

# Seed Dispersal as A Search Strategy: Dynamic and Fragmented Landscapes Select for Multi-Scale Seed Dispersal

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## Research

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# Abstract

**Background** – Plant dispersal is a critical factor driving ecological responses to global changes. Knowledge on the mechanisms of dispersal is rapidly advancing, but selective pressures responsible for the evolution of dispersal strategies remain elusive. Recent advances in animal movement ecology identified general strategies that may optimize efficiency in animal searches for food or habitat. We here explore the potential for evolution of similar general movement strategies for plants.

**Methods** – We propose that seed dispersal in plants can be viewed as a strategic search for suitable habitat, where the probability of finding such locations has been optimized through evolution of appropriate dispersal kernels. Using model simulations, we demonstrate how dispersal strategies can optimize key dispersal trade-offs between finding habitat, avoiding kin competition, and colonizing new patches. These trade-offs depend strongly on the landscape, resulting in a tight link between optimal dispersal strategy and spatiotemporal habitat distribution.

**Results** – Our findings reveal that multi-scale seed dispersal strategies that combine short-distance and long-distance dispersal, including Lévy-like dispersal, are optimal across a wide range of dynamic and patchy landscapes. Static patchy landscapes select for short-distance dominated dispersal strategies, while uniform and highly unpredictable landscapes both select for long-distance dominated dispersal strategies.

**Conclusions** – By viewing plant seed dispersal as a strategic search for suitable habitat, we provide a reference framework for the analysis of plant dispersal data. This reference framework helps identify plant species' dispersal strategies, the evolutionary forces determining these strategies and their ecological consequences, such as a potential mismatch between plant dispersal strategy and altered spatiotemporal habitat dynamics due to land use change. Our perspective opens up directions for future studies, including exploration of composite search behaviour and 'informed searches' in plant species with directed dispersal.

## Background

Dispersal plays a crucial role in the population dynamics and ecological interactions of plant species. In light of ongoing habitat fragmentation and climate change, dispersal is a particularly critical determinant of local, regional and global plant species survival (1–4). This realisation has elevated plant dispersal to a research priority in the last decades. Quantitative information on plant species' dispersal distance distributions (or 'dispersal kernels') is needed for adequate species management, as dispersal kernels determine colonization probabilities and restoration success, as well as speeds of range expansions and invasions. Indeed, significant progress has been made in understanding how mechanisms of seed dispersal determine seed dispersal kernels (5–8), and how these may be affected by global changes (1, 9–11). However, the selective pressures responsible for the evolution of dispersal strategies remain elusive.

Excellent overviews of studies on the evolution of dispersal in plants and animals are given in Ronce (12) and Duputié and Massol (13). For plants, a long line of research has developed on how (kin) competition, facilitation, inbreeding, and density dependent mortality translate to selective pressures for dispersal propensity (the tendency of an individual to disperse) (e.g., (14–24)). In addition, theoretical studies have shown that increasing dispersal propensity can serve as an effective bet-hedging strategy to deal with spatiotemporal environmental variability(22).

Few studies to date included dispersal kernels in their evolutionary analysis (25–27). These studies usually focus on a single aspect of dispersal (e.g., long-distance dispersal) or compare dispersal strategies in a relative sense (e.g., how dispersal propensity increases or decreases in response to e.g. stress-related factors). However, many of the driving processes are acting at different spatial scales (13), so that flexibility in the shape of dispersal kernels is required to balance trade-offs between driving processes at a range of scales. Here, we move beyond dispersal propensity or focus on a single aspect of the dispersal distance distribution, and argue that the entire distribution of seed dispersal distances matters and may optimally balance dispersal over shorter and longer distances.

We propose that plant dispersal strategies evolve as search strategies for suitable habitat, in a way comparable to stochastic searches made by other moving organisms. Reynolds (28) already hypothesized that plants may maximize the likelihood of finding the nearest unoccupied site by adopting a Lévy flight-shaped inverse power-law seed dispersal kernel. We propose that plant species have a wide range of dispersal strategies, that each evolved in search of *all* suitable habitat of the species, and therefore depend strongly on the spatial and temporal distribution of their habitat. Using a theoretical framework inspired by animal movement ecology, we show how recent conceptual developments in analysing animal movement data can advance the field of plant dispersal ecology towards identification of evolutionary drivers and ecological consequences of seed dispersal strategies.

Over the past decade, analyses of high-resolution movement data from a wide range of animals have broadly identified the signatures of complexity in movement patterns. Movement paths can be decomposed into consecutive movement steps of a specific length (move length) that are separated by changes in direction (turns) (29, 30). Move length distributions can be described by power-law relationships ( $p(x) \sim x^{-\mu}$ ; Fig. 1) with a scaling exponent  $\mu$  ranging from  $\sim 1$  (promoting long-distance movements, where long steps are as abundant as short steps) to  $> 3$  (promoting Brownian motion, where short steps are abundant and long steps are very rare). At an intermediate  $\mu \sim 2$ , many consecutive short-distance movements are alternated with infrequent long-distance movements, producing complex multi-scale movement patterns where many different move lengths occur. In such multi-scale movement strategies, the relationship between move length and frequency decays neither too quickly (so that one scale predominates) nor too slowly (so that all scales are equally frequent) (30–34). These complex multi-scale movement strategies are known as Lévy flights or walks (31).

In a random search, the move length distribution that maximizes search efficiency depends on the spatiotemporal distribution of targets being sought (e.g., food, mates; (32, 35, 36)). Theoretical studies

have shown that various strategies may effectively balance short-distance and long-distance movements, depending on the spatiotemporal environmental conditions (34–38). Importantly, this balance is determined by the entire move length distribution. Experimental studies have shown that complex animal movement patterns indeed have intrinsic underlying patterns that optimize random search efficiency, thereby greatly enhancing individual fitness (34, 39–41).

Although these recent developments have significantly advanced our understanding of the evolution and ecology of animal movement (41), the potential for evolution of similar random search strategies has not been explored for plants. We propose that the move length distribution (i.e., seed dispersal distance distribution or dispersal kernel) generated by all the seeds coming from a single plant can be viewed as a movement strategy to search for suitable habitat, or more specifically, suitable sites for germination, establishment and reproduction. As adult plants are otherwise immobile, we expect that there is strong selective pressure on such dispersal kernels.

Here, we provide a theoretical framework that identifies null models for (evolution of) dispersal strategies in plant populations and explores the impact of spatiotemporal landscape structure (habitat fragmentation and patch turnover dynamics) on dispersal evolution, considering dispersal as a search strategy. We acknowledge that evolved plant dispersal strategies should match relevant biotic and abiotic factors determining eventual offspring success, such as the spatial structure of density-dependent mortality (42), competition, and facilitation (43, 44). However, in this study, we first explore the evolution of dispersal strategies in a neutral context where plants are identical except for dispersal strategy. By focussing primarily on dispersal strategy in relation to spatiotemporal habitat distribution, we derive fundamental null models that can serve as the basis for extension in the future to explore effects of additional relevant factors.

## Methods

We developed a straightforward spatiotemporal lattice model to explore the evolution of plant dispersal strategies in landscapes differing in their degree of fragmentation (patch size and inter-patch distance) and landscape dynamics (patch turnover). We excluded any variation in life history traits and competitive interactions between plants; all plants were completely similar entities that only differed in the shape of their dispersal kernels. To explore different dispersal strategies, we simulated seed dispersal kernels using a truncated two-dimensional (isotropic) Pareto distribution with discrete values of shape parameter  $\mu$  ranging from 1.1 to 5 (Table 1; see Appendix S1 in Supporting Information for derivation of 2D form):

Table 1  
Parameter ranges used in the different simulation scenarios.

Landscape parameters	Parameter values
Patch size [diameter, # grid cells]	1, 2, 4, 8, 16, 32, 64, 128, 256, continuous
Inter-patch distance [# grid cells]	2, 4, 16, 64, 256, 1024
Patch turnover rate	0, 0.01, 0.05, 0.1, 0.5, 1
Dispersal parameters	Parameter values
Dispersal kernel (Pareto scale parameter $\mu$ )	U <sup>1</sup> , 1.1, 1.5, 2, 2.5, 3, 3.5, 4, 4.5, 5, MN <sup>2</sup>
Number of seeds per individual <sup>3</sup>	(10), 100, (1000), (10000)
<sup>1</sup> Alternative ('benchmark') kernel 1: uniform dispersal	
<sup>2</sup> Alternative ('benchmark') kernel 2: Moore neighbourhood dispersal	
<sup>3</sup> Number of seeds per individual was 100 in main simulations; 10, 1000, 10000 were used in sensitivity analyses only.	

$$p(l) = \frac{1}{2\pi} \left[ \frac{2 - \mu}{l_{max}^{2-\mu} - l_{min}^{2-\mu}} \right] l^{-\mu} \quad (1)$$

where  $l_{min}$  is the minimum distance (radius of a grid cell),  $l_{max}$  is the maximum distance (equal to the domain size) and  $\mu$  is the scaling exponent. The scaling exponent determines the power-law decay of the dispersal kernel. This scaling exponent makes the 2D-Pareto kernel a very convenient tool to explore different dispersal strategies; by changing only one parameter, the kernel can cover a full range of dispersal strategies ranging from very local (short-distance dispersal dominated,  $\mu > 3$ ) to non-local (relatively high probability of long-distance dispersal,  $\mu \rightarrow 1$ ). For  $\mu \sim 2$  (i.e., canonical Lévy), this kernel produces a highly heterogeneous, multi-scale distribution of dispersal distances. We compared these 2D-Pareto kernels to 'benchmark' kernels or limiting cases on both ends of the spectrum: uniform dispersal across the entire domain (as benchmark for minimum  $\mu$ ) and dispersal only to the 8 nearest neighbours (Moore neighbourhood) in equal probabilities (as benchmark for maximum  $\mu$ ). In each model-run, two plant types with different dispersal kernels competed in a landscape with specified fragmentation and patch turnover characteristics. Plants were initially randomly placed in equal proportions throughout a landscape. For simplicity, plants only produced seeds once per generation and then died (i.e., we simulated semelparous plants). Between generations, the types were redistributed over the landscape following these event-driven steps: 1) dispersal, 2) death, 3) patch turnover, and 4) colonization. The type that remained after multiple generations was assumed to have the better dispersal strategy. We then related these dispersal strategies to three important dispersal metrics that quantify the success of dispersal in terms of (i) the success rate of finding habitat (hereafter referred to as 'habitat encounter'), (ii)

the success rate of avoiding kin competition (hereafter 'kin avoidance'), and (iii) the success rate of colonizing new patches (hereafter 'colonization'). A conceptual figure illustrating the model and model details are provided in Appendix S2.

## Simulations

We characterized landscapes by the parameters patch size, inter-patch distance, and patch turnover rate, and determined how evolved dispersal kernels depend on these landscape characteristics. Table 1 shows the parameter ranges used in our simulations.

For each set of parameter combinations, model simulations ran until one of the types was outcompeted, *i.e.* when it occupied less than 5% of all habitat grid cells, while the other type increased to at least 80% of all habitat grid cells or reached a stable equilibrium (no significant decrease over 200 generations). If both types were maintained after 1000 generations, we assigned no 'winner' and scored this as no strong selection on dispersal strategy. For each landscape, all possible combinations of dispersal kernels were used to determine the evolutionarily stable strategy (ESS). We repeated each simulation 12 times to test robustness of results. We summarized the outcome of these 12 replicate runs as follows: 1) a clear winner (one population won in at least 11 out of 12 repetitions), 2) extinction of both populations, or 3) no clear winner or no convergence. Per landscape, these results are presented in pairwise invasibility plots (PIPs, (45)). From each PIP, we extracted the ESS (expressed by parameter  $\mu$ ) and used this to identify changes of evolved strategy in relation to patch size, inter-patch distance, and patch turnover rate. We performed robustness tests of our model results to variations in plant seed number (Appendix S3) and our FFT approach (Appendix S4), which both had no significant impact on model output.

## Dispersal metrics

We expected that, similar to random searches by animals, evolutionarily stable dispersal kernels would adequately balance a complex trade-off between short-distance and long-distance dispersal conditioned to the landscape configuration (habitat patch size, inter-patch distance and patch turnover). To facilitate interpretation of these underlying trade-offs, we calculated a number of dispersal metrics that relate to the success of dispersal for each landscape configuration. First, we calculated the success rate of finding habitat (hereafter referred to as 'habitat encounter'), as the fraction of seeds landing in suitable habitat. Second, we calculated the success rate of avoiding kin competition (hereafter 'kin avoidance'). Grid cells close to parent plants typically receive a high quantity of seeds ( $> 1$ ), but only one individual can occupy a cell in the next time step. For each parent, we summed all fractions of seeds above one and then normalized these for the number of grid cells where kin competition took place to calculate the fraction of seeds involved in kin competition. We calculated kin avoidance as  $1 - \text{kin competition}$ . Third, we determined the success rate of colonizing new patches (hereafter 'colonization') as the fraction of seeds landing in a new patch that emerged due to patch turnover.

## Results

Evolutionarily stable dispersal strategies are tightly connected to the spatiotemporal distribution of plant habitat

Our simulations show that all types of movement strategies (ranging from strategies dominated by short-distance dispersal, to multi-scale dispersal, to long-distance dispersal) can be an ESS, depending on the spatiotemporal distribution of habitat in the landscape. The spatiotemporal distribution of habitat determines the optimal balance between short-distance and long-distance dispersal following trade-offs in habitat encounter, kin avoidance and colonization. In general, we found that in the most static and in the most unpredictable landscapes, the two extremes (Moore nearest-neighbour dispersal and uniform dispersal, respectively) are ESS's. When patch distributions are dynamic and fragmented, the trade-off between short-distance and long-distance dispersal results in a wide range of multi-scale dispersal strategies (including Lévy-like Pareto kernels) that are tightly connected to the spatiotemporal habitat distribution.

## Short-distance and long-distance dominated dispersal strategies

When the distribution of habitat is patchy in space and static in time, the landscape is highly predictable and movement strategies dominated by short-distance dispersal are evolutionarily stable (Fig. 2a-c). The shape of these short-distance dispersal kernels varies with patch size, with decreasing patch sizes corresponding to shorter dispersal distances (larger  $\mu$ ) (Fig. 2c). These movement strategies are essentially driven by the optimization of both habitat encounter and kin avoidance (Fig. 2d-f). With increasing patch size, the edge-to-area ratio decreases and habitat encounter increases accordingly, allowing for strategies with somewhat longer dispersal, which improves kin avoidance.

When the distribution of habitat is continuous in space (the most predictable scenario) or when the distribution of habitat is unpredictable, either in space (patch size = 1, i.e. patches can hold one individual only) or in time (patch turnover rate = 1), dispersal strategies dominated by long-distances were evolutionarily stable (Fig. 3a-c). In these situations, dispersal strategies are driven exclusively by avoidance of kin competition (Fig. 3d-f). Maximizing habitat encounter does not contribute to selecting the optimal strategy, because habitat encounter is similar for all possible values of  $\mu$ , either because the landscape consists of homogeneous habitat, or because the habitat distribution is so unpredictable that no  $\mu$  optimizes habitat encounter better than another (Fig. 3d-f).

## Multi-scale dispersal strategies

In many landscapes, habitat distribution is patchy and dynamic to some extent. In these situations, evolved dispersal strategies are dominated by multi-scale dispersal strategies, i.e. broadly heterogeneous and heavy tailed kernels (e.g. Lévy-like Pareto distributions). These strategies balance local, within-patch dispersal to provide high habitat encounter and non-local dispersal to avoid kin competition and colonize new patches. This balance is driven by all patch distribution characteristics: patch size, inter-patch distance and patch turnover rate (Fig. 4, Appendix S5). The ESS's for these landscapes, as reflected by  $\mu$ ,

are most strongly determined by patch turnover rates (Fig. 4, 5, S5), which very strongly increase the need to colonize new patches. Higher patch turnover rates correspond to lower values of  $\mu$ , with  $\mu \sim 2$  for a wide range of landscapes with patch turnover rates between 0.1 and 1 (Fig. 5). Secondly, evolutionarily stable dispersal strategies are also driven by the relative importance of colonization of new patches in relation to habitat encounter and kin competition, which decreases with patch size and inter-patch distance (Fig. 4, S5). Under low dynamic conditions, this translates to multi-scale dispersal strategies with more local dispersal when patch sizes are small and inter-patch distances short (as the role of habitat encounter becomes more important,  $\mu \rightarrow 3$ ). Under highly dynamic conditions, this translates to more long-distance dispersal when inter-patch distances are large (as the effects on colonization are strengthened by the role of kin avoidance,  $\mu \rightarrow 1.5$ ; Fig. 4, S5). The short-distance dominated dispersal strategies that we found to be ESS's in static landscapes with small patch sizes (2–8) and large inter-patch distances (> 50) changed immediately when patch turnover rate was even slightly larger than zero, as winning the local competition within patches was no longer a stable strategy in the long term.

In some dynamic landscapes with large inter-patch distances, no dispersal strategy could ensure population survival. In these cases, the probability of seeds ending up in new habitat was too low to overcome the loss of habitat due to patch turnover.

## Discussion

Studies of animal movement behaviour have identified general optimal movement strategies based upon the spatial distribution of resources (32, 36). Using a similar analytical approach, we show that general optimal dispersal strategies can be identified for plants based purely on the shape of the entire seed dispersal kernel in relation to the spatiotemporal distribution of the plant habitat. While earlier studies have shown how dispersal propensity may evolve in response to landscape structure, cost of dispersal and other (density-dependent) processes (13, 25–27, 46), we here show that the entire shape of the dispersal kernel can be seen as a multi-scale search strategy that needs to balance incentives to disperse over short-distances, long distances and everything in between.

The model used in this study is very simple, with individual plants being identical except for differences in dispersal strategies. Competition is not explicitly parameterized in the model, but implicitly there is some form of density dependence due to the role of kin avoidance. Multi-scale dispersal strategies emerge as optimal strategy even within this simple and straightforward framework, suggesting that they are of importance as a baseline in the natural setting where more processes play a role in spatial population dynamics. The reference framework following from our results is visualised conceptually in Fig. 6. The main hypotheses for real plant data generated from our findings are: (1) In static, but patchy habitats, short-distance dispersal (e.g.  $\mu > 3$ ) dominates multi-scale dispersal strategies, due to the importance of optimizing habitat encounter. Particularly when patches are small and inter-patch distances are large, there is a strong selection in favour of extremely short-distance dispersal. (2) In contrast, extreme long-distance dispersal ( $\mu \rightarrow 1$ , or even uniform dispersal kernels) is favoured in both stable, continuous habitats as well as in unpredictable and dynamic landscapes. These dispersal strategies are driven by



avoidance of kin competition and need to colonize newly formed patches. (3) In patchy and dynamic environments, a complex trade-off between finding habitat, avoiding kin competition and colonizing new patches results in multi-scale dispersal strategies with  $\mu$  correlated to average patch size, inter-patch distance and, most importantly, patch turnover rate. Our results suggest that multi-scale kernels similar to Lévy flights ( $\mu \sim 2$ ) would be selected for in patchy landscapes with intermediate patch sizes ( $\sim 2$  to 100 times the plant size), intermediate inter-patch distances ( $\sim 5$  to 100 times the plant size) and relatively high patch turnover rates of around 50% per generation.

Some aspects of our findings are in line with well-known patterns observed in plant communities: Plant species in patchy and highly dynamic habitats typically have dispersal strategies dominated by long-distance dispersal and species from patchy but highly static landscapes tend to display predominantly short-distance dispersal that promotes the chance of success in 'winning the home patch' (22, 47–49). Yet, such hypotheses are not trivial. For example, in static but patchy landscapes short-distance dispersal strategies may rapidly evolve. Colonization has been followed by rapid loss of long-distance dispersal in plants on islands and patches in urban environments (50–52). Such species are extremely vulnerable to habitat loss and fragmentation, as their dispersal strategy is not adapted to colonizing new areas (53). With ongoing global change, such dispersal-limited species are under great threat of extinction – an example of such a case is the endemic and highly threatened *Centaurea corymbosa* which is adapted to long term persistent, but isolated rocky outcrops (54).

Some hypotheses generated within our study may appear counterintuitive. For example, species in homogeneous habitats are suggested to have uniform dispersal kernels. This hypothesis would explain why, indeed, many species of large-scale, more or less continuous habitats, such as primary forest (55) and heathlands (56), have adaptations for very long-distance dispersal. Previous studies may have suggested that these adaptations serve to avoid density-dependent mortality close to the parent (16, 57, 58), but this would not explain dispersal over more than a few tens of m (the decay rate of pest-induced mortality, (24)). Our results suggest that selection for kin avoidance may explain these long-distance dispersal syndromes, although escaping density-dependent mortality may be an additional, enforcing factor.

Our analyses also lead to interesting untested hypotheses: species subjected to patchy environments should have multi-scale dispersal strategies that vary in the fatness of their tail in relation to patch size and inter-patch distances, but primarily in relation to patch turnover rates. Analyses of measured plant dispersal kernels across real landscapes should reveal whether these hypotheses indeed reflect reality. It is, however, difficult to obtain complete dispersal kernels from field measurements, as long-distance dispersal events are extremely difficult to measure and at the same time form a vital component of the dispersal strategy. For wind dispersal, mechanistic models have been developed that simulate complete dispersal kernels (including long-distance dispersal events), and these have withstood tests against field tracking and trapping data (e.g., CELC, (59); and WALD, (60)). Simulations of tree dispersal kernels using WALD indicate that forest trees such as *Liriodendron tulipifera* in oak-hickory forests, one of the largest and most continuous forest habitats in temperate regions, could have tails with power laws of  $\mu \sim 1.5$

(60) and species such as *Pinus taeda* are likely to have even fatter tails (55). These kernels are close to the long-distance dominated dispersal kernels that would be expected for species in continuous habitats. Simulations of wind dispersal using the CELC model for herbs characteristic of patchy and temporary wet grasslands ((59); data from (61)) generate dispersal kernels that are best fitted by 2D-Pareto distributions with  $\mu \sim 2$  (1.9 for *Cirsium dissectum*, 2.0 for *Hypochaeris radicata*). These values match the Lévy-like multi-scale dispersal kernels expected for species in successional, patchy habitats. For species typical of highly disturbed sites, such as *Tussilago farfara* in disturbed open sites, extreme long-distance dispersal has been reported - up to 4000 m in one generation (62), with a roughly estimated  $\mu$  of 0.59 (63). Another species typical of disturbed sites is *Cecropia obtusifolia*, a pioneer tree colonizing forest gaps. Seed trap data of this species in young forests are best fit by a 2D-Pareto distribution with  $\mu = 1.1$  (data from (64)). We summarize these first lines of evidence in Fig. 6.

By proposing to analyse plant seed dispersal as a search strategy for finding suitable habitat and using kernels with different scaling behaviour to compare dispersal strategies across different landscape dynamics, we break with the tradition of investigating dispersal propensity or only a single aspect of plant dispersal kernels such as the tail or modal distance. With methodological hurdles to the study of long-distance dispersal being overcome (55, 65), much research has focused on quantifying the tail of the dispersal kernel (5, 65–67). This has resulted in rapid progress in our understanding of, and ability to predict, the connectivity of plant populations in fragmented landscapes (68, 69) and has helped to explain species' abilities to track climate change (3, 70) or become invasive (71). At the same time, other studies have focused on the mode of the dispersal distribution to facilitate cross-species comparisons (72), as modal distance is an attractive parameter to study, representing the distance where most seeds end up and being far easier to measure. We however stress that *the entire dispersal kernel* defines the movement strategy of plants, and as such is relevant for local, landscape-scale and global species survival. Such an integrated approach to plant dispersal has also been advocated in the general 'movement ecology paradigm' (73), and an important first step in making large cross-species comparisons of entire dispersal kernels has recently been taken (11). The simplicity of our approach, which uses a flexible dispersal function parameterized by a single parameter,  $\mu$ , facilitates further comparisons across large numbers of species with widely differing dispersal strategies, while also allowing for the exploration of relations between species' dispersal strategies and their traits, life history strategy or habitat characteristics.

As a final point, we hope our framework facilitates plant ecological research to benefit from conceptual advances in animal movement ecology. Promising future directions for plant ecological research include exploring how different costs of dispersal (e.g. due to investments in traits) modify the optimal search strategy (cf. (36)) and examining plant dispersal kernels for the existence of 'composite walks', which combine multiple movement types into one dispersal strategy (cf. (74)). The latter would be relevant in species with dispersal dimorphisms or species using multiple dispersal vectors. Another interesting direction would be to explore to what extent plant searches can be considered as 'informed searches'. There is a growing body of evidence that plants dispersed by animals, water, and wind utilize 'directed dispersal' strategies, in which they use environmental cues or select specific vectors that result in

disproportionate arrival of seeds at more suitable sites (75–77). In a recent study, ‘informed dispersal’ has been suggested as a strategy to escape competition and environmental stress (78). Thus, future research could explore these strategies in the light of ‘informed searches’ in plants, similar to how animals use cues to guide their search towards suitable sites (cf. (79)). Insights in how these factors shape the evolution of dispersal strategies, and progress in knowledge of dispersal mechanisms can mutually inspire each other, and thereby improve the understanding and quantification of dispersal in plants.

## Conclusions

Our results clearly show that the full range of dispersal kernels, from extreme long-distance to short distance dispersal, can be adaptive, depending on the spatiotemporal habitat distribution across the landscape. Intermediate landscape dynamics and fragmentation would lead to the most complex and heterogeneous (multi-scale) kernels in terms of seed distributions. These multiple scales reflect an intensive-extensive search trade-off that determines the success rates of habitat encounter, kin avoidance, and colonization of new patches. Our analysis can serve as a framework that generates null hypotheses for dispersal strategies of plant species based on the spatiotemporal distribution of their habitat that can be used to analyse and compare plant dispersal data.

## Abbreviations

2D	two-dimensional
ESS	evolutionarily stable strategy
FFT	fast-fourier transform
IPD	inter-patch distance
NN	nearest neighbour
PIP	pairwise invasability plot
PS	patch size
PT	patch turnover rate
U	uniform

# Declarations

**Ethics approval and consent to participate** – Not applicable.

**Consent for publication** – Not applicable.

**Availability of data and materials** – The model code will be made available on Github; the model data supporting the results will be archived in the public repository Dryad.

**Competing interests** – The authors declare that they have no competing interests.

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**Authors' contributions** – JT and MBS conceived the idea. JT, MdJ and MBS designed the study. JT performed the modelling work and analysed output data in collaboration with MdJ, MBS and FB. JT wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

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# References

1. Damschen EI, Baker DV, Bohrer G, Nathan R, Orrock JL, Turner JR, et al. How fragmentation and corridors affect wind dynamics and seed dispersal in open habitats. *Proc Natl Acad Sci U S A*. 2014 Mar;4(9):3484–9. 111(.
2. Ozinga WA, Roemermaann C, Bekker RM, Prinzing A, Tamis WLM, Schaminee JHJ, et al. Dispersal failure contributes to plant losses in NW Europe. *Ecol Lett*. 2009 Jan;12(1):66–74.
3. Nathan R, Katul GG, Bohrer G, Kuparinen A, Soons MB, Thompson SE, et al. Mechanistic models of seed dispersal by wind. *Theor Ecol*. 2011 May;4(2)(1):113–32.
4. Renton M, Shackelford N, Standish RJ. Habitat restoration will help some functional plant types persist under climate change in fragmented landscapes. *Glob Change Biol*. 2012 Jun;18(6):2057–70.
5. Carlo TA, Garcia D, Martinez D, Gleditsch JM, Morales JM. Where do seeds go when they go far? Distance and directionality of avian seed dispersal in heterogeneous landscapes. *Ecology*. 2013 Feb;94(2):301–7.
6. Pazos GE, Greene DF, Katul G, Bertiller MB, Soons MB. Seed dispersal by wind: towards a conceptual framework of seed abscission and its contribution to long-distance dispersal. *J Ecol*. 2013 Jul;101(4):889–904.
7. Jansen PA, Visser MD, Wright SJ, Rutten G, Muller-Landau HC. Negative density dependence of seed dispersal and seedling recruitment in a Neotropical palm. *Ecol Lett*. 2014 Sep;17(9):1111–20.

8. Kleyheeg E, Treep J, de Jager M, Nolet BA, Soons MB. Seed dispersal distributions resulting from landscape-dependent daily movement behaviour of a key vector species, *Anas platyrhynchos*. *J Ecol*. 2017 Sep;105(5):1279–89.
9. Mokany K, Prasad S, Westcott DA. Loss of frugivore seed dispersal services under climate change. *Nat Commun*. 2014 May;5:3971.
10. Moran-Lopez T, Fernandez M, Luis Alonso C, Flores-Renteria D, Valladares F, Diaz M. Effects of forest fragmentation on the oak-rodent mutualism. *Oikos*. 2015 Nov;124(11):1482–91.
11. Bullock JM, Gonzalez LM, Tamme R, Gotzenberger L, White SM, Partel M, et al. A synthesis of empirical plant dispersal kernels. *J Ecol*. 2017 Jan;105(1):6–19.
12. Ronce O. How does it feel to be like a rolling stone? Ten questions about dispersal evolution. In: *Annual Review of Ecology Evolution and Systematics*. Palo Alto: Annual Reviews; 2007. pp. 231–53.
13. Duputie A, Massol F. An empiricist's guide to theoretical predictions on the evolution of dispersal. *Interface Focus*. 2013 Dec;6(6):20130028. 3(.
14. Hamilton W, May R. Dispersal in Stable Habitats. *Nature*. 1977;269(5629):578–81.
15. Comins H, Hamilton W, May R. Evolutionarily Stable Dispersal Strategies. *J Theor Biol*. 1980;82(2):205–30.
16. Howe H, Smallwood J. Ecology of Seed Dispersal. *Annu Rev Ecol Syst*. 1982;13:201–28.
17. Janzen D. Dispersal of Small Seeds by Big Herbivores - Foliage Is the Fruit. *Am Nat*. 1984;123(3):338–53.
18. Frank S. Dispersal Polymorphisms in Subdivided Populations. *J Theor Biol*. 1986 Oct 7;122(3):303–9.
19. Gandon S. Kin competition, the cost of inbreeding and the evolution of dispersal. *J Theor Biol*. 1999 Oct 21;200(4):345–64.
20. Perrin N, Mazalov V. Dispersal and inbreeding avoidance. *Am Nat*. 1999 Sep;154(3):282–92.
21. Perrin N, Mazalov V. Local competition, inbreeding, and the evolution of sex-biased dispersal. *Am Nat*. 2000 Jan;155(1):116–27.
22. Levin SA, Muller-Landau HC, Nathan R, Chave J. The ecology and evolution of seed dispersal: A theoretical perspective. *Annu Rev Ecol Evol Syst*. 2003;34:575–604.
23. Cheptou P-O, Massol F. Pollination Fluctuations Drive Evolutionary Syndromes Linking Dispersal and Mating System. *Am Nat*. 2009 Jul;174(1):46–55.
24. Comita LS, Queenborough SA, Murphy SJ, Eck JL, Xu K, Krishnadas M, et al. Testing predictions of the Janzen-Connell hypothesis: a meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. *J Ecol*. 2014 Jul;102(4):845–56.
25. Bolker BM, Pacala SW. Spatial moment equations for plant competition: Understanding spatial strategies and the advantages of short dispersal. *Am Nat*. 1999 Jun;153(6):575–602.
26. Rousset F, Gandon S. Evolution of the distribution of dispersal distance under distance-dependent cost of dispersal. *J Evol Biol*. 2002 Jul;15(4):515–23.

27. North A, Cornell S, Ovaskainen O. Evolutionary Responses of Dispersal Distance to Landscape Structure and Habitat Loss. *Evolution*. 2011 Jun;65(6):1739–51.
28. Reynolds AM. Beating the Odds in the Aerial Lottery: Passive Dispersers Select Conditions at Takeoff That Maximize Their Expected Fitness on Landing. *Am Nat*. 2013 Apr;181(4):555–61.
29. Turchin P. Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Animals and Plants. Massachusetts: Sinauer Associates Sunderland; 1998.
30. Méndez V, Campos D, Bartumeus F. Stochastic Foundations in Movement Ecology: Anomalous Diffusion, Front Propagation and Random Searches. Springer Science & Business Media; 2013.
31. Viswanathan GM, Afanasyev V, Buldyrev SV, Murphy EJ, Prince PA, Stanley HE. Levy flight search patterns of wandering albatrosses. *Nature*. 1996 May;30(6581):413–5. 381(.
32. Viswanathan GM, Buldyrev SV, Havlin S, da Luz MGE, Raposo EP, Stanley HE. Optimizing the success of random searches. *Nature*. 1999 Oct 28;401(6756):911–4.
33. Reynolds AM, Bartumeus F. Optimising the success of random destructive searches: Levy walks can outperform ballistic motions. *J Theor Biol*. 2009 Sep 7;260(1):98–103.
34. de Jager M, Weissing FJ, Herman PMJ, Nolet BA, van de Koppel J. Levy Walks Evolve Through Interaction Between Movement and Environmental Complexity. *Science*. 2011 Jun 24;332(6037):1551–3.
35. Bartumeus F, Raposo EP, Viswanathan GM, da Luz MGE. Stochastic Optimal Foraging: Tuning Intensive and Extensive Dynamics in Random Searches. *Plos One*. 2014 Sep 12;9(9):e106373.
36. Humphries NE, Sims DW. Optimal foraging strategies: Levy walks balance searching and patch exploitation under a very broad range of conditions. *J Theor Biol*. 2014 Oct 7;358:179–93.
37. Benhamou S. How many animals really do the Levy walk? *Ecology*. 2007 Aug;88(8):1962–9.
38. Reynolds AM, Rhodes CJ. The Levy flight paradigm: random search patterns and mechanisms. *Ecology*. 2009 Apr;90(4):877–87.
39. Kolzsch A, Alzate A, Bartumeus F, de Jager M, Weerman EJ, Hengeveld GM, et al. Experimental evidence for inherent Levy search behaviour in foraging animals. *Proc R Soc B-Biol Sci*. 2015 May 22;282(1807):20150424.
40. Franks NR, Richardson TO, Keir S, Inge SJ, Bartumeus F, Sendova-Franks AB. Ant search strategies after interrupted tandem runs. *J Exp Biol*. 2010 May 15;213(10):1697–708.
41. Bartumeus F, Campos D, Ryu WS, Lloret-Cabot R, Mendez V, Catalan J. Foraging success under uncertainty: search tradeoffs and optimal space use. *Ecol Lett*. 2016 Nov;19(11):1299–313.
42. Nathan R, Casagrandi R. A simple mechanistic model of seed dispersal, predation and plant establishment: Janzen-Connell and beyond. *J Ecol*. 2004 Oct;92(5):733–46.
43. Gilman SE, Urban MC, Tewksbury J, Gilchrist GW, Holt RD. A framework for community interactions under climate change. *Trends Ecol Evol*. 2010 Jun;25(6):325–31.
44. Soliveres S, Smit C, Maestre FT. Moving forward on facilitation research: response to changing environments and effects on the diversity, functioning and evolution of plant communities. *Biol Rev*.

- 2015 Feb;90(1):297–313.
45. Geritz S, Kisdi H, Meszina E, Metz G, a. J. J. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol Ecol*. 1998 Jan;12(1):35–57.
  46. Bonte D, Van Dyck H, Bullock JM, Coulon A, Delgado M, Gibbs M, et al. Costs of dispersal. *Biol Rev*. 2012 May 1;87(2):290–312.
  47. Tilman D. Competition and Biodiversity in Spatially Structured Habitats. *Ecology*. 1994 Jan;75(1):2–16.
  48. Kisdi E, Geritz S, a. H. On the coexistence of perennial plants by the competition-colonization trade-off. *Am Nat*. 2003 Feb;161(2):350–4.
  49. Muller-Landau HC. The tolerance-fecundity trade-off and the maintenance of diversity in seed size. *Proc Natl Acad Sci U S A*. 2010 Mar;2(9):4242–7. 107(.
  50. Cheptou P-O, Carrue O, Rouifed S, Cantarel A. Rapid evolution of seed dispersal in an urban environment in the weed *Crepis sancta*. *Proc Natl Acad Sci*. 2008 Mar 11;105(10):3796–9.
  51. Cody ML, Overton JM. Short-term evolution of reduced dispersal in island plant populations. *J Ecol*. 1996 Feb;84(1):53–61.
  52. Kavanagh PH, Burns KC. The repeated evolution of large seeds on islands. *Proc R Soc B-Biol Sci*. 2014 Jul 7;281(1786):20140675.
  53. Cheptou P-O, Hargreaves AL, Bonte D, Jacquemyn H. Adaptation to fragmentation: evolutionary dynamics driven by human influences (vol 372, 20160037, 2016). *Philos Trans R Soc B-Biol Sci*. 2017 Apr 5;372(1717):20160541.
  54. Colas B, Olivieri I, Riba M. *Centaurea corymbosa*, a cliff-dwelling species tottering on the brink of extinction: A demographic and genetic study. *Proc Natl Acad Sci U S A*. 1997 Apr 1;94(7):3471–6.
  55. Nathan R, Katul GG, Horn HS, Thomas SM, Oren R, Avissar R, et al. Mechanisms of long-distance dispersal of seeds by wind. *Nature*. 2002 Jul;418(6896):409.
  56. Bullock JM, Clarke RT. Long distance seed dispersal by wind: measuring and modelling the tail of the curve. *Oecologia*. 2000 Sep;124(4):506–21.
  57. HilleRisLambers J, Clark JS, Beckage B. Density-dependent mortality and the latitudinal gradient in species diversity. *Nature*. 2002 Jun 13;417(6890):732–5.
  58. Bell T, Freckleton RP, Lewis OT. Plant pathogens drive density-dependent seedling mortality in a tropical tree. *Ecol Lett*. 2006 May;9(5):569–74.
  59. Soons MB, Nathan R, Katul GG. Human Effects on Long-Distance Wind Dispersal and Colonization by Grassland Plants. *Ecology*. 2004;85(11):3069–79.
  60. Katul GG, Porporato A, Nathan R, Siqueira M, Soons MB, Poggi D, et al. Mechanistic analytical models for long-distance seed dispersal by wind. *Am Nat*. 2005 Sep;166(3):368–81.
  61. Soons MB, Messelink JH, Jongejans E, Heil GW. Habitat fragmentation reduces grassland connectivity for both short-distance and long-distance wind-dispersed forbs. *J Ecol*. 2005 Dec;93(6):1214–25.

62. Bakker D. A comparative life history of *Cirsium arvense* (L.) Scop. and *Tussilago farfara* L., the most troublesome weeds in the newly reclaimed polders of the former Zuiderzee. In: *The Biology of Weeds*. Oxford: Blackwell.
63. Willson M. Dispersal, Mode, Seed Shadows, and Colonization Patterns. *Vegetatio*. 1993 Jun;108:261–80.
64. Alvarezbuylla E, Martinezramos M. Seed Bank Versus Seed Rain in the Regeneration of a Tropical Pioneer Tree. *Oecologia*. 1990;84(3):314–25.
65. Jones FA, Muller-Landau HC. Measuring long-distance seed dispersal in complex natural environments: an evaluation and integration of classical and genetic methods. *J Ecol*. 2008 Jul;96(4):642–52.
66. Nathan R, Schurr FM, Spiegel O, Steinitz O, Trakhtenbrot A, Tsoar A. Mechanisms of long-distance seed dispersal. *Trends Ecol Evol*. 2008 Nov;23(11):638–47.
67. Gillespie RG, Baldwin BG, Waters JM, Fraser CI, Nikula R, Roderick GK. Long-distance dispersal: a framework for hypothesis testing. *Trends Ecol Evol*. 2012 Jan;27(1):47–56.
68. Herrmann JD, Carlo TA, Brudvig LA, Damschen EI, Haddad NM, Levey DJ, et al. Connectivity from a different perspective: comparing seed dispersal kernels in connected vs. unfragmented landscapes. *Ecology*. 2016 May;97(5):1274–82.
69. Auffret AG, Rico Y, Bullock JM, Hooftman DAP, Pakeman RJ, Soons MB, et al. Plant functional connectivity - integrating landscape structure and effective dispersal. *J Ecol*. 2017 Nov;105(6):1648–56.
70. Kremer A, Ronce O, Robledo-Arnuncio JJ, Guillaume F, Bohrer G, Nathan R, et al. Long-distance gene flow and adaptation of forest trees to rapid climate change. *Ecol Lett*. 2012 Apr;15(4):378–92.
71. Wilson JRJ, Dormontt EE, Prentis PJ, Lowe AJ, Richardson DM. Something in the way you move: dispersal pathways affect invasion success. *Trends Ecol Evol*. 2009 Mar;24(3):136–44.
72. Thomson FJ, Moles AT, Auld TD, Kingsford RT. Seed dispersal distance is more strongly correlated with plant height than with seed mass. *J Ecol*. 2011 Nov;99(6):1299–307.
73. Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, et al. A movement ecology paradigm for unifying organismal movement research. *Proc Natl Acad Sci U S A*. 2008 Dec 9;105(49):19052–9.
74. Morales JM, Haydon DT, Frair J, Holsiner KE, Fryxell JM. Extracting more out of relocation data: Building movement models as mixtures of random walks. *Ecology*. 2004 Sep;85(9):2436–45.
75. Fraaije RGA, ter Braak CJF, Verduyn B, Verhoeven JTA, Soons MB. Dispersal versus environmental filtering in a dynamic system: drivers of vegetation patterns and diversity along stream riparian gradients. *J Ecol*. 2015 Nov;103(6):1634–46.
76. Soons MB, de Groot GA, Cuesta Ramirez MT, Fraaije RGA, Verhoeven JTA, de Jager M. Directed dispersal by an abiotic vector: wetland plants disperse their seeds selectively to suitable sites along the hydrological gradient via water. *Funct Ecol*. 2017 Feb;31(2):499–508.



77. Spiegel O, Nathan R. Empirical evaluation of directed dispersal and density-dependent effects across successive recruitment phases. *J Ecol.* 2012 Mar;100(2):392–404.
78. Martorell C, Martinez-Lopez M. Informed dispersal in plants: *Heterosperma pinnatum* (Asteraceae) adjusts its dispersal mode to escape from competition and water stress. *Oikos.* 2014 Feb;123(2):225–31.
79. Clobert J, Le Galliard J-F, Cote J, Meylan S, Massot M. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecol Lett.* 2009 Mar;12(3):197–209.

## Figures

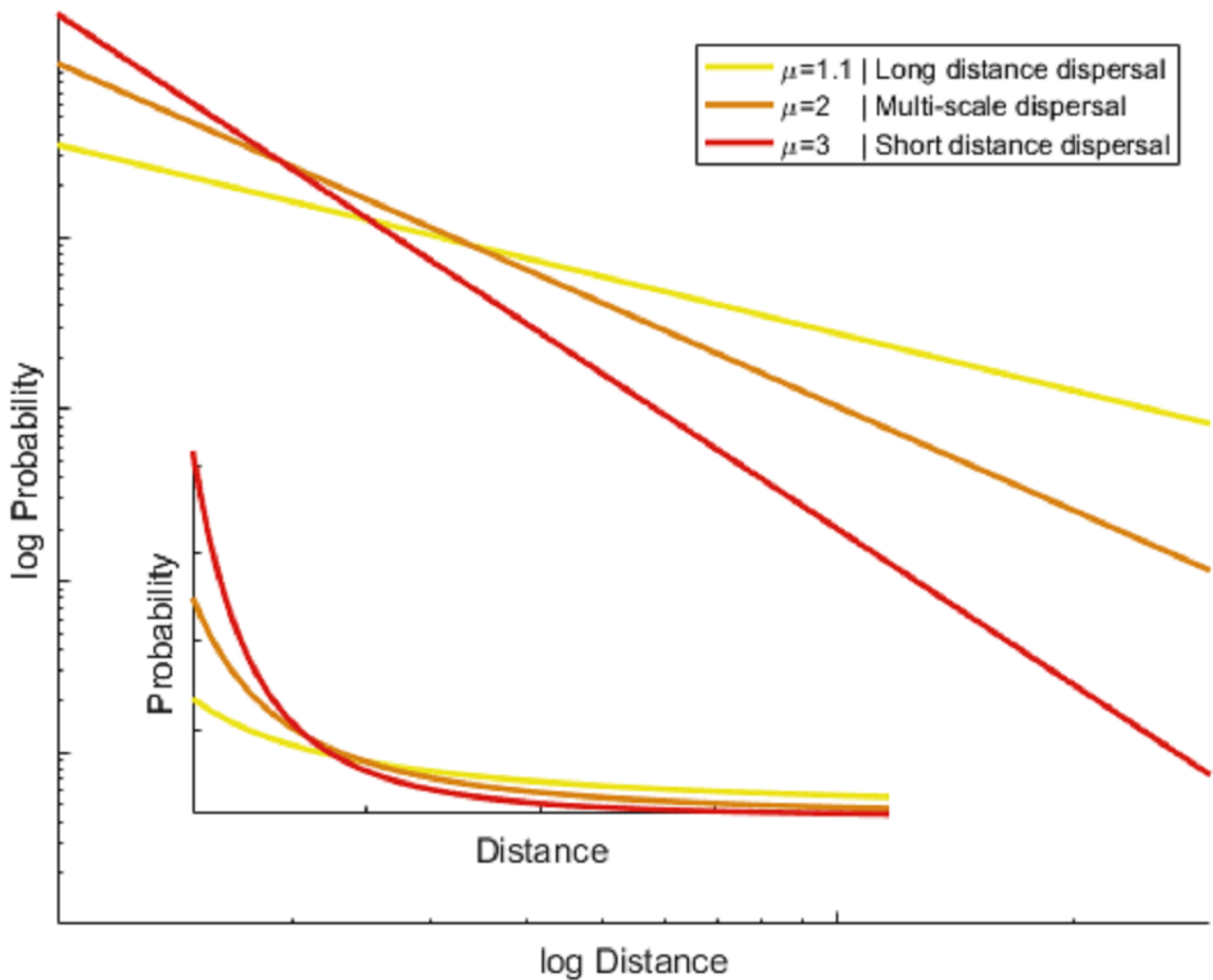
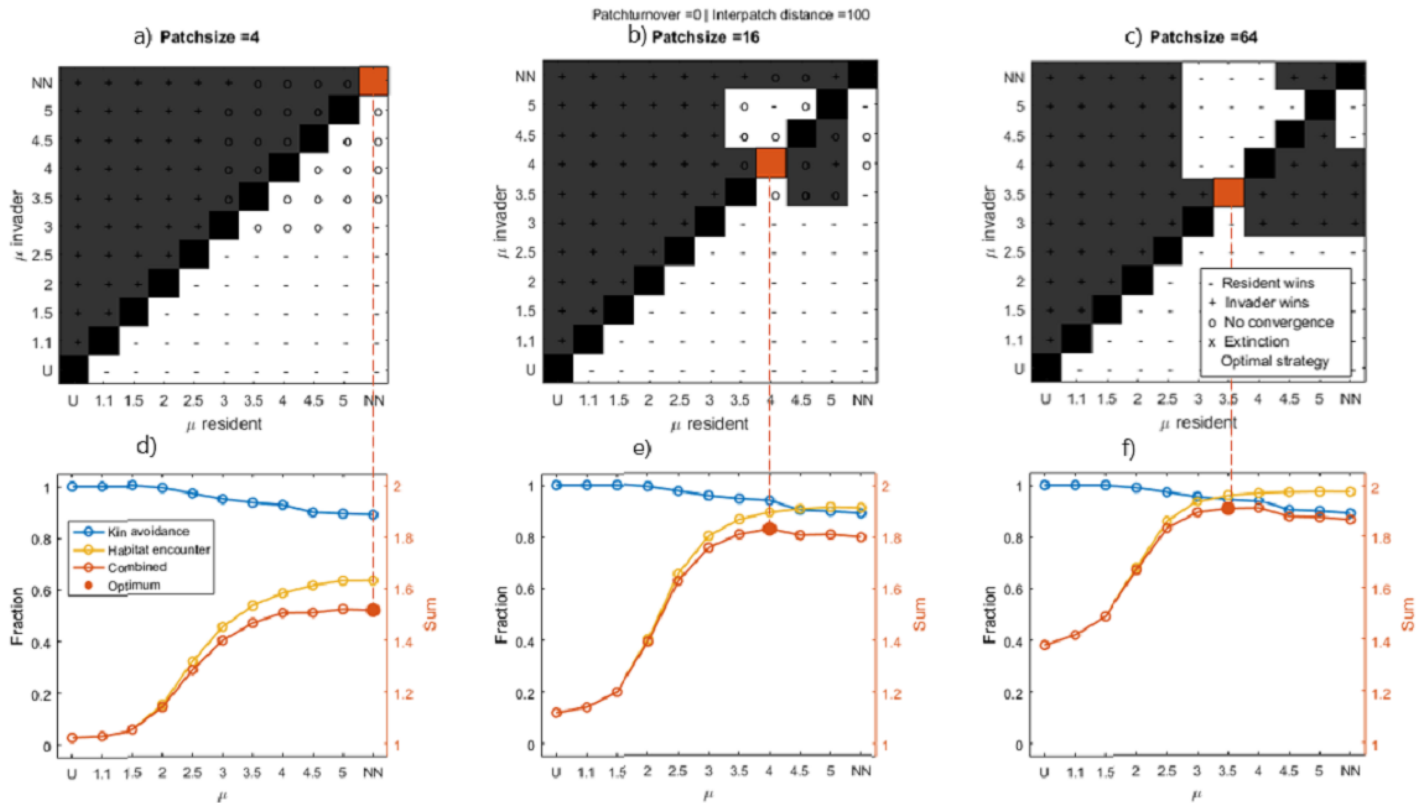


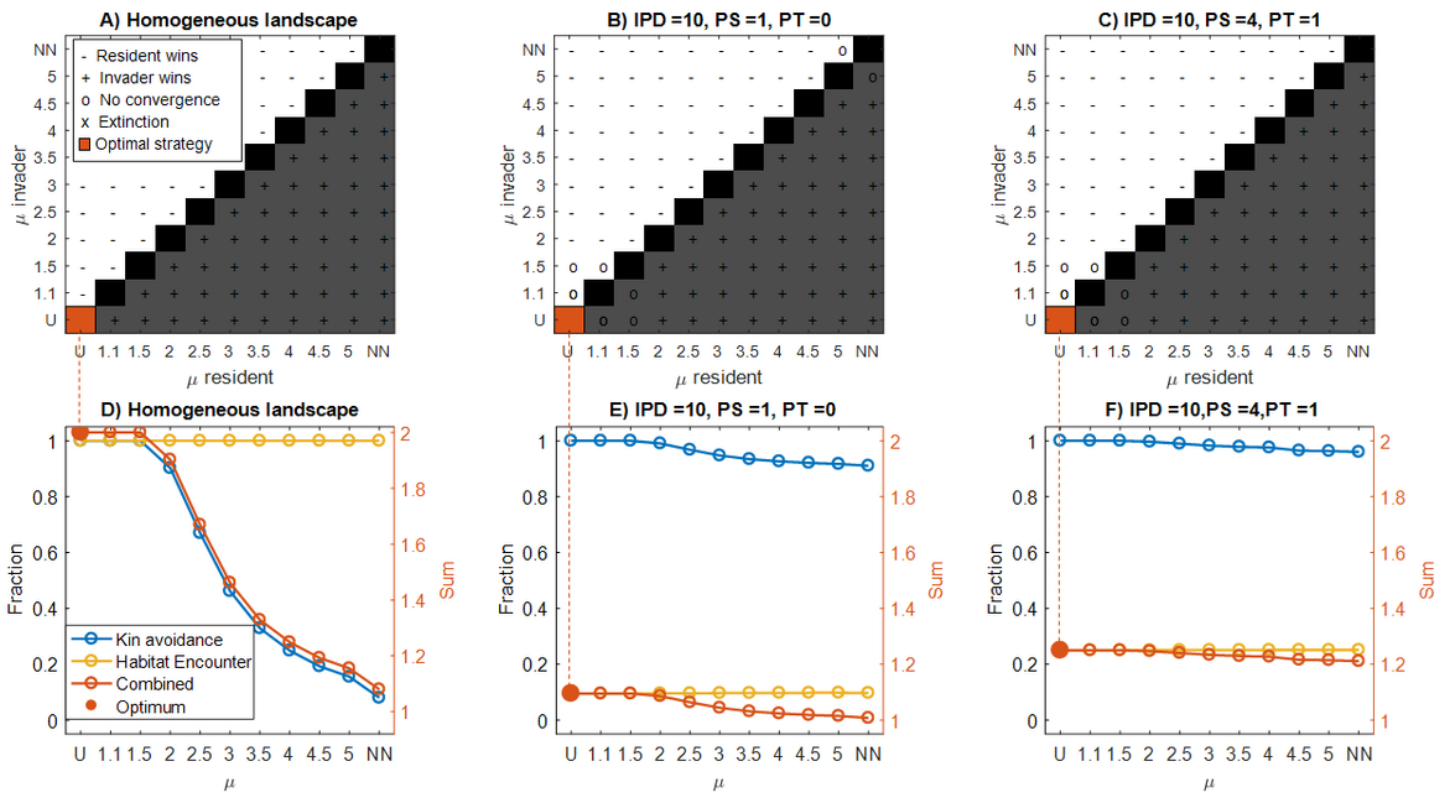
Figure 1

Move length distributions can be described using a Pareto distribution ( $p(x) \sim x^{-\mu}$ ). Shape parameter  $\mu$  determines whether dispersal strategies are characterized by a high probability of long-distance dispersal, by balancing long- and short-distance dispersal strategies, or dominated by short-distance dispersal only.



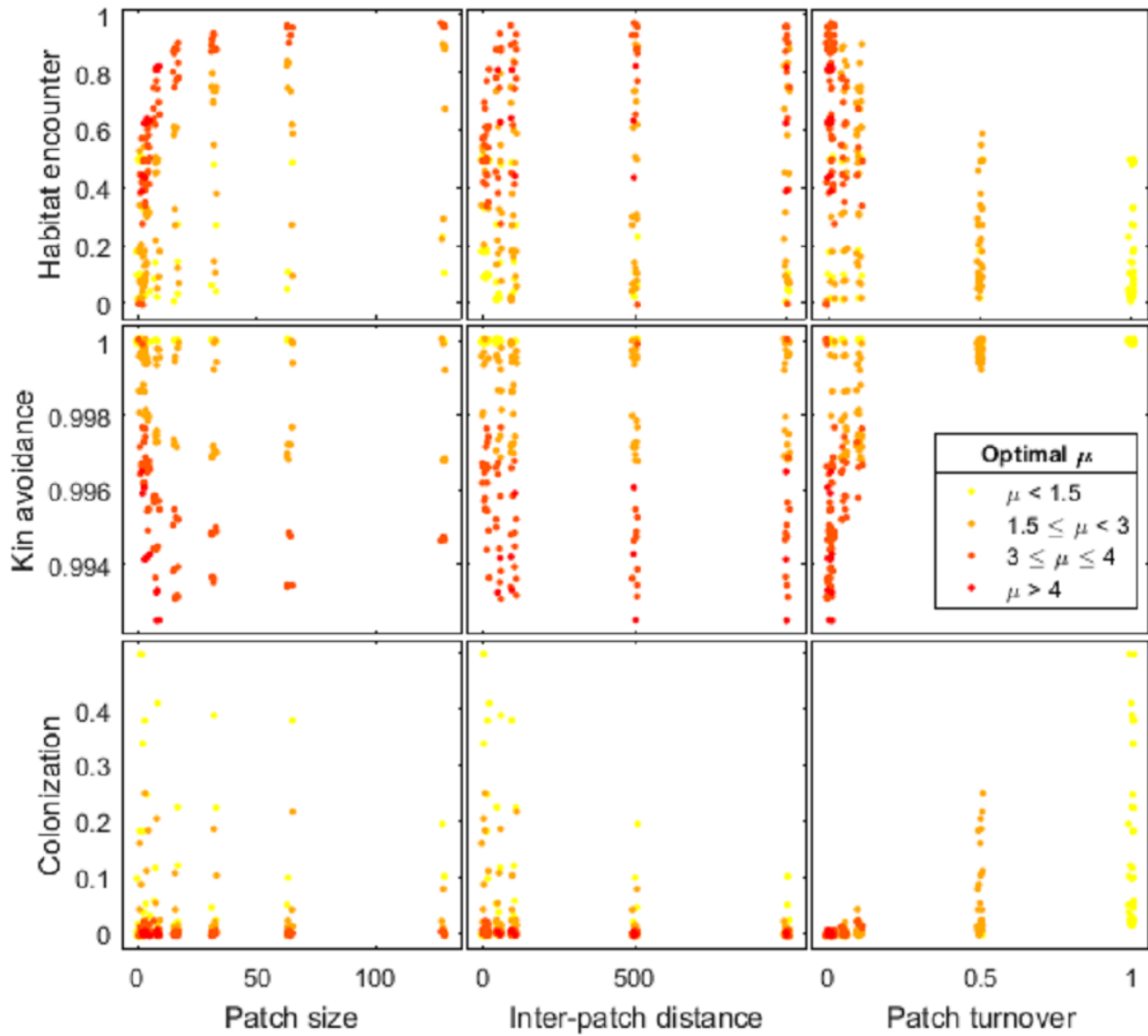
**Figure 2**

Upper panels (a-c): pairwise invasibility plots for dispersal strategies with different values of  $\mu$  (and the extreme cases of uniform and nearest-neighbour dispersal), highlighting the evolutionary stable strategy in red. Grey shading indicates the resident-invader combinations where the invasive type outcompetes the resident type in more situations than vice versa; a '+' indicates that this happened in at least 11 out of 12 replicate runs. No convergence ('0') means that either no winner was identified after 1000 generations or no stable outcome was achieved (winning 11 out of 12 replicate runs). 'X' indicates extinction of both types. Lower panels (d-f): seed fates for dispersal strategies with different values of  $\mu$ , showing on the left y-axis the fractions of seeds that landed in suitable habitat ('habitat encounter', yellow line), and the fractions of seeds that avoided kin competition ('kin avoidance', blue line). On the right y-axis, the sum of both fractions ('Combined', red line) and the optimal  $\mu$  are represented.



**Figure 3**

Upper panels (a-c): pairwise invasibility plots for dispersal strategies with different values of  $\mu$  (and the extreme cases of uniform and nearest-neighbour dispersal), highlighting the evolutionary stable strategy in red. Grey shading indicates the resident-invader combinations where the invasive type outcompetes the resident type in more situations than vice versa; a '+' indicates that this happened in at least 11 out of 12 replicate runs. No convergence ('0') means that either no winner was identified after 1000 generations or no stable outcome was achieved (winning < 11 out of 12 replicate runs). 'X' indicates extinction of both types. Lower panels (d-f): seed fates for dispersal strategies with different values of  $\mu$ , showing on the left y-axis the fractions of seeds that landed in suitable habitat ('habitat encounter', yellow line), and the fractions of seeds that avoided kin competition ('kin avoidance', blue line). On the right y-axis, the sum of both fractions ('Combined', red line) and optimal  $\mu$  are represented. IPD = Inter-patch distance, PS = patch size, PT = patch turnover rate.



**Figure 4**

Scatterplots showing the dispersal metrics shaping the dispersal kernel ('Habitat encounter', 'Kin avoidance', and 'Colonization') as a function of landscape parameters ('Patch size', 'Inter-patch distance', and 'Patch turnover'). The dots in the scatterplots represent the optimal dispersal kernels.

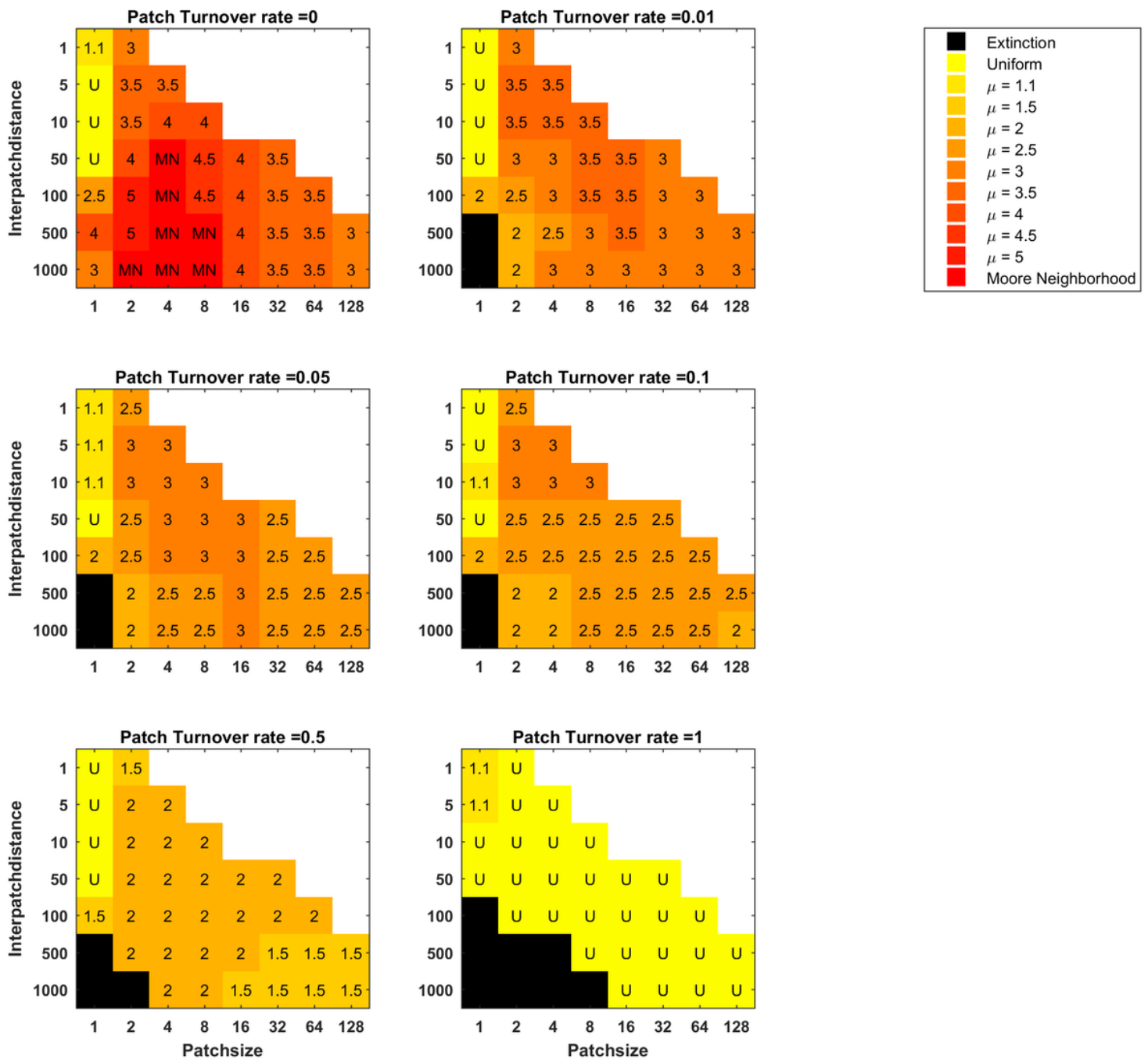
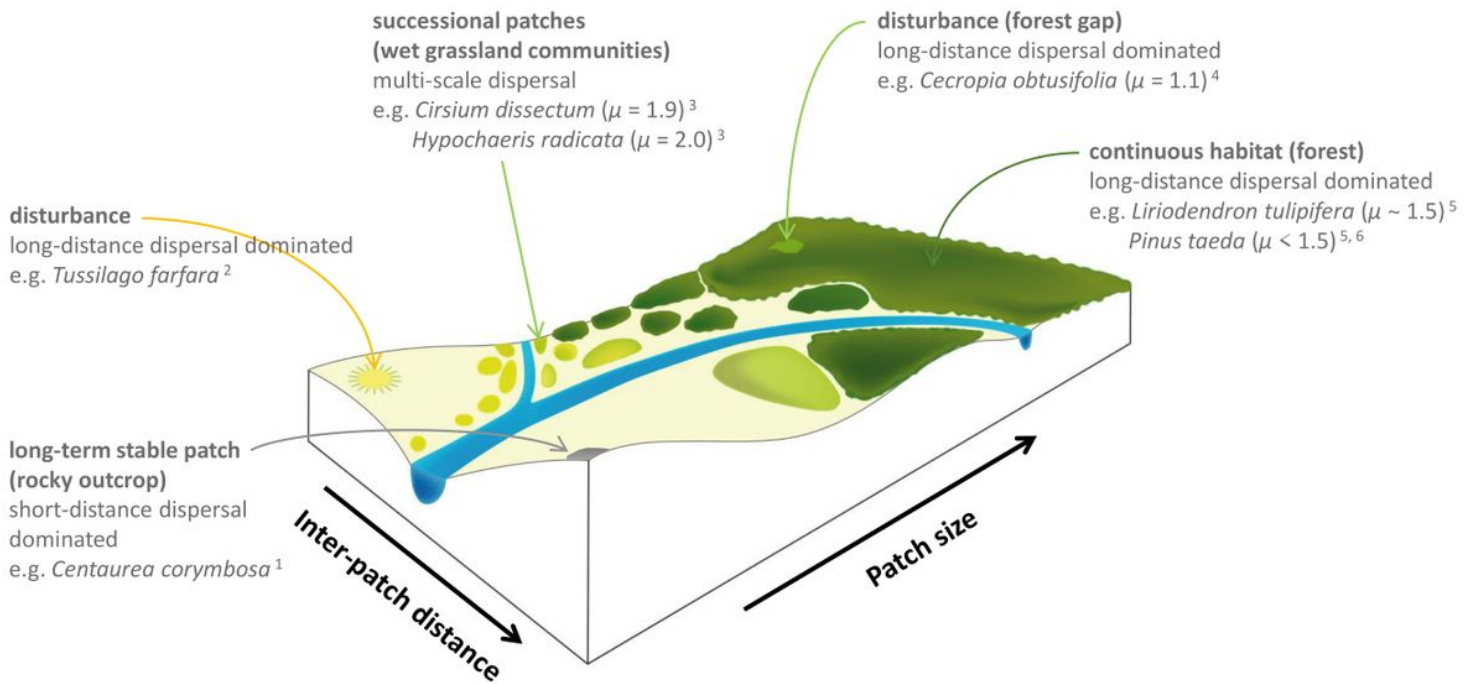


Figure 5

Heat maps showing the evolutionary stable dispersal strategies of all possible pairwise invasibility plots for landscapes with increasing patch turnover rates (from 0, top left, to 1, bottom right), as a function of both patch size and inter-patch distance.



**Figure 6**

Conceptual diagram showing a range of dynamic (disturbances, successional grassland, forest gaps) and static (rocky outcrops, forests) habitats across gradients in inter-patch distance and patch size. In static, but patchy habitats, short-distance dispersal ( $\mu > 3$ ) dominates dispersal strategies. Extreme long-distance dispersal ( $\mu \rightarrow 1$ ) is favoured in both stable, continuous habitats or in extremely unpredictable and dynamic landscapes. In patchy and dynamic habitats, Lévy-like, multi-scale dispersal strategies are optimal, with  $\mu$  correlated to average patch size, inter-patch distance and, most importantly, patch turnover rate. Species examples are given; data from 1Colas et al. 1997 (54), 2Bakker 1961 (62), 3Soons et al. 2005 (61), 4Alvarez -Buylla & Martinez-Ramos 1990 (64), 5Katul et al. 2005 (60), 6Nathan et al. 2002 (55).

## Supplementary Files

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