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

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

1. Introduction

Theory on the evolution of dispersal has almost entirely been constructed on the assumption that individuals have no knowledge of the possible destination patches to which they might recruit if they emigrate [1–4]. In reality, many organisms do not make such blind dispersal decisions; instead, they may often invest considerable time and/or energy in prospecting potential breeding habitats before deciding on where to settle [5,6]. While there has recently been a surge of interest in the importance of information acquisition and use within ecology [7], these ideas have yet to be properly integrated into our understanding of dispersal evolution. Importantly, recent developments incorporating greater realism by modelling dispersal as a three-stage process (of departure, transient and settlement [8]) are readily extendable to explore the evolution of prospecting behaviour in the context of dispersal. Here, we take some initial steps to building up a theory on the joint evolution of habitat prospecting and dispersal, and evaluate its consequences for the persistence of populations.
The field of dispersal evolution has provided clear examples where predictions from theory have subsequently been tested by empiricists (kin competition driving emigration rates being an excellent example; reviewed in [9]) and, vice versa, where field observations have resulted in new modelling directions being taken (e.g. density-dependent emigration; [10]). We suggest here that one area in which the development of theory lags well behind empirical studies is the joint evolution of prospecting and dispersal strategies.

Accumulation of empirical evidence demonstrates that organisms condition their dispersal strategy on informative cues from the environment at the different stages of the dispersal process, from departure to settlement (see [9,11,12], for extensive reviews). As such, it has become clear that models need to integrate this information use in order to predict spatial dynamics in a realistic manner [8]. Several factors might influence an organism’s tendency to leave or to settle on a given patch. For example, density-dependent dispersal models have found that emigrating individuals may be sensitive to habitat quality [13], to patch size [14] or to the presence of conspecifics [4,15] in their local patches. Ruxton & Rohani [13] were the first to introduce the concepts of fitness-dependent dispersal to highlight that other environmental factors (e.g. carrying capacity) at sites that an individual visits during transience are expected to influence individuals’ decisions about whether to settle. In their model, individuals moved between patches until they found a patch of suitable quality, thereby generating variation in dispersal distance strategies and the subsequent dispersal kernel. In common with almost all models to date on context-dependent dispersal, these aforementioned models assume that individuals make their decisions based on perfect knowledge of the local conditions. Thus, there exists a clear dichotomy between the many models that assume context-independent (i.e. blind or no information) processes and those that have incorporated context-dependent dispersal assuming perfect information on, for example, local density.

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

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

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

2. Material and methods

To study the evolution of informed dispersal strategies and examine their population consequences, we modelled the population and evolutionary dynamics of annual organisms dispersing in a two-dimensional, continuous patchy landscape. The choice of the breeding site is done according to information about patch quality and individual genetically determined preferences. We consider specifically prospecting by individuals for a potential breeding site. Depending upon the strategy adopted, we assumed that some individuals prospect for breeding sites as soon as they depart from a natal patch. Then the subsequent decision on where to settle was sufficient in terms of providing dispersal distance. In other cases, selection pressures may act to favour greater dispersal distances. In this case, the process of prospecting and settling was supplemented by an additional, potentially less-informed, displacement from the natal patch.

(a) Model structure

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

The landscape consists of 1000 circular habitat patches of unit radius, randomly distributed over a square area of size $2000 \times 2000$ units (so average nearest-neighbour distance to patch is about 11.3 units). The patch quality varies spatially owing to the variation in the carrying capacity, and temporally, owing to changes in the local population size. The patches’ carrying capacities, $K_i$, were normally distributed around the mean of 50, with standard deviation of 10 (or zero if negative numbers occurred).

(b) Information acquisition

The ability of individuals to acquire information is determined in our model by:

1. their perceptual range, $a$, restricting the individual's ability to acquire information about the locations of potential patches and
2. their preferred dispersal kernel, which is determined by the preferred dispersal distance and the variance around it. This kernel sets the total spatial extent over which an individual acquires information (figure 1). We modelled the preference of an individual for a patch as a Gaussian function, as it allows for the easy manipulation of the preference area through the mean distance and its extent

$$p_{ij} = \frac{1}{\sigma \sqrt{2\pi}} e^{\frac{(d_{ij} - \tau)^2}{2\sigma^2}},$$

where $d_{ij}$ is the distance to the patch $i$ from individual $j$, $\tau$ is the individual’s most preferred distance and $\sigma$ is the deviation of the preference. Therefore, the individual preference kernel is defined by two parameters $\tau$ and $\sigma$ (figure 2).

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

$$L_j = \frac{A(\rho_u) - A(\rho_l)}{A(\tau)} \times \frac{2\tau}{A(\tau)} + 2\rho_l = \frac{2}{A(\tau)} - \rho_l^2 \quad \text{or} \quad \rho_l = 0$$

where the proportion of the prospecting area (delimited by the two radii $\rho_l$ and $\rho_u$) to the area that can be perceived from a single location (of radius of perceptual range $\tau$) is multiplied by the distance made between two sampling locations ($2\alpha$), and twice the inner radius is added to account for the way from the natal patch and to the selected target patch (figure 1). The lower bound is $\rho_l = \tau - 2\alpha$, when $\tau > 2\alpha$ or $\rho_u = 0$ when $\tau < 2\alpha$, and upper bound is $\rho_u = \tau + 2\alpha$ from the natal patch.

(c) Information use

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

After the prospecting has been completed, the individual moves to the target patch. The choice of the settlement/target patch was based on the perceived patch quality, $q$, within the
preferred dispersal range, and an individual’s preference, \( p \), towards a certain dispersal distance (see equation (2.1)). The quality \( q \) of a patch was assessed as its ‘underpopulation’ (i.e. the remaining capacity), and calculated as the difference between the patch’s carrying capacity \( K_i \) and its current population size \((N_i)\). Weights \( p_i, K_i \) were used as selection probabilities for the target patch. If no patches were present within the individual’s preferred dispersal range, we assumed that the individual died. Once the target patch was selected, the individual settles on it. When all individuals settle (or die in the process of dispersal), a reproduction phase takes place.

### (d) Reproduction (population model)

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

\[
N_i \sim \text{Poisson} \left( \frac{\lambda \alpha \varphi}{\alpha(1+\varphi)} \right),
\]

where \( \lambda \) is the mean, population-wide, number of offspring when no costs incurred, \( \alpha \) is the perceptual range and \( \varphi \) is the cost of (developing) perceptual ability, paid in decreased fecundity (figure 4a). Adults die immediately after reproduction, and then juveniles compete. If the number of juveniles \( J_i \) in a patch \( i \) exceeds the carrying capacity \( K_i \), juveniles suffer mortality with probability \( K_i/J_i - 1 \).

### (e) Simulations

(i) Prospecting and dispersal: their eco-evolutionary dynamics

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

(ii) Prospecting and dispersal: their implications for population patterns

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

For the first set, we fixed all the individual traits (i.e. assuming no evolution), and ran a simulation for 250 generations for each combination of perceptual range \( (15 \text{ values ranging from } 0 \text{ to } 50) \) and preferred dispersal distance \( (15 \text{ values ranging from } 5 \text{ to } 100) \), performing 15 replicates for each. We did not vary preferred distance range, the value \( \varphi = 5 \) was common to all simulations. At the end of each simulation, we recorded.
population performance, measured as both patch occupancy and population size.

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

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

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

There is now a consensus that information affects the evolution of dispersal strategies [17–19,30]. These previous studies used different assumptions about the type of information (including spatial extent and precision) that an individual makes use of, and then analysed how different situations might influence the evolution of informed dispersal strategies. However, individuals need to first update their perception of the biotic and abiotic environments (i.e. information acquisition; [31,32]) either from their own experience [33] or from observing the gains obtained by conspecifics [34–36]. Only then, should they be able to compare different alternatives and thus benefit to increasing their likelihood of choosing the best-matching dispersal strategy (i.e. information use). Doing so might entail costs, however, because individuals must redirect valuable resources, including energy and time to information gathering at the expense of other basic biological demands [32]. Here, we clearly demonstrate the emergence of coevolutionary dynamics between prospecting and dispersal movement strategies, which differed in sign and magnitude depending on their respective costs (figure 5). The results were qualitatively robust to the emigration probability, i.e. similar patterns for the evolution of informed dispersal strategies evolved when considering different emigration rates (50 and 80%), as well as when we allowed this trait to evolve (results not shown).

On the one hand, selection always aims to maximize the individual’s chances of reproduction, which in our model is primarily determined by survival during prospecting. The duration of prospecting movement (as implemented in our model) can be much longer for those individuals that need to make some spiral turns in order to cover the whole prospecting area (i.e. when preferred mean dispersal distance is long; figure 2) compared with those individuals which just follow a straight line from the natal to the selected patch (i.e. when they are able to perceive most of the potential dispersal area; figure 2). Thus, it was at this stage where most opportunity for evolutionary cost-cutting occurred. On the other hand, selection tends to favour a large dispersal distance (i.e. large margin for freely choosing the best-quality patch). This was generally achieved by expanding the

![Figure 3. Evolved emigration probabilities as a function of movement mortality and under three different costs of perceptual range, $\varphi$.](image-url)

![Figure 4. Trade-offs applied in the model: (a) between the exploration range of surrounding patches and fecundity ($\varphi$ is the cost of the perceptual range paid in fecundity, here $\lambda = 1$), (b) between dispersal distance and survival ($\mu$ is movement mortality).](image-url)
preferred distance variance ($\sigma$), and therefore there was a strong correlation between $\sigma$ and the realized dispersal distance (figure 5). Quite obviously, prospecting length decreased with increasing mortality risk during movements, but we also observed that it increased with the increasing cost of perceptual range (figure 5). Yet, the cost of perceptual range has a moderately lower effect on dispersal distance compared with the mortality cost.

Depending on the relative costs of movements and perceptual range, selection minimized each of these traits, compensating the deficiency of one trait by the other. For instance, as moving became increasingly risky, the preferred distance variance decreased, but simultaneously a large perceptual range evolved. This allowed the duration of prospecting to be minimized while still permitting individuals to move a reasonably large dispersal distance (figure 5). That is, large perceptual ranges evolved only when the cost of its development was low and when the movement during dispersal was relatively costly (figure 5). This finding is in line with the few empirical studies because the perceptual range has been linked to many aspects of dispersal, including the choice of search strategy and the movement behaviour during dispersal, which is directly related to an individual’s effectiveness at finding new habitat patches [37]. A well-developed perception of habitat patches by individuals should lead to more efficient, oriented movements.

Figure 5. Characteristics of prospecting and dispersal evolved along the movement mortality gradient, under three different costs of perceptual range. The phenotype (i.e. actual length of prospecting trajectory and realized dispersal distance) results from the genetic parameters: preferred mean distance, its variance and perceptual range.
that can reduce the time and energy spent in risky environment during dispersal [38] and influence the ability to respond to habitat disturbance and fragmentation [39]. As informed individuals are able to make firmer decisions as a function of the current state of the biotic and abiotic environment, they are expected to enhance their fitness [21,32]. However, as collecting information usually entails costs, including committing time, energy or the use of bodily resources at the expense of other biological demands, such as growth or reproduction [22], selection should only favour the acquisition of information when its value exceeds the costs of its use [33].

When the cost of information acquisition are high, and consequently a limited perceptive range evolves (figure 5) individuals can be selected to move to a long distance and prospect a narrow area at that distance, making just one prospecting round (as depicted in the lower left panel of figure 2). Such a strategy minimizes information acquisition and mortality costs, still allowing individuals to maintain sufficient environmental sampling for good-quality patches. Therefore, dispersers possessing a low perceptual range are still likely to detect particularly good patches (either empty or well below carrying capacity). In some cases, overreliance on cues can be costly if it attracts individuals into sink habitats where they have little chance of breeding successfully (ecological traps; [40]). For example, in species where dispersal is at least partly based on copying conspecifics, informational cascades can occur if the copied behaviour is occasionally wrong [22]. Under certain conditions (e.g. high-density habitats leading to poor individual success; [41]), it might therefore be beneficial to evolve a long-distance dispersal strategy as opposed to simply increasing one’s perceptual range. The observed selection for long dispersal distances when the individual perceptual range is low has important consequences for population viability, given that for a population divided into patches, and where each patch has a finite lifetime because of random events, such as local extinctions, long dispersal distance events are crucial for its persistence [40,41]. In addition, short-range prospecting evolving by a high mortality costs will increase local competition because all individuals will choose to settle in a patch within a small area around their natal patch. Increasing dispersal distance should result in a lower saturation rate of the environment and an overall increased reproduction success. This competition effect would possibly have been different if we had considered directional dispersal, i.e. the individual chooses an initial direction and prospect the area located in that direction. Such preselection of the search area would reduce the cost of movement, allowing the evolution of large dispersal distances, also diversifying the choice of settlement site among individuals. Moreover, depending on the spatio-temporal variability of the landscape, we expect the strength of selection for the spatial extent in which individuals choose a breeding site to vary.

(b) Prospecting and dispersal: their implications for population patterns

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

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

4. Conclusion

An increased understanding of the coevolutionary dynamics between prospecting and dispersal is of crucial importance
in linking individual behaviour to population dynamics and distribution. Some early theoretical studies have already investigated the consequences of cognitive abilities on several important properties of populations. Thus far, these studies were based on the rather general assumption of an information-free world or have simply incorporated perceptual range as a distance from which habitat patches can be recognized. Empirically, studies addressing the possible trade-off between costs and benefits of developing different perceptual ranges are still lacking. Yet, if information is available, of a certain quality and predictable over space and time, the individual-level decisions to acquire and use information are traits under selection that may have important consequences for the persistence and dynamics of ecological systems [7]. Our contribution goes beyond previous work by (i) jointly considering information acquisition and use as evolving traits that vary across space and time in response to the balance between costs and benefits at the individual level and (ii) evaluating the population-level success of the evolved informed dispersal rules. We have shown that, under certain conditions, the information acquisition and use that evolves (owing to the balance between risks and benefits of information acquisition and use at the individual level) may not be those that maximize the population abundance or patch occupancy. There is a need to increase our fundamental understanding of how information use evolves in the context of dispersal behaviours at each of three stages of dispersal [8]. Here, we fixed the emigration probability and an obvious extension is to integrate ideas presented here with those exploring information and emigration decisions [19]. Ultimately, gaining a more sophisticated understanding and capability for modelling informed dispersal promises to improve our ability to predict and manage how species will respond to multiple environmental changes.

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**Figure 6.** Colours represent population size and proportion of patch occupancy (from dark grey, low, to white, high) as a result of simulations where individuals were forced to acquire (i.e. perceptual range; y-axis) and disperse a certain distance (i.e. preferred dispersal distance; x-axis). Costs in fecundity ($\varphi$) and in mortality ($\mu$) were fixed at (a) $\varphi$: 0.001, $\mu$: 0.001; (b) $\varphi$: 0.01, $\mu$: 0.001 and (c) $\varphi$: 0.01; $\mu$: 0.01. We assumed the patch extinction rate ($e$) of 15%. Black dots indicate the informed dispersal strategy favoured by natural selection. Hatching denotes the area of parameter space where the population went extinct before 5000 generations.