

# Implications of drift and rapid evolution on negative niche construction

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## **Author contribution**

MC, and NL conceived the idea of the project. PLN contributed to the main design of the model, MC and NL contributed to further developments of the model, and provided additional suggestions and modifications. PLN analysed the model with the help of MC and NL. PLN wrote the first draft of the manuscript. MC and NL revised, commented and made further modifications.

## 1 Abstract

2 1. Organisms throughout their lives constantly modify their surrounding environment; such  
3 activities are often termed niche construction. An important property of niche construction is  
4 that its consequences can persist for a long period of time and several subsequent generations  
5 can be affected. This phenomenon is described as a time lag in niche construction, or ecological  
6 inheritance.

7 2. Studies have suggested that time lag in niche construction can help avoiding the tragedy of  
8 the commons. In other words, it can lead to evolution of contribution to a common good,  
9 which is associated with positive niche construction, or to the limitation of a common bad,  
10 which is associated with negative niche construction.

11 3. In this article, we will study the evolutionary consequences of incorporating time lags in  
12 a negative niche construction process: waste production. We consider a population that  
13 extrudes waste into its environment as it consumes resources to grow and reproduce. Higher  
14 consumption rates can lead to higher waste production. Individuals that adopt this selfish  
15 strategy are expected to be selected as toxic effects are equally shared among all individuals.

16 4. We show that indeed this tragedy of the commons persists in many cases and selfish strategies  
17 evolve in general. When evolution is rapid and intragenerational time lag is incorporated, how-  
18 ever, selfish strategies are no longer favoured and strategies resulting in less waste production  
19 can be selected. Importantly, heavy pollution results in smaller population sizes, so that  
20 drift becomes more important than natural selection and limits the evolution of higher waste  
21 production.

22 **Key words** Adaptive dynamics, drift, intragenerational time lag, negative niche construction,  
23 rapid evolution, stochastic simulations, tragedy of the commons.

## 24 **1 Introduction**

25 Niche construction is a process whereby organisms modify their surrounding environment. It can  
26 be as sophisticated and noticeable to the human eye as beaver dams or termite mounds (Naiman  
27 et al. 1988; Wright et al. 2002; Korb 2011). Yet, it can simply be a change in chemical concen-  
28 trations induced by the activities of organisms such as the enrichment of environmental oxygene  
29 by cyanobacteria billions of years ago (Mazard et al. 2016). In fact, any living being is a niche  
30 constructor because by merely existing, organisms interact with their surrounding environment,  
31 thereby chemically and physically modifying it. Such modifications can be positive (positive niche  
32 construction) or negative (negative niche construction) when considering the fitness of individuals  
33 of the constructing species. It is suggested that niche construction have important ecological and  
34 evolutionary consequences (Odling-Smee et al. 2003).

35 An important property of niche construction is that environmental modifications can persist on  
36 long timescales, which is often known as legacy effects or ecological inheritance (Cuddington 2011;  
37 Odling-Smee et al. 2003; Danchin et al. 2011; Hastings et al. 2007). In particular, changes in the  
38 niche can be inherited within a generation and between generations of a niche constructing species  
39 (Krebs and Davies 1993; Laland et al. 2000; Edeline et al. 2016; Hastings et al. 2007). Environmental  
40 changes can also be inherited by other species that live within the same area (Hastings et al. 2007;  
41 Kidwell and Jablonski 1983).

42 Understanding the evolutionary dynamics related to niche construction therefore requires the  
43 careful consideration of three different timescales: the population timescale, the niche construc-  
44 tion timescale, and the evolutionary timescale. The population dynamic timescale encompasses all  
45 demographic processes of niche constructors and recipients of niche construction. The niche con-  
46 struction timescale covers the variations in the environment born from niche construction processes,  
47 including ecological inheritance. Finally, the evolutionary timescale refers to the changes in gene  
48 frequencies, emergence and invasion of new mutants, or the birth and death of new species. For  
49 instance, a termite mound may grow as the termite colony grows; this happens along the population  
50 dynamic timescale. The changes of the mound could then affect local environments for millennia

51 (Martin et al. 2018), so that the niche construction timescale here is very large. Associated en-  
52 vironmental changes can have large consequences, affecting vegetation patterns at various spatial  
53 scales (Bonachela et al. 2015; Tarnita et al. 2017; Ashton et al. 2019) thereby creating new sources  
54 of selection that act on a long evolutionary timescale.

55 The three timescales thus interact in complex ways and do not necessarily match. If niche con-  
56 struction persists for a long time, its timescale may completely lag behind the population dynamic  
57 timescale. For instance, mollusca or crustacean species leave behind their shells when dead, which  
58 accumulate under the ocean. This gradually forms hard substrata which facilitate or inhibit the oc-  
59 cupation of subsequent species (Kidwell and Jablonski 1983). In this case, several populations may  
60 exist, reach their dynamical equilibrium, and even go extinct, while the dynamics of the substrata  
61 remains at its quasi-stable state. Thus, the substrata dynamics may not have a significant effect on  
62 a particular species within a short period of time, but when considering a sufficiently long period,  
63 the effect becomes more significant and concerns evolution of multiple species. The lag between the  
64 population and niche construction timescales need not be so extreme (Odling-Smee et al. 2003).  
65 For instance, earthworms modify soil properties which has been suggested to make the environment  
66 become favourable for not only the starting communities, but also their future generations (Caro  
67 et al. 2014). In the study of Edeline et al. (2016), when juvenile and adult mekada fishes consume  
68 the same resources, adults 'inherit' the resources degraded by juveniles, and this facilitates the  
69 evolution of semelparity.

70 Theoretical frameworks of evolution often assume the separation of the evolutionary and popu-  
71 lation dynamic timescales, such that the former is much slower than the latter (Metz et al. 1995;  
72 Koch et al. 2014). However, more and more evidence pointed out that evolutionary processes can  
73 be much faster than previously thought (Thompson 1998; Hairston et al. 2005; Carroll et al. 2014),  
74 so that evolutionary and ecological timescales may not be easily separated. If the dynamics of  
75 niche construction are also taken into account, then lags among the three timescales can happen  
76 in many ways, leading to unexpected ecological and evolutionary results. For instance, Gurney  
77 and Lawton (1996) showed that a time lag between population and resources dynamics, can lead  
78 to cyclic dynamics. Laland et al. (1996) showed that a lag in the effect of resources construction

79 delays the spread of the allele that is favoured by the increasing amount of resources. Both studies  
80 concern positive niche construction where a focal population can increase resources dynamics.

81 Effects of niche construction, positive or negative, are often shared among coexisting individuals  
82 and may result in the tragedy of the commons. It is often difficult for positive niche construction to  
83 evolve but easy for negative niche construction to spread. To avoid this tragedy, classical theoretical  
84 studies include a direct benefit to the restriction of negative niche construction or impose a direct  
85 cost by coercion and punishment, or add spatial structure and kinship (Rankin et al. 2007). They  
86 have one thing in common: explicit dynamics of niche construction are not taken into account,  
87 that is, organisms can impact the environment but feedback loops between the environment and  
88 organisms are disregarded. Such feedback loops are however suggested to change evolutionary  
89 dynamics (Odling-Smee et al. 2003; Estrela et al. 2019).

90 In this article, we explicitly include all three dynamics: population, niche construction and  
91 evolution and consider possible lags among the three associated timescales. We study the evolution  
92 of negative niche construction, here the production of waste. Waste production is assumed to  
93 be positively linked to consumption rates such that individuals that consume more produce more  
94 waste (Zarco-Perello et al. 2019; Besiktepe and Dam 2002; Tanner et al. 2019), and have higher  
95 reproduction, growth or maturation rates (Greenberg et al. 2003; Morton 1986). However, waste  
96 production also pollutes the environment, thereby reducing the fitness of the population. When  
97 such fitness reductions lead to smaller population sizes, they may increase the significance of genetic  
98 drift compared to natural selection. We found that in almost all cases, negative niche construction  
99 is favoured, possibly leading to population extinction. To counterselect for it, we need to introduce  
100 intragenerational time lags between niche construction and population dynamics. Also, evolutionary  
101 timescale needs to be overlapped with the other two timescales. More importantly, since negative  
102 niche construction leads to small population sizes, drift plays an increasing role compared to natural  
103 selection which may limit negative niche construction activities.

## 104 **2 Model**

105 The analysis is structured as follows: we first use the adaptive dynamics approach to analyse  
106 scenarios of slow evolutionary dynamics (Metz et al. 1995). The most important assumption of  
107 this approach is that the evolutionary timescale completely lags behind the other two timescales.  
108 Therefore, mutation is so rare that when a new mutant arises, the resident population is already  
109 at its ecological equilibrium, setting the environmental conditions, and the mutant will replace the  
110 resident if its invasion fitness is positive. We then incorporate intragenerational time lags using a  
111 structured population model, where the population is divided into juvenile and adult states. Here,  
112 the intragenerational time lag implies that adults are affected by the environment constructed by  
113 juveniles. Negative niche construction thereby directly affects individual fitness. Finally, we relax  
114 the assumption of slow evolution imposed by the adaptive dynamics approach. Multiple mutants  
115 can arise at the same time when resident populations need not be at the equilibrium. As a result,  
116 offspring with different strategies inherit the environment created by previous generations. We use  
117 the Tau-leap method to simulate the dynamics (Gillespie 2001). This method enables an overlap  
118 between the evolutionary timescale and the population and niche construction timescales. We will  
119 denote this overlap as rapid evolution. This also allows us to study the effect of drift because birth  
120 and death processes are modelled as stochastic drawings. As negative niche construction can lead  
121 to smaller population sizes, the role of drift can become more significant.

### 122 **2.1 A complete lag of the evolutionary timescale**

#### 123 **Negative niche construction without intragenerational time lag**

124 We model a species  $S$  that impoverishes its environment by consuming resources  $R$  and pollutes it by  
125 producing waste  $W$ . A higher consumption rate  $c$  results in more offspring, given a fixed efficiency  $\rho$   
126 of converting resources into new individuals. It also leads to higher rates of waste production  $f(c)$ ,  
127 where  $df(c)/dc > 0$ . The pollution level  $W$  adds a mortality rate  $\omega(W)$  to the natural mortality  
128 rate  $d$  of the consumer. Since higher waste densities lead to higher additional mortality rates, we  
129 assume  $d\omega(W)/dW > 0$ . The dynamics of resources and waste follow a chemostat dynamic, where

130  $I_R/\delta_R$  and  $I_W/\delta_W$  are their respective natural turnover rates. The ODEs that describe the whole  
131 system can be written as

$$\begin{cases} \frac{dR}{dt} = -cRS + I_R - \delta_R R, & (1a) \\ \frac{dW}{dt} = Sf(c) + I_W - \delta_W W, & (1b) \\ \frac{dS}{dt} = c\rho RS - dS - \omega(W)S. & (1c) \end{cases}$$

132 In order to derive analytical results, we use linear functions for the production of waste and  
133 additional mortality due to pollution, thus,  $f(c) = hc$  and  $\omega(W) = vW$ . System (1) has three  
134 equilibria: an equilibrium where the species does not survive, an equilibrium where the density of  
135 the species is always negative, and an equilibrium where the species persists if the consumption  
136 rate is sufficiently large, i.e. a positive equilibrium. This positive equilibrium is unstable only if  
137 the niche construction activity has little effect on the waste dynamics or if the population is not at  
138 all vulnerable to pollution. This results in the population increasing to infinity, and it corresponds  
139 to extremely small values of  $h$  and  $v$  (details of the equilibrium is in Supplementary Document 1).  
140 In our analysis, we only consider sufficiently large values of  $h$  and  $v$ , such that the equilibrium is  
141 always stable.

142 We study the evolution of consumption rate  $c$ . A mutant that adopts a different consumption  
143 value than the resident can invade if its invasion fitness is positive. This is the equivalent to a mutant  
144 having its reproduction ratio  $F_m(c_m, c)$  greater than one. In other words, a mutant can spread if  
145 it is replaced by more than one offspring (details of the expression is in Supplementary Document  
146 2). The reproduction ratio of a mutant, which is derived from the invasion fitness condition, can  
147 be written as

$$F_m(c_m, c) = \frac{c_m \rho R^*(c)}{d + vW^*(c)}$$

148 The value of the reproduction ratio depends on the mutant strategy ( $c_m$ ) and the environment

149 that is constructed by the resident, which is evaluated at equilibrium ( $W^*(c), R^*(c)$ ). It can be  
 150 shown that the selection gradient on higher consumption rate is always positive (see details in  
 151 Supplementary Document 2). As a consequence, we always observe selection for higher consumption  
 152 rates, leading to a continuous increase in pollution and more scarcity of resources (figure 1). The  
 153 consumer population eventually settles to a certain value, when increasing consumption rates are  
 154 exactly balanced by increased costs due to pollution. Note that the selection pressure remains  
 155 positive, but its value decreases as the consumption rate increases (purple line in figure 1), so that  
 156 evolution becomes progressively slower.

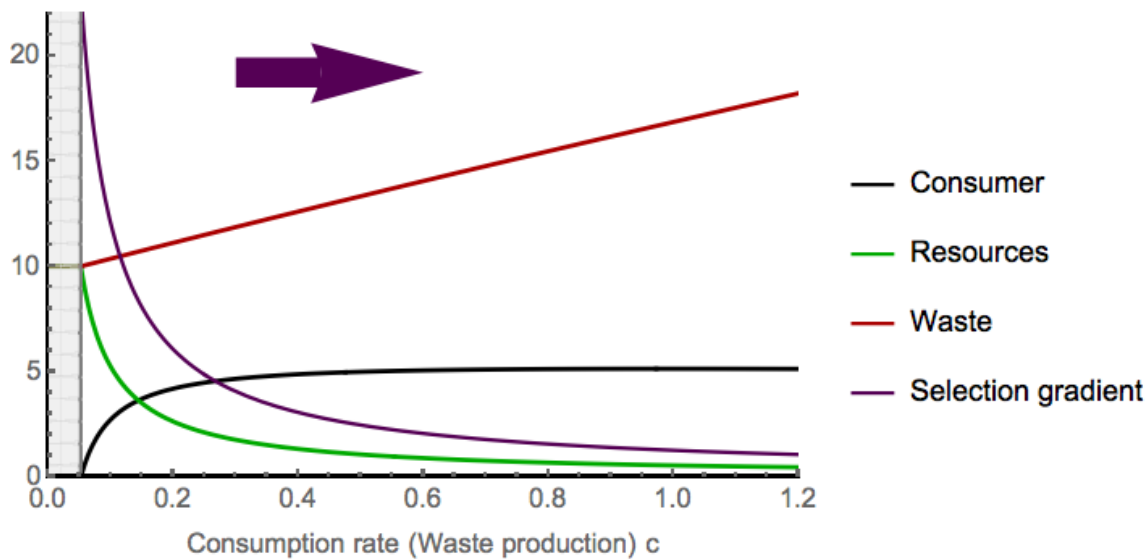


Figure 1: Changes in equilibrium value ( $W^*(c), R^*(c), S^*(c)$ ) with respect to the trait value. Gray area corresponds to population extinction. Parameters:  $\rho = 2.3, d = 1.1, I_R = 3, \delta_R = 0.3, I_W = 3, \delta_W = 0.3, v = 0.01, h = 0.4$

157 In this model, there is no direct cost on over-exploitation, and the tragedy of the commons per-  
 158 sists. All individuals, consumptive or frugal, share the damage caused by high pollution levels and  
 159 resource degradation but the benefits to reproduction is attributed immediately to the individuals  
 160 that adopt the selfish strategy of overexploitation.



161 **Negative niche construction with intragenerational time lag**

162 Intragenerational time lag is incorporated using an age-structured population, in which a consumer  
 163 has a juvenile state ( $J$ ) and an adult state ( $A$ ). Juveniles mature into adults at a rate  $g$  and adults  
 164 reproduce at a rate  $\rho$ . Both the maturation rate and the reproduction rate are functions of juvenile  
 165 and adult consumption rates ( $c_J, c_A$ ) and of resources availability ( $R$ ). In consuming resources,  
 166 both juveniles and adults emit waste at a rate  $p_J(c_J)$  and  $p_A(c_A)$  respectively. These rates depend  
 167 on the consumption rates of adults and juveniles, such that the more they consume, the more they  
 168 pollute their environment. Juveniles and adults have an additional mortality rate due to pollution  
 169 ( $\omega_J(W)$  and  $\omega_A(W)$ ). The intragenerational time lag in niche construction is depicted by the fact  
 170 that the negative effect of resource degradation and pollution is transmitted from juvenile to adult  
 171 states. The natural mortality rates of juveniles and adults are  $d_J$  and  $d_A$  respectively. As before,  
 172 the dynamics of the resources and waste follow a chemostat dynamic. Their natural turnover rates  
 173 are respectively  $I_R/\delta_R$  and  $I_W/\delta_W$ . The ODEs that describe the dynamics of the system read

$$\begin{cases} \frac{dJ}{dt} = A\rho(c_A, R) - d_J J - \omega_J(W)J - Jg(c_J, R), & (2a) \\ \frac{dA}{dt} = Jg(c_J, R) - d_A A - \omega_A(W)A, & (2b) \\ \frac{dR}{dt} = I_R - \delta_R R - c_J J R - c_A A R, & (2c) \\ \frac{dW}{dt} = I_W - \delta_W W + p_J(c_J)J + p_A(c_A)A. & (2d) \end{cases}$$

174 System (2) is rather complicated to analyse theoretically. The number of equilibria depends  
 175 much on the explicit forms of the additional mortality functions ( $\omega_J(W)$  and  $\omega_A(W)$ ), and the  
 176 reproduction and maturation functions ( $\rho(c_A, R)$  and  $g(c_J, A)$ ). Even when we use all linear func-  
 177 tions, it is still difficult to obtain analytical results. This complicates our evolutionary analysis as  
 178 the invasion fitness of a mutant depends on the value of the resident at equilibrium. Therefore,  
 179 we simplify the model to gain a better understanding of how the environment affects the selective  
 180 pressure.

181 We only consider negative niche construction as increases in pollution levels, disregarding the dy-

182 namics (and overexploitation) of resources. In addition, we use linear relationships in all functions.

183 System (2) can now be simplified into

$$\begin{cases} \frac{dJ}{dt} = \rho RA - d_J J - v_J W J - c_J R J & (3a) \\ \frac{dA}{dt} = c_J R J - d_A A - v_A W A & (3b) \\ \frac{dW}{dt} = I_W - \delta_W W + h c_J J + p_A A & (3c) \end{cases} .$$

184

185 Now, resource density  $R$ , reproduction rate  $\rho$  and waste production rate of adults  $p_A$  are con-  
186 stants.  $v_J, v_A$  are the vulnerabilities of juveniles and adults to pollution. In disregarding the  
187 resources dynamics and considering exclusively linear functions, the population dynamics are en-  
188 tirely governed by the waste dynamics. There is thus no resource competition among individuals,  
189 adult and juvenile alike. Our model becomes similar to models of maturation (Roos et al. 2007;  
190 Gardmark et al. 2003; Poos et al. 2011). Very often in these models, there is a trade-off between  
191 adult reproduction and juvenile maturation, such that, when an individual invests more in matura-  
192 tion, it invests less in reproduction because it has a fixed energy budget. In our model, considering  
193 such a trade-off would correspond to the consideration of an intrinsic constraint of the negative  
194 niche construction activity, which, similar to the study of Kylafis and Loreau (2008), may result  
195 in selection of lower negative niche construction. In this article, we investigate whether such re-  
196 ductions in negative niche construction may arise only from variations in the different timescales,  
197 and therefore do not include direct costs. Therefore, we assume no direct link between juvenile and  
198 adult traits.

199 System (3) has three equilibria: one trivial equilibrium where no adults and juveniles can survive,  
200 one equilibrium where the waste density is always negative, and one equilibrium that is positive if  
201  $F > 1$ , where

$$F = \frac{c_J R}{D_J(c_J, W_0)} \frac{\rho R}{D_A(W_0)} \quad (4)$$

202 is the reproduction ratio of a resident consumer. Here,  $1/D_J(c_J, W_0) = 1/(d_J + c_J R + W_0)$  is the  
203 expected time that the consumer spends as juvenile, and  $1/D_A(W_0) = 1/(d_A + W_0)$  is the expected  
204 time that the consumer spends as adult, with  $W_0 = I_W/\delta_W$  is the waste density in the environment  
205 when the consumer is rare.  $F$  includes both adult and juvenile components, thus,  $F > 1$  requires  
206 that the adult reproduction rate and the juvenile maturation rate are sufficiently large, while the  
207 waste turnover has to be sufficiently small so that the environment is livable. When  $F > 1$ , the  
208 equilibrium is most likely stable (details of the equilibrium are in Supplementary Document 3 and  
209 4).

210 We analyse the evolution of the juvenile consumption rate. A lower consumption rate indicates  
211 lower rates of maturation and waste production. A mutant with a consumption rate  $c_{Jm}$  can  
212 invade a resident population whose dynamics are at equilibrium if its invasion fitness is positive.  
213 This condition is satisfied whenever the mutant reproduction ratio  $F_m$  is greater than one (details  
214 in 5), where

$$F_m = \frac{c_{Jm}R}{D_J(c_{Jm}, W^*)} \frac{\rho R}{D_A(W^*)} \quad (5)$$

215 Here,  $1/D_J(c_{Jm}, W^*) = 1/(d_J + c_{Jm}R + v_J W^*)$  is the expected time the mutant spends as a  
216 juvenile, and  $1/D_A(W^*) = 1/(d_A + v_A W^*)$  is the expected time the mutant spends as an adult.  
217  $W^*$  is the waste density at equilibrium, which depends on the growth rate value  $c_J$  of the resident.  
218 The reproduction ratio of a mutant ( $F_m$ ) is rather similar to the reproduction ratio of a resident  
219 ( $F$ ), except that the latter depends on a 'virgin' environment whereas the former depends on the  
220 environment constructed by a resident. Expression (5) suggests that higher juvenile consumption  
221 reduces the time that a consumer spends as an adult because it increases the pollution level so that  
222 the consumer might die before it can even reproduce. Thus, a lower juvenile consumption might  
223 be selected under certain conditions. This happens when the selection gradient is negative, which  
224 requires

$$\begin{cases} v_A > v_J & (6a) \\ W^*(c_J) > \frac{d_J + \rho R - d_A}{v_A - v_J} & (6b) \end{cases}$$

225 Condition (6) suggests that the direction of the selection gradient does not depend on the mutant  
226 trait value, and essentially depends on the pollution level created by the resident. Condition (6a)  
227 implies that adults have to be more vulnerable to pollution than juveniles. Intuitively, if juveniles  
228 are more prone to pollution than adults, those who mature slower remain juvenile for a longer  
229 time and suffer pollution, whereas those who mature faster escape the (vulnerable) juvenile state.  
230 Selection then always favours higher juvenile consumption. Thus, in order for lower trait values to  
231 be selected, adults have to be more vulnerable to pollution than juveniles. The second condition  
232 (6b) implies that if the waste density at equilibrium is sufficiently large, the environment becomes  
233 too toxic, and traits that reduce pollution levels (i.e. lower consumption) may be selected.

234 However, under the assumptions of adaptive dynamics, condition (6b) can never be satisfied.  
235 When the environment is not too polluted, we observe a strong selection pressure for higher con-  
236 sumption rate (figure 2A, S. 2A). As the consumption rate increases, so does waste density (figure  
237 2A) (see Supplementary Document 6 for more details). Because mutants can only arise when the  
238 resident population is at equilibrium, and because the waste density at equilibrium is asymptotic  
239 to  $(\rho R - d_A)/v_A$  as the evolving trait increases, which is smaller than the threshold set by the  
240 right-hand side of condition (6b) (figure 2, Figure S. 2), higher consumption is always favoured.  
241 This selection leads to a continuous increase the pollution level (Figure S. 3), and so the tragedy of  
242 the commons persists. Note, however, that the selection gradient fastly becomes extremely small,  
243 so that we expect selection for higher consumption rates to become very weak, and evolutionary  
244 dynamics to be very slow.

## 245 **2.2 Rapid evolution and the role of drift**

246 From condition (6), we infer that if, out of equilibrium, the waste density exceeds its equilibrium  
247 value, it can satisfy condition (6b), resulting in selection for mutants with lower trait values. In

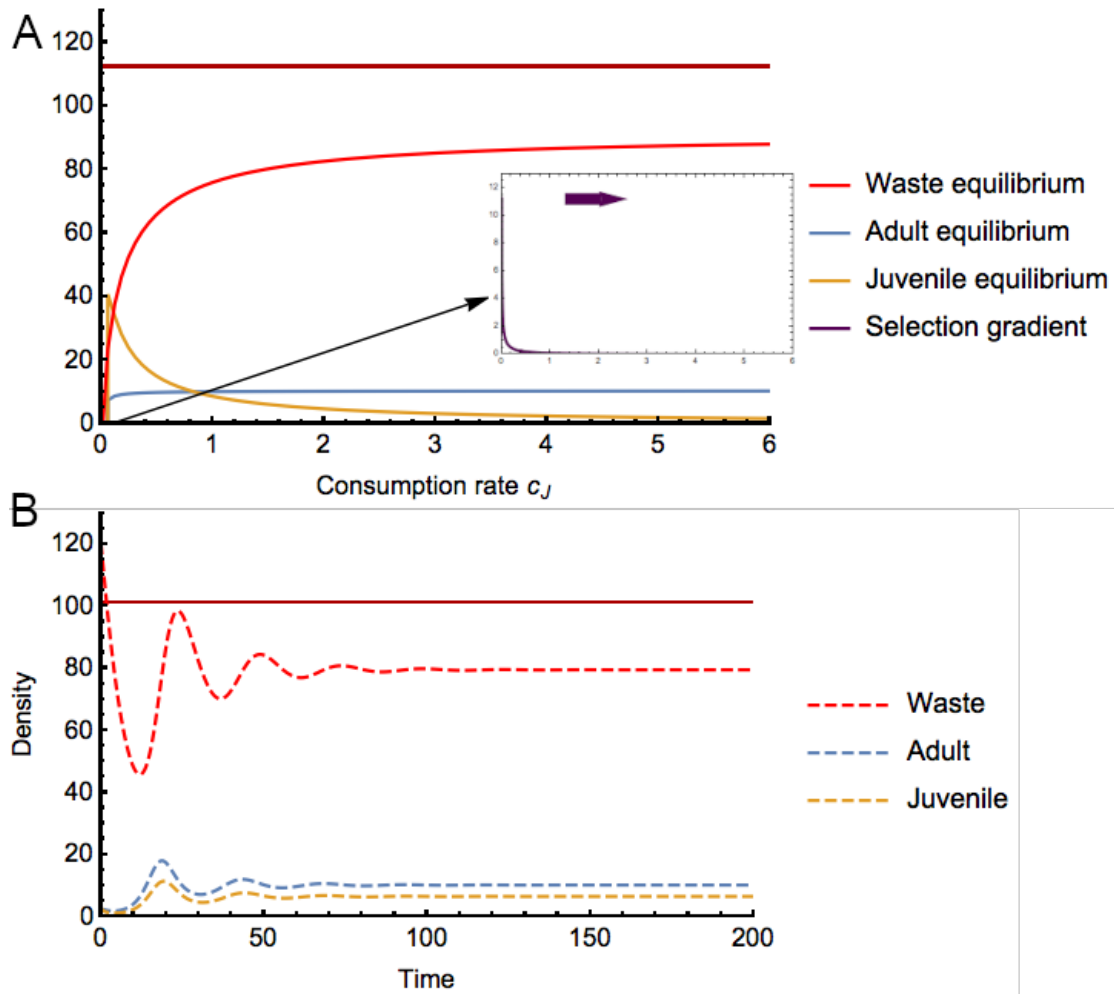


Figure 2: A) Changes of the equilibrium values of system (3) with respect to the growth rate values. The small frame illustrates the selection gradient, and corresponds to a zoom of the general figure B) Ecological dynamics of waste and a resident population that adopts a growth rate value  $c_J = 1.4$ . Thick lines indicate equilibrium while dashed lines indicate the value of density of a resident population. The dark red line indicates the threshold beyond which lower growth rate can be selected. Other parameters:  $R = 1, v_J = 0.001, d_J = d_A = 0.1, h_J = 1.1, v_A = 0.01, \rho = 1.01, I_W = 0.3, \delta_W = 0.13, p_A = 0.001$

248 addition, when the environment is polluted, population density decreases and the selection pres-  
 249 sure is weakened (figure 2A), suggesting that drift can play an increasingly dominant role in the  
 250 evolutionary dynamics. To investigate these aspects, we relax the assumption of slow evolution and

251 introduce stochasticity using mathematical simulations.

252 In particular, we use the Tau-leap algorithm (Gillespie 2001). At each interval  $\tau$ , we calculate all  
253 rates for maturation, reproduction, mortality of juveniles and adults, and the influx and outflux of  
254 the waste concentration. Changes in the number of juveniles and adults and in waste concentration  
255 are then drawn from a Poisson distribution depending on their respective rates. An increase in  
256 the number of juveniles implies birth events. Mutations can happen at a certain rate  $m$ , and new  
257 mutants will adopt juvenile consumptions that are drawn from a normal distribution whose mean  
258 is the value of the mother and the standard deviation is  $\sigma$ . When  $m$  is extremely small, we recover  
259 the adaptive dynamics scenarios. Rapid evolution takes place when we increase the mutation rate.  
260 It should be noted that here rapid evolution implies overlaps between the three timescales and not  
261 indicates larger standing variation or stronger selection as in Koch et al. 2014 and Hairston et al.  
262 2005. In fact, the evolutionary speed could vary in the simulations.

263 In contrast with the adaptive dynamics approach where the population dynamics are determ-  
264 inistic and small populations are guaranteed to survive as long as they satisfy survival conditions,  
265 in stochastic simulations, small populations with selective advantages can go extinct whereas those  
266 with selective disadvantages can survive simply due to chance, so that the stochastic simulations  
267 allows us to consider drift. In each simulation, we start with a monomorphic population and an  
268 initial value of waste density that is drawn from a uniform distribution with a range of (1, 10). Such  
269 initial values allow the existence of initial populations that are sufficiently large, in an environment  
270 that is not too polluted.

### 271 **Negative niche construction with intragenerational time lag**

272 Our simulations suggest that in the long term, an increase in juvenile consumption rate that leads  
273 to an increase in waste production is inevitable. However quasistationary states of the trait value  
274 are obtained mostly because the low population sizes allow a strong effect of drift, that may easily  
275 compensate for the low selection gradient we observed in the adaptive dynamics analysis (figure  
276 2A). Note also that higher trait values are also counterselected whenever the waste density crosses  
277 the threshold  $(d_J + \rho R - d_A)/(v_A - v_J)$  in condition (6b) (figure 3, 4).

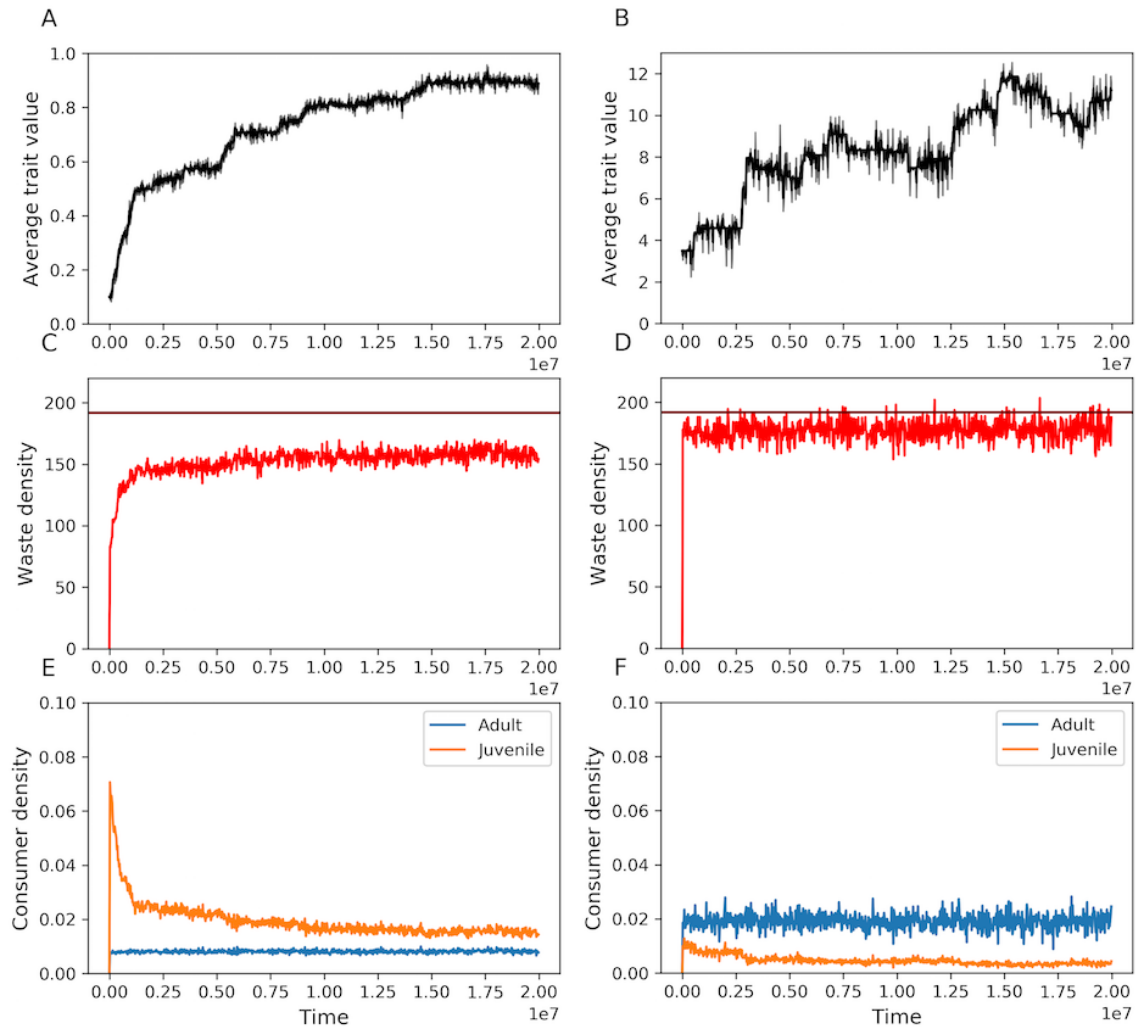


Figure 3: Simulations with moderately fast population and waste dynamics compared to evolutionary dynamics. A, C, E) The starting population has low growth rate  $c_J = 0.1$ . B, D, F) The starting population has higher growth rate  $c_J = 3.5$ . Other parameters for dynamics of populations and waste:  $d_J = d_A = 0.1$ ,  $h_J = 1.1$ ,  $v_J = 0.0001$ ,  $v_A = 0.01$ ,  $u_A = 1$ ,  $u_J = 1$ ,  $I_W = 0.3$ ,  $\delta_W = 0.13$ ,  $\rho = 1.9$ ,  $p_A = 0.001$ . Parameters for evolutionary dynamics  $\sigma = 0.02$  for low growth rate and  $\sigma = 0.7$  for higher growth rate,  $m = 0.001$ . Red horizontal lines indicate the threshold for the waste density beyond which selection will favour lower growth rate.

278 When the initial population has an extremely small juvenile consumption rate ( $c_J = 0.1$ ), higher  
 279 trait values will be immediately selected because the starting environment is rather clean and the

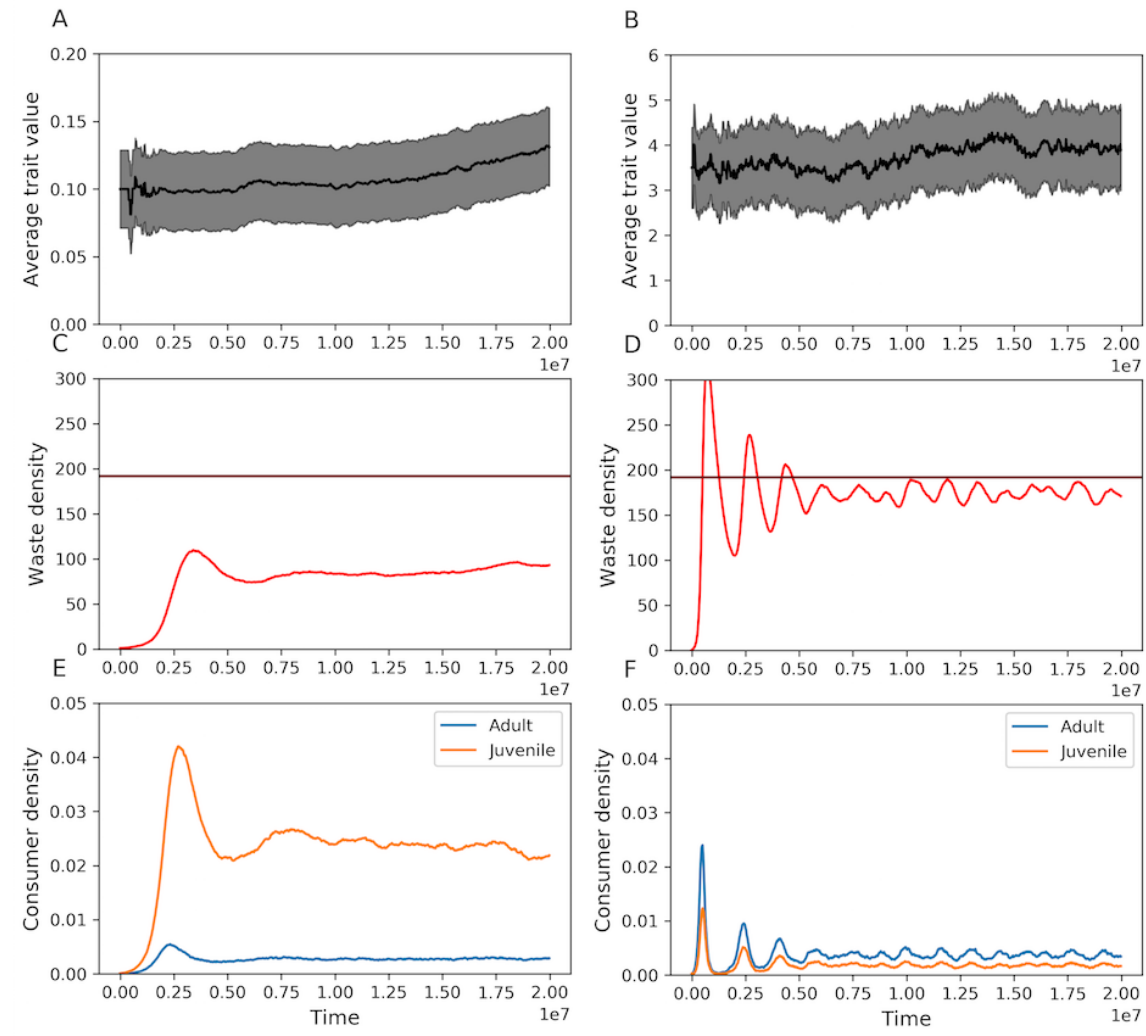


Figure 4: Simulations with slow population and waste dynamics compared to evolutionary dynamics. The dynamics of population and waste are three order of magnitude slower than in figure 3. Mutation rate is increased to  $m = 0.01$ . Red horizontal lines indicate the threshold for the waste density beyond which selection will favour lower growth rate. The gray area is the standard deviation of the trait value.

280 selection pressure is rather strong (left panels of figure 3). This will lead to a rapid increase of  
281 waste density. As the environment becomes polluted, the selection pressure for higher consumption  
282 is progressively eroded, so that evolution rapidly slows down. When the initial population possesses  
283 an already high juvenile consumption rate ( $c_J = 3.5$ ), the environment becomes instantly heavily



284 polluted and the waste density crosses the threshold. This leads to the counter selection of high  
285 trait values. Polluted environments then reduce population density, which subsequently leads to  
286 a decrease in the pollution level below the threshold. Higher consumption rates are then again  
287 favoured. However, as long as the pollution level is not too far below the threshold, selection  
288 pressure for higher consumption rates remains weak while population density is low, so that drift  
289 becomes increasingly important. Also, low population sizes lead to few mutations, further limiting  
290 evolution toward higher trait values. For all these reasons (limited mutations, weak selection,  
291 important drift), we observe that the trait value fluctuates around a quasistationary state that  
292 maintains the system close to the pollution threshold (right panels of figure 3).

293 When the population and waste dynamics are extremely slow whereas evolution remains rapid,  
294 a higher juvenile consumption rate is still selected for when the initial population has a small trait  
295 value (figure figure 4A). However, the increase in the trait value is much slower than when the  
296 population and waste dynamics are fast. When the initial population has a higher trait value, we  
297 observe a longer period of quasistationary state of the trait value (figure 4B). In both cases, the  
298 variation of the trait values is much higher than when the population and waste dynamics are fast.  
299 What is more interesting is that the quasistationary state is initially obtained as a result of counter  
300 selection of higher consumption rates because the waste density is above the threshold. However,  
301 in the long term, stasis in the trait is maintained mostly by drift, as the waste density remains  
302 slightly below the threshold most of the time (right panels of figure 4).

### 303 **Negative niche construction without intragenerational time lag**

304 Our results so far suggest that intragenerational time lag alone is not sufficient to prevent higher  
305 waste production. This requires both drift and rapid evolution. In this section, we revisit the  
306 unstructured system (1) and analyse whether including drift and rapid evolution is sufficient to  
307 avoid higher waste production.

308 We run simulations adopting the Tau-leap method just as we did for the structured system  
309 (3). We found that in all cases, selection for lower consumption rate that is linked to lower waste  
310 production, never takes place (figure 5) (more simulations with different parameter values can be

311 found in figure S. 7). The effect of drift is less significant in this case because the population density  
312 is large as higher consumption rate is now associated with higher reproduction rate. Selection for  
313 higher consumption rate is therefore stronger than the drift effect, and even quasistationary state  
314 of the trait value cannot be maintained. This result suggests that rapid evolution and drift do not  
315 suffice for the counter selection of negative niche construction, and that an intragenerational effect  
316 of niche construction is additionally required.

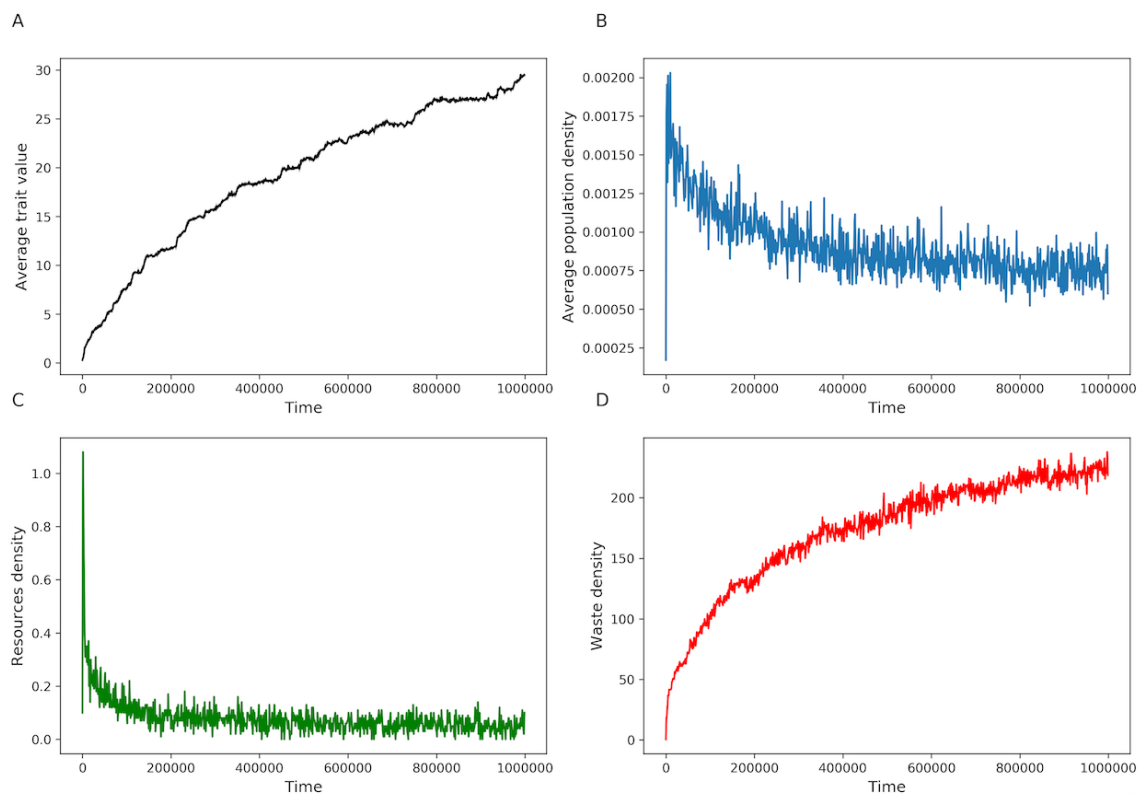


Figure 5: Simulation using Tau-leap method. Parameters:  $\rho = 2.3, d = 1.1, I_R = 3, \delta_R = 0.3, I_W : 3, \delta_W = 0.3, h = 1.1, v = 0.01, m = 0.1, \sigma = 0.2$ .

### 317 **3 Discussion**

318 Along their life cycles, organisms consume resources and produce metabolic wastes, which inev-  
319 itably results in resource depletion and pollution. Such environmental modifications may lead to  
320 population extinction if the resources become too scarce or the environment too toxic. These poor  
321 conditions can persist for a long period of time, and so do their negative effects on the organisms.  
322 This is often known as the time lag in niche construction or ecological inheritance (Odling-Smee  
323 et al. 2003; Danchin et al. 2011; Cuddington 2011).

324 In this article, we use mathematical models to study the evolution of negative niche construction  
325 manipulating explicitly three different timescales: population, niche construction, and evolution. In  
326 addition, because negative niche construction can be associated with decreasing population sizes,  
327 we also consider how these small population sizes can affect the evolutionary dynamics. In such  
328 conditions, mutations are limited and drift eventually compensates natural selection so that negative  
329 niche construction is slowed down. Our results also suggest that intragenerational time lag in niche  
330 construction is the precondition but rapid evolution is required for the counter selection of negative  
331 niche construction. In addition, drift plays a more important role than natural selection to maintain  
332 quasistationary states of the trait value.

333 Increasing environmental pollution is unavoidable under the adaptive dynamics approach, which  
334 assumes that the evolutionary timescale lags far behind the population and niche construction times-  
335 cale. A mutant with a higher reproduction rate always replaces a resident population despite the  
336 fact that it will worsen the environment for both of them. When the environment is heavily pol-  
337 luted, a strain that adopts an overexploitation strategy may die faster but it also reproduces faster  
338 to maintain its existence. Eventually, evolution leads to increasing pollution level and decreasing  
339 population density, possibly threatening the evolving population. This result has been observed in  
340 the study of Ratzke et al. (2018), in which a strain of soil bacteria increases the environmental PH,  
341 which in turn becomes toxic to the bacterial population. The bacterial population then collapses  
342 quickly because they cannot live in a highly acidic environment.

343 To prevent such tragedy of commons, direct benefits are usually added to positive niche con-

344 struction and direct costs are imposed on negative niche construction. For instance, Krakauer et al.  
345 (2009) shows that benefits can come from the ability of organisms to monopolise their niches and  
346 prevent free riders; Kylafis and Loreau (2010) and Chisholm et al. (2018) suggest that benefits could  
347 also be attributed to the ability to better exploit or adapt to the constructed niche. The benefits  
348 from positive niche construction in Lehmann (2008) comes from kinship and transgenerational time  
349 lag in niche construction.

350 In the present work, the cost on waste production lies in the intragenerational time lag in niche  
351 construction. This potentially creates a threshold of pollution beyond which strains that produce  
352 less waste and mature slower have more advantages than strains that mature fast but produce  
353 more waste. However, under the adaptive dynamics approach, the waste density always settles at  
354 its ecological equilibrium which is below the threshold. Therefore, the advantageous environment  
355 for having a slow maturation rate vanishes when mutations emerge. That is why rapid evolution  
356 is mandatory, where the evolutionary dynamics can be on a similar timescale as the waste and  
357 population dynamics. In such a case, high pollution levels may persist while strains with slow and  
358 fast maturation rates coexist. Juveniles who produce more waste mature faster into adults and  
359 pay a higher cost. By contrast, juveniles who produce less waste mature slower, remain juvenile  
360 for longer and pay a smaller cost. Halting negative niche construction also requires that adults are  
361 more vulnerable to pollution than juveniles. Here, the negative effects of pollution are shared among  
362 individuals but the costs on different strategies are unequal. In our model, rapid evolution allows  
363 rapid feedback loops between evolutionary dynamics, niche construction and population dynamics.  
364 It has been shown that such rapid feedback loops play a key role in the evolution of positive niche  
365 construction. In the studies of Weitz et al. (2016) and Tilman et al. (2020), reckless consumption  
366 cannot prevail. It is beneficial in a nutrient rich environment, and so the frequency of individuals  
367 that adopt this strategy will increase. However, along with this increase, they impoverish the  
368 environment and the reckless consumption strategy is now at a disadvantage compared to the  
369 prudent consumption strategy.

370 Evidence for rapid evolution is rich. For instance, changes in beak and body size of Darwin's  
371 finches and changes in the diapause timing of a copepod species happen within a few generations

372 (Grant and Grant 1995; Hairston and Dillon 1990). Many more examples can be found in Hairston  
373 et al. (2005) and Thompson (1998). Studies on the effect of intragenerational time lag of niche  
374 construction are however rare. A study of positive niche construction in *Coenobita compressus*,  
375 a terrestrial hermit crab, may give a hint of the importance of intragenerational time lag. *C.*  
376 *compressus* has been shown to be able to modify the shells they reside in (Laidre et al. 2012; Laidre  
377 2012a), and when they outgrow their current shell, they change to a bigger shell. Laidre (2012b)  
378 shows that the crabs prefer modified shells that have been used by other crabs because the modified  
379 shells increase their survivorship. The used shells that they abandoned will serve as new shells for  
380 other smaller and younger crabs. Here, “juveniles” are affected by positive niche construction  
381 activities of “adults”. As generations overlap, such modifications would still be considered as  
382 intragenerational time lags in our population structured framework. Importantly, juveniles and  
383 adults involved in this example do not have to be kin.

384 One important result is that in the long term, drift plays a key role in preventing the increase  
385 of waste production. Early rapid evolution leads to the selection of highly consumptive traits that  
386 lead to a heavily polluted environment. As the waste density may temporarily reach high values  
387 (above the threshold), strains that produce less waste can become temporarily advantageous. This  
388 then results in smaller population density and a less polluted environment in which strains that  
389 produce more waste and mature faster again have more advantage. However, as the environment  
390 becomes progressively occupied by many strains, the pollution level remains high. This situation  
391 has two immediate consequences: (i) population density is kept at a low value, and (ii) the selective  
392 force favouring higher waste production becomes very small. Drift then becomes dominant and  
393 evolutionary trajectories fluctuate without a clear direction (quasi stationary state). It should be  
394 noted that the effect of drift is specifically important in our model on negative niche construction  
395 because negative niche construction may lead to decreasing population size. We expect that the  
396 drift effects we observe may not be that important if niche construction is positive because positive  
397 niche construction by definition leads to higher fitness within the population which may often (but  
398 not always) lead to higher population sizes. Such higher population sizes should favour the action  
399 of natural selection over drift.

400 In our intragenerational model, we exclude the effect of resources availability on the selection  
401 pressure, which could be an important component to prevent the increase of waste production. In  
402 fact, Kawecki (1993) showed that if there is competition for resources among juveniles and adults,  
403 individuals that delay maturation may grow larger, obtain more resources and therefore produce  
404 more offspring than individuals that mature early. Future studies that take into account resources  
405 dynamics would provide a deeper understanding.

406 Our models are simple but they take into account two most fundamental elements: a niche  
407 constructing population and the niche construction dynamics. In nature, species do not live alone,  
408 and the most common mechanisms to prevent habitat degradation and population extinction are  
409 probably interactions among different species in a network. These interactions may open possibilities  
410 to new niches; negative effects for a species may be positive effects for others; and the complex  
411 feedback loops may maintain the stability of the whole network. This multidimensional aspect of  
412 niche construction is beyond the scope of the present article. Nevertheless, our study shows that  
413 rapid evolution, drift and intragenerational time lag in niche construction are important in delaying  
414 the spread of negative niche construction, therefore, it may buy more time for new species to come  
415 colonise and interact with the focal species and help establish a stable network. Lion et al. (2011)  
416 suggested that structured population, demographic and spatial alike, could favour the evolution  
417 of common goods and limit the spread of common “bads”. Our models suggest that a structure  
418 in time may contribute another dimension to the avoidance of such tragedies of commons. Here,  
419 time is particularly structured into population, niche construction and evolutionary dynamics, but  
420 it is not necessarily the only way. This further raises questions of how time could be structured in  
421 different ways.

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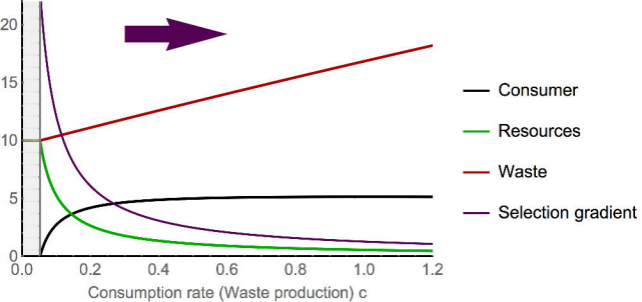
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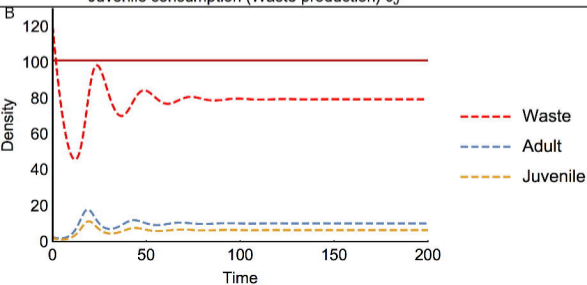
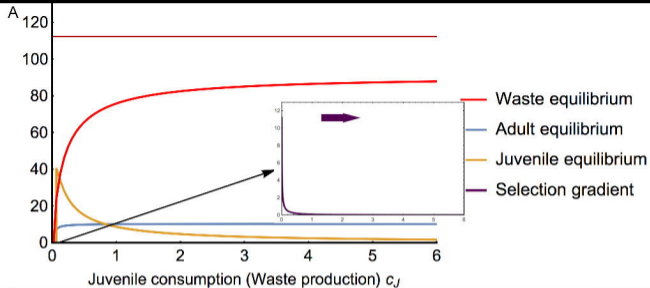


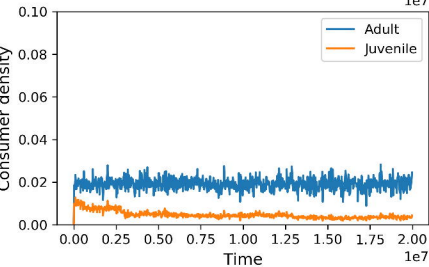
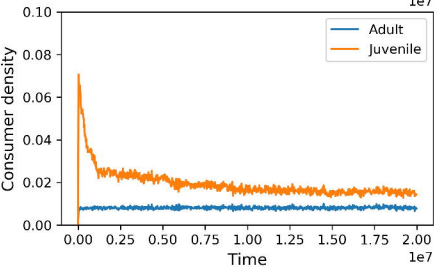
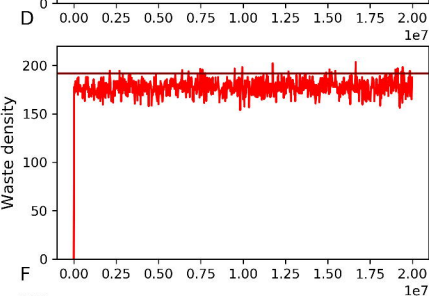
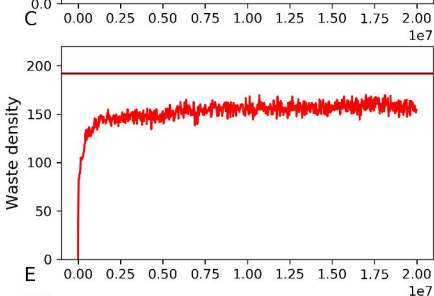
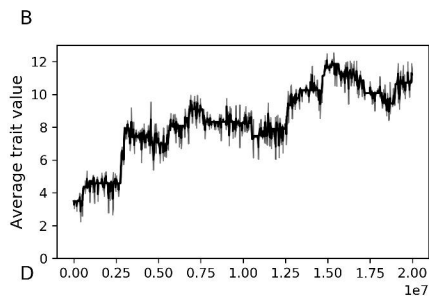
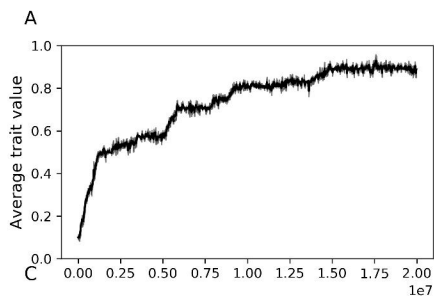
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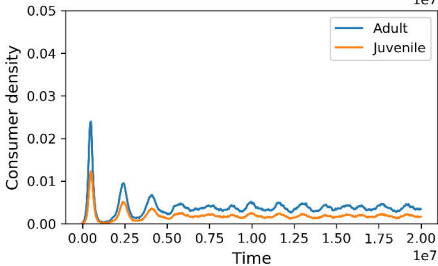
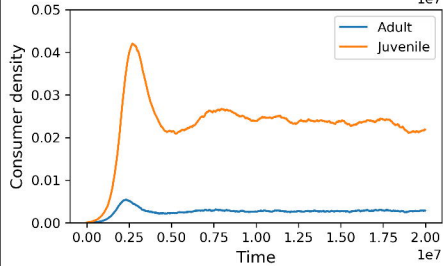
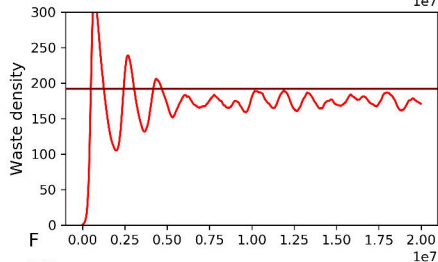
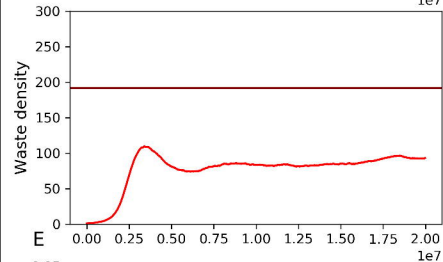
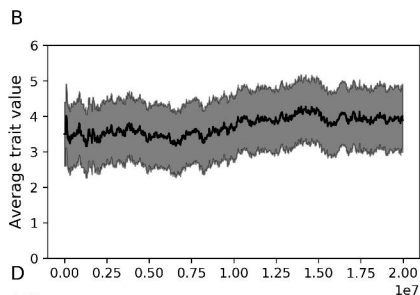
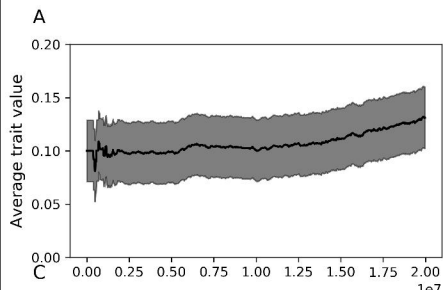
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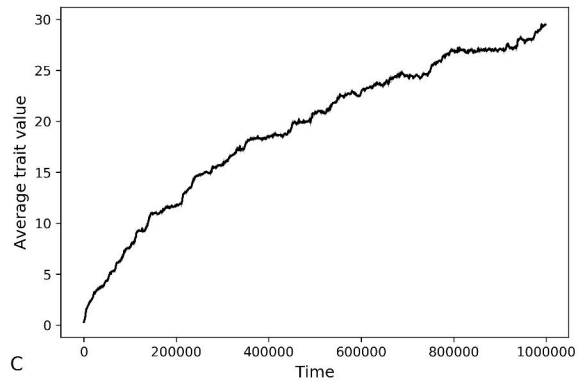




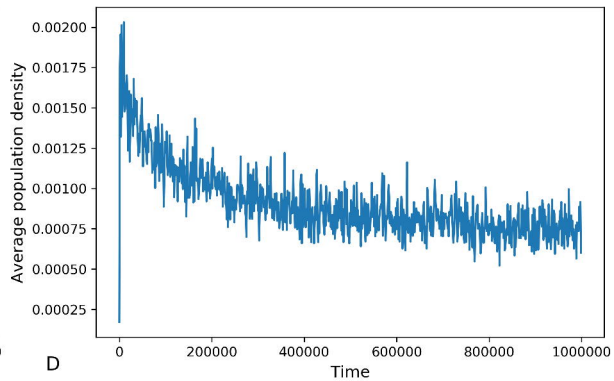




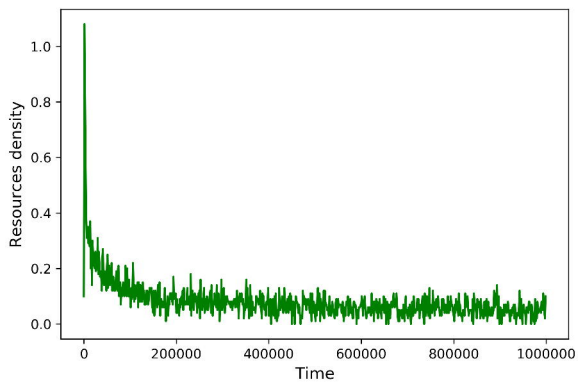
A



B



C



D

