

University of Nebraska - Lincoln

DigitalCommons@University of Nebraska - Lincoln

Faculty Publications in the Biological Sciences

Papers in the Biological Sciences

2023

Ecological boundaries and constraints on viable eco-evolutionary pathways [Pre-print]

Kyle E. Coblenz

University of Nebraska - Lincoln, kyle.coblenz@unl.edu

John DeLong

University of Nebraska-Lincoln, jpdelong@unl.edu

Follow this and additional works at: <https://digitalcommons.unl.edu/bioscifacpub>



Part of the [Biology Commons](#)

Coblenz, Kyle E. and DeLong, John, "Ecological boundaries and constraints on viable eco-evolutionary pathways [Pre-print]" (2023). *Faculty Publications in the Biological Sciences*. 963.

<https://digitalcommons.unl.edu/bioscifacpub/963>

This Article is brought to you for free and open access by the Papers in the Biological Sciences at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Faculty Publications in the Biological Sciences by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

1 **Ecological boundaries and constraints on viable eco-evolutionary pathways**

2 Kyle E. Coblentz^{a,1} and John P. DeLong^{a,2}

3 a: School of Biological Sciences, University of Nebraska—Lincoln, Lincoln, NE 68588

4 1: Email: kyle.coblentz@unl.edu; [ORCID ID: 0000-0002-0069-8491](https://orcid.org/0000-0002-0069-8491)

5 2: Email: jpdelong@unl.edu; [ORCID ID: 0000-0003-0558-8213](https://orcid.org/0000-0003-0558-8213)

6

7 **Ecological boundaries and constraints on viable eco-evolutionary pathways**

8 **Abstract**

9 Evolutionary dynamics are subject to constraints ranging from limitations on what is physically possible
10 to limitations on the pathways that evolution can take. One set of evolutionary constraints, known as
11 ‘demographic constraints’, constrain what can occur evolutionarily due to the population demographic or
12 population dynamical consequences of evolution leading to conditions that make populations susceptible
13 to extinction. These demographic constraints can limit the strength of selection or rates of environmental
14 change populations can experience while remaining extant and the trait values a population can express.
15 Here we further hypothesize that the population demographic and population dynamical consequences of
16 evolution also can constrain the eco-evolutionary pathways that populations can traverse by defining
17 ecological boundaries represented by areas of likely extinction. We illustrate this process using a model of
18 predator evolution. Our results show that the populations that persist over time tend to be those whose
19 eco-evolutionary dynamics have avoided ecological boundaries representing areas of likely extinction due
20 to stochastic deviations from a deterministic eco-evolutionary expectation. We term this subset of
21 persisting pathways viable eco-evolutionary pathways. The potential existence of ecological boundaries
22 constraining evolutionary pathways has important implications for predicting evolutionary dynamics,
23 interpreting past evolution, and understanding the role of stochasticity and ecological constraints on eco-
24 evolutionary dynamics.

25 *Keywords:* Adaptive Landscapes, Demographic Stochasticity, Extinction, Genetic Drift, Natural
26 Selection, Predator-Prey Interactions, Stochasticity

27

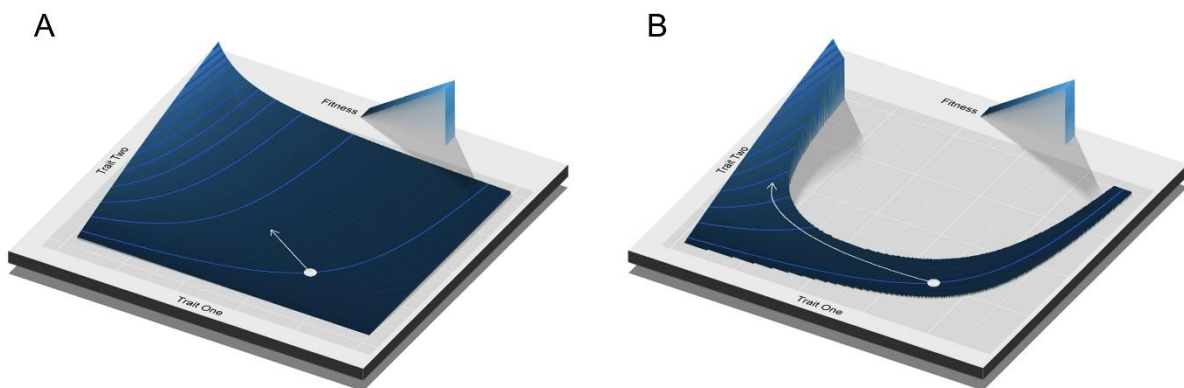
28 **Introduction**

29 A diverse set of processes place constraints on evolution. These constraints occur on multiple levels from
30 genetic constraints that limit evolutionary responses to selection to functional constraints that are due to
31 limits on what is physically or physiologically possible (Arnold 1992, Kempes et al. 2012, 2019).
32 Constraints also can limit the evolutionary pathways that evolution can traverse. For example, pathways
33 in protein evolution can be limited to steps that retain protein function and evolution on genetic adaptive
34 landscapes may have to occur in a manner that avoids ‘holes’ of low fitness on the landscape (Maynard
35 Smith 1970, Gavrilets 1997, Poelwijk et al. 2007). The identification and understanding of these
36 constraints on evolution is powerful because it allows us to narrow the domain over which evolutionary
37 changes can occur.

38 An additional set of constraints on evolution are due to the consequences of evolution on
39 population dynamics or population demography (Gomulkiewicz and Houle 2009, Amarasekare 2022).
40 Population dynamic and demographic consequences of evolution are likely to constrain evolution because
41 these can lead to situations in which populations become susceptible to extinction, even if the underlying
42 genetics makes it physically possible for individuals to function. Therefore, these evolutionary dynamics
43 are inaccessible for populations that are to remain persistent. For example, Gomulkiewicz and Houle
44 (2009) have shown that populations are evolutionarily constrained because overly strong selection or
45 rapid rates of environmental change are likely to lead to extinction. Similarly, a wide range of theoretical
46 models have shown that natural selection can cause populations to evolve in a way that leads to their own
47 extinction either deterministically or by causing populations to reach densities low enough to be
48 susceptible to stochastic extinction in a process known as ‘Darwinian extinction’ or ‘evolutionary suicide’
49 (Matsuda and Abrams 1994, Webb 2003, Rankin and López-Sepulcre 2005, Parvinen and Dieckmann
50 2013). These studies suggest that populations that experience these sorts of selective forces without other
51 sources of evolutionary constraints will not persist. Last, evolution may cause trait changes that lead to
52 the destabilization of systems such as the development predator-prey cycles in which populations can

53 become susceptible to stochastic extinction during the troughs of the cycles (Amarasekare 2022). Thus,
54 evolutionary dynamics may be constrained away from these areas because populations with destabilizing
55 traits are unlikely to persist over time. Altogether, these results suggest that, for populations that are to
56 remain persistent, evolutionary dynamics may be constrained such that the demographic and population
57 dynamic consequences of evolution do not lead to extinction.

58 Here we further this idea by developing the hypothesis that the demographic consequences of
59 evolution also create ecological boundaries that constrain the eco-evolutionary pathways that populations
60 can traverse. To illustrate this, imagine a population evolving on an adaptive landscape portraying fitness
61 as a function of phenotypic trait values (Wright 1932, Simpson 1944, Svensson and Calsbeek 2013;
62 Figure 1). Evolutionary theory predicts that the population will evolve towards peaks on the adaptive
63 landscape following the path with the steepest fitness gradient (Figure 1A). However, evolution along the
64 steepest fitness gradient may cause the population to reach trait values in which the extinction of the
65 population is likely to occur (represented by the cut-out areas of the adaptive landscape in Figure 1B).
66 This suggests that for populations that persist, evolution is more likely to proceed along trajectories that
67 avoid these ecological boundaries through stochastic deviations from evolution along the steepest fitness
68 gradient (Figure 1B). We term the resulting set of trajectories that avoid extinction viable eco-
69 evolutionary pathways.



70

71 **Figure 1.** (A) *Evolutionary theory predicts that populations will evolve towards higher fitness following*
72 *the steepest fitness gradient. (B) However, some trait combinations may lead to ecological conditions in*
73 *which the population is likely to go extinct, shown as areas cut out from the landscape. These boundaries*
74 *will constrain persisting populations to a portion of the adaptive landscape, requiring their eco-*
75 *evolutionary dynamics to follow only the viable eco-evolutionary pathways.*

76 As a proof-of-concept that the demographic and population dynamic consequences of evolution
77 can constrain viable eco-evolutionary pathways, and that populations may traverse these pathways by
78 chance, we use a computational model of eco-evolutionary dynamics that directly incorporates
79 demographic stochasticity and extinction. We specifically model predator feeding rate evolution in the
80 widely used Rosenzweig-MacArthur predator prey model (Rosenzweig and MacArthur 1963). We use
81 this model because the ecological properties of this model are well-known (e.g., what parameter values
82 lead to stable vs. unstable dynamics and feasible vs. infeasible equilibria), the evolutionary expectations
83 for the parameters governing the predator's feeding rate (the space clearance (aka attack) rate and
84 handling time) are well-known, and a recent study has shown that areas in which the dynamics of this
85 model lead to predator-cycles are likely to cause extinction constraining the values that the predator's
86 feeding rate parameters can take (Rosenzweig and MacArthur 1963, Rosenzweig 1973, Johnson and
87 Amarasekare 2015, Amarasekare 2022). In our analysis, we first use stochastic simulations in the absence
88 of evolution to determine which areas of trait space are likely to lead to population dynamics that result in
89 extinction. We then perform simulations in which the predator's feeding rate parameters evolve to
90 determine whether these identified regions of high extinction risk constrain the pathways that persistent
91 populations can take. Overall, our results illustrate that the demographic and population dynamic
92 consequences of evolution can constrain the viability of eco-evolutionary pathways.

93 **Methods**

94 *Model*

95 To examine the ability of ecological boundaries to constrain viable eco-evolutionary pathways, we
96 analyze the evolution of a predator's functional response parameters in the classic Rosenzweig-
97 MacArthur predator-prey model (Rosenzweig and MacArthur 1963) in which the prey dynamics are
98 described as:

$$99 \quad \frac{dR}{dt} = R((b - q_b R) - (d + q_d R)) - \frac{aRC}{1 + ahR}$$

100 where R is the density of the prey, b is the birth rate of the prey, d is the natural mortality rate of the prey,
101 q_b and q_d describe the density-dependence of the birth and natural mortality rates of the prey
102 respectively, a is the predator's space clearance rate of the prey, h is the predator's handling time on the
103 prey, and C is the predator density (parameter definitions are also given in Table 1). We explicitly model
104 the prey's birth and death rates and their density dependence to allow for a stochastic birth-death process
105 and facilitate the use of the eco-evolutionary modeling approach we employ (see below). This form of
106 logistic growth is equivalent to the classical model of logistic growth with intrinsic growth rate $r = b -$
107 d and carrying capacity $K = \frac{b-d}{q_b+q_d}$ (DeLong and Coblentz 2022; See Supplemental Information S1). The
108 predator's dynamics are described as:

$$109 \quad \frac{dC}{dt} = C \left(\frac{eaR}{1 + ahR} - m \right)$$

110 where e is the conversion efficiency of prey into predators, m is the per capita mortality rate of the
111 predator, and all other parameters are defined above. This model has well-known stability and feasibility
112 boundaries related to the predator's functional response parameters (a and h , Murdoch *et al.*, 2013;
113 Johnson & Amarasekare, 2015). Specifically, the equilibrium of the model with positive densities of the
114 predator and prey is unstable and leads to limit cycles when $ahK > \frac{e+hm}{e-hm}$ (Murdoch *et al.* 2013, Johnson
115 and Amarasekare 2015). The predator cannot persist in the system when $aK < \frac{m}{(e-hm)}$ (Murdoch *et al.*
116 2013, Johnson and Amarasekare 2015). The evolution of the predator's functional response parameters

117 are also easily predicted as the selection gradient is always positive for a and negative for h (Rosenzweig
118 1973). That is, predator fitness increases with increasing space clearance rates and decreasing handling
119 times.

120 *GEMs and How They Work*

121 To model predator evolution in the Rosenzweig-MacArthur model, we used Gillespie Eco-
122 evolutionary Models (GEMs, (DeLong and Gibert 2016, Luhring and DeLong 2020, DeLong and
123 Coblentz 2022, DeLong and Cressler in press)). GEMs work by adding an evolutionary component to the
124 Gillespie algorithm for stochastic simulations of ordinary differential equations (ODEs; Gillespie, 1977).
125 In short, GEMs are individual-based models that simulate differential equations and approximate the
126 results of quantitative genetic analyses of phenotypic evolution while incorporating the effects of
127 individual heterogeneity, demographic stochasticity, genetic drift, and the degradation of phenotypic
128 variation with selection that are typically lacking from studies of eco-evolutionary dynamics. As
129 stochasticity in evolutionary pathways and extinction are central to our hypothesis on ecological
130 boundaries generating viable eco-evolutionary pathways, GEMs provide a useful tool for examining this
131 hypothesis that would be difficult to examine using other tools for eco-evolutionary modelling.

132 Here we provide an in-depth explanation to how GEMs operate. First, the GEM is initiated with a
133 matrix in which each row represents an individual from one of the considered populations (in the case
134 here, either predators or prey). The columns of the matrix give the traits and parameters for each
135 individual. For traits or parameters that evolve, the initial trait or parameter values for individuals are
136 drawn from a log-normal distribution with a specified mean and coefficient of variation. All other traits or
137 parameters receive the same value for all individuals within a population.

138 During each step of the GEM algorithm a random individual from each population is selected.
139 The traits or parameters of these individuals are used to parameterize the ODE model underlying the
140 GEM. The parameterized ODE is then broken up into corresponding ‘events’ as in the original Gillespie

141 algorithm and which event occurs is determined randomly. For example, in our predator-prey model, the
142 possible events are the birth of a prey, the natural death of a prey, the death of a prey via consumption by
143 a predator, the birth of a predator, and the death of a predator. Which of these events occur during each
144 iteration of the algorithm is randomly determined based on the relative magnitudes of the rates for each of
145 the possible events. Specifically, we take a cumulative sum over all the possible events and then draw a
146 random number determining which event occurs.

147 After determining which event occurs, that event is then played out through the modification of
148 the matrix of individuals. In the case of a death in one of the populations, the individual selected from that
149 population at the beginning of the step is removed from the population by deleting its corresponding row
150 from the matrix. If a birth in a population occurs, a new row is added to the matrix of individuals. For
151 traits or parameters that are not evolving, the values for these traits or parameters are simply placed in the
152 corresponding column. For traits or parameters that are evolving, the new value of the trait is determined
153 based on the value of the individual from the corresponding population selected at the beginning of the
154 step and a chosen heritability of that trait or parameter using formulas derived from parent-offspring
155 regression (DeLong and Belmaker 2019). Specifically, the new value is drawn from a log-normal
156 distribution. The mean of the log-normal distribution is equal to $h_x^2 p + \bar{p}(1 - h_x^2)$ where h_x^2 is the
157 narrow-sense heritability of trait x , p is the trait of the parent, and \bar{p} is the average of the trait in the
158 population (DeLong and Belmaker 2019). The standard deviation of the log-normal distribution is equal

159 to $\sigma_x \sqrt{1 - (h_x^2)^2}$ where σ_x is the heritability-weighted mean of the initial and current standard deviations

160 of the trait x or $\sigma_x = (1 - h_x^2)\sigma_{init} + h_x^2\sigma_{current}$ (DeLong and Belmaker 2019). Thus, new

161 individuals have a similar, but generally not identical, trait to their ‘parent’. Due to these methods of
162 adding and removing individuals from populations, the algorithm performs a computational process
163 analogous to natural selection with individuals with traits making them more ‘fit’ on average adding more
164 similar individuals to the population on average compared to less ‘fit’ individuals. As in the original
165 Gillespie algorithm, after an event resolves, the time is then advanced based on the expected time for the

166 event to occur. This algorithm is repeated until a specified end time is reached with descriptions of
167 population numbers and distributions of traits saved at standard times throughout the algorithm. Overall,
168 this process then models the stochastic dynamics and trait evolution of populations based on a description
169 of the system given by ODEs.

170 *Analysis Methods*

171 Using GEMs, we first evaluated whether the analytical stability and feasibility boundaries of the
172 model with respect to the predator's functional response parameters defined a parameter space in which
173 persistence was likely in the absence of evolution. To do so, we first simulated the dynamics of the
174 predator and prey populations across a grid on the space clearance rate-handling time plane (*a-h* plane) on
175 which the feasibility and stability boundaries of the system are defined. For each grid point on the plane,
176 we performed 100 simulations over 50 time steps and calculated the proportion of simulations in which
177 the predator or prey went extinct (i.e. reached a population size of zero). For the starting population
178 values, we used the average population sizes following any transient dynamics from the deterministic
179 solution. We also performed linear stability analysis of the deterministic model for each of the points on
180 the *a-h* plane to determine the deterministic qualitative dynamics for that point (stable steady state,
181 damped oscillations to a stable steady state, an unstable steady state leading to a stable limit cycle, or an
182 infeasible steady state) and the resilience of the steady state equilibrium at that point measured by the
183 maximum eigenvalue of the Jacobian matrix evaluated at the steady state (this eigenvalue determines the
184 rate of return of the system to the equilibrium given a pulse perturbation away from the equilibrium;
185 (McCann 2011, Murdoch et al. 2013)). For each point on the grid, we also determined the minimum
186 population size of the deterministic dynamics after transient dynamics. In these simulations, no evolution
187 occurred as we set the heritability of the space clearance rate and handling times and their variance within
188 the population to zero. We did this for two carrying capacities ($K = 200$ and $K = 2000$) because higher
189 carrying capacities lead to higher equilibrium population sizes which are likely to show different patterns

190 of extinction due to demographic stochasticity (Giles Leigh 1981, Lande 1993, Ovaskainen and Meerson
191 2010).

192 After assessing the space in the a - h plane in which the predator and prey were likely to persist for
193 each of the two carrying capacities in the absence of evolution, we then allowed predator populations'
194 space clearance rates and handling times to evolve directly and determined 1) whether the evolutionary
195 pathways of populations that persisted differed from those of populations that went extinct and 2) whether
196 extinction occurred in the areas of likely extinction identified in the absence of evolution. Although the
197 selection gradients for the space clearance rate and handling time have constant signs, meaning that they
198 are predicted to evolve to extreme and unrealistic values (infinity and zero, respectively), we are only
199 interested in the trajectories of populations that persist over some time frame and the direct evolution of
200 the functional response parameters is sufficient. Nevertheless, using an alternative model that assumes
201 that the space clearance rate has a maximum, the handling time has a minimum value, and the predator
202 has an evolving trait that determines both the space clearance rate and handling time gives similar
203 answers to the model allowing the parameters to evolve directly (Supplemental Information S2). To
204 match the simulations determining persistence on the a - h plane, these simulations also were run over 50
205 time steps. As we were particularly interested in whether stochastic eco-evolutionary dynamics could
206 allow populations to take trajectories that avoided extinction, we specifically chose heritabilities and
207 coefficients of variation for the space clearance rates and handling times that led to deterministic
208 evolution to or near areas of likely extinction over the period of our simulations in quantitative genetics
209 models.

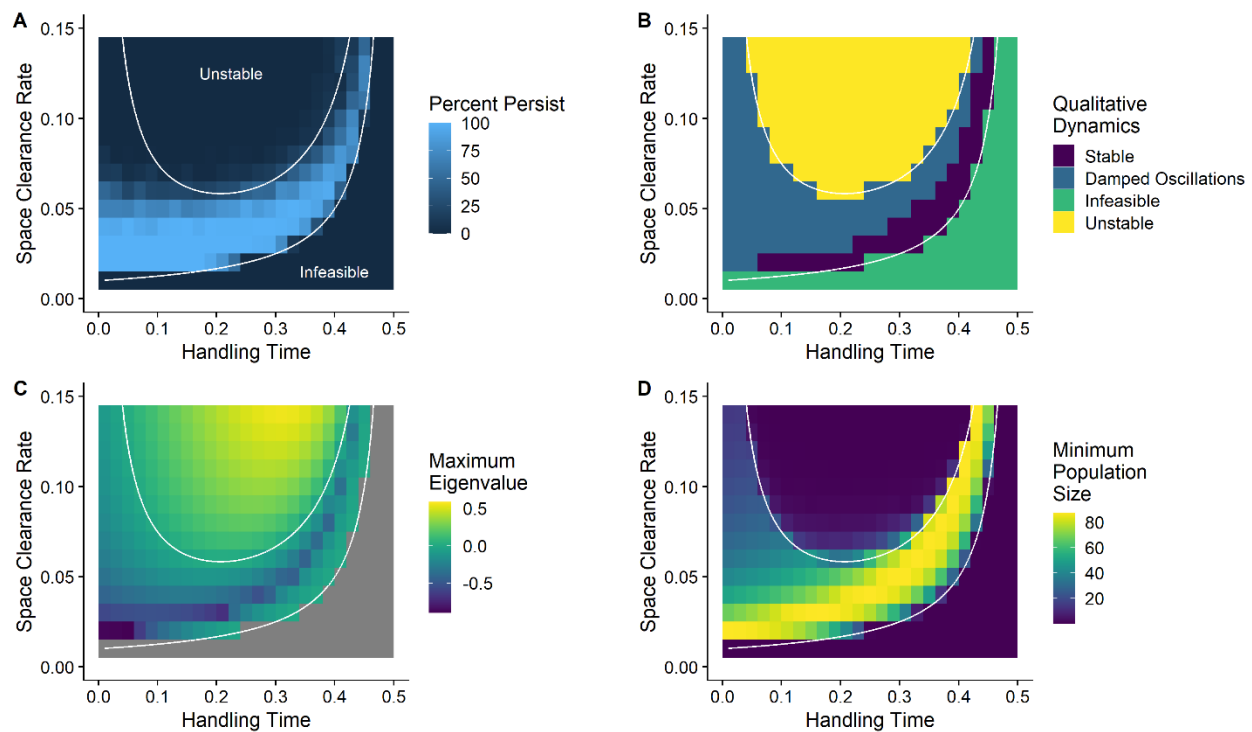
210 Matlab and Mathematica code for the numerical analyses of the model are available (See Data
211 Availability Statement).

212 **Results**

213 *No Predator Evolution*

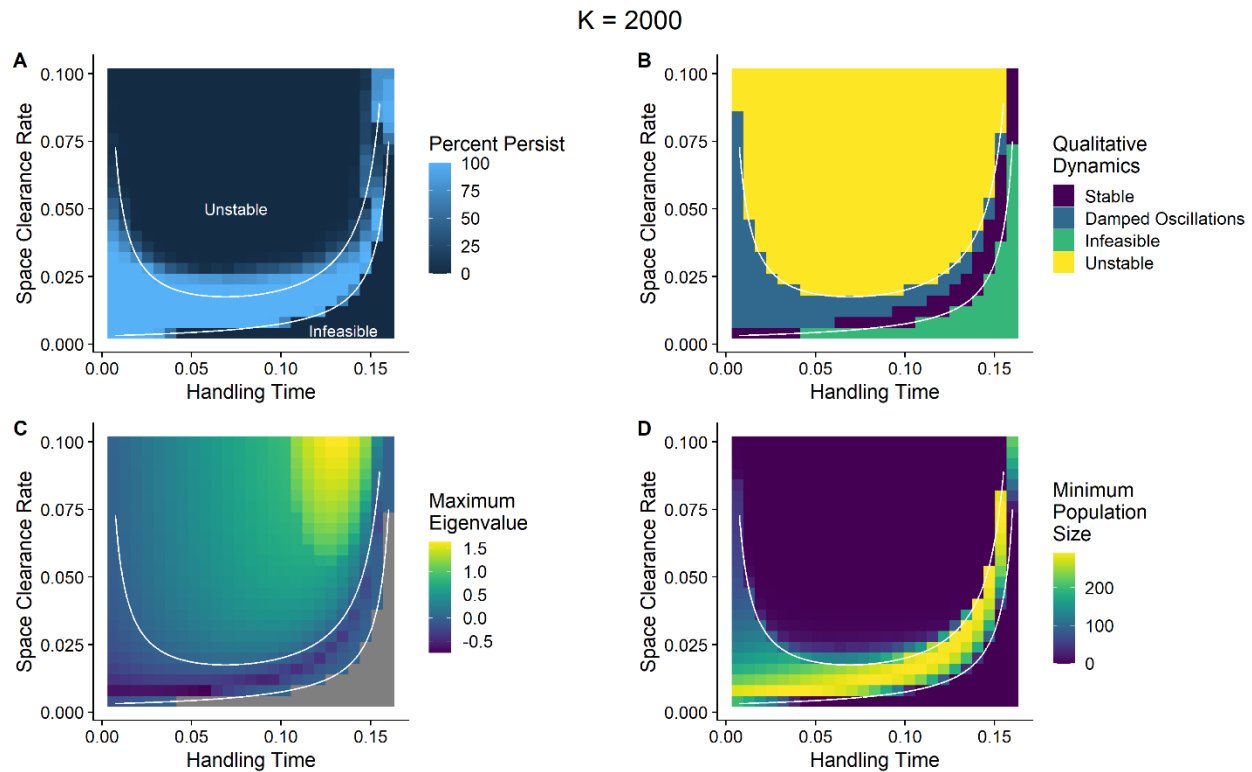
214 The analytical stability and feasibility boundaries did largely define areas of likely population extinction
215 with no evolution in the predator (Figures 2, 3). However, just considering these deterministic boundaries
216 missed areas of likely extinction and persistence (Figures 2,3). For a carrying capacity of 200, an area of
217 extinction occurred within the stability and feasibility boundaries at high space clearance rates and low
218 handling times (Figure 2A). This area is associated with deterministic population dynamics that lead to
219 damped oscillations to a steady state and stochastic dynamics that lead to quasi-cycles (cycles due to an
220 interaction between the deterministic damped oscillations and stochasticity (Bartlett 1957, Gurney and
221 Nisbet 1998, Pineda-Krch et al. 2007; Figures 2B). For areas in which the deterministic dynamics lead to
222 damped oscillations and the stochastic dynamics lead to quasi-cycles, extinctions are more likely for the
223 areas of the $a-h$ plane that have lower resilience (a higher maximum eigenvalue; Figure 2C) and lower
224 minimum population sizes of the deterministic dynamics (Figure 2D). For a carrying capacity of 2000, the
225 area of extinction within the feasibility and stability boundaries at high space clearance rates and low
226 handling times was reduced due to higher minimum population sizes and greater resilience despite the
227 occurrence of quasi-cycles (Figure 3). Furthermore at a carrying capacity of 2000, there were some areas
228 beyond but near the stability boundary where populations were able to persist despite dynamics leading to
229 limit cycles of predator and prey abundances (Figure 3; note that the areas of persistence beyond the
230 stability boundary at high handling times and space clearance rates occur because the simulation time of
231 50 time steps was shorter than the period of the limit cycles at these parameter values and all populations
232 at these values would go extinct with longer simulation times).

K = 200



233

234 **Figure 2.** (A) In stochastic simulations of a predator-prey model, the percent of persistent populations
 235 varied within the stability and feasibility constraints predicted from the deterministic model (the white
 236 lines in Figures 2A-2D). Areas of extinction in the stochastic models occurred within the stability and
 237 feasibility boundaries. (B) Linear stability analysis of the deterministic models gives four areas with
 238 qualitatively different dynamics: a stable steady state (Stable), a stable steady state approached through
 239 damped oscillations (Damped Oscillations), an infeasible steady state with both predator and prey
 240 (Infeasible), and an unstable equilibrium leading to a stable limit cycle (Unstable). Areas within the
 241 stability and feasibility boundaries that lead to damped oscillations (B) but lead to persistent populations
 242 are associated with greater resilience (lower Maximum Eigenvalue, C) and higher minimum population
 243 sizes in deterministic dynamics (D). The non- a and $-h$ parameters used are: $b = 4.5$, $d = 1$, $q_b = q_d =$
 244 0.00875 , $e = 0.3$, $m = 0.6$.



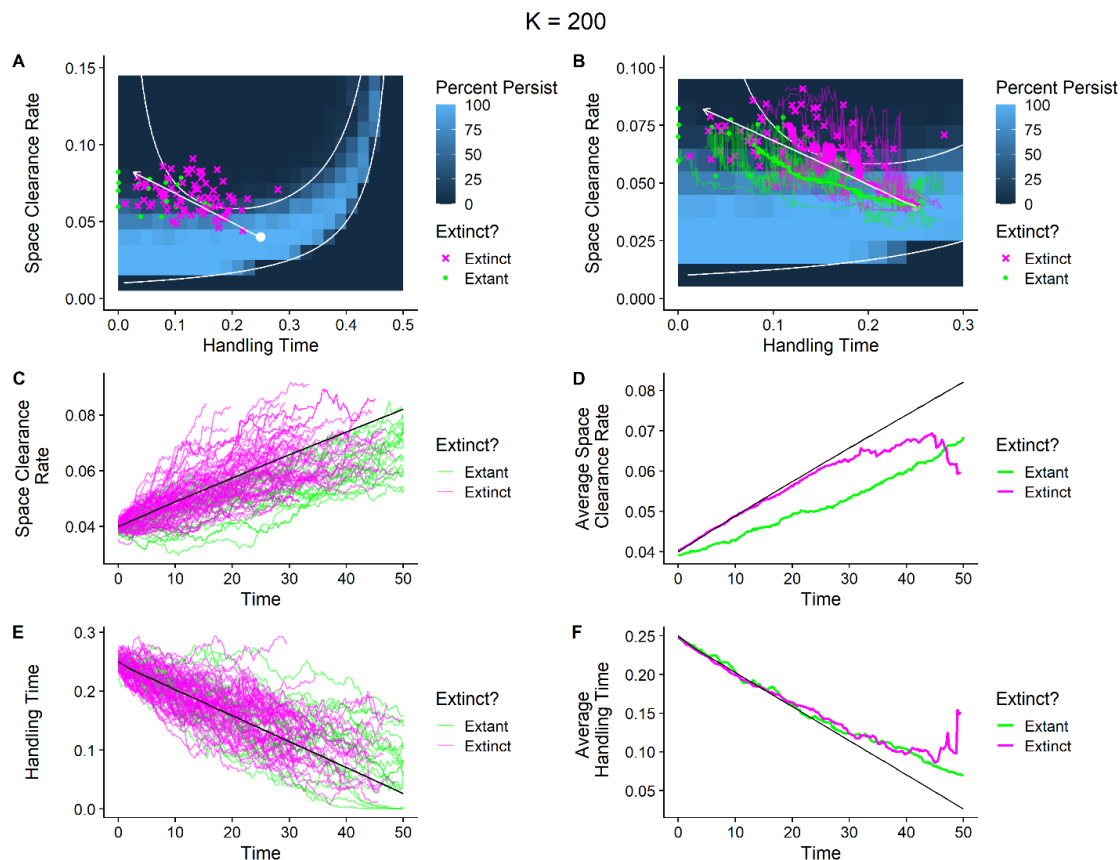
245

246 **Figure 3.** (A) In stochastic simulations of a predator-prey model, the percent of persistent populations
 247 varied within the stability and feasibility constraints predicted from the deterministic model (the white
 248 lines in Figures 2A-2D). Areas of extinction in the stochastic models occurred within the stability and
 249 feasibility boundaries and areas of persistence occurred beyond the stability boundary. (B) Linear
 250 stability analysis of the deterministic models gives four areas with qualitatively different dynamics: a
 251 stable steady state (Stable), a stable steady state approached through damped oscillations (Damped
 252 Oscillations), an infeasible steady state with both predator and prey (Infeasible), and an unstable steady
 253 state leading to a stable limit cycle (Unstable). Areas within the stability and feasibility boundaries that
 254 lead to damped oscillations (B) but lead to persistent populations are associated with greater resilience
 255 (lower Maximum Eigenvalue, C) and higher minimum population sizes in deterministic dynamics (D).
 256 The non- a and $-h$ parameters used are: $b = 4.5$, $d = 1$, $q_b = q_d = 0.000875$, $e = 0.1$, $m = 0.6$.

257 *Predator Evolution*

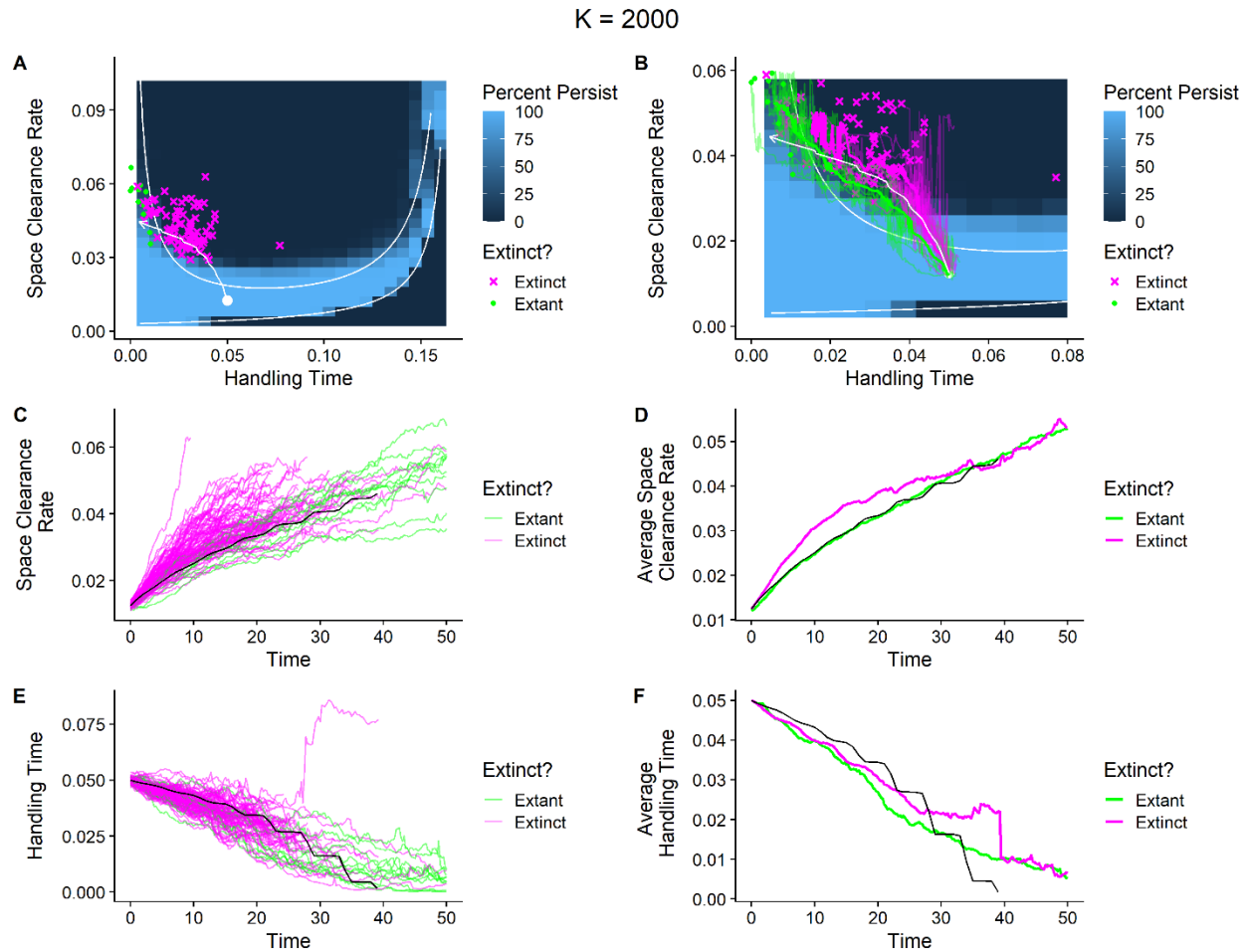
258 When predator populations evolved, populations that persisted evolved to parameter space that largely
259 avoided the areas of likely extinction identified in the cases with no evolution (Figures 4, 5). In contrast,
260 populations that went extinct tended to evolve higher space clearance rates at longer handling times
261 causing the population to cross into areas of likely extinction (Figures 4A,B; 5A,B).

262 For a carrying capacity of 200 and populations that began with low space clearance rates and
263 moderate handling times, the populations that persisted were those whose evolutionary dynamics
264 stochastically led to slower evolution of the space clearance rate (Figures 4B-D). These populations on
265 average showed a shallower evolutionary trajectory than that predicted by deterministic quantitative
266 genetics (the white lines in Figures 4A,B and the black lines in Figures 4C-F). The evolutionary decrease
267 in handling times of extant and extinct populations were similar and largely followed the quantitative
268 genetics predictions but eventually slowed relative to the quantitative genetics prediction likely due to a
269 decrease in trait variation over time (Figures 4E-F, Supplementary Information S3).



271 **Figure 4.** (A) *Predator populations that persist (green points) after evolution tend to avoid areas of likely*
272 *extinction, whereas predator populations that went extinct (magenta crosses) tended to evolve higher*
273 *space clearance rates earlier at higher handling where extinction is more likely. The white arrow is the*
274 *evolutionary pathway predicted by quantitative genetics. The white dot is the average starting values of*
275 *the populations at the beginning of the simulation. (B,C,D) The evolutionary trajectories of space*
276 *clearance rates for populations that went extinct (magenta lines) tended to reach higher space clearance*
277 *rates earlier than for populations that were extant until the end of the simulations (green lines; thin lines*
278 *in B represent the trajectories of 10 randomly chosen extinct and extant populations and the thick line is*
279 *the average trajectory). (E,F) The evolutionary trajectories of handling times for populations that went*
280 *extinct (magenta lines) showed no clear differences relative to populations that were extant and the end*
281 *of the simulations (green lines). Black lines in C-F are the evolutionary trajectories predicted by*
282 *quantitative genetics. The non- a and $-h$ parameters used are: $b = 4.5$, $d = 1$, $q_b = q_d = 0.00875$, $e = 0.3$,*
283 *$m = 0.6$. The heritability of a and h were 0.33 and 0.33 and the starting coefficients of variation in a and*
284 *h among predators were 0.55 and 0.6, respectively.*

285 For a carrying capacity of 2000 and populations that began with low space clearance rates and
286 moderate handling times, the populations that persisted were those whose evolutionary dynamics
287 stochastically led to initially faster evolution of the handling time compared to extinct populations and the
288 quantitative genetics prediction (Figures 5A-B, E-F). This initially fast decrease in the handling time kept
289 evolutionary trajectories within areas where persistence was more likely (Figure 5B). In contrast, the
290 evolutionary increase in the space clearance rate in the space clearance rate for persistent populations was
291 similar to that predicted by quantitative genetics and generally slower than the populations that went
292 extinct (Figures 5B-D).



293

294 **Figure 5.** (A) Predator populations that persist (green points) after evolution tend to avoid areas of likely
295 extinction, whereas predator populations that went extinct (magenta crosses) tended to evolve higher
296 space clearance rates earlier into areas where extinction is more likely. The white arrow is the
297 evolutionary pathway predicted by quantitative genetics. The white dot is the average starting values of
298 the populations at the beginning of the simulation. (B, C, D) The evolutionary trajectories of space
299 clearance rates for populations that went extinct (magenta lines) tended to reach higher space clearance
300 rates earlier than for populations that were extant until the end of the simulations (green lines; thin lines
301 represent the trajectories of 10 randomly chosen extinct and extant populations and the thick line is the
302 average trajectory). (E, F) The evolutionary trajectories of handling times for populations that went
303 extinct (magenta lines) evolved faster on average than populations that were extant and the end of the
304 simulations (green lines). Black lines in C-F are evolutionary trajectories predicted by quantitative

305 *genetics. The non- a and $-h$ parameters used are: $b = 4.5$, $d = 1$, $q_b = q_d = 0.00875$, $e = 0.3$, $m = 0.6$.*
306 *The heritability of a and h were 0.33 and 0.33 and the starting coefficients of variation in a and h among*
307 *predators were 0.55 and 0.6, respectively.*

308 **Discussion**

309 Previous research has suggested that the population demographic and dynamical consequences of
310 evolution can lead to constraints on the types of selection that species can experience and still persist
311 (Gomulkiewicz and Houle 2009, Amarasekare 2022). Here using a stochastic, computational model of
312 predator evolution, we show that areas that are likely to lead to population extinction establish ecological
313 boundaries that define a set of viable eco-evolutionary pathways. This is because evolutionary dynamics
314 that stochastically follow different trajectories can lead to two qualitatively different outcomes. First,
315 some populations evolve trait combinations that lead to extinction by entering unstable, unfeasible, or low
316 abundance ecological conditions susceptible to demographic stochasticity (i.e., Darwinian suicide).
317 Second, populations that deterministically or by chance avoid ecological boundaries persist, following
318 what become the viable subset of eco-evolutionary pathways.

319 Our results have implications for both forecasting evolutionary dynamics and interpreting past
320 evolution. In terms of forecasting, our results illustrate the importance of considering the ecological
321 consequences of evolutionary changes and incorporating the ecological environment into evolutionary
322 forecasts (Nosil et al. 2020). Although a selection gradient may predict that a population evolve along a
323 certain trajectory, if that trajectory leads to a trait space in which the ecological conditions are likely to
324 lead to extinction, persistent populations may end up being those that have evolved along an alternative
325 trajectory differing from that expected from the selection gradient. Operationalizing the existence of
326 ecological barriers to predict actual empirical eco-evolutionary dynamics will require an increased
327 connection between species' traits and the parameters used in such models, although this may already be
328 achievable in some laboratory eco-evolution systems (Yoshida et al. 2003, Kasada et al. 2014).
329 Considering viable eco-evolutionary pathways is also important for interpreting past evolution. The

330 persistence of a population suggests that that population's evolution has avoided trait combinations likely
331 to lead to that population's extinction (Webb 2003, Borrelli et al. 2015). Thus, a population may not have
332 evolved along the exact selection gradients occurring in the past and instead persisted because – possibly
333 by chance alone – its evolutionary dynamics avoided ecological extinction boundaries. This suggests that
334 past evolutionary dynamics may not always be informative about past selection gradients due to survivor
335 bias (for other examples of survivor bias influencing evolutionary inference, see Budd and Mann (2018)
336 and Weis (2018)). For example, if one observed the starting values of populations in Figure 4A and the
337 ending values of the populations that persisted, they might infer a weaker selection gradient on predator
338 space clearance rates than existed.

339 Stochasticity plays an important role in allowing populations to traverse viable eco-evolutionary
340 pathways. First, because viable eco-evolutionary pathways may not match selection gradients, genetic
341 drift is essential in allowing evolutionary dynamics to diverge from deterministic expectations. In our
342 models, genetic drift is incorporated because individuals with traits or parameters that deterministically
343 would lead to high fitness can stochastically die leaving few or no offspring (i.e. individual stochasticity
344 *sensu* Caswell (2009)), while individuals with traits or parameters that would deterministically lead to low
345 fitness may stochastically leave many offspring similar to themselves. Second, demographic stochasticity
346 plays important roles in our models in both determining which areas of trait space represent high
347 extinction risk and in generating variation among evolutionary trajectories. In terms of the areas that
348 represent high extinction risk, our results show some mismatches between the predicted areas of high
349 extinction risk from the deterministic model (i.e. the unstable and unfeasible areas of parameter space)
350 and the areas of extinction that occurred in simulations with demographic stochasticity. At low carrying
351 capacities, some of the areas of extinction not predicted by the deterministic model involved the presence
352 of quasi-cycles that are the product of the interaction of damped oscillations in the deterministic model
353 and demographic stochasticity and cannot occur without demographic stochasticity (Bartlett 1957,
354 Gurney and Nisbet 1998, Pineda-Krch et al. 2007). At high carrying capacities, the simulations without

355 evolution suggested that some parameter combinations that lead to predator-prey cycles may nevertheless
356 still lead to persistent populations because populations do not reach low enough sizes to be susceptible to
357 extinction via demographic stochasticity. In terms of the effects of demographic stochasticity in
358 generating variation in evolution trajectories among populations, this is because the selection gradients on
359 the predator's space clearance rates and handling times depend on the densities of the prey (Rosenzweig
360 1973, Amarasekare 2022, DeLong and Coblenz 2022). Because demographic stochasticity can alter
361 population abundances relative to deterministic expectations, two predator populations with exactly the
362 same distribution of traits could experience different selection gradients because their prey population
363 abundances are stochastically different. Altogether, the importance of stochasticity in generating our
364 results highlights the importance of including stochasticity into theory on eco-evolutionary dynamics
365 (Benaïm and Schreiber 2019, DeLong and Cressler in press).

366 Although our results highlight the role of stochasticity in allowing populations to traverse viable
367 eco-evolutionary pathways, evolutionary constraints on traits also may operate to prevent species from
368 evolving to areas in which ecological conditions are likely to lead to extinction. For example,
369 counteracting selection from other sources or a lack of heritable variation may operate to prevent species
370 from evolving into ecological scenarios likely to cause extinction (Arnold 1992, Vuorinen et al. 2021). In
371 fact, if our simulations were run long enough eventually all populations would end up extinct. Thus, the
372 existence of factors slowing or counteracting evolution are likely important and could possibly lead to a
373 form of selection bias across populations in which populations that do exhibit evolutionary constraints
374 that prevent their evolution to ecologically risky trait spaces are more likely to be observed (Webb 2003,
375 Rankin and López-Sepulcre 2005, Parvinen and Dieckmann 2013). Note, however, that viable eco-
376 evolutionary pathways also can occur in models in which the predator and prey will not evolve to
377 extinction (Supplemental Information S2).

378 Despite our use of a predator-prey model to illustrate the concept of viable eco-evolutionary
379 pathways, this process should be general to systems in which certain trait combinations lead to high

380 likelihoods of extinction (e.g. low population sizes). We view this work as analogous to past research on
381 limits to evolutionary trajectories. For example, Gavrillets (1997) suggested that adaptive landscapes
382 representing the fitness of genotypic frequencies contain genotypes of low fitness (or inviability) creating
383 'holes' in the fitness landscape in which evolutionary trajectories must evolve around. Similarly, our
384 results suggest that eco-evolutionary trajectories must avoid certain trait combinations that lead to
385 ecological conditions with high extinction risk even while being genetically viable. Studies on protein
386 evolution also have shown that amino acid substitutions may have to occur in a certain order for the
387 evolving protein to remain functional or provide a fitness benefit (Maynard Smith 1970, Poelwijk et al.
388 2007). Similarly, ecological barriers may require that certain traits evolve before others for the population
389 to follow the viable eco-evolutionary pathway. For example, in the scenario with evolution and a high
390 carrying capacity, populations that evolved lower handling times quickly at the beginning of the
391 simulation were able to achieve higher space clearance rates later in time while still persisting. In general,
392 we expect that the ecological consequences of evolutionary changes along with intrinsic evolutionary
393 constraints act to limit the evolutionary pathways persistent lineages can traverse.

394 **Literature Cited**

- 395 Amarasekare, P. 2022. Ecological Constraints on the Evolution of Consumer Functional Responses. -
396 *Frontiers in Ecology and Evolution* in press.
- 397 Arnold, S. J. 1992. Constraints on Phenotypic Evolution. - *The American Naturalist* 140: S85–S107.
- 398 Bartlett, M. S. 1957. Measles Periodicity and Community Size. - *Journal of the Royal Statistical Society.*
399 *Series A (General)* 120: 48–70.
- 400 Benaim, M. and Schreiber, S. J. 2019. Persistence and extinction for stochastic ecological models with
401 internal and external variables. - *J. Math. Biol.* 79: 393–431.
- 402 Borrelli, J. J. et al. 2015. Selection on stability across ecological scales. - *Trends in Ecology & Evolution*
403 30: 417–425.
- 404 Budd, G. E. and Mann, R. P. 2018. History is written by the victors: The effect of the push of the past on
405 the fossil record. - *Evolution* 72: 2276–2291.
- 406 Caswell, H. 2009. Stage, age and individual stochasticity in demography. - *Oikos* 118: 1763–1782.
- 407 DeLong, J. P. and Gibert, J. P. 2016. Gillespie eco-evolutionary models (GEMs) reveal the role of
408 heritable trait variation in eco-evolutionary dynamics. - *Ecology and Evolution* 6: 935–945.
- 409 DeLong, J. P. and Belmaker, J. 2019. Ecological pleiotropy and indirect effects alter the potential for
410 evolutionary rescue. - *Evolutionary Applications* 12: 636–654.
- 411 DeLong, J. P. and Coblenz, K. E. 2022. Prey diversity constrains the adaptive potential of predator
412 foraging traits. - *Oikos* in press.
- 413 DeLong, J. P. and Cressler, C. E. Stochasticity directs adaptive evolution toward nonequilibrium
414 evolutionary attractors. - *Ecology* n/a: e3873.
- 415 Gavrilets, S. 1997. Evolution and speciation on holey adaptive landscapes. - *Trends in Ecology &*
416 *Evolution* 12: 307–312.
- 417 Giles Leigh, E. 1981. The average lifetime of a population in a varying environment. - *Journal of*
418 *Theoretical Biology* 90: 213–239.
- 419 Gillespie, D. T. 1977. Exact stochastic simulation of coupled chemical reactions. - *J. Phys. Chem.* 81:
420 2340–2361.
- 421 Gomulkiewicz, R. and Houle, D. 2009. Demographic and Genetic Constraints on Evolution. - *The*
422 *American Naturalist* 174: E218–E229.
- 423 Gurney, W. and Nisbet, R. M. 1998. *Ecological dynamics*. - Oxford University Press.
- 424 Johnson, C. A. and Amarasekare, P. 2015. A Metric for Quantifying the Oscillatory Tendency of
425 Consumer-Resource Interactions. - *The American Naturalist* 185: 87–99.

- 426 Kasada, M. et al. 2014. Form of an evolutionary tradeoff affects eco-evolutionary dynamics in a predator–
427 prey system. - PNAS 111: 16035–16040.
- 428 Kempes, C. P. et al. 2012. Growth, metabolic partitioning, and the size of microorganisms. - Proceedings
429 of the National Academy of Sciences 109: 495–500.
- 430 Kempes, C. P. et al. 2019. The Scales That Limit: The Physical Boundaries of Evolution. - Frontiers in
431 Ecology and Evolution in press.
- 432 Lande, R. 1993. Risks of Population Extinction from Demographic and Environmental Stochasticity and
433 Random Catastrophes. - The American Naturalist 142: 911–927.
- 434 Luhring, T. M. and DeLong, J. P. 2020. Trophic cascades alter eco-evolutionary dynamics and body size
435 evolution. - Proc. R. Soc. B. 287: 20200526.
- 436 Matsuda, H. and Abrams, P. A. 1994. Runaway Evolution to Self-Extinction Under Asymmetrical
437 Competition. - Evolution 48: 1764–1772.
- 438 Maynard Smith, J. 1970. Natural Selection and the Concept of a Protein Space. - Nature 225: 563–564.
- 439 McCann, K. S. 2011. Food Webs (MPB-50). - Princeton University Press.
- 440 Murdoch, W. W. et al. 2013. Consumer-Resource Dynamics (MPB-36). - Princeton University Press.
- 441 Nosil, P. et al. 2020. Increasing our ability to predict contemporary evolution. - Nat Commun 11: 5592.
- 442 Ovaskainen, O. and Meerson, B. 2010. Stochastic models of population extinction. - Trends in Ecology &
443 Evolution 25: 643–652.
- 444 Parvinen, K. and Dieckmann, U. 2013. Self-extinction through optimizing selection. - Journal of
445 Theoretical Biology 333: 1–9.
- 446 Pineda-Krch, M. et al. 2007. A Tale of Two Cycles: Distinguishing Quasi-Cycles and Limit Cycles in
447 Finite Predator-Prey Populations. - Oikos 116: 53–64.
- 448 Poelwijk, F. J. et al. 2007. Empirical fitness landscapes reveal accessible evolutionary paths. - Nature
449 445: 383–386.
- 450 Rankin, D. J. and López-Sepulcre, A. 2005. Can adaptation lead to extinction? - Oikos 111: 616–619.
- 451 Rosenzweig, M. L. 1973. Evolution of the Predator Isocline. - Evolution 27: 84–94.
- 452 Rosenzweig, M. L. and MacArthur, R. H. 1963. Graphical Representation and Stability Conditions of
453 Predator-Prey Interactions. - The American Naturalist 97: 209–223.
- 454 Simpson, G. G. 1944. Tempo and Mode in Evolution. - Columbia University Press.
- 455 2013. The Adaptive Landscape in Evolutionary Biology (E Svensson and R Calsbeek, Eds.). - Oxford
456 University Press.
- 457 Vuorinen, K. E. M. et al. 2021. Why don't all species overexploit? - Oikos 130: 1835–1848.

- 458 Webb, C. 2003. A Complete Classification of Darwinian Extinction in Ecological Interactions. - The
459 American Naturalist 161: 181–205.
- 460 Weis, A. E. 2018. Detecting the “invisible fraction” bias in resurrection experiments. - Evolutionary
461 Applications 11: 88–95.
- 462 Wright, S. 1932. The roles of mutation, inbreeding, crossbreeding and selection in evolution. -
463 Proceedings of the Sixth Annual Congress of Genetics 1: 356–366.
- 464 Yoshida, T. et al. 2003. Rapid evolution drives ecological dynamics in a predator–prey system. - Nature
465 424: 303–306.
- 466

467 **Table 1. Parameters used in the models, their definitions, and the values taken in this study.**

Parameter	Definition	Values Used
b	Birth rate	3.5
q_b	per capita density-dependent decrease in the birth rate	0.00875 when $K = 200$ 0.000875 when $K = 2000$
d	Death rate	1
q_d	Per capita density-dependent increase in the death rate	0.00875 when $K = 200$ 0.000875 when $K = 2000$
K	Carrying capacity $K = \frac{b - d}{q_b + q_d}$	200 or 2000
a	Space clearance rate	varied or evolves
h	Handling time	varied or evolves
e	Conversion efficiency	0.3 when $K = 200$ 0.1 when $K = 2000$
m	Per capita predator mortality rate	0.6
h_a^2	Narrow-sense heritability of the space clearance rate in the predator	0.55 when $K = 200$ 0.6 when $K = 2000$
h_h^2	Narrow sense heritability of the handling time in the predator	0.6 when $K = 200$ 0.6 when $K = 2000$
CV_a	Coefficient of variation of the initial log-normal distribution of the predator space clearance rate	0.33 when $K = 200$ 0.8 when $K = 2000$

CV_h	Coefficient of variation of the initial log-normal distribution of the predator handling time	0.325 when $K = 200$ 0.4 when $K = 2000$
--------	---	---