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► To cite this version:

Thibaut Morel-Journal, Marjorie Haond, Lana Dunan, Ludovic Mailleret, Elodie Vercken. Colonisation debt: when invasion history impacts current range expansion. 2023. hal-04236191v1

HAL Id: hal-04236191

<https://hal.inrae.fr/hal-04236191v1>

Preprint submitted on 6 Jul 2023 (v1), last revised 10 Oct 2023 (v2)

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Colonisation debt: when invasion history impacts current range expansion

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1 Abstract

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

16 Introduction

17 The demographic processes occurring among invasive populations are essential for understanding and
18 modeling range expansion at large scales (Gurevitch et al., 2011, Caplat et al., 2012, Blackburn et al.,
19 2015). Indeed, range expansion is the result of successive colonisation events beyond the edge of the
20 invaded area (Blackburn et al., 2011), whose failure causes the invasion to slow down or even come
21 to a halt. (Keitt et al., 2001, Morel-Journel et al., 2022). The dynamics of these new, initially small
22 colonies may be influenced by various ecological mechanisms, including a positive density dependence
23 of growth and dispersal. Positive density-dependent growth, commonly referred to as the Allee effect
24 (Allee et al., 1949, Courchamp et al., 2008), corresponds to lower *per capita* growth rates at low densities
25 because of biological mechanisms generally affecting survival or reproduction (Courchamp et al., 1999).
26 Positive density-dependent dispersal describes the greater propensity of individuals to disperse from large
27 populations than from small ones, often to avoid intraspecific competition at high densities (Altwegg et al.,
28 2013). Previous studies have shown that both types of density-dependence create a causal relationship
29 between expansion speed and the size of the populations in the core of the invaded area, behind the
30 invasion front (Stokes, 1976, Lewis and Kareiva, 1993, Roques et al., 2012, Haond et al., 2021). The
31 larger these populations, the greater the number of individuals reaching the front, thus mitigating adverse
32 effects of positive density-dependence in small populations.

33 The influence of positive density dependence may also depend on the amount of habitat available,
34 which influences the carrying capacity, i.e. the maximum attainable individual density. Previous mod-
35 elling and experimental evidence from Haond et al. (2021) and Morel-Journel et al. (2022) have shown
36 that, in presence of positive density dependence, the carrying capacity of the invaded environment im-
37 pacts invasion speed, potentially up to a stop of the invasion front for low carrying capacities. Conversely,
38 invasion speed remains unaffected by carrying capacity in the absence of any density-dependence. These
39 studies only considered constant carrying capacities over space. Yet the amount of habitat is rarely
40 spatially homogeneous, especially at the scale of an invasion. Other works have studied the impact of
41 spatial heterogeneity on invasive spread (e.g Shigesada et al., 1986, Kinezaki et al., 2006, Schreiber and
42 Lloyd-Smith, 2009, Vergni et al., 2012), some of them including positive density dependence (e.g Dewhurst
43 and Lutscher, 2009, Pachepsky and Levine, 2011, Maciel and Lutscher, 2015). However, heterogeneity
44 was considered in these studies through its impact on the growth rate of populations rather than on their
45 carrying capacity. Although carrying capacity could still change as a result, it was not explicitly consid-
46 ered as a controlled parameter. Moreover, many of them considered binary cases, separating habitat from
47 non-habitat (Shigesada et al., 1986, Dewhurst and Lutscher, 2009, Pachepsky and Levine, 2011, Maciel
48 and Lutscher, 2015). Yet, the amount of habitat, which plays an important role in defining the carrying
49 capacity, often varies gradually rather than starkly over space.

50 For this study, we consider gradients of carrying capacity, i.e. monotonic variations of carrying capacity
51 over space. In this context, gradients are different from the environmental gradients defining for instance
52 defining range limits, which rather correspond to a set of changes in habitat quality, often susceptible of
53 affecting individual fitness and population growth rates. In this study, we focus on variations of carrying
54 capacity, which does not limit by itself the ability of individuals to survive or reproduce, but rather
55 their maximal numbers. These gradients are considered ‘upward’ if the invasion fronts move towards
56 increasing carrying capacities, and ‘downward’ if it moves towards decreasing carrying capacities, with
57 the slope of the gradient characterizing the average change in carrying capacity over space, in absolute
58 value. According to previous studies considering constant carrying capacities over space, colonisation with
59 positive density dependence is expected to be more difficult and slower at smaller carrying capacities, and
60 thus smaller population sizes (Haond et al., 2021). Therefore, colonisation along a downward gradient is
61 expected to slow down as carrying capacity decreases. However, information on the rate of decrease and
62 its relationship to the gradient slope is lacking. While the carrying capacity of the patch on the front is
63 still expected to impact invasion speed, so are those of the patches behind the front in that case. Indeed,
64 density dependence links colonisation success to the dynamics of populations behind the invasion front.
65 Thus, the front should advance faster in downward gradients because of the large influx of dispersed
66 individuals from larger populations behind. Conversely, the front should be impeded by the smaller size
67 of the populations behind the front in upward gradients. This impact is expected to be stronger as
68 gradient slope, and thus the difference in carrying capacities, increases.

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

80 Using mechanistic models and experiments, we tested the existence of the colonisation debt during
81 invasions in environments with heterogeneous carrying capacity. On the one hand, we simulated invasions
82 across a one-dimensional landscape with positive density dependence on growth, dispersal, or neither.
83 As the impact of carrying capacity on invasion speed with positive density-dependence has already been
84 shown (Haond et al., 2021), we aimed at comparing here landscapes with the same average carrying

85 capacity but exhibiting different gradients. To do so, we considered periodic successions of gradients
86 of increasing and decreasing carrying capacity, with identical mean but different slopes. On the other
87 hand, we performed artificial invasions in microcosm landscapes using *Trichogramma chilonis*, a biological
88 model known to exhibit positive density-dependent dispersal in particular experimental conditions (Morel-
89 Journal et al., 2016, Haond et al., 2021). Two types of landscapes, with different slopes, were used for
90 this experiment.

91 Material and Methods

92 *Simulations*

93 A stochastic model was used to generate invasions in a one-dimensional landscape (see Supplementary
94 material 1 for details). The model was discrete in space, i.e. the landscape was represented as a linear
95 chain of patches. It was also discrete in time, with each time step divided into a growth phase and a
96 dispersal phase. Growth potentially included positive density-dependence, through an Allee threshold
97 ρ , i.e. a population size under which the mean population growth rate was negative. Hence, there was
98 positive density-dependent growth if $\rho > 0$. Dispersal was local and stochastic, i.e. individuals travelled
99 to the neighboring patch with a probability d . This probability could either be constant if dispersal was
100 density-independent, or increase with individual density according to a Hill function of parameters α and
101 τ , to include density-dependent dispersal.

102 This model was used to simulate invasions, using the R software (RCoreTeam, 2018). The landscapes
103 considered were infinite on the right but finite on the left. Only the leftmost patch was initially colonised,
104 with a population size of K_{max} . The landscape was divided into two parts. The first n_b leftmost
105 patches made up the ‘burn-in part’. These patches all had a carrying capacity of K_{max} , so the invasion
106 started in a homogeneous space and the invasion front was created before the invasion entered the second
107 part of the landscape. The dynamics in this burn-in part were not analysed further, as this type of
108 invasion in homogeneous landscapes has already been documented in previous studies (e.g Haond et al.,
109 2021). The remaining patches made up the ‘periodic part’ of the landscape. Their carrying capacity
110 varied periodically between K_{max} and K_{min} with a period length $2q$ (Fig. 1). Each period included
111 one downward gradient followed by one upward gradient, each with q patches. The two gradients were
112 symmetrical, and the carrying capacity K_i of patch i was defined as follows:

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

113 with j the closest patch to the left of i so that $K_j = K_{max}$. The gradients were symmetrical, and

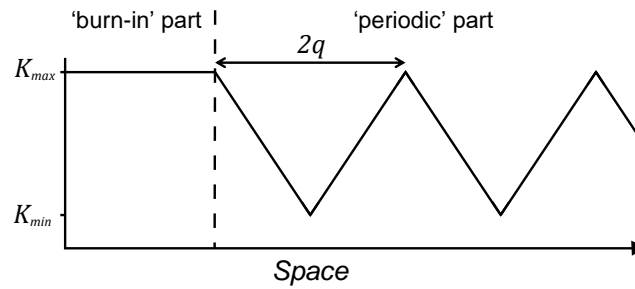


Figure 1: Schematic representation of the variations in the carrying capacity in the landscape considered for the simulations. The burn-in part is of finite length (corresponding to n_b patches), but the periodic part continues infinitely to the right.

114 their slope – the differences in carrying capacity between two neighbouring patches – increased when q
 115 decreased. Since the value of K_{max} and K_{min} were constant, the length of a gradient q was inseparable
 116 from the slope, computed as $(K_{max} + K_{min})/q$. Therefore, low values of q correspond to steeper gradients
 117 whereas high values of q correspond to shallower ones.

118 As a convention, patches were numbered in ascending order, starting from $-n_b$ for the leftmost patch.
 119 Therefore, the first patch of the periodic part was the patch 0. Previous results showed the link between
 120 the average carrying capacity of the landscape and invasion speed because of positive-density dependence
 121 (Haond et al., 2021). Considering such periodic landscapes allowed us to consider landscapes that all had
 122 the same average carrying capacity in their periodic part for any value of q , of value $(K_{max} + K_{min})/2$.

123 Simulations were performed for landscapes with $K_{max} = 450$, $K_{min} = 45$, $n_b = 10$, and q an integer
 124 between 1 and 10. They all lasted for $t_{max} = 1000$ generations – including the burn-in part – and
 125 assumed an intrinsic growth rate $r = 0.2$ and a dispersal rate without density dependence $d_{ind} = 0.1$ (see
 126 Supplementary material 1). Three scenarios were tested for each landscape: (i) a null scenario, without
 127 any positive density-dependence, (ii) with positive density-dependent growth with $\rho = 15$, and (iii) with
 128 positive density-dependent dispersal with $\alpha = 4$ and $\tau = K_{max}/2 = 225$ (see Supplementary material 1).
 129 Each of the 3 scenarios \times 10 landscape combinations was simulated 1000 times.

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

135 Invasion speed was computed at three scales: the whole landscape, the gradient and the patch. The
 136 average speed of the front was defined at the landscape level, as the ratio between the last position of the
 137 front and the duration of the invasion proper $P(t_{max})/(t_{max} - t_s)$. The gradient speed was defined at
 138 the scale of one (upward or downward) gradient, as the ratio between q and the number of generations
 139 the invasion front spent between the two extremities of the gradient. For a downward gradient, the

140 extremities were patch a and patch $a + q$, such that $K_a = K_{max}$. For upward gradients, they were patch
141 b and patch $b + q$, such that $K_b = K_{min}$. For a given simulation, the difference between the average
142 upward and downward gradient speeds was also computed. A gradient was not considered if the invasion
143 never reached its extremity. The instantaneous speed of the front was defined at the patch level, as the
144 inverse of the number of generations during which the invasion front remained stationary in the patch.
145 To compare instantaneous speeds for different q , the average instantaneous speed in the middle patch
146 was computed for each simulation with an even value of q . Then, the carrying capacity of this middle
147 patch was always $K = (K_{max} + K_{min}) / 2 = 247.5$. As there was no middle patch when q was odd, these
148 cases were not considered.

149 To assess the impact of the periodic structure of the landscape, we also performed simulations with
150 the same parameter values as indicated above, but for a a single gradient, either upward or downward.
151 For these simulations, we computed the gradient speed, as well as the instantaneous speed in the middle
152 patch of the gradient (see Supplementary material 2).

153 *Microcosm experiments*

154 Artificial invasions of microcosm stepping-stone landscapes were performed in addition to the simulations
155 (see Supplementary material 3 for details). The biological model used was a strain of the parasitoid
156 wasp *Trichogramma chilonis*, which is known to exhibit positive density-dependent dispersal (Morel-
157 Journal et al., 2016). As carrying capacity was previously shown to not affect invasions speed without
158 positive density-dependence (Haond et al., 2021), we focused on this strain to test for the existence of the
159 colonisation debt. In our experiment, the carrying capacity was manipulated by changing the number
160 of host eggs available for *T. chilonis*, which were used as a resource. Two landscapes defined for the
161 simulations were recreated for the experiment (Fig. 2). The first one (called thereafter the ‘shallow’
162 landscape) was a downward gradient from 450 to 45 eggs, similarly to the simulated landscape with
163 $q = 7$. The second one (called thereafter the ‘steep’ landscape) alternated between patches with 450
164 eggs and patches with 90 eggs, similarly to the simulated landscapes for $q = 1$. Patches with 90 eggs
165 were used rather than with 45 eggs to buffer the very strong demographic stochasticity displayed by *T.*
166 *chilonis*. Indeed, populations in patches with 45 eggs would have been too likely to go extinct because
167 of stochasticity or over-competition (see Supplementary material 3), without allowing for additional
168 colonisation over the 18 generations of the experiment. Likewise, we did not consider invasion in a single
169 upward slope because starting invasions in such small patches would likely have lead to establishment
170 failures during the experiment.

171 As for simulations, the position of the front was recorded at every generation as the rightmost patch
172 with more than 5 individuals. The stop duration, i.e. the number of generations during which the invasion
173 front remained stationary in a given patch, was used to assess instantaneous speed across the landscape.

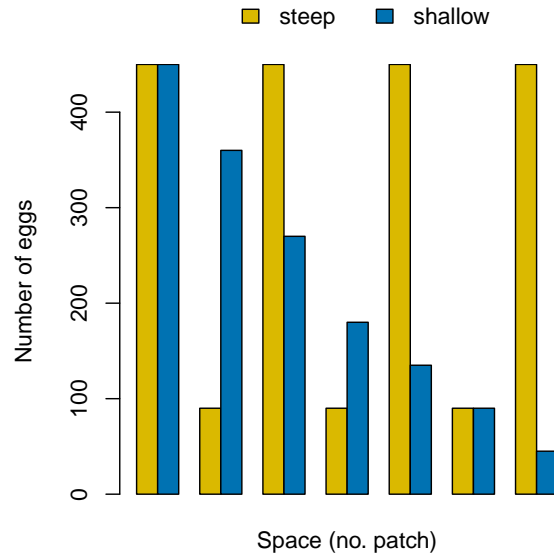


Figure 2: Number of eggs in the patches in the ‘steep’ (yellow) and ‘shallow’ (blue) landscapes. The invasion are initiated by colonizing patch 1 for each replicate of the experiment.

174 The stop duration was computed for every colonized patch but the last one, and was a count of generations
175 following a Poisson distribution. It was therefore analysed using a generalized linear mixed model, with
176 a log link function and the experimental replicate as a random effect. Three explanatory variables were
177 considered: the type of landscape, the carrying capacity on the front, the carrying capacity of the patch
178 preceding the front. Models with every combination of these parameters were compared according to
179 AIC. Models within 2 AIC points of the smallest value were compared using likelihood ratio tests, to
180 define the most parsimonious among the best ones.

181 Results

182 *Simulation results for average speed*

183 The average invasion speed was substantially reduced by positive density dependence. Indeed, 90% of
184 the simulated invasions without any positive density dependence had an average speed between 0.159
185 and 0.181 patches/gen, whereas they ranged from 0.009 to 0.024 patches/gen and from 0.014 to 0.026
186 patches/gen for simulations with density-dependent growth and dispersal, respectively. There was no
187 major impact of the half-period size q on the average speed, likely because the average carrying capacity
188 in the landscape was identical in every landscape. The variations in speed across upward and downward
189 gradients averaged out in the long run, leading to similar landscape speeds for different q even though
190 gradient speeds themselves could differ. However, the variance tended to increase with q for simulated
191 invasions with density-dependent growth (standard deviation from 0.0019 for $q = 1$ to 0.0083 for $q = 10$)

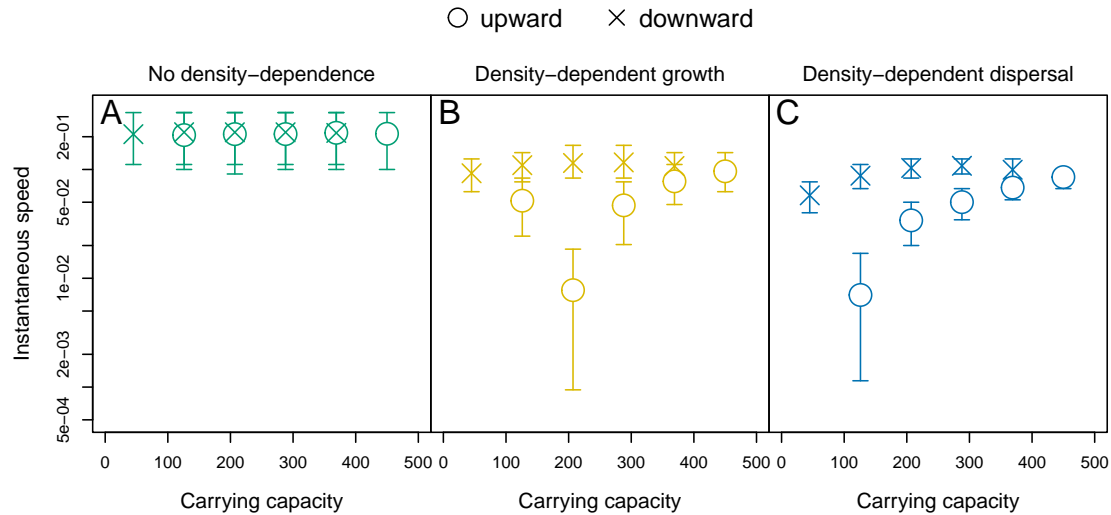


Figure 3: Example of instantaneous speed as a function of carrying capacity of the patch where the front is located, for $q = 5$ and either no density dependence (A, green), density-dependent growth (B, yellow) and dispersal (C, blue). Average values over all patches with the same carrying capacity are represented by crosses if the patch is in a downward gradient, and as circles if the patch is in an upward gradient. Intervals contain 80% of the simulated instantaneous speeds.

192 and dispersal (standard deviation from 0.0019 for $q = 1$ to 0.0064 for $q = 10$). The variance was
 193 independent from q and overall greater for simulated invasions without density-dependence (standard
 194 deviation between 0.0076 and 0.0082).

195 *Simulation results for instantaneous speed*

196 Instantaneous speeds for each value of q considered are presented in Supplementary material 4 (Fig.
 197 S5), while Fig. 3 presents the results for the simulations with $q = 5$, which is in the middle of the
 198 range of values considered. Like the average speed, the instantaneous speed was systematically higher in
 199 simulations with no positive density dependence. Furthermore, the invasion speed without any mechanism
 200 was largely independent of carrying capacity, remaining around 0.215 gen^{-1} for each patch (Fig. 3A).
 201 In presence of density dependence, the instantaneous speed varied not only with the carrying capacity
 202 of the patch, but also with the carrying capacity of previous patches (Fig 3B, 3C). Indeed, with positive
 203 density dependence, separating instantaneous speeds according to whether the patch was in an upward or
 204 downward gradient revealed substantial differences. Firstly, speeds were consistently higher in downward
 205 gradients, for the same value of K . Secondly, the minimum instantaneous speed was not observed in the
 206 patch with $K = 45$ (i.e. K_{min}), but one (with density-dependent dispersal) or two patches (with density-
 207 dependent growth) further in upward gradients. This created a lag in the variation of instantaneous
 208 speed, compared to the variation in carrying capacity.

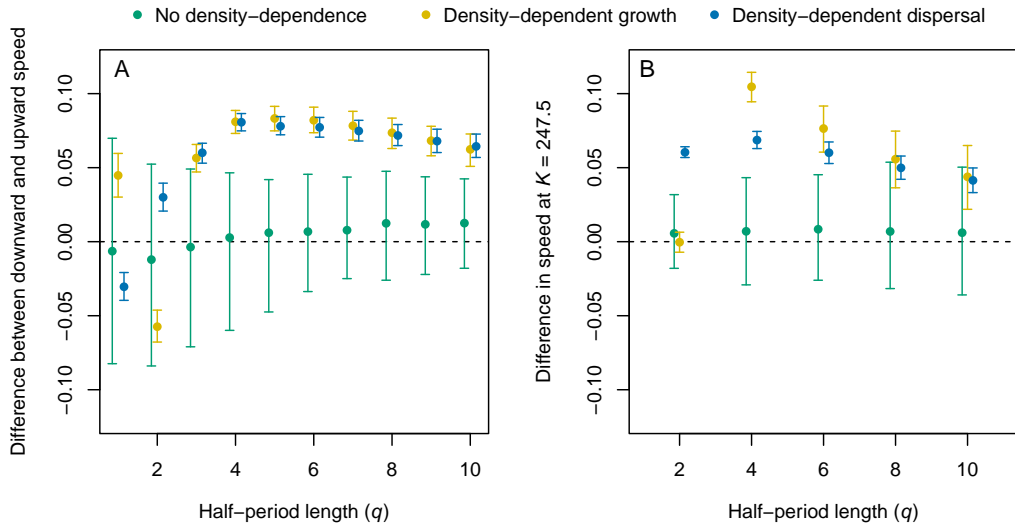


Figure 4: Difference between the downward and upward gradient speed (A) and instantaneous speed in the middle patch (B), for simulations without density dependence (green), density-dependent growth (yellow) and dispersal (blue), averaged over every gradient crossed by a simulated invasion. Positive values 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.

209 *Impact of gradient slope on simulated speed*

210 The impact of gradient slope (inversely proportional to the value of q) was assessed by comparing invasion
211 speeds in upward and in downward gradients, based on gradient speeds (Fig 4A) and on instantaneous
212 speed in the middle patch of the gradient (Fig 4B). Consistently with the results presented above, there
213 was no significant difference in speed between downward and upward gradients in the absence of positive
214 density dependence. However, the difference in speed was generally positive with both types of density
215 dependence, with faster speeds in the downward gradients. The difference in gradient speed was maximal
216 around $q = 4$ and decreased for larger values of q , i.e. for the shallower gradients (Fig 4A). For smaller
217 values of q , the gradients were so short that the invasion front was always close to, and therefore impacted
218 by, patches with a large carrying capacity, even in the upward gradient. The very short gradient size was
219 also likely the cause of the reversed patterns observed for $q = 1$ and density-dependent dispersal and for
220 $q = 2$ and density-dependent growth. These corresponded to the lag described in the previous section:
221 as the slowest speeds were respectively reached 1 and 2 patches after the smallest patch, the downward
222 gradient speed suffered from the influence of the previous smallest patch. A similar pattern was observed
223 for the instantaneous speed in the middle patch, with differences decreasing as q increased (Fig 4B). As
224 with the gradient speed, the lack of difference observed for $q = 2$ and density-dependent growth was also
225 likely the result of the lag. The additional results for a single gradient (Supplementary material 3) show
226 faster downward gradient speeds for any value of q , thus supporting our hypothesis that this lag stems
227 from the downward gradient preceding the upward one.

Fixed variables	AIC	Δ AIC
$K_i + K_{i-1}$	442.391	0.000
landscape + $K_i + K_{i-1}$	442.797	0.406
K_{i-1}	444.427	2.036
Null	445.555	3.164
landscape + K_{i-1}	445.824	3.433
landscape	447.205	4.815
K_i	447.515	5.124
landscape + K_i	449.189	6.798

Table 1: AIC and Δ AIC (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}). Δ AIC values lower than 2 are noted in bold.

228 *Experimental results*

229 Our statistical analysis on stop duration confirms that the speed also depends on the carrying capacity
230 of the patch behind the front. Firstly, it should be noted that including the carrying capacity of the
231 previous patch (noted K_{i-1} in Table 1) reduced the AIC value of any of the models considered (Table
232 1), indicating that taking this factor into account always improved the model. Secondly, the two best
233 models according to Δ AIC ≤ 2 were nested within each other, so they were compared using likelihood
234 ratio tests. The model including the carrying capacities on the front and behind the front ($K_i + K_{i-1}$
235 in Table 1) was not significantly worse than the one with all variables ($\chi^2_{df=1} = 1.5941, p = 0.2067$),
236 while being more parsimonious. This model was therefore selected. According to it, the stop duration
237 decreased with the carrying capacity of the patch ($z = -1.969, p = 0.0490$) and of the previous patch
238 ($z = -2.591, p = 0.0096$). As instantaneous speed (as defined to analyse the simulation results) was the
239 inverse of the stop duration, these results confirm experimentally the positive impacts of the carrying
240 capacities of the current and previous patches on invasion speed.

241 Besides, experimental results show a clear decrease in velocity for lower carrying capacities in shallow
242 landscapes, but a much smaller decrease in steep landscapes. (Fig. 5). The difference in speed in the
243 largest and smallest patches was therefore greater when the gradient was shallower. This is consistent
244 with the simulation results, for which the difference between speeds in the largest and smallest patch
245 were greater as the value of q increased (see Supplementary material 4). However, the pattern observed
246 in the simulations of steep gradients ($q < 4$) was not observed experimentally.

247 **Discussion**

248 *Main results*

249 Simulation and experimental results provide evidence for the existence of a ‘memory’ of past carrying
250 capacities impacting on the speed of invasion, which we refer to here as ‘colonisation debt’, when there

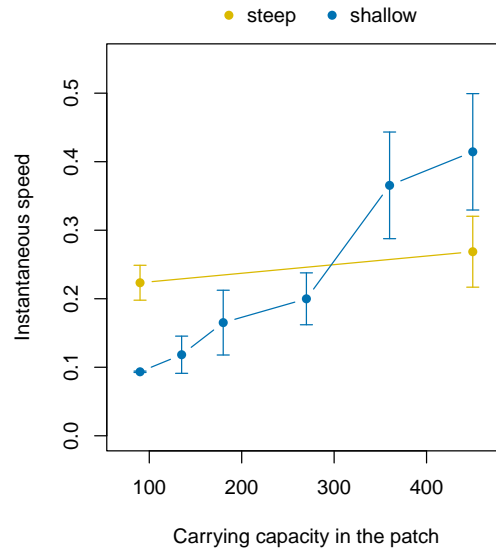


Figure 5: Average instantaneous speed (inverse of the stop duration) observed in the experiments, as a function of the carrying capacity in the patch, in shallow (blue) and steep landscapes (yellow). Intervals represent 2 standard errors around the average.

251 is a positive density dependence in per capita growth or dispersal. In these cases, taking into account
252 habitat on the front alone was not sufficient to predict the invasion rate. Our simulation results show that
253 the carrying capacity encountered previously by the front could substantially affect colonisation success
254 and speed. We notably showed that invasions were faster overall in downward gradients than in upward
255 gradients, as were instantaneous speeds, i.e. measured at the scale of a single patch, for the same carrying
256 capacity. As hypothesized, a lag between changes in K and changes in invasion rate was also observed for
257 both types of positive density dependence. Hence, the slowest invasion rate was reached a fixed number
258 of patches after the lowest-quality patch encountered: one patch for density-dependent dispersal and two
259 for density-dependent growth. This discrepancy can be explained by the functioning of the two density
260 dependence mechanisms. With both mechanisms, the invasion managed to establish in the colony, after
261 the smallest patch because of the influx of dispersing individuals from the previous patches. With density-
262 dependent dispersal, this population on the front was too small to produce dispersing individuals, which
263 momentarily stopped the front one patch after the smallest one. With density-dependent growth, this
264 population produced enough dispersing individuals to be detected in the next patch (two patches after
265 the smallest one), but not enough to overcome the Allee effects. These individuals might not have been
266 detected if population sizes had been recorded after the growth phase rather than after the dispersal
267 phase.

268 Our experimental results using a species known to exhibit positive density-dependent dispersal also
269 show differences in invasion speed as a function of the carrying capacity on the front, depending on the
270 size of the patch behind the front. Indeed, invasion speed decreased more strongly with carrying capacity
271 in the shallow landscapes than in the steep ones, which is consistent with the simulation results.

272 The impact of the gradient slope on invasion speed varied with the scale considered. At the scale of
273 a single patch, the upward and downward speeds for the same carrying capacity on the front became
274 closer as the gradients became shallower (higher values of q). Indeed, the difference between the carrying
275 capacities of the patches behind the front in the two gradients became smaller as q increased, thus making
276 the effect of colonisation debt less visible. At the scale of the whole invasion, slope had little impact on
277 the average invasion speed. However, the variance in speed increased with q , indicating that the speed
278 of invasions in shallower gradients was less predictable.

279 *Extent of the memory of past carrying capacities*

280 Our results are consistent with a limited memory of invasions in time and space, with the impact of the
281 last few colonized patches predominating. The difference in carrying capacity between these patches and
282 the front was smaller when the gradients were shallower, as was the impact on invasion rate. At the
283 gradient level, this lead to more extreme slowest and fastest speeds with increasing values of q . At the
284 whole landscape level, this lead to less predictable average invasion speeds. Indeed, crossing the areas
285 with small carrying capacity patches became increasingly difficult for the invader as q increased, leading
286 to more frequent stops of the invasion front during simulations. As dispersal was stochastic, so were
287 these stops and their duration, generating additional variability in the overall invasion speed. This is
288 consistent with modeling studies using binary landscapes rather than gradients, which showed that a
289 larger non-habitat gap was more likely to alter the spread of density-dependent invaders (Dewhurst and
290 Lutscher, 2009, Morel-Journel et al., 2018). Although this was not tested for this study, experimental
291 invasion fronts have proved to be inherently stochastic and hardly predictable (Melbourne and Hastings,
292 2009). The speed of real invasions along shallow gradients might therefore be even more unpredictable.

293 The influence of distant patches on the speed of the front is also expected to be modulated by the
294 dispersal abilities of individuals (Dewhurst and Lutscher, 2009). This is likely the case in our study,
295 when dispersal is local and mostly driven by nearby patches, Not only should lower dispersal distances
296 limit this influence, but also the ability of invasion fronts to overcome areas with low carrying capacities.
297 Indeed, studies show that the pinning of invasion fronts is more likely if the size of the gap in habitat is
298 greater relative to the dispersal distance (Keitt et al., 2001, Morel-Journel et al., 2022). Our simulations
299 do not exhibit actual pinning, but the very slow instantaneous speeds observed near the smallest patch
300 correspond to temporary front stops over long time periods. The duration of those stops was greater in
301 landscapes with shallower gradients, i.e. when large populations were further from the location of the
302 stop. This suggests that even shallower gradients or smaller dispersal distances could generate pinning.

303 Conversely, the influence of patches behind the front is expected to be even greater when individuals
304 also disperse on long distances. Studies have shown that even rare long-distance dispersal events have
305 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
carrying capacity 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.

Link with pushed invasions

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. It should however be noted that other mechanisms have
been shown to generate pushed waves, among them shifts in environmental conditions (Bonneton et al.,
2014). While the spatial variations in carrying capacity considered in this study reflect variations in the
amount of habitat available, landscapes are also heterogeneous in other environmental factors susceptible
to constrain species ranges. Garnier and Lewis (2016) notably showed that shifting climate envelopes
could generate pushed waves without any mechanism of positive density-dependence. Conversely to our
study, climate envelope limits the colonisable habitat in space, so that a slow shift due to climate change
constrains the colonisation of new habitats by the species, regardless of density-dependence mechanisms.
It could be interesting to test for the colonisation debt in these pushed waves that exhibit none without
a shifting climate envelope.

Interaction with genetic diversity

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

339 during spread (Roques et al., 2012, Bonnefon et al., 2014). We could therefore expect genetic diversity to
340 maintain at higher levels along downward gradients, thus limiting the apparition of genetic bottlenecks
341 because of decreasing carrying capacity and population size.

342 The density-dependence mechanisms themselves are susceptible to evolve along the invasion, and
343 therefore affect the colonisation debt. On the one hand, increased genetic variance has been shown to
344 help invasive population to evolve towards a mitigation of positive density-dependent growth (Kanarek
345 and Webb, 2010, Kanarek et al., 2015). The maintenance of genetic variance in pushed invasions could
346 therefore also facilitate a weakening of the mechanism on the front. Similarly, studies indicate that
347 positive density-dependent dispersal is expected to be reduced along invasions, by evolving towards
348 density-independent dispersal (Travis et al., 2009, Erm and Phillips, 2020), although recent results suggest
349 that this evolution might not be systematic (Dahirel et al., 2022). Dispersal from the populations behind
350 the front underlying the colonisation debt might therefore also enable the invader to evolve out of the
351 density-dependence mechanisms generating the colonisation debt.

352 *Consideration for the management of invasions*

353 Considering the colonisation debt could improve the management of actual invasions or other range
354 shifts. Firstly, the variations in speed it generates in heterogeneous environments might help identify
355 density-dependent mechanisms among invasive populations. Our results show that the correlation be-
356 tween carrying capacity and invasion speed expected according to Haond et al. (2021) might not be as
357 clear if the amount of habitat varies over space, because of the lag generated by the colonisation debt.
358 The occurrence of such discrepancies in nature might be an indicator that the invasive population ex-
359 hibits positive density-dependence. Secondly, targeting populations behind the invasion front has already
360 been identified as a way to prevent long-distance dispersal that could increase the spread of invaders
361 (e.g. Johnson et al., 2006). Our results show that it could also reduce the colonisation capabilities of the
362 populations on the front themselves, and potentially further reduce the speed of invasion. Reducing the
363 suitability of the environment for an invader to hinder its spread might appear inefficient at first, because
364 the invading populations still benefit from the last colonisation events, but it might also have a more
365 durable impact on further colonisation events. These results suggest that targeting core populations as
366 well as the invasion front itself might prove more efficient to slow down invasions.

367 **Acknowledgements**

368 This work is part of the PhD thesis of Marjorie Haond, funded by INRAE (plant health division) and
369 the regional council of Provence Alpes Côte d'Azur. It was also supported by the TriPTIC (ANR-14-
370 CE18-0002) and PushToiDeLa (ANR-18-CE32-0008) projects, funded by the French National Agency for

371 Research.

372 Conflicts of interest

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

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