Mechanistic modelling of animal dispersal offers new insights into range expansion dynamics across fragmented landscapes

Greta Bocedi, Damaris Zurell, Björn Reineking and Justin M. J. Travis

G. Bocedi (greta.bocedi@abdn.ac.uk) and J. M. J. Travis, Inst. of Biological and Environmental Sciences, Univ. of Aberdeen, Zoology Building, Tillydrone Avenue, Aberdeen, AB24 2TZ, UK. – D. Zurell, Dynamic Macroecology, Swiss Federal Inst. WSL, Zürcherstraße 111, CH-8903 Birmensdorf, Switzerland, and Plant Ecology and Nature Conservation, Inst. for Biochemistry and Biology, Univ. of Potsdam, Maulbeerallee 2, DE-14469 Potsdam, Germany. – B. Reineking, UR EMGR Écosystèmes Montagnards, Irstea, 2 rue de la Papeterie-BP 76, FR-38402 St-Martin-d'Hères, France, and Biogeographical Modelling, Bayreuth Center for Ecology and Environmental Research BayCEER, Univ. of Bayreuth, Universitätstraße 30, DE-95447 Bayreuth, Germany.

Understanding and predicting the dynamics of range expansion is a major topic in ecology both for invasive species extending their ranges into non-native regions and for species shifting their natural distributions as a consequence of climate change. In an increasingly modified landscape, a key question is 'how do populations spread across patchy landscapes?' Dispersal is a central process in range expansion and while there is a considerable theory on how the shape of a dispersal kernel influences the rate of spread, we know much less about the relationships between emigration, movement and settlement rules, and invasion rates. Here, we use a simple, single species individual-based model that explicitly simulates animal dispersal to establish how density-dependent emigration and settlement rules interact with landscape characteristics to determine spread rates. We show that depending on the dispersal behaviour and on the risk of mortality in the matrix, increasing the number of patches does not necessarily maximise the spread rate. This is due to two effects: first, individuals dispersing at the expanding front are likely to exhibit lower net-displacement as they typically do not travel far before finding a patch; secondly, with increasing availability of high quality habitat, density-dependence in emigration and settlement can decrease the number of emigrants and their net-displacement. The rate of spread is ultimately determined by the balance between net travelled distance, the dispersal mortality and the number of dispersing individuals, which in turn depend on the interaction between the landscape and the species' dispersal behaviour. These results highlight that predicting spread rates in heterogeneous landscapes is a complex task and requires better understanding of the rules that individuals use in emigration, transfer and settlement decisions.

Dispersal is one of the two most important ecological processes in determining the dynamics of range expanding populations. Classic models established that the equilibrium rate of spread is determined by both the intrinsic growth rate of a population and its dispersal ability (Skellam 1951, Hastings et al. 2005). Further advances have demonstrated that fat-tailed kernels generate more rapid and potentially ever-accelerating spread rates (Kot et al. 1996), that Allee effects can dramatically lower spread rates (Veit and Lewis 1996, Keitt et al. 2001, Johnson et al. 2006, Tobin et al. 2009) and that ignoring the fact that not all the population stages equally contribute to dispersal and demographic processes can lead to overestimation of the rate of spread (Neubert and Caswell 2000, Clark et al. 2001). Although most of these analytical models have assumed homogenous

landscapes, there has been some progress in extending them, or in developing alternative approaches, to ask questions related to dispersal success (King and With 2002, With 2002, Skelsey et al. 2013) and expansion dynamics (Schwartz 1992, Collingham and Huntley 2000, King and With 2002, Higgins et al. 2003, McInerny et al. 2007, Schurr et al. 2008, Dewhirst and Lutscher 2009, Travis et al. 2010, Pachepsky and Levine 2011, Hodgson et al. 2012, Gilbert et al. 2014) on fragmented and heterogeneous landscapes.

Similar modelling approaches have been applied quite widely to predict the expansion dynamics of invasive (With 2002, Neubert and Parker 2004, Hastings et al. 2005, Jongejans et al. 2008, Miller and Tenhumberg 2010) and, more rarely, threatened species (Tinker et al. 2008). Recently, they have started to be applied to questions relating to how species will shift their distributions under climate change (Hill et al. 2001, Engler and Guisan 2009, Willis et al. 2009, Midgley et al. 2010, Nathan et al. 2011, Leroux et al. 2013). Particularly, over the last few years there has been major progress in the field of projecting spe-

cies responses to climate change (Guisan and Thuiller 2005, Elith and Leathwick 2009, Dormann et al. 2012). Models that link spatial population dynamics with statistical projections of future-suitable climate space have already been used to explore the potential future distributions and extinction risk of, for example, trees (Iverson et al. 2004, Regan et al. 2012), plants in the South African fynbos (Keith et al. 2008), high-mountain Alpine plants (Dullinger et al. 2012), insects (Fordham et al. 2012, Leroux et al. 2013) and birds (Zurell et al. 2012). Additionally, there has been development of at least one alternative approach for incorporating demography and dispersal that relies on Bayesian techniques to infer how demographic rates vary according to local environmental conditions (Pagel and Schurr 2012, Schurr et al. 2012). Whilst various approaches have been taken, such as the integration of population level demographic models and dispersal (Iverson et al. 2004, Keith et al. 2008, Engler and Guisan 2009, Midgley et al. 2010, Dullinger et al. 2012, Fordham et al. 2012, Pagel and Schurr 2012, Regan et al. 2012), individual-based approaches (Zurell et al. 2012) or integro-difference modelling methods (Leroux et al. 2013), these approaches have typically assumed that individuals disperse according to some form of a dispersal kernel (but see Zurell et al. 2012) and that this kernel is a fixed property of a species. However, the assumption of fixed dispersal kernels may be strongly violated for many animal species, for animal-dispersed plants and even for passively dispersed organisms such as wind-dispersed plants (Schurr et al. 2008).

In parallel to the rapid development of methods for species distribution modelling, there have been significant improvements in our understanding of (Clobert et al. 2012) and ability to model (Travis et al. 2012) dispersal. The process of dispersal has, for some time, been recognised as comprising three key phases of emigration, transfer and settlement (Clobert et al. 2009, 2012). Each of these phases has its own mechanisms, context-dependencies and costs associated (Bowler and Benton 2005, Bonte et al. 2012).

Among others, two conditions upon which dispersal behaviours are likely to be highly dependent are conspecific density and mate availability. A dispersal strategy conditional to con-specific density, in both emigration and settlement decisions, is expected from theory to enhance individual fitness relative to a density-independent strategy, unless changes in the environment are highly unpredictable (Travis et al. 1999, Metz and Gyllenberg 2001, Poethke and Hovestadt 2002, Kun and Scheuring 2006, Bach et al. 2007). Depending on the environment and the social conditions, density-dependence in emigration and settlement can either be positive or negative. For example, there can be negative density-dependence in emigration and positive in settlement when con-specifics are used as a cue for good quality habitat and mating opportunities, or when being in groups is advantageous as defence against predators. The contrary can occur when dispersal is prompted by competition for resources, including mates, or by increasing probability of aggressive interactions (Matthysen 2005 and references therein). Empirical evidence for both types of density-dependence are still relatively sparse but accumulating for invertebrates (Denno and Roderick 1992, Enfjäll and Leimar 2005, De Meester and Bonte 2010, Nowicki and Vrabec 2011), vertebrates (Léna et al. 1998, Matthysen 2005, Kim et al. 2009, Le Galliard et al. 2012, Pärn et al. 2012, White et al. 2012)

and even for protozoa (Fellous et al. 2012) and plants (Lu et al. 2012, Martorell and Martínez-López 2013).

In the context of range-expansion, most theoretical models have assumed density-independent emigration and settlement, with the exception of a few recent works (Best et al. 2007, Altwegg et al. 2013). The main expectations drawn from Altwegg et al. (2013) is that positive density-dependence in emigration and in settlement should slow range expansion, which should be faster in the case of negatively density-dependent emigration. Additionally, an evolutionary model showed that during period of range spread, the reaction norm to density in emigration is expected to evolve towards higher emigration at lower densities, causing an acceleration of the rate of spread (Travis et al. 2009).

As well as con-specific density, mate availability, in interaction with the species' mating system, is expected to be an important determinant of dispersal for sexually-reproducing species, influencing both emigration and settlement decisions and their evolution (Meier et al. 2011, Trochet et al. 2013). Mate-finding is one of the main mechanisms recognized to generate a component Allee effect, which may or may not translate into demographic Allee effect and affect a species' population and expansion dynamics (Gascoigne et al. 2009). For example, in the invasion dynamics of the gypsy moth in North-America, mate-finding failure has been demonstrated to be the main cause of low population growth rate in newly established, low density populations (Tobin et al. 2009).

Most of the studies on mate-finding Allee effect have focussed on invasive species (Taylor and Hastings 2005), while there is still little theory on how mate limitation can affect species' spread rate over fragmented landscapes and more applied models rarely incorporate this behaviour. Recently, Gilroy and Lockwood (2012) showed, with a simulation model over homogeneous landscape, how including mate-finding in settlement decisions produces increasingly fat-tailed dispersal kernels at low population densities.

Overall, we still have rather little theoretical understanding of how a species' behaviours at each of the three dispersal phases influence the expected rate of population spread. To date, most of the theoretical and applied models for species' range expansion on fragmented landscape represent dispersal in a rather simplified way, not explicitly considering its different phases and processes (Travis et al. 2012). Even the few exceptions where dispersal is modelled with some condition dependencies, still use simple, fixed dispersal kernels. Therefore we still lack understanding on how the three dispersal phases together interact with habitat fragmentation in determining rates of spread and species' spatial dynamics in general. On the other hand, a growing body of empirical evidence is emphasising the ecological and evolutionary consequences of habitat fragmentation (Baguette and Van Dyck 2007, Baguette et al. 2012) on all stages of the dispersal process, emphasising a clear need for more theoretical work considering this complexity.

Here, we seek to advance beyond existing theory on how the shape of a dispersal kernel influences the dynamics of range expansion by linking the recent advances in modelling dispersal in its three phases with demographic modelling. We use an individual-based model (Bocedi et al. 2014) that explicitly models the dispersal process, to explore how context dependencies in emigration and settlement, in particular density-dependence and mate availability, influ-

ence the spread rate of a population. We run simulations across landscapes varying both in the amount of suitable habitat and the properties of the matrix (risk of mortality) that dispersing individuals move through, to seek insight on how differing dispersal characteristics in the three phases interact in determining species' range expansion on landscapes with different levels of habitat availability. Our results suggest that the rate of expansion in response to habitat availability and matrix properties can vary substantially depending upon dispersal characteristics. We consider implications of these results for conservation management.

The model

We used a spatially explicit, individual-based model, RangeShifter ver. 1.0 (Bocedi et al. 2014), for simulating range shifting dynamics of species. We simulate hypothetical species, differing in their dispersal behaviour, spreading across artificial landscapes with varying habitat availability and mortality risk in the matrix.

Population dynamics

We modelled sexual species with discrete generations. Population dynamics were modelled with a single species, individual based and stochastic formulation of the Maynard Smith and Slatkin's (1973) population model. At the time of reproduction, each female produces a Poisson-distributed number of offspring, M, according to Eq. 1:

$$M \sim Poisson\left(\frac{R}{1+|R-1|*\left(\frac{N_{i,t}}{K_i}\right)^{b_c}}\right) \quad (1)$$

where R is the maximum growth rate at low densities, $N_{i,t}$ is the number of individuals in cell i at time t and K_i is the cell's carrying capacity. b_c is the competition coefficient which describes the type of density-dependence (under-compensatory: $b_c < 1$; compensatory: $b_c = 1$; over-compensatory: $b_c > 1$). For all the simulations we assumed $R = 3$, $K = 20$ individuals ha^{-1} and $b_c = 1$, with the exception of one experiment where four different values of K were considered (20, 40, 80 and 160 individuals ha^{-1}). A female reproduces only if at least one male is present in the same cell. The offspring sex ratio is 1:1. After reproduction, all adults die and offspring can disperse.

Dispersal

Dispersal is modelled explicitly in its three phases of emigration, transfer and settlement. Offspring have a certain probability, d, of emigrating from their natal cell, and this probability can be density-independent or dependent. d is given by

$$d = \frac{D_0}{1+e^{-\left(\frac{N_{i,t}}{K_i}-\beta\right)\alpha}} \quad (2)$$

where D_0 is the maximum emigration probability, β is the inflection point of the reaction norm and α is its slope at β (Kun and Scheuring 2006 and Fig. 1). $\alpha = 0$ corresponds to density-independent emigration. A Bernoulli trial determines if an individual emigrates or not. We like to use this three parameter function to model density dependence in emigration as it provides considerable flexibility in terms of the shape of relationships between local density and emigration that it can describe. However, we acknowledge that others equally strongly prefer to use a simpler, but less flexible, one parameter function (Hovestadt et al. 2010). The appeal of this simpler function is in its derivation from the marginal value theorem and the fact that in competition experiments it has been shown to outperform the more complex model (Hovestadt et al. 2010). However, it is worth noting that these competition experiments were conducted for populations in a stationary range. Here, we model an expanding range and previous theory (Travis et al. 2009) suggests that evolution of density dependent dispersal strategies might be substantially modified as a population spreads into unoccupied space, such that key assumptions made in deriving the Hovestadt et al (2010) function are unlikely to remain valid. Most importantly in the context of this paper, while a discussion on the relative merits of the functions is likely to continue, importantly, the exact form of the function used is unlikely to qualitatively alter the key results obtained.

The transfer phase is modelled with the Stochastic Movement Simulator (SMS; Palmer et al. 2011), a discrete, step-wise movement algorithm. At each step the individual moves to one of the eight neighbouring cells. The probabilities of an individual moving to each of the neighbouring cells are given by the normalised reciprocals of the effective costs of moving to each cell. The effective cost of a neighbouring cell is given as the product of three factors: 1) movement costs based on landscape composition within the animal's perceptual range (PR), 2) distance to the current cell (i.e. 1 for rook neighbours and sqrt(2) for diagonal, bishop neighbours), and 3) directional bias depending on the animal's directional persistence (DP).

Movement costs are calculated as the harmonic mean of the per-cell costs of all cells within the perceptual range. We assume a constant value of perceptual range $PR = 3$ cells (i.e. individuals can perceive the landscape within a rectangular area of 3×3 cells in each of the eight possible directions, so that the movement decision is influenced by habitat composition in a rectangular area of 7×7 cells centred around the current cell). The per-cell costs of habitat and matrix were kept constant and equal to 1 and 10 respectively. Note that per-cell costs are intended as resistance to moving through a particular land-cover, as it would be in least cost modelling (Adriaensen et al. 2003), and not as actual fitness costs. Directional bias is calculated as DP raised to the power of the absolute value of the turning angle in degrees divided by 45, i.e. in a homogeneous landscape individuals are, for example, $DP^{180/45} = DP4$ times less likely to make a 180° turn than continuing in the same direction. We use a constant value of directional persistence DP of 2.5. We assume non-periodic boundary conditions; the probability of moving into a cell outside the landscape is zero. When calculating movement costs at the border of the landscape, the harmonic mean is taken only over those cells that are within the landscape.
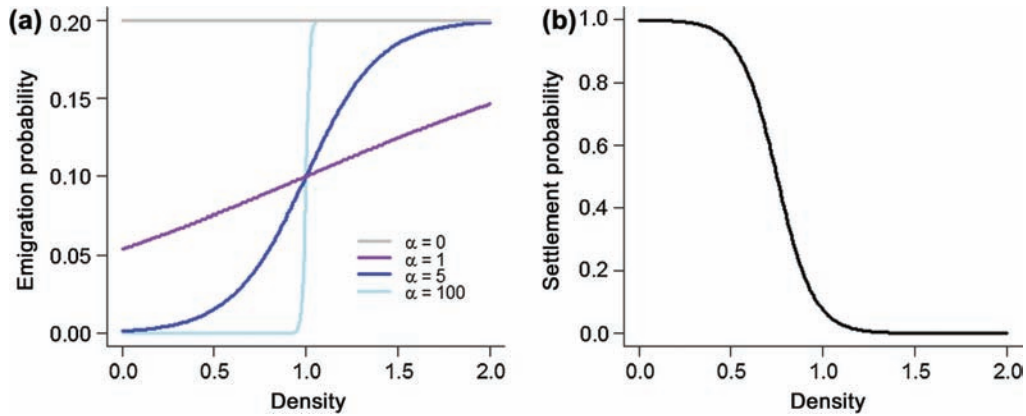
Figure 1. Density-dependent reaction norms for emigration and settlement probabilities. (a) The three types of density-dependent emigration functions used in this study ($D_0 = 0.2$, $\beta = 1.0$; Eq. 2) and the density-independent strategy (grey; $D_0 = 0.4$, $\beta = 1.0$). (b) Density-dependent settlement function used for the settlement strategies HD and HMD ($\beta_s = 0.75$, $\alpha_s = -10$; Eq. 3).

At each step individuals have a certain mortality probability (per-step mortality, SM) that can vary depending on the land-cover type. We kept the habitat per-step mortality (SM_h) constant and equal to 0.01, and varied the matrix per-step mortality (SM_m) between 0.01 (the default) and 0.2. At every step, all dispersers move simultaneously to a new cell and the ones that survive evaluate the arrival cell for settlement. When the settlement strategy involves density-dependence, individuals take their decision based on all the individuals present in the cell at that particular point in time, which includes non-emigrants born in that cell, individuals settled at previous steps and transiting dispersers (potential settlers). If it does not settle each individual keeps moving either until it settles in a cell or until it dies.

The settlement decision is taken according to different rules. We explored four different strategies, denoted H, HD, HM and HDM. With strategy H, an individual settles as soon as it finds a cell with suitable habitat. The other three strategies all require suitable habitat but with additional conditions. In HD the settlement probability, p_s, is negatively density-dependent and is given by

$$P_s = \frac{1}{1 + e^{-\left(\frac{N_i}{K_i} - \beta_s\right)\alpha_s}} \quad (3)$$

where β_s is the inflection point of the curve and α_s the slope at β_s. We assume $\beta_s = 0.75$ and $\alpha_s = -10$ (Fig. 1). The settlement decision is determined with a Bernoulli trial. Individuals settling according to the third strategy, HM, settle only if there is at least one individual of the opposite sex in the cell. Finally, HDM combines HD and HM: individuals settle only if there is a mate in the cell and, if so, with the probability given by Eq. 3. In all cases, individuals are not allowed to settle in their natal cell. Once all the dispersing individuals have settled or died, the year is concluded and the surviving individuals are able to reproduce the following year. For simplicity, we ignore non-dispersal related mortality risks within the individuals' life cycle.

Simulation experiments

We generate a series of binary (i.e. with two land-cover types: breeding habitat and unsuitable matrix), gridded landscapes of 300 (rows) × 50 (columns) cells, with a cell resolution of 100 m. Habitat cells were uniformly randomly distributed in the landscape. We considered eight different proportions of habitat cells (*p*), namely 0.01, 0.02, 0.04, 0.08, 0.16, 0.32, 0.64 and 1; we generated twenty replicated landscapes for each proportion, resulting in a total of 160 landscapes. Landscapes that did not contain any suitable cell in the first 10 rows (*y*) were discarded and replaced with new ones.

We ran a series of simulation experiments to test the influence of different emigration and settlement strategies as well as matrix per-step mortalities on the rate of range expansion. All simulations were run for 50 yr after initialising all the habitat cells in the first 10 rows (*y*) with a number of individuals equal to *K*.

In experiment I, we varied the emigration strategy, first considering density-independent ($D_0 = 0.4$, $\alpha = 0$ and $\beta = 1.0$) and subsequently three different parameterisations of the density-dependent ($\alpha = 1$, 5 and 100) emigration function (Fig. 1). For the three density-dependent strategies, D_0 and β were kept constant at 0.2 and 1.0 respectively. The values of α correspond to increasing strengths of density-dependence. For example, at density 0.5, $\alpha = 1$ corresponds to an emigration probability $d = 0.15$, $\alpha = 5$ to $d = 0.03$ and $\alpha = 100$ to $d = 0$. Note that at carrying capacity (density equal to 1.0) all the emigration strategies give the same emigration probability, $d = 0.2$. This allows the comparison between strategies and avoids the resulting rates of range expansion being confounded by individuals with different emigration probabilities from the core of the range where populations are typically saturated (see Altwegg et al. 2013 for similar approach). In this experiment we assumed the per-step mortality to be homogeneous across the landscape, $SM_h = SM_m = 0.01$, and individuals settled with strategy H. We then repeated the same experiment with higher habitat quality: $K = 40$, 80 and 160 individuals ha^{-1}.

In experiment II, we varied SM_m, considering values of 0.01, 0.05, 0.1 and 0.2. Individuals settled as soon as they

found suitable habitat (strategy H). Additionally, we tested the effect of the four different settlement strategies, H, HD, HM and HDM. For this experiment we used density-dependent emigration probability with $\alpha = 5$ and kept $K = 20$ individuals ha^{-1}. All experiments were run for all the different landscapes described above that varied in the proportion of available habitat. For all simulations we calculated the mean rate of spread (rows/year) as the total number of additional occupied rows (y) at the end of the simulation divided by 50.

Results

Effect of emigration behaviour, habitat availability and habitat quality

Under the assumption that individuals settle as soon as they found suitable habitat (strategy H), results from experiment I highlight that the population's rate of spread depended on the type of emigration behaviour in interaction with the proportion of habitat cells in the landscape and their carrying capacity (Fig. 2a and b). The most striking result is that spread rate was often highest with relatively low proportion of available habitat. Spread rates were not maximised in homogeneous landscapes ($p = 1$), where, on the contrary, they were the lowest of the all scenarios considered. The amount of habitat that maximised the rate of spread was always rather low (0.01, 0.02 or 0.04; Fig. 2a), the exact value depending upon K: the higher the carrying capacity, the lower the proportion of habitat maximising spread. Generally, increasing K increased the rate of spread but, with a high proportion of habitat available, the impact of K on the rate of expansion diminished and was close to being negligible for density-dependent emigration strategies in homogeneous landscapes (Fig. 2b).

Experiment I also revealed the interacting effects of patch quality (K) and the form of emigration in determining spread rates. At relatively low K (20 individuals ha^{-1}) and very low habitat availability ($p = 0.01$ and 0.02; Fig. 2a and b), the density-independent emigration strategy led to the lowest spread rates, which increased considerably with increasing density-dependence in emigration probability. This trend faded as p increased and the four emigration strategies all yielded similar rates of spread. With increasing K, the effect of density-dependence in emigration probability on spread rates was reversed and spread rates increased with decreasing density-dependence, this effect being more pronounced for higher values of K (Fig. 2a and b).

Especially at low p, density-independent emigration and low density regulation on emigration ($\alpha = 1$) led to rates of spread that were typically higher than all the other strategies. Again, the effect of density-dependence decreased with increasing p.

Effect of mortality during transfer and settlement behaviour

Results from experiment II revealed interactions between the proportion of habitat, the matrix per-step mortality (SM_m) and the settlement strategy to determine maximum spread rates (Fig. 3). Generally, the rate of spread decreased with increasing SM_m independently of the settlement strategy. Increasing SM_m had the overall effect of shifting the value of p that maximised the rate of spread towards higher values. With SM_m greater than 0.01, low habitat availability ($p = 0.01$, 0.02 and 0.04), which led to some of the highest rates of spread before, actually resulted in a range contraction (negative rates of spread in Fig. 3). For settlement strategies requiring the presence of a mate, increasing SM_m led to a linear or accelerating increase of the spread rate with increasing p (Fig. 4).

The settlement behaviour also strongly influenced the resulting rate of spread and the optimal proportion of habitat that maximised it (Fig. 4). In the case of relatively low per-step mortality in the matrix ($SM_m = 0.01$), the relationship between rate of spread and p was hump-shaped, with the maximum changing depending on the settlement strategies. When the settlement requirements were finding suitable habitat (H) or suitable habitat plus density-dependence (HD), the maximum spread was achieved at low values of p (0.02 and 0.04 respectively). Much higher values of p maximised spread rates when individuals had to find a mate to settle, with (HDM) or without density-dependence (HM). Interestingly, the strategy that led to the highest rate of range expansions changed depending upon p. At low habitat availability, strategies that did not include mating requirements (H and HD) resulted in higher rates of spread, while the opposite was observed for high values of p, especially if comparing between strategies with and without density-dependence (HD vs HDM and H vs HM).

Net displacement and mortality during dispersal

Figure 5 shows the distances travelled by individuals (net-displacement) and their realised mortality during dispersal. Regardless of the amount of available habitat p, individuals travelled much longer distances when they had to find a mate in order to settle (HM and HDM). If there were no mating constraints (H and HD), individuals travelled further when there was little habitat, while they settled almost immediately in landscapes with high p. However, while in the absence of mating constraints individuals travelled less and thus a high proportion of them survived and settled, having to find a mate forced individuals to be exposed to a considerably higher mortality, especially when there was little suitable habitat available. The balance between net-displacement and realised mortality explains the patterns shown in Fig. 4. Without mating constraints on settlement, a lower proportion of habitat maximised the rate of spread because individuals travelled further and the additional mortality they suffered was moderate. When individuals had to find a mate, finding suitable habitat was not the main constraint in settlement, hence their net-displacements did not differ much between landscapes with different p. However, the additional mortality that individuals travelling long distances in landscapes with little suitable habitat were exposed to, was considerably higher, increasing as p decreased to the point that when $p = 0.01$, less than 2–3% of individuals that dispersed beyond the range front survived. Hence, when
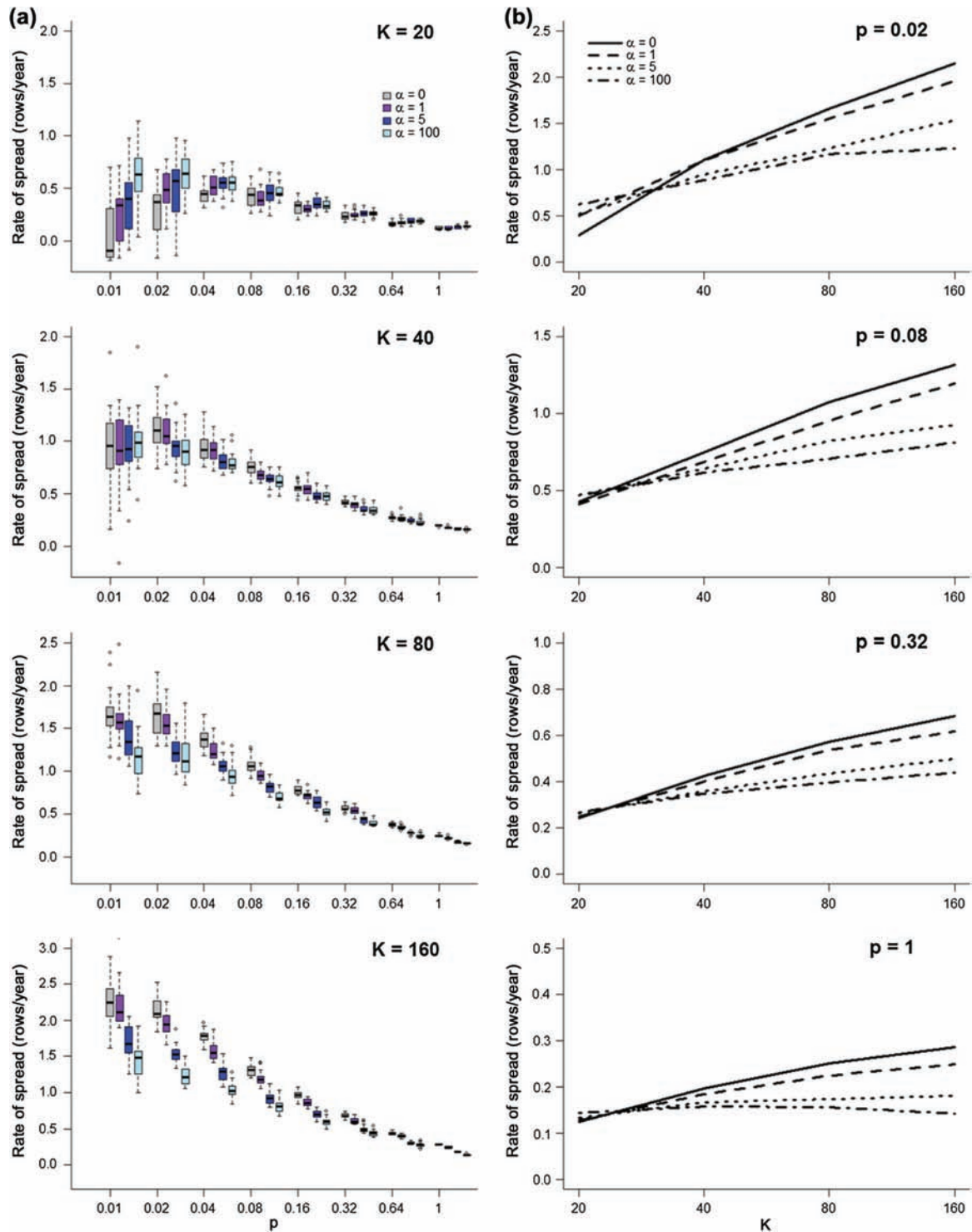
Figure 2. Effect of emigration behaviour, habitat availability (p) and habitat quality (K) on the rate of range expansion. (a) Rate of spread (rows/years) across p values, for the four different emigration strategies (density-independent: $\alpha = 0$; density-dependent: $\alpha = 1$, 5 and 100) and for four values of K (20, 40, 80 and 160 individuals ha^{-1}). (b) Mean rate of spread (rows/years) across K values for the four different emigration strategies and four values of p (0.02, 0.08, 0.32 and 1). Note that with increasing p, the scale on the y axis has been changed to lower values to show the patterns more clearly. In all cases, $SM_h = SM_m = 0.01$ and settlement strategy = H. 20 replicates were run for each parameter combination. Colours refer to the functions presented in Fig. 1.

mate finding limited the settlement, the spread rate increased as the habitat availability increased (Fig. 4). Increasing the matrix per-step mortality (Fig. 5, $SM_m = 0.05$) reduced net-displacement and decreased the proportion of dispersers that survived, especially at low habitat availability. However, the patterns described above remained the same. Interestingly, and perhaps not immediately intuitive, the density and mate dependent settlement strategy, HDM, led to slightly higher
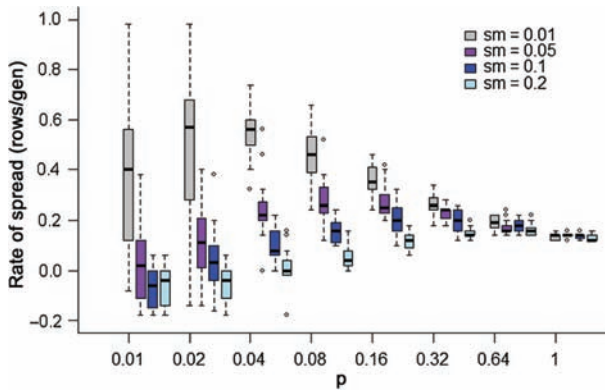
Figure 3. Effect of per-step dispersal mortality (SM_m) on the rate of range expansion across landscapes with different proportions of breeding habitat (p). Results are shown for simulations where emigration is density-dependent with $\alpha = 5$ (the pattern is similar for the other emigration strategies), carrying capacity is set to $K = 20$ and individuals settle with strategy H. All parameters combinations were run for 20 replicates.

net-displacements and most importantly to lower mortality than the HM strategy, especially where the habitat availability was higher. This is not the case for strategies that do not involve mate finding (H and HD); in this case, mortalities

were comparable and the higher rates of spread given by HD at high values of p were mainly due to greater net-displacements.

Discussion

We demonstrated that the rate of range expansion in fragmented landscapes depends on complex interactions between landscape characteristics, specifically the amount of available habitat, its quality and the quality of the matrix, and species characteristics, specifically the behavioural decisions made during dispersal. By explicitly modelling the three phases of dispersal (emigration, transfer and settlement), we were able to show how density-dependence in emigration and settlement, the need to find a mate for settling, and mortality during transfer affect the rate of spread at different levels of habitat availability.

Perhaps the most striking result is that the highest rates of spread do not always coincide with the highest amount of available habitat. Thus, in contrast to results from previous theory (Schwartz 1992, Collingham and Huntley 2000, With 2002, Dewhirst and Lutscher 2009), our work suggests that we should not expect homogenous, suitable landscapes to yield the greatest rates of range expansion in all
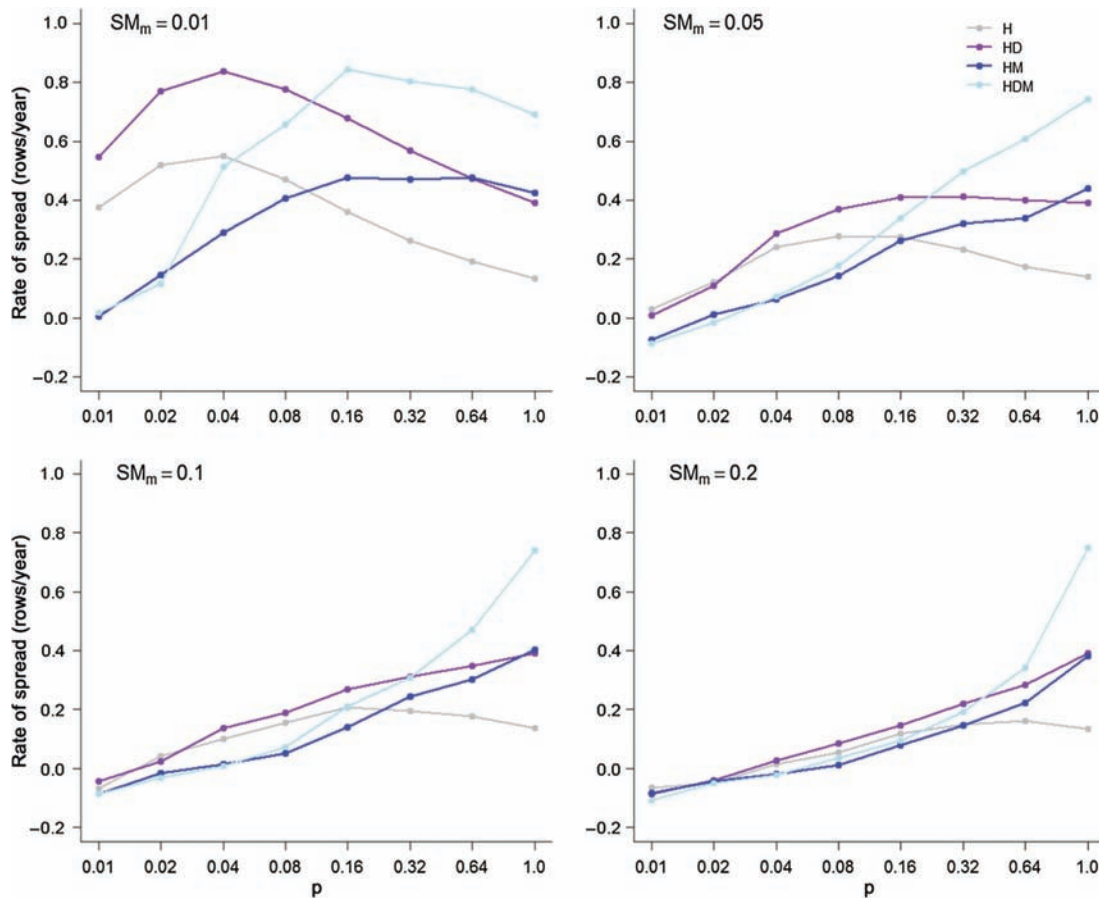

Figure 4. Effect of different settlement strategies on the rate of range expansion in relation to different values of habitat availability (p) and matrix per-step mortality (SM_m). In all cases individuals had density-dependent emigration ($D_0 = 0.2$, $\alpha = 5$ and $\beta = 0.75$). The figure reports the mean of 20 replicates for each parameters combination. For clarity we omitted the error bars which are reported in Supplementary material Appendix 1, Fig. A1.
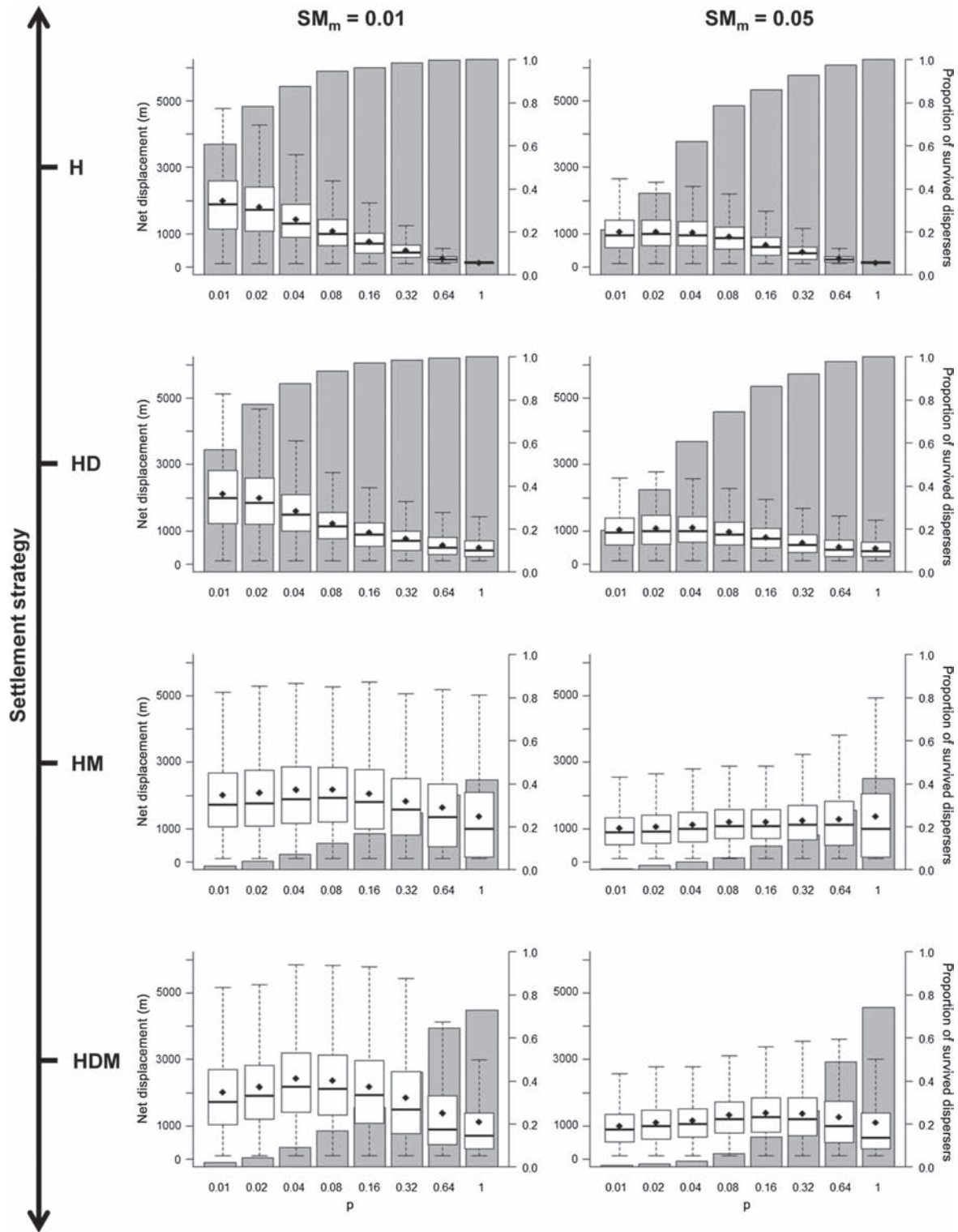
Figure 5. Mechanisms behind the effect of settlement and per-step mortality on the rate of range expansion. The resulting rate of spread from different settlement strategies and SM_m is emerging from the combination of the individuals' net displacement (left axes, boxplots) and their realised mortality, here illustrated with the proportion of dispersers that survive and settle (right axes, grey bars). The plots refer to those individuals that dispersed beyond the current range front (determined by the farthest occupied cell along the y axis of the landscape before the dispersal phase). The net displacements refer to alive and dead individuals. For clarity outliers have been omitted from the boxplots. Black diamonds represent the mean net displacements. In all cases individuals had density-dependent emigration $(\alpha = 5)$ and each parameter combination was replicated 20 times.

circumstances. Rather, our results indicate that under certain conditions, rates of spread are maximised by intermediate or even very low habitat availability. We found that the type of settlement behaviour and the movement costs of crossing the matrix strongly determined the amount of habitat maximising the spread rate. Particularly, settlement strategies that relied either on just finding suitable habitat (H), or on a combination of finding suitable habitat while avoiding high-density patches (HD), led to maximum rates of spread in landscapes with very low habitat availability (between 1 and 4% in scenarios with low matrix per-step mortality). On the other hand, when individuals had to find a mate in order to settle, a higher amount of suitable habitat was needed for achieving maximum spread rates.

One possible mechanism behind these results is the 'shadow effect' (Hein et al. 2004, Heinz et al. 2005) for which, at higher patch densities, individuals immediately stop in patches that are closer to their natal one and shadow the ones farther away, with the consequence of slowing the expansion. In our results, this effect is most influential when the cost of movement through the matrix is low. The interaction between settlement strategy and dispersal mortality shown here may, in fact, constitute the missing component needed to explain positive effects of fragmentation on population persistence that were found empirically but, so far, were not adequately captured by existing models (Fahrig 2002). Increasing the per-step mortality in the matrix decreases the proportion of successful dispersers especially in landscapes where individuals have to travel farther and through high proportions of unsuitable and risky habitat. Hence, when the matrix is highly hostile, a higher proportion of suitable habitat is needed to maximise the rate of spread. This is in line with previous studies showing that with increasing dispersal mortality the minimum amount of habitat required for species' persistence increases (Fahrig 2001, 2002).

The need to find a mate before settling in a habitat patch effectively dilutes the 'shadow effect'; individuals travel farther as they have to find a con-specific of the opposite sex, which at the expansion front will be very scarce. This results in individuals being subjected to higher chance of dying and a higher proportion of habitat increases their chances of encountering a mate and decreases their movement mortality, especially when the matrix is very hostile. Thus, our results clearly show that mate-finding, as part of the settlement rules, may constitute an important process shaping species expansion. The effects, however, may be more diverse in reality because of more complex mate-searching strategies. For example, we have not considered animals biasing their movement if they can perceive a potential mate within their perceptual range. Clearly, different animal species can have a range of complex strategies for efficiently finding con-specifics during dispersal (Gascoigne et al. 2009, Gilroy and Lockwood 2012). For example, in many species individuals can perceive the opposite sex over long distances through pheromones, scents or calls (Leonard and Hedrick 2010, Metzger et al. 2010, Ziegler et al. 2011, Kapranas et al. 2013, Llusia et al. 2013). Sexes may also have different strategies, with one settling in suitable habitat and then waiting for the other to find it or actively attracting it (Fincke 1985, Fisher et al. 2009, Samelius et al. 2012). We can expect that any strategy that improves the efficiency

of mate finding would decrease the proportion of habitat that maximises the rate of spread. The same is true also for species employing more efficient strategies for finding suitable habitat (Heinz and Strand 2006). In this case, even within moderately hostile matrix we could expect the expansion being faster for lower amounts of habitat.

In this work we did not consider different landscape structures. Previous work focussing on the effect of the degree of fragmentation (i.e. level of habitat aggregation rather than amount of habitat) on range expansion or shifting, has suggested that when the amount of habitat available is above the extinction threshold, higher fragmentation levels can actually enhance dispersal success and range expansion, especially for species with good dispersal abilities relative to the size of the gaps (McInerny et al. 2007, Hodgson et al. 2012). Additionally, in the presence of an Allee effect the invasion threshold (i.e. the minimum amount of habitat required for the population spread) has been shown to decrease with fragmentation (Dewhirst and Lutscher 2009). Another recent study suggests that dispersal success should always be maximised at intermediate scales of fragmentation relative to the species' dispersal abilities (Skelsey et al. 2013). We used random landscapes which have a very high degree of fragmentation for a given amount of habitat. Hence, we might expect that for higher habitat aggregation, more habitat would be required to achieve comparable rates of range expansion. However, all the studies cited above used very simplified dispersal models, such as dispersal kernels, and did not account mechanistically for dispersal behaviours. Therefore, it is not immediately obvious how these two results would combine and this warrants further investigation. For example, we might expect that, for species that have to find a mate to settle, higher habitat aggregation could enhance the rate of range expansion at moderate levels of habitat availability by reducing the mortality risk and increasing the chance of con-specific encounters.

As expected from previous theory (Best et al. 2007, Travis et al. 2009, Pachepsky and Levine 2011, Altwegg et al. 2013), density-dependence in emigration and settlement affects the expansion rate. Recently, the importance of density-dependent emigration in determining the rate of spread, especially in the early phases of range expansion, has also been detected for the invasion of bank voles in Ireland (White et al. 2012). In our simulations, increasing density-dependence in emigration decreased the spread rate, especially with increasing carrying capacity. Generally increasing the carrying capacity led to higher rates of spread. However, with a high proportion of available habitat and strong density-dependence in the emigration probability, the increase in carrying-capacity did not cause an increase in the expansion rate. This is likely to be due to the rate at which the habitat patches saturate. The higher the carrying capacity the longer the time a newly colonised cell takes to reach K, hence the longer the time the cell takes to send emigrants out in the case of strong positive density-dependence in emigration. On the other hand, higher carrying capacities mean more individuals in the landscape, more emigrants and hence a higher propagule pressure which determines higher rates of spread. The resulting expansion rate depends on the balance between the time lag in emigration and the increased propagule pressure.

Negative density-dependence in settlement caused an increase in the rate of range expansion relative to density-independent strategies, with greater differences observed for higher proportions of available habitat. This is in contrast with Altwegg et al. (2013), who found no change with negative density-dependence in immigration. We suggest that the difference in results probably arises because of the difference in the dispersal models. In Altwegg et al. (2013), dispersal is modelled with kernels and an individual is displaced either into the sampled cells or into one of the eight nearest neighbours; this limits the scope for detecting an effect of negative density-dependence in settlement. Overall, our results suggest that the effect of density-dependencies in dispersal could be greater than suggested by previous studies. Interestingly, when comparing the settlement strategies involving mate finding, with and without negative density-dependence, the higher rate of range expansion for the first strategy, especially at higher levels of habitat availability, appeared to be due not so much to individuals travelling farther but rather to those individuals at the front suffering from lower mortality (Fig. 5). We suggest the explanation is likely to be that with mate finding and density-dependent settlement, substantial numbers of individuals that emigrated from some distance behind the front actually reach the front as they fail to find patches of sufficiently low density close to their natal patch. This will result in a greater abundance of dispersing individuals beyond the front, mates will become easier to find, and thus the mortality associated with being a disperser in this expansion region is reduced. There is a clear need for further work focussing on the emergence and consequences of spatial and temporal heterogeneity in dispersal mortality associated with different settlement rules.

We chose some representative examples of dispersal behaviours to highlight how mechanistically considering the whole dispersal process, context-dependencies and associated mortalities can change our expectations on the amount of habitat that will enhance a species' spread. However, these are not, by any means, exhaustive of all the possible conditions that can affect dispersal and hence rate of range expansion. For example, we did not consider the effect of sex-specific dispersal and sex ratio-dependent strategies. Depending on the mating system, variability in mating opportunities can strongly influence dispersal behaviour, both in emigration, leading in some cases to sex-biased dispersal, and in settlement (Lawrence 1987, Chaput-Bardy et al. 2010, Steifetten and Dale 2012, Saino et al. 2013, Trochet et al. 2013). In reality, con-specific density and mating opportunities (hence, sex-ratio in interaction with the mating system) are likely to interact in determining dispersal behaviours. Sex-biased dispersal and sex-ratio can ecologically and evolutionary influence each other (Bonte et al. 2009, Meier et al. 2011, Nelson and Greeff 2011), with considerable consequences for species' rate of spread (Miller et al. 2011, Miller and Inouye 2013).

Here, we have explored the ecological consequences of a range of fixed behavioural rules at each of the three dispersal stages. In reality, selection is likely to operate on these behaviours and the processes of habitat fragmentation and range expansion are already well known to exert selective pressure on dispersal strategies (Travis and Dytham 2002, Simmons and Thomas 2004, Schtickzelle et al. 2006, Baguette and Van Dyck 2007, Hughes et al. 2007, Urban et al. 2008, Phillips et al. 2010, Travis et al. 2010, 2013, Wang et al. 2011, Bartoń et al. 2012, Boeye et al. 2013, Henry et al. 2013, Lombaert et al. 2014). Species' dispersal rules are likely to vary both in space – depending on the landscape type in which they evolved and/or on the position within the species' range, and also in time – depending on the time since fragmentation and/or the phase of range expansion/shifting that is considered (Schtickzelle et al. 2006, Baguette and Van Dyck 2007, Dytham 2009, Baguette et al. 2013, Lindström et al. 2013). An implication of this is that the landscape structure optimising a species' rate of range expansion following, for example, the onset of climate change (when we might generally expect species to be relatively poorly dispersive), may not be the same as for a species that has already been expanding its range for a sufficiently long period of time for spatial sorting or evolution of dispersal to take place.

Habitat fragmentation has been demonstrated to select for reduced emigration propensity in some species (Van Dyck and Matthysen 1999, Bonte et al. 2006, Schtickzelle et al. 2006, Baguette and Van Dyck 2007) while selecting for increased emigration in others (Hanski and Mononen 2011, North et al. 2011, Wang et al. 2011). Species evolving in a highly fragmented landscape are expected to evolve traits that enhance colonisation ability (Merckx and Van Dyck 2007, Bartoń et al. 2009), such as increased perceptual range and movement in straighter lines. Moreover, the degree of spatial autocorrelation in habitat quality has been shown to affect density-dependent strategies, for example in emigration, where negative density-dependent is expected to evolve when the spatial autocorrelation is low (Baguette et al. 2011). Importantly, there is likely to be an interplay between the evolution of behavioural characteristics acting at each of the three phases of dispersal. For example, in a fragmented landscape selection might act to have a high level of emigration but then a low risk movement behaviour in the transfer phase, or it might lead to a low rate of emigration but with these emigrants engaging in much riskier movement (Travis et al. 2012). To date, we have an absence of theory (or empirical data) on how the three dispersal phases jointly evolve during range expansions and gaining an improved understanding represents an important area for future work. Ultimately, eco-evolutionary dispersal dynamics should be incorporated in models trying to predict the rate of spread of expanding or shifting populations over fragmented landscapes.

Finally, like most models focussing on the rate of population spread, we consider a single species expanding into empty space. However, inter-specific interactions have been demonstrated to play a potentially important role in species' spatial dynamics and range expansion or shifting (Singer et al. 2012, Bocedi et al. 2013, Wisz et al. 2013, Svenning et al. 2014). Inter-specific interactions, including competition and predation could have important impacts on each of the three phases of dispersal and this might have important consequences for the dynamics of range expansions across patchy landscapes. As an example, inter-specific competition may result in density-dependent emigration or settlement decisions somewhat similar to those generated by intra-specific behaviours – with individuals more likely to emigrate or less likely to settle when the density of a second

species is high (Denno and Roderick 1992). As a second example, the mortality cost of the matrix may be increased if a predator is present, while it may be reduced in the presence of an energy source (e.g. a prey species or a preferred flower; Driscoll et al. 2013). This is an unexplored area that warrants further investigation.

Our results have potentially important consequences for conservation planning. There is a current debate surrounding the relative value of improving (or extending) existing patches of suitable habitat versus increasing the connectivity of a landscape by creating new habitat patches and/or improving the quality of the matrix (Hodgson et al. 2009, 2011, Mortelliti et al. 2010, Doerr et al. 2011). Our results suggest that almost all species that exhibit active dispersal will exhibit higher rates of range expansion if patch quality is improved (Fig. 2b) or if the matrix is made less costly (Fig. 3). In many cases, the rates of expansion can be substantially increased by improvement to habitat and/or matrix. The picture is much less clear in relation to the proportion of suitable habitat. While some species will undoubtedly expand their range faster with an increase in the availability of suitable habitat, others may not, or even experience reduced spread rates. It is too early to provide any definite advice. Yet, our results emphasise that expected spread rates depend on complex interactions between species' behaviour and the landscape. Thus, for deciding whether to invest in improving habitat quality, in adding habitat to existing patches, in creating new patches of habitat or in managing the matrix, it is important to consider the likely consequences across a range of species with different behaviours within the community. Further work that moves away from dispersal kernel based modelling and instead uses and extends the type of approach adopted here can, we believe, play an important role in informing this debate. Importantly, the development of this type of modelling is now assisted by the rapid development in the field of movement ecology (Nathan et al. 2008, Jeltsch et al. 2013) which, together with progress in dispersal ecology (Clobert et al. 2012), is providing increasing mechanistic understanding of fundamental dispersal/ movement rules.

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Supplementary material (Appendix ECOG-01041 at <www.ecography.org/readers/appendix>). Appendix 1.