

1 Abstract

2 An important property of niche construction is that its consequences can persist for a long period of
3 time, affecting several subsequent generations. This phenomenon is known as the niche construction
4 time lags.

5 Time lags in niche construction can result in the evolution of cooperation. Here, we study the
6 evolutionary consequences of cooperation by incorporating time lags in a negative niche construction
7 process. We consider a population that extrudes waste into its environment as it consumes resources.
8 Higher consumption rates can lead to higher waste production, as it is associated with higher *per*
9 *capita* growth and reproduction rates.

10 We showed that increasing consumption rates often evolve as pollution is equally experienced by
11 the whole population while benefits are at the individual level. When we consider rapid evolution,
12 intragenerational time lags, and stochasticity, however, such increases are no longer favoured and
13 lower consumption rates resulting in less waste production can be an outcome. Interestingly, in the
14 long term, drift becomes more important than natural selection, as selection becomes progressively
15 weaker while population sizes are severely depressed by the cumulative effects of pollution.

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-

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

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

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

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

2 Model

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

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

2.1 A complete lag of the evolutionary timescale

2.1.1 Negative niche construction without intragenerational time lags

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

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

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

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

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

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

2.1.2 Negative niche construction with intragenerational time lags

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

2.2 Rapid evolution and the role of drift

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

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

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

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

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

3 Discussion

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

Increasing environmental pollution is unavoidable under the adaptive dynamics approach, which assumes that the evolutionary timescale lags far behind the population and niche construction timescales. A mutant with a higher consumption rate always replaces a resident population, despite the fact that it worsens the environment for both of them. When the environment is heavily polluted, a strain that adopts an overexploitation strategy may die faster, but it also reproduces 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.

References

- L. A. Ashton, H. M. Griffiths, C. L. Parr, T. A. Evans, R. K. Didham, F. Hasan, Y. A. Teh, H. S. Tin, C. S. Vairappan, and P. Eggleton. Termites mitigate the effects of drought in tropical rainforest. *Science*, 363(6423):174–177, 2019. doi: 10.1126/science.aau9565. URL <https://doi.org/10.1126/science.aau9565>.
- Mahdi Balali-Mood, Adel Ghorani-Azam, and Bamdad Riahi-Zanjani. Effects of air pollution on human health and practical measures for prevention in iran. *Journal of Research in Medical Sciences*, 21(1):65, 2016. doi: 10.4103/1735-1995.189646. URL <https://doi.org/10.4103/1735-1995.189646>.
- S Besiktepe and HG Dam. Coupling of ingestion and defecation as a function of diet in the calanoid copepod *acartia tonsa*. *Marine Ecology Progress Series*, 229:151–164, 2002. doi: 10.3354/meps229151.
- Juan A. Bonachela, Robert M. Pringle, Efrat Sheffer, Tyler C. Coverdale, Jennifer A. Guyton, Kelly K. Caylor, Simon A. Levin, and Corina E. Tarnita. Termite mounds can increase the robustness of dryland ecosystems to climatic change. *Science*, 347(6222):651–655, February 2015. doi: 10.1126/science.1261487. URL <https://doi.org/10.1126/science.1261487>.
- A.N.M. Bot, C.R. Currie, A.G. Hart, and J.J. Boomsma. Waste management in leaf-cutting ants. *Ethology Ecology & Evolution*, 13(3):225–237, July 2001. doi: 10.1080/08927014.2001.9522772. URL <https://doi.org/10.1080/08927014.2001.9522772>.
- James H. Brown, James F. Gillooly, Andrew P. Allen, Van M. Savage, and Geoffrey B. West. Toward a metabolic theory of ecology. *Ecology*, 85(7):1771–1789, July 2004. doi: 10.1890/03-9000. URL <https://doi.org/10.1890/03-9000>.
- Gael Caro, Christian Hartmann, Thibaud Decaens, Sebastien Barot, Philippe Mora, and Jerome Mathieu. Impact of soil engineering by two contrasting species of earthworms on their dispersal rates. *Applied Soil Ecology*, 84:223–230, 2014. doi: 10.1016/j.apsoil.2014.08.004. URL <https://doi.org/10.1016/j.apsoil.2014.08.004>.

404 S. P. Carroll, P. S. Jorgensen, M. T. Kinnison, C. T. Bergstrom, R. F. Denison, P. Gluckman, T. B.
 405 Smith, S. Y. Strauss, and B. E. Tabashnik. Applying evolutionary biology to address global
 406 challenges. *Science*, 346(6207):1245993–1245993, 2014. doi: 10.1126/science.1245993.

407 Peter Chesson. MacArthur’s Consumer- Resource Model. *Theoretical Population Biology*, 37:26–38,
 408 1990. doi: 10.1016/0040-5809(90)90025-q .

409 Rebecca H. Chisholm, Brian D. Connolly, Benjamin Kerr, and Mark M. Tanaka. The role of
 410 pleiotropy in the evolutionary maintenance of positive niche construction. *The American Natu-*
 411 *ralist*, 192(1):35–48, July 2018. doi: 10.1086/697471. URL <https://doi.org/10.1086/697471>.

412 Kim Cuddington. Legacy effects: The persistent impact of ecological interactions. *Bi-*
 413 *ological Theory*, 6(3):203–210, September 2011. doi: 10.1007/s13752-012-0027-5. URL
 414 <https://doi.org/10.1007/s13752-012-0027-5>.

415 Étienne Danchin, Anne Charmantier, Frances A. Champagne, Alex Mesoudi, Benoit Pujol, and
 416 Simon Blanchet. Beyond DNA: integrating inclusive inheritance into an extended theory of
 417 evolution. *Nature Reviews Genetics*, 12(7):475–486, June 2011. doi: 10.1038/nrg3028. URL
 418 <https://doi.org/10.1038/nrg3028>.

419 Eric Edeline, Osamu Terao, and Kiyoshi Naruse. Empirical evidence for competition-driven semel-
 420 parity in wild medaka. *Population Ecology*, 58(3):371–383, June 2016. doi: 10.1007/s10144-016-
 421 0551-4. URL <https://doi.org/10.1007/s10144-016-0551-4>.

422 Sylvie Estrela, Eric Libby, Jeremy Van Cleve, Florence Debarre, Maxime Deforet, William R.
 423 Harcombe, Jorge Pena, Sam P. Brown, and Michael E. Hochberg. Environmentally mediated
 424 social dilemmas. *Trends in Ecology & Evolution*, 34(1):6 – 18, 2019. ISSN 0169-5347. doi:
 425 <https://doi.org/10.1016/j.tree.2018.10.004>.

426 G Fuchs. Diversity of metabolic pathways. In *Biology of the Prokaryotes*, pages 163–232. Blackwell
 427 Science, 1999.

- 428 A. Gardmark, U. Dieckmann, and P. Lundberg. Life-history evolution in harvested populations:
429 the role of natural predation. *Evolutionary Ecology Research*, 5:239–257, 2003.
- 430 S.A.H. Geritz, É. Kisdi, G. Meszéna, and J.A.J. Metz. Evolutionarily singular strategies and the
431 adaptive growth and branching of the evolutionary tree. *Evolutionary Ecology*, 12(1):35–57, Jan-
432 uary 1998. doi: 10.1023/a:1006554906681. URL <https://doi.org/10.1023/a:1006554906681>.
- 433 Daniel T. Gillespie. Approximate accelerated stochastic simulation of chemically reacting systems.
434 *The Journal of Chemical Physics*, 115(4):1716–1733, July 2001. doi: 10.1063/1.1378322. URL
435 <https://doi.org/10.1063/1.1378322>.
- 436 Catalina Gonzalez-Quevedo, Lewis G. Spurgin, Juan Carlos Illera, and David S. Richardson. Drift,
437 not selection, shapes toll-like receptor variation among oceanic island populations. *Molecular*
438 *Ecology*, 24:5852–5863, 2015 . doi: <https://doi.org/10.1111/mec.13437>.
- 439 S. M. Greenberg, T. W. Sappington, D. W. Spurgeon, and M. Sétamou. Boll weevil (coleoptera:
440 Curculionidae) feeding and reproduction as functions of cotton square availability. *Environmental*
441 *Entomology*, 32(3):698–704, 2003. doi: 10.1603/0046-225x-32.3.698.
- 442 W. S. C. Gurney and J. H. Lawton. The population dynamics of ecosystem engineers. *OIKOS*, 76:
443 273–283, 1996. doi: 10.2307/3546200.
- 444 Nelson G. Hairston, Stephen P. Ellner, Monica A. Geber, Takehito Yoshida, and Jen-
445 nifer A. Fox. Rapid evolution and the convergence of ecological and evolutionary time.
446 *Ecology Letters*, 8(10):1114–1127, 2005. doi: 10.1111/j.1461-0248.2005.00812.x. URL
447 <https://doi.org/10.1111/j.1461-0248.2005.00812.x>.
- 448 Alan Hastings, James E. Byers, Jeffrey A. Crooks, Kim Cuddington, Clive G. Jones, John G.
449 Lambrinos, Theresa S. Talley, and William G. Wilson. Ecosystem engineering in space and time.
450 *Ecology Letters*, 10(2):153–164, February 2007. doi: 10.1111/j.1461-0248.2006.00997.x. URL
451 <https://doi.org/10.1111/j.1461-0248.2006.00997.x>.

452 Tadeusz J. Kawecki. Age and size at maturity in a patchy environment: Fitness maximiza-
 453 tion versus evolutionary stability. *Oikos*, 66(2):309, 1993. doi: 10.2307/3544819. URL
 454 <https://doi.org/10.2307/3544819>.

455 S.M. Kidwell and D. Jablonski. *Taphonomic Feedback Ecological Consequences of Shell Accumula-*
 456 *tion*, volume 3. Springer, 1983. doi: https://doi.org/10.1007/978-1-4757-0740-3_5.

457 Hanna Koch, Jens Frickel, Martha Valiadi, and Lutz Becks. Why rapid, adap-
 458 tive evolution matters for community dynamics. *Frontiers in Ecology and Evo-*
 459 *lution*, 2:17, 2014. ISSN 2296-701X. doi: 10.3389/fevo.2014.00017. URL
 460 <https://www.frontiersin.org/article/10.3389/fevo.2014.00017>.

461 Judith Korb. *Termite Mound Architecture, from Function to Construction*, pages 349–373. Springer
 462 Netherlands, Dordrecht, 2011. ISBN 978-90-481-3977-4. doi: 10.1007/978-90-481-3977-4_13.
 463 URL https://doi.org/10.1007/978-90-481-3977-4_13.

464 David C. Krakauer, Karen M. Page, and Douglas H. Erwin. Diversity, dilemmas, and monopolies
 465 of niche construction. *The American Naturalist*, 173(1):26–40, 2009. doi: 10.1086/593707.

466 John R. Krebs and Nicholas B. Davies. Predators versus prey: Evolutionary arms races. In *An*
 467 *Introduction to Behavioural Ecology (Third Edition)*, chapter 4, pages ”77–101”. Wiley-Blackwell,
 468 1993.

469 Grigoris Kylafis and Michel Loreau. Ecological and evolutionary consequences of niche construc-
 470 tion for its agent. *Ecology Letters*, 11(10):1072–1081, October 2008. doi: 10.1111/j.1461-
 471 0248.2008.01220.x. URL <https://doi.org/10.1111/j.1461-0248.2008.01220.x>.

472 Grigoris Kylafis and Michel Loreau. Niche construction in the light of niche theory. *Ecol-*
 473 *ogy Letters*, 14(2):82–90, November 2010. doi: 10.1111/j.1461-0248.2010.01551.x. URL
 474 <https://doi.org/10.1111/j.1461-0248.2010.01551.x>.

475 K. N. Laland, F. J. Odling-Smee, and M. W. Feldman. The evolutionary consequences of
 476 niche construction: a theoretical investigation using two-locus theory. *Journal of Evo-*

477 *lutionary Biology*, 9(3):293–316, 1996. doi: 10.1046/j.1420-9101.1996.9030293.x. URL
 478 <https://onlinelibrary.wiley.com/doi/abs/10.1046/j.1420-9101.1996.9030293.x>.

479 Kevin N. Laland, John Odling-Smee, and Marcus W. Feldman. Niche construction, biological
 480 evolution, and cultural change. *Behavioral and Brain Sciences*, 23(1):131–146, 2000. ISSN 0140-
 481 525X. doi: 10.1017/S0140525X00002417.

482 Laurent Lehmann. The adaptive dynamics of niche constructing traits in spatially subdivided
 483 populations: Evolving posthumous extended phenotypes. *Evolution*, 62(3):549–566, 2008. doi:
 484 10.1111/j.1558-5646.2007.00291.x.

485 Sébastien Lion, Vincent A.A. Jansen, and Troy Day. Evolution in structured populations: beyond
 486 the kin versus group debate. *Trends in Ecology & Evolution*, 26(4):193–201, April 2011. doi:
 487 10.1016/j.tree.2011.01.006. URL <https://doi.org/10.1016/j.tree.2011.01.006>.

488 Robert Mac Arthur. Species packing, and what competition minimizes. *PNAS*, 64(4):1369–1371,
 489 1969. doi: 10.1073/pnas.64.4.1369.

490 Stephen J. Martin, Roy R. Funch, Paul R. Hanson, and Eun-Hye Yoo. A vast 4, 000-year-old
 491 spatial pattern of termite mounds. *Current Biology*, 28(22):R1292–R1293, November 2018. doi:
 492 10.1016/j.cub.2018.09.061. URL <https://doi.org/10.1016/j.cub.2018.09.061>.

493 Sophie Mazard, Anahit Penesyan, Martin Ostrowski, Ian Paulsen, and Suhelen Egan. Tiny microbes
 494 with a big impact: The role of cyanobacteria and their metabolites in shaping our future. *Marine*
 495 *Drugs*, 14(5):97, 2016. doi: 10.3390/md14050097. URL <https://doi.org/10.3390/md14050097>.

496 J.A.J. Metz, S.A.H. Geritz, G. Meszena, F.J.A. Jacobs, and J.S. van Heerwaarden. Adaptive
 497 dynamics: A geometrical study of the consequences of nearly faithful reproduction. Iiasa working
 498 paper, IIASA, Laxenburg, Austria, 1995. URL <http://pure.iiasa.ac.at/id/eprint/4497/>.

499 Brian Morton. Reproduction, juvenile growth, consumption and the effects of starvation upon
 500 the south china sea whelk *hemifusus tuba* (gmelin) (prosobranchia: Melongenidae). *Journal*

501 *of Experimental Marine Biology and Ecology*, 102(2):257 – 280, 1986. ISSN 0022-0981. doi:
502 [https://doi.org/10.1016/0022-0981\(86\)90181-4](https://doi.org/10.1016/0022-0981(86)90181-4).

503 Robert J. Naiman, Carol A Johnston, and James C. Kelley. Alteration of north american streams
504 by beaver. *BioScience*, 38(11):753–762, 1988. doi: 10.2307/1310784.

505 F. John Odling-Smee, Kevin N. Laland, and Marcus W. Feldman. *Niche Construction*.
506 Princeton University Press, 2003. ISBN 0691044376. doi: 10.2307/j.ctt24hqpd. URL
507 <https://doi.org/10.2307/j.ctt24hqpd>.

508 Stéphane Pinhal, Delphine Ropers, Johannes Geiselmann, and Hidde de Jong. Acetate metabolism
509 and the inhibition of bacterial growth by acetate. *Journal of Bacteriology*, 201(13), July 2019.
510 doi: 10.1128/jb.00147-19. URL <https://doi.org/10.1128/jb.00147-19>.

511 J.J. Poos, Å. Brännström, and U. Dieckmann. Harvest-induced maturation evolu-
512 tion under different life-history trade-offs and harvesting regimes. *Journal of The-*
513 *oretical Biology*, 279(1):102–112, June 2011. doi: 10.1016/j.jtbi.2011.03.001. URL
514 <https://doi.org/10.1016/j.jtbi.2011.03.001>.

515 Daniel Rankin, Katja Bargum, and Hanna Kokko. The tragedy of the commons in evolution-
516 ary biology. *Trends in Ecology & Evolution*, 22(12):643–651, 2007. ISSN 0169-5347. doi:
517 10.1016/j.tree.2007.07.009.

518 Christoph Ratzke and Jeff Gore. Modifying and reacting to the environmental pH can drive bacterial
519 interactions. *PLOS Biology*, 16(3):e2004248, March 2018. doi: 10.1371/journal.pbio.2004248.
520 URL <https://doi.org/10.1371/journal.pbio.2004248>.

521 Christoph Ratzke, Jonas Denk, and Jeff Gore. Ecological suicide in microbes. *Nature Ecology*
522 *& Evolution*, 2(5):867–872, 2018. ISSN 2397-334X. doi: 10.1038/s41559-018-0535-1. URL
523 <https://doi.org/10.1038/s41559-018-0535-1>.

524 Andre M. De Roos, Tim Schellekens, Tobias van Kooten, Karen van de Wolfshaar, David Claessen,
525 and Lennart Persson. Food-dependent growth leads to overcompensation in stage-specific

526 biomass when mortality increases: The influence of maturation versus reproduction regula-
527 tion. *The American Naturalist*, 170(3):E59–E76, September 2007. doi: 10.1086/520119. URL
528 <https://doi.org/10.1086/520119>.

529 Richelle L. Tanner, Lindsay E. Faye, and Jonathon H. Stillman. Temperature and salinity sensitivity
530 of respiration, grazing, and defecation rates in the estuarine eelgrass sea hare, *phyllaplysia taylori*.
531 *Marine Biology*, 166(8), 2019. doi: 10.1007/s00227-019-3559-4.

532 Corina E. Tarnita, Juan A. Bonachela, Efrat Sheffer, Jennifer A. Guyton, Tyler C. Coverdale,
533 Ryan A. Long, and Robert M. Pringle. A theoretical foundation for multi-scale regular veg-
534 etation patterns. *Nature*, 541(7637):398–401, January 2017. doi: 10.1038/nature20801. URL
535 <https://doi.org/10.1038/nature20801>.

536 John N Thompson. Rapid evolution as an ecological process. *Trends in Ecology & Evolution*, 13
537 (8):329 – 332, 1998. ISSN 0169-5347. doi: [https://doi.org/10.1016/S0169-5347\(98\)01378-0](https://doi.org/10.1016/S0169-5347(98)01378-0). URL
538 <http://www.sciencedirect.com/science/article/pii/S0169534798013780>.

539 Andrew R. Tilman, Joshua B. Plotkin, and Erol Akçay. Evolutionary games with environmental
540 feedbacks. *Nature Communications*, 11(1):915, 2020. ISSN 2041-1723. doi: 10.1038/s41467-020-
541 14531-6. URL <https://doi.org/10.1038/s41467-020-14531-6>.

542 Carl Veller, Pavitra Muralidhar, George W A Constable, and Martin A Nowak. Drift-Induced
543 Selection Between Male and Female Heterogamety. *Genetics*, 207(2):711–727, 2017. doi:
544 <https://doi.org/10.1534/genetics.117.300151>.

545 Joshua S. Weitz, Ceyhun Eksin, Keith Paarporn, Sam P. Brown, and William C. Ratcliff. An
546 oscillating tragedy of the commons in replicator dynamics with game-environment feedback.
547 *Proceedings of the National Academy of Sciences*, 113(47):E7518–E7525, November 2016. doi:
548 10.1073/pnas.1604096113. URL <https://doi.org/10.1073/pnas.1604096113>.

549 Justin P. Wright, Clive G. Jones, and Alexander S. Flecker. An ecosystem engineer, the beaver,
550 increases species richness at the landscape scale. *Oecologia*, 132(1):96–101, 2002. ISSN 00298549,
551 14321939. URL <http://www.jstor.org/stable/4223313>.

552 Salvador Zarco-Perello, Tim J. Langlois, Thomas Holmes, Mathew A. Vanderklift, and Thomas
553 Wernberg. Overwintering tropical herbivores accelerate detritus production on temperate
554 reefs. *Proceedings of the Royal Society B: Biological Sciences*, 286(1915):20192046, 2019. doi:
555 10.1098/rspb.2019.2046.

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
δ_R	Resource outflux
I_W	Waste influx
δ_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
ρ	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.