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Roger William Shaw
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**The Dissertation Committee for Roger William Shaw Certifies that this is
the approved version of the following dissertation:**

**Sex and Social Hierarchies Affect Populations Across
Landscapes**

Committee:

Mathew Leibold, Supervisor

Daniel Bolnick

Shalene Jha

Timothy Keitt

Volker Rudolf

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Landscapes**

by

Roger William Shaw, B.A.

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Sex and Social Hierarchies Affect Populations Across Landscapes

Roger William Shaw, Ph.D.

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Supervisor: Mathew Leibold

Ecologists have long been interested in the factors that drive the species composition of ecological communities. I propose that variation within species, particularly in dispersal behavior, plays an underappreciated role, as it affects population distributions across landscapes. To study this in the field, I censused dragonflies in a north Texas metacommunity, differentiating between adult males, adult females, and larvae. I found that while adult males were not well-explained by any environmental or spatial variables, adult females and larvae were significantly explained by their environment. Therefore, considering variation within species (in this case, sex and life stage) can clarify our understanding of species distributions. This is one example of sex-biased dispersal, which is universal amongst animals. However, research has mostly been focused on its potential benefits, while its costs remain largely unexplored. I developed an individual-based simulation model, to see how populations with varying degrees of sex-biased dispersal were able to persist in the face of frequent disturbances. I found that increasing sex-biased dispersal made it difficult for individuals to find mating partners in suitable habitat, and so these populations did not persist very long, in comparison to populations with equal

dispersal. These heavy costs may be alleviated by habitat selection or alternative mating systems, however these costs should remain in the discussion of understanding sex-biased dispersal. Even within males, there may be significant variation in social status and physical condition, which can then affect dispersal strategies; these differences could then produce unique signatures in the distributions of populations. I developed another individual-based simulation model, in which individuals were sensitive to crowds, to environment, to both, or to neither. In comparison to passive dispersal, I found that crowd-sensitive populations were disproportionately abundant in medium-quality patches. In contrast, environment-sensitive populations were scarce in these patches. This approach requires fine-scale environmental data, but may be easier to acquire than the fine-scale demographic data that would otherwise be required. Overall, considering variation between individuals, particularly in their dispersal behavior, can improve our understanding of species distributions.

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Within-species variation better explains community composition in dragonflies (Insecta: Odonata) of a north Texas landscape

The composition of ecological communities is shaped by many factors, both biotic and abiotic. However, intraspecific variation has not been well-incorporated into this thinking. One simple form of variation within species is sex differences, and an abundant example is sex-biased dispersal, in which the sexes differ in their dispersal behavior. When the composition of particular animal communities are difficult to explain, it may be useful to separately examine the distributions of males and females as a consequence of sex-biased dispersal. I surveyed adult male, adult female, and larval communities of dragonflies (Insecta: Odonata) at 45 ponds in the Lyndon B. Johnson National Grasslands in north Texas, which included a wide array of pond characteristics across a landscape. I used variation decomposition analysis to examine whether variation in community composition between ponds could be explained by environmental variables, spatial distance, or environmental-spatial interactions. I found that adult males could not be well-explained by the measured variables. In contrast, adult females were fairly well-explained by environmental factors, while larvae were explained by both environmental and spatial factors. Previous studies of adult dragonfly communities had either focused solely on males, or pooled males and females together. By analyzing the sexes separately, clearer patterns emerged, illustrating the usefulness of considering intraspecific variation such as sex-biased dispersal in community ecology.

INTRODUCTION

Many forces interact to determine the composition of an ecological community. Exactly which forces, and the importance of each, has remained a foundational question in ecological science throughout its history. It has indirectly led to and presided over many historically important debates, including the role of top-down vs. bottom-up forces [1-4], the importance of selection and competition vs. neutral randomness [5-8], and whether productivity encourages or discourages species turnover [9-14]. Yet despite (or because of?) these debates, we still don't have a clear understanding of how communities are specifically influenced by different forces.

Recent statistical methods have underlined exactly how little we still understand. A meta-analysis by Cottenie [15], using variation partitioning to examine how much environmental and spatial variables influence community composition, found that even in the best cases, we are only able to explain 48% of the variation in community composition. But often, our best natural history and sampling knowledge performs even much worse than that. Many theories have been put forward to explain this unexplained residual variation, hypothesizing that it is due to "random chance", assembly history, sampling errors, or unmeasured factors [7,16-19]. But one additional important angle has yet to be fully explored: variation between individuals, within species.

Recent work has emphasized that intraspecific variation is poorly incorporated into ecological thinking, despite the fact that it often produces large impacts on ecological patterns and processes [20-22]. For instance, intraspecific genetic variation in an alga was found to produce predator-prey cycles that differed considerably from those of populations with little or no variation [23]. Recent

conceptual reviews have described the potential importance of individual differences in dispersal [24,25]. Some empirical work suggests that individual dispersal differences may influence species range expansions [26-28]. However, many other ecological consequences of individual dispersal differences have not received concrete attention.

Sex-biased dispersal, where males and females differ in their dispersal behavior, may be one particularly common form of intraspecific dispersal variation. Empirical studies of sex-biased dispersal have historically focused on birds and mammals [29-31], though more recent work has examined other organisms such as fish and insects [32-35]. Theory has shown that sex-biased dispersal likely evolved as a mechanism of inbreeding avoidance [29,36,37]. However, the consequences of sex-biased dispersal on ecological processes remain poorly understood, though conceptual theory suggests that it could affect diverse processes such as population demography, range expansion dynamics, and metapopulation persistence in changing environments [25].

One natural system where sex-biased dispersal may be relatively easy to evaluate involves insects in the order Odonata, commonly known as dragonflies and damselflies. Adult odonates are terrestrial, and disperse widely, with individuals of some species capable of dispersing upwards of 100km in their lifetimes [38]. Meanwhile, larval odonates are aquatic, and incapable of dispersing between closed aquatic habitats. In other words, larval odonates cannot escape unsuitable habitat, and so their survival is dependent upon the dispersal decisions of their parents.

The survival of larval odonates is regulated by several factors, most notably the presence or absence of fish, their primary predators. The larvae of some odonate species are unable to coexist with fish because of high mortality, while other species

have developed adaptations for tolerating fish, such as camouflaging or tunneling [39-43]. Other factors, such as substrate type and vegetation structure, have also been shown to play a minor role in the suitability of habitat for the larvae of some species [38]. Thus, in general, the distribution and abundance of larval odonates appears to be heavily constrained by the presence or absence of fish, and to a lesser extent by other environmental factors.

Adults, on the other hand, do not seem to be constrained by environmental factors [44,45]. Variables such as shade, aboveground vegetation, and distance from the individual's natal pond have been hypothesized to play a minor role [38], however no clear patterns have emerged in previous studies [44,45].

Males of most odonate species are highly territorial, and conduct all of their foraging and mating within their territories. The losers of territorial competitions disperse to other bodies of water, with more dominant males remaining at their presumably-suitable natal ponds [46]. Contrastingly, females spend most of their time away from water, and come to water only to mate and lay eggs [38]. The dispersal decisions of satellite males and of females are not well studied [38].

We aimed to understand the forces that determine community composition in dragonflies, but with the potential added power of investigating each life stage and sex on their own, thereby incorporating intraspecific variation.

METHODS

This field survey was conducted at the Lyndon B. Johnson (LBJ) National Grasslands, in Wise County, Texas, USA. The LBJ Grasslands support hundreds of small ponds that cover a wide spectrum of environmental characteristics, with some

containing fish and others none, various amounts of shade, differing substrates and vegetation, and other variables. These ponds dry up during periods of extreme drought, and the frequency of these drought events have large effects on pond communities [47]. The landscape matrix surrounding the ponds is relatively free of significant barriers to dispersal, or potential funnels or other biases in dispersal direction.

The size of each pond, as well as its spatial location, was determined using Google Earth and ImageJ [48] software. Shade amount was determined using a canopy cover densiometer from Forestry Suppliers, Inc. Total phosphorus and nitrogen levels for these ponds had been previously established by past studies [49]. Fish presence or absence had also been established previously, and was also confirmed visually. Each year, the extent of shoreline vegetation and emergent macrophytic vegetation was graded on a 1–5 scale. Photographs were taken of each pond annually, and images were compared to ensure consistent grading.

A total of 43 ponds at the Grasslands were surveyed in the summers of 2010, 2011, and 2013. For adult male dragonflies, abundances were noted using ten minutes of stationery observation. The territorial behavior of most species made these counts relatively easy. The presence or absence of any adult females was also noted during this time. Egg-laying behavior by females was specially noted as a definite indicator of habitat selection. Larval samples were collected using a ‘D’-shaped aquatic dip net from Bioquip, Inc., which was dragged through the substrated three times for two meters in each pond. Specimens were preserved in 70% ethanol, and identified to the specific level in the lab using published keys [50,51] and a dissecting microscope.

I analyzed these data using a method of variation decomposition, in which a redundancy analysis ordination was used to explain variation in the species

composition of communities using environmental, spatial, or residual variables [52,53]. This analysis was performed on the data using the statistical software R, with the *vegan* package. To allow for comparison with other similarly-analyzed studies, the methodology of the meta-analysis by Cottenie [15] was followed. Abundances of adult males were Hellinger-transformed, and the size and nutrient values of each pond were log-transformed. Larvae, adult females, and adult males were each analyzed separately as if they were distinct communities. In addition, Generalized Linear Models summarized with Akaike's Information Criteria were used to develop models to explain each species' distribution. This species-level analysis was used to further support the community-level variance decomposition analysis.

RESULTS

Across 43 ponds, a total of 606 individual adult males were counted, of 25 different species. Of adult females, 81 presences were observed of 15 species, while of larvae, 76 presences were observed of 15 species.

Adult male dragonfly communities were constrained both by environment and by space (Table 1). However, compared to other natural systems, these adult male dragonfly communities are very poorly explained by the measured variables (Cottenie). At the species level, the presence or absence of fish significantly explained the distributions of the males of some species, but the majority were not well explained by any combination of environmental variables (data not shown).

Adult female communities are significantly explained by environmental characteristics, as are larval communities (Table 1), to a degree comparable with other natural systems that are heavily influenced by environmental characteristics. At

the species level, the distributions of females and larvae of most species were significantly affected by the presence or absence of fish in each pond, with other variables adding significant explanatory power for only a small handful of species (data not shown).

DISCUSSION

Adult male dragonflies had relatively unpredictable distributions, that did not cleanly match either environmental variables or spatial locations, particularly compared with other natural systems. This is in sharp contrast to adult female and larval dragonflies, which were consistently found only in precise environments for each species. These highly divergent patterns provide a much cleaner understanding of what drives the distributions of each species, compared to an approach that considers each individual without regards to sex, life stage, or other within-species differences.

This indicates that adult female dragonflies make highly adaptive dispersal decisions. The larvae of each species can only survive within an often-narrow band of environmental attributes, and after spending much of their lives wandering across the landscape, adult females disperse to ponds at which their larvae can successfully thrive. Whether adult females accomplish this adaptive dispersal behavior through an active search or through simple philopatry appears to remain an open question, as adult female dragonfly dispersal has not been well-studied. Mark-recapture studies of emerging adult females may be necessary to elucidate their exact dispersal behaviors, and whether that behavior allows them to adapt to the changing mosaic of the landscape.

Adult male dragonflies have highly unpredictable distributions, which seems to indicate that they are not sensitive to any environmental attributes, a seemingly wasteful and un-adaptive strategy. This strange non-pattern may be explained by male-male competition. In many species, adult males defend territories at each pond. The winners of these territorial battles are more likely to mate with females that visit the ponds through their territories [38]. The loser satellite males may be forced to disperse elsewhere, if they are unable to establish a territory [46].

Therefore, the unpredictability of adult male dragonfly distributions may be explained by the behavior of satellite males, who are forced to leave their natal ponds, and may simply settle for any pond at which male-male competitive pressure is lower. This results in strong dominant males establishing territories in ponds suitable for that species, and satellite males distributed randomly across the landscape. That behavior of satellite males may mask any true habitat preferences of each species, producing a weaker overall signal.

To confirm these findings, I plan to further investigate the relationships between adult males, adult females, and larvae in this dataset. Converting adult male abundances to a simpler presence/absence measure would allow for easier comparison with adult females and larvae, particularly analysis such as Permutational Multivariate Analysis of Variance (PERMANOVA) using the 'adonis' function in R, which can determine whether these groups significantly overlap in their response to spatial and environmental variables. In addition, it would be fruitful to focus further on abundant species that were particularly well-sampled across all groups, to better investigate the spatial distributions of each group, and whether spatial distance may play a larger role in their distributions. Finally, the distributions of larvae could be influenced by an interaction between local environment and the presence of

ovipositing females, and exploring this interaction could lead to a stronger understanding of their distributions.

Throughout this study then, a finer within-species understanding of the behavior of individuals produces a clearer understanding of the forces that drive the distributions of species. In many natural systems, the overall distributions may be difficult to explain. But here, a finer look at the adult females, larvae, adult dominant males, and adult satellite males produces a much clearer picture. Each of these small groups have simple behaviors that drive simple distributions, but they interact to produce messier and more complex communities.

For many ecologists then, it may be fruitful to consider a study of within-species differences. Though such work is more labor-intensive, such work can counter-intuitively simplify the often-tangled complexities of nature.

FIGURES AND TABLES

Table 1: Results of variation partitioning analysis on adult male, adult female, and larval dragonflies from 43 ponds at the Lyndon B. Johnson National Grasslands, Wise County, Texas, USA. Significance values were obtained by running an Analysis of Variance (ANOVA) test on the redundancy analyses, as recommended by Borcard et al. [53].

	<i>Environment</i>	<i>Space</i>	<i>Environment x Space</i>	<i>Residual</i>
<i>Adult males</i>	6.684	2.966	2.144	88.206
<i>Adult females</i>	12.244 *	2.458	0	86.271
<i>Larvae</i>	10.031 **	0	2.183	93.308

* $p < 0.1$

** $p < 0.05$

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How costly is sex-biased dispersal?

Sex-biased dispersal, in which males and females exhibit differing dispersal behavior, is extremely common in animals. It appears to be a byproduct of mating/social systems, and is also an efficient means of avoiding inbreeding depression and kin competition. But sex-biased dispersal also seems inherently inefficient; it results in unbalanced sex ratios across a landscape, which could result in some individuals never finding mating partners, among other effects. To understand the strength of these costs, I developed an agent-based model, in which males and females disperse across a heterogeneous and changing landscape. When individuals came in contact with a member of the opposite sex in a suitable patch, reproduction occurred. The length of each metapopulation's persistence was compared. Sex-biased dispersal heavily affected population persistence time; it strongly decreased the proportion of individuals that found mating partners in suitable patches, which strongly undermined population success. To explain why sex-biased dispersal remains so prevalent in nature, this model does not consider which specific individuals mate and disperse. In addition, non-random directed dispersal could ease these costs considerably. In any case, future discussions of sex-biased dispersal should include some attention to these costs for populations.

BACKGROUND

Sex-biased dispersal, in which males and females of a species exhibit differing dispersal behaviors, is extremely common in animals. It is particularly well-studied in birds and in mammals [1-4], but more recent work has discovered the pattern in diverse taxa such as fish, insects, and amphibians as well [5-8]. It seems as if nearly all

animal groups with significant behavior exhibit some degree of sex-biased dispersal; it is clearly a common pattern throughout the animal kingdom. Explanations for the prevalence of sex-biased dispersal have often depended on the specifics of each system, but general patterns have also been discussed and explored [1,2].

Often, it appears as a byproduct of certain social and mating systems. If there are significant behavioral differences between males and females, encoded as part of a social system, then sex-biased dispersal often appears to emerge as a consequence [1,2]. For instance, species in which males defend territories, and females move around the landscape assessing males and their territories, will often result in female-biased dispersal. In species where males defend a harem of females, then male-biased dispersal will often result [1]. Though these examples are likely mechanistically oversimplified [4], they do illustrate potential pathways. Broadly then, sex-biased dispersal becomes prevalent as a byproduct of a widespread process, in this case social and mating systems.

As a more direct and inherent advantage, evolutionary theory has shown that sex-biased dispersal is an efficient strategy for avoiding inbreeding depression, compared to equal dispersal between the sexes [9-15]. This is likely of particular importance when sub-populations are small and isolated, therefore increasing the likelihood of inbreeding. In addition, sex-biased dispersal may also be an effective strategy for avoiding competition between kin, for both resources and for mates [16,17]. In these scenarios, sex-biased dispersal becomes prevalent across nature due to its direct, effective benefits.

But from a population ecology perspective, sex-biased dispersal seems inherently inefficient, costly, and disadvantageous. The mismatches in movement behavior have been shown to produce unbalanced local sex ratios across a landscape

[18,19]. These imbalances would seemingly lead to some individuals not having mating opportunities; this would reduce the number of potential offspring in the population, and the long-term growth and stability of the population as a whole.

In addition, unbalanced sex ratios could cause one sex to become disproportionately affected by disturbances. If the more philopatric sex is clustered in space, the population may be more vulnerable to catastrophic disturbances to these source patches, as the philopatric sex becomes disproportionately scarce over the landscape. In addition, the more dispersive sex may be similarly disproportionately vulnerable to changes in the landscape matrix or connectivity between patches. While these types of disturbances always affect species, having them disproportionately affect one sex creates a sort of population bottleneck that would otherwise not exist. In one example, American Redstarts (*Setophaga ruticilla*) wintering in lowland forests of Jamaica segregate by sex into slightly different habitats, which differ in quality. This strongly and differentially affects the survivorship of each sex; this results in much higher male survivorship year-over-year, and unbalanced sex ratios on the breeding grounds [20]. While this kind of habitat segregation is not necessarily caused by sex-biased dispersal in this specific instance, other systems have found that sex-biased dispersal leads to unbalanced sex ratios across a landscape [18,19], similar to this case. Though sex-biased dispersal does have some advantages as discussed above, potential costs such as this raise the question of why it is so prevalent across nature, and these potential costs have been largely overlooked in the literature.

While these conceptual explanations for the potential costs of sex-biased dispersal are a start, it would be useful to quantitatively establish exactly how costly it may be for populations, in comparison to equal dispersal. Here, I have developed a

computer simulation to explore the costs of sex-biased dispersal on populations; the primary hypothesis being that sex-biased dispersal greatly hinders population success because too many individuals are unable to find mating partners.

METHODS

To measure the costliness of sex-biased dispersal, I developed an agent-based (individual-based) simulation model using the software NetLogo [21]. In these types of models, individuals are given simple sets of rules that govern their movement and behavior, and complex results emerge from these simple interactions. Compared to classic dynamic equations traditionally used in ecological theory, agent-based models are much more well-suited for studying variation between individuals [22,23]. One potential drawback of agent-based models are that the results are largely heuristic and qualitative, rather than giving precise quantitative results. They are also sensitive to small adjustments in the individuals' governing rules, though well-developed models that emphasize simplicity can limit this over-sensitivity.

In this model, male and female individuals are distributed across a heterogeneous landscape, consisting of patches in a wrapped 10x10 torus. Each patch possesses a randomly-determined environmental value; patches with a value within a specified window are deemed to be 'suitable' patches, while all other patches are deemed to be 'unsuitable' patches.

At each time step, all individuals disperse in a random direction, at a distance drawn from their respective sex's poisson-distributed dispersal kernel.

If individuals then encounter a member of the opposite sex in a suitable patch, they produce a clutch of new individuals, with the clutch size being density-dependent.

Individuals lose health through time, and are removed from the model if their health drops below zero. Therefore, in order for populations to grow or remain stable, a majority of individuals must find a partner in a suitable patch and reproduce during their short lifespans. Once dispersal, breeding, and health accounting have been completed, the next time step begins.

A random selection of patches in the landscape experience local disturbance events, which were simulated by adjusting each affected patch's environmental value to a degree drawn from a Normal distribution. This slowly produces a landscape that is increasingly extreme in its distribution of habitat suitabilities. Because of this, no population is able to persist forever, but the length of persistence does vary considerably, as the ability of individuals to find partners is affected by the dispersal kernels of each sex.

Simulations run until the entire metapopulation becomes extinct, and this persistence time is logged. The spread of each sex's dispersal kernel was varied, with 36 combinations of kernels, and 200 replicates for each kernel pair. The strength of dispersal bias was calculated as the difference between the spread-values of the two sex's dispersal kernels, with zero indicating equal dispersal, and higher values indicating increasing degrees of dispersal bias.

In addition to population persistence time, additional variables that were logged included the sex ratio in each patch, the proportion of suitable patches in the landscape that were successfully colonized, and the proportion of unmated individuals at each time-step (Table B1). All model parameters were chosen to most

closely approximate natural systems, with adjustments to ensure realistic population dynamics. The NetLogo code for this model is open-source and available for adaptation, via <https://github.com/aredoubles/SexBiasedDispersal>.

One-way ANOVAs were used to evaluate the effects of dispersal bias, and correlations were used to inspect relationships between population persistence time and other variables.

RESULTS

Dispersal bias significantly affected population persistence time, as increasing dispersal led to sharply decreased population success ($F = 1173.6$, $df = 5$, $p < 2.2 \times 10^{-16}$, one-way test, Fig. 1). Variances between bias strengths were not equal according to a Levene Test ($F = 33.822$, $df = 5$, $p < 2.2 \times 10^{-16}$), and so one-way ANOVA was used. A *post-hoc* Tukey-HSD Test shows that while populations with a slight dispersal bias were statistically equivalent to populations with equal dispersal, all other degrees of sex-bias led to significantly worse-performing populations (Table B2).

The degree of sex-biased dispersal also significantly affected global sex ratios, sex ratios in suitable and unsuitable patches, the degree of spatial segregation between patches, and the proportion of suitable patches that were successfully colonized (Table B3). All of these patterns were significantly correlated with population persistence time (Fig. B1).

The strongest candidate mechanism was the proportion of unmated individuals in the population, which sex-biased dispersal significantly affected ($F = 4119$, $df = 5$, $p < 2.2 \times 10^{-16}$, Fig. 2), with a *post-hoc* Tukey-HSD Test showing that while populations with a slight dispersal bias were statistically equivalent to

populations with equal dispersal, all other degrees of sex-bias produced significantly worse-performing populations (Table B4). The proportion of unmated individuals in the populations was significantly correlated with population persistence time ($R^2 = 0.57, p < 2.2 \times 10^{-16}$, Fig. 3).

Disturbance frequency and extent affected the persistence time of populations, but not the qualitative effects of sex-biased dispersal (data not shown).

DISCUSSION

Sex-biased dispersal clearly has significant costs, as populations with equal dispersal persisted for nearly a full order of magnitude longer on average than populations with strong dispersal biases (Fig. 1). Even when regarding extreme outliers of success, populations with strong dispersal biases could still only match the average population with equal dispersal.

It appears that sex-biased dispersal causes many individuals to never find mating opportunities, and that this produces the strong effects on population persistence time. These individuals were unable to find mates either because of unbalanced local sex ratios, and/or because they dispersed into unsuitable patches. That sex-biased dispersal led to unbalanced local sex ratios (Fig. B1) confirms the findings of empirical studies [18,19], and it seems intuitive that this would then affect reproductive opportunities for individuals. Though many other variables also linked sex-biased dispersal with population success, the proportion of unmated individuals in the population was the strongest measure by far.

Given that these costs exist, the question of why sex-biased dispersal is so universal becomes even more interesting. It must be true that in nature, these costs

are overcome regularly, in order for it to be so widespread. The hypotheses of inbreeding avoidance and kin competition avoidance have been previously discussed, and may counteract these costs to some degree. But the costs revealed by this model suggest several other hypotheses to explain the prevalence of sex-biased dispersal.

First, this model does not consider the identity or characteristics of which individuals go unmated, and which do mate. In natural systems, one would expect that mated individuals would be highly-fit, with strong and well-adapted traits, while unmated individuals would be poorly-fit, with weak and maladapted traits. This produces a quantity-quality trade-off in the offspring of the species. Sex-biased dispersal produces much fewer matings and offspring, but these few offspring would likely be highly fit for their environment. In contrast, equal dispersal between the sexes results in many more matings and offspring, but this would likely include many weak individuals. In addition, this model only considered a monogamous mating system. If polygamous or polygynous systems are considered, that may ease these costs of sex-biased dispersal, as more individuals would be able to mate, and these offspring would likely be highly fit. Therefore, considering the traits and fitness of the individuals in this population may considerably alleviate the costs of sex-biased dispersal.

In addition, the direction of dispersal in this model was wholly random, as individuals picked a random heading at every time step. This made it somewhat unlikely that individuals would find suitable patches, and find mating partners in those patches. In comparison, non-random and intelligently directed dispersal would do much to ease these issues. Individuals would be more likely to find suitable patches, and more likely to find mating partners. Therefore, directed dispersal would greatly reduce the proportion of unmated individuals in the population, and thus

greatly increase population persistence times. In general, directed dispersal is a greatly under-appreciated force in ecology, particularly in theoretical and conceptual work, and there are many other ecological processes that could be profoundly impacted by considering its effects [24-27].

These strong costs also raise the question of whether the parameters of this model are empirically realistic, particularly the strongest degrees of sex-biased dispersal. With these types of agent-based models, it is admittedly difficult to assess realism, as empirical data can not fit with the model's parameter values neatly. In particular, the exact nature of spatial and temporal scaling in agent-based models is difficult to match with empirical data, and since these scales are the basis of nearly every other model parameter, such empirical-simulation comparisons are difficult. I have done my best to choose parameter values that fit within the range of empirical systems that I am familiar with, but this process was admittedly subjective. A more rigorous model that fully incorporates empirical data would likely have to take the form of ordinary dynamic equations, rather than an agent-based model.

Future work on this model should successively address some of these complexities. Investigating how non-monogamous mating systems, habitat selection, and inbreeding costs affect these results would add more useful context for these results. Of particular interest would be investigating how sex-biased dispersal can drive population dynamics on range expansion fronts, as has been observed in at least one prominent example [28,29]. Sex-biased dispersal could even become demographically positive in certain instances, even outside of inbreeding costs, for instance when dynamics surrounding Batesman's Principle and reproductive variance are considered. Exploring these further complexities would add useful context for the pure costs that have been explored thus far.

Sex-biased dispersal has historically been of interest due to its prevalence throughout nature, and so research has been focused on its potential benefits. But this model shows that sex-biased dispersal also introduces significant costs to populations, which complicates the picture significantly. Though there may be easy paths to easing these costs, any future discussion of sex-biased dispersal would require attention to these costs and a consideration of how they are overcome in nature.

FIGURES AND TABLES

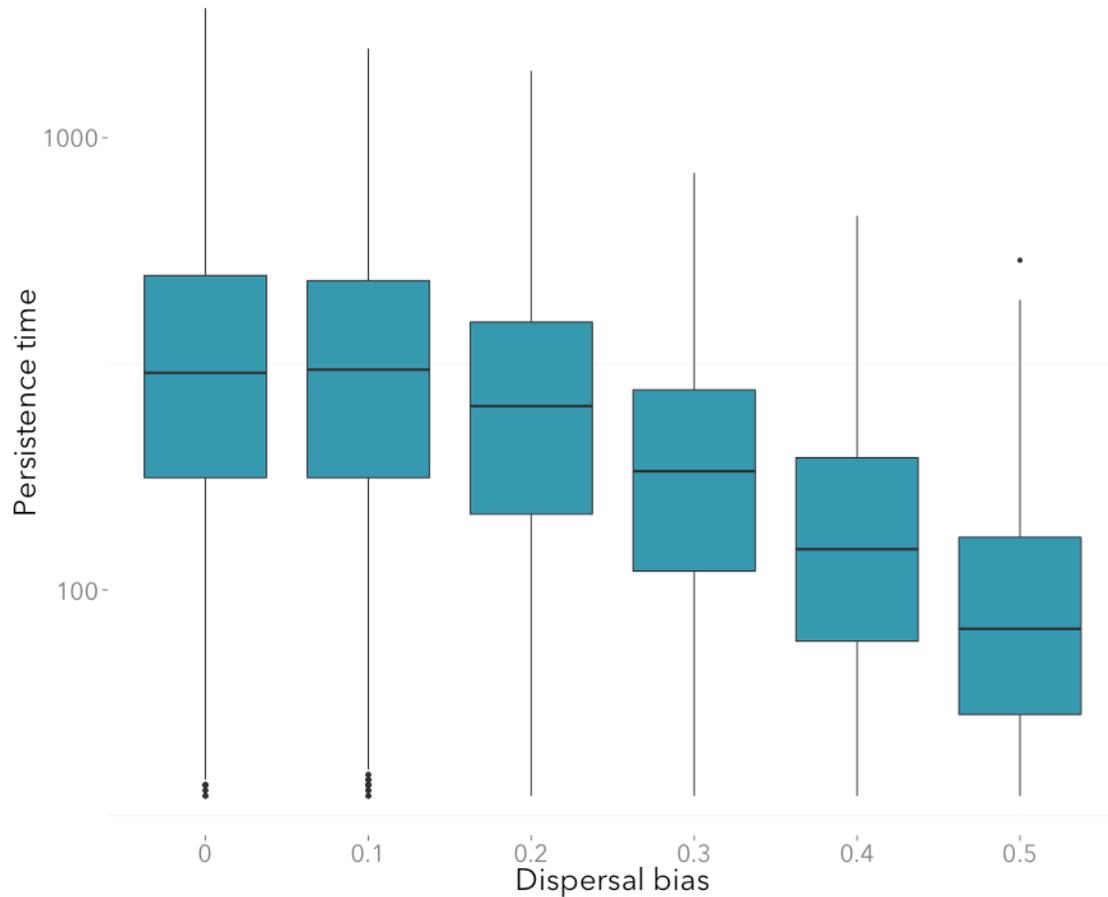


Fig. 1. Dispersal bias significantly affected population persistence time, as increasing dispersal biases led to sharply decreased population success ($F = 1173.6$, $df = 5$, $p < 2.2 \times 10^{-16}$, one-way test). Variances between bias strengths were not equal according to a Levene Test ($F = 33.822$, $df = 5$, $p < 2.2 \times 10^{-16}$), and so one-way ANOVA was used.

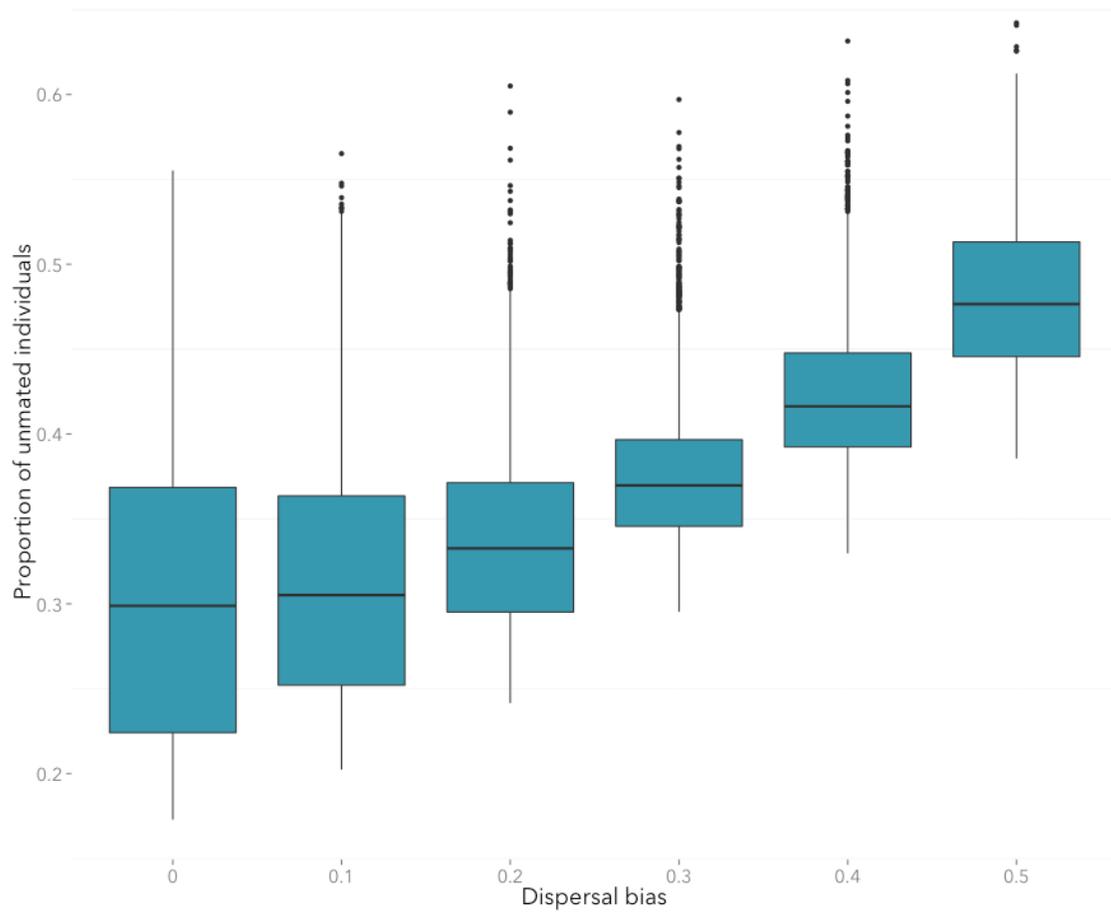


Fig. 2. The proportion of unmated individuals in the population was significantly affected by the strength of sex-biased dispersal ($F = 4119$, $df = 5$, $p < 2.2 \times 10^{-16}$)

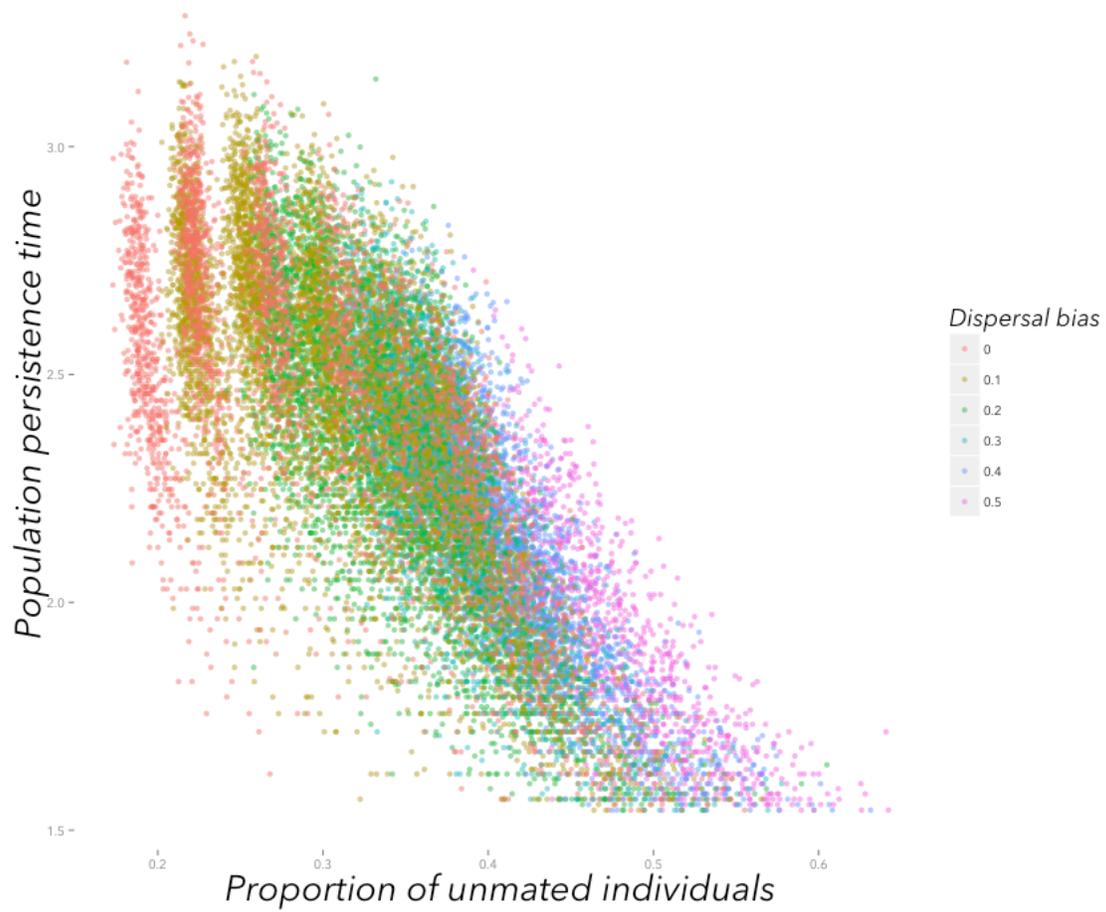


Fig. 3. The proportion of unmated individuals in the populations was significantly correlated with population persistence time ($R^2 = 0.57$, $p < 2.2 \times 10^{-16}$). Colours indicate the strength of sex biased dispersal, showing that it strongly affects the number of unmated individuals in the population, which then effects population success.

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Dispersal strategies of satellite males leave signatures in population distributions

Individuals can differ in their dispersal behavior, as their physical condition, social status, and local suite of environmental cues can influence each individual's decision-making calculus. This variation in dispersal behavior creates unique challenges for ecologists, as it changes the scale of interactions. However, studying these dispersal differences can be challenging, as a comprehensive study requires following the movements of known individuals, as well as mapping local conditions. Alternatively, a coarser but more widely applicable strategy is to study existing distributions of individuals and their local conditions, to determine *post-facto* what potential dispersal strategies were involved. This study aimed to assess how different habitat selection strategies affected the spatial distributions of populations, hoping to uncover unique signatures of each dispersal strategy. I developed an individual-based simulation model, in which individuals either dispersed passively/randomly, were sensitive to crowds, were sensitive to environmental cues, or were sensitive to both of the above. Coefficients from generalized linear models were compared, to assess if unique signatures emerged from these dispersal strategies. I found that compared to passive/random dispersal, populations with crowd-sensitive or both-sensitive individuals were disproportionately found in medium-quality patches, while populations with environment-sensitive individuals were disproportionately scarce in medium-quality patches. These results can be interpreted through the lens of opportunity costs, as passively-dispersing individuals perished in both low-quality and high-quality (over-crowded) patches, whereas individuals sensitive to crowds settled in medium-quality patches instead and survived. Environment-sensitive

populations were the least successful as a whole, while populations sensitive to both crowds and environment were the most successful. To classify empirical data as belonging to one of these dispersal strategies therefore requires fine-scale data on the environmental suitability of each patch, but such an approach can refine our understanding of species distributions beyond what could be done while ignoring individual differences.

INTRODUCTION

An individual's decision to disperse draws upon many factors, both biotic and abiotic. These can include local environmental conditions, population density, and genetic relatedness to nearby individuals, amongst other factors [1]. While many of these factors affect all individuals equally, an individual's phenotypic condition is of particular interest, as it can vary significantly between individuals. In some systems, individuals in good condition are more likely to disperse, as they are more physically capable, while in other systems it is the poor-condition individuals that disperse in search of better opportunities [2,3]. This variation produces a spectrum of dispersal proclivities within a population, and opens up a variety of intriguing ecological questions. For instance, how do residents and migrants interact locally, and how does that affect local and regional ecological dynamics? Might phenotypic condition and dispersal proclivity become linked, creating dispersal syndromes [4-6], and even assortative mating [7]? Variation between individuals has generally been poorly incorporated into ecological thinking [8], and variation in dispersal behavior creates unique problems as it changes the scale of interactions.

However, studying intraspecific variation in dispersal in the field is often difficult. For a comprehensive study, it requires following the movements of known individuals over the long-term, as well as the traits of those individuals [9,10]. There are some systems where such comprehensive work has been performed, with useful insights [3,11-13]. However, gathering this kind of data is highly labor-intensive, and may be impossible in many systems. Experimental manipulation of local densities could also provide insights into individuals's habitat selection strategies [14], but again this may not be possible in many systems.

An alternative approach is to study the existing distributions of individuals, and analyze this data to ascertain the most likely dispersal dynamics that could have produced those empirical patterns. While this approach is more presumptive rather than comprehensive, it requires less labor is more widely applicable across systems. For instance, Rosenzweig and Abramsky applied a theoretical model of habitat selection to a dataset of desert rodents, with only a spatial matrix and population densities in each patch. Using that simple dataset, they found a variety of habitat selection strategies amongst each species in the community. However, they were only able to ascertain the strength of habitat selection across different population densities, but not the specifics of which individuals were dispersing, what cues informed their settlement decisions, etc. [14]. In other words, this study ascertained the strength of habitat selection, but not the direction or mechanism except by anecdotal observation.

The exact mechanisms driving habitat selection decisions could affect the direction of settlement decisions. For instance, individuals may be sensitive to cues of the abiotic environment, density of present individuals, fitness of present individuals, or some combination of these and other cues [15]. While these cues may

be correlated in many instances, exceptions could be exceedingly beneficial (uncolonized but suitable habitat) or harmful (ecological traps and attractive sinks [16-18]) to individuals. Exactly how individuals navigate the settlement cues in their landscape [19,20] could profoundly shape their distributions across landscapes, and the success of their populations.

The goal of this study was to assess how different habitat selection strategies affected the spatial distributions of populations. Ideally, each dispersal strategy would produce unique spatial or environmental response signatures that could be used to classify empirical data. While populations would always heavily inhabit the most suitable patches, I predicted that the dispersal strategies would affect the number of individuals in medium-quality patches. In particular, I hypothesized that populations where individuals avoided densely-occupied patches would disproportionately colonize medium-quality patches, as compared to populations with random/passive dispersal.

METHODS

In order to explore how dispersal strategies of satellite males can affect spatial distributions of populations, I developed an individual-based (agent-based) simulation model using the software NetLogo [21]. In these types of models, the movement and behavior of individuals are governed by simple sets of rules, which then interact to produce complex, emergent results. As discussed in the previous chapter, individual-based models can easily account for variation between individuals, but must be kept simple in order to avoid overfitting, and the results are best interpreted heuristically.

The empirical system of dragonflies provided a loose basis for the rules governing this model. Here, dominant males establish territories at their natal ponds [22], while satellite males are forced to disperse elsewhere in search of their own defensible territories [12,22]. It is unclear what the dispersal strategies of these satellite males are, but they may respond to certain environmental cues [22,23], and/or to the existing presence or absence of conspecifics [22]. For each species, ponds vary in their environmental suitability, in a relatively random distribution across space.

Model setup

In this model, the heterogeneous 30x30 landscape consists of patches that vary in their suitability score on a scale from 0 to 11, with a value of '11' representing an ideal suitable patch, and '0' indicating a wholly unsuitable patch. Individuals lose health in every time step, at a linear proportion relative to the quality of the patch they are in, and losing all health results in death. An individual's probability of successfully reproducing in a given patch is determined by a logistic function, where a patch with a suitability score of 8 gives each individual there a 50% probability of successful reproduction. A steepness value of 1.0 was chosen; this ensures that reproduction is often (but not always) successful in patches with a score of 9 and above, and are typically unsuccessful in patches with a score of 7 or below.

During initialization, each individual is given a random 'trait' score, which affects the outcomes of intraspecific battles. Given a pre-determined carrying capacity for each patch, that number of individuals with the highest trait values are assigned as 'dominant males', while all others (with the lower trait values) are

assigned as satellite males. Dominant males remain philopatric, while satellite males disperse according to given dispersal strategies, described below. Only dominant males are capable of reproducing, and if an individual successfully reproduces given the reproductive odds of its patch, it hatches a single individual offspring, with a trait value drawn from a Normal distribution centered on the parents' trait value, and full health.

Dispersal strategies

In each run of the model, all satellite males followed one of four possible dispersal strategies: sensitivity to environment, sensitivity to crowds, sensitivity to both, or no sensitivity (random/passive dispersal). When sensitive to the environment, individuals assessed all patches within a given search radius, and dispersed to the patch with the greatest suitability score, other than its current patch. This search radius was drawn randomly from a poisson distribution at each time step for each individual, with a mean value of 3, which pilot study models showed to effectively link the entire landscape. In this dispersal strategy, individuals dispersed to the most suitable patch even if it was already crowded with individuals; therefore these individuals would be taking a chance that their trait values would be stronger in this new patch, compared to their original home.

When sensitive to crowds, individuals ignored all patches within their search radius that were already filled with individuals up to the carrying capacity. Among the remaining available patches, they dispersed to one chosen at random. This model assumes that individuals are blind to the suitability of a patch.

When sensitive to both environment and to crowds, individuals again ignored all patches in their search radius that were already full to the carrying capacity. Among the remaining available patches, they dispersed to the one with the best environment. This dispersal strategy is the closest to ideal habitat selection, though they remain limited by their search radius, and do not explicitly weigh individual benefits and costs.

When individuals were not sensitive to environment nor to crowds, they dispersed to a random patch within their search radius, mimicking passive movement. This strategy serves as a null model, to which the other strategies were compared to.

Each run of the simulation lasted for 150 time steps, which was more than enough for the spatial distributions of the population to become fixed. Each dispersal strategy was run through 10 replicates.

Model assessment and data analysis

I tracked the environmental quality and final abundance in each patch, as well as supplementary measures such as the cumulative number of births, deaths, immigrants, and emigrants during the run.

Spatial autocorrelation in each run was checked using the PCNM (Principle Coordinates of Neighbor Matrices) method, and testing for significant values of Moran's I [24].

Variation between runs of the model were evaluated by using runs as a random effect in a Generalized Linear Mixed Model [25].

The relationship between patch environment and abundance, births, deaths, immigrants, and emigrants was examined using a Generalized Linear Model (GLM) for each response separately, where the responses were related to environment and environment² crossed by each dispersal strategy, with random dispersal serving as the reference level. Abundance count data was used as the response variable, but because the highest counts were capped due to a carrying capacity, I transformed these counts into proportions, and assumed a quasi-binomial error distribution and used a logit link function. All other responses assumed a quasi-poisson error distribution and used a log-log link function.

Mean overall population sizes were compared using one-way ANOVA, and a *post-hoc* Games-Howell test.

I performed this analysis using base packages in the statistical software R [26].

RESULTS

Variation between runs was insignificant, precluding use of the GLMM, and allowing data from multiple runs to be pooled together in a simpler GLM (data not shown).

No significant spatial autocorrelation was found in the PCNM method, and so analysis in the GLM focused solely on environment (data not shown).

Abundance in each patch was significantly explained by environment crossed with dispersal strategy ($p = 2.692 \times 10^{-5}$), and environment² crossed with dispersal strategy ($p = 3.537 \times 10^{-6}$). All dispersal strategies produced regression coefficients that significantly differed from random dispersal, the reference level ($p < 2 \times 10^{-16}$,

Fig. 4). In the crowd-sensitive and both-sensitive strategies, individuals were disproportionately found in medium-quality patches, compared to the random dispersal strategy. In contrast, the environment-sensitive strategy produced disproportionately few individuals in medium-quality patches, as the vast majority of individuals were found exclusively in the best-quality patches (Fig. 4).

Immigration to each patch was significantly explained by environment crossed with dispersal strategy ($p = 3.707 \times 10^{-15}$), and environment² crossed with dispersal strategy ($p < 2.2 \times 10^{-16}$). All dispersal strategies produced regression coefficients that significantly differed from random dispersal, the reference level ($p < 2 \times 10^{-16}$, Fig. 5). When individuals dispersed randomly/passively or were sensitive to the environment, most immigration was into high-quality patches, particularly in the latter dispersal strategy. In crowd-sensitive and both-sensitive dispersal strategies, most immigration was into medium-quality patches (Fig. 5).

Mean overall population sizes significantly differed between dispersal strategy ($p < 2.2 \times 10^{-16}$), and a *post-hoc* Games-Howell test found that every group significantly differed from one another (Table C1, Fig. 6).

DISCUSSION

Each dispersal strategy produced a unique signature in the population's distribution, and the differences were largely expressed in the medium-quality patches. Populations with environment-sensitive individuals were rarely found in medium-quality patches, while crowd- and both-sensitive populations were disproportionately abundant there.

These results can be interpreted through the lens of opportunity costs. Under random/passive dispersal, some individuals dispersed into poor-quality patches, and were unable to survive or reproduce. When individuals were sensitive to the environment in some degree, those individuals dispersed elsewhere, to more suitable patches.

But more subtly, under random dispersal, many individuals also dispersed into already-full suitable patches, where they could not compete with the existing residents, and therefore perished. Under the crowd-sensitive strategies, these individuals would have persisted in other patches instead, often in medium-quality patches where they had an opportunity to survive and reproduce.

Therefore, under random dispersal, individuals perished in both the poor- and the high-quality patches, while under crowd- and both-sensitive strategies these individuals persisted in medium-quality patches instead. This can be confirmed by examining the numbers of births and deaths across patch types (Fig. C1), as well as overall population sizes (Fig. 6).

Environment-sensitive populations were almost exclusively found in high-quality patches. However, their overall population sizes were quite low (Fig. 6), as individuals largely failed to settle for medium-quality patches (Fig. 5), and is therefore a poor strategy when there is a carrying capacity in high-quality patches. Depending on their search radius, populations with this dispersal strategy could be vulnerable to catastrophic disturbance events.

While the both-sensitive dispersal strategy is the closest analog to the classical Ideal Free Distribution and perfect habitat selection, it somewhat-ironically results in the highest proportion of individuals in medium-quality patches. However, in overall population size, it is the most successful dispersal strategy overall (Fig. 6).

If empirical studies find many individuals in sub-optimal environments, that is not necessarily a sign of poor habitat selection. Instead, it could be that optimal patches are saturated, and that the landscape is filled with population sinks or pseudo-sinks [27].

It could be suggested, then, that the disproportionate abundance or scarcity in medium-quality patches is due solely to population success, rather than any direct signature of dispersal strategy. If the best patches are saturated, the amount of spillover into medium-quality patches would simply be in relation to population size as a whole. Indeed, the overall population sizes of each strategy do correspond exactly with the proportion of individuals in medium-quality patches (Fig. 4, Fig. 6). Or could it be that dispersal strategies do leave a signature on medium-quality patches, and that this leads to more successful populations?

This chicken-egg conundrum can be resolved to some degree by examining the mechanisms of population growth. The most successful dispersal strategies (crowd-sensitivity and both-sensitivity) showed high rates of immigration into medium-quality patches, while random/passive and environment-sensitive dispersal showed most of the immigration going into high-quality patches (Fig. 5). But for all dispersal strategies, medium-quality patches served as population sinks, with deaths greatly outnumbering births; only high-quality patches served as population sources (Fig. C1).

However, dispersal does alter the number of patches in the landscape that are occupied at a given time. And so the crowd-sensitive and both-sensitive dispersal strategies, with their high immigration rates into medium-quality patches, are increasing the population's coverage of the landscape. Because there is a carrying capacity in each patch, landscape coverage is the only way in which the strategies

could differentiate themselves in overall population size. Therefore, the disproportionate abundance or scarcity of individuals in medium-quality patches are a signature of these dispersal strategies, which ultimately affect population success.

Disentangling these dispersal strategies in empirical data may remain difficult. The signatures of these strategies are only obvious in comparison with other strategies, and with fine-scale data on local environmental suitability. Implementing disturbance regimes could potentially uncover clearer signatures, as each strategies affects colonization rates of new patches. In addition, it would be interesting to allow individuals within the population to adopt differing dispersal strategies, and investigate how the frequencies of these dispersal phenotypes vary given certain environmental conditions, and what stable equilibria the populations settle into. Broadly however, dispersal strategies do affect the spatial distributions of populations across landscapes, and accounting for this could help to produce more nuanced models of how species are influenced by their environments.

FIGURES

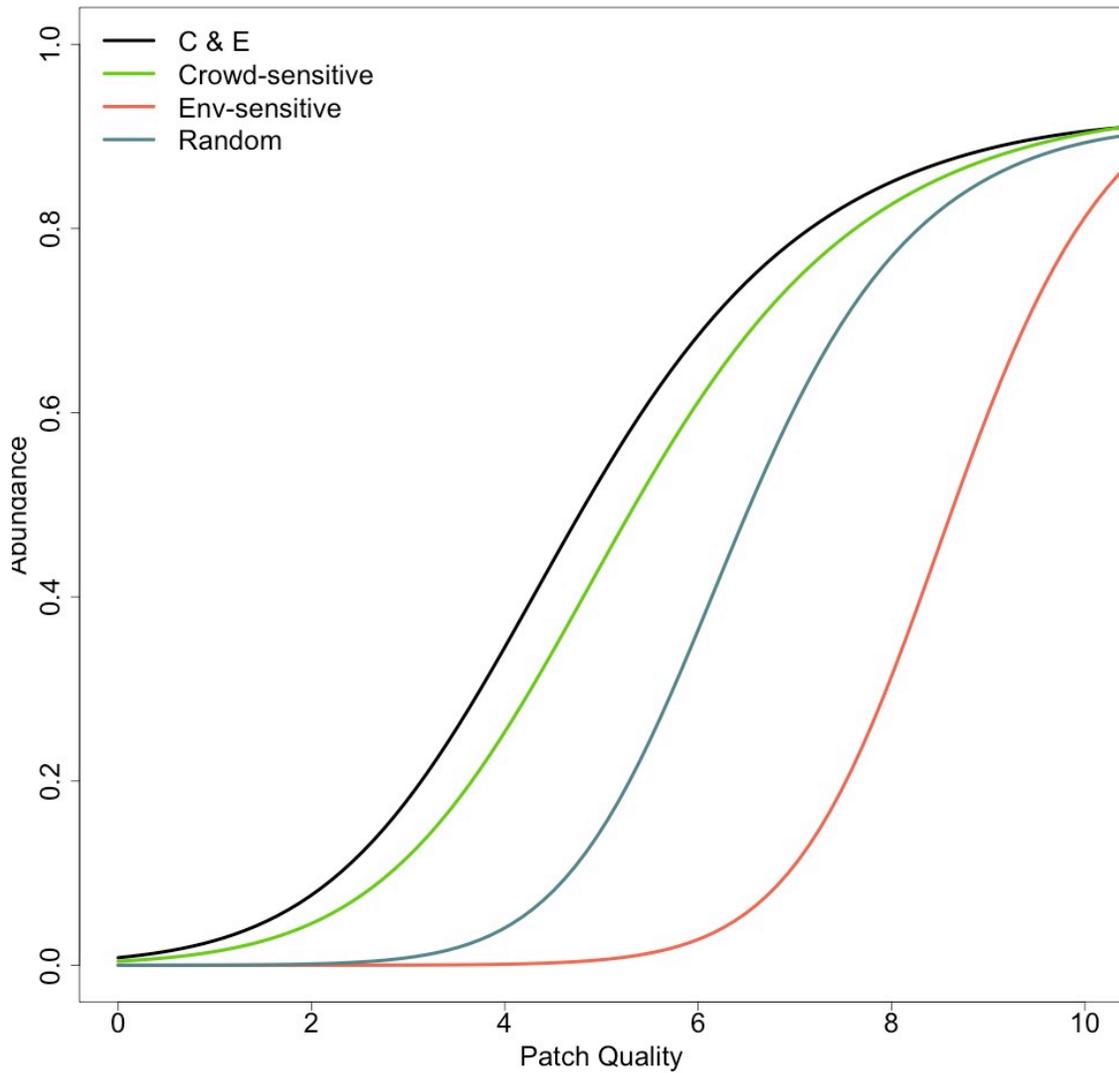


Fig. 4. Abundance in each patch was significantly related to environment crossed with dispersal strategy ($p = 2.692 \times 10^{-5}$), in a Generalized Linear Model. All dispersal strategies produced regression coefficients that significantly differed from random/passive dispersal, the reference level. Curves represent the average coefficient values across runs.

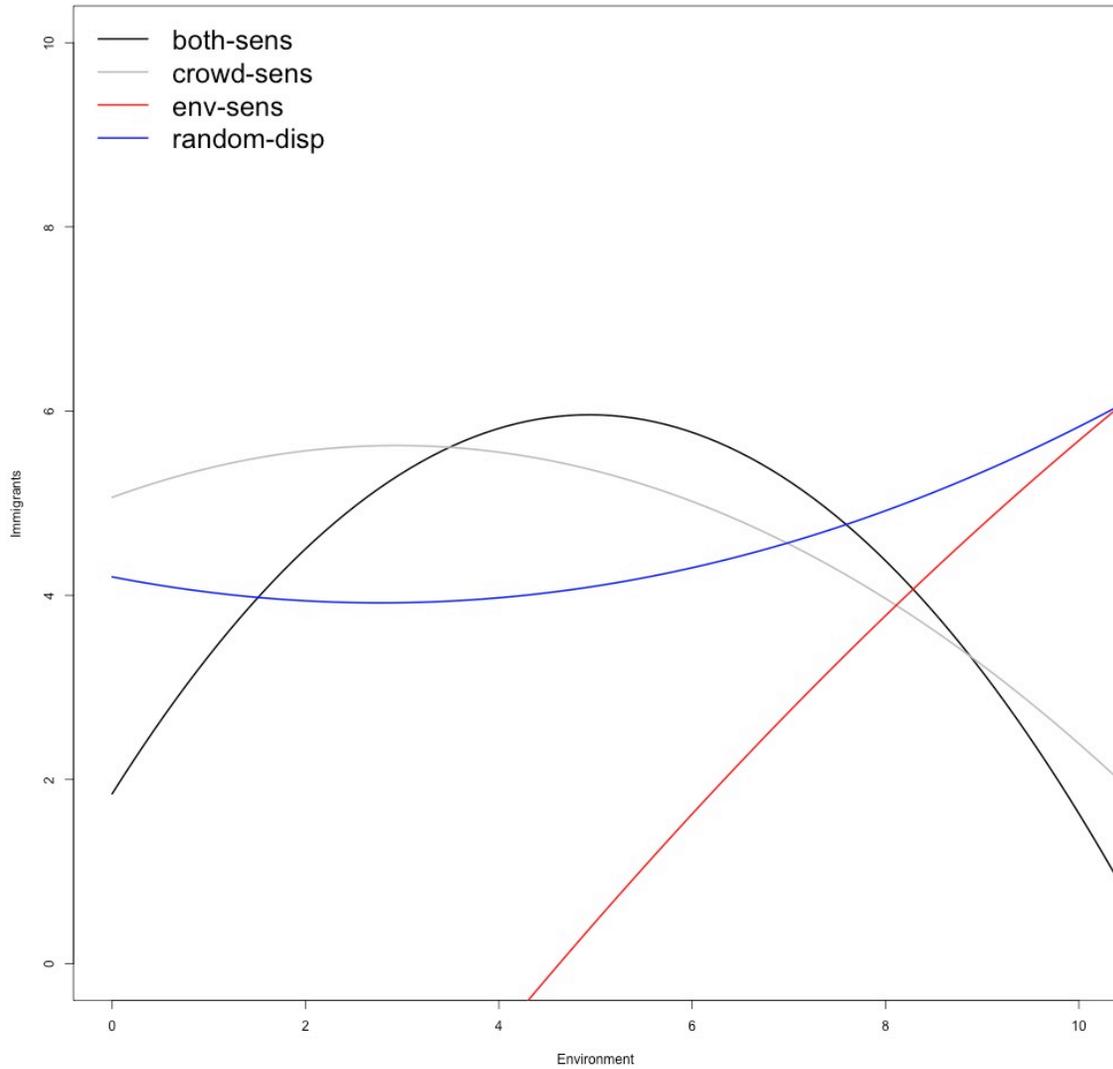


Fig. 5. Immigration into each patch was significantly related to environment crossed with dispersal strategy ($p = 3.707 \times 10^{-15}$), in a Generalized Linear Model. All dispersal strategies produced regression coefficients that significantly differed from random/passive dispersal, the reference level. Curves represent the average coefficient values across runs.

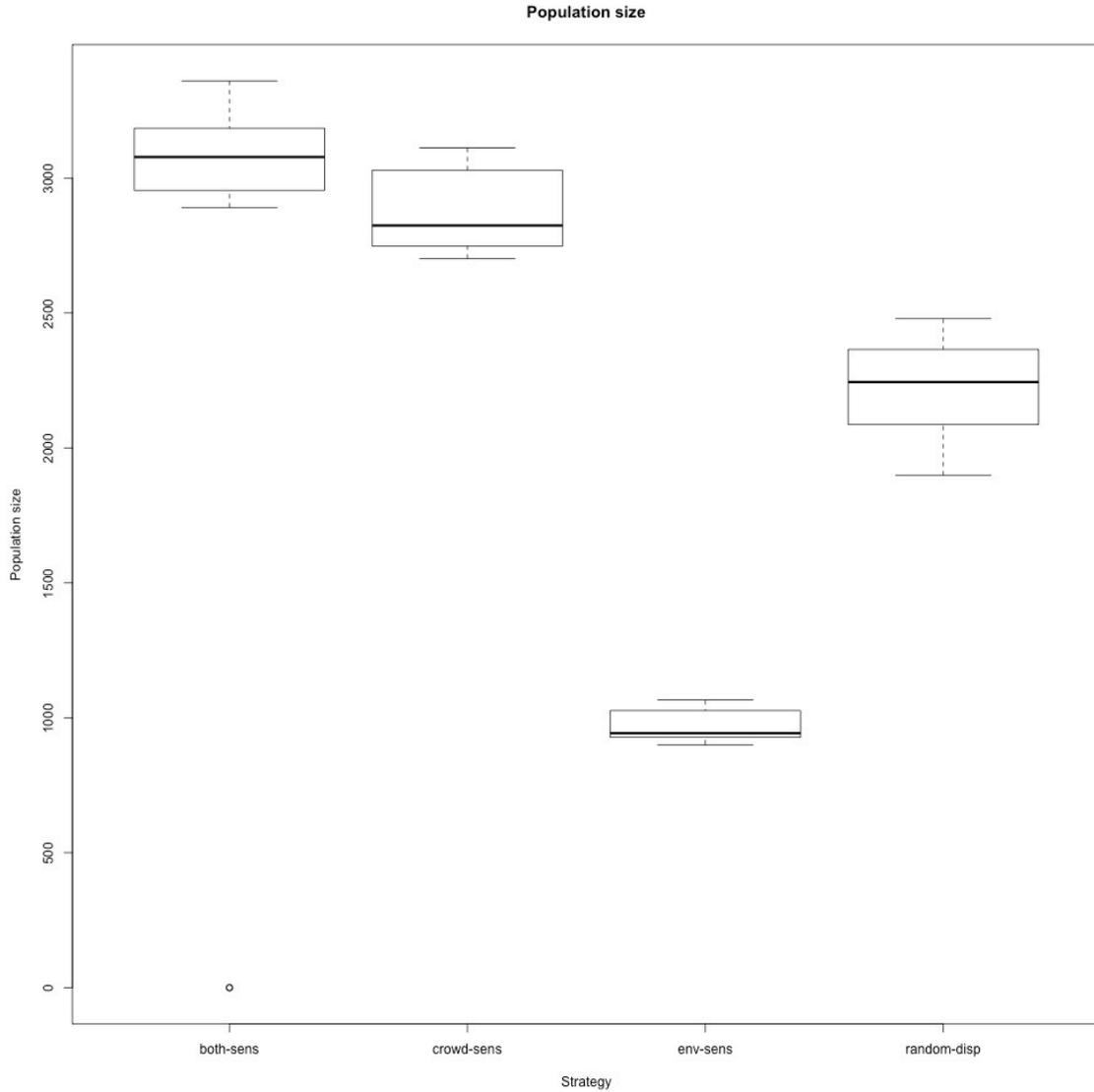


Fig. 6. Mean overall population sizes significantly differed for each dispersal strategy ($p < 2.2 \times 10^{-16}$). A *post-hoc* Games-Howell test found that every group significantly differed from one another (Table C1).

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Appendices

APPENDIX A: DRAGONFLIES IN THE LBJ GRASSLANDS

No supplementary material.

APPENDIX B: SEX-BIASED DISPERSAL COSTS

Table B1: Definitions for all model output variables that were considered, including method of calculation. For more details, please refer to the model code, available at <https://github.com/aredoubles/SexBiasedDispersal>

Variable	Definition, calculation
Dispersal bias	<i>The dispersal kernel of each sex is a Poisson distribution, with the lambda-value of this distribution varied, in order to affect spread. The strength of dispersal bias was calculated as the absolute value of the difference between these lambda values.</i>
Global sex ratio	<i>In each time step, of all individuals alive, what proportion are male? Calculated as an average across all time-steps in the model run, to arrive at a pseudo-equilibrium value. This pseudo-equilibrium value was then subtracted from 0.5, and the absolute value of this 'difference value' represents the final value that was used in statistical analysis.</i>
Suitable-patch sex ratio	<i>In each time step, of all the individuals that are located on suitable patches, what proportion are male? Calculated as an average across all time-steps in the model run, to arrive at a pseudo-equilibrium value. This pseudo-equilibrium value was then subtracted from 0.5, and the absolute value of this 'difference value' represents the final value that was used in statistical analysis.</i>
Unsuitable-patch sex ratio	<i>In each time step, of all the individuals that are located on suitable patches, what proportion are male? Calculated as an average across all time-steps in the model run, to arrive at a pseudo-equilibrium value. This pseudo-equilibrium value was then subtracted from 0.5, and the absolute value of this 'difference value' represents the final value that was used in statistical analysis.</i>
Spatial sex segregation	<i>The pseudo-equilibrium values of the sex ratios in suitable and unsuitable patches were subtracted; the absolute value of this represents the final value that was used in statistical analysis.</i>
Proportion of unmated individuals	<i>In each time step, of all the individuals alive, what proportion did not find a mating partner? Calculated as an average across all time-steps in the model run, to arrive at a pseudo-equilibrium value. This value was then log-transformed, for the final values that were used in statistical analysis.</i>
Suitable patches colonized	<i>In each time step, of all the suitable patches in the landscape, how many are occupied by individuals? Calculated as an average across all time-steps in the model run, to arrive at a pseudo-equilibrium value.</i>

Table B2: Output of a Tukey-HSD test, on how the degree of dispersal bias affects the persistence time of the population. All pairwise comparisons are highly significant, except for the lowest pair (0.1 difference in dispersal kernel spread, versus equal dispersal between the sexes).

```
> TukeyHSD(aov(log(newsb$ticks) ~ newsb$bias))
```

```
Tukey multiple comparisons of means
```

```
95% family-wise confidence level
```

```
Fit: aov(formula = log(newsb$ticks) ~ newsb$bias)
```

```
$`newsb$bias`
```

	diff	lwr	upr	p adj
0.1-0	-0.002416185	-0.04533383	0.04050146	0.9999853
0.2-0	-0.189299394	-0.23417716	-0.14442163	0.0000000
0.3-0	-0.482446054	-0.53063680	-0.43425531	0.0000000
0.4-0	-0.830659679	-0.88546058	-0.77585878	0.0000000
0.5-0	-1.189408946	-1.26179573	-1.11702216	0.0000000
0.2-0.1	-0.186883208	-0.22625305	-0.14751337	0.0000000
0.3-0.1	-0.480029868	-0.52313809	-0.43692165	0.0000000
0.4-0.1	-0.828243494	-0.87863307	-0.77785391	0.0000000
0.5-0.1	-1.186992761	-1.25610005	-1.11788547	0.0000000
0.3-0.2	-0.293146660	-0.33820671	-0.24808661	0.0000000
0.4-0.2	-0.641360286	-0.69342946	-0.58929111	0.0000000
0.5-0.2	-1.000109553	-1.07045091	-0.92976819	0.0000000
0.4-0.3	-0.348213626	-0.40316391	-0.29326334	0.0000000
0.5-0.3	-0.706962893	-0.77946283	-0.63446295	0.0000000
0.5-0.4	-0.358749267	-0.43580141	-0.28169713	0.0000000

Table B3: Results of ANOVAs, comparing the degree of dispersal bias to an assortment of variables. Sex-biased dispersal significantly affected all of these variables.

	F	df	p-value
Global sex ratio	20191	5	2.2e-16
Suitable-patch sex ratio	29945	5	2.2e-16
Unsuitable-patch sex ratio	10666	5	2.2e-16
Spatial sex segregation	30095	5	2.2e-16
Proportion of unmated individuals (log)	4119	5	2.2e-16
Suitable patches colonized	543.0	5	2.2e-16

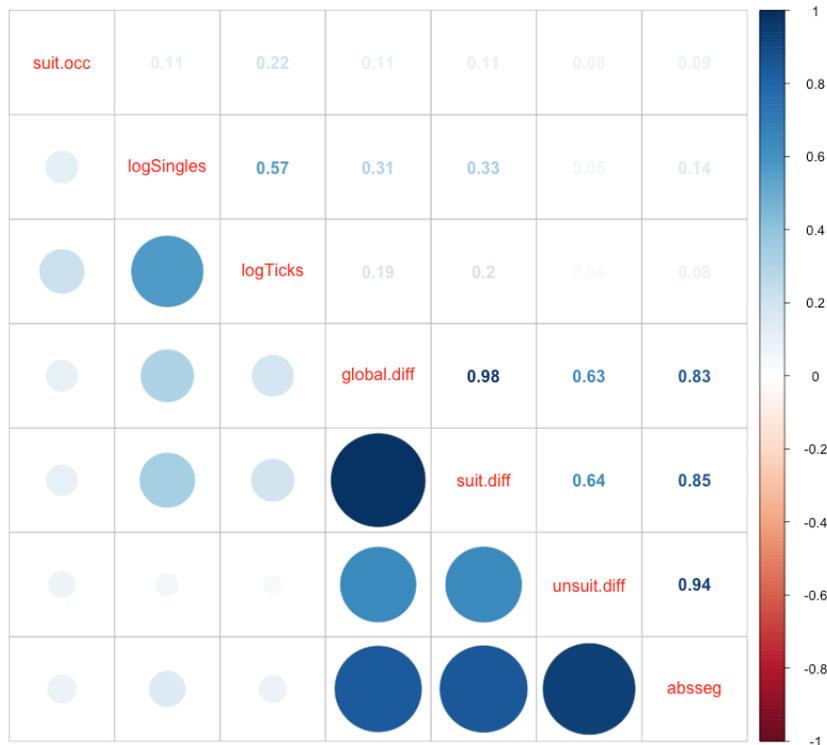


Fig. Br: Correlation matrix, showing R^2 coefficient of determination values for an assortment of correlation analyses. Size of circles represents a visualization of the strength of the coefficient of determination between those variables. Of particular interest, the persistence time of populations (logTicks) was most strongly correlation with the proportion of unmated individuals (logSingles).

suit.occ = Suitable patches colonized
 logSingles = Proportion of unmated individuals (log)
 logTicks = Persistence time of the population (log)
 global.diff = Global sex ratio
 suit.diff = Suitable-patch sex ratio
 unsuit.diff = Unsuitable-patch sex ratio
 absseg = Spatial sex segregation

Table B4: Output of a Tukey-HSD test, on how the degree of dispersal bias affects the proportion of unmated individuals in the population. All pairwise comparisons are highly significant.

```
> TukeyHSD(aov(newsb$singles.prop ~ newsb$bias))
```

```
Tukey multiple comparisons of means
```

```
95% family-wise confidence level
```

```
Fit: aov(formula = newsb$singles.prop ~ newsb$bias)
```

diff	lwr	upr	p adj	
0.1-0	0.009481719	0.005773108	0.01319033	0
0.2-0	0.036512733	0.032634744	0.04039072	0
0.3-0	0.075189916	0.071025645	0.07935419	0
0.4-0	0.124273737	0.119538268	0.12900921	0
0.5-0	0.180678075	0.174422970	0.18693318	0
0.2-0.1	0.027031014	0.023628977	0.03043305	0
0.3-0.1	0.065708197	0.061983119	0.06943328	0
0.4-0.1	0.114792018	0.110437741	0.11914630	0
0.5-0.1	0.171196356	0.165224640	0.17716807	0
0.3-0.2	0.038677183	0.034783442	0.04257092	0
0.4-0.2	0.087761004	0.083261589	0.09226042	0
0.5-0.2	0.144165342	0.138086986	0.15024370	0
0.4-0.3	0.049083821	0.044335443	0.05383220	0
0.5-0.3	0.105488159	0.099223276	0.11175304	0
0.5-0.4	0.056404338	0.049746089	0.06306259	0

APPENDIX C: DISPERSAL STRATEGIES OF SATELLITE MALES

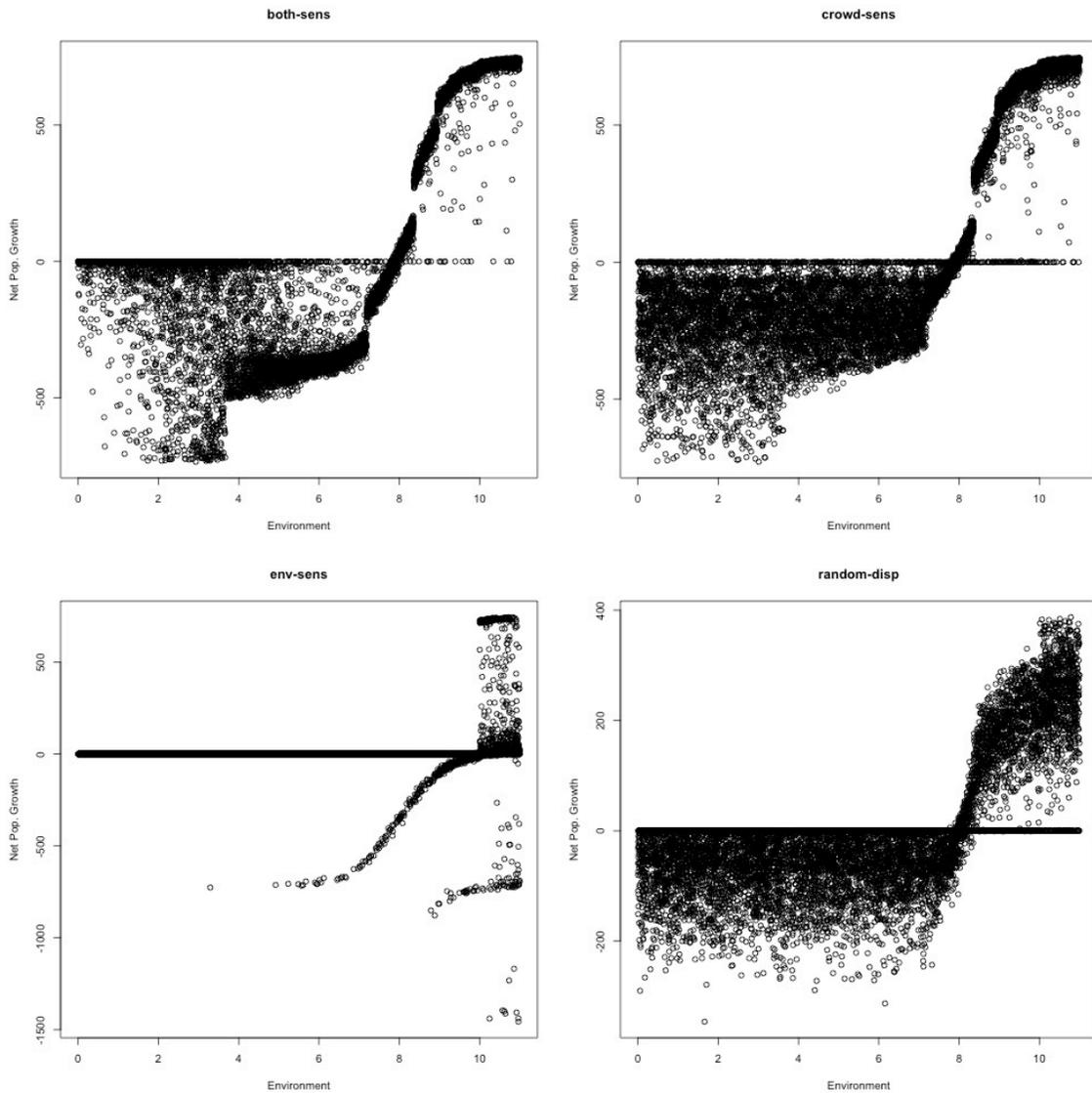


Fig. C1. Total population growth (= total births – total deaths) in each patch was related to environment for each dispersal strategy. In every strategy, population growth exclusively occurred in patches with an environment greater than 8, with all other patches in the landscape becoming population sinks.

Table C1. A *post-hoc* Games-Howell test found that every group significantly differed from one another in overall population success.

One-way analysis of means (not assuming equal variances)

data: pop and strat

F = 840.66, num df = 3.000, denom df = 16.849, p-value < 2.2e-16

	n	means	variances
both-sens	9	3135	24686
crowd-sens	10	2881	24638
env-sens	10	964	3418
random-disp	10	2225	36997

	t	df	p
both-sens:crowd-sens	3.5	17	1.3e-02
both-sens:env-sens	39.1	10	3.7e-11
both-sens:random-disp	11.3	17	1.5e-08
crowd-sens:env-sens	36.2	11	0.0e+00
crowd-sens:random-disp	8.4	17	9.7e-07
env-sens:random-disp	19.8	11	5.1e-09

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CHAPTER I

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