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.

Models and Methods

The Eco-evolutionary model

To study whether trait evolution confers stability to food web communities, we developed and

simulated the dynamics of a stochastic, individual-based eco-evolutionary quantitative genetics model.

The model consists of N_B basal species and N_C consumer species. Basal species are autotrophs (i.e., do

not need to consume other individuals in order to reproduce), and are assumed to have no intraspecific

trait variation, and thus do not evolve in our model. Consumer species, on the other hand, have

intraspecific trait variation, and can evolve over time. These species are omnivorous (i.e., can

potentially eat both basal and other consumer species), however, cannibalistic interactions are

forbidden. Inclusion of cannibalism is beyond the scope of our current study, but we recognize it's

potential importance for ecological communities (Fox 1975; Rudolf 2007). While only consumer

species are able to evolve in our model, both consumer and basal species exhibit ecological dynamics,

and can go extinct.

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

rate, R_i is the density of the basal species, and *S* is the maximal number of occupiable sites available to

species *i*. In the absence of predation, the per-capita death rates of all basal species are a constant *d*.

The attack rate of a consumer individual on a hetereospecific individual depends on the trait values of

the interacting individuals (Nuismer and Doebeli 2004; Nuismer et al. 2005; Schreiber et al. 2011;

Patel and Schreiber 2015). That is, an individual with trait value *y* attacks an individual with trait value

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 hetereospecific 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. 1*B*). 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 regime*s. 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   6*C*). 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   extensions (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. 4*A,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 4*F*, 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 though 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.

Acknowledgements

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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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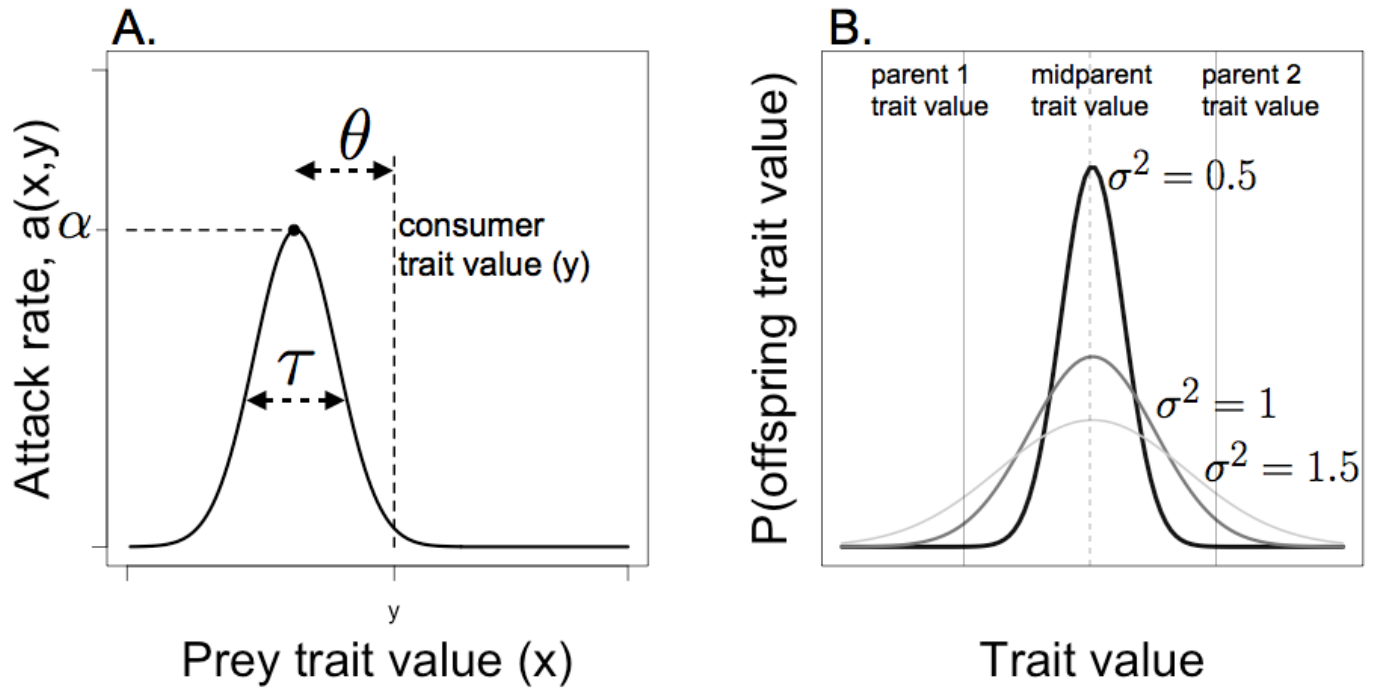
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638   **Figure 2:** Representative ecological and evolutionary dynamics. (A) Ecological dynamics of basal

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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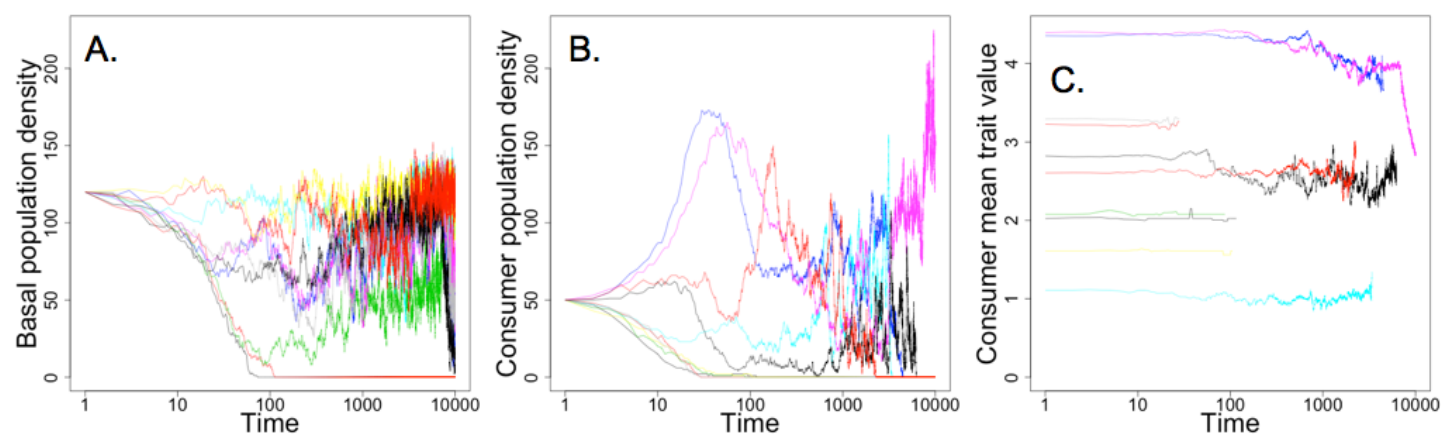
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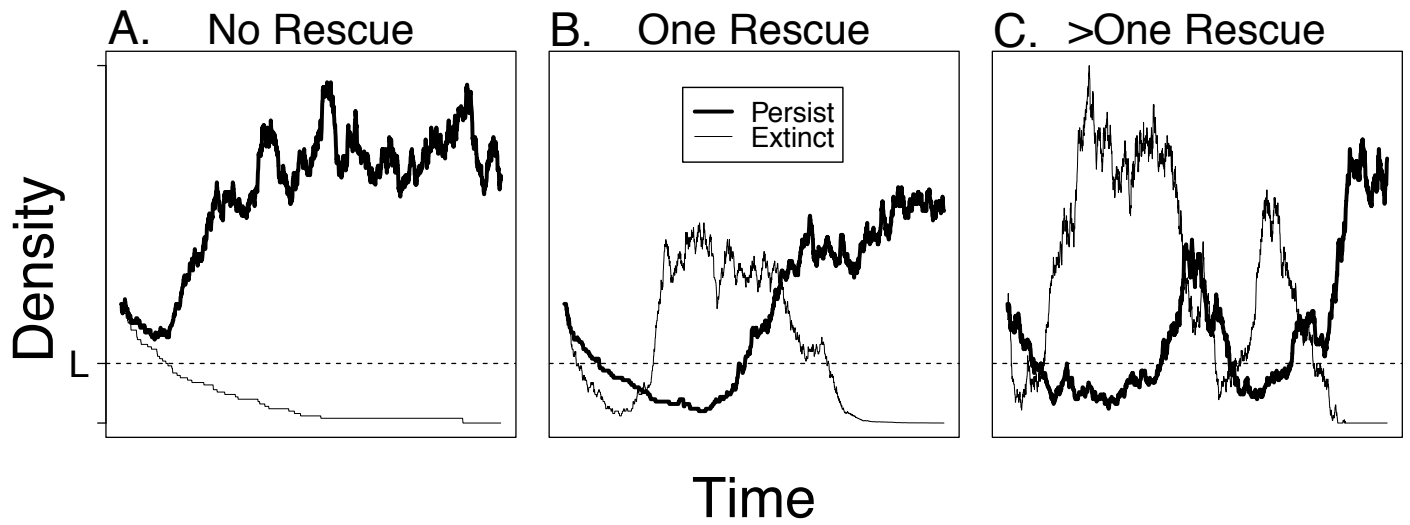
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656   **Figure 3:** Classification of population rescues. Dashed line at *L* shows the low density threshold for

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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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.
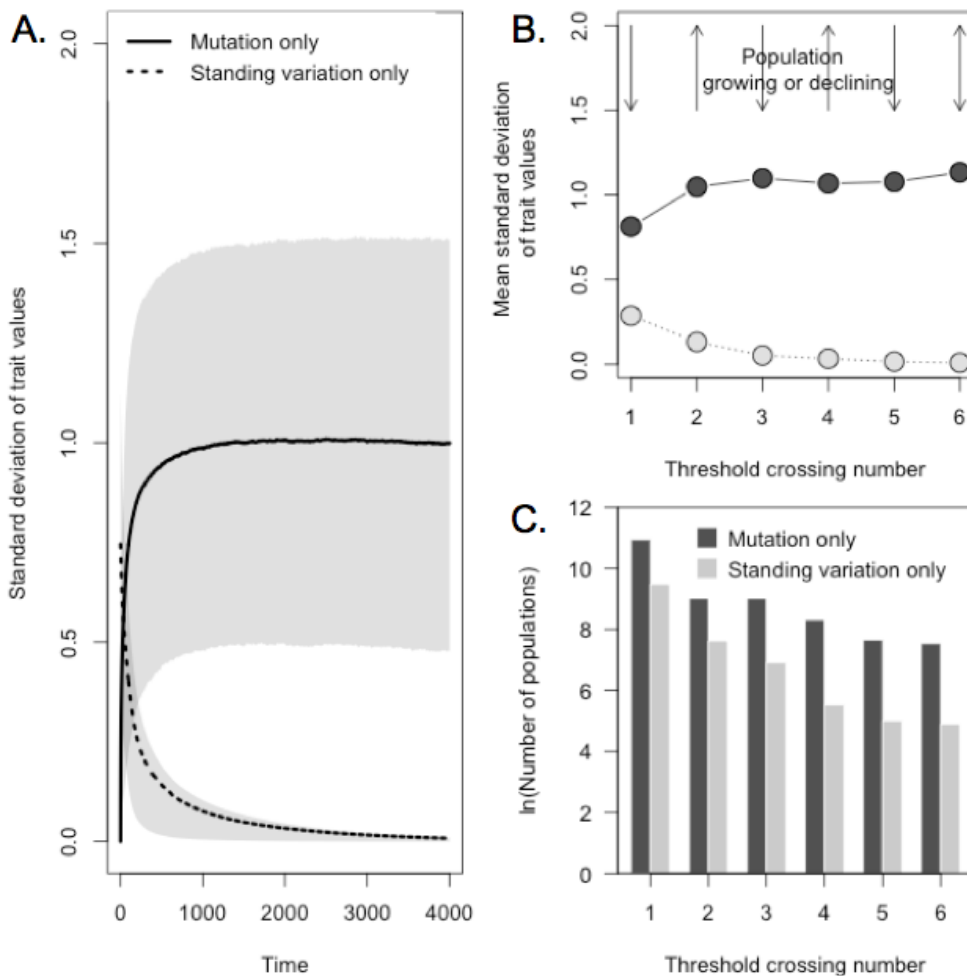
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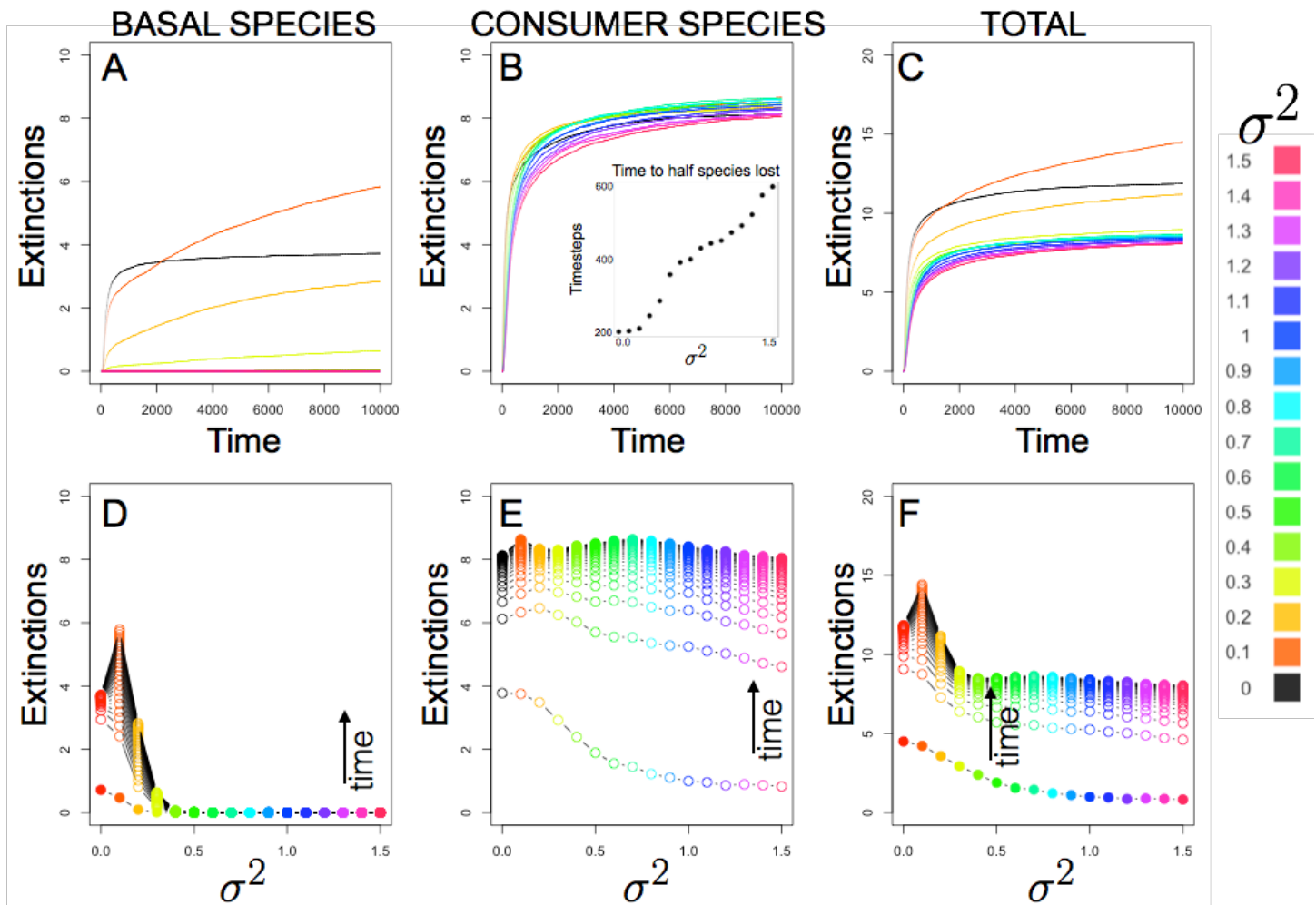
683   **Figure 5:** Evolution increases proportion of populations rescued. (A) Evolutionary effect on rescue

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.

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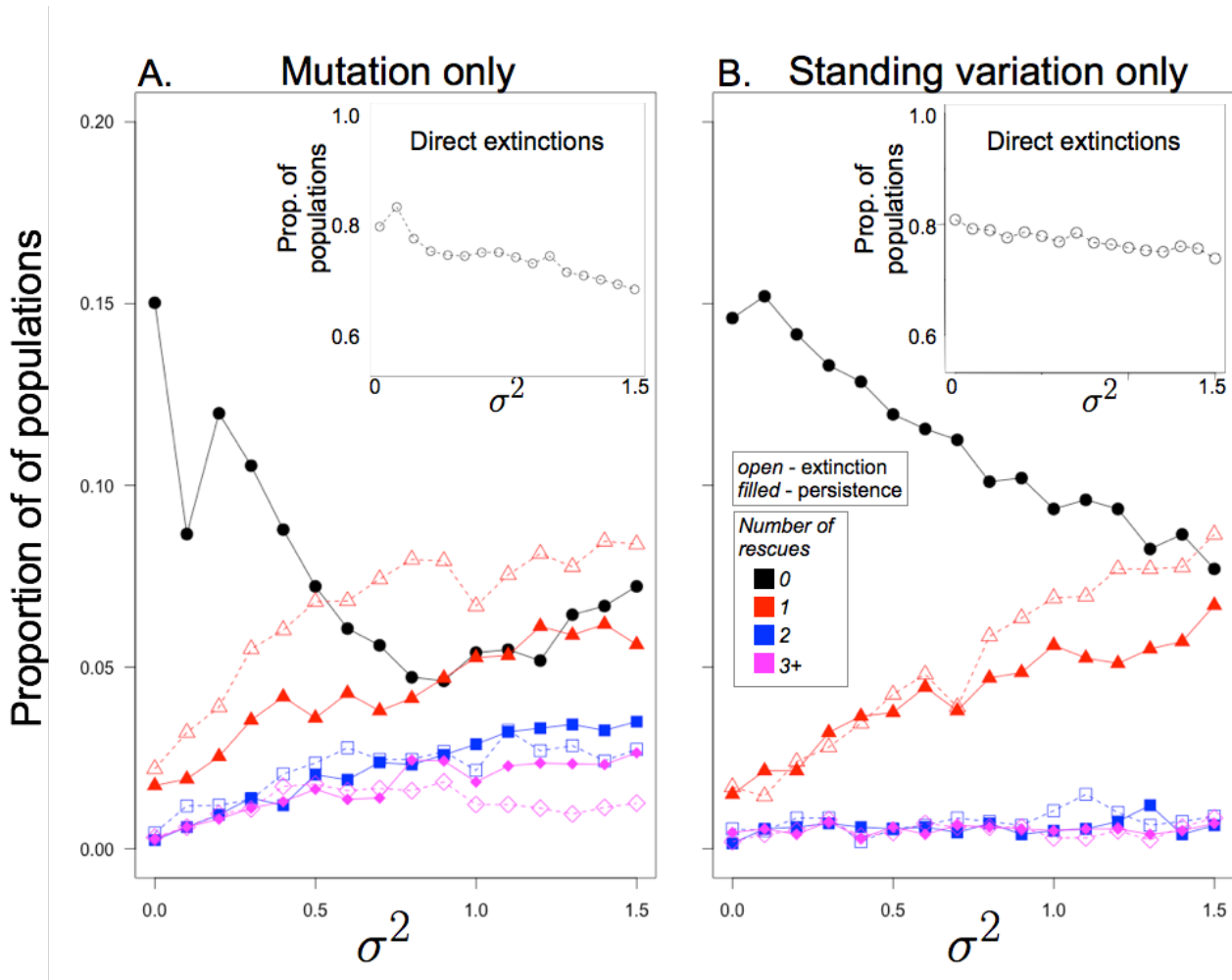
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693 **Figure 6:** Standing variation only regime exhausts trait variation more quickly than mutation only

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.

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