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Coevolution of species colonisation rates controls food-chain length in spatially structured food webs

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Abstract

How the complexity of food webs depends on environmental variables is a long-standing ecological question. It is unclear though how food-chain length should vary with adaptive evolution of the constitutive species. Here we model the evolution of species colonisation rates and its consequences on occupancies and food-chain length in metacommunities. When colonisation rates can evolve, longer food-chains can persist. Extinction, perturbation and habitat loss all affect evolutionarily stable colonisation rates, but the strength of the competition-colonisation trade-off has a major role: weaker trade-offs yield longer chains. Although such eco-evo dynamics partly alleviates the spatial constraint on food-chain length, it is no magic bullet: the highest, most vulnerable, trophic levels are also those that least benefit from evolution. We provide qualitative predictions regarding how trait evolution affects the response of communities to disturbance and habitat loss. This highlights the importance of eco-evolutionary dynamics at metacommunity level in determining food-chain length.

KEY WORDS

dispersal, eco-evolutionary dynamics, habitat destruction, metacommunity, patch occupancy model

INTRODUCTION

An important puzzle in ecology is how food web topology, and in particular food-chain length, is determined (Cohen & Briand, 1984; Cohen & Newman, 1988; Hutchinson, 1959; May, 1983; Pimm, 1982; Stenseth, 1985; Williams & Martinez, 2004). Food-chain length is a measure of the number of feeding links between resources and top predators (e.g. Sabo et al., 2009). Ecological theory has long tried to understand what limits this length. For instance, the energetic constraint hypothesis (Hutchinson, 1959) invokes imperfect transfers of energy and resources along food chains, the dynamics constraint hypothesis (Pimm & Lawton, 1977) argues that long food chains are more vulnerable to perturbation than short ones, and the community area hypothesis

combines the diversity-area relationship of island biogeography (MacArthur & Wilson, 1967) with the link scaling law (Cohen & Briand, 1984) to predict a concave increase in food-chain length with habitat area (Cohen & Newman, 1991). Empirical studies have identified three major determinants of food-chain length: productive space (i.e. ecosystem size \times productivity), disturbance and ecosystem size (Post, 2002). While confirming the roles of resource limitation and perturbation, these results argue against single explanations, and also stress the need to incorporate space in theoretical models. Indeed, despite ample evidence that food-chain length correlates with habitat area or ecosystem size (Post et al., 2000; Schoener, 1989; Takimoto et al., 2008), spatial processes are still understudied in theoretical models of food webs (Amarasekare, 2008; Holt, 2002). Calcagno

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et al. (2011) extended the model of Holt (2002) to provide predictions under conditions encompassing top-down and habitat selection effects, while Pillai et al. (2011) studied the effect of colonisation rates on the complexity of food webs at the metacommunity level. More recently, Wang et al. (2021) reanalysed a similar ecological model of spatial food chains to assess how metacommunity dynamics should influence maximum food-chain length. They rendered the model spatially realistic and provided some empirical support for its predictions in a butterfly-parasitoid system.

The spatial structure of populations, on the other hand, has inspired a prolific research line in evolutionary biology, namely the evolution of dispersal (Duputié & Massol, 2013; Ronce, 2007). Indeed, there has been an early realisation that spatial structure, beyond its population dynamical consequences, also imposed strong selection pressures, and that the key parameter in this context, the colonisation, dispersal or migration rate, could be shaped by evolution. Several selective forces should act on the dispersal rate, and determine its evolutionarily stable value, depending among others on patch size, connectivity, spatio-temporal environmental variability and dispersal costs. In the case of metapopulation occupancy models (Hastings, 1980; Levins, 1969; Tilman, 1994), one can translate a purely ecological statement of the problem ('what is the occupancy of competing species when they obey a competition-colonisation trade-off?', Calcagno et al., 2006) into an evolutionary question ('how should this competition-colonisation trade-off drive the evolution of colonisation rates of co-existing species?', Aubree et al., 2020). This leads to investigating the eco-evolutionary dynamics of adaptation of colonisation rates in a metacommunity.

These two lines of research have often remained disconnected. The rising recognition that ecological and evolutionary processes are feeding themselves in feedback loops (Hendry, 2017; Loreau, 2010; McPeck, 2017) suggests that they should be considered together when modelling and analysing biodiversity patterns. In spatially structured ecological systems, the environmental structure is known to influence the evolution of dispersal (Laroche et al., 2016; Massol et al., 2011), while the evolution of the dispersal rate may affect ecological patterns (Aubree et al., 2020; Laroche et al., 2016), for example, through the spatial structuring of diversity within and among species. We also know that the outcome of species interactions can be affected by considering the evolutionary dynamics, as shown by Osmond et al. (2017) for predator-prey interactions with predators favouring the persistence of preys when they sufficiently increase their adaptedness. What happens in longer food chains has, however, not been sufficiently considered.

The purpose of this article was precisely to connect the ecological limit on food-chain length and the evolutionary dynamics of dispersal, and to determine how they can interact. Two distinct constraints on food-chain

length arising from metacommunity structure have been identified. First, bounded colonisation rates limit predator occupancy to a subset of prey-occupied sites. Second, extinction rates accumulate along food chains. For instance, if prey go extinct at a rate of 1 year^{-1} and predators also go extinct on their own at a rate of 1 year^{-1} , predators effectively go extinct at a rate of 2 year^{-1} because they cannot persist locally without their prey. Both processes concur to decrease maximal and average food-chain length in metacommunities. In an eco-evolutionary framework, the evolution of colonisation rates in response to competition within trophic levels might mitigate the two constraints. Here, we investigate this question by incorporating evolutionarily explicit adaptive change into a metacommunity model. This model allows assessing how habitat destruction and extinction rates induce adaptive changes in colonisation rates, and how these alter predictions compared to metacommunities that do not evolve. The model is specifically used to predict how food-chain length responds to environmental deterioration when evolution is taken into account.

MODEL AND METHODS

Spatial food chain model

We model the dynamics of the fraction q_i of patches containing trophic level i . In such a patch, all lower trophic levels are present (Figure 1), but the upper trophic levels can be present or absent. The dynamics of q_i are expressed similarly to Levins' metapopulation model (as in Calcagno et al., 2011 and similarly to Wang et al., 2021):

$$\frac{dq_i}{dt} = c_i q_i (q_{i-1} - q_i) - (\langle e_i \rangle + \mu) q_i \quad (1)$$

where for the first trophic level ($i=1$), $q_0 = h$ is the proportion of habitat patches available (Nee & May 1992; level 0 is therefore not counted in food-chain length), μ is the perturbation rate, which causes all trophic levels to disappear simultaneously, $\langle e_i \rangle$ is the extinction rate experienced by species i (more explicitly defined below) and c_i is its colonisation rate. A fully developed set of equations is described in Appendix S1 for a two-level trophic chain.

The effective extinction rate $\langle e_i \rangle$ is experienced independently by each trophic level, and incorporates a basal extinction rate e , potentially modified by bottom-up and top-down effects. Bottom-up effects reflect the fact that if a given trophic level goes extinct in a patch, all upper trophic levels must go extinct too. Top-down effects represent how the presence of upper trophic levels may increase extinction of the focal trophic level, for example, through a reduction of local population size. If an occupied site also contains the $i+1$ trophic level (probability $= q_{i+1} / q_i$), top-down effects increase the extinction rate

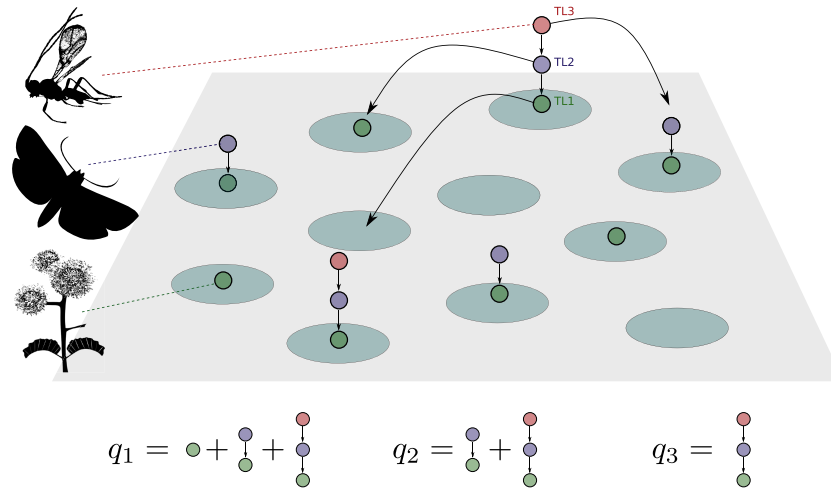


FIGURE 1 A graphical illustration of the spatial food chain model. The habitat consists of many interconnected patches. Each patch can be colonised by one or more trophic levels. The first trophic level can colonise any empty available habitat patch, whereas the second trophic level can only colonise patches where the first trophic level is found, etc. Each trophic level can disappear from a patch at some basal extinction rate e , and local extinction of one trophic level causes the local extinction of all upper trophic levels. Patches can also undergo catastrophic perturbation events, at rate μ , causing all trophic levels to be removed at once. The dynamical variables of interest in Equation (1) are the q_i , that is, the proportion of patches occupied by the i th trophic level (and possibly upper trophic levels too), as illustrated at the bottom of the figure. Images of organisms are from phylopic.org.

by some constant e_{TD} . This yields $\langle e_i \rangle$ to be expressed as $e + (i - 1)(e + e_{TD}) + e_{TD}q_{i+1}/q_i$ (Calcagno et al., 2011; Wang et al., 2021).

Evolutionary dynamics of colonisation rate

The above model has been studied for arbitrary, fixed, colonisation rates (Calcagno et al., 2011). Here, we further let colonisation rates evolve under the effect of natural selection (other parameters are fixed). Metapopulation structure (i.e. the subdivision of a large population into smaller populations connected by costly dispersal and the occurrence of local extinctions) is known to control selection pressures on dispersal, and hence on colonisation rate (Duputié & Massol, 2013). Two forces select for higher dispersal rates: the presence of empty available patches (Comins et al., 1980) and kin competition. Conversely, dispersal is counter-selected by competitive trade-offs, that is, the fact that high dispersal rates come at the expense of local growth and/or competitive strength, which is the case when dispersal is costly. We here use a simple representation of these evolutionary dynamics, which can be derived from competition-colonisation trade-offs (Calcagno et al., 2017), or alternatively from spatially structured population models (Appendix S1). The model incorporates the three selective forces listed above, and yields the following equation for the dynamics of c_i :

$$\frac{dc_i}{dt} = V_G [(q_{i-1} - q_i) + (\phi + 2c_i\psi)q_i] \quad (2)$$

V_G represents the genetic variance in colonisation (from a quantitative genetics perspective, Lande, 1979; see Dieckmann & Law, 1996 for an alternative interpretation). The other two evolutionary parameters describe the strength of the trade-off between local competitiveness and colonisation (Appendix S1). ϕ is the probability that immigrants replace residents with identical colonisation rates. It falls in (0,1), and can also be understood as a within-patch relatedness coefficient (Appendix S1). Parameter ψ is the (negative) slope quantifying how much increasing colonisation rate comes at the expense of decreased local competitiveness (i.e. dispersal is costly). The first term in brackets represents positive selection for dispersal due to the presence of empty patches (fraction $q_{i+1} - q_i$), and the second term $(\phi + 2c_i\psi)q_i$ represents the (usually negative) selection caused by local competition. More specifically, ϕ represents the (weak) positive selection caused by kin competition (Appendix S1), whereas the term involving ψ represents counter-selection imposed by competitive trade-offs and costs of dispersal.

Equation (2) admits a unique positive equilibrium that is always convergence stable and is an evolutionarily stable strategy (ESS) in most cases of interest (Appendix S1). The ESS represents a balance of selective forces for and against colonisation. Parameter V_G controls the speed of evolutionary change, and thus of progress towards the ESS. Setting $V_G = 0$ implies no evolutionary change, yielding the usual no-evolution scenario (Calcagno et al., 2011; Holt, 2002). A positive V_G allows traits to evolve in response to changing environmental conditions (e.g. habitat loss): the larger V_G , the faster the species responds to environmental conditions.

When V_G is very large (fast evolution), species traits effectively attain the equilibrium almost immediately on the scale of environmental change.

Computing equilibria and maximum food-chain length

Equation (1) can be used directly with fixed colonisation rates to compute equilibrium occupancies and maximum food-chain length in the no-evolution scenario (Calcagno et al., 2011; Wang et al., 2021). To introduce evolution, we let $V_G > 0$ and study the coupled dynamics of Equations (1) and (2), retaining the common simplification that Equation (1) is at equilibrium, that is, that metapopulation dynamics are faster than evolutionary dynamics. Given the nature of ecological and evolutionary attractors, this is not expected to have important dynamical consequences (Sanchez et al., 2011).

To obtain maximum food-chain length in a computationally efficient way, we further assume Equation (2) is at equilibrium (see Aubree et al., 2020). This amounts to considering V_G as large enough (fast evolution scenario). We can thus implement an iterative algorithm to jointly solve Equations (1) and (2) for arbitrary numbers of trophic levels (Appendix S1). With this algorithm, we computed maximum food-chain length, defined as the maximum number of trophic levels that could persist for given parameter values.

In all cases, we define persistence as having an equilibrium occupancy above some small threshold level $\epsilon = 10^{-3}$ (any trophic level should occupy at least one patch in one thousand; results presented here hold qualitatively for any small value of ϵ).

Parameter values will be varied systematically over their feasible range, with, when needed, reference values given in Table S2. All rates (e , μ , c) have dimension time^{-1} ; ψ is time; V_G time^{-2} ; h and ϕ a dimensionless.

Comparing no-evolution and evolution scenarios

To investigate how eco-evolutionary outcomes depend on evolution speed, we first provide numerical examples with small numbers of trophic levels, by numerically integrating Equation (2) through time for different values of V_G , while keeping Equation (1) at equilibrium. In such conditions, species colonisation traits gradually evolve as environmental variables (e.g. the extinction rate e) are continuously deteriorated. Although evolution cannot ‘rescue’ species with non-viable trait values (as Equation 1 is at equilibrium), it allows viable species to adjust to environmental conditions, delaying, or avoiding extinction entirely. For the sake of comparison with existing literature, we chose the initial trait values equal to those used by Wang et al. (2021).

In a second step, to facilitate comparisons between no-evolution and evolution scenarios, all species initially have colonisation traits set at the ESS. Then, some environmental variable (e , h or μ) is varied at a constant rate, mimicking a trend of habitat deterioration. Species traits remain constant in the no-evolution scenario, whereas with evolution their colonisation rates evolve to track environmental change, with an efficiency determined by V_G . This ensures that communities are initially equally adapted, in both evolution and no-evolution scenarios.

RESULTS

The evolution of dispersal in a predator–prey metacommunity

Figure 2a,b presents results for the simplest possible case with two trophic levels. When the basal extinction rate e increases, the occupancies of the two trophic levels decline, eventually driving them to extinction, one after the other. In the absence of evolution, the figure was parameterised to mimic Wang et al. (2021)'s Figure 1, thus including top-down control of the predator and using initial colonisation rates equal to 10 for the two species (which is not an ESS). When $c = 10$ and $e = 1$, the first trophic level would occupy 90% of patches in the absence of predation, which is large but not uncommon in natural metacommunities (e.g. Pantel et al., 2022; Wang et al., 2021). In this case, our mathematical model faithfully reproduces the spatially realistic simulation results of Wang et al. (2021). Other choices would yield qualitatively similar conclusions.

Without evolution, occupancy of the higher trophic level quickly decreases with extinction rate, as expected from classic metapopulation models. The higher trophic level disappears at rather low extinction values ($e = 3.5$). The lower trophic level can sustain itself at much larger extinction rates, until e reaches a value of 10, at which point it is no longer viable (Figure 2a). This difference in persistence is entirely attributable to the processes described in Calcagno et al. (2011), that is, limited colonisation rates and the accumulation of extinction rates up the food chain. Due to the absence of trait dynamics, the colonisation rates, and therefore the metapopulation colonisation-to-extinction ratios (c/e), of the two trophic levels remain identical throughout (Figure 2b).

Figure 2c–h shows how important differences emerge with evolution. In particular, colonisation changes under the action of evolution, and the upper trophic level evolves larger colonisation rates than the lower trophic level, as one would expect (Figure 2 right panels). If evolution is slow (Figure 2c,d), that is, at low V_G in Equation (2), evolution has little impact, and does not significantly ‘delay’ the predator extinction, in the sense of allowing persistence at higher extinction rates. Despite the predator beginning to evolve higher

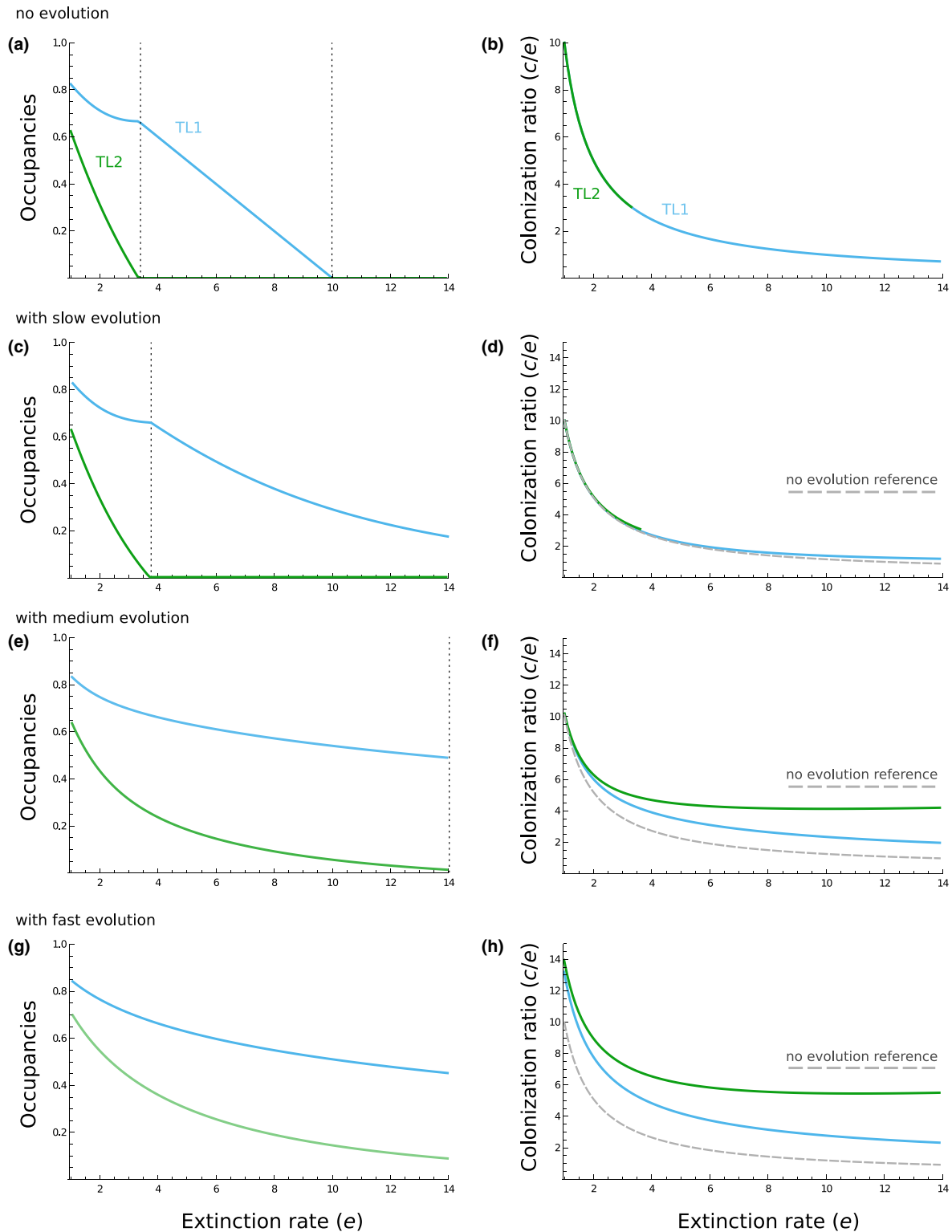


FIGURE 2 The impact of an increasing extinction rate in a system with two trophic levels. (a, b) No evolution. The extinction rate is gradually increased from its baseline value ($e=1$). The equilibrium occupancies of the prey (blue) and the predator (green) gradually decline until extinction (a), as the colonisation ratios (c/e) decline with the increase in e (b). These results very closely reproduce Wang et al. (2021)'s Figure 1 results. (c, d) Introducing evolution at low speed relative to the change in e ($V_G = 0.1$). (e, f) Introducing evolution at an intermediate speed relative to the change in e ($V_G = 1$). (g, h) Introducing evolution at a large speed relative to the change in e ($V_G = 100$). The two trophic levels initially had colonisation rates $c = 10$; without evolution they retained these values throughout, whereas with evolution the values could evolve according to Equation (2). In (c–f), occupancies and evolved (c/e) values constitute time series, as colonisation trait values evolved gradually on the same timescale as the increase in extinction rate (x -axis). In (g, h), the time-series nature vanishes since trait values immediately reached their equilibrium values, regardless of previous history. To help comparisons, the colonisation ratios without evolution shown in (b) were also shown in panels d, f, and h, as grey dashed curves. Other parameters were at default values ($h=1$, $e=1$, $\phi = 0.5$, $\psi = -0.1$), except $\mu=0$ and $e_{TD}=2e$.

colonisation rate when approaching extinction, the effect is not sufficiently strong. This is mostly because the prey occupancy declines (Figure 2d), an effect potentially amplified by the prey evolving lower colonisation rates (Figure S4). However, once the prey itself becomes threatened with extinction (around $e=7$), it manages to persist despite the sustained increase in extinction rate. It does so by evolving higher colonisation rates, maintaining its colonisation-to-extinction ratio c/e above its value without evolution (Figure 2d; Figure S3). Prey occupancy still declines, but the decline is mitigated by evolution, preventing extinction in the range of extinction rates considered (Figure 2c).

When evolution is faster (larger V_G ; Figure 2e,f), the predator can evolve sufficiently to delay its extinction, persisting until larger values of the extinction rate ($e = 4$). This is achieved because the evolutionary increase of its colonisation rate is fast enough relative to the increase in extinction rate. It eventually outpaces the latter, so that the predator colonisation ratio turns into an increasing function of extinction rate (Figure 2f). This effect is, however, insufficient to prevent eventual extinction, because of the concomitant decline in prey occupancy, potentially reinforced by the effects of prey evolution (Figure 2f).

Eventually, when evolution is fast enough (Figure 2g,h), the predator also manages to escape extinction, like the prey. The predator colonisation rate increases fast enough to maintain persistence despite the diminishing occupancy of the prey. However, the predator never gets very frequent and persists at very low occupancy (Figure 2g). It must be stressed that since the prey (and to a lesser extent the predator) are initially not threatened with extinction, adaptive evolution may actually drive the colonisation rates to values smaller than they would be in the absence of evolution (Figure S3). This effect is detrimental to persistence, amplifying the effect of habitat deterioration. It is only when a species approaches extinction that the evolutionary effect becomes beneficial. Since this occurs much later in the prey than in the predator, evolution in the prey counteracts the (beneficial) effects of trait evolution in the predator. This shows that adaptive evolution can have opposing effects on food-chain length at different trophic levels.

From Equation (2), it can be seen that as a species approaches extinction, $q_i \rightarrow 0$, c_i always increases, acting to counteract extinction. However, comparing among trophic levels when they are on the verge of extinction ($q_i \approx \epsilon$), one can deduce that (i) the positive selection pressure caused by available habitat is lower for higher trophic levels (since q_{i-1} decreases with i), and (ii) the negative selection pressure caused by local competition is stronger (since the colonisation rate c_i will generally be increasing with trophic position). Both effects make selection for larger colonisation rates less efficient at higher trophic levels, providing a rationale for the results shown in Figure 2.

Overall, the evolution of colonisation rate is beneficial to species persistence and thus food-chain length. Higher trophic levels evolve larger colonisation rates than lower trophic levels. However, while all trophic levels are selected for higher colonisation when approaching extinction, the intensity of this effect decreases with trophic level. Furthermore, evolution at low trophic levels, when they are not threatened by extinction, can often be detrimental to the persistence of upper trophic levels. For these two reasons, the beneficial effects of evolution on food-chain length are not as effective as one might expect. These conclusions are qualitatively unchanged when considering other parameter values, even when the initial trait values are initially lower than the ESS (Figure S4). In the latter case, the initially detrimental effects of trait evolution, which can amplify the effects of habitat degradation, vanish. Evolutionary dynamics is thus even more beneficial to food-chain persistence (Figure S4).

Since fast and slow evolution entail qualitatively similar results, in the following we consider fast evolution only, comparing results with the no-evolution scenario. This provides an upper bound on the potential consequences of evolution on food-web dynamics, and captures the two extreme situations, most real situations probably falling somewhere in between.

Maximum food-chain length under habitat degradation

We considered two forms of habitat degradation: (i) an increase in extinction rate (as above) and (ii) habitat destruction (i.e. reduced fraction of available patches h ; Equation [1]).

As expected, increasing the extinction rate decreases maximum food-chain length in the absence of evolution (Figure 3a; Calcagno et al., 2011; Wang et al., 2021). In the presence of evolution, however, the decline is much reduced. This is mostly caused by an increase in the colonisation rate of the upper trophic levels, which evolve towards higher values (Figure 3b). The higher colonisation rates evolved are, however, insufficient to completely overcome the increasing extinction rate and the reduced occupancy of lower trophic levels (Figure 3b). With or without evolution, the decline of maximum food-chain length with extinction rate always has an overall convex shape (i.e. an initially rapid loss of many trophic levels followed by a more gradual loss of the remaining levels, as extinction rate increases; Figure 3a).

Destroying habitat patches (reducing h) yields the same tendency: evolution allows longer food chains to persist (Figure 3c). However, all trophic levels jointly evolve higher colonisation-to-extinction ratios, even the lower ones, contrary to what was observed when extinction rate was manipulated (Figure 3d). This is because decreasing h affects the first trophic level just as strongly

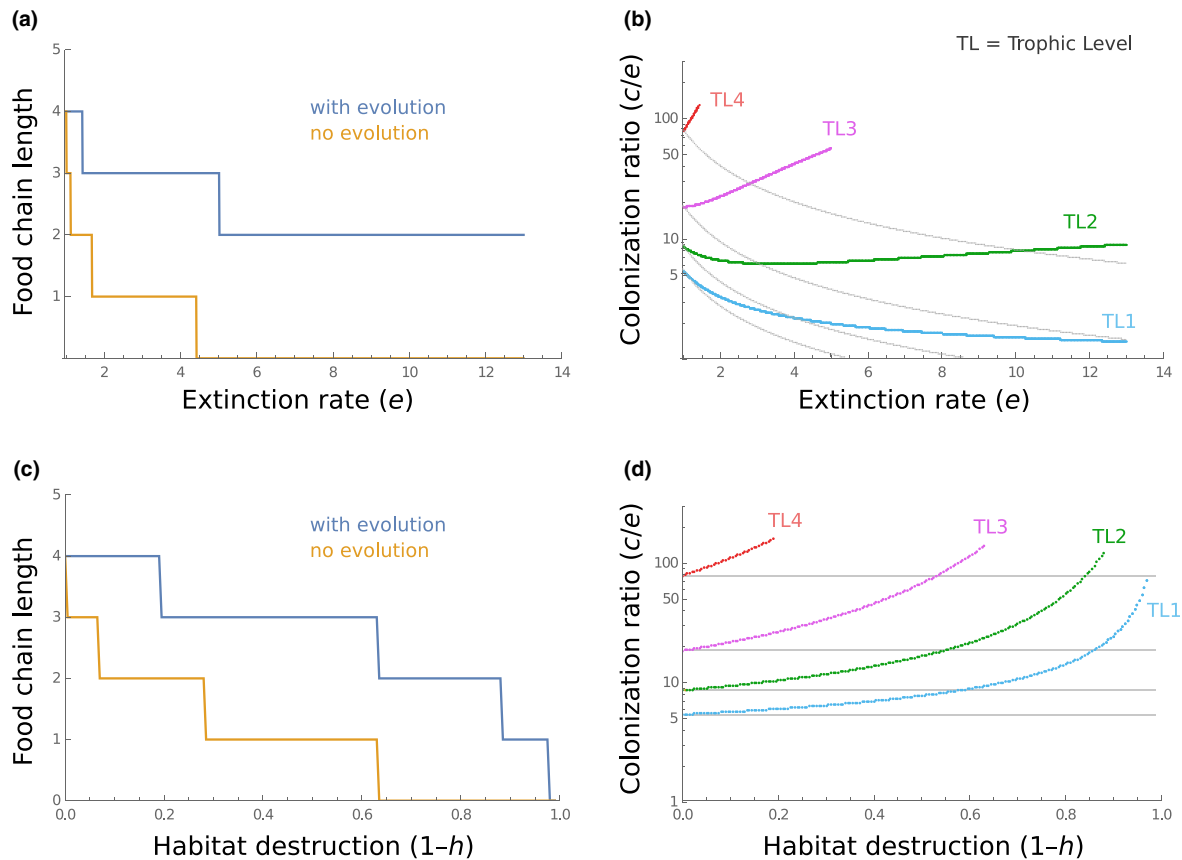


FIGURE 3 Maximum food-chain length under habitat deterioration. (a, b) The effect of increasing the extinction rate on maximum food-chain length (a), without evolution (orange) and with evolution (blue). In the case of evolution, the colonisation ratio values at each trophic level are shown in (b). (c, d) Same as (a, b), except that the level of habitat destruction ($1-h$) was increased instead of e . Initially (i.e. for $e=0$ or $h=1$), species have the same colonisation rates in the two scenarios (with or without evolution), set at the corresponding ES values. These values do not change in the no evolution scenario, whereas they changed in the other scenario. As in Figure 2, the dim grey curves in the right panels show the colonisation ratio values in the no evolution scenario.

as the others, unlike increasing the extinction rate, which has a disproportionate effect on the higher trophic levels. We also remark a qualitative impact of evolution: the decline in food-chain length with habitat destruction follows a convex sequence in the absence of evolution (first many losses, then fewer losses), as it does when increasing extinction rate. However, with evolution, increasing habitat destruction on the contrary generates a concave decline of food-chain length, with two trophic levels (out of four) abruptly going extinct when habitat destruction reaches 80–100% (Figure 3c).

Consequences of trade-off intensity

We showed that increasing the intensity of the trade-off between colonisation and local competitiveness (i.e. decreasing the basal competitiveness of immigrants ϕ and/or making the slope ψ more negative) increases the negative selection pressure on the colonisation rates (see Equation 2). Therefore, it should select for lower colonisation rates, which should in turn negatively affect persistence and maximum food-chain length. This is

indeed what we find (Figure 4a). In quantitative terms, we remark that parameter ϕ has very little impact, compared to the trade-off slope ψ , consistent with the results of Calcagno et al. (2017). If the trade-off slope is very shallow, colonisation rates are free to evolve to high values, thereby allowing much longer food chains to persist (Figure 4b). Conversely, if the slope is very negative, selection favours small colonisation values, especially at lower trophic levels, at the expense of population persistence and food-chain length (Figure 4b). Costs of dispersal (trade-off intensity) are therefore critical in determining the consequences of dispersal evolution for food-chain length.

Relationship between food-chain length and the proportion of empty patches

In the absence of evolution, a negative correlation is expected between food-chain length and the fraction of empty patches. In other words, long food chains can be observed only if total occupancy is high. This is shown in Figure 5, where inter-community variability was

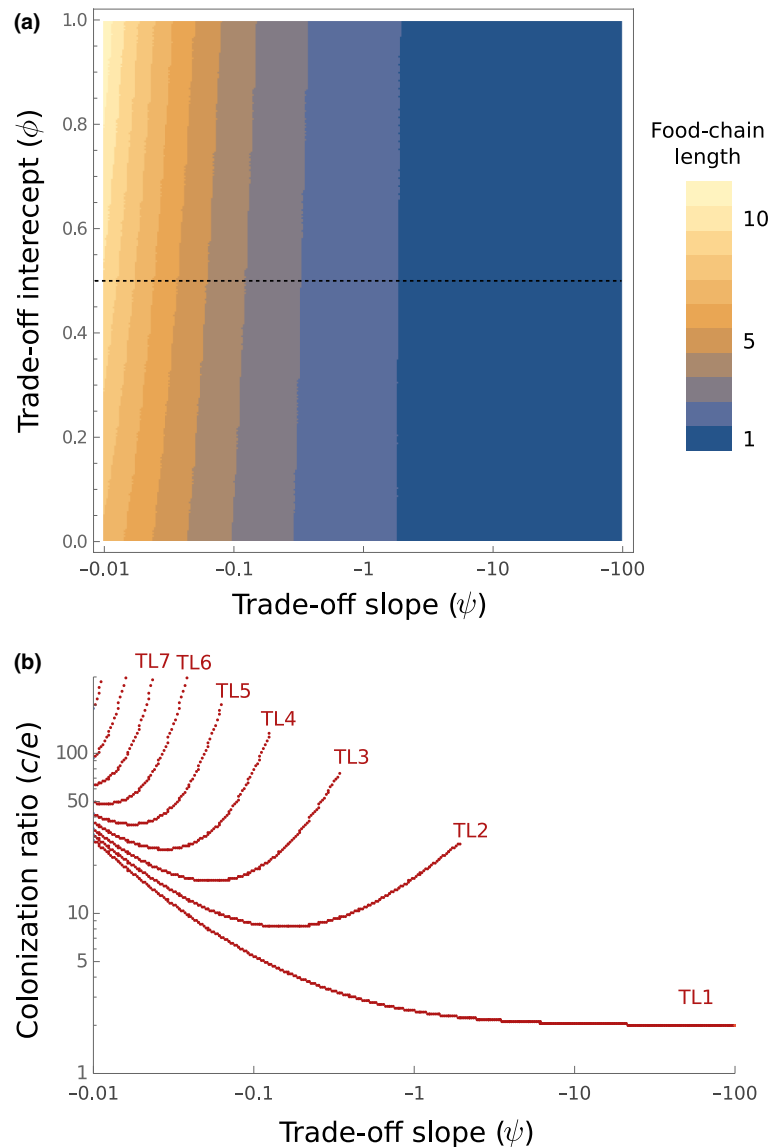


FIGURE 4 Consequences of varying the competitive trade-off intensity. (a) A contour plot of maximum food-chain length, with evolution, as a function of the two competitive trade-off parameters (ϕ ; y-axis) and (Ψ ; note the logarithmic scale). (b) For a fixed $\phi=0.5$ (corresponding to the dotted line in panel a), the colonisation ratios of the different trophic levels as a function of Ψ . Note the logarithmic scales on both axes.

generated from different sources of parameter variation (extinction rate, habitat destruction and trade-off intensity). When ecosystems differ in their extinction rate e , evolution changes the pattern quantitatively, but not qualitatively (Figure 5a,b). Things are different when the amount of habitat destruction (h) is the source of variation: without evolution, we observe the classic convex relationships between food-chain length and the fraction of empty patches or, at best, linear relationships (Figure 5c), but concave negative relationships emerge when evolution is allowed (Figure 5d).

Interestingly, this difference is reminiscent of the one observed between food-chain length and habitat destruction (Figure 3c,d). We checked that varying other parameters (specifically the perturbation rate μ) could not produce concave relationships, with or without evolution (Figure S2). It therefore seems that habitat destruction

elicits specific evolutionary responses, and ultimately brings up a qualitative difference between evolved and unevolved food chains. Specifically, with evolution, relationships that are otherwise convex can become concave. Such a qualitative difference in the shape of the relationships might be looked for in empirical or experimental data as a trace of the action of evolutionary dynamics.

DISCUSSION

Both ecology and evolutionary biology aim at understanding the dynamics of biodiversity (Vellend, 2016). Trophic diversity is certainly a major component of the latter, and metacommunities are suitable objects to address its interaction with spatial dynamics. Indeed, the persistence of long food chains in spatially structured

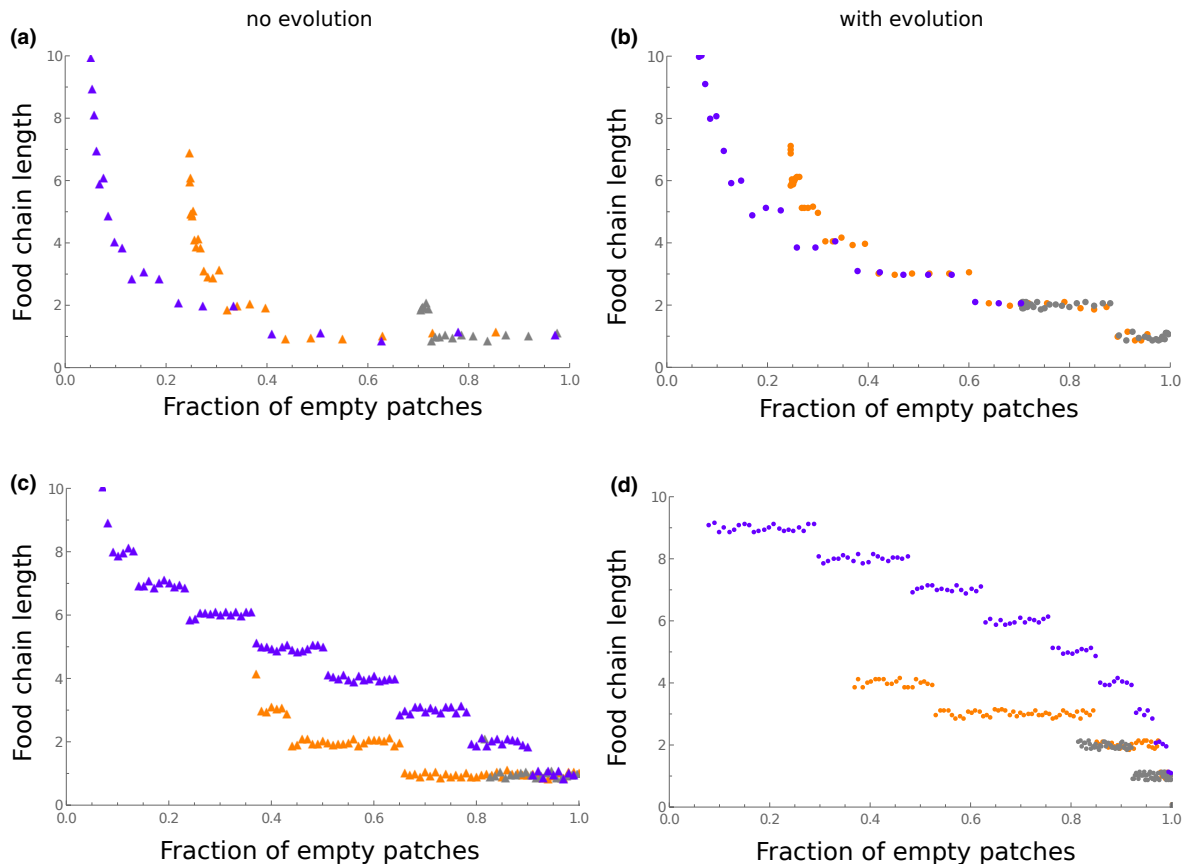


FIGURE 5 The relationship between food-chain length and the fraction of empty patches without evolution (left panels) and with evolution (right panels). (a, b) Each dot represents a different parameter value, where the extinction rate varies between 0.01 and 100, under three different values of Ψ . (c, d) Each dot represents a different parameter value, where the habitat destruction level $1-h$ varies between 0 and 1, under three values of Ψ . In all panels, the three values of Ψ were -1 (grey dots), -0.1 (orange dots) and -0.01 (blue dots). As in Figure 3, species had colonisation rates set at the ES values for the initial parameter value, and these values remained constant in the no evolution scenarios, whereas they adapted in the evolution scenarios. Points were slightly jittered vertically for better readability.

habitats requires quite constrained conditions (Calcagno et al., 2011; Holt, 2002; Wang et al., 2021). Higher trophic levels are vulnerable to extinction from multiple processes, and, paraphrasing Robert May, they must arguably deploy ‘devious strategies’ in order to persist (May, 1973, chap. 7). The most obvious strategy in this context is the adoption of systematically higher colonisation rates by higher trophic levels through evolution, but other strategies are possible, such as behavioural ones (Calcagno et al., 2011). At this point, evolution has not formally been integrated in the analysis of trophic structure in a spatial context. Our work aimed at bringing an eco-evolutionary perspective into the theory of food-chain length.

We have shown that the evolutionary dynamics of colonisation rates, that is, the evolution of dispersal at each trophic level, provides a potent way to alleviate the spatial constraint on food-chain length. Natural selection does favour larger colonisation rates at upper trophic levels and an evolutionary increase in colonisation rate can, if fast enough, allow longer food chains to persist. The selection pressures imposed on colonisation rates by trophic relationships and spatial structure

cause evolutionary responses, which can sustain the persistence of more trophic levels in the face of habitat degradation, for example, increased disturbance or habitat destruction.

It could seem at first glance that such eco-evolutionary dynamics are the ultimate ‘devious strategy’ that trophic levels deploy to persist, as it allows colonisation rates to evolve larger values as needed. This could potentially remove any limit on food-chain length, as spatial persistence is ensured with large enough colonisation rates. This might be considered a form of evolutionary rescue, operating at a larger spatio-temporal scale than ‘classic’ examples (Gonzalez et al., 2013). However, our results show that things are not so simple. Indeed, when all trophic levels are allowed to evolve, two factors limit the efficiency of evolution in rescuing food-chain length. First, the lowest trophic levels, which are usually not facing the most pressing danger of spatial extinction, experience little selection for increased colonisation. Quite the opposite: they can readily be selected for lower colonisation rates, because of intraspecific competition or, equivalently, costs of dispersal. These negative selection pressures lower their spatial occupancy, directly jeopardising

the persistence of superior trophic levels. Second, the strength of selection for larger colonisation rates typically declines, all else being equal, as trophic level increases. This is because positive selection declines as the fraction of hospitable patches decreases, while at the same time, the larger colonisation rates that higher trophic levels must adopt increase the strength of selection against dispersal caused by intraspecific competition (Equation 2). Combined, these two factors make eco-evolutionary dynamics at lower trophic levels potentially detrimental to food-chain length. In short, even when efficient, evolutionary dynamics is not the silver bullet to ensure the persistence of higher trophic levels. Therefore, even with no particular constraint on the speed or extent of adaptive evolution, eco-evolutionary dynamics does not totally suppress the spatial constraint on food-chain length. When it does permit longer food-chains to persist, trophic levels are typically kept at low spatial occupancies, thus vulnerable to environmental perturbations or other random events.

In the evolutionary context considered here, the question of understanding what devious strategies higher trophic levels must deploy to persist remains, though the range of available strategies is more precisely defined. Theoretically, factors favouring the persistence of longer food-chains are: (i) higher trophic levels having greater evolution rates or (ii) competition-colonisation trade-off intensities being weaker at higher trophic levels. These two possibilities remain to be investigated empirically. We can nonetheless remark that one of the components affecting trade-off intensity is local population size (Appendix S1). The larger the local population size, the weaker the trade-off, all else equal. Since we would often expect higher trophic levels to have smaller local population sizes, this should make ψ more negative as trophic level goes up. If so, this would be yet another factor detrimental to food-chain length under eco-evolutionary dynamics. Regarding heterogeneity in evolution rates among trophic levels, good evidence is also lacking, but if evolution were generally faster in prey than predators, or vice versa, this should leave a potentially detectable mark on the predator–prey time series (Hiltunen et al., 2014; Yoshida et al., 2003).

We did not impose any restriction on the range of the evolvable colonisation rates. This may be unrealistic; other selective forces or constraints could obviously interfere with the effects reported here. For instance, colonisation rates may have upper bounds (see Appendix S1 for a mechanistic example). If the upper bound is low enough, this could prevent at least some trophic levels from persisting through the evolution of greater colonisation rates. Large colonisation rates are especially selected for at higher trophic levels, so the latter would need to have less stringent bounds.

One direct way to test our predictions is experimental, with appropriate systems such as ciliates or other microorganisms (Altermatt et al., 2015; Fox & Morin, 2001;

Pennekamp et al., 2014). More generally, we might use observational data from the field to look for some of the qualitative patterns we have identified – these patterns could indeed be diagnostic of whether eco-evolutionary dynamics are at play or not. Of course, natural communities and food chains experience processes and contingencies left out in models (e.g. autocorrelation and/or clustering of perturbations, diffuse trophic levels). This would often complicate the task, but datasets such as the one used in Wang et al. (2021) exist and are extremely useful in this context, especially if extending to three or more trophic levels. The patterns reported in Figures 3 and 5 appear especially valuable for empirical assessments. Indeed, we found that among systems differing in their level of habitat destruction, either spontaneously or upon experimental manipulation, the maximum food-chain length declines in a generically convex manner in the absence of eco-evolutionary dynamics, whereas it could have a concave decline with evolution (Figure 3c). A concave shape is never observed without evolution. Observing a concave relationship would therefore be a strong indication that eco-evolutionary dynamics are at play. Alternatively, the correlation between total occupancy (and thus the fraction of unoccupied patches) and maximum food-chain length offers the same qualitative prediction (Figure 5). Such qualitative differences between ecological and eco-evo models are usually the most susceptible to be detected, and might even leave their mark in real-world patterns (e.g. Dwyer et al., 2022). Datasets or experiments documenting the impact of habitat destruction on maximum food-chain length and overall occupancy should thus offer the best potential to evaluate the importance of eco-evolutionary dynamics for food-web dynamics.

Our results derive from a spatially homogeneous and mean-field patch-occupancy model. Interestingly, such a simple model faithfully reproduces the results presented in Wang et al. (2021), who used stochastic simulations of a spatially realistic model. This gives additional credence to our predictions. Our results could be extended in different ways, including more complex food-web topologies (omnivory), introducing several species per trophic level (apparent predation at the metacommunity scale) or using trophic level-specific patch definitions (McCann et al., 2005). We also used a simple description of how the mean species trait evolved, which proved to affect ecological dynamics, and reciprocally. This is a fair basic description of eco-evolutionary dynamics (Hendry, 2017), but it would be interesting to model the entire distribution of phenotypes within species (e.g. Osmond et al., 2017), and its dynamical interactions with food-chain dynamics (Bassar et al., 2021). In any case, our results reveal some fundamental ways in which the evolution of dispersal and spatial food-webs dynamics are interconnected. They suggest a lot is to be gained from bringing more eco-evolutionary dynamics into food-web ecology.

AUTHOR CONTRIBUTIONS

The initial idea of this work originated from François Massol during his PhD thesis with Philippe Jarne and Patrice David. Vincent Calcagno and François Massol designed and conducted the research. Vincent Calcagno and François Massol wrote the initial manuscript, all co-authors contributed to manuscript preparation.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

No new data were used in this manuscript. The scripts and codes used to generate the results are available at <https://doi.org/10.5281/zenodo.7825156>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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