Colonisation debt: when invasion history impacts current range expansion

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Abstract

Demographic processes that occur at the local level, such as positive density dependence in growth or dispersal, are known to shape population range expansion by linking carrying capacity to invasion speed. As a result of these processes, the advance of an invasion front depends both on populations in the core of the invaded area and on small populations at the edge. While the impact on velocity is easily tractable in homogeneous environment, information is lacking on how speed varies in heterogeneous environment due to density dependence. In this study, we tested the existence of a 'colonisation debt', which corresponds to the impact of conditions previously encountered by an invasion front on its future advances. Due to positive density dependence, invasions are expected to spread respectively slower and faster, along the gradients of increasing and decreasing carrying capacity, with stronger differences as the gradient slope increases. Using simulated invasions in a one-dimensional landscape with periodically varying carrying capacity, we confirmed the existence of the colonisation debt when density-dependent growth or dispersal was included. Additional experimental invasions using a biological model known to exhibit positive density-dependent dispersal confirmed the impact of the carrying capacity of the patch behind the invasion front on its progression, the mechanism behind the extinction debt.

Introduction

The demographic processes occurring among invasive populations are essential for understanding and modeling range expansion at large scales (Gurevitch et al., 2011, Caplat et al., 2012, Blackburn et al., 2015). Expansions are the result of multiple colonisation events in not yet invaded habitats (Blackburn et al., 2011). Populations located at the edge of the invaded area - referred to as the "front" of the invasion - are thus characterized by low densities and transient population dynamics, compared to the larger, older populations located in the core of the invaded area. If they manage to become firmly established, these new colonies created by dispersal from the core will themselves become part of the core, and will be the source of new dispersing individuals that will further the invasion front. Conversely, their inability to establish will cause the invasion front to slow down or even come to a halt (Keitt et al., 2001, Morel-Journel et al., 2022). These transient dynamics at the edge of an invaded area, which play a major role in shaping range changes, can be influenced by several ecological mechanisms, among which positive density-dependence.

Positive density dependence, either in growth or dispersal, directly impacts the ability of small populations on the invasion front to colonize further. In presence of density-dependent growth, commonly referred to as the Allee effect (Allee et al., 1949, Courchamp et al., 2008), small populations experience lower growth rates *per capita* due to biological mechanisms that reduce individual fitness (Courchamp et al., 1999). Positive density-dependent dispersal describes the greater propensity of individuals to disperse from large populations than from small ones, often to avoid intraspecific competition at high densities (Altwegg et al., 2013). Because growth and dispersal are central parameters in the expansion of invaded areas, their density dependence creates a causal relationship between expansion and the dynamics of the core populations behind the invasion front (Stokes, 1976, Lewis and Kareiva, 1993, Roques et al., 2012, Haond et al., 2021). The larger these populations, the more likely emigration is, as well as the creation of colonies large enough to establish and advance the front.

The influence of positive density dependence may also depend on the quality of the environment, more specifically on the carrying capacity, i.e. how the local environment limits the maximum attainable individual density. Previous modelling and experimental evidence from Haond et al. (2021) and Morel-Journel et al. (2022) have shown that, in presence of positive density dependence, the carrying capacity of the invaded environment impacts invasion speed, potentially up to a stop for low carrying capacities. Conversely, speed remained unaffected by carrying capacity in the absence of any density-dependence. However, these studies only considered constant carrying capacities over space. Yet habitat quality is rarely spatially homogeneous, especially at the scale of an invasion. Other works have studied the impact of spatial heterogeneity on invasive spread (e.g Shigesada et al., 1986, Kinezaki et al., 2006, Schreiber and Lloyd-Smith, 2009, Vergni et al., 2012), some of them including positive density dependence (e.g Dewhirst

and Lutscher, 2009, Pachepsky and Levine, 2011, Maciel and Lutscher, 2015). However, heterogeneity was considered in these studies through its impact on the growth rate of populations rather than on their carrying capacity. Moreover, many of them considered binary cases, separating habitat from non-habitat (Shigesada et al., 1986, Dewhirst and Lutscher, 2009, Pachepsky and Levine, 2011, Maciel and Lutscher, 2015). Yet, carrying capacity is directly tied to habitat quality, most notably through resource availability, whose natural variations are often rather progressive than stark, resulting in successive gradients over space.

For this study, environmental gradients are defined as monotonic variations of the carrying capacity in space. They are considered 'upward' if the invasion fronts move toward increasing carrying capacities, and 'downward' otherwise, with the slope of the gradient characterizing the average change in carrying capacity over space, in absolute value. On a downward gradient, for example, colonisation with positive density dependence is expected to become increasingly difficult as carrying capacity - and thus population size - decreases. However, information on the rate of decrease and its relationship to the gradient slope is lacking. Because density dependence links colonisation success to the dynamics of populations behind the invasion front, carrying capacities in the core are expected to influence colonisation success as well. Thus, the front should advance faster in downward gradients, because of the large influx of dispersed individuals from larger populations behind. Conversely, the front should be impeded by the smaller size of the populations behind the front in upward gradients. This impact is expected to be stronger as gradient slope, and thus the difference in carrying capacities, increases.

In this study, we hypothesize that this impact of the environmental conditions previously encountered by an invasion front on its future advance may create a 'colonisation debt'. This term echoes extinction debt, defined by Tilman et al. (1994) as the impact of previous demographic events on the probability of a population going extinct. We hypothesize that only invaders affected by positive density dependence exhibit such a 'memory' of past carrying capacities, while the others should remain memoryless. When encountering a succession of downward and upward environmental gradients, the colonisation debt should create a lag in the relationship between invasion speed and environmental quality. In a downward gradient, a patch of a given carrying capacity should be crossed faster than if it were in an upward gradient, due to the influence of the previous, larger patches. For a strong enough impact of the carrying capacities encountered earlier, the slowest and fastest rates should be reached after colonisation of the smallest and largest habitat, respectively.

Using mechanistic models and experiments, we tested the existence of colonisation debt during invasions in environments with heterogeneous carrying capacity. On the one hand, we simulated invasions across a one-dimensional landscape with positive density dependence on growth, dispersal, or neither. The landscapes were periodic successions of gradients of increasing and decreasing carrying capacity, with identical mean but different slopes. On the other hand, we performed artificial invasions in microcosm

landscapes using *Trichogramma chilonis*, a biological model known to exhibit positive density-dependent dispersal in particular experimental conditions. Two types of landscapes, with different slopes, were used for this experiment.

Material and Methods

Simulations

A stochastic model was used to generate invasions in a one-dimensional landscape (see Supplementary Material 1 for details). The model was discrete in space, i.e. the landscape was represented as a linear chain of patches. It was also discrete in time, with each time step divided into a growth phase and a dispersal phase. The growth phase could include density-dependent growth, with an Allee threshold (the size under which the deterministic population growth rate is negative) ρ. The dispersal phase could include density-dependent dispersal, with a dispersal rate d either constant or increasing with individual density according to a parameter τ.

This model was used to simulate invasions, using the R software (RCoreTeam, 2018). The landscapes considered were infinite on the right but finite on the left. Only the leftmost patch was initially colonised, with a population size of K_{max}. The landscape was divided into two parts. The first n_b leftmost patches made up the 'burn-in part'. These patches all had a carrying capacity of K_{max}, so the invasion started in a homogeneous space and the invasion front was created before the invasion entered the second part of the landscape. The dynamics in this burn-in part were not analysed further, as this type of invasion in homogeneous landscapes has already been documented in previous studies (e.g Haond et al., 2021). The remaining patches made up the 'periodic part' of the landscape. Their carrying capacity varied periodically between K_{max} and K_{min} with a period length $2q$ (Fig. 1). Each period included one downward gradient followed by one upward gradient, each with q patches. The two gradients were symmetrical, and the carrying capacity K_i of patch i was defined as follows:

$$K_i = \begin{cases} K_{max} - \frac{1}{q}(i-j)(K_{max} - K_{min}) & \text{if } i \in [j, j+q[\\ K_{max} - \frac{1}{q}(2q - i + j)(K_{max} - K_{min}) & \text{if } i \in [j+j, i+2q[\end{cases},$$

with j the closest patch to the left of i so that $K_j = K_{max}$. The gradients were symmetrical, and their slope – the differences in carrying capacity between two neighbouring patches – increased when q decreased. As a convention, patches were numbered in ascending order, starting from $-n_b$ for the leftmost patch. Therefore, the first patch of the periodic part was the patch 0.

Simulations were performed for landscapes with $K_{max} = 500$, $K_{min} = 50$, $n_b = 10$, and q an integer between 1 and 10. They all lasted for $t_{max} = 1000$ generations and assumed an intrinsic growth rate

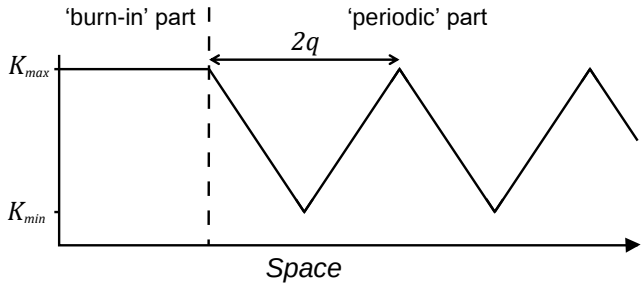

Figure 1: Schematic representation of the variations in the carrying capacity in the landscape considered for the simulations. The burn-in part is of finite length (corresponding to n_b patches), but the periodic part continues infinitely to the right.

$r = 0.2$ and a dispersal rate without density dependence $d_{ind} = 0.1$ (see Supplementary Material 1). Three scenarios were tested for each landscape: (i) a null scenario, without any positive density-dependence, (ii) with positive density-dependent growth and $\rho = 20$, and (iii) with positive density-dependent dispersal according to a Hill function of parameters $\alpha = 4$ and $\tau = K_{max}/2 = 250$ (see Supplementary Material 1). Each of the 3×10 combinations of landscape and scenario was simulated 1000 times.

The position of the invasion front $P(t)$ at time t was recorded throughout the simulation, as the number of the rightmost patch with more than 5 individuals. This threshold was chosen to mitigate the effects of demographic and dispersal stochasticity on the front. The starting time of the invasion proper t_s was defined as the first generation at which the invasion front reached the periodic part of the landscape, i.e. $P(t_s) \geq 0$.

Invasion speed was computed at three scales: the whole landscape, the gradient and the patch. The average speed of the front was defined at the landscape level, as the ratio between the last position of the front and the duration of the invasion proper $P(t_{max})/(t_{max} - t_s)$. The gradient speed was defined at the scale of one (upward or downward) gradient, as the ratio between q and the number of generations the invasion front spent between the two extremities of the gradient. For a downward gradient, the extremities were patch i and patch $i + q$, such that $K_i = K_{max}$. For upward gradients, they were patch j and patch $j + q$, such that $K_j = K_{min}$. For a given simulation, the difference between the average upward and downward gradient speeds was also computed. A gradient was not considered if the invasion never reached its extremity. The instantaneous speed of the front was defined at the patch level, as the inverse of the number of generations during which the invasion front remained stationary in the patch. To compare instantaneous speeds for different q, the middle patch of the each gradient was considered. As there was no middle patch when q was odd, only landscapes with an even value of q were considered. Then, the carrying capacity of the middle patch was always $K = \frac{K_{min}+K_{max}}{2} = 274.5$.

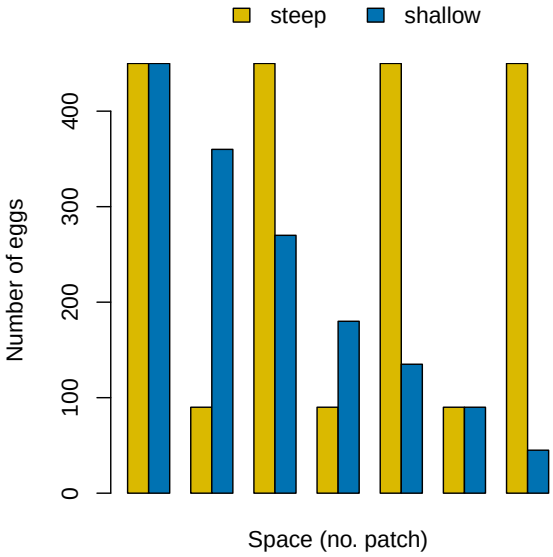

Figure 2: Number of eggs in the patches in the 'steep' (yellow) and 'shallow' (blue) landscapes. The invasion are initiated by colonizing patch 1 for each replicate of the experiment.

Microcosm experiments

Artificial invasions of microcosm stepping-stone landscapes were performed in addition to the simulations (see Supplementary Material 2 for details). The biological model used was a strain of the parasitoid wasp *Trichogramma chilonis*, which is known to exhibit positive density-dependent dispersal (Morel-Journel et al., 2016, Haond et al., 2021). The carrying capacity was manipulated by changing the number of host eggs available for *T. chilonis*, which were used as a resource. Two landscapes defined for the simulations were recreated for the experiment (Fig. 2). The first one (called thereafter the 'shallow' landscape) was a downward gradient from 450 to 45 eggs, similarly to the simulated landscape with $q = 7$. The second one (called thereafter the 'steep' landscape) alternated between patches with 450 eggs and patches with 90 eggs, similarly to the simulated landscapes for $q = 1$. Patches with 90 eggs were used rather than with 45 eggs to buffer the highly stochastic dynamics of small populations of *T. chilonis*.

As for simulations, the position of the front was recorded at every generation as the rightmost patch with more than 5 individuals. The stop duration, i.e. the number of generations during which the invasion front remained stationary in a given patch, was used to assess speed along the landscape. The stop duration was computed for every colonized patch but the last one, and followed a Poisson distribution, and was therefore analysed using a generalized linear mixed model, with a log link function and the experimental replicate as a random effect. Three explanatory variables were considered: the type of landscape, the carrying capacity on the front, the carrying capacity of the patch preceding the front. Models with every combination of these parameters were compared according to AIC. Models within 2 AIC points of the smallest value were compared using likelihood ratio tests, to define the most

parsimonious among the best ones.

Results

Simulation results for average speed

The average invasion speed was substantially reduced by positive density dependence. Indeed, 90% of the simulated invasions without any positive density dependence had an average speed between 0.159 and 0.181 patches/gen, whereas they ranged from 0.009 to 0.024 patches/gen and from 0.014 to 0.026 patches/gen for simulations with density-dependent growth and dispersal, respectively. There were no major impact of q on the average speed, although variance tended to increase with q for simulated invasions with density-dependent growth (standard deviation from 0.0019 for $q = 1$ to 0.0083 for $q = 10$) and dispersal (standard deviation from 0.0019 for $q = 1$ to 0.0064 for $q = 10$).

Simulation results for instantaneous speed

Instantaneous speeds for each value of q considered are presented in Supplementary Material 3 (Fig. S2), while Fig. 3 presents the results for the simulations with $q = 10$. Like the average speed, the instantaneous speed was systematically higher in simulations with no positive density dependence. Furthermore, the invasion speed without any mechanism was largely independent of carrying capacity, remaining around 0.215 gen^{-1} for each patch (Fig. 3A). In presence of density dependence, the instantaneous speed varied not only with the carrying capacity of the patch, but also with the carrying capacity of previous patches (Fig 3B, 3C). Indeed, with positive density dependence, separating instantaneous speeds according to

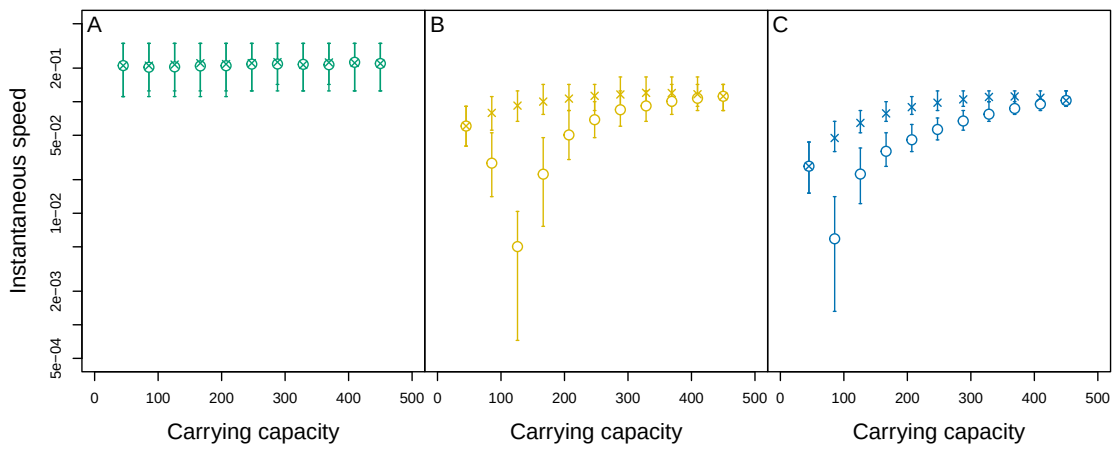

Figure 3: Instantaneous speed as a function of carrying capacity of the patch where the front is located, for $q = 10$ and either no density dependence (A, green), density-dependent growth (B, yellow) and dispersal (C, blue). Average values over all patches with the same carrying capacity are represented by crosses if the patch is in a downward gradient, and as circles if the patch is in an upward gradient. Patches with $K = K_{min} = 45$ and $K = K_{max} = 450$ are represented as belonging to both gradients (cross and circle). Intervals contain 80% of the simulated instantaneous speeds.

whether the patch was in an upward or downward gradient revealed substantial differences. Firstly, speeds were consistently higher in downward gradients, for the same value of K. Secondly, the minimum instantaneous speed was not observed at $K = 45$, but one (with density-dependent dispersal) or two patches (with density-dependent growth) further in upward gradients. This created a lag in the variation of instantaneous speed, compared to the variation in carrying capacity.

Impact of gradient slope on simulated speed

The impact of gradient slope (inversely proportional to the value of q) was assessed by comparing invasion speeds in upward and in downward gradients, based on gradient speeds (Fig 4A) and on instantaneous speed in the middle patch of the gradient (Fig 4B). Consistently with the results presented above, there was no significant difference in speed between downward and upward gradients in the absence of positive density dependence. However, the difference in speed was generally positive with both types of density dependence, with faster speeds in the downward gradients. The difference in gradient speed was maximal around $q = 4$ and decreased for larger values of q, i.e. for the shallower gradients (Fig 4A). For smaller values of q, the gradients were so short that the invasion front was always close to, and therefore impacted by, patches with a large carrying capacity, even in the upward gradient. The very short gradient size was also likely the cause of the reversed patterns observed for $q = 1$ and density-dependent dispersal and for $q = 2$ and density-dependent growth. These corresponded to the lag described in the previous section: as the slowest speeds were respectively reached 1 and 2 patches after the smallest patch, the downward

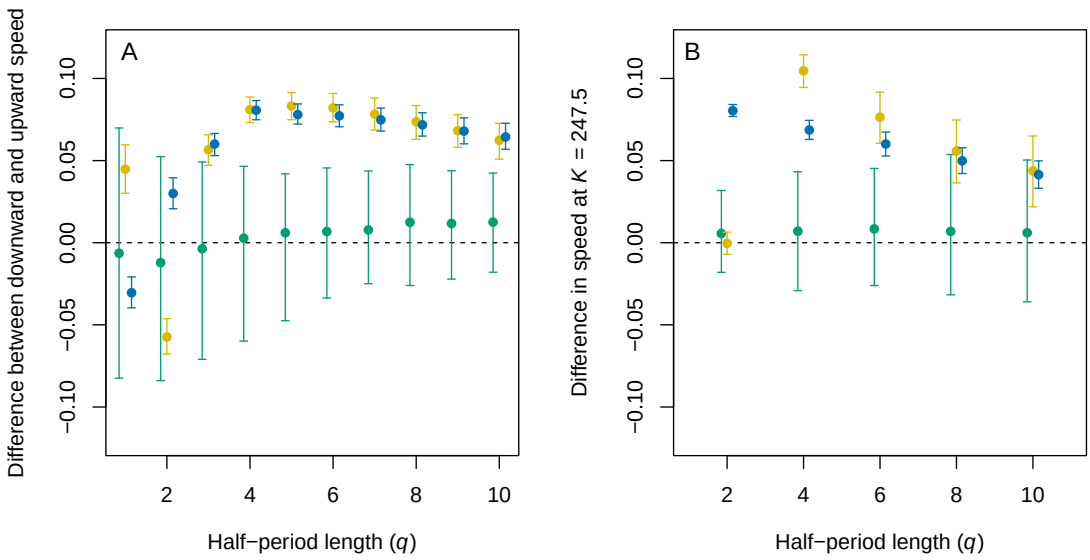

Figure 4: Difference between the downward and upward gradient speed (A) and instantaneous speed in the middle patch (B), for simulations without density dependence (green), density-dependent growth (yellow) and dispersal (blue), averaged over every gradient crossed by a simulated invasion. Positive values indicate faster invasions in downward gradients compared to the upward ones. Intervals contain 80% of the simulations. Results were slightly shifted on the x-axis for better readability.

gradient speed suffered from the influence of the previous smallest patch. A similar pattern was observed for the instantaneous speed in the middle patch, with differences decreasing as q increased (Fig 4B). As with the gradient speed, the lack of difference observed for $q = 2$ and density-dependent growth was also likely the result of the lag.

Experimental results

The three best models among those considered had a ΔAIC ≤ 2 (Table 1). As they were nested within each other, they were compared using likelihood ratio tests. The model including the carrying capacities on the front and behind the front ($K_i + K_{i-1}$ in Table 1) was significantly better than the one with only the carrying capacity behind the front ($\chi^2_{df=1} = 9.251, p = 0.0024$), and not significantly worse than the one with all variables ($\chi^2_{df=1} = 0.064, p = 0.8004$), while being more parsimonious. This model was therefore selected. According to it, the stop duration decreased with the carrying capacity of the patch ($z = -3.645$, $p = 0.0003$) and of the previous patch ($z = -2.428$, $p = 0.0152$). As instantaneous speed (as defined to analyse the simulation results) was the inverse of the stop duration, these results confirm experimentally the positive impacts of the carrying capacities of the current and previous patches on invasion speed.

Discussion

Simulation and experimental results provide evidence for the existence of a colonisation debt during invasions affected by positive density dependence in per capita growth or dispersal, i.e. a 'memory' of past carrying capacities impacting their speed. In these cases, taking into account habitat quality on the front alone was not sufficient to predict the invasion rate. Our results show in particular that the carrying capacity encountered previously by the front could substantially affect colonisation success and speed. We notably showed that invasions were faster overall in downward gradients than in upward gradients, as were instantaneous speeds, i.e. measured at the scale of a single patch, for the same carrying capacity.

Fixed variables	AIC	ΔAIC
Null	434.996	2.145
landscape	436.652	3.801
K_i	436.962	4.111
K_{i-1}	434.289	**1.438**
landscape + K_i	438.639	5.788
landscape + K_{i-1}	435.703	2.852
$K_i + K_{i-1}$	432.851	**0.000**
landscape + $K_i + K_{i-1}$	433.321	**0.470**

Table 1: AIC and ΔAIC (difference with the smallest AIC) of GLMMs defined for the experiment. Every model includes the experimental block as a random variable. Fixed variables included are the landscape type, the carrying capacity on the front (K_i) and the carrying capacity of the patch behind the front (K_{i-1}). ΔAIC values lower than 2 are noted in bold.

As hypothesized, a lag between changes in K and changes in invasion rate was also observed for both types of positive density dependence. Hence, the slowest invasion rate was reached a fixed number of patches after the lowest-quality patch encountered: one patch for density-dependent dispersal and two for density-dependent growth. This discrepancy can be explained by the functioning of the two density dependence mechanisms. In the case of density-dependent dispersal, the colony after the smallest patch remained too small to produce a substantial amount of dispersing individuals. In the case of density-dependent growth, the colony after the smallest patch produced dispersing individuals that were detected in the next patch (i.e. two patches after the smallest one), but they were too few to actually establish.

The impact of gradient slope on invasion speed varied with the scale considered. At the scale of one or a few patches, the velocities in the upward gradients approached those in the downward gradients as q increased. This means that the impact of colonisation debt was reduced in shallower gradients, i.e., where the difference in carrying capacity between the front and the patches of the core decreased. At the scale of the whole invasion, slope had little impact on the average invasion speed. However, the variance in speed increased with q, indicating that the speed of invasions in shallower gradients was less predictable when considered at large scales.

These results are consistent with a limited memory of invasions in time and space, with the impact of the last few colonized patches predominating. The difference in carrying capacity between these patches and the front was smaller when the gradients were shallower, as was the impact on invasion rate. At the gradient level, this lead to more extreme slowest and fastest speeds with increasing values of q. At the whole landscape level, this lead to less predictable average invasion speeds. Indeed, crossing the areas with small carrying capacity patches became increasingly difficult for the invader as q increased, leading to more frequent stops of the invasion front during simulations. As dispersal was stochastic, so were these stops and their duration, generating additional variability in the overall invasion speed. This is consistent with modeling studies using binary landscapes rather than gradients, which showed that a larger non-habitat gap was more likely to alter the spread of density-dependent invaders (Dewhirst and Lutscher, 2009, Morel-Journel et al., 2018). Although this was not tested for this study, experimental invasion fronts have proved to be inherently stochastic and hardly predictable (Melbourne and Hastings, 2009). The speed of real invasions along shallow gradients might therefore be even more unpredictable.

The influence of distant patches on the speed of the front is also expected to be modulated by the dispersal abilities of individuals (Dewhirst and Lutscher, 2009). This is likely the case in our study, when dispersal is local and mostly driven by nearby patches, but is even more important when individuals also disperse on long distances. Studies have shown that even rare dispersal long-distance dispersal events have a disproportionate impact on invasion speed (Johnson et al., 2006, Nehrbass et al., 2007, Pergl et al., 2011), and they have been shown to mitigate the impact of habitat heterogeneity (Marco et al., 2011). Similarly, we might expect them to limit the strength of the colonisation debt in our context

of gradual environmental change. Indeed, stratified dispersal, i.e. the combination of short-distance and long-distance dispersal, should diversify the origins of the individuals dispersing to the front, and therefore the habitat quality of the patches involved. It could be interesting to investigate the interaction between long-distance dispersal and the colonisation debt, in order to quantify this interaction.

The colonisation debt only appeared when either growth or dispersal was density-dependent. Otherwise, invasion speed remained independent from the carrying capacity, on the front or in the core of the invasion. Such links between a local mechanism and an invasion-wide pattern were previously documented, notably in the study of pushed waves (Stokes, 1976, Roques et al., 2012). Pushed waves also stem from a link between the population dynamics of the core of the invaded area and the spreading speed. Besides, they are generally associated with positive density-dependent growth, i.e. Allee effects, although they can also be the result of positive density-dependent dispersal (Haond et al., 2021). Therefore, our results can be relevantly considered in this framework. Studies concerning pushed waves have notably identified conditions for invasion pinning, i.e. the stop of the invasion front (Keitt et al., 2001, Wang et al., 2019, Morel-Journel et al., 2022). Our simulations do not exhibit actual pinning, but the very slow instantaneous speeds observed near the smallest patch correspond to temporary front stops over long time periods. The duration of those stops was greater in landscapes with shallower gradients, i.e. when large populations were further from the location of the stop. This suggests that the colonisation debt might also reduce the chances of pinning occurring in downward gradients, especially if they are steep.

The colonisation debt identified in this study is strictly the result of demographic mechanisms. Indeed, the simulations carried out for this study did not take into account the genetic background of the individuals, and the strain used for the experiments has a very low genetic diversity, being maintained in the laboratory through inbreeding. Yet, the colonisation debt can be expected to interact with the genetic diversity during real invasions. On the one hand, low genetic diversity could be an additional hurdle to colonisation for invading populations moving along an upward gradient of carrying capacity and having already suffered from a genetic bottleneck. On the other hand, pushed waves, which are generated by the same mechanisms as the colonisation debt, are also known to prevent the loss of genetic diversity that can be observed during spread (Roques et al., 2012, Bonnefon et al., 2014). We could therefore expect genetic diversity to maintain at higher levels along downward gradients, thus limiting the apparition of bottleneck because of decreasing carrying capacity and population size.

Considering the colonisation debt could improve the management of actual invasions or other range shifts. Firstly, the variations in speed it generates in heterogeneous environments might help identify density-dependent mechanisms among invasive populations. Our results show that the correlation between carrying capacity and invasion speed expected according to Haond et al. (2021) might not be perfect if habitat quality varies over space, because of the lag generated by the colonisation debt. The occurrence of such discrepancies in nature might be an indicator that the invasive population exhibits

positive density-dependence. Secondly, targeting populations behind the invasion front has already been identified as a way to prevent long-distance dispersal that could increase the spread of invaders (e.g. Johnson et al., 2006). Our results show that it could also reduce the colonisation capabilities of the populations on the front themselves, and potentially further reduce the speed of invasion. Reducing the suitability of the environment for an invader to hinder its spread might appear inefficient at first, because the invading populations still benefit from the last colonisation events, but it might also have a more durable impact on further colonisation events. These results suggest that targeting core populations as well as the invasion front itself might prove more efficient to slow down invasions.

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Conflicts of interest

The authors declare no financial conflict of interest with the content of this article.

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