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1 **Do species population parameters and landscape characteristics affect the relationship**
2 **between local population abundance and surrounding habitat amount?**

3

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23

1 Abstract

2 In Landscape Ecology, correlational approaches are typically used to analyse links
3 between local population abundance, and the surrounding habitat amount to estimate
4 biologically-relevant landscape size (extent) for managing endangered or pest populations.
5 The direction, strength, and spatial extent of the correlations are then sometimes interpreted in
6 terms of species population parameters. Here we simulated the population dynamics of
7 generalized species across spatially explicit landscapes that included two distinct habitat
8 types. We investigated how characteristics of a landscape (structure), including the variation
9 in habitat quality and spatial aggregation of the habitat, and the precise population-dynamic
10 properties of the simulated species (dispersal and growth rates) affect the correlation between
11 population abundance and amount of surrounding, favourable habitat in the landscape. To
12 evaluate the spatial extent of any correlation, proportions of favourable habitats were
13 calculated in several circular buffers of increasing radii centred on sample patches of
14 favourable, where population abundance was recorded.

15 We found that the value of the correlation coefficients depended both on population
16 dynamics parameters and landscape characteristics. Correlation coefficients increased with
17 the variation in habitat quality and with aggregation of favourable habitat in the landscape.
18 The distance to highest correlation was sensitive to the interaction between landscape
19 characteristics and the population dynamic properties of the simulated species; in particular
20 between the variation in landscape quality and the dispersal rate. Our results corroborate the
21 view that correlational analyses do provide information on the local population dynamics of a
22 species in a given habitat type and on its dispersal rate parameters. However, even in
23 simplified, model frameworks, direct relationships are often difficult to disentangle and global
24 landscape characteristics should be reported in any studies intended to derive population-
25 dynamic parameters from correlations. Where possible, replicated landscapes should be

1 examined in order to control for the interaction between population dynamics and landscape
2 structure. Finally, we recommend using species-specific, population-dynamic modelling in
3 order to interpret correctly the observed patterns of correlation in the landscape.

4

5 **Keywords**

6 dispersal, habitat quality, spatial aggregation, metapopulation, spatially explicit model.

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1. Introduction

Understanding species abundance, as function of the habitat characteristics of a landscape and the population-dynamic properties of the species, is important for guiding landscape management policy for biodiversity conservation (Jeanneret et al., 2003; Aldridge and Boyce, 2007; Ockinger and Smith, 2007), and the control of invasive species (Sebert-Cuvillier et al., 2008; McKee et al., 2009) and of crop pests (Bianchi et al., 2006).

Correlations between local population abundance in focal sampling patches and the surrounding habitat amount in buffers of increasing size have been used to identify both the important landscape features that compose the habitat of a species and their scale of effect (Brennan et al., 2002). This ‘focal sampling patches approach’ has been widely used by Conservation Ecologists for a number of years (Vos and Chardon, 1998) and is now used for pests in agro-ecosystems with a view to landscape-level management (e.g. Schmidt et al., 2005; Decante and Van Helden, 2006; Zaller et al., 2008; Ricci et al., 2009; Rusch et al., 2010). Observed correlations between population abundance and the amount of surrounding habitat have been interpreted in an intuitive fashion; a positive correlation between population abundance and the area of a landscape feature indicates that this feature is a “good quality” habitat for the species, and *vice versa*. Numerous empirical studies have thus interpreted the direction and the value of landscape correlations in terms of quality of the habitat (Roschewitz et al., 2005; Bianchi et al., 2006; Moser et al., 2009; Ricci et al., 2009; Veres et al., 2012). The spatial extent of the correlations has also been interpreted in terms of underlying ecological processes (Wiegand et al., 1999; Jepsen et al., 2005; Turner, 2005; Schroder and Seppelt, 2006). For example, the amount of habitat in a given buffer can be treated as a simple metric of patch connectivity that explains the frequency of colonization events (Moilanen and Nieminen, 2002; Bender et al., 2003). Some authors have investigated the spatial extent at which correlations arise, using empirical approaches, in order to shed light on the scale of

1 effect of particular landscape features of species habitat (Thies et al., 2003; Carrière et al.,
2 2006). The maximal extent of significant correlation (e.g. Carrière et al., 2006), range of
3 distances that provide significant correlations (e.g. Roschewitz et al., 2005; Thies et al., 2005)
4 and the distance that has the strongest correlation (e.g. Thies et al., 2003) are statistics that
5 have all been used to infer the spatial scale of landscape characteristics. More recently, it has
6 become clear that landscape correlation effects depend both on population-demographic
7 processes and landscape structure. Jackson and Fahrig (2012) demonstrated through simulated
8 population-dynamic models that the scale of effect (measured as the distance that has the
9 strongest correlation) depends on species population parameters, most notably species-
10 specific dispersal. The spatial distribution of a species over a landscape depends, in turn, not
11 only on its population dynamics but also on the landscape composition and structure
12 (Tischendorf, 2001, Campagne et al., 2009).

13 The impact of landscape structuring (habitat amount and spatial aggregation) on the
14 outcome of focal sampling patches approaches has been found to depend on efficiency of
15 dispersal over the landscapes. The efficient movement of individuals among habitats, at the
16 landscape scale, depends both on the dispersal abilities of a species and on the subsequent
17 realised probability of success of immigration; a probability that is directly related to the
18 aggregation of good quality habitat (Ricketts, 2001; Baguette and Van Dyck, 2007; Reeve et
19 al., 2008). These population-dynamic effects of aggregation of the habitat on the correlation
20 between local abundance and surrounding habitat amount remain to be deeply explored (but
21 see Wiegand et al. 1999).

22 The relative proportion of high vs. low quality habitat, and the intensity of the contrast
23 between these habitat types are also important factors affecting landscape correlations. By
24 definition, high quality habitat provides enough resources to allow higher population growth
25 rates and/or carrying capacities than low quality habitat (Moilanen and Hanski, 1998). Low

1 quality habitats may act as population dynamic sinks (Pulliam, 1988) and/or slow down
2 population expansions from high quality habitats (Thomas and Kunin, 1999). Models of
3 heterogeneous landscape usually simulate extreme cases, with only patches of favourable
4 habitat set in an unfavourable matrix (Wiegand et al 1999; Jackson and Fahrig, 2012). In real
5 landscapes, however, species are often able to grow and survive across a variety of different
6 habitat types with a range of levels of success. The effects of the quality contrast between
7 habitats and the relative proportions of each habitat in landscape on focal sampling patches
8 approach correlations have yet to be documented, although we would expect that
9 heterogeneity in habitat qualities should markedly impact the magnitude of landscape
10 correlation.

11 This paper explores how species population parameters (dispersal, growth rate) and
12 landscape properties (amount and spatial aggregation of favourable habitat) mediate the
13 correlations between local abundance in focal sampling patches and surrounding habitat
14 amount. Using a spatial population dynamic model, we simulate the spatial distribution of
15 population abundance in landscape composed of low and high quality habitat at differing
16 levels of spatial aggregation. We sample the population abundance in 25 focal patches in each
17 landscape and calculate the correlation between local population abundance in these focal
18 patches and the amount of high quality habitat across buffers of increasing size. We analyse
19 how this correlation is influenced by: i) variation in habitat quality, both across differing
20 relative amounts of high and low quality habitat and for a variety of quality contrast between
21 habitat types; and, ii) an interaction of landscape structure (level of spatial aggregation of each
22 habitat) and species dispersal parameters (dispersal rate and dispersal function).

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1 2. Material and Methods

2 2.1. General approach

3 Our scheme of spatially-explicit simulation modelling took place in two clear steps (Fig.
4 1 and Table 1). In the first set, we investigated the effect of variation in habitat quality on the
5 overall pattern of correlation by varying both the proportion of low vs. high quality habitat
6 and the difference in population growth rate between high and low quality habitats. In the
7 second set, we addressed the impact of landscape spatial aggregation and dispersal on the
8 pattern of correlation by varying the amount of aggregation of high quality habitat and the
9 population dispersal parameters (dispersal rate and dispersal type). This second step in the
10 simulation modelling fixed as constant the habitat quality at the values which provided
11 maximal correlations in the first step of the simulation scheme.

13 2.2. Landscape modelling

14 2.2.1. Landscape composition

15 The simulations took place across landscapes of 3600 cells in a regular 60×60 grid. The
16 square cells had sides of one arbitrary unit, D , were either of high quality habitat H (in
17 proportion P_H), in which any population would have a high growth rate ($r_H = 0.07$), or of low
18 quality habitat L (in proportion $1 - P_H$), in which a population would had a low growth rate
19 (r_L). Contrasted effects between high and low quality cells, were simulated by varying the
20 growth rate differences between H- and L-habitats ($\delta = r_H - r_L$). In the first set of simulations,
21 each combination of proportions of H-cells ($P_H = 0.10, 0.25, 0.50, 0.75$ or 0.90) and habitat
22 contrasts ($\delta = 0.02, 0.04, 0.06$) was considered in order to compare landscapes with differing
23 qualities (Fig. 1 and Table 2). In the second set of simulations, P_H and δ were fixed as
24 constants, respectively at 0.5 and 0.06 , as this combination of values was found to maximize
25 the correlation coefficients in step 1 (see results below).

1

2 2.2.2. Spatial aggregation of habitat quality within the landscape

3 For the first set of simulations, we generated random landscapes (S_0) in which L-cells
4 and H-cells were distributed in a spatially random pattern on the grid for each proportion of
5 high quality cells (10 replicates for each P_H value). For the second set of simulations, we
6 generated landscapes with spatial aggregation of habitat quality, for the given value of $P_H =$
7 0.5, using the method detailed by Wiegand et al. (1999). At 250 spatially random locations
8 (x_0), we calculated two-dimensional Gaussian functions of form:

$$9 \quad G(x) = \frac{1}{\sigma\sqrt{2\pi}} \exp\left(-\frac{(x-x_0)^2}{2\sigma^2}\right)$$

10 These functions were superimposed, forming a surface of different elevations that we split by
11 a horizontal plane thus classifying areas of the landscape above or below the plane into either
12 H-cells or L-cells. The height of the plane was chosen so that the proportion of cells H was
13 equal to 0.5. Two values of σ were used to design landscapes with aggregation of habitat
14 quality with either relatively small ($\sigma=1$, designated landscape-type S_1) or relatively large
15 ($\sigma=3$, designated landscape-type S_2) clusters of high and low quality cells. Ten replicates of
16 each S_1 and S_2 landscapes were generated for the second set of simulations and we reused the
17 10 replicates of S_0 from the first set. Example maps of the generated landscapes are provided
18 in Fig 2 (see also Fig. A1 and Fig. A2 in the Supplementary Material).

19

20 2.3. Population dynamics

21 2.3.1. Population growth

22 Each cell hosted a population initially composed of two individuals that grew
23 logistically. The carrying capacity of each cell was set to $K=100$ and the growth rate was r_H or
24 r_L depending on whether the population was in a H- or L-cell, respectively. The growth rate in

1 H-cells was kept constant ($r_H=0.07$), defining a reference situation. In the first set of
2 simulations, growth rates in L-cells were either $r_L = 0.01$ or 0.03 or 0.05 in order to vary cell
3 quality contrasts ($\delta = r_H - r_L = 0.06, 0.04, 0.02$) between H- and L-habitats (Fig. 1). In the
4 second set of simulations, δ was kept constant ($\delta=0.06, r_L=0.01$).

5 Preliminary simulations showed that the maximal difference between the mean
6 population abundance in H- and L-cells, in random landscapes, occurred after 75 time steps
7 (See Fig. A3 in the Supplementary Material). 75 time steps was therefore chosen as the
8 terminal duration of each simulation.

10 2.3.2. Dispersal

11 At each time step, a proportion m (dispersal rate) of the population in each cell dispersed
12 to other cells according to one of four, predefined dispersal models:

- 13 • *Stepping stone (Step)*: individuals dispersing from a given cell had an equal
14 probability of moving to each of the four nearest cells situated at a distance of 1. This
15 model corresponds to a classical two dimensional stepping stone.
- 16 • *Twelve nearest neighbours (12nn)*: individuals dispersing from a given cell had an
17 equal probability of moving to each of the twelve nearest cells; corresponding to a
18 maximal distance of 2 from the source cell.
- 19 • *Long distance dispersal (2Dt)*: this dispersal model intended to simulate a process in
20 which most individuals moved to nearby cells, while a few individuals dispersed to
21 cells further away. A bivariate Student's dispersal distribution (2Dt) was used to
22 determine the probability of a individual dispersing from one cell arriving in any
23 other, as given by:

$$24 \quad P = \frac{b-1}{\pi a^2} \left(1 + \frac{d^2}{a^2} \right)^{-b}$$

1 where d is the distance between the two cells, a is a scale parameter and b is a
 2 parameter that determines the weight of the distribution tail. The parameters a and b
 3 were set at $a = 3$ and $b = 3.5$, so that the mean distance of dispersal was approximately
 4 2 and about 25% of dispersal events were above this mean distance. The probability
 5 was then normalized to ensure that all dispersing individuals from any source cell
 6 found a target cell.

7 • *Random*: all individuals dispersing from a cell moved randomly with equal probability
 8 to other cells (Wright, 1931). This dispersal model was used as a control, with the
 9 expectations that no significant correlations should be observed.

10 The probability distributions associated to these four models have different average
 11 dispersal distances (\bar{d}). The average dispersal distance progressively increases from the *Step*
 12 model ($\bar{d} = 1$) to the *Random* dispersal model ($\bar{d} = 31.28$ in a 60 x 60 grid), with the *12nn*
 13 ($\bar{d} = 1.47$) and the *2Dt* ($\bar{d} = 2.12$) models displaying intermediate average distances of
 14 dispersal (see Fig. A4 in the Supplementary Material for the shapes of the dispersal
 15 functions). Only the *12nn* dispersal model was used for the first set of simulations. The four
 16 dispersal models were contrasted in the second set of simulations (Fig. 1).

18 2.4. Details of the two simulation sets

19 2.4.1. Set 1

20 In the first set of simulations (Fig. 1), the effect of the variation in landscape-level
 21 habitat quality, Q , on correlation patterns was assessed on random landscapes, S_0 , using
 22 constant dispersal parameters (dispersal model *12nn* and $m=0.075$). Q was calculated as the
 23 coefficient of variation of growth rates over all cells from the grid:

$$24 \quad Q = \frac{\sqrt{P_H (r_H - \bar{r})^2 + (1 - P_H) (r_L - \bar{r})^2}}{\bar{r}},$$

1 where P_H is the proportion of high quality habitat, r_H the growth rate in high quality habitat, r_L
2 the growth rate in low quality habitat and \bar{r} the mean growth rate over the landscape
3 calculated as:

$$4 \quad \bar{r} = P_H r_H + (1 - P_H) r_L$$

5 Q varied across the five values of P_H , each with 10 replicates, and the three values of quality
6 contrast between the habitats ($\delta = r_H - r_L = 0.06, 0.04, 0.02$), yielding a total of 150
7 simulations (Table 2).

8 9 2.4.2. Set 2

10 In a second set of simulations (Fig. 1), we assessed the effect of landscape spatial
11 aggregation and dispersal on the patterns of correlation. For this set of simulations, we fixed
12 as constant landscape-level variation in habitat quality at $Q=0.75$ (i.e. $P_H=0.5$ and $\delta=0.06$),
13 which the preceding set of simulations demonstrated to provide maximal correlation
14 coefficients. Simulations were run over 10 replicates of each of the three levels of aggregation
15 of habitat quality (S_0, S_1 and S_2) for each combination of the four dispersal models (*Step*,
16 *12nn*, *2Dt* and *Random*) and three different dispersal rates ($m=0.05, 0.075$ and 0.100). This
17 gave a total of 360 simulations (30 landscapes x 4 dispersal models x 3 dispersal rates).

18 19 2.5. Correlations between local population abundances and amount of 20 surrounding high quality habitats

21 For each suite of demographic and landscape parameters, the simulation results were
22 analysed after 75 time steps using a focal sampling patches approach. We randomly picked 25
23 H-cells, as focal patches, such that each of these selected cells was situated at a: i) distance
24 $d>4$ from the border of the grid to avoid border effects; and, ii) distance $d>8$ from any other
25 focal cell to avoid overlapping of buffer zones (maximum buffer radius = 4; see example

1 maps in Fig. 2). We then calculated and evaluated the significance of Spearman correlations
2 between population abundances in each of the 25 focal cells and the proportions of H-cells
3 surrounding the focal cells. In order to describe and compare correlation patterns among
4 simulations, correlation coefficients were calculated in four buffer zones ($D1$, $D2$, $D3$ and $D4$)
5 of different radii d surrounding each focal cells ($d=1, 2, 3$ and 4 , respectively). Three
6 commonly used indicators were recorded to describe correlation patterns (Table 1): the value
7 R_m of the highest correlation coefficient, and two measures of the scale of effect namely the
8 distance D_m at which R_m was achieved (e.g. Jackson and Fahrig, 2012) , and the greatest
9 distance D_s at which a significant correlation occurred (e.g. Carrière et al., 2006). D_s was
10 assumed to be 0 when no correlation was significant.

11

12 **3. Results**

13 All significant correlations (85% of correlations) were positive in simulations with the
14 *Step*, *12nm* and *2Dt* dispersal models, indicating that local population abundances in sampling
15 cells were higher in cells surrounded by a large proportion of H-cell. Correlations averaged
16 $0.65 \pm \text{sd } 0.22$ for the three dispersal models (Table 3). As expected, in the *Random* dispersal
17 model used as reference, 6% of correlations were significant, which is little more than that
18 expected by chance.

19

20 *3.1. Effects of the variation in habitat quality on the correlation patterns*

21 The shape of the correlation coefficient curves with increasing Q was similar for all
22 buffer zones, rising to a maximum before declining (Fig. 3A). For the $D1$ and $D2$ buffers, the
23 value of the correlation reached a maximum at $Q=0.750$, while for the $D3$ and $D4$ buffers this
24 was at $Q=1.039$. The maximal correlation, R_m , followed a similar trajectory, increasing with
25 Q to a maximum at $Q=0.75$ (Fig. 3B). The correlation coefficients were globally smaller for

1 the smallest buffer, $D1$, and larger for the buffer, $D2$ (Fig. 3A). The mean of the distance of
2 the highest correlation, Dm , was 2.61. Dm did not present a clear response to variation in Q
3 (Fig. 3C). The greatest distance with a significant correlation, Ds , showed the same tendency
4 as the maximal correlation, Rm , increasing with Q to a maximum at $Q=0.75$ (Fig. 3D).

5 The value of $Q=0.75$ was chosen to perform the second set of simulations. This Q
6 gave an intermediate value of the proportion of high quality habitat ($P_H=0.5$) and the highest
7 contrast in growth rates between high and low quality habitat ($\delta=0.06$, Table 2).

8 9 3.2. Effects of aggregation of the habitat and dispersal on the correlation 10 patterns

11 For each of the four buffer radii, the correlation between the local population
12 abundance in each cell and the proportion of surrounding H-habitat increased with the spatial
13 aggregation of the habitat across the landscape (Fig. 4). The correlation patterns also
14 depended on the dispersal model (Fig. 5), particularly for the two first buffer radii ($D1$ and
15 $D2$), for which the correlation was higher for the *Step* than for the *12nn* dispersal model and
16 also higher for the *12nn* than for the *2Dt* dispersal model. The correlation value was not
17 influenced by the dispersal rate (mean correlation for $m=0.05$: $0.47 \pm \text{sd } 0.34$; $m=0.075$: 0.49
18 $\pm \text{sd } 0.35$; $m=0.1$: $0.50 \pm \text{sd } 0.37$).

19 Rm increased with increasing spatial aggregation of the habitat and decreased with
20 increasing dispersal distance, irrespective of the level of aggregation of the habitat (Fig. 6A).
21 Dm increased both with increasing dispersal distances and level of aggregation of the habitat
22 (Fig. 6B). Ds was higher in landscapes with spatial aggregation than in random landscapes,
23 but did not vary with the dispersal distance (Fig. 6C).

24

25

1 4. Discussion

2 In the present study, we show that both species population parameters and landscape
3 characteristics simultaneously affect patterns of landscape correlation. The value and distance
4 of maximal correlation were sensitive to variation in habitat quality, dispersal distances and
5 the level of aggregation of the habitat; the greatest distance of significant correlation was
6 affected by landscape variation in habitat quality.

8 4.1. Effects of the variation in habitat quality on the correlation patterns

9 As expected, the correlations between local population abundance in sampling cells
10 and the surrounding amount of favourable habitat were positive in the case of non-random
11 dispersal (Fig. 3). The correlation increased with increasing variation in the habitat quality of
12 the whole landscape, up to a maximal value that corresponded to equal proportions of H- and
13 L-habitat (i.e. maximal habitat heterogeneity) and maximal difference in quality between H-
14 and L-habitat types. These results provide support for our interpretation that higher
15 correlations are a consequence of highly contrasted habitat qualities and/or high global
16 proportion of high quality habitat over the landscape. This might result from the proportion of
17 high quality habitats, within buffers, following a binomial distribution, with maximum
18 variance at $P_H = 0.5$. This cannot be the only explanation, however, as correlations were
19 higher at $P_H = 0.25$ than at $P_H = 0.75$ (both for $\delta = 0.04$ and $\delta = 0.06$), which would not be
20 expected for the binomial distribution. A practical issue for Landscape Ecologists is,
21 therefore, that ranking habitat quality for species based on values of correlation will produce
22 misleading or anomalous results if the proportions of habitat are not constant over the
23 landscape (Tischendorf, 2001; Rusch et al., 2011).

24 We found that, the scale of effect measured as Dm neither depended on proportion of
25 good quality habitat nor on differences of quality, δ , between H- and L-habitats; H- and L-

1 habitat quality differences largely determined the local population size and global abundance
2 over the landscape. This finding contrasts with the conclusion of Jackson and Fahrig (2012)
3 that “population size (and the underlying population growth rate that leads to population size)
4 may be a strong negative predictor of scale of effect”. As with Jackson and Fahrig (2012), the
5 exact mechanism for our result is difficult to pinpoint. However, the discrepancy between the
6 results may be due to differences in the modelling approaches used for dispersal. In our first
7 set of simulations, dispersal distances were short implying that, at each time step, it was only
8 the population abundance within the close neighbourhood that affected abundance of focal
9 patch. In Jackson and Fahrig (2012), individuals could move longer distances, and the
10 abundance of the whole population abundance may impact abundance of focal patch. Such
11 ‘heavy-tails’ to the distribution of dispersal distances can lead to ‘super-diffusion’ (Clark,
12 1998; Viswanathan et al., 2011) and decrease the correlation pattern between local abundance
13 and surrounding habitat amount.

15 *4.2. Effects of the aggregation of the habitat and dispersal parameters on the* 16 *correlation patterns*

17 Our findings for the aggregation of the type of habitat quality and species dispersal
18 were more intuitive. The value of a correlation depended on the dispersal model, with the
19 strength of the correlations decreasing with increasing average dispersal distance (Fig. 5). The
20 effect was consistent with increasing dispersal homogenizing the abundance of populations
21 among cells, through an exchange of individuals (Bowler and Benton, 2009). Dispersal
22 reduces correlation values because all cells will tend to have similar population abundances.
23 Long distance dispersers will also tend not to perceive small scale landscape heterogeneities
24 because heterogeneity among buffers decreases as dispersal distances increase (Baguette and
25 Van Dyck, 2007). Correlation coefficients also increased between random landscapes and

1 landscapes with aggregated habitat (Fig. 6), probably in part because the level of aggregation
2 increased the apparent contrast between H- and L-habitat landscape composition. However,
3 there was no effect of the level of aggregation, despite the highly contrasted maps we used
4 (Fig. A2 in the Supplementary Material). Increasing the aggregation of the habitat within the
5 landscape impacts the connectivity of good quality habitat cells, independent of habitat
6 proportion, and affects the spatial structure of populations over the landscape (Tischendorf,
7 2001).

8 As explained, we found that landscape correlations depended on the dispersal model
9 (Fig. 5), with the strength of the correlation decreasing with increasing average dispersal
10 distance; and effect consistent with homogenization. However, where migration is restricted
11 to the near neighbourhoods, strong spatial structuring of population abundances can result.
12 Populations close to high quality habitat would tend to have higher abundances (e.g. Ockinger
13 and Smith, 2007); thus increasing correlation. We did not, though, detect an expected
14 influence of dispersal rate on the pattern of correlation. The value of the correlation was more
15 related to the spatial distribution of displacement events than to the rate (frequency) of
16 displacements. Interestingly, the variation in correlation coefficients achieved with the
17 different dispersal models was consistent across the three levels of aggregation of the habitat
18 across the landscape.

20 4.3. Accuracy of the indices describing correlation patterns

21 The indices of correlation that might be used by landscape ecologists (R_m , D_m and
22 D_s) were found to be related both to population dynamics parameters and global landscape
23 characteristics. The highest correlation coefficient, R_m , appeared to summarize all the
24 correlation effects. High values of R_m occurred in landscapes with aggregated habitat and/or
25 landscapes with a high variation in habitat quality and for species with lower distances of

1 dispersal. This would suggest that correlations are unlikely to be observed for species with
2 relatively long distance dispersal, with respect to the scales of habitat heterogeneity.

3 Landscape characteristics and population dispersal also impacted the distances of
4 observed correlations between the local population abundance and the proportion of high
5 quality cells. In empirical studies, the maximal extent of significant correlation (e.g. Carrière
6 et al., 2006), the range of distances that provided significant correlations (e.g. Roschewitz et
7 al., 2005; Thies et al., 2005) and the distance providing the strongest correlation (e.g. Thies et
8 al., 2003) have been used to infer both the spatial scales that species are influenced by
9 landscape characteristics and, more rarely, dispersal ability. Here, we analysed D_m and D_s as
10 two synthetic variables to evaluate the distance effects of favourable habitat quantity. D_m was
11 found to be very sensitive to the dispersal model and increased with average dispersal
12 distance, as has been assumed in empirical studies. However, it was also sensitive to the
13 aggregation of the habitat (Fig. 6). As a consequence, we believe it would be difficult to
14 derive the mean dispersal distance of a given species using the measurement of the distance of
15 the highest correlation, D_m , alone. We also found that D_s did not depend on population
16 dynamics parameters or on landscape structure (for landscapes with aggregated habitat), but
17 increased only with the variation in habitat quality. It thus does not appear to be a very useful
18 statistic to infer dispersal. Perhaps most interestingly, all the indices of correlation we
19 considered in this study were found not to be affected by the rate of dispersal. This would
20 suggest to us that estimates of dispersal rate cannot be derived from observed patterns of
21 correlation.

22 23 24 4.4. Modelling context

1 In this study, we used representations of simple natural landscapes and population
2 dynamics in order to understand qualitative landscape-correlation relationships. We chose to
3 focus solely only on the representation of the spatial variation of habitat quality and to keep it
4 stable along the simulations, which would likely not be the case in all landscapes (Le Féon et
5 al., 2012). The dynamics of the populations were also greatly simplified and rather than
6 modelling particular taxa, we considered only simple, general processes. This generic
7 approach allowed us to highlight general trends that can be readily interpreted and gave
8 important insight into analysing correlation patterns between local population abundances and
9 landscape features. However, some of the simulation characteristics we used may be more
10 representative of some systems than others. The modelled local population dynamics
11 described the dynamics of an annual species with population growth during a favourable
12 season, bracketed by large death rates in winter that re-set the populations to low levels for the
13 start of the following year. This population dynamic system resembles that of many pest
14 arthropods in temperate agriculture.

16 **5. Conclusion**

17 Our results indicate that global landscape structure and composition affect the patterns
18 of correlation between population abundance and amounts of favourable habitat. Such global
19 landscape characteristics therefore need to be considered in analyses that intend to derive
20 population dynamic parameters from empirical, landscape correlation studies. Inferring either
21 the quality of a habitat from the intensity of the correlation or the distance of dispersal from
22 the distance of the highest correlation requires knowledge of whether the habitat is aggregated
23 or not. Our work confirms that it is necessary to control for the interaction between landscape
24 structure and population dynamics parameters, such as dispersal distance, possibly by using
25 landscape replication, and to report details about the proportion and spatial distribution of the

1 investigated habitats to facilitate comparison among studies in different landscapes. These
2 results also reaffirm the importance of modelling to predict, test and correctly interpret
3 observed patterns of correlation (Zurell et al., 2010).

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8 modelling spatial dynamics and insect dispersal. This work was supported by the ECOGER
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10 region.

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1 **References**

- 2 Aldridge, C.L., Boyce, M.S., 2007. Linking occurrence and fitness to persistence: Habitat-
3 based approach for endangered Greater Sage-Grouse. *Ecol. Appl.* 17, 508-526.
- 4 Baguette, M., Van Dyck, H., 2007. Landscape connectivity and animal behavior: functional
5 grain as a key determinant for dispersal. *Landscape Ecol.* 22, 1117-1129.
- 6 Bender, D.J., Tischendorf, L., Fahrig, L., 2003. Using patch isolation metrics to predict
7 animal movement in binary landscapes. *Landscape Ecol.* 18, 17-39.
- 8 Bianchi, F.J.J.A., Booij, C.J.H., Tschardtke, T., 2006. Sustainable pest regulation in
9 agricultural landscapes: a review on landscape composition, biodiversity and natural pest
10 control. *Proc. R. Soc. Lond. B Biol. Sci.* 273, 1715-1727.
- 11 Bowler, D.E., Benton, T.G., 2009. Impact of dispersal on population growth: the role of inter-
12 patch distance. *Oikos* 118, 403-412.
- 13 Brennan, J.M., Bender, D.J., Contreras, T.A., Fahrig, L., 2002. Focal patch landscape studies
14 for wildlife management: optimizing sampling effort across scales. In: Liu J, Taylor WW
15 (eds) *Integrating landscape ecology into natural resource management*. Cambridge
16 University Press, Cambridge.
- 17 Campagne, P., Buisson, E., Varouchas, G., Roche, P., Baumel, A., Taton, T., 2009. Modeling
18 landscape structure constraints on species dispersal with a cellular automaton: Are there
19 convergences with empirical data? *Ecol. Complex.* 6, 183-190.
- 20 Carrière, Y., Ellsworth, P.C., Dutilleul, P., Eilers-Kirk, C., Barkley, V., Antilla, L., 2006. A
21 GIS-based approach for areawide pest management: the scales of *Lygus hesperus*
22 movements to cotton alfalfa, weeds, and cotton. *Entomol. Exp. Appl.* 118, 203-210.
- 23 Clark, J.S., 1998. Why trees migrate so fast: confronting theory with dispersal biology and the
24 paleorecord. *Am. Nat.* 152, 204-224.

- 1 Decante, D., Van Helden, M., 2006. Population ecology of *Empoasca vitis* (Gothe. and
2 Scaphoideus titanus, Ball) in Bordeaux vineyards: Influence of migration and landscape.
3 Crop Prot. 25, 696-704.
- 4 Jackson, H.B., Fahrig, L., 2012. What size is a biologically relevant landscape? Landscape
5 Ecol. 27, 939-941.
- 6 Jeanneret, P., Schupbach, B., Pfiffner, L., Walter, T., 2003. Arthropod reaction to landscape
7 and habitat features in agricultural landscapes. Landscape Ecol. 18, 253-263.
- 8 Jepsen, J.U., Baveco, J.M., Topping, C.J., Verboom, J., Vos, C.C., 2005. Evaluating the effect
9 of corridors and landscape heterogeneity on dispersal probability: a comparison of three
10 spatially explicit modelling approaches. Ecol. Model. 181, 445-459.
- 11 Le Féon, V., Burel, F., Chifflet, R., Henry, M., Ricroch, A., Vaissière, B.E., Baudry, J., 2012.
12 Solitary bee abundance and species richness in dynamic agricultural landscapes. Agric.
13 Ecosyst. Environ. In press, doi:10.1016/j.agee.2011.06.020.
- 14 McKee, G.J., Goodhue, R.E., Zalom, F.G., Carter, C.A., Chalfant, J.A., 2009. Population
15 dynamics and the economics of invasive species management: The greenhouse whitefly in
16 California-grown strawberries. J. Environ. Manage. 90, 561-570.
- 17 Moilanen, A., Hanski, I., 1998. Metapopulation dynamics: Effects of habitat quality and
18 landscape structure. Ecology 79, 2503-2515.
- 19 Moilanen, A., Nieminen, M., 2002. Simple connectivity measures in spatial ecology. Ecology
20 83, 1131-1145.
- 21 Moser, D., Drapela, T., Zaller, J.G., Frank, T., 2009. Interacting effects of wind direction and
22 resource distribution on insect pest densities. Basic Appl. Ecol. 10, 208-215.
- 23 Ockinger, E., Smith, H.G., 2007. Semi-natural grasslands as population sources for
24 pollinating insects in agricultural landscapes. J. Appl. Ecol. 44, 50-59.
- 25 Pulliam, H., 1988. Sources, sinks, and metapopulation regulation. Am. Nat. 132, 652-661.

- 1 Reeve, J.D., Cronin, J.T., Haynes, K.J., 2008. Diffusion models for animals in complex
2 landscapes: incorporating heterogeneity among substrates, individuals and edge
3 behaviours. *J. Anim. Ecol.* 77, 898-904.
- 4 Ricci, B., Franck, P., Toubon, J.F., Bouvier, J.C., Sauphanor, B., Lavigne, C., 2009. The
5 influence of landscape on insect pest dynamics: a case study in southeastern France.
6 *Landscape Ecol.* 24, 337-349.
- 7 Ricketts, T.H., 2001. The matrix matters: Effective isolation in fragmented landscapes. *Am.*
8 *Nat.* 158, 87-99.
- 9 Roschewitz, I., Hücker, M., Tschardtke, T., Thies, C., 2005. The influence of landscape
10 context and farming practices on parasitism of cereal aphids. *Agric. Ecosyst. Environ.*
11 108, 218-227.
- 12 Rusch, A., Valantin-Morison, M., Sarthou, J.P., Roger-Estrade, J., 2010. Biological control of
13 insect pests in agroecosystems: effects of crop management, farming systems, and
14 seminatural habitats at the landscape scale: a review. *Adv. Agron.*, vol 109 (ed D.L.
15 Sparks), pp 219-259. Elsevier Academic Press Inc., San Diego.
- 16 Rusch, A., Valantin-Morison, M., Sarthou, J.P., Roger-Estrade, J., 2011. Multi-scale effects of
17 landscape complexity and crop management on pollen beetle parasitism rate. *Landscape*
18 *Ecol.* 26, 473-486.
- 19 Schmidt, M.H., Roschewitz, I., Thies, C., Tschardtke, T., 2005. Differential effects of
20 landscape and management on diversity and density of ground-dwelling farmland spiders.
21 *J. Appl. Ecol.* 42, 281-287.
- 22 Schroder, B., Seppelt, R., 2006. Analysis of pattern-process interactions based on landscape
23 models - Overview, general concepts, and methodological issues. *Ecol. Model.* 199, 505-
24 516.

- 1 Sebert-Cuvillier, E., Simon-Goyheneche, V., Paccaut, F., Chabrierie, O., Goubet, O., Decocq,
2 G., 2008. Spatial spread of an alien tree species in a heterogeneous forest landscape: a
3 spatially realistic simulation model. *Landscape Ecol.* 23, 787-801.
- 4 Thies, C., Steffan-Dewenter, I., Tschardtke, T., 2003. Effects of landscape context on
5 herbivory and parasitism at different spatial scales. *Oikos* 101, 18-25.
- 6 Thies, C., Roschewitz, I., Tschardtke, T., 2005. The landscape context of cereal aphid-
7 parasitoid interactions. *Proc. R. Soc. Lond. B Biol. Sci.* 272, 203-210.
- 8 Thomas, C.D., Kunin, W.E., 1999. The spatial structure of populations. *J. Anim. Ecol.* 68,
9 647-657.
- 10 Tischendorf, L., 2001. Can landscape indices predict ecological processes consistently?
11 *Landscape Ecol.* 16, 235-254.
- 12 Turner, M.G., 2005. Landscape ecology: What is the state of the science? *Annu. Rev. Ecol.*
13 *Evol. Syst.* 36, 319-344.
- 14 Veres, A., Petit, S., Conord, C., Lavigne, C. 2012. Does landscape composition affect pest
15 abundance and their control by natural enemies? *Agric. Ecosyst. Environ.* In press,
16 doi:10.1016/j.agee.2011.05.027.
- 17 Viswanathan, G.M., da Luz, M.G.E., Raposo, E.P., Stanley, H.E., 2011. The physics of
18 foraging: an introduction to random searches and biological encounters. Cambridge
19 University Press, Boston.
- 20 Vos, C.C., Chardon, J.P., 1998. Effects of habitat fragmentation and road density on the
21 distribution pattern of the moor frog *Rana arvalis*. *J. Appl. Ecol.* 35, 44-56.
- 22 Wiegand, T., Moloney, K.A., Naves, J., Knauer, F., 1999. Finding the missing link between
23 landscape structure and population dynamics: A spatially explicit perspective. *Am. Nat.*
24 154, 605-627.

- 1 Zaller, J.G., Moser, D., Drapela, T., Schmoger, C., Frank, T., 2008. Effect of within-field and
- 2 landscape factors on insect damage in winter oilseed rape. *Agric. Ecosyst. Environ.* 123,
- 3 233-238.
- 4 Zurell, D., Berger, U., Cabral, J., Jeltsch, F., Meynard, C., Muenkemueller, T., Nehrbass, N.,
- 5 Pagel, J., Reineking, B., Schroeder, B., Grimm, V., 2010. The virtual ecologist approach:
- 6 simulating data and observers. *Oikos* 119, 622-635.
- 7

1 TABLES

2 Table 1. Variable names and description.

Category	Parameter name	Description
Population growth	r_H	Growth rate in high quality habitat
	r_L	Growth rate in low quality habitat
	$\delta = r_H - r_L$	Growth rate difference between habitats
Dispersal	m	Dispersal rate
	$disp$	Dispersal model (qualitative)
Landscape	P_H	Proportion of high quality habitat
	S	Aggregation of habitat quality across the landscape (qualitative)
	Q	Variation in habitat quality
Correlation description	Rm	Maximal correlation
	Dm	Distance of maximal correlation
	Ds	Greatest distance with a significant correlation

3

- 1 Table 2. Variation in habitat quality (Q) for different proportions P_H of high quality habitat
- 2 and different values of growth rate contrast δ between high and low quality habitats.

P_H	$\delta = 0.06$	$\delta = 0.04$	$\delta = 0.02$
0.10	1.125	0.353	0.115
0.25	1.039	0.433	0.158
0.50	0.750	0.400	0.167
0.75	0.472	0.289	0.133
0.90	0.281	0.182	0.088

3

4

- 1 Table 3. Mean correlation between population abundance and surrounding proportion of high
- 2 quality habitat, and percentage of significant positive or negative correlations.

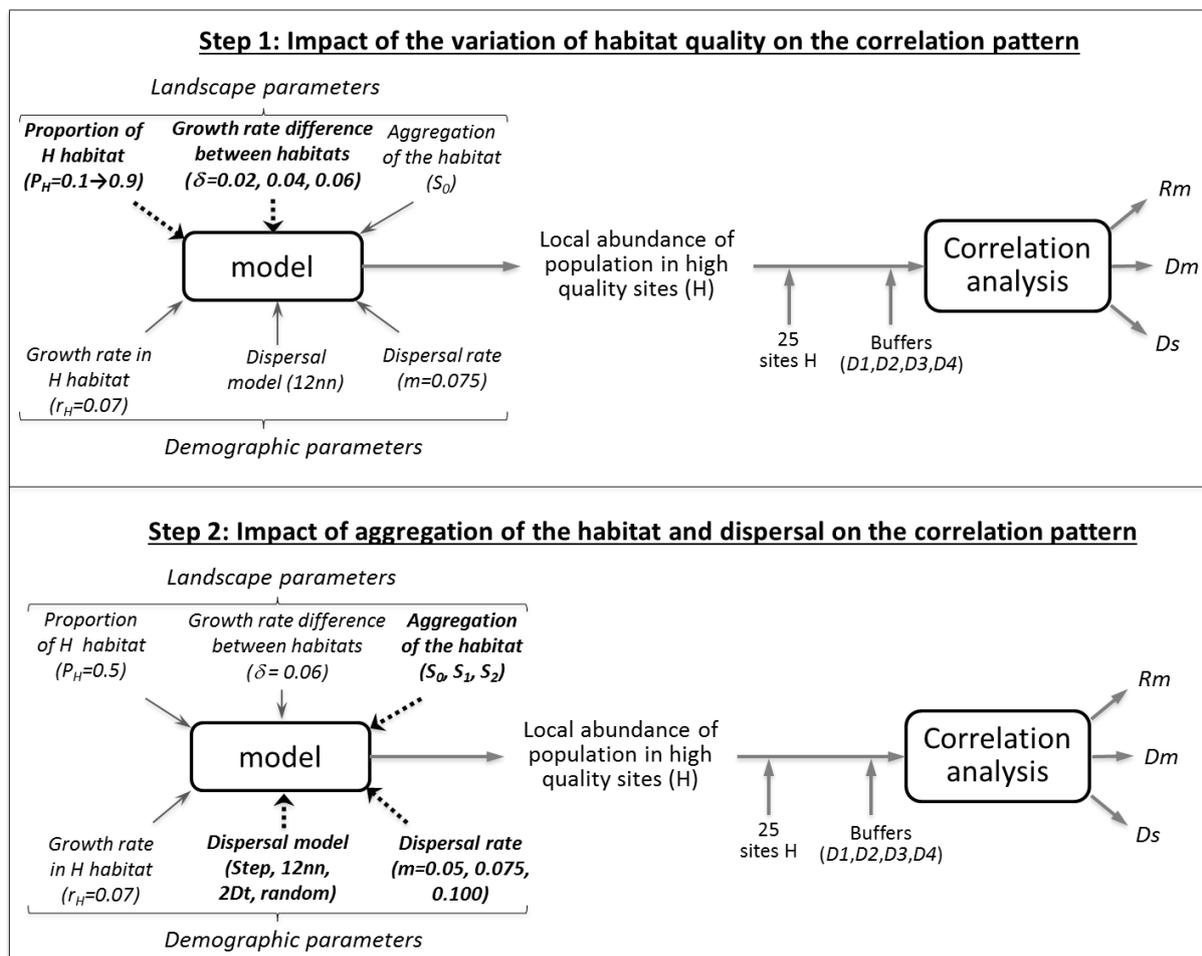
Disperal model	Mean correlation	Percentage of significant and positive correlations	Percentage of significant and negative correlations
<i>Step</i>	0.73 (\pm SE 0.011)	92.2	0
<i>12nn</i>	0.66 (\pm SE 0.011)	86.7	0
<i>2Dt</i>	0.56 (\pm SE 0.012)	76.9	0
<i>Random</i>	0.01 (\pm SE 0.011)	2.2	4.2

3

4

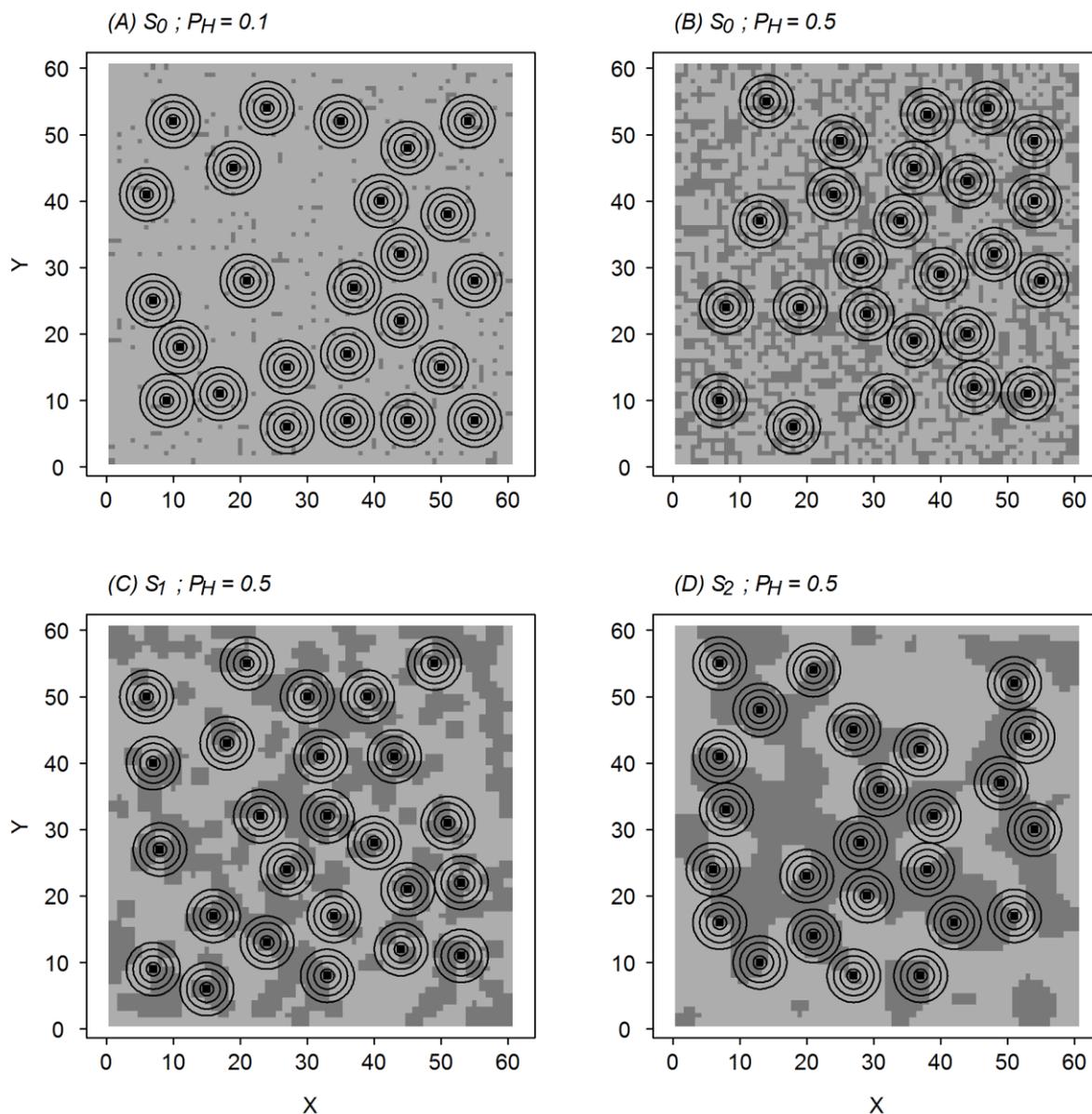
1 **FIGURES CAPTION**

2

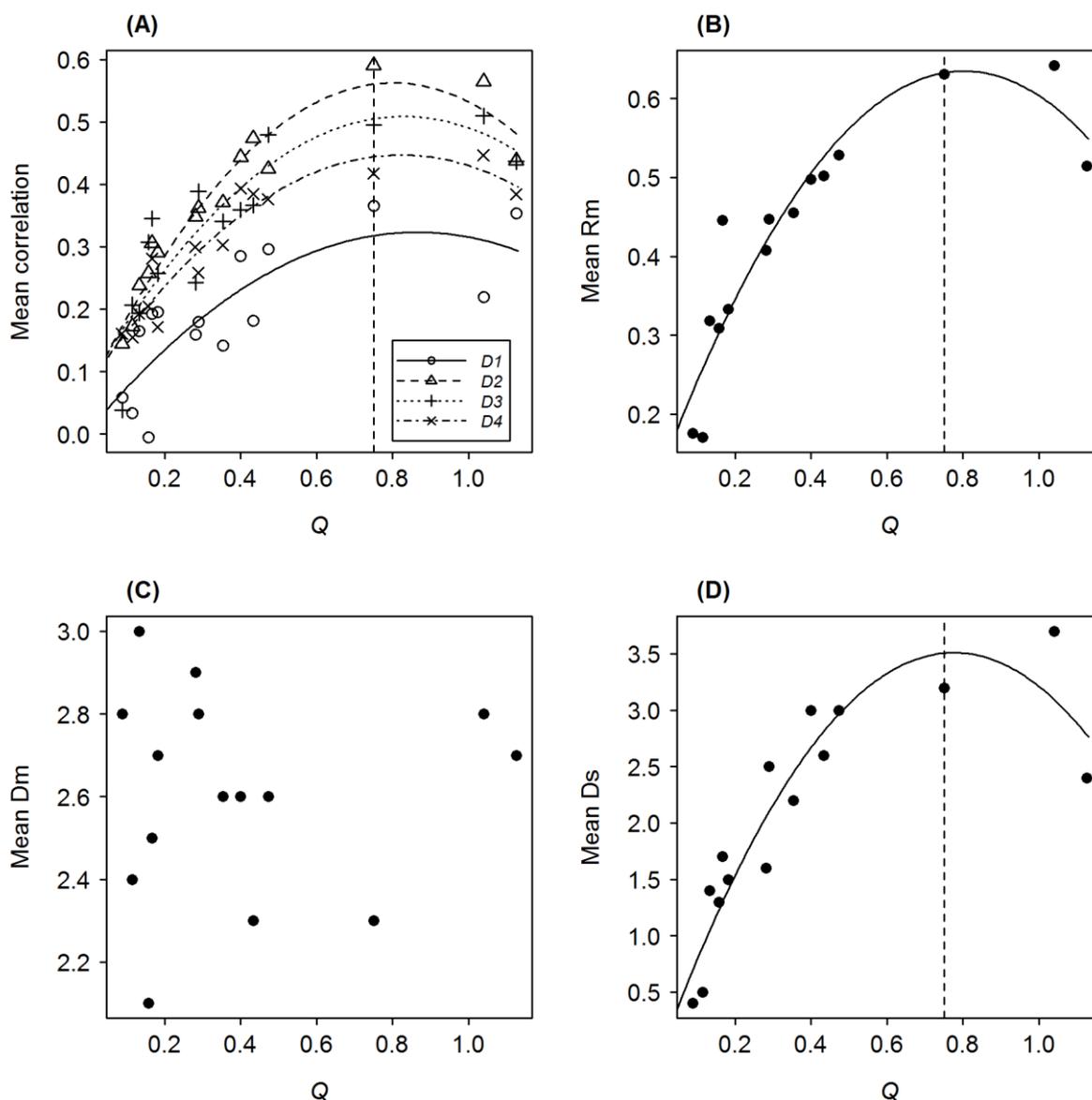


3

4 **Fig. 1.** Simulation designs for each one of the two studied questions. On the left part of the
 5 scheme describing the landscape and population demographic parameters used in the
 6 simulating model (Table 1), variable parameters are indicated in bold with dashed arrows and
 7 fixed parameters are indicated with small full-line arrows. On the right part of the scheme
 8 describing the correlation analysis, three output parameters were computed to describe
 9 intensity (R_m) and spatial extent of the correlations (D_m and D_s) according to simulations.

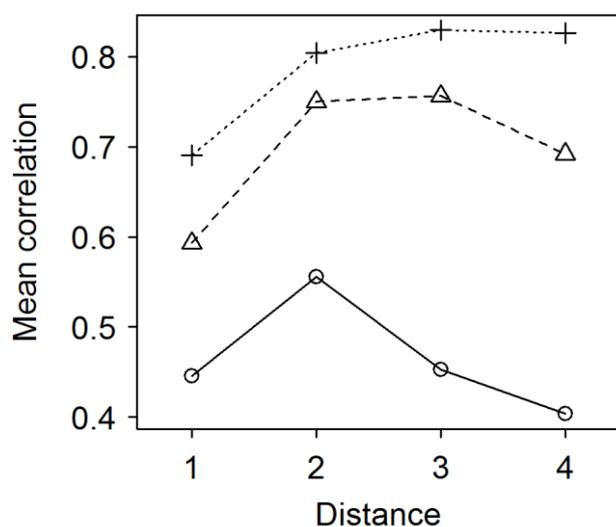


1
 2 **Fig. 2.** Maps of some landscape configuration used for the simulations, including position of
 3 the selected cells and the four buffer zones ($D1$, $D2$, $D3$, $D4$) used for the calculation of
 4 correlations: random landscape with a proportion of H-habitat $P_H = 0.1$ (A) and 0.5 (B),
 5 landscapes with low (C) and high (D) level of aggregation of the habitat. Cells corresponding
 6 to L-habitat are represented by light grey dots; cells corresponding to H-habitat by dark grey
 7 dots. The 25 selected H-cells used for the correlation between population abundance and the
 8 proportion of surrounding H-habitat are indicated by black dots and are surrounded by the
 9 four buffer zones of increasing radius distances.



1
 2 **Fig. 3.** Effect of the variation of habitat quality Q on (A) the correlation between local
 3 population abundance and surrounding proportion of H-habitat, (B) the highest correlation,
 4 (C) the distance of the highest correlation and (D) the greatest distance at which a significant
 5 correlation occurred. Each point is a mean value over the ten replicates of a given value of Q .
 6 Curves are second-order polynomial regressions: (A)-D1: $R^2=0.64$; (A)-D2: $R^2=0.94$; (A)-D3:
 7 $R^2=0.77$, (A)-D4: $R^2=0.91$; (B): $R^2=0.87$; (D): $R^2=0.87$.

8



1

2 **Fig. 4.** Effect of the aggregation of the habitat ($\circ S_0$, $\triangle S_1 + S_2$) on the value of the

3 correlation between local population abundance and surrounding proportion of H-habitat in

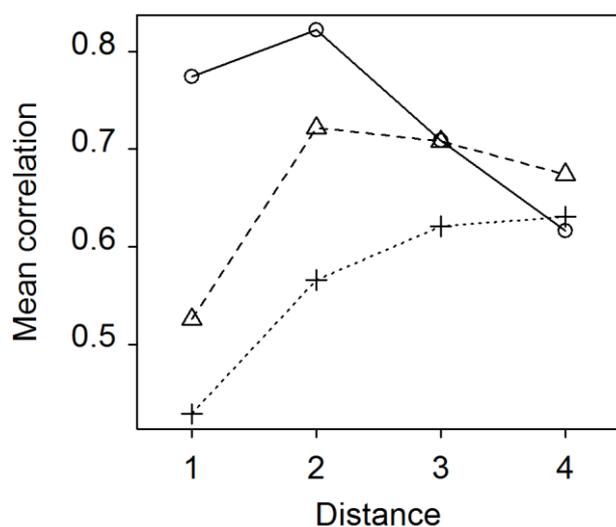
4 buffer zones of increasing radius distances ($D1$, $D2$, $D3$ and $D4$). Each point is a mean over

5 ten replicates of a given level of aggregation (S_0 , S_1 , S_2) and the combination of dispersal

6 parameters, except the *Random* dispersal model (three dispersal rates m and three dispersal

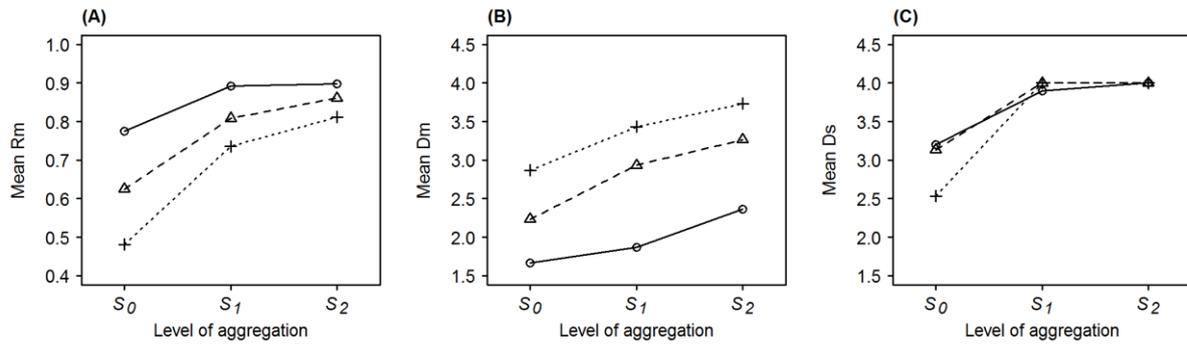
7 models *Step*, *12nn*, *2Dt*).

8



1
 2 **Fig. 5.** Effect of the dispersal model (\circ Step, \triangle $12nn$, $+ 2Dt$) on the value of the correlation
 3 between local population abundance and surrounding proportion of H-habitat in buffer zones
 4 of increasing radius distances ($D1$, $D2$, $D3$ and $D4$). Each point is a mean over the
 5 combinations of other parameters (three dispersal rates ($m = 0.05, 0.075, 0.100$), three levels
 6 aggregation of the habitat (S_0, S_1, S_2) and ten replicates of a given landscape structure).

7



1
 2 **Fig. 6.** Effect of aggregation of the habitat (S_0, S_1, S_2) and the dispersal model (\circ Step, Δ
 3 $12nn$, $+ 2Dt$) on (A) the highest correlation, R_m ; (B) the distance of the highest correlation,
 4 D_m ; and (C) the greatest distance at which a significant correlation occurred, D_s . Each point
 5 is a mean value over the three dispersal rates and the ten replicates of a given level of
 6 aggregation (S_0, S_1, S_2).
 7