

1 **Prospecting and dispersal: their eco-evolutionary dynamics**
2 **and implications for population patterns**

3 **M. M. Delgado^{1,2}, K. A. Bartoń³, D. Bonte⁴ and J. M. J. Travis³**

4
5 ¹*Metapopulation Research Group, Department of Biosciences, FI-00014, University of*
6 *Helsinki, Finland*

7 ²*Department of Conservation Biology, Estación Biológica de Doñana, C.S.I.C., c/*
8 *Americo Vespucio s/n, 41092 Seville, Spain*

9 ³*Institute of Biological and Environmental Sciences, Zoology Building, University of*
10 *Aberdeen, AB24 2TZ, UK*

11 ⁴*Terrestrial Ecology Unit, Department of Biology, Ghent University, K.L.*
12 *Ledeganckstraat 35, 9000, Gent, Belgium*

13
14 *Author for correspondence (maria.delgado@helsinki.fi).

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1 **ABSTRACT**

2 Dispersal is not a blind process, and evidence is accumulating that individual dispersal
3 strategies are informed in most, if not all, organisms. The acquisition and use of
4 information are traits that may evolve across space and time as a function of the balance
5 between costs and benefits of informed dispersal. If information is available, individuals
6 can potentially use it in making better decisions, thereby increasing their fitness.
7 However, prospecting for and using information likely entail costs that may constrain
8 the evolution of informed dispersal, potentially with population-level consequences. By
9 using individual-based, spatially explicit simulations, we detected clear co-evolutionary
10 dynamics between prospecting and dispersal movement strategies that differed in sign
11 and magnitude depending on their respective costs. More specifically, we found that
12 informed dispersal strategies evolve when the costs of information acquisition during
13 prospecting are low but only if there are mortality costs associated with dispersal
14 movements. That is, selection favours informed dispersal strategies when the
15 acquisition and use processes themselves were not too expensive. When non-informed
16 dispersal strategies evolve, they do so jointly with the evolution of long dispersal
17 distance because this maximises the sampling area. In some cases selection produces
18 dispersal rules different from those that would be ‘optimal’ (i.e. the best possible
19 population performance – in our context quantitatively measured as population density
20 and patch occupancy - among all possible individual movement rules) for the
21 population. That is, on the one side, informed dispersal strategies led to population
22 performance below its highest possible level. On the other side, un- and poorly
23 informed individuals nearly optimised population performance, both in terms of density
24 and patch occupancy.

25 **Keywords:** cost of information; extinction; information; natural selection; perceptual
26 range; population dynamics

1 1. INTRODUCTION

2 Theory on the evolution of dispersal has almost entirely been constructed on the
3 assumption that individuals have no knowledge of the possible destination patches to
4 which they might recruit if they emigrate [1-4]. In reality, many organisms do not make
5 such blind dispersal decisions; instead, they may often invest considerable time and/or
6 energy in prospecting potential breeding habitats before deciding on where to settle [5,
7 6]. Whilst there has recently been a surge of interest in the importance of information
8 acquisition and use within ecology [7], these ideas have yet to be properly integrated
9 into our understanding of dispersal evolution. Importantly, recent developments
10 incorporating greater realism by modelling dispersal as three stage process (of
11 departure, transient and settlement [8]) are readily extendable to explore the evolution
12 of prospecting behaviour in the context of dispersal. Here, we take some initial steps to
13 building up a theory on the joint evolution of habitat prospecting and dispersal, and
14 evaluate its consequences for the persistence of populations.

15 The field of dispersal evolution has provided clear examples where predictions from
16 theory have subsequently been tested by empiricists (kin competition driving emigration
17 rates being an excellent example; reviewed in [9]) and, vice versa, where field
18 observations have resulted in new modelling directions being taken (e.g. density-
19 dependent emigration; [10]). We suggest here that one area in which development of
20 theory lags well behind empirical studies is the joint evolution of prospecting and
21 dispersal strategies.

22 Accumulation of empirical evidence demonstrates that organisms condition their
23 dispersal strategy on informative cues from the environment at the different stages of
24 the dispersal process, from departure to settlement (see [9, 11, 12] for extensive
25 reviews). As such, it has become clear that models need to integrate this information use
26 in order to predict spatial dynamics in a realistic manner [8]. Several factors might
27 influence an organism's tendency to leave and to settle on a given patch. For example,
28 density dependent dispersal models have found that emigrating individuals may be
29 sensitive to habitat quality [13], to patch size [14] or to the presence of conspecifics [4,
30 15] in their local patches. Ruxton and Rohani [13] were the first to introduce the
31 concepts of fitness-dependent dispersal to highlight that other environmental factors
32 (e.g. carrying capacity) at sites that an individual visits during transience are expected to

1 influence individuals' decisions about whether to settle. In their model, individuals
2 moved between patches until they found a patch of suitable quality, thereby generating
3 variation in dispersal distance strategies and the subsequent dispersal kernel. In
4 common with almost all models to date on context-dependent dispersal, these
5 aforementioned models assume that individuals make their decisions based on perfect
6 knowledge of the local conditions. Thus, there exists a clear dichotomy between the
7 many models that assume context-independent (i.e. blind or no information) processes
8 and those that have incorporated context-dependent assuming perfect information on,
9 for example, local density.

10 In reality, whilst individuals are likely to acquire and use information in order to reduce
11 the costs of uncertainty and thus make more adaptive dispersal decisions [11, 16], they
12 will have neither the ability nor the time to acquire perfect information. Thus, there is a
13 pressing need to develop a greater body of theory that considers how dispersal evolves
14 when individuals have access to imperfect information, and additionally to ask how
15 much time and/or energy individuals should be selected to invest in gaining and using
16 information for dispersal decisions. To date, only very few modelling studies attempted
17 to deal explicitly with how information should influence the nature of evolved dispersal
18 strategies. Schjørring [17] was, to our knowledge, the first to develop an optimality
19 model that explicitly considered the use of information as an important factor for
20 individual-decision making during dispersal. She concluded that when high-quality
21 habitats are sparse, information is predictable over time and survival rate is high,
22 prospecting strategies maximise fecundity. More recently, it has been demonstrated that
23 because dispersal is a costly process, non-informed emigration strategies may lead to
24 higher dispersal rates relative to informed strategies [18]. In a recent paper, the extent to
25 which individuals invest in acquiring information for making an emigration decision is
26 also allowed to evolve [19]. Slightly informed dispersal strategies are always selected
27 for, except in highly unpredictable environments when there is no investment in
28 information acquisition. Importantly, selection rarely favours investment in acquisition
29 of high-precision information, and the propensity to invest in information acquisition is
30 greatest in predictable environments when the associated cost was low [19]. However, it
31 is unclear whether this result emerges, at least in part, because individuals were only
32 able to acquire information on their natal patch before making their emigration decision.

1 Likewise, previous empirical and theoretical studies have shown that natural selection
2 acting at the individual level may promote traits that are advantageous for individuals
3 but which can have negative effects on the population (reviewed in [20]). A high chance
4 to enhance individual fitness tends to favour an inclination to prospect, insofar as
5 prospecting can be achieved without much cost [21, 22]. However, when prospecting is
6 costly (e.g. in time and/or energy; [22]), individuals may be selected to sample habitats
7 at levels that differ from what would be ideal for population performance. This
8 discrepancy between individual and population levels is expected to be strong when
9 costs of information acquisition and use are high and hence, there is potential for
10 considerable tension between selections operating at individual and lineage level (often
11 termed the metapopulation level effect; [23]). To date, while examples have shown that
12 the use of information in dispersal decisions can be either beneficial or detrimental at
13 the population level [13, 24], general theory on when information acquisition and use
14 lead to positive or negative population consequences is still lacking.

15 Here, our first objective was to quantify explicitly how information acquisition
16 (including spatial extent of patch quality assessment) and use (i.e. how individuals
17 weight the information on patch quality and preferred distribution of dispersal distances
18 to decide where to settle) influence the evolution of dispersal strategies. Using an
19 individual-based, spatially explicit simulation model, we allow these two quantitative
20 traits to experience different selection pressures as a function of different costs and
21 trade-offs in a range of environments with different levels of spatio-temporal
22 stochasticity. Second, by looking at both patch occupancy and population size, we
23 addressed our attention to the population consequences of the evolved individual
24 informed strategies to examine whether and under what conditions natural selection
25 may produce individual prospecting rules that might not maximize the population
26 performance.

27 **2. METHODS**

28 To study the evolution of informed dispersal strategies and examine their population
29 consequences, we modelled the population and evolutionary dynamics of annual
30 organisms dispersing in a two-dimensional, continuous patchy landscape. Choice of the
31 breeding site is done according to information about patch quality and individual
32 genetically determined preferences. We consider specifically prospecting by individuals

1 for a potential breeding site. Depending upon the strategy adopted, we assumed that
2 some individuals prospect for breeding sites as soon as they depart from a natal patch.
3 Then the subsequent decision on where to settle was sufficient in terms of providing
4 dispersal distance. In other cases, selection pressures may act to favour greater dispersal
5 distances. In this case, the process of prospecting and settling was supplemented by an
6 additional, potentially less-informed, displacement from the natal patch.

7 ***Model structure***

8 The dispersal event is divided into two steps, corresponding to the prospecting and the
9 settlement phases. In the first step, the individual assesses the quality of the patches
10 surrounding its natal patch within its preferred dispersal range (i.e. dispersal kernel; as
11 explained in the previous section; Fig. 1). In the second step, the individual selects its
12 target patch and moves into it (Fig. 1 and Fig. 2). This settlement decision is based upon
13 the gathered information about patch quality combined with the individual preference
14 for dispersal distance (Fig. 2).

15 The landscape consists of 1000 circular habitat patches of unit radius, randomly
16 distributed over a square area of size 2000×2000 units (so average nearest-neighbour
17 distance to patch is about 11.3 units). The patch quality varies spatially due to variation
18 in the carrying capacity, and temporally, due to changes in the local population size.
19 The patches' carrying capacities, K , were normally distributed around the mean of 50,
20 with standard deviation of 10 (or zero if negative numbers occurred).

21 ***Information acquisition***

22 The ability of individuals to acquire information is determined in our model by:
23 (1) their perceptual range, a , restricting the individual's ability to acquire information
24 about the locations of potential patches; and
25 (2) their preferred dispersal kernel, which is determined by the preferred dispersal
26 distance and the variance around it. This kernel sets the total spatial extent over which
27 an individual acquires information (see Fig. 1). We modelled the preference of
28 individual for a patch as a Gaussian function, as it allows for easy manipulation of the
29 preference area through the mean distance and its extent:

$$1 \quad p_{i,j} = \frac{1}{\sigma_j \sqrt{2\pi}} e^{-\frac{(d_{i,j}-r_i)^2}{2\sigma_j^2}}, \quad (1)$$

2 where $d_{i,j}$ is the distance to the patch i from individual j , r_i is the individual's most
3 preferred distance, and σ is the deviation of the preference. Therefore, the individual
4 preference kernel is defined by two parameters r and σ (see Fig. 2).

5 We assumed individuals acquire information within an area comprising approximately
6 95% of its preference (i.e. the area under the preference curve, within $\pm 2\sigma_i$ from r_i).
7 This prospecting area thus increases both when r or σ increase (Fig. 1). As the
8 individual travels over this potential region for dispersal, it collects information on the
9 quality of the patches within its perceptual range. The perceptual range (a) determines
10 the searching efficiency, and, consequently, the trajectory length (duration of the
11 prospecting movement; see Fig. 2). One of the simplest movement strategies to cover
12 such a ring-shaped or circular area is spiralling, in which the prospecting individual
13 moves in a straight line from the natal patch at the distance of the perception from the
14 inner radius of the ring and circles around increasing the radius by twice the perceptual
15 range after completing each round (see Fig. 1 and Fig. 2). Assuming such a trajectory in
16 our model, we can approximate the length of the path needed to cover the whole
17 prospecting area to be explored by individual j as

$$18 \quad l_j = (A(\rho_u) - A(\rho_l)) * \frac{2a}{A(a)} + 2\rho_l = \left(2/a(\rho_u^2 - \rho_l^2)\right) + 2\rho_l$$

$$19 \quad l_j = (16r\sigma/a) - 4\sigma + 2r, \quad \text{for } r_j \geq 2\sigma_j, \quad (2)$$

$$20 \quad l_j = 2(r_j + 2\sigma_j)^2 / a_j, \quad \text{for } r_j < 2\sigma_j$$

21 where the proportion of prospecting area (delimited by the two radii ρ_l and ρ_u) to the
22 area that can be perceived from a single location (of radius of perceptual range a) is
23 multiplied by the distance made between two sampling locations ($2a$), and twice the
24 inner radius is added to account for the way from the natal patch and to the selected
25 target patch (see Fig. 1). The lower bound is $\rho_l = r_j - 2\sigma_j$ when $r_j \geq 2\sigma_j$ or $\rho_l =$
26 0 when $r_j < 2\sigma_j$, and upper bound is $\rho_u = r_j + 2\sigma_j$ from the natal patch.

1 ***Information use***

2 Individuals leave their natal patches with a constant probability of 0.2. It is worth noting
3 here that in each of the simulated scenarios (see below for more details), the evolved
4 emigration rate was mostly below 0.2 (Fig. 3). Thus, our choice of this specific fixed
5 emigration probability yield results close to the ones expected with this trait evolving.
6 Once moving, the dispersers suffer mortality with per-unit length probability μ . The
7 probability of survival from departure to settlement, so including prospecting
8 movements, is $S = (1 - \mu)^l$, where l is the total path length. We assumed that the
9 development of perceptual abilities entails a cost paid in fecundity, φ , based on
10 previous evidence on dispersal costs and their trade-offs against other life-history
11 characteristics [12]. Thus, development of both wide dispersal range and perceptual
12 range is penalized by their costs (Fig. 4; [8, 12]). In addition, given that individuals with
13 a short perceptual range need to make more spiral turns compare to individuals with
14 large perceptual range in order to cover the same area, they are exposed to higher
15 mortality risk. Therefore, the cost of large preferred dispersal area is paid in mortality
16 rather than fecundity when perceptual range is small.

17 After the prospecting has been completed, the individual moves to the target patch. The
18 choice of the settlement/target patch was based on the perceived patch quality, q , within
19 the preferred dispersal range, and an individual's preference, p , towards certain
20 dispersal distance (see equation 1). The quality q of a patch was assessed as its
21 'underpopulation' (i.e. the remaining capacity), and calculated as the difference between
22 the patch's carrying capacity (K_i) and its current population size (N_i). Weights $p_{i,j}q_j$ were
23 used as selection probabilities for the target patch. If no patches were present within the
24 individual's preferred dispersal range, we assumed that the individual died. Once the
25 target patch was selected, the individual settles on it. When all individuals settle (or die
26 in the process of dispersal), they reproduce.

27 ***Reproduction (population model)***

28 Individuals that successfully settled, give birth to a number of offspring described by
29 equation:

$$30 \quad N_i = \text{Poisson} \left(\lambda - \frac{\lambda \alpha}{\alpha^{\frac{1}{\varphi}}} \right) \quad (3)$$

1 where λ is the mean, population-wide, number of offspring when no costs incurred, α is
2 the perceptual range, and φ is the cost of (developing) perceptual ability, paid in
3 decreased fecundity (see upper panel in Fig. 4). Adults die immediately after
4 reproduction and then juveniles compete. If the number of juveniles (J_i) in a patch i
5 exceeds the carrying capacity (K_i), juveniles suffer mortality with probability $K_i J_i - 1$.

6 *Simulations*

7 *(a) Prospecting and dispersal: their eco-evolutionary dynamics*

8 In order to quantify explicitly how information acquisition and use influence the
9 evolution of dispersal strategies, we run different simulations allowing all individual
10 traits considered (i.e. perceptual range a , preferred dispersal distance r and its range σ)
11 to evolve by varying costs of fecundity φ (from 0.001 to 0.01) and costs of movement μ
12 (from 0.00001 to 0.01) between simulations. In these evolutionary simulations,
13 offspring inherited the three genetic parameters (a , r and σ) that determined these traits
14 asexually from their haploid parent with a 1% probability of a mutation (i.e. probability
15 that a mutation occurs in a whole ‘genome’ is 1% and only one mutation at a time
16 happens). We run simulations for 5000 generations and recorded all values of the
17 evolved traits, as well as the resulting phenotype (i.e. length of prospecting trajectory
18 and actual dispersed distance). The duration of the evolutionary simulations was chosen
19 after initial examination of transient dynamics.

20 *(b) Prospecting and dispersal: their implication for population patterns*

21 We next turn our attention to the population level consequences for the different
22 informed dispersal strategies evolved. Examining the evolved informed dispersal rules
23 on their own does not provide the information required to assess relative population-
24 level performance, because they do not contain information on how efficiently the
25 population would have performed under informed dispersal rules other than those that
26 did evolve. We thus next conducted two sets of simulations, where we fixed and
27 combined both cost of mortality and fecundity (μ , from 0.001 to 0.01) and fecundity (φ ,
28 from 0.001 to 0.01), assuming a patch extinction rate (e) of 15%.

29 For the first set, we fixed all the individual traits (i.e. assuming no evolution), and ran a
30 simulation for 250 generations for each combination of perceptual range (15 values
31 ranging from 0 to 50) and preferred dispersal distance (15 values ranging from 5 to

1 100), performing 15 replicates for each. We did not vary preferred distance range, the
2 value $\sigma = 5$ was common to all simulations. At the end of each simulation, we recorded
3 population performance, measured as both patch occupancy and population size.

4 For the second set, we ran 20 replicates for 5000 generations, with the same
5 combinations of costs mentioned above, but we allowed the genetic parameters to
6 evolve. We recorded evolved values of perceptual range and preferred dispersal distance
7 (preferred distance range was again fixed) to examine whether evolved informed
8 dispersal strategies produced by individual-level selection differ from that which
9 maximise patch occupancy or population size.

10 The model was implemented in a C++ language (source code and binaries are available
11 upon request), and the output was analysed using R environment [25].

12 **3. RESULTS AND DISCUSSION**

13 *Prospecting and dispersal: their eco-evolutionary dynamics*

14 To date, there has been substantial progress in moving beyond the most commonly
15 made assumptions of e.g. density-independent emigration rates [26-28] towards models
16 that represent the different stages of dispersal explicitly [8] and incorporate assessment
17 of habitat quality [19, 29]. Yet, there remains a knowledge gap in terms of how
18 organisms should evolve strategies to acquire and use information in order to make
19 informed dispersal decisions. Here, by developing a model that allows both perceptual
20 range and preferred dispersal kernel to jointly evolve we provide some important
21 insights into the evolution of informed dispersal.

22 There is now a consensus that information affects the evolution of dispersal strategies
23 [17-19, 30]. These previous studies used different assumptions about the type of
24 information (including spatial extent and precision) that an individual makes use of, and
25 then analysed how different situations might influence the evolution of informed
26 dispersal strategies. However, individuals need to first update their perception of the
27 biotic and abiotic environments (i.e. information acquisition; [31, 32]) either from their
28 own experience [33] or from observing the gains obtained by conspecifics [34-36]. Only
29 then, they should be able to compare different alternatives and thus benefit to increasing
30 their likelihood of choosing the best-matching dispersal strategy (i.e. information use).

1 Doing so might entail costs, however, because individuals must redirect valuable
2 resources, including energy and time to information gathering at the expense of other
3 basic biological demands [32]. Here, we clearly demonstrate the emergence of co-
4 evolutionary dynamics between prospecting and dispersal movement strategies, which
5 differed in sign and magnitude depending on their respective costs (Fig. 5). The results
6 were qualitatively robust to the emigration probability, i.e. similar patterns for the
7 evolution of informed dispersal strategies evolved when considering different
8 emigration rates (50% and 80%), as well as when we allowed this trait to evolve (results
9 not shown).

10 On the one hand, selection always aims to maximise the individual's chances of
11 reproduction, which in our model is primarily determined by survival during
12 prospecting. The duration of prospecting movement (as implemented in our model) can
13 be much longer for those individuals that need to make some spiral turns in order to
14 cover the whole prospecting area (i.e. when preferred mean dispersal distance is long;
15 Fig. 2) compared to those individuals which just follow a straight line from the natal to
16 the selected patch (i.e. when they are able to perceive most of the potential dispersal
17 area; Fig. 2). Thus, it was at this stage where most opportunity for evolutionary cost-
18 cutting occurred. On the other hand, selection tends to favour large dispersal distance
19 (i.e. large margin for freely choosing the best quality patch). This was generally
20 achieved by expanding the preferred distance variance (σ), and therefore there was a
21 strong correlation between σ and the realised dispersal distance (Fig. 5). Quite
22 obviously, prospecting length decreased when increasing mortality risk during
23 movements, but we also observed that it increased with increasing cost of perceptual
24 range (Fig. 5). Yet, cost of perceptual range has a moderately lower effect on dispersal
25 distance compared to mortality cost.

26 Depending on the relative costs of movements and perceptual range, selection
27 minimized each of these traits, compensating the deficiency of one trait by the other.
28 For instance, as moving became increasingly risky, the preferred distance variance
29 decreased, but simultaneously a large perceptual range evolved. This allowed
30 minimising the duration of prospecting while still permitting individuals to move a
31 reasonably large dispersal distance (Fig. 5). That is, large perceptual ranges evolved
32 only when the cost of its development was low and when movement during dispersal
33 was relatively costly (Fig. 5). This finding is in line with the few empirical studies

1 because perceptual range has been linked to many aspects of dispersal, including the
2 choice of search strategy and the movement behaviour during dispersal, which is
3 directly related to individual's effectiveness at finding new habitat patches [37]. A well-
4 developed perception of habitat patches by individuals should lead to more efficient,
5 oriented movements that can reduce the time and the energy spent in risky environment
6 during dispersal [38], and influence the ability to respond to habitat disturbance and
7 fragmentation [39]. As informed individuals are able to make firmer decisions as a
8 function of the current state of the biotic and abiotic environment, they are expected to
9 enhance their fitness [21, 32]. However, since collecting information usually entails
10 costs, including committing time, energy or the use of bodily resources at the expense
11 of other biological demands such as growth or reproduction [22], selection should only
12 favour the acquisition of information when its value exceeds the costs of its use [33].

13 When cost of information acquisition are high, and consequently a limited perceptive
14 range evolves (Fig. 5), individuals can be selected to move to a long distance and
15 prospect narrow area at that distance, making just one prospecting round (as depicted in
16 the lower left panel of Fig. 2). Such a strategy minimises information acquisition and
17 mortality costs, still allowing individuals to maintain sufficient environmental sampling
18 for good quality patches. Therefore, dispersers possessing low perceptual range are still
19 likely to detect particularly good patches (either empty or well below carrying capacity).
20 In some cases, overreliance on cues can be costly if it attracts individuals into sink
21 habitats where they have little chance of breeding successfully (ecological traps; [40]).
22 For example, in species where dispersal is at least partly based on copying conspecifics,
23 informational cascades can occur if the copied behaviour is occasionally wrong [22].
24 Under certain conditions (e.g. high density habitats leading to poor individual success;
25 [41]), it might be therefore beneficial to evolve a long-distance dispersal strategy as
26 opposed to simply increasing ones perceptual range. The observed selection for long
27 dispersal distances when individual perceptual range is low has important consequences
28 for population viability, given that for a population divided into patches of suitable
29 habitat, and where each patch has a finite life-time because of random events like local
30 extinctions, long dispersal distance events are crucial for its persistence [40, 41]. In
31 addition, short-range prospecting evolving by a high mortality costs will increase local
32 competition since all individuals will choose to settle in a patch within a small area
33 around their natal patch. Increasing dispersal distance should result in a lower saturation

1 rate of the environment and an overall increased reproduction success. This competition
2 effect would possibly have been different if we would have considered directional
3 dispersal, i.e. the individual chooses an initial direction and prospect the area located in
4 that direction. Such pre-selection of the searching area would reduce costs of
5 movements, allowing the evolution of large dispersal distances, also diversifying the
6 choice of settlement site among individuals. Moreover, depending on the spatiotemporal
7 variability of the landscape, we expect the strength of selection for the spatial extent in
8 which individuals choose a breeding site to vary.

9 *Prospecting and dispersal: their implications for population patterns*

10 Previous studies have demonstrated that the perceptual range of dispersing animals
11 directly affects spatial patterns and biological processes at multiple spatio-temporal
12 scales, by influencing the probability of detecting new patches, as well as the duration
13 of searches [39, 42, 43]. Pe´er and Kramer-Schadt [44] theoretically demonstrated that
14 population connectivity was enhanced if large perceptual range was assumed. However,
15 more information does not always mean better population performance [24]. Given the
16 various costs of information acquisition and use at the level of individual, the
17 motivation of individuals to sample environment is an individual trait that under certain
18 condition might not evolve to produce optimal behaviour at the population level [20].
19 We observed that while informed dispersal strategies led to population performance
20 below its highest possible level (Fig. 6A), un- and poorly informed individuals nearly
21 optimised population performance, both in terms of density and patch occupancy (Fig.
22 6B). We assumed that the time individuals spend in prospecting is directly correlated
23 with the distance moved. Therefore, if an individual has very low perceptual range it has
24 to move around to find sites which results in a species having a more uniform
25 distribution. These results are in line with Vuilleumier and Perrin [24], and are likely
26 explained by the fact that individuals with no/small perceptual range are unable to find
27 available patches easily. Therefore, they have to search more extensively, even though
28 this yields a high mortality, which results in more optimal population performance.
29 Indeed, another study has demonstrated that, under certain conditions, individuals may
30 even decide to ignore information on the proximity of non-natal patches, thereby
31 moving further than strictly necessary [30]. This has a positive effect on connectivity
32 but reduces individual lifetime reproduction success, and thus these studies highlight an

1 important potential discrepancy between different organizational levels of selection
2 (reviewed in [20]).

3 This discrepancy between the individual and the population good is also evident when
4 both information acquisition and use are very costly (Fig. 6C). Under these conditions,
5 we observed individuals to still evolve their perceptual range and dispersal distance
6 despite high immediate costs at the individual level (Fig. 6C). This pattern evolved here
7 under conditions where the population is at the brink of extinction because considering
8 the same costs but increasing patch extinction rate (from 15% to 20%) lead to
9 population extinction (results not shown). A number of factors are known to influence
10 how much an individual invests in dispersal [2], one being the probability of success in
11 a dispersal attempt. A high chance of success tends to favour the evolution of dispersal
12 rate, insofar as dispersal can be achieved without much cost. However, the finding of
13 selection for information acquisition and use when dispersal is increasingly risky is
14 another expected evolutionary outcome, which is explained as a response to severely
15 lowered patch occupancy due to decreased dispersal success. Under these conditions
16 (i.e. a small nonzero probability of success in a dispersal attempt), dispersal survival is
17 difficult, but this is balanced by the few successful dispersers having a high probability
18 to find excellent habitat (i.e. ‘unsaturated’) which offers good breeding prospects. Even
19 though the dispersal strategy emerged under the new, less favourable conditions might
20 not be the one maximising the long-term persistence of the population [26], such
21 evolutionary response will still enhance its persistence.

22 **4. CONCLUSIONS**

23 An increased understanding of the co-evolutionary dynamics between prospecting and
24 dispersal is of crucial importance in linking individual behaviour to population
25 dynamics and distribution. Some early theoretical studies have already investigated the
26 consequences of cognitive abilities on several important properties of populations. Thus
27 far, these studies were based on the rather general assumption of an information-free
28 world or have simply incorporated perceptual range as a distance from which habitat
29 patches can be recognized. Empirically, studies addressing the possible trade-off
30 between costs and benefits of developing different perceptual ranges are still lacking.
31 Yet, if information is available, of a certain quality and predictable over space and time,
32 the individual-level decisions to acquire and use information are traits under selection

1 that may have important consequences for the persistence and dynamics of ecological
2 systems [7]. Our contribution goes beyond previous work by (1) jointly considering
3 information acquisition and use as evolving traits that vary across space and time as a
4 response to the balance between costs and benefits at the individual level; and (2)
5 evaluating the population-level success of the evolved informed dispersal rules. We
6 have shown that, under certain conditions, the information acquisition and use that
7 evolves (due to the balance between risks and benefits of information acquisition and
8 use at the individual level) may not be those that maximise the population abundance or
9 patch occupancy. There is a need to increase our fundamental understanding of how
10 information use evolves in the context of dispersal behaviours at each of three stages of
11 dispersal [8]. Here we fixed the emigration probability and an obvious extension is to
12 integrate ideas presented here with those exploring information and emigration
13 decisions [19]. Ultimately, gaining a more sophisticated understanding and capability
14 for modelling informed dispersal promises to improve our ability to predict and manage
15 how species will respond to multiple environmental changes.

16 **ACKNOWLEDGEMENTS**

17 This study was funded by a research project of the Spanish Ministry of Science and
18 Innovation (CGL2008-02871/BOS; with FEDER co-financing), and the Junta of
19 Andalucía (Excellence Project, RNM-5090) and FWO project G.0610.11 (D.B.). M.D
20 received a postdoctoral fellowship from the Spanish Ministry of Science and Innovation
21 and a postdoctoral grant from the Academy of Finland (no. 140367). KB and JMJT
22 were supported by the project TenLamas funded through the EU FP6
23 BiodivERsA Eranet, DB by the FWO network on eco-evolutionary dynamics
24 (EVENET)

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1 FIGURE LEGENDS

2 Fig. 1. Schematic representation of dispersal in the model. (Upper) Individual is
3 characterized by its preferred dispersal distance (r being a most preferred distance, and
4 the preference decreases asymptotically with distance from r , the ring-shaped region
5 within the distances set by $r \pm 2\sigma$ from natal patch represents roughly the 95%
6 ‘preference interval’ (i.e. the area with 95% probability of dispersing assuming equal
7 quality of homogeneously distributed patches within it, in which case it is equivalent to
8 *dispersal kernel*), and perceptual range (a). (Lower) Individual emigrates from the natal
9 patch and explores the potential dispersal area. Length of the exploration path depends
10 on the size of the perceptual range (a , here a is two times smaller than the range of
11 favoured distances, so the individual must traverse the perimeter at least twice to cover
12 the whole area). Eventually the individual selects a patch and moves there in order to
13 settle.

14

15 **Fig. 2.** Prospecting behaviour as implemented in the model. Individual preferred
16 dispersal distance follows a Gaussian distribution with mean r and standard deviation σ
17 (represented by the intensity of black colours; left hand side of the upper plots) from the
18 natal patch (marked as star) and patch quality $K - N$ (represented by colour intensities;
19 middle figure of the upper plots) are combined yielding patch selection probabilities
20 (right hand side of the upper plots). The searching area constitutes the 95% of the area
21 under the preference curve, delineated in the figures with dashed circles. The searching
22 area and the distribution of preferred dispersal distances vary as a function of the mean r
23 and standard deviation σ (lower three panels). When $r - 2\sigma > a$ (a being the perceptual
24 range), the individual moves away from the natal patch before starting to prospect,
25 otherwise the searching area is within a circle. Even though the searching area may be
26 of the same size for different values of r and σ , the distribution of the preferred dispersal
27 distance may be different, as depicted by a two-dimensional cross-section showing the
28 distribution of the preference for dispersal distance at the bottom of the plots. The right
29 hand side panel of the figure shows the relationship between the perceptual range (a),
30 path length (l), and the survival related to it (p_{surv}). Individuals with low perceptual
31 range need to make more spiral turns in order to cover the same searching area (shaded).

1 Therefore, there is a trade-off between developing a large perceptual range (at a cost of
2 fecundity) and longer prospecting path (at the cost of mortality).

3

4 Fig. 3. Characteristics of prospecting and dispersal evolved along the movement
5 mortality gradient, under three different costs of perceptual range. The phenotype (i.e.
6 actual length of prospecting trajectory and realized dispersal distance) results from the
7 genetic parameters: preferred mean distance, its variance, and perceptual range.

8

9 Fig. 4. Trade-offs applied in the model: (A) between the exploration range of
10 surrounding patches and fecundity (φ is the cost of perceptual range paid in fecundity,
11 $\lambda = 1$), (B) between dispersal distance and survival (μ is movement mortality).

12

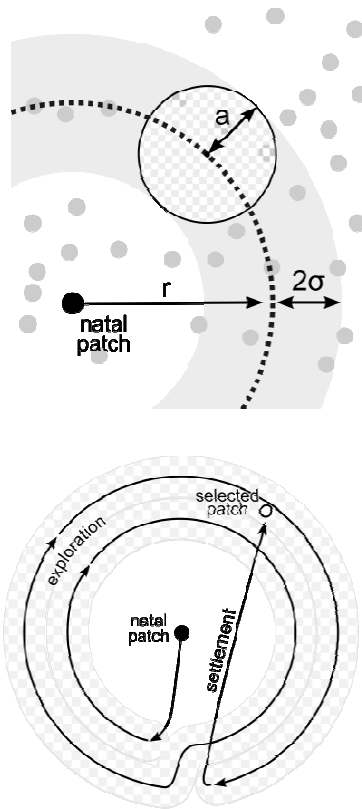
13 Fig. 5. Evolved emigration probabilities as a function of movement mortality and under
14 three different costs of perceptual range.

15

16 Fig. 6. Colours represent population size and proportion of patch occupancy (from dark
17 grey – low, to white – high) as a result of simulations where individuals were forced to
18 acquire (i.e. perceptual range; y-axis) and disperse a certain distance (i.e. preferred
19 dispersal distance; x-axis). Costs in fecundity (φ) and in mortality (μ) were fixed at (A)
20 $\varphi: 0.001, \mu: 0.001$; (B) $\varphi: 0.01, \mu: 0.001$; and (C) $\varphi: 0.01; \mu: 0.01$. We assumed patch
21 extinction rate (e) of 15%. Black dots indicate the informed dispersal strategy favoured
22 by natural selection. Hatching denote parts of parameter space where population went
23 extinct before 5000 generation.

24

1 FIGURES



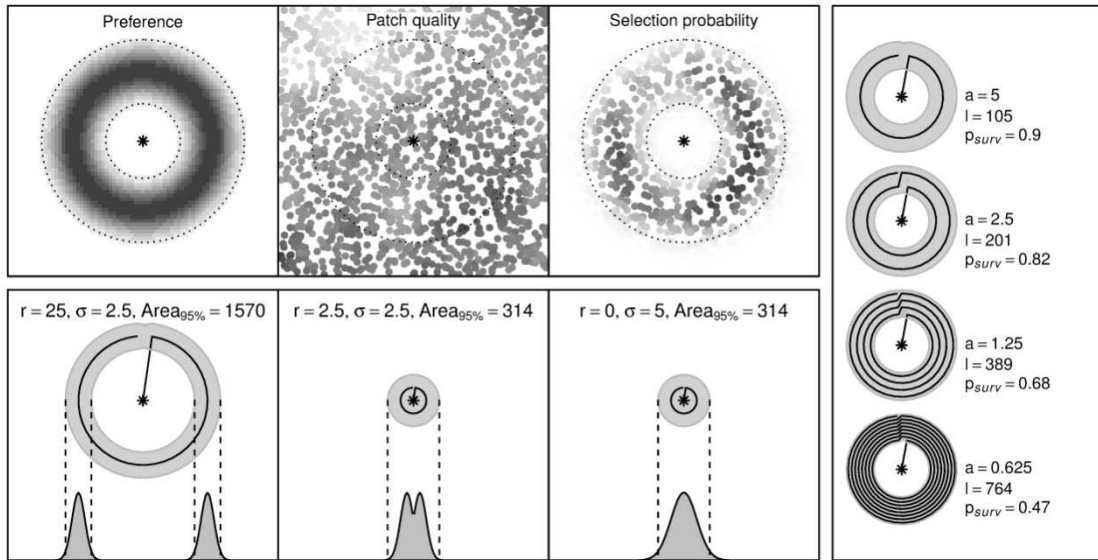
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Fig.1

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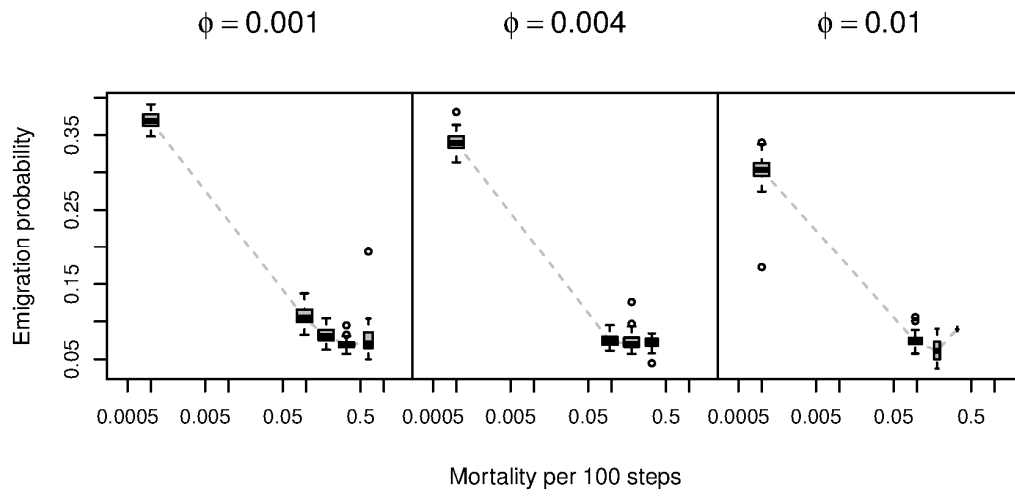


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Fig.2

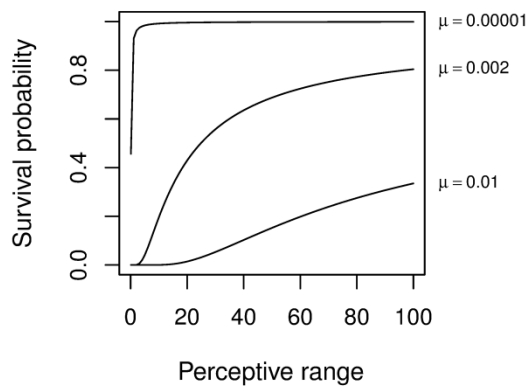
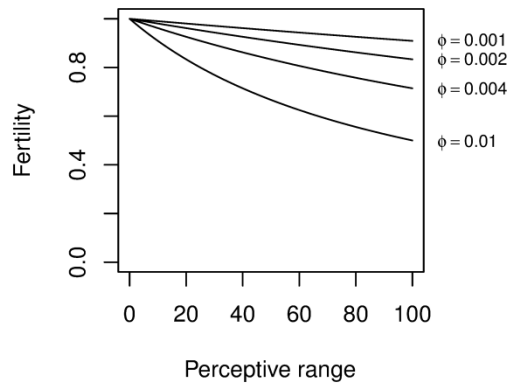
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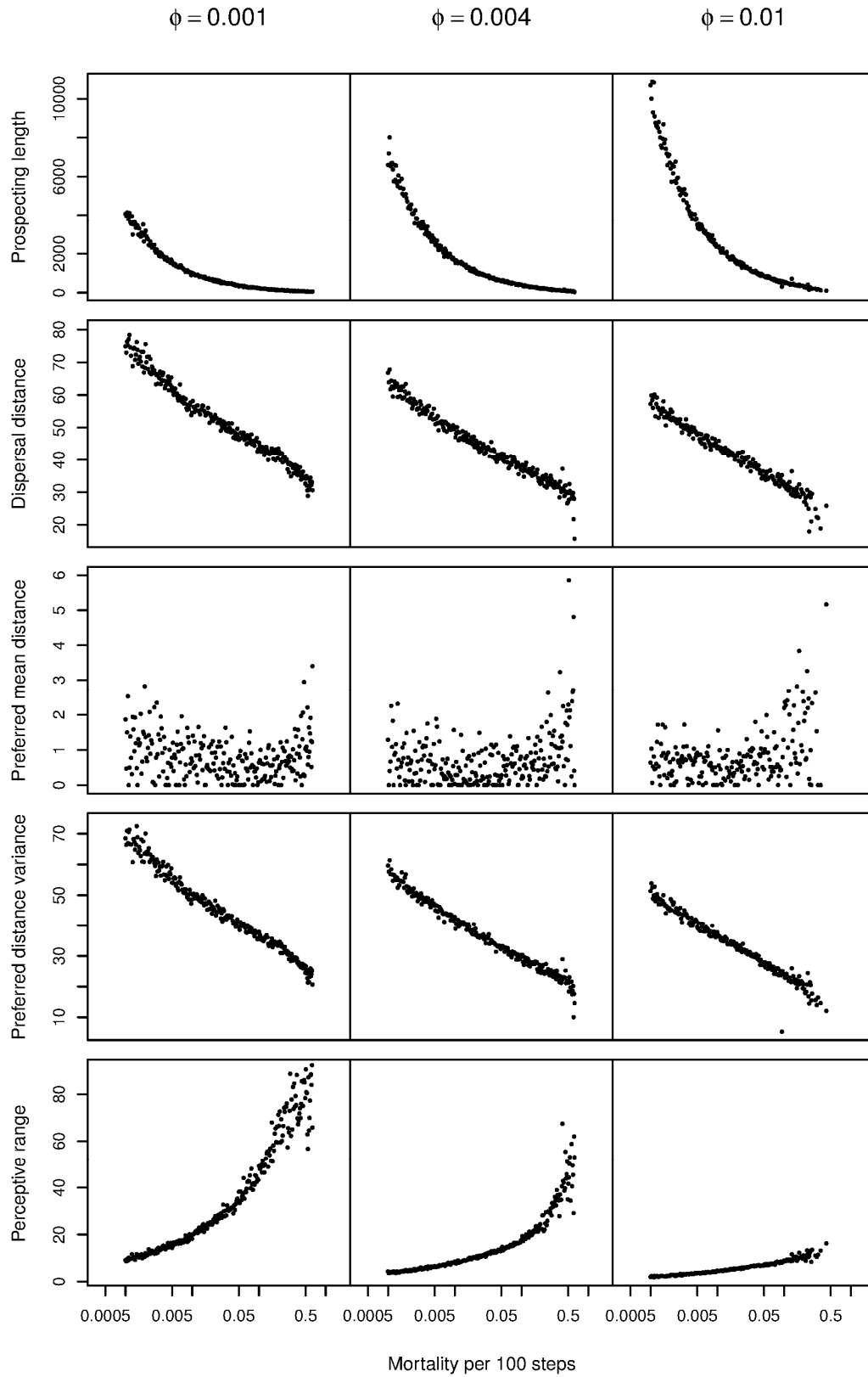
Fig.3



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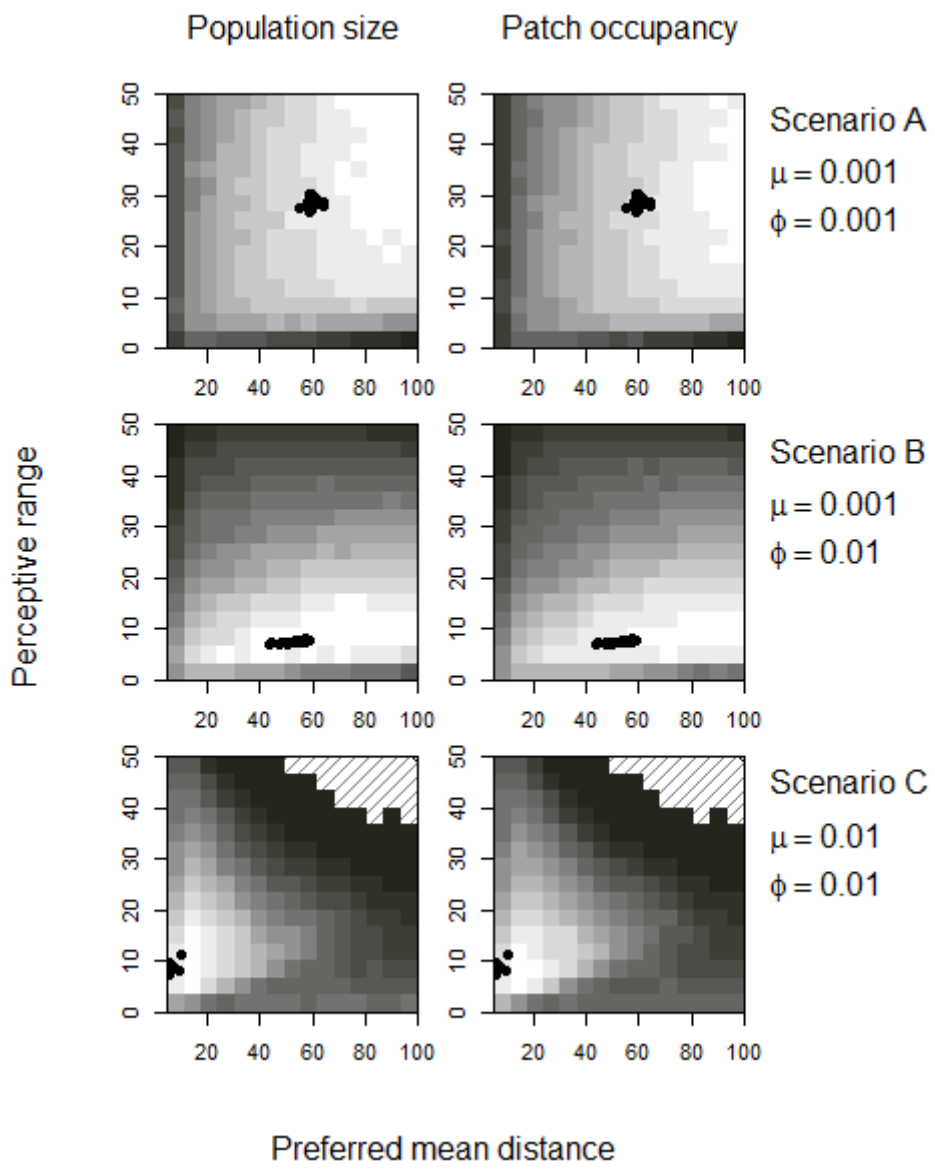
Fig.4



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Fig.5



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Fig.6