolution increases proportion of populations rescued. (A) Evolutionary effect on rescue
684 under the ‘mutation only’ trait variation regime. Increased mutational variance (σ^2) leads to more
685 trajectories with rescues (and multiple rescues). (B) ‘Standing variation only’ trait variation regime.
686 Here, probability of a trajectory having multiple rescues is not elevated. In both panels, the black
687 points show a decrease in the populations that have zero crossing, i.e., persist at high density. In all
688 cases, closed black circles represent the proportion. Upper panels (open black circles) in all cases show
689 the proportion of populations that directly go extinct (one crossing). Note that the y-axis scales are
690 different for lower and upper panels.
691



692

693 **Figure 6:** Standing variation only regime exhausts trait variation more quickly than mutation only
694 regime. (A) The mean standard deviation of the trait values decreases to zero in the standing variation
695 only regime, but stays level for the mutation only regime. Lower and upper bounds of shaded areas
696 represent the first and third quartiles, respectively. (B) At the time of threshold crossings, there is
697 significantly less intraspecific trait variation in the standing variation only regime (light) compared to
698 the mutation regime (dark). Arrows at top represent whether the populations are increasing or
699 decreasing in density at the time of threshold crossing. (C) Dark (mutation only) and light (standing
700 variation only) bars represent the total number of populations for each regime with each crossing. Note
701 the y-axis of (C) is on logarithmic scale.
702

