

# Implication of drift and rapid evolution on negative niche construction

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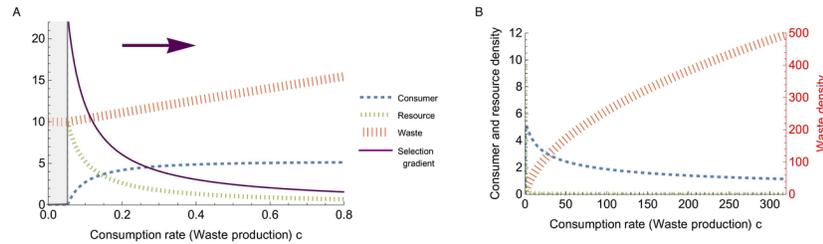
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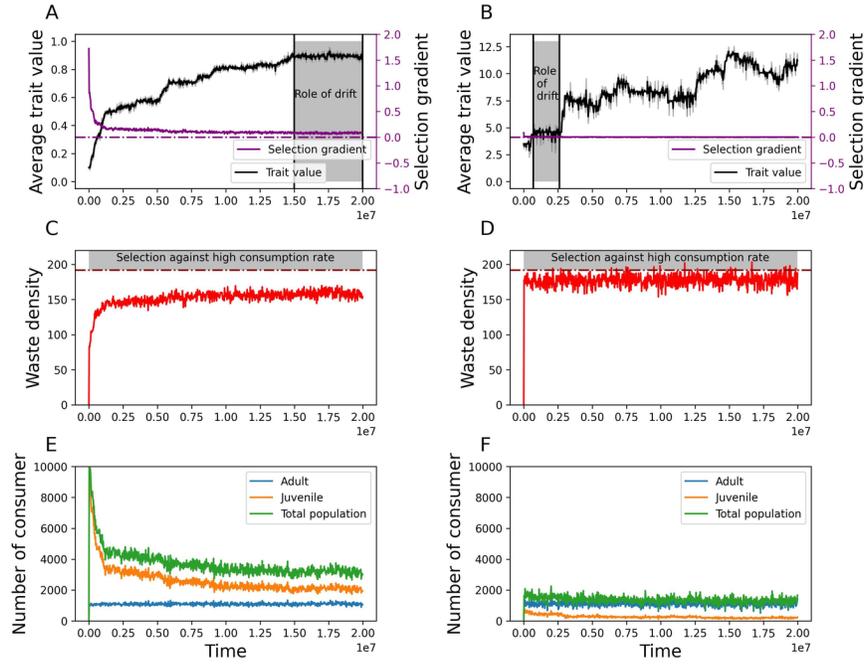
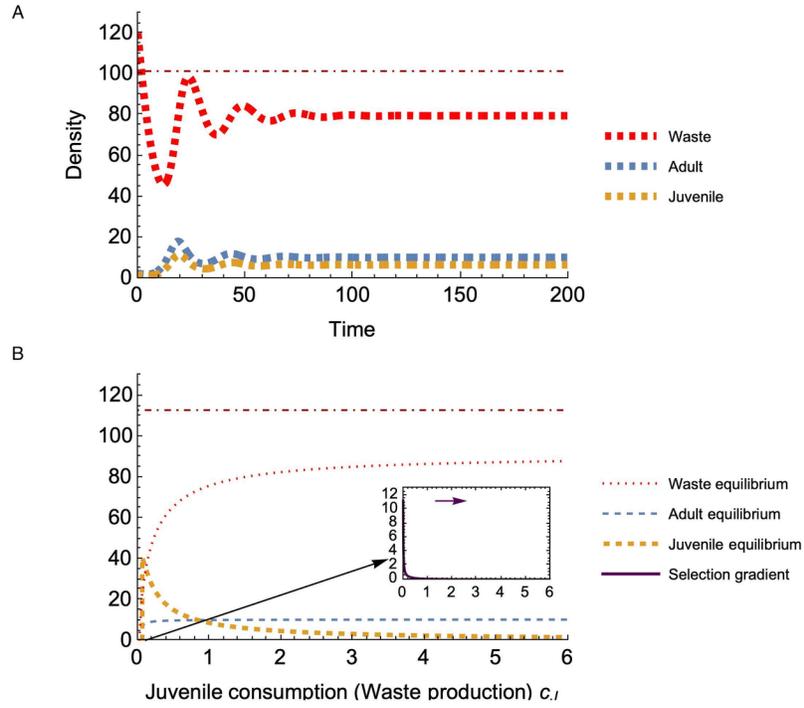
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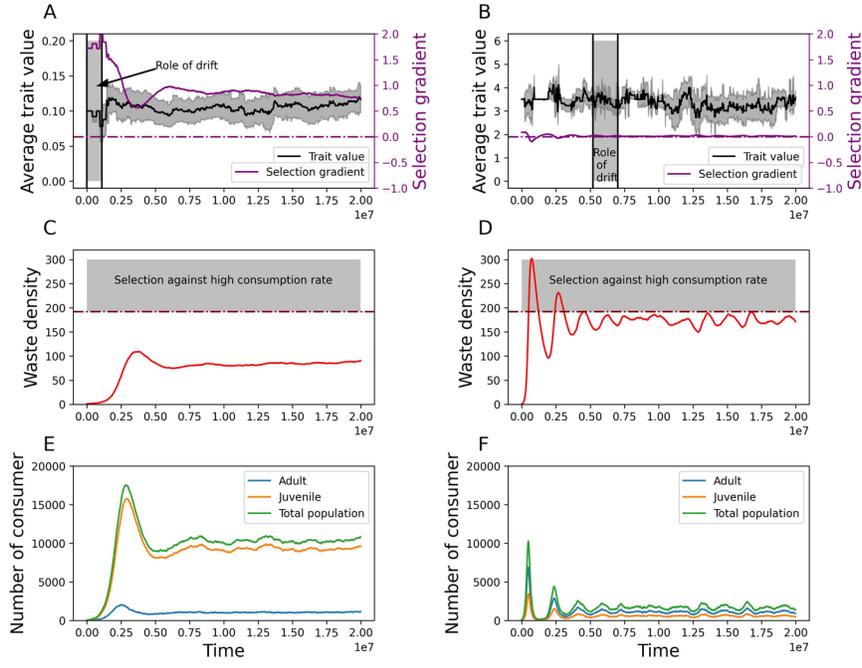
November 11, 2022

## Abstract

An important property of niche construction is that its consequences can persist for a long period of time, affecting several subsequent generations. This phenomenon is known as the niche construction time lags. Time lags in niche construction can result in the evolution of cooperation. Here, we study the evolutionary consequences of cooperation by incorporating time lags in a negative niche construction process. We consider a population that extrudes waste into its environment as it consumes resources. Higher consumption rates can lead to higher waste production, as it is associated with higher  $\textit{per capita}$  growth and reproduction rates. We showed that increasing consumption rates often evolve as pollution is equally experienced by the whole population while benefits are at the individual level. When we consider rapid evolution, intragenerational time lags, and stochasticity, however, such increases are no longer favoured and lower consumption rates resulting in less waste production can be an outcome. Interestingly, in the long term, drift becomes more important than natural selection, as selection becomes progressively weaker while population sizes are severely depressed by the cumulative effects of pollution.







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16 **Keywords:** Adaptive dynamics, Ecological inheritance, legacy effects, pollution, rapid evolu-  
17 tion, stochastic simulation, tragedy of the commons.

# 1 Introduction

Niche construction is a process whereby organisms modify their surrounding environment. It can be as sophisticated and noticeable to the human eye as beaver dams or termite mounds (Korb (2011); Naiman et al. (1988); Wright et al. (2002)). Yet, it can simply be a change in chemical concentrations induced by the activities of organisms, such as the enrichment of environmental oxygen by cyanobacteria billions of years ago (Mazard et al. (2016)). Any living being could be a niche constructor because by merely existing, organisms interact with their surrounding environment, thereby chemically and physically modifying it. The modified environment can in turn have ecological and evolutionary consequences on the organisms, which can be positive niche construction or negative niche construction when considering the fitness of individuals of the constructing species (Odling-Smee et al. (2003)). Environmental changes also affect other species that live within the same area (Hastings et al. (2007); Kidwell and Jablonski (1983)).

Environmental modifications due to niche construction can persist on long timescales, which are often known as legacy effects or ecological inheritance (Cuddington (2011); Danchin et al. (2011); Hastings et al. (2007); Odling-Smee et al. (2003)). In particular, changes in the niche can be experienced by individuals within a generation or between generations of a niche constructing species (Edeline et al. (2016); Hastings et al. (2007); Krebs and Davies (1993); Laland et al. (2000)). Understanding the evolutionary consequences of niche construction therefore requires careful consideration of three different timescales: population timescale, niche construction timescale, and evolutionary timescale. The population dynamic timescale encompasses all demographic processes of the niche constructor population. The niche construction timescale covers variations in the environment as a result of niche construction processes, including ecological inheritance. Finally, the evolutionary timescale refers to changes in gene frequencies, emergence and invasion of new mutants, or the birth and death of new species.

The three timescales interact in complex ways and do not necessarily match. For instance, a termite mound expands as the termite colony grows, which happens along the population dynamic timescale. Changes of the mound's size, shape and structure could then affect local environments for

45 millennia (Martin et al. (2018)), so that the niche construction timescale spans a long period of time.  
46 Such environmental changes can have large consequences, affecting vegetation patterns at various  
47 spatial scales (Ashton et al. (2019); Bonachela et al. (2015); Tarnita et al. (2017)) thereby creating  
48 new sources of selection that act on a long evolutionary timescale. The niche construction timescale  
49 may completely lag behind the population dynamic timescale. For instance, molluscs or crustaceans  
50 leave behind their shells when dead, which accumulate under the ocean. This gradually forms  
51 hard substrata, which may facilitate or inhibit the occupation of subsequent species (Kidwell and  
52 Jablonski (1983)). In this case, several populations may exist, reach their dynamical equilibrium,  
53 and even go extinct, while the dynamics of the constructed niche remain at its quasi-stable state.  
54 Within a short period, the dynamics of the constructed niche may not have a significant effect on a  
55 particular species. Given a sufficiently long period, however, they can have important evolutionary  
56 consequences on various species. Lags between the population and niche construction timescales  
57 need not be so extreme (Odling-Smee et al. (2003)). Relatively short intergenerational time-lags  
58 occur in earthworms where the worms modify soil properties, which have been suggested to make  
59 the environment favourable for the ancestors and their immediate future generations (although the  
60 benefits may last for many years) (Caro et al. (2014)). The time-lags can be intragenerational as  
61 shown in Edeline et al. (2016), in which juvenile and adult medaka fishes compete for the same  
62 resources. Adult fishes can be starved due to resources degradation by juveniles, which facilitates  
63 the evolution of semelparity.

64 Many theoretical frameworks tackling eco-evolutionary dynamics assume that variations in the  
65 ecological/environmental context happen on a shorter timescale that is separated from the long  
66 evolutionary timescale (Koch et al. (2014); Metz et al. (1995)). Given that niche construction  
67 processes may span a large timeframe, and that evolution can happen in a short timescale, we here  
68 propose to investigate how the interplay of the three time scales (i.e. population, niche construction,  
69 and evolution) affect evolutionary outcomes.

70 Effects of niche construction, positive or negative, are often experienced by coexisting individu-  
71 als, which often leads to the tragedy of the commons. Positive niche construction often comes with  
72 a cost for the niche constructing individuals, while benefits are shared among the whole popula-

73 tion. In the same vein, negative niche construction are experienced by the whole population, while  
74 the benefits are often private to the niche constructing individuals. It is thus often difficult for  
75 positive niche construction to evolve yet easy for negative niche construction to spread. To avoid  
76 this tragedy, classical theoretical studies include a direct benefit to the restriction of negative niche  
77 construction, or impose a direct cost by coercion and punishment, or add spatial structure and  
78 kinship (Rankin et al. (2007)). Even though eco-evolutionary feedback loops are taken into account  
79 in various work on the tragedy of the commons (Estrela et al. (2019)), explicit dynamics of the  
80 constructed niche are rarely considered. The eco-evolutionary feedback including niche construc-  
81 tion dynamics however play a key role in evolutionary outcomes (Estrela et al. (2019); Odling-Smee  
82 et al. (2003)).

83 To study the effects of niche construction and the impact of ecological inheritance on the evo-  
84 lution of cooperation, we explicitly include all three dynamics: population, niche construction and  
85 evolution, and consider possible lags among the three associated timescales. Transgenerational time  
86 lags in niche construction have been considered in various theoretical studies (Gurney and Lawton  
87 (1996); Laland et al. (1996); Lehmann (2007)), our work specifically considers intergenerational  
88 time lags. We focus on the evolution of negative niche construction, in particular, the production of  
89 wastes, which are metabolites such as lactic acid, acetate, or hydrogen in cases of bacteria (Fuchs  
90 (1999)), or more complex material such as excrement or toxin in other groups (Balali-Mood et al.  
91 (2016); Bot et al. (2001)). These substances have been shown to be toxic to the population, es-  
92 pecially when their concentrations are high (Balali-Mood et al. (2016); Bot et al. (2001); Pinhal  
93 et al. (2019); Ratzke and Gore (2018); Ratzke et al. (2018)). Waste production is assumed to be  
94 positively linked to consumption rates such that individuals that consume more produce more waste  
95 (Besiktepe and Dam (2002); Tanner et al. (2019); Zarco-Perello et al. (2019)). Higher consumption  
96 rates may be associated with higher reproduction, growth or maturation rates (Greenberg et al.  
97 (2003); Morton (1986)). This is consistent with the metabolic theory, where metabolic rates, and  
98 hence catabolism and waste production, is intimately linked to intrinsic growth rate (Brown et al.  
99 (2004)). A high rate of waste production may mean higher individual fitness, but it can lead to  
100 higher pollution in the environment, which in turn imposes negative effects on the whole popula-

101 tion. When such negative effects lead to smaller population sizes, drift can play an increasingly  
102 important role. Genetic drift has been shown to be crucial in many evolutionary processes, espe-  
103 cially when natural selection force is weak and population sizes are small (Gonzalez-Quevedo et al.  
104 (2015); Veller et al. (2017)). We also consider the effect of drift in our work.

105 We found that negative niche construction is generally favoured, leading to populations prone  
106 to extinction in many cases. However, when evolutionary timescale overlaps with the population  
107 and niche construction timescales, introducing intragenerational time lags in niche construction  
108 establishes conditions that prevent the negative niche constructing activities. Interestingly, on the  
109 long evolutionary course, drift plays an increasing role compared to natural selection, and even  
110 becomes the main factor to impede the negative niche construction.

## 111 2 Model

112 The analysis is structured as follows: we first use an adaptive dynamics approach to investigate  
113 scenarios of slow evolutionary dynamics (Geritz et al. (1998); Metz et al. (1995)). Under this frame-  
114 work, we incorporate intragenerational time lags using a structured population model with juvenile  
115 and adult stages. The intragenerational time lags imply that juveniles construct an environment  
116 that will be experienced by adults. An individual may benefit from a niche construction activity  
117 conducted when being juvenile, but it then suffers the negative effect when becoming adult.

118 We then relax the assumption of slow evolution in the adaptive dynamics approach using the  
119 Tau-leap simulation (Gillespie (2001)). This algorithm enables overlaps between the evolutionary  
120 timescale, the population timescale, and the niche construction timescale. We denote these overlaps  
121 as rapid evolution. The algorithm allows us to study the effect of drift because birth and death events  
122 are modelled as stochastic processes. As negative niche construction can lead to smaller population  
123 sizes, the drift component may eventually dominate selection and become the key evolutionary  
124 force, especially when selective pressures become weak.

## 125 2.1 A complete lag of the evolutionary timescale

### 126 2.1.1 Negative niche construction without intragenerational time lags

127 We adapt a resource-consumer model (Chesson (1990); MacArthur (1969)), adding waste dynamics,  
128 and using a chemostat dynamic for both resources ( $R$ ) and wastes ( $W$ ). Our model focuses on a  
129 species ( $S$ ) that consumes a resource at a rate  $c$ , where increasing  $c$  results in more offspring but  
130 also a higher rate of waste production, which add mortality  $v$  to the population. The ODEs that  
131 describe the whole system can be written as

$$\begin{cases} \frac{dR}{dt} = -cRS + I_R - \delta_R R & (1a) \\ \frac{dW}{dt} = hcS + I_W - \delta_W W & (1b) \\ \frac{dS}{dt} = crRS - dS - vWS & (1c) \end{cases}$$

133 where  $d$  is the natural mortality rate of the consumer.  $I_W/\delta_W$  and  $I_R/\delta_R$  are the turn-over rates  
134 of the waste and resource dynamics respectively. Definitions of the parameters and variables can  
135 be found in table 1. System (1) has three equilibria: a trivial equilibrium where the species does  
136 not survive, a non-feasible equilibrium where the density of the species is always negative, and an  
137 equilibrium where the species persists. This positive equilibrium, which is always stable, requires  
138 that the consumption rate is sufficiently larger than a threshold value (details of the equilibrium  
139 and its stability are in supplementary 1).

140 We study the evolution of the consumption rate  $c$  and show that, without any constraint, the  
141 selection gradient on the consumption rate is always positive so that higher consumption rates  
142 are always favoured (figure 1) (supplementary 2). Here, we use the adaptive dynamics approach,  
143 which assumes that the resident population always approach its ecological equilibrium when a  
144 mutant with a different consumption rate appears. The approach focuses on the role of selection  
145 and is completely deterministic, such that drift is not taken into account at this stage. On the  
146 course of evolution, the population of consumer increases at first because higher consumption rates  
147 mean higher reproduction rates (figure 1A). However, it eventually decreases asymptotically to zero

148 when increasing consumption rates are exactly balanced by increased costs due to pollution and  
 149 resource degradation (figure 1B) (see supplementary 3 for analytical results). Note that the selection  
 150 pressure remains positive, but its magnitude constantly decreases and becomes vanishingly small as  
 151 the consumption rate increases (figure 1A), indicating that the selective force becomes progressively  
 152 weaker.

153 Here, there is no direct individual cost on overexploitation and pollution. All individuals,  
 154 consumptive or frugal, share the damage caused by high pollution levels and resource degradation,  
 155 but the benefits from higher reproduction is attributed immediately to the consumptive individuals.  
 156 As a consequence, selection of higher consumption rates is inevitable.

### 157 2.1.2 Negative niche construction with intragenerational time lags

158 We introduce a cost to higher consumption rate by including intragenerational time lags. To do this,  
 159 we use an age-structured population where a consumer has a juvenile stage ( $J$ ) and an adult stage  
 160 ( $A$ ). Here, we make a couple of simplifications to better understand how the environment affects the  
 161 selective pressure. First, we focus on the negative construction, which is the increase in pollution  
 162 levels, and disregard the dynamics of resources. The resources  $R$  is now simply a parameter.  
 163 Juveniles mature into adults at a rate that is proportional to their consumption rate  $c_J$ . Higher  
 164 consumption rates of juveniles are associated with faster maturity and higher waste production.  
 165 Adults excrete waste into the environment at a rate  $p_A$ , which we assume no relationship with  
 166 juvenile's waste production. Environmental waste adds mortality on all individuals, but adults and  
 167 juveniles have different vulnerabilities to pollution ( $v_J$  and  $v_A$  for juveniles and adults respectively).  
 168 Definitions of each parameter can be found in table 1. The ODEs that describe the dynamics of  
 169 the system read

$$\begin{cases}
 \frac{dJ}{dt} = \rho RA - d_J J - v_J W J - c_J R J & (2a) \\
 \frac{dA}{dt} = c_J R J - d_A A - v_A W A & (2b) \\
 \frac{dW}{dt} = I_W - \delta_W W + h c_J J + p_A A & (2c)
 \end{cases}$$

171

172 The population dynamics are now entirely governed by the waste dynamics. There is thus no  
 173 resource competition among individuals, adult and juvenile alike. Our model becomes similar to  
 174 models of maturation (Gardmark et al. (2003); Poos et al. (2011); Roos et al. (2007)), except that  
 175 we do not consider a trade-off between adult reproduction and juvenile maturation, a common  
 176 assumption of these models. Including such a trade-off would indeed lead to an intrinsic constraint  
 177 of the negative niche construction activity, which, similar to the study of Kylafis and Loreau (2008),  
 178 may result in selection of lower negative niche construction. Our work aims to investigate whether  
 179 reductions in negative niche construction may arise only from variations in the different timescales,  
 180 and thus do not include any intrinsic cost.

181 System (2) has three equilibria: one trivial equilibrium where no adults and juveniles can  
 182 survive, one equilibrium where the waste density is always negative, and one equilibrium that is  
 183 positive if the reproduction ratio of the consumer is greater than one (the details can be found  
 184 in supplementary 4). We consider the evolution of the consumption rate of juveniles. A mutant  
 185 with a consumption rate  $c_{Jm}$  that is different from that of a resident  $c_J$ , can invade the resident  
 186 population if its reproduction ratio  $F_m$  is greater than one (see supplementary 5), where

$$187 \quad F_m = \frac{c_{Jm}R}{D_{Jm}} \frac{\rho R}{D_{Am}} \quad (3)$$

189 Here,  $1/D_{Jm} = 1/(d_J + c_{Jm}R + v_JW^*)$  is the expected time a mutant spends as a juvenile,  
 190 and  $1/D_{Am} = 1/(d_A + v_AW^*)$  is the expected time a mutant spends as an adult.  $W^*$  is the waste  
 191 density set by the resident at equilibrium. Expression (3) suggests that higher consumption rate  
 192 may lead to faster maturation, but adults who rapidly mature from juveniles are then exposed to  
 193 pollution, and might die before they can even reproduce. Lower consumption rates can be selected  
 194 if the selection gradient is negative, which is equivalent to

$$\begin{cases} v_A > v_J & (4a) \\ W^*(c_J) > \frac{d_J + \rho R - d_A}{v_A - v_J} & (4b) \end{cases}$$

Condition (4) suggests that the sign of the selection gradient uniquely depends on the pollution level created by the resident (details on the selection gradient can be found in supplementary 5). Condition (4a) implies that adults have to be more vulnerable to pollution than juveniles. Intuitively, if juveniles are more prone to pollution than adults, those who mature slower remain juvenile for a longer time and suffer pollution, whereas those who mature faster escape the (more vulnerable) juvenile state. Selection then always favours higher consumption rate of juveniles. Thus, in order for lower consumption rates to be selected, adults have to be more vulnerable to pollution than juveniles. The second condition (4b) implies that if the waste density at equilibrium is sufficiently large, the environment becomes too toxic, and lower consumption rate may be selected. At this stage, condition (4b) is evaluated under the assumptions of adaptive dynamics, that is, the waste density is always at its equilibrium  $W^*(c_J)$  when a mutant arises. We show that  $W^*(c_J)$  is always lower than the right-hand side and condition (4b) can never be satisfied (figure 2, supplementary 6). It means that the fitness gradient is always positive, resulting in continuously selection for higher values of the trait (figure 2 B, figure S2, S3, supplementary 6). As a result, if the evolutionary timescale is decoupled from the population and niche construction timescale, i.e. evolution process is extremely slow compared to ecological process, incorporating intragenerational time lags in niche construction can hardly prevent higher consumption rates.

The results of this model are much similar to those of the model without intragenerational time-lags in that they suggest the inevitable of excessive consumption rates. Both models show that as the consumption rate increases, the selection gradient continuously weaken and nearly vanishes, and the population sizes declines due to accumulated pollution. These two conditions suggest the role of drift, which we focus on in the following sections.

## 218 **2.2 Rapid evolution and the role of drift**

219 We relax the assumption of slow evolution such that mutation happens even when the waste density  
220 does not yet settle at its equilibrium (i.e. condition (4b) can be satisfied). In addition, we introduce  
221 stochasticity in the population dynamics to study the role of genetic drift. We use the Tau-leap  
222 algorithm where the birth-death processes are drawn randomly from a distribution that depends  
223 on the consumption rate. The algorithm allows a direct manipulation of the evolutionary timescale  
224 through changing mutation rates (Gillespie (2001)). A pseudocode to run the algorithm can be  
225 found in supplementary 7. Rapid evolution scenarios explicitly imply higher mutation rates, and  
226 thus, overlaps between the three timescales, but do not indicate stronger selection as in Hairston  
227 et al. (2005) (in fact, the evolutionary speed could vary in the simulations). In our simulations,  
228 when rapid evolution takes place, multiple strains with different consumption rates co-occur while  
229 the ecological dynamics need not settle at equilibrium.

230 In contrast with the adaptive dynamics approach where population variations are deterministic  
231 and small populations never reach extinction in finite time, in stochastic simulations, the fate of  
232 small populations may be determined by random components more than by differences in fitness.  
233 Stochastic simulations allow us to consider drift. In each simulation, we start with a monomorphic  
234 population and an initial value of waste density that is drawn from a uniform distribution with a  
235 range of  $[10, 100]$ . Such initial values allow the existence of initial populations that are sufficiently  
236 large, in an environment that is not too polluted.

237 Consistent with the results of the deterministic model (adaptive dynamics approach), higher  
238 consumption rates of juveniles are initially selected, as we always start the simulation with relatively  
239 low pollution levels. Increasing consumption rates leads to a heavily polluted environment (figure  
240 3C, D), which has two effects: a weak selection pressure for high consumption rate (figure 3 A, B)  
241 and low population sizes (figure 3 E, F). Low population sizes allow a strong effect of drift that easily  
242 compensate for the extremely weak selection gradient. As a result, the increase in the consumption  
243 rate eventually slows down and quasi-stationary states of the trait value can be obtained.

244 In particular, starting from a small consumption rate ( $c_J = 0.1$ ), higher trait values are imme-

245 diately selected because the selection pressure is strong (left column of figure 3). Such an increase  
246 rapidly raise the waste density, although it never crosses the threshold beyond which the selection  
247 gradient is negative (figure 3C). Yet, quasi-stationary state of the consumption rates is possible.  
248 This is because the selection pressure for higher consumption rates is progressively eroded while  
249 adult density is low because they are more vulnerable to pollution than juveniles (figure 3E). The  
250 combined conditions of weak selection and small population sizes favours drift over natural selec-  
251 tion. That is why, individuals with higher consumption rates cannot dominate and spread readily  
252 even though nature selection favours them, while individuals with lower consumption rates per-  
253 sist for a long period of time (quasi-stationary state). When starting from a higher consumption  
254 rate ( $c_J = 3.5$ ), the environment becomes instantly heavily polluted, and waste density occasion-  
255 ally crosses the threshold above which the selection gradient becomes negative, favouring lower  
256 consumption rates (right column of figure 3). However, the pollution rapidly settle below the  
257 threshold, resulting in positive selection gradient most of the time (3B, D). What then keeps the  
258 consumption rate in stasis for several short intervals is mainly genetic drift because again, in this  
259 case, adult population sizes are extremely small suggesting very few mutations, and the selection  
260 gradient is extremely weak (it is very close to zero) (figure 3B, F).

261 When the population and waste dynamics are extremely slow whereas the mutation rate is  
262 high, the trait variation is much larger than when the mutation rate is moderate (figure 4A, B).  
263 Higher consumption rates of juveniles are still favoured when starting from a small trait value, as  
264 the selection gradient is highly positive (left column of figure 4, figure S9A). However, the trait  
265 value increases much slower and even stays at the quasi-stationary state compared to the case  
266 of relatively moderate mutation rate and rapid population and waste dynamics. The underlying  
267 reason is that when ecological dynamics are slow and the consumption rates of juveniles are small,  
268 the adult population is scant in the beginning as maturation is delayed. The effects of drift become  
269 much stronger than natural selection even though the selection pressure remains high (figure 4A,  
270 E). In the case of rapid ecological dynamics (left column of figure 3), there is an immediate surge  
271 in the adult population in the beginning, and combining with a strong selection pressure, the  
272 average consumption rate increases rapidly before settling at its quasi-stationary state when the

273 selection pressure weakens and drift takes over. Starting at a higher consumption rate, the waste  
274 density crosses the threshold for a longer period of time due to the slow ecological dynamics, and  
275 lower consumption rates are selected at this interval (right column of figure 4, figure S8B, S9B).  
276 Interestingly, negative selections for higher consumption rates only occur in the beginning of the  
277 course of evolution. As the waste dynamics reach the threshold, the population regulates itself  
278 at a very small density (4F), which also stabilizes the waste density near but rarely above the  
279 threshold. Again, what keeps the consumption rates from increasing is the effect of drift because  
280 the two conditions for drift to dominate (small population size and weak selection) are satisfied. A  
281 robustness analysis confirms that such dynamics occur for various sets of parameters (figure S4 -  
282 S12 in supplementary 9).

### 283 **3 Discussion**

284 In this article, we use mathematical models to study the evolution of negative niche construction,  
285 manipulating explicitly three different timescales: population, niche construction, and evolution.  
286 Negative niche construction can be associated with decreasing population sizes, we thus consider  
287 how these small population sizes can affect evolutionary dynamics. In such conditions, mutations  
288 are limited and drift eventually compensates natural selection so that negative niche construction is  
289 slowed down. Our results suggest that intragenerational time lags in niche construction and rapid  
290 evolution are required for the counter selection of negative niche construction. As population sizes  
291 becomes smaller and selection gradient weaker, drift eventually dominates natural selection, leading  
292 to quasi-stationary states of the trait value.

293 Increasing environmental pollution is unavoidable under the adaptive dynamics approach, which  
294 assumes that the evolutionary timescale lags far behind the population and niche construction  
295 timescales. A mutant with a higher consumption rate always replaces a resident population, despite  
296 the fact that it worsens the environment for both of them. When the environment is heavily  
297 polluted, a strain that adopts an overexploitation strategy may die faster, but it also reproduces  
298 faster than strains that adopt more prudent strategies. Eventually, consumptive strains are favoured

299 and evolution leads to increasing pollution levels and decreasing population densities, possibly  
300 threatening the evolving population. Such dynamics may be related to empirical observations. For  
301 instance, Ratzke et al. (2018) investigates a situation in which a strain of soil bacteria increases  
302 the environmental PH, which in turn becomes toxic to the bacterial population. The bacterial  
303 population eventually collapses due to highly acidic conditions.

304 Most theoretical studies usually consider direct benefits or costs to avoid a systematic directional  
305 selection. For instance, Krakauer et al. (2009) proposes that benefits can come from the ability  
306 of organisms to monopolize their niches and prevent free riders. Kylafis and Loreau (2010) and  
307 Chisholm et al. (2018) suggest that benefits could also be attributed to the ability to better exploit  
308 or adapt to the constructed niche. Benefits from positive niche construction in Lehmann (2007)  
309 come from kinship and transgenerational time lags in niche construction. In the present work,  
310 we do not incorporate a direct cost for higher values of consumptive strategies. Rather, the cost  
311 lies in the intragenerational time lags in niche construction. This creates a potential threshold of  
312 pollution, above which strains that produce less waste and mature slower could in theory be selected.  
313 Limiting negative niche construction also requires that adults are more vulnerable to pollution than  
314 juveniles. More importantly, the evolutionary timescale has to overlap with the population and  
315 niche construction timescale. In other words, we need to relax the assumption of slow evolution in  
316 the adaptive dynamics framework. When evolution is slow and mutants are rare, long term waste  
317 density settles at its ecological equilibrium, which is always below the threshold beyond which low  
318 consumption rates are selected. The advantageous environment for having a low consumption rate  
319 is never reached in the long term. When the timescale of evolutionary dynamics overlaps with  
320 those of the waste and population dynamics, high pollution levels may be transiently reached, and  
321 lower consumption rates are temporarily selected. Here, the negative effects of pollution are shared  
322 among individuals but the costs on different strategies and stages of life are unequal.

323 In our model, rapid evolution is extremely important because it allows rapid feedback loops  
324 between evolutionary dynamics, niche construction and population dynamics. Indeed, it has been  
325 shown that such rapid feedback loops play a key role in the evolution of positive niche construction.  
326 In the studies of Weitz et al. (2016) and Tilman et al. (2020), reckless consumption cannot prevail.

327 It is beneficial in a nutrient rich environment, and so the frequency of individuals that adopt this  
328 strategy will increase. However, along with this increase, they impoverish the environment and  
329 the reckless consumption strategy is now at a disadvantage compared to the prudent consumption  
330 strategy.

331 One important result of our model is that in the long term, drift plays a key role in preventing  
332 the increase of waste production. Early in the course of evolution, selection strongly favours higher  
333 consumption rates, resulting in heavy pollution. As the waste density may temporarily reach high  
334 values (above the threshold where the selection gradient on consumption rate is negative), strains  
335 that produce less waste can become temporarily advantageous. This results in smaller population  
336 sizes and a less polluted environment, in which strains that consume more and produce more waste  
337 are again selected. Pollution levels however remain near the threshold. This situation has two  
338 immediate consequences: (i) population sizes are kept at a small value, and (ii) the selective force  
339 favouring higher waste production becomes very small. Drift then dominates and evolutionary  
340 trajectories fluctuate without a clear direction (i.e. quasi-stationary state). It should be noted that  
341 this effect of drift is specifically important here because negative niche construction may lead to  
342 decreasing population size. We expect that the drift effects may not be that important if niche  
343 construction is positive because positive niche construction by definition leads to higher fitness  
344 within the population, which may often (but not always) lead to higher population sizes. Such  
345 higher population sizes should favour the action of natural selection over drift.

346 Drift alone is not sufficient to stop increasing consumption rates. In fact, without intragen-  
347 erational time lags between population and niche construction, higher consumption rates evolve  
348 continuously in all cases and quasi-stationary state cannot be maintained. This is shown in the  
349 Tau-leap simulations for the system without intragenerational time lags (figure S13, figure S14).  
350 This result suggests that higher consumption rates can easily spread unless all three conditions  
351 are met: rapid evolution, stochasticity in the dynamics (i.e. genetic drift), and intragenerational  
352 time lags in niche construction. More interestingly, intragenerational time lags select for lower  
353 consumption rate in the short term while in the long term, evolution of stasis in consumption rates  
354 is maintained largely by drift when population is small and selection becomes weak.

355 In our intragenerational model, we exclude resource dynamics. This allows us to simplify niche  
356 construction dynamics, making them uni-dimensional, that is, we only consider waste production.  
357 Therefore, we are able to focus on the aspect of relative time scales and on the role of drift. Resource  
358 dynamics, however, could be an important component affecting the evolution of the consumption  
359 trait. For instance, Kawecki (1993) showed that if there is competition for resources among juveniles  
360 and adults, individuals that delay maturation may grow larger, obtain more resources and therefore  
361 produce more offspring than individuals that mature early. Such a situation would substantially  
362 shift the selective pressures here acting on the consumption trait. Studying the two-dimensional  
363 feedback loop of niche construction (resource vs pollution levels) would be a natural extension of  
364 the present work.

365 We kept our models simple and focused on a monospecific situation in order to have deeper  
366 insights into the effect of time lags and drift. In nature, species do not live alone, and niche  
367 construction may substantially lead to indirect effects in natural communities. Such interactions  
368 among different species may open new niches. Moreover, negative effects for a species could be  
369 positive effects for others, such that niche construction may lead to complex feedback loops and  
370 affect the stability of the whole network. This multidimensional and multispecies aspect of niche  
371 construction go beyond the scope of the present article. Our models show that rapid evolution, drift  
372 and intragenerational time lags in niche construction can be key to delay the spread of negative  
373 niche construction. They may thereby allow more time for new species to colonize and interact with  
374 the focal species and help establish a stable network. Lion et al. (2011) suggested that structured  
375 population, demographic and spatial alike, could favour the evolution of common goods and limit  
376 the spread of common bads. Our study suggests that a structure in time may add another dimension  
377 to the avoidance of the tragedy of commons.

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Table 1: Definitions of variables and parameters of system (1) and (2)

Variables and parameters	Definition
$R$	Resource density
$W$	Waste density
$S$	Consumer density
$c$	Consumption rate of system (1)
$I_R$	Resource influx
$\delta_R$	Resource outflux
$I_W$	Waste influx
$\delta_W$	Waste outflux
$r$	Efficiency of converting resource into new individuals
$d$	Natural death rate of the consumer (system (1))
$v$	Vulnerability to pollution of the consumer (system (1))
$h$	Intensity of waste production
$J$	Juvenile density
$A$	Adult density
$\rho$	Reproduction rate of adults
$c_J$	Consumption rate of juveniles
$p_A$	Rate of waste production of adults
$d_J, d_A$	Natural death rate of respectively juveniles and adults (system (2))
$v_J, v_A$	Vulnerability to pollution of respectively juveniles and adults (system (2))

## Figure legends

Figure 1: Changes in the equilibrium value ( $W^*(c), R^*(c), S^*(c)$ ) of system (1) with respect to the trait value. The population goes extinct in the gray area. The arrow indicates the direction of selection. A) When the trait value ranges from  $[0, 1.2]$ , B) When the trait value ranges from  $[0, 320]$ . Parameters:  $r = 2.3, d = 1.1, I_R = 3, \delta_R = 0.3, I_W = 3, \delta_W = 0.3, v = 0.01, h = 0.4$

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

Figure 3: Simulations with moderately fast population and waste dynamics compared to evolutionary dynamics, mutation rate is  $m = 0.001$ . A, C, E) The starting population has a small consumption rate  $c_J = 0.1$ . B, D, F) The starting population has a larger consumption rate  $c_J = 3.5$ . Other parameters for dynamics of populations and waste:  $d_J = d_A = 0.1, h_J = 1.1, v_J = 0.0001, v_A = 0.01, I_W = 0.3, \delta_W = 0.13, \rho = 1.9, p_A = 0.001, V = 100$ . Parameters for evolutionary dynamics  $\sigma = 0.02$  for small consumption rate and  $\sigma = 0.7$  for large consumption rate. The dashed-dotted horizontal line indicates the threshold for the waste density above which selection favours smaller consumption rates. The gray area around the average trait value indicates the standard deviation of the trait value. The gray area within the black vertical line is an example when drift takes over natural selection (i.e. selection gradient is positive but higher consumption rate is not selected).

Figure 4: Simulations with slow population and waste dynamics compared to evolutionary dynamics. The dynamics of population and waste are three orders of magnitude slower than in figure 3. Mutation rate is increased to  $m = 0.01$ . The annotations and legends are the same as in figure 3.