PERSPECTIVE

Dispersers' habitat detection and settling abilities modulate the effect of habitat amount on metapopulation resilience

Louise Riotte-Lambert [ID] · **Fabien Laroche** [ID]

Abstract

Context Metapopulation theory makes useful predictions for conservation in fragmented landscapes. For randomly distributed habitat patches, it predicts that the ability of a metapopulation to recover from low occupancy level (the "metapopulation capacity") linearly increases with habitat amount. This prediction derives from describing the dispersal between two patches as a function of their features and the distance separating them only, without interaction with the rest of the landscape. However, if individuals can stop dispersal when hitting a patch ("habitat detection and settling" ability), the rest of habitat may modulate the dispersal between two patches by intercepting dispersers (which constitutes a "shadow" effect).

Objectives We aim at evaluating how habitat detection and settling ability, and the subsequent shadow effect, can modulate the relationship between the metapopulation capacity and the habitat amount in the metapopulation.

Methods Considering two simple metapopulation models with contrasted animal movement types, we used analytical predictions and simulations to study the relationship between habitat amount and metapopulation capacity under various levels of dispersers' habitat detection and settling ability.

Results Increasing habitat detection and settling ability led to: (i) larger metapopulation capacity values than expected from classic metapopulation theory and (ii) concave habitat amount–metapopulation capacity relationship.

Conclusions Overlooking dispersers' habitat detection and settling ability may lead to underestimating the metapopulation capacity and misevaluating the conservation benefit of increasing habitat amount. Therefore, a further integration of our mechanistic understanding of animals' displacement into metapopulation theory is urgently needed.

Keywords Animal movement · Conservation · Perception · Reserve design · Spatial network · SPOM

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Introduction

The spatial distributions of many animals living in fragmented habitats can be represented as metapopulations, i.e. networks of populations connected by dispersal and undergoing frequent extinction/re-colonization (e.g. snails: Lamy et al. 2013, frogs: Chandler et al. 2015, beetles: Laroche et al. 2018, voles: Sutherland et al. 2014). The classic metapopulation theory (Levins 1969) emphasizes that the long-term persistence of metapopulations essentially depends on the species' colonization abilities overweighing the extinction rate of populations. Understanding the mechanisms underpinning colonization dynamics is therefore a crucial step to assess the degree of threat to metapopulations and to design management measures.

Notwithstanding the deep conceptual contributions of Levins' simple spatially-implicit model (1969), it is however quite limited to draw conclusions about real metapopulations, especially about how habitat spatial configuration affects the colonization dynamics (but see Ovaskainen 2002). Spatially-explicit stochastic patch occupancy models (SPOMs), like the Incidence Function models (Hanski 1994) and the spatially realistic Levins model (Hanski and Gaggiotti 2004), contribute to bridge this gap by analyzing the impact of metapopulation spatial structure on its persistence. In particular, they allow deriving the expected time to extinction of the metapopulation, i.e. extinction of all local populations, and the 'metapopulation capacity' (Hanski and Ovaskainen 2000), which quantifies its ability to recover from low occupancy level. The metapopulation capacity has been widely used in applied conservation studies. It allows the evaluation of metapopulation persistence in a changing environment (Shen et al. 2015; Che-Castaldo and Neel 2016), the ranking of patches' (Blazquez-Cabrera et al. 2014; Rubio et al. 2014) and corridors' conservation values (Brodie et al. 2016; Foster et al. 2017), and the comparison of metapopulation configurations (Schnell et al. 2013; Larrey-Lassalle et al. 2018).

Most spatially-explicit metapopulation models simulate the colonization process with a kernel function. The kernel depicts the probability of colonization C_{ij} from a habitat patch j to patch i as a function of their attributes (A_j, A_i; e.g. their respective areas) and the distance separating them (d_{ij}; Hanski 1994; Hanski and Ovaskainen 2000): $C_{ij} = C \times$ a$(A_j) \times$ b$(A_i) \times$ c(d_{ij}) where C is a normalizing

constant and a,b and c are functions that vary depending on models. Under this simple set of assumptions, current metapopulation theory predicts that decreasing the distance among patches or increasing habitat density always increases metapopulation capacity (Hanski and Ovaskainen 2000; Etienne 2004; Grilli et al. 2015). When habitat patches are located randomly in space, current theory further predicts that this relationship is linear (Grilli et al. 2015). Overall, this suggests that increasing the total area of habitat in a defined area is a robust conservation strategy.

The kernel-based approach depicted above integrates over the entire metapopulation all the phases of the dispersal process (emigration, transfer, and immigration phases; Clobert et al. 2009) into one single probability formula. However, simulating dispersal within a metapopulation using a kernel means considering that individuals' probability to reach a given destination does not depend on the habitat quality they may encounter during the transfer phase of their dispersal, i.e. does not depend on the landscape spatial configuration. Although many different dispersal motivations exist, this assumption seems questionable for dispersers that can alter their movement according to the environment and conditions they encounter, i.e. most animals (Revilla and Wiegand 2008; Nathan et al. 2008). Efforts are therefore needed to build metapopulation models that account for the effects of the interactions between the landscape configuration and dispersers' sensory, cognitive and navigational abilities on dispersal fluxes between two patches.

First steps in that direction have been to account for the limitation of the number of dispersers leaving a source patch. This limitation induces a "competition" for dispersers among destination patches, which depends on the distance from the source (e.g. Ranius et al. 2010) and on the dispersers' habitat preferences (e.g. Vinatier et al. 2011). The competition for dispersers among patches implies that the addition of a new habitat patch within a metapopulation will necessarily lead to a decrease in the fluxes among the preexisting patches, because the new patch will attract some of the dispersers. This effect violates the kernel assumption from the classic metapopulation theory.

However, acknowledging the competition for dispersers does not capture the full complexity of how the landscape spatial configuration can affect the dispersal fluxes among patches. Here we aim at illustrating this point by considering a basic aspect of most animals'

dispersal: the voluntary interruption of dispersal when local conditions are suitable. This ability, which we call "habitat detection and settling ability" (HDSA) hereafter, can generate a phenomenon called the "shadow effect" that is covered neither by the classic kernel approach (Hein et al. 2004; Bode et al. 2008) nor by extensions including competition for dispersers determined by the distance to the source patch (Ranius et al. 2010). When a new patch is made available for habitat-perceptive dispersers, it intercepts dispersers and thus decreases the probability of dispersal among other patches (Fig. 1). Heinz et al. (2006) showed that the shadow effect can drastically change usual rules of thumb provided by classic metapopulation models: for organisms with localized dispersal movements (e.g. Brownian motion or looping), decreasing the distance among patches below some threshold can become detrimental for metapopulation persistence, contrary to what was predicted by Etienne (2004). Moreover, Hein et al. (2004) showed that when dispersers perform a highly directed movement, a proper adjustment of a classic kernel to the realized dispersal distances is not possible, because dispersal is then highly spatially heterogeneous. However, whether the shadow effect also changes the effect of patch density upon metapopulation capacity and affects the robustness of increasing the total habitat area as a conservation strategy remains unexplored.

Here, we investigated whether HDSA can modulate the effect of patch density on metapopulation capacity. Because metapopulation dynamics are known to be sensitive to dispersers' movement type (Hein et al. 2004; Heinz et al. 2006; Bode et al. 2008; Hawkes 2009), we used two movement models – random walk and straight-line movement—to investigate the shapes of the relationships between the metapopulation capacity and the density of patches for species with various levels of HDSA. Our intuitions were that a higher HDSA may: (i) lead to a faster-increasing relationship between the metapopulation capacity and the density of habitat patches when patches are rare, because dispersers are more efficient at finding habitat; and (ii) generate saturation (or even a decrease) of metapopulation capacity at high patch density because of the shadow effect among patches.

Methods

Metapopulation dynamics and persistence criterion

We model the metapopulation dynamics using the continuous-time mean-field approximation of Hanski and Ovaskainen (2000) for a spatially-explicit metapopulation model. We consider N identical habitat patches. Patches either harbour a population or are empty. We call $p_i(t)$ the probability that patch i is occupied by a population at time t. A population located in a patch emits dispersers at rate β. We call $\mathbf{\Pi}$ the dispersal success matrix. Π_{ij} is the probability that a disperser leaving patch j successfully reaches patch i as its final destination. Dispersers cannot settle in their
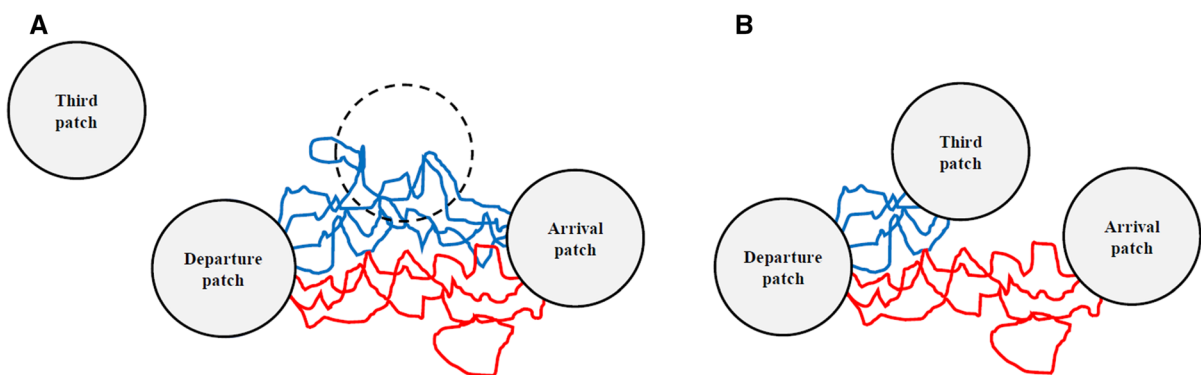

Fig. 1 Illustration of the "shadow effect". The distances between the departure patch and the two other patches are identical in the two panels. Seven transfer phase events are represented. In panel **a**, all of the seven dispersers reach the arrival patch. In panel **b**, the probability of reaching the arrival patch is lower because some dispersers stop in the third patch lying in between

origin patch, so all diagonal entries of $\mathbf{\Pi}$ are set to 0. A population in patch j thus emits dispersers that settle in patch i at rate $\beta\Pi_{ij}$. When a disperser reaches a patch already occupied, it is absorbed in the existing population. By contrast, when a disperser stops in a patch devoid of individuals, it has a probability γ of creating a new population. This implies that the colonization rate C_{ij} of an empty patch i by a population occupying patch j verifies $C_{ij} = \gamma\beta\Pi_{ij}$. We further call e the extinction rate of populations in patches. Then one can approximate the master equation of the patch dynamics as (Hanski and Ovaskainen 2000):

$\forall i | 1 \leq i \leq N,$

$$\frac{dp_i}{dt} = \beta\gamma[1 - p_i(t)]\left[\sum_{\substack{j=1 \\ j \neq i}}^{N} \Pi_{ij}p_j(t)\right] - ep_i(t) \tag{1}$$

We define the metapopulation persistence as the ability of the species to recover when reaching low occupancy. Mathematically speaking, a metapopulation is persistent if and only if it harbours an unstable equilibrium point at $\boldsymbol{p} = 0$ in (1). Linearizing system (1) around $\boldsymbol{p} = 0$ yields:

$$\frac{d\boldsymbol{p}}{dt} \approx (\beta\gamma\mathbf{\Pi} - e\mathbf{I})\boldsymbol{p}(t) \tag{2}$$

where $\mathbf{I}$ is the identity matrix. We call λ the maximum real part of eigenvalues of $\beta\gamma\mathbf{\Pi} - e\mathbf{I}$. The metapopulation is persistent if and only if $\lambda > 0$. We define λ_Π as the maximum real part of eigen values of $\mathbf{\Pi}$. It is straightforward to show that $\lambda = \beta\gamma\lambda_\Pi - e$, which implies that the metapopulation is persistent if and only if:

$$\lambda_\Pi > \frac{e}{\beta\gamma} \tag{3}$$

We show in Online Appendix 4 that criterion (3) is robust to considering the true stochastic metapopulation dynamics rather than the mean-field approximation, except for situations combining very low habitat density with low extinction rate.

We then focus on deriving λ_Π—the metapopulation capacity ("MC" below; Hanski and Ovaskainen 2000)—as a function of (i) dispersers' movement ability T, defined as the average distance dispersers can travel before stopping, limited by the energy available for dispersal, and (ii) dispersers' habitat detection and settling ability (HDSA) q, defined as the probability of settling when encountering a patch. $q = 0$ means that the disperser is unable to differentiate patches from the matrix, whereas $q = 1$ means that the disperser can distinguish a patch from the matrix with perfect accuracy and always stops when encountering a patch. Generally, for $q > 0$, the path length of dispersers is smaller than their movement ability T.

We consider two contrasting dispersal models: (i) random walk on a grid where patches are cells, and (ii) straight-line walk across a continuous landscape. Random walk models are very common in ecology studies (along with its continuous space approximate, diffusion). However, most animals do not follow a random walk with uncorrelated turns, but tend to move forward (Codling et al. 2008). We thus contrast the random walk model with the other extreme of movement persistence: a straight-line walk in continuous space. In the "Discussion" section, we will detail the potential effects of four key simplifying assumptions we make: (1) the randomness of patch location, (2) the absence of any perception radius, (3) the absence of social behaviour or heterogeneity in patch quality, and (4) the choice of absorbing boundaries.

Random walker

We first consider a model where space is a $L \times L$ grid where each cell is either a patch or unhospitable matrix. In our simulations below, we set $L = 10$ and we varied the number of patches N from 2 to 99 (one single empty cell). For each value of N, we considered 100 landscape replicates where we randomly selected the N cells that correspond to patches.

When a disperser starts moving from its natal patch, it repeats the following procedure until stopping:

Step 1   choose with equal probability 0.25 among the four non-diagonal neighboring cells (i.e. Von Neumann neighbourhood) of the current cell and move on it; if this cell is out of the $L \times L$ grid then the disperser dies, else go to step 2;

Step 2   if the new cell is not a patch, then go to step 3, else stop with probability q or go to step 3 with probability $1 - q$.

Step 3   with probability μ, stop in current cell, with probability $1 - \mu$ go to Step 1.

If the disperser stops in a patch, dispersal is successful. If it stops in the matrix, it dies. Probability μ is negatively related to the movement ability T of the dispersers: $T = (1-\mu)/\mu$ distance units in the absence of habitat patches. We developed an exact method adapted from Morales et al. (2017) for algebraically computing Π under this dispersal strategy and we tested the validity of our analytical derivation using numerical simulations (see Online Appendix 2). λ_{Π} was then analytically computed for each particular Π.

Straight-line motion

We then considered a continuous-time and -space model of dispersal. The environment is a $L \times L$ square with absorbing boundaries, where N identical and non-overlapping circular patches with radius r are randomly distributed within an inhospitable matrix. Dispersers leave their source patch in a random direction and walk on a straight line. The potential dispersal distance of dispersers follows a negative exponential distribution of rate μ. The dispersers' movement ability is thus equal to $T = 1/\mu$ distance units. On its dispersal path, when a perceptive disperser encounters a patch, it interrupts its dispersal and settles there with probability $q > 0$ or continues in the same direction with probability $1 - q$. If the disperser has not settled in a patch before reaching its potential dispersal path length, it stops. If, by chance, it stops within a patch, the disperser settles there. Otherwise, it dies.

We parameterized this model in a similar way as the grid model by setting $L = 10$ and $r = 0.5$. We varied N, q and T. For each parameter combination, we considered 100 landscape replicates, and for each patch within these landscapes, we simulated 1000 dispersal events in random directions. We simulated this model using Julia v. 0.5.0 (Bezanson et al. 2012).

Results

We theoretically showed for the random walk model that better habitat detection ability (HDSA) always increased the metapopulation capacity (MC), but that the MC was never larger than 1 for both dispersal models (see Figs. 2 and 3 and proof in Online Appendix 1). Increasing HDSA to perfect ability ($q = 1$) did not necessarily imply that the MC saturated to 1. This only occurred for high movement ability ($T > 31.6$ and $T > 10$ for the random walk and straight-line models respectively, Fig. 2b, d) and high patch density ($N > 80$ for both movement models, Fig. 2b, d).

The effect of patch density on metapopulation capacity

The MC always increased with patch density (Figs. 2 and 3). Without HDSA ($q = 0$), the MC-patch density relationship was linear for all movement abilities T (level curves are evenly spaced along the x-axis in Fig. 2a, c; see also Fig. 3b, d). This linear profile reached maximum slope for intermediate T values (T around 10 and 1.78 for the random walk and straight-line models respectively; Fig. 2a, c) and became close to null when T took extreme (low or high) values.

Increasing HDSA changed the shape of the MC—patch density relationship from linear to concave. Higher HDSA implied that the MC increased faster with patch density when patches were rare but increased more slowly with patch density when patches were abundant (space between level curves increases along the x-axis in Fig. 2b, d; see also Fig. 3b, d). When movement ability increased, higher values of MC were reached at lower patch density values (Fig. 2b, d), which resulted in a more concave MC patch-density relationship.

The effect of movement ability on metapopulation capacity

When dispersers did not detect habitat patches, the MC was a hump-shaped function of movement ability (Fig. 2a, c). For habitat-perceptive dispersers, the hump-shaped profile vanished and the MC increased monotonically with movement ability (Fig. 2b, d). For high values of habitat detection, the MC-movement ability relationship was markedly saturating to 1 when patch density was above $N = 80$ (Fig. 2d). In these situations, increasing movement ability had no effect on MC beyond a threshold of approximately $T = 10$.

Discussion

A very common (and intuitive) conservation strategy consists in increasing the density of patches available
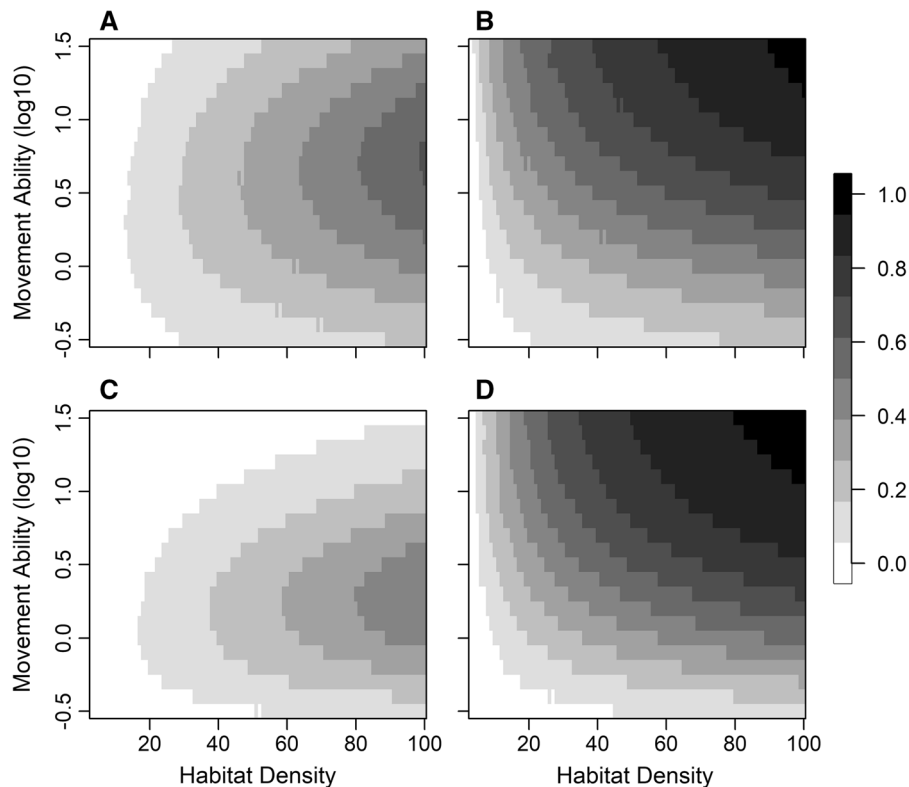
Fig. 2 Mean metapopulation capacity as a function of habitat density (expressed as the number of habitat patches) and movement ability, for two contrasted values of habitat detection and settling ability (HDSA): $q = 0$ (panels **a** and **c**) and $q = 1$ (panel **b** and **d**) and for the random walk (panels **a** and **b**) and straight-line (panels **c** and **d**) models

for the metapopulation. Based on current metapopulation theory, the metapopulation capacity (MC) is thought to increase linearly with patch density when patches are randomly located (Hanski and Ovaskainen 2000; Grilli et al. 2015). We confirmed this expectation when dispersers have no habitat detection and settling ability (HDSA). Taking into account the HDSA of dispersers induced two major changes in the patch density—MC relationship. First, for a given patch density, the MC was higher for habitat-perceptive dispersers, hence validating our first prediction. This pattern stemmed from the fact that HDSA led to fewer dispersers exiting the metapopulation without settling (a phenomenon that we call the "disperser saving effect" hereafter). This effect was particularly strong when the movement ability was high. Second, HDSA induced a marginally decreasing contribution of patch density to MC, as a consequence of the shadow effect. We thus validated our expectation that HDSA increases the positive effect of adding patches to a metapopulation when patch density is small, but

generates a saturation effect at high patch density. We did not observe that the shadow effect could be sufficiently strong to overcome the disperser saving effect. First, we never observed a negative effect of adding habitat patches on the metapopulation capacity. Second, higher HDSA always increased the metapopulation capacity. Our qualitative conclusions were not affected by the choice of the dispersal model, suggesting that they are robust.

The concave relationship between patch density and the MC suggests that when habitat patches are randomly spread in space, the marginal gain of adding patches could decrease, a phenomenon largely overlooked by classic metapopulation theory. For habitat-perceptive species, the conservation strategy consisting of increasing patch density is thus very effective when only a little amount of habitat can be protected, but is ineffective beyond some patch density threshold that decreases with their movement ability. When increasing patch density becomes ineffective, an
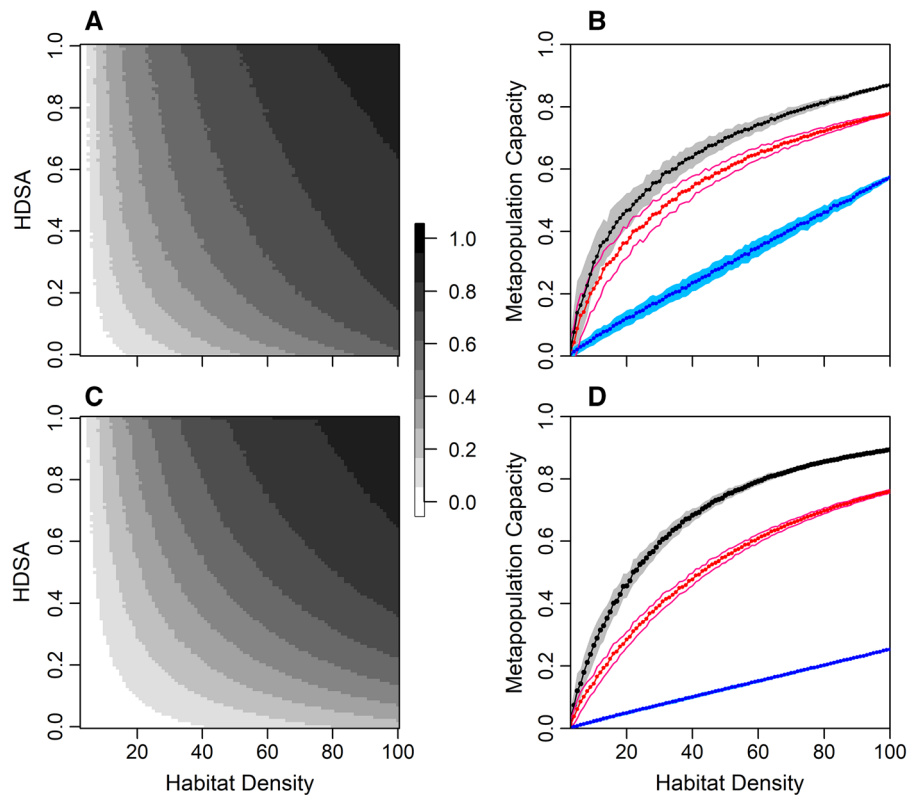
Fig. 3 Mean metapopulation capacity as a function of HDSA (q, Habitat Detection & Settling Ability) and habitat density (expressed as the number of patches), for the random walk (panels **a** and **b**) and straight-line (panels **c** and **d**) models. Left panels (**a** and **c**): levels of grey indicate the average value of metapopulation capacity. Parameter q was varied from 0 to 1

with a 0.01 step. Right panels (**b** and **d**): mean ± SD metapopulation capacity as a function of the number of patches for three contrasted values of q. Black line: $q = 1$, red line: $q = 0.5$, blue line: $q = 0$. Note that the standard deviations around the bottom line in panel **d** are too small to be visible. For all panels, $T = 10$

alternative strategy suggested by Eq. (3) is to improve the quality of the patches.

Hanski and Ovaskainen (2000) showed that, for a classic kernel dispersal model, a concave relationship between the density of habitat patches and the metapopulation capacity can exist when new habitat is added non-randomly, in large blocks. This suggests that, even for passive dispersers (e.g. anemochorous plants), optimizing the location of patches can lead to a faster increase of metapopulation capacity at low patch density compared to random spatial distribution. This faster initial increase is necessarily followed by a marginally decreasing effect of adding patches, because in a landscape with a large proportion of habitat, the habitat configuration (random vs. aggregated) should make little difference for the MC, hence bringing back the aggregated landscapes to similar MC values than random ones. This result suggests that

combining the HDSA of dispersers with some spatial aggregation of habitat patches should lead to an even more concave MC—patch density relationship, hence strengthening even more our conclusion.

Our two dispersal models aimed at illustrating how HDSA can generate marked deviations from the predictions of the classic metapopulation theory, with potentially strong implications for conservation strategies. However, they remain too simple to account for all the complex species-dependent behavioural rules intervening at each major phases of the dispersal process (emigration, transfer and immigration phases; Clobert et al. 2009). From a management and conservation perspective, our models should therefore be refined towards custom-made spatially explicit, mechanistic modelling of dispersal, which should improve the predictions of the efficiency of conservation measures. This is in accordance with a more general

call to move from pattern-based to process-based studies in ecology to improve predictions in changing conditions (Krebs 2002; Morin and Lechowicz 2008; Riotte-Lambert et al. 2017). Our model is a crucial first step towards these practical applications, since it contributes to defining processes that will be used to build and interpret the outcome of more complex models. For example, here we have assumed that μ, the probability for the individual to stop at each time step due to limited energy budget allocated to movement, does not vary in space. However, in nature, space can have a modulating effect on μ if the cost of movement is spatially heterogeneous, for example due to physical obstacles, or local wind conditions. Considering the effect of spatially heterogeneous μ could thus be the focus of future research. Future studies could also investigate the effects of more complex movement models, such as the Biased Correlated Random Walk or the Generic Random Walk (Benhamou 2014), or of the size of the perceptual range and of habitat selection. We can expect that habitat selection, associated with a moderate perceptual range, would enable individuals to avoid unsuitable habitat in a more forward-looking sense and thus increase the shadow effect.

As an example of much needed extension, one may note that we only used a single parameter, q, to control the propensity of dispersers to settle in a patch they encounter. This simple formulation enabled us to describe the full range of possible behaviours between "blind" dispersal ($q = 0$), whereby dispersers are completely unable to distinguish a habitat patch from the matrix, and $q = 1$, whereby dispersers detect patches with perfect accuracy and stop at the first patch they detect. The value of q thus represents the combination of two processes: patch detection and the decision of the disperser to stop (or not) in a detected patch. In nature, there is a wide variation in both processes. Patch detection ability depends on individuals' sensory system and on environmental conditions (e.g. openness) (Spiegel and Crofoot 2016). Dispersers' propensity to prospect before settling also varies between species and conditions (Delgado et al. 2014). Here, we assumed that the propensity to stop dispersal into an encountered patch was the same for all patches. However, in nature the propensity to stop may depend on the disperser's state, and on the species' social behaviour, for example, territorial or aggregative. Moreover, before deciding whether to settle in a patch, many individuals use cues about patches' quality, or social cues such as conspecifics' or heterospecifics' density or breeding performance (Ponchon et al. 2014). Future theoretical work should thus implement q as a function of patches' characteristics and occupancy status, and investigate the effect of sociality, because conspecific attraction is likely to decrease colonization of new populations (Ray et al. 1991; Delgado et al. 2010). In general, we can expect that when dispersers favor settlement in already occupied patches, the shadow effect will be increased, while when they favor settlement in empty patches, the shadow effect will be lessened.

In the metapopulation models presented here, we assumed absorbing boundaries. It implies that a very high movement capacity can have a negative effect on metapopulation capacity (MC), because dispersers are lost outside of the landscape. This explains the hump-shaped pattern of MC as a function of movement capacity for dispersers without HDSA. We used absorbing boundaries because we were interested in the conditions making the metapopulation a "source", able to maintain without immigration and being a net provider of dispersers for the larger spatial scale, which is a desirable goal for any conservation strategy. This is why we ignored immigration from outside the metapopulation: we were not interested in the conditions ensuring the persistence of the metapopulation as a "sink", maintaining only thanks to immigration from outside its boundaries.

Conclusions

Recently, several studies have highlighted the need to relax the simplifying assumptions about animal movement in population dynamics studies (Morales et al. 2010; Riotte-Lambert et al. 2017). Our main results suggest that, for species that have some control over the patches in which they settle, the expectations coming from metapopulation theory simulating the dispersal matrix by using a classic dispersal kernel may be invalid. This can limit our general understanding of metapopulation persistence, and our ability to design efficient conservation measures. Future extensions of metapopulation theory are thus needed for the investigation of the effect of dispersers' habitat detection ability on metapopulation dynamics. The models we developed will be amenable for further

enquiry of the impact of habitat-perceptive dispersal on metapopulation dynamics, and we hope to have stimulated a line of theoretical investigations that could be of high practical importance.

Code availability The R and Julia codes supporting this article are freely available on Figshare (Riotte-Lambert and Laroche 2021).

Compliance with ethical standards

Conflict of interest We declare no competing interest.

Informed consent All the authors have read and approved the revised manuscript, and all persons entitled to authorship have been included.

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