Flying cheap

Modelling the passive movement of plants and animals

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1

General Introduction

Jelle Treep

Movement of plants and animals in a changing world

Movement - the “change in the spatial location of the whole individual in time” (Nathan *et al.* 2008a) - is a key process determining the life history of individuals, the dynamics of populations and the distribution of species in many organisms, ranging from soil microbes to plants to whales. Organismal movement enables colonisation of habitat and gene flow between populations. Furthermore, movements have consequences for other taxa: moving animals can transport plant seeds and a wide range of other organisms (van Leeuwen *et al.* 2012; Soons *et al.* 2016), and plant seeds carry microbial communities (Barret *et al.* 2015). Mankind has long been fascinated by the diversity and creativity of biological movement. Evolution has led to an amazing repertoire of movement solutions, from the ability to rely on sheer speed (e.g. hunting cheetahs and falcons), to extremes in covering great distances (e.g. fish migration and dispersal of moss spores), and from achieving high efficiency (e.g. soaring birds and mud snails hitching a ride on waterbirds), to pure inventiveness (e.g. exploding cucumbers).

Because movement is fundamental to the ecology of species, understanding of movement is of particular importance in light of recent trends in biodiversity loss caused by habitat loss, deterioration, fragmentation, hunting, and climate change (Vitousek *et al.* 1997; Butchart *et al.* 2010). Movement is also fundamental to species invasions and the spread of toxic materials and diseases, which pose threats to biodiversity and human health. Adequate measures for managing and restoring landscapes and biodiversity in a changing world depends significantly on the understanding of the movement ecology of target species and vector species (species that transport other species, materials or diseases).

The field of movement ecology has been growing rapidly in the 21st century. The number of publications per year on movement ecology has grown exponentially, from 135 in 2000 to 602 in 2016, and a scientific journal fully dedicated to movement ecology was even established in 2013 (Nathan & Giuggioli 2013). To a large extent, this growth has been driven by advances in technologies for studying movement (Cagnacci *et al.* 2010; Börger 2016) e.g. GPS tracking, cameras and radar. A wealth of information is becoming available to study organismal movement in different environments across a wide range of spatiotemporal scales, and increasing volumes of this information are publicly available in (open source) databases. The rapid growth of movement observations has advanced (and sometimes changed) movement theories and changed research questions (Hays *et al.* 2016). Especially in large animals, which can be tracked with data loggers, movement research has shifted from population-level studies to detailed individual tracks for studying individual behaviour and consequences for population dynamics (Börger 2016).

Besides movement data, there is also a rapid increase of available environmental data originating from e.g. satellite- or avian-based remote sensors and Earth system models. These data can be annotated to movement tracks (Mandel *et al.* 2011), creating opportunities to study interactions between organismal movement and their environment in great detail (Shamoun-Baranes *et al.* 2010; Hays *et al.* 2016).

A major challenge in movement ecology is bridging the gap between theory and data (Kays *et al.* 2015). Simple theoretical models (or strategic models) aid in the understanding of general ecological processes and are usually inspired by observed patterns from the natural world. These theoretical models, however, are typically developed for theoretical, simplified, environments and do not adequately describe real world systems (Evans *et al.* 2013). On the contrary, observations provide information on a specific individual at a specific place at a specific time in a complex environment. This complexity arises from interacting (biotic and abiotic) processes across a range of spatiotemporal scales. Making predictions, e.g. about the effects of land cover change on changing movement patterns and species dynamics with both theoretical models and empirical models based on observations is, therefore, problematic. Complex mechanistic models (e.g. spatially explicit simulation models), however, are developed from conceptual ideas and constructed from variables that can be physically observed, making them more suitable for extrapolations (or predictions) across different contexts.

A combination of detailed movement data and mechanistic models can be used to evaluate hypotheses addressing interactions between organisms and their environment, identify important variables or species traits determining movements, or explore the consequences of movement for species dynamics - eventually resulting in high quality predictions. Increased computational power, through high performance computing clusters, now makes it possible to translate existing movement theory into (dynamical) models that can integrate multiple spatiotemporal scales. This, however, remains challenging due to the interdisciplinary nature of such studies and the large data volumes involved. This thesis aims to connect movement theory, movement data and environmental data. As such, it combines modelling and data analysis approaches to study the movement ecology of plant and bird species in relation to their environment. This chapter will briefly introduce a general framework regarding the movement ecology of birds and plants, and introduce the work performed in this thesis by positioning the main chapters within this framework.

Movement Ecology framework

Organisms move in distinct environments (air, water, soil) and in a variety of different ways, either actively (flying, swimming, walking, crawling) or passively (floating, gliding, hitching). Movement is required for a range of activities and functions: e.g. feeding, foraging, hunting, reproduction, protecting territory, escaping competition, exploring, escaping predation or colonising new habitats. These uses are all related to either maintaining or acquiring energy or involve interactions with conspecifics or other species and thus always related to the biotic and abiotic environment.

Birds are typically highly mobile throughout their lifetimes, transporting themselves by flying, walking or sometimes swimming. Their lifetime movement path consists of varying patterns that are related to different behavioural modes. Plants on the other hand are sessile organisms, typically only being able to move once in a lifecycle: during the seed stage. This movement is often referred to as seed dispersal, a type of movement defined as unidirectional movement away from the parent source (Levin *et al.* 2003b). Seed dispersal is passive, as seeds require an external energy source for transportation (although some plants have a ballistic form of dispersal in which seeds are ejected from the plant with force). This external energy source can be an abiotic dispersal vector such as wind or water, but seeds can also be transported by biotic vectors such as moving birds.

Despite the differences in life forms, common principles of movement apply to plants and birds, as well as many other organisms. The 'movement ecology paradigm', as developed by Nathan et al. (2008) (Fig. 1.1), provides a framework that can be used to better understand movement patterns in relation to driving forces that are responsible for the observed movement patterns. According to this framework, the movement path is a result of a combination of the 'Internal state' of the organism (*Why move?*, Fig. 1), the 'Navigation capacity' (*Where to move?)*, the 'Motion capacity' (*How to move?*) and external factors.

Why move?

Movements can be driven by several motivations that act on very short to very long timescales. These motivations are related to the internal state of an individual. For birds, the internal state is a combination of physiological and psychological state. For example: if energy levels run low the bird needs to feed and if a bird is in danger the bird needs to find safety. These are typically short term motivations, but also longer term motivations can play an important role, such as finding a partner, finding safe breeding grounds, or finding resource rich environments. An example outcome of such long term motivations is migratory behaviour. So besides movements driven by a direct payoff in terms of e.g. food, movement patterns can also be shaped by intrinsic motivations that have selective advantage over evolutionary timescales (Salewski & Bruderer 2007). Many internal state variables are related to external biotic and abiotic factors such as weather, food availability and interactions with others. Over time, birds change flight behaviour due to a changing internal state and thus changing motivations for movement.

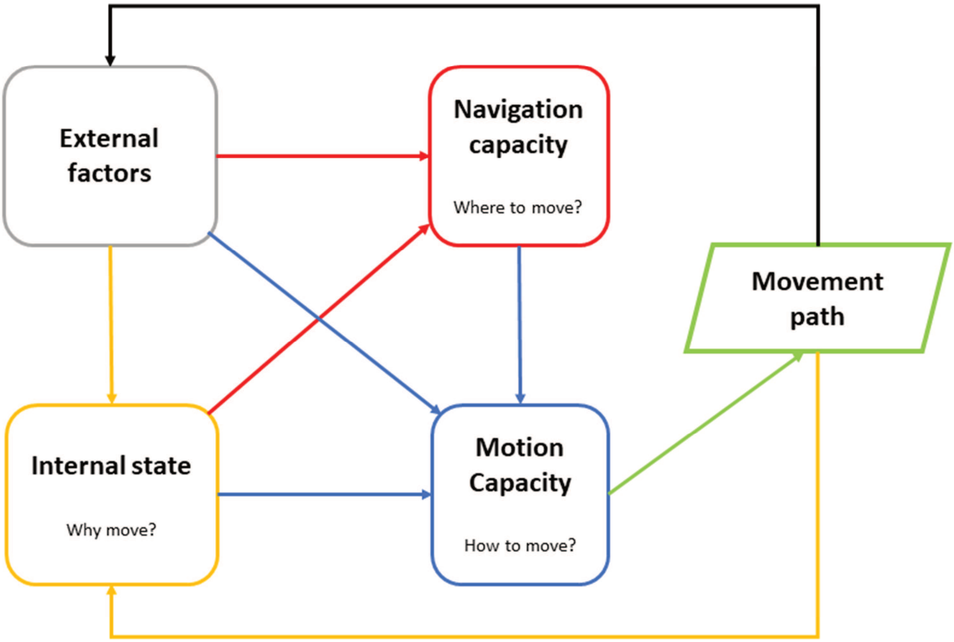

Figure 1.1. The general movement ecology framework (after Nathan et al. 2008).

Movement trajectories of plant seeds are not influenced by internal state dynamics since plants only move passively, and only during the seed stage. The internal (physiological) state of the parent plant determines the amount of resources allocated to and the timing of seed production. Short term motivations may be induced by competition and environmental stress, which can impact dispersal through phenotypic plasticity (Imbert & Ronce 2001). However, seed dispersal is mainly driven by long term motivations, which have shaped dispersal syndromes with a fitness advantage on evolutionary time scales. Plants disperse seeds to enable gene flow, colonize new habitats, and escape mortality and competition for resources in subsequent generations (Howe & Smallwood 1982). There, again, is a clear interaction with biotic and abiotic external factors such as the spatiotemporal distribution of resources, herbivores and competitors.

Where to move?

Organisms rely on information about where to move in order to achieve a desired goal. This can be information that is actively gathered by sensing, but can also be based on experience or even behaviour that is 'genetically coded' (Nathan *et al.* 2008a). Birds have excellent vision and can benefit from their own experience or follow conspecifics to navigate to a known target (e.g. breeding area, or prey). However, sometimes the target is unknown. For example, during foraging, there is a level of uncertainty involved due to stochasticity in the spatiotemporal distribution of resources. Stochastic search behaviour in animals has received considerable attention in recent years (Bartumeus *et al.* 2016). Many organisms with varying cognitive abilities have been found to exhibit movement patterns that optimize target encounter in stochastic environments (Bartumeus *et al.* 2010; Franks *et al.* 2010; De Jager *et al.* 2011; Kölzsch *et al.* 2015), which suggests selection for behaviour that optimizes search efficiency.

Motivations for seed dispersal are well known, but not much is known about **where** plants should disperse their seeds. Seeds should land on locations where their fitness is highest ('dispersal effectiveness'; Schupp and Jordano 2010). However, where seeds have the highest fitness depends on the spatiotemporal distribution of habitat, competitors, pathogens, herbivores, etc. (Soons *et al.* 2017). Theoretical models have been used to explore how qualitative gradients of these processes impact dispersal (Nathan & Casagrandi 2004). Environments can be highly variable in space and time, which means that there is uncertainty in the distribution of suitable habitat. Hence, there is a clear parallel with stochastic searches in animals. **Chapter 2** of this thesis uses random search theory from animal movement ecology to show how plant dispersal may optimize seed arrival and population persistence in a range of dynamic fragmented landscapes. We use a dynamic lattice model to explore how the shape of the dispersal kernel influences population dynamics in a two-species system. We suggest that consistency in the spatiotemporal variability of the environment selects for seed dispersal strategies that optimize fitness. Seed dispersal is passive, which means that the trajectory of a dispersed plant seed depends for a large part on the dispersal vector (which could be wind, water or moving animals). However, several traits influence the transport of seeds by a given vector. For instance, in the case of wind dispersal, a lower terminal fall velocity of seeds increases the time in the air and the probability of long-distance dispersal. We expect that a combination of traits optimizes short term and long term fitness of seeds through optimizing distributions of dispersed plant seeds.

How to move?

Most animals move by active locomotion. Birds can move by flying, walking or swimming. Since flying birds move in atmospheric flows, the efficiency of flight is strongly related to meteorological conditions (Shamoun-Baranes *et al.* 2010). One could imagine the atmosphere as an energy landscape with flows that benefit and obstruct movement, in which birds try to move with the lowest possible energetic cost of movement (Shepard *et al.* 2013). Examples of beneficial flows include tailwinds and thermal convection, whereas headwinds or strong turbulence greatly reduces flight efficiency. Especially large birds or birds that travel large distances have adapted well to flying efficiently by selecting proper weather conditions (Bohrer *et al.* 2012; McLaren *et al.* 2012), whereas flight efficiency may be less relevant in small birds flying short distances.

Plants seeds require an external energy source for movement (Nathan *et al.* 2008b). For instance, birds can act as an important vector of seed dispersal. Birds can transport seeds, either internally via ingestion or externally on their feathers and feet, and thereby are directly involved in the movement of plant seeds (Soons *et al.* 2016). Therefore, the movement patterns of seed-carrying birds dictate hitching seed dispersal distributions. If birds are flying between habitat sites, such as waterfowl travelling between wetlands, they provide opportunities for long-distance dispersal and, importantly, directed dispersal towards habitats similar to the site of origin (Carlo *et al.* 2013). The motion capacity of seeds consists of adaptive traits that influence dispersal patterns. Traits in bird-mediated dispersal include: capacity for attachment to plumage or feet, buoyancy, seed size and ability to survive the digestive tract (Vivian-Smith & Stiles 1994; Soons *et al.* 2008). In **chapter 4** we link seed traits to movement patterns of ducks in a dynamic model to show how seed dispersal by waterfowl can be quantified. This model provides the first integrated approach where seed dispersal kernels are quantified based on seed traits and movement data. This model framework allows for the determination of the relative importance of seed traits and movement patterns in determining seed dispersal distributions and arrival in suitable habitats.

Wind is another common dispersal vector for seeds (Nathan *et al.* 2008b). In contrast to animal-mediated dispersal, wind dispersal is not directed to certain habitat types. Seed trajectories depend on atmospheric flows (external factor) and coupling between seed and flow dynamics (Bohrer *et al.* 2008). Besides seed morphology, the exact moment and location of seed release may be important factors as wind speeds increase with altitude and are highly variable in time (Pazos *et al.* 2013). Thus, adaptive traits that are involved in wind dispersal include: terminal fall velocity of the seed (seed aerodynamics), seed release height and timing of seed release. These traits may change over evolutionary timescales to optimize the dispersal kernel. This may happen when certain dispersal kernel characteristics result in higher fitness (e.g. increased long-distance dispersal), as illustrated in **chapter 2**. In **chapter 3** we developed a model that integrates a seed trajectory model and a time-series of environmental (atmospheric) data to explore how non-random seed release interacts with realistic weather patterns in the Netherlands. We show how non-random timing of seed release can maximize dispersal distances.

External factors

All factors that determine the movement path interact with biotic and abiotic external factors. The internal state is determined by e.g. temperature, water availability, resource availability or presence of enemies. Navigation capacity can be dependent on the spatiotemporal distribution of e.g. food, predators, competitors, and beneficial or adverse meteorological conditions. As movements take place in a fluid medium, the motion capacity can be related to flow dynamics. For example, bird flight is tightly linked to atmospheric conditions, especially for large birds or birds travelling long-distances, as flight efficiency depends on air flows. For plants this is even more the case, as seeds disperse passively, which makes the relation between the motion capacity and external factors such as air flows very strong.

In **chapter 5,** we link GPS data of the soaring behaviour of griffon vultures to high resolution meteorological data. Here we solve an 'inverse problem' of determining air flow patterns. By understanding of movement ecology of birds and collecting high resolution movement data, one can glean relevant information about external factors, i.e. wind and thermal convection.

The 'movement ecology paradigm', discussed above, provides a powerful framework for linking various internal and external factors involved in the movement ecology of plants and animals. All organisms have an internal physiological (and potentially psychological) state that gives a motivation for movement. Organisms need information through direct sensing, experience or intrinsic drivers (or genetic "memory" by selection) for navigation (Nathan *et al.* 2008a). The motion capacity determines how to move effectively towards a target. All these factors link tightly together in an environmental context and ultimately determine the movement path that can be observed in nature.

In **chapter 6** the conclusions from chapters 2-5 are synthesized in the context of this movement ecology framework. I discuss how mechanistic models can help to integrate components of the framework to obtain a quantitative understanding of movement patterns and their most important drivers.

2

Plant dispersal as a search strategy: dynamic and fragmented landscapes select for multi-scale seed dispersal strategies

Jelle Treep, Monique de Jager, Frederic Bartumeus, Merel B. Soons

Abstract

Over the past decade, animal ecologists have identified multi-scale movement behaviour as a key search strategy across animal species. Surprisingly, the potential for evolution of such general movement strategies has not been explored for plants. We propose that seed dispersal in plants can be viewed as a strategic search for suitable habitat and that plants optimize the probability of finding such locations by evolving appropriate dispersal kernels. Using model simulations, we demonstrate how dispersal strategies optimize key dispersal trade-offs between finding habitat, avoiding kin competition, and colonizing new patches. These trade-offs depend strongly on landscape structure, resulting in multi-scale dispersal strategies, including Lévy-like dispersal, across a wide range of dynamic 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. Our findings reveal that multi-scale seed dispersal is optimal in fragmented landscapes and highlight the tight link between dispersal strategy and spatiotemporal habitat distribution. We provide a reference framework for the analysis of plant dispersal data. This helps to identify the evolutionary forces determining species' dispersal strategies and opens up new directions for future studies, including exploration of composite search behaviour and 'informed searches' in plant species with directed dispersal.

Introduction

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 (Damschen *et al.* 2008; Ozinga *et al.* 2009; Nathan *et al.* 2011a; Renton *et al.* 2012). This realisation has elevated plant dispersal to a research priority in recent years. Significant progress has been made in understanding the mechanisms of seed dispersal, including resultant seed dispersal distributions (e.g. Carlo *et al.* 2013; Pazos *et al.* 2013; Jansen *et al.* 2014; Kleyheeg *et al.* 2017) and how these may be affected by global changes (e.g. Bullock *et al.* 2012; Damschen *et al.* 2014; Mokany *et al.* 2014; Kleyheeg *et al*. 2017). Yet, while our knowledge of the mechanisms of plant seed dispersal is rapidly advancing, our understanding of the selective pressures responsible for the evolution of dispersal strategies lags behind. 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. Using a theoretical framework inspired by animal movement ecology, we show how recent conceptual developments in analysing animal movement data can help advance the field of plant dispersal ecology.

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. Key features of animal movement patterns are turning angles and displacement distributions (Turchin 1998; Méndez *et al.* 2013). Displacements or move length distributions can be described by inverse power-law relationships with a scaling exponent μ ranging from ~ 1 (promoting super-diffusive motion, where all step lengths are equally likely to occur) to > 3 (promoting Brownian motion, where short steps are abundant and long steps are rare). At an intermediate $\mu \sim 2$, many consecutive short-distance movements are infrequently alternated with long-distance movements, producing complex multi-scale movement patterns where many different spatial scales are well represented, albeit with different intensities. Here, the relationship between displacement lengths and frequency decays neither too quickly (so that one scale predominates) nor too slowly (so that all scales are equally frequent) (Viswanathan *et al.* 1996, 1999; Reynolds & Rhodes 2009; De Jager *et al.* 2011; Méndez *et al.* 2013). These complex multi-scale movement strategies are known as Lévy flights or walks (Viswanathan *et al.* 1996, 1999; Reynolds & Rhodes 2009; De Jager *et al.* 2011; Méndez *et al.* 2013). In a random search, the optimal move length distribution depends on the spatiotemporal distribution of targets being sought (e.g.

food, a mate etc.; Viswanathan *et al.* 1999; Bartumeus *et al.* 2014; Humphries & Sims 2014). Theoretical studies of search behaviour have shown that various optimal strategies may adequately balance intensive and extensive movement patterns, depending on the spatiotemporal environmental conditions (Benhamou 2007; Reynolds & Rhodes 2009; De Jager *et al.* 2011; Bartumeus *et al.* 2014; Humphries & Sims 2014). Importantly, this balance is determined not only by the tail or the mode, but the entire displacement length distribution. Experimental studies have shown that complex animal movement patterns that are not expected to be driven by taxis nor by high-cognitive processes, may indeed have intrinsic underlying patterns that optimize random search efficiency, thereby greatly enhancing individual fitness and species survival under uncertainty (Franks *et al.* 2010; De Jager *et al.* 2011, 2014; Kölzsch *et al.* 2015; Bartumeus *et al.* 2016).

Alghough these recent developments in random search theory have significantly advanced our understanding of the evolution and ecology of animal movement (Bartumeus *et al.* 2016), it is surprising that the potential for evolution of similar movement strategies has not been explored for plants. Do plants have movement strategies with similar general underlying patterns? Considering this, there are two major differences between animal movement and plant dispersal. First, animals move by way of consecutive steps and may use internal or external cues to adjust step length and direction as they go. In contrast, plants produce a number of propagules (seeds or fruits, hereafter collectively referred to as 'seeds') that each disperse by one displacement step with a given orientation. A second major difference is that animals move actively and thereby spend energy during movement, which means that longer steps have higher energy costs. For the vast majority of plant species, seeds move passively, and the cost of a displacement may not increase linearly with dispersal distance. However, in plant species with long-distance dispersal, longer dispersal distances often require specialized structures that need to be made by the plant and/or seed. For instance, in wind-dispersed species, plants may release seeds high above the canopy, have seed structures that slow down the fall rate, or have special connecting tissue between the plant and seed that determines seed release during favourable conditions (Nathan *et al.* 2002; Soons *et al.* 2004; Pazos *et al.* 2013). The frequent occurrence of such specialized structures implies that, in many plant species, increasing the probability of longer steps requires higher investment costs. We propose that the displacement length distribution (i.e. seed shadow 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 suggest that there is strong selective pressure to select for optimal dispersal kernels.

We provide a theoretical reference framework that identifies null models for optimal dispersal strategies in plant populations and explores the impact of spatiotemporal landscape structure (fragmentation and patch turnover dynamics) on optimal dispersal. We acknowledge that optimal plant dispersal strategies should match relevant biotic and abiotic factors determining eventual offspring success, such as the spatial structure of density-dependent mortality (Nathan & Casagrandi 2004), competition and facilitation (Gilman *et al.* 2010; Soliveres *et al.* 2014), as well as landscape heterogeneity (North & Ovaskainen 2007). However, in this study, we focus primarily on abiotic factors to derive fundamental null models, as we explore the effects of habitat fragmentation and patch turnover rates on optimal dispersal kernels. For landscapes of varying habitat fragmentation and patch turnover, we evaluate the efficiency of different dispersal strategies using a simple simulation model, where competing plant populations are equivalent in all traits except the shape of their dispersal kernels. These simulations illustrate how different combinations of habitat fragmentation and patch turnover rates impact dispersal efficiency and hence the evolution of dispersal strategies in plant populations.

Model and simulations

We developed a spatiotemporal lattice model to explore the evolution of dispersal strategies under isotropic conditions and generate a reference framework for optimal dispersal 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 of the plants. The model plants were completely similar entities (producing an equal number of seeds per individual and per time step) that only differed in the shape of their dispersal kernels. In each model-run, two populations with different dispersal kernels competed in a landscape with specified fragmentation and patch turnover characteristics. They 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 populations were redistributed over the landscape following these event-driven steps: 1) dispersal, 2) death, 3) patch turnover, and 4) colonization (see below). The population that remained after a number of generations was assumed to have a better dispersal strategy. Figure 2.1 provides a visualisation of a model run.

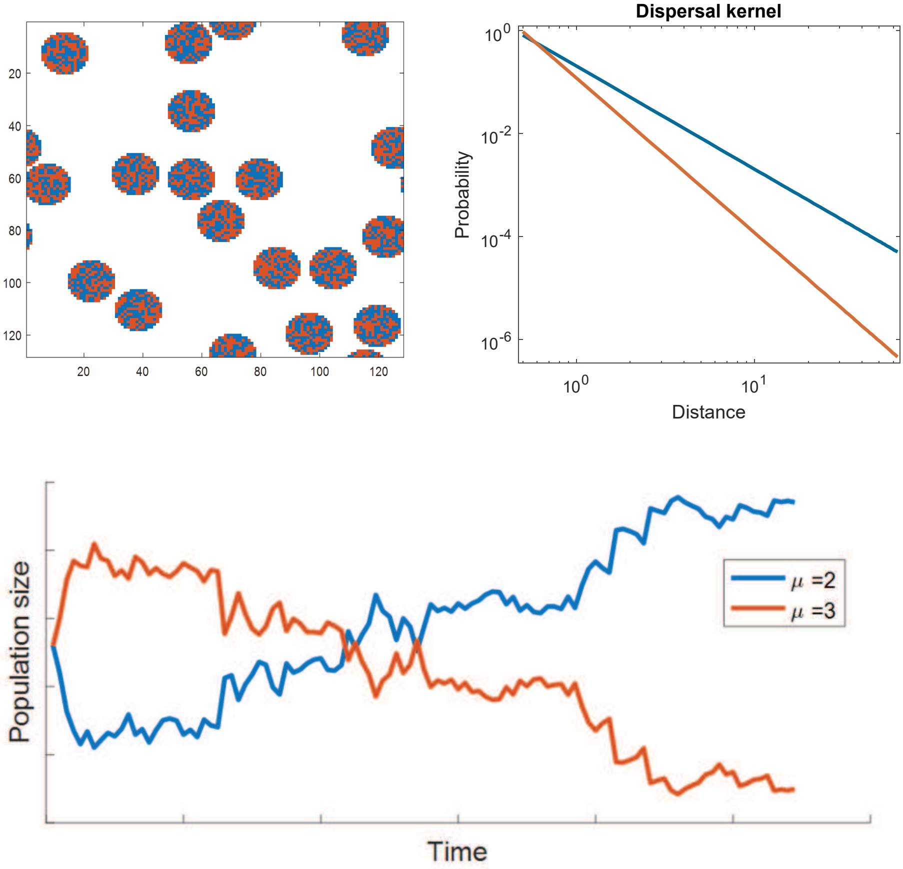

Figure 2.1. The top left panel represents a randomly generated initial landscape for patch size 8 and inter-patch distance 50 (note: for visualization purposes a domain of 128 by 128 grid cells is used here instead of 512). The top right panel shows examples of two 1D dispersal kernels on log-log scale (before transformation to 2D kernels) of the two species competing in a model run. The bottom panel shows the population size of both species as a function of time. In this specific run, the population with a relatively high probability of short distance dispersal (μ = 3) increases in size in the first generations. However, due to patch turnover, patches where this population dominates disappear and the better colonizer (μ = 2) eventually wins.

Initial conditions

In order to simulate spatiotemporal population dynamics of two competing plant populations, we constructed a lattice model with a 2D spatial domain of 512 by 512 grid cells. The landscape was simplified to have each grid cell represent either suitable or unsuitable habitat. Landscape configurations were generated randomly using a predefined patch size and inter-patch distance. Patches were circular-shaped and patch size was defined as patch diameter in number of grid cells. We defined a landscape's inter-patch distance as the average distance from the border of a patch to the border of the nearest patch in all directions. This distance is equal to the mean free path minus the patch radius. Mean free path (λ) relates to patch size as follows:

$$\lambda = \frac{N}{2L^2 r} \qquad \textit{Eq. 2.1}$$

where N is the number of patches, L^2 the size of the lattice and r the patch radius. Patches were randomly placed in the landscape so that they did not overlap, but could potentially adjoin other patches.

Each grid cell which was classified as habitat could be occupied by only a single individual from one of the two populations.

Dispersal

Each individual dispersed 100 seeds to neighbouring cells according to a truncated Pareto 2D kernel distribution (see Appendix S2.1 in Supporting Information for derivation of 2D form);

$$p(l) = \frac{1}{2\pi}\left[\frac{2-\mu}{{l_{max}}^{2-\mu} - {l_{min}}^{2-\mu}}\right] l^{-\mu} \qquad \textit{Eq. 2.2}$$

where l_{min} is the minimum distance (radius of a grid cell), l_{max} is the maximum distance (equal to the domain size) and μ is the scaling exponent. The scaling exponent determines the power-law decay of the dispersal kernel. The 2D dispersal kernels were predefined for an individual in the centre of the domain, bounded by the domain boundaries (l_{max}) and normalized, so that the probability over the entire domain summed to one. The 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 (equally distributed dispersal distances, $\mu \rightarrow 1$). For $\mu \sim 2$ (i.e., canonical Lévy), this kernel produces a highly heterogeneous, multi-scale distribution of dispersal distances. In our simulations, we used discrete values of μ ranging from 1.1 to 5 (Table 2.1). 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 μ) and dispersal only to the 8 nearest neighbours (Moore neighbourhood) in equal probabilities (as benchmark for maximum μ). In all cases, there was no dispersal to the grid cell of the parent plant (distance = 0). For each landscape, all possible combinations of two dispersal kernels were simulated.

The domain was isotropic and had periodic boundaries. Seed dispersal from all individuals of a population was calculated simultaneously by convolution using Fast Fourier Transformations (FFT) (Powell 2002).

Table 2.1. 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 μ)	U[1], 1.1 ,1.5, 2, 2.5, 3, 3.5, 4, 4.5, 5, MN[2]
Number of seeds per individual[3]	(10), 100, (1000), (10000)

[1] Alternative ('benchmark') kernel 1: uniform dispersal

[2] Alternative ('benchmark') kernel 2: Moore neighbourhood dispersal

[3] Number of seeds per individual was 100 in main simulations; 10, 1000, 10000 were used in sensitivity analyses only.

Death

After seed dispersal, all individuals died, thereby resembling semelparous species that have only a single reproductive event in their lifetime.

Patch turnover

Patch turnover was determined stochastically for each patch using a fixed probability of turnover per patch per time step (each time step equalling the time between two generations). When patch turnover occurred, the patch disappeared and a new patch was randomly placed at a different location in the lattice.

Colonization

Colonization of empty habitat cells by the dispersed seeds was simulated. We calculated the expected number of seeds arriving at a grid cell as the sum of the probability density functions of all individuals of this population (obtained using FFT), multiplied by the number of produced seeds. Using FFT is computationally much more efficient than simulation of discrete dispersal events, however, in doing so, one neglects some of the stochasticity naturally involved in the dispersal process. Instead, we introduced stochasticity in the translation of the continuous seed arrival expectations into discrete colonization events (as a grid cell can only hold one individual). First, we determined for both populations whether they colonized a certain grid cell. When the expected number of seeds of a population was above 1, the grid cell was colonized by this population. When the expected number was below 1, a random number determined whether the grid cell was colonized by this population or not; $X \sim U(0,1) < p_i$, where p_i is the expected number of seeds either from population 1 or 2. This resulted in three possible outcomes: 1) neither population colonized the grid cell, 2) one of the populations colonized the grid cell, or 3) both populations colonized the grid cell. When both populations colonized a grid cell, a second random number determined which population would occupy the grid cell in the next time step; $X \sim U(0,1) < p_1/(p_1 + p_2)$. An individual of population 1 or 2 occupied the grid cell when $X = 1$ or $X = 0$, respectively.

Simulations

We characterized landscapes by the parameters patch size, inter-patch distance, and patch turnover rate, and determined how optimal dispersal kernels depend on these landscape characteristics. Table 2.1 shows the parameter ranges used in our simulations.

For each set of parameter combinations, model simulations ran until one of the populations was outcompeted. We assumed that a population was outcompeted when it occupied less than 5% of all habitat grid cells, while the other population increased to at least 80% of all habitat grid cells or reached a stable equilibrium (no significant decrease over 200 generations). If both populations were maintained after 1000 generations, we assigned no 'winner' and scored this as no strong selection on dispersal strategy. For each simulated landscape, all possible combinations of dispersal kernels were used to determine the optimal strategy. We repeated each simulation 12 times to test the robustness of the 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 (Geritz *et al.* 1998). From each pairwise invasibility plot, we extracted the optimal dispersal strategy (expressed by parameter μ from the 2D Pareto distribution) and used this to identify changes of optimal strategy in relation to patch size, inter-patch distance, and patch turnover rate.

Robustness tests

We performed a sensitivity analysis to plant seed number, by varying the amount of seeds dispersed per plant several orders of magnitude, representing a realistic range for annual plant species (10, 1000, 10000) (Jakobsson & Eriksson 2000). We ran these simulations for a sub-set of 10 landscape configurations, which were selected to cover all interesting patterns in the parameter space, and compared these results to the results for seed number = 100. In general, seed number hardly effected optimal dispersal strategies (see Appendix S2.2) and we present only results for seed number = 100.

We also tested whether our FFT approach affected our results compared to purely stochastic dispersal events. To do so we ran the model for a subset of 2 landscape configurations using stochastic discrete dispersal events. In these simulations, we sampled dispersal events of individual seeds from the 2D-Pareto kernel, and summed the total amount of arrived seeds in each grid cell instead of summing up FFT-derived probabilities. We found no qualitative differences in optimal dispersal between the two model types (see Appendix S2.3). We therefore only present the results of the FFT models.

Dispersal metrics

We expected that, similar to random searches by animals, the optimal dispersal kernels would adequately balance a complex trade-off between local and non-local dispersal conditioned to the landscape configuration (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 - 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

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 optimal, depending on the spatiotemporal distribution of habitat in the landscape. The spatiotemporal distribution of habitat determines the optimal balance between local and non-local dispersal following trade-offs in habitat encounter, kin avoidance and colonization. In general, we found that in the most static as well as in the most unpredictable landscapes, the two extremes (nearest-neighbour dispersal and uniform dispersal, respectively) are most likely to be optimal. When patch distributions are dynamic and fragmented, the trade-off between local and non-local dispersal results in a wide range of multi-scale dispersal strategies (including Lévy-like Pareto kernels), 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 optimal (Fig. 2.2 a-c). The shape of these short-distance dispersal kernels varies with patch size, with decreasing patch sizes corresponding to shorter dispersal distances (larger μ) (Fig. 2.2c). These movement strategies are essentially driven by the optimization of both habitat encounter and kin avoidance (Fig. 2.1d-f). With increasing probability of short-distance dispersal, averaged habitat encounter increases considerably as more seeds land in the patch of origin. At the same time, kin avoidance decreases, albeit to a lesser extent. 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.

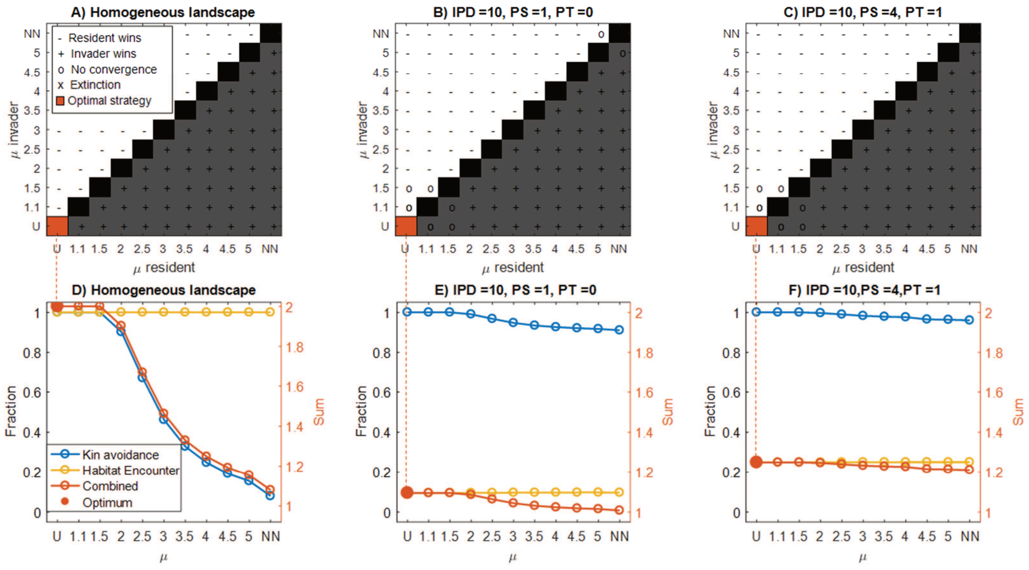

Figure 2.2. Upper panels (a-c): pairwise invasibility plots for dispersal strategies with different values of μ, highlighting the evolutionary stable strategy in red. Grey shading indicates the resident-invader combinations where the invasive population outcompetes the resident population in more situations 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 populations. Lower panels (d-f): seed fates for dispersal strategies with different values of μ, 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 μ are represented.

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 so patches able to hold one individual only) or in time (patch turnover rate = 1), dispersal strategies dominated by long-distance distance dispersal were optimal (Fig. 2.3a-c). In these situations, dispersal strategies are driven exclusively by avoidance of kin competition (Fig. 2.3d-f). Maximizing habitat encounter does not contribute to selecting the optimal strategy, because habitat encounter is similar for all possible values of μ, either because the landscape consists of homogeneous habitat, or because the habitat distribution is so unpredictable that no μ optimizes habitat encounter better than another (Fig. 2.3d-f).

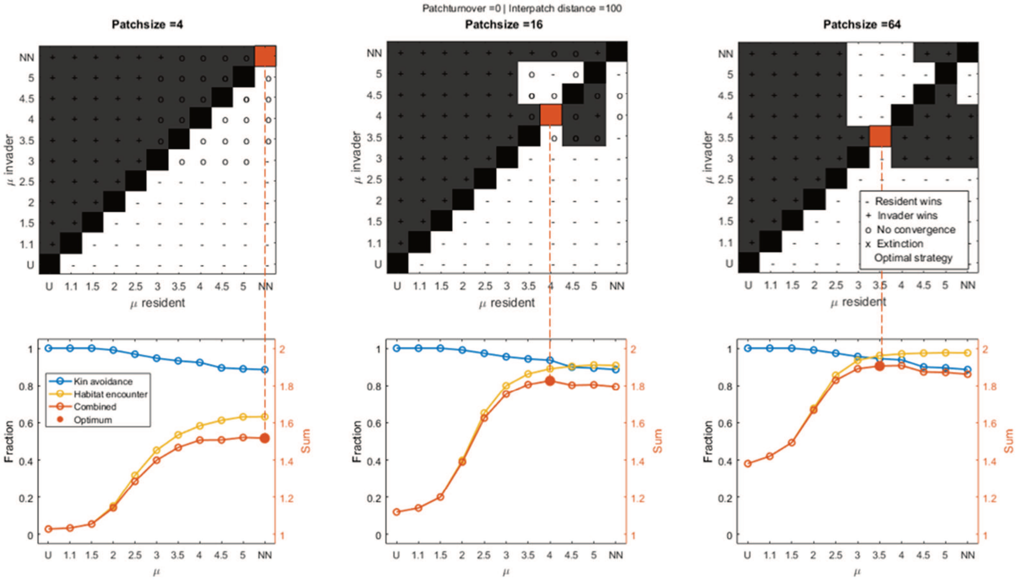

Figure 2.3. Upper panels (a-c): pairwise invasibility plots for dispersal strategies with different values of μ, highlighting the evolutionary stable strategy in red. Grey shading indicates the resident-invader combinations where the invasive population outcompetes the resident population in more situations 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 populations. Lower panels (d-f): seed fates for dispersal strategies with different values of μ, 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 μ are represented.

Multi-scale dispersal strategies

In many landscapes, habitat distribution is patchy and dynamic to some extent. In these situations, 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. 2.4, Appendix S2.4). The optimal strategies for these landscapes, as reflected by μ, are most strongly determined by

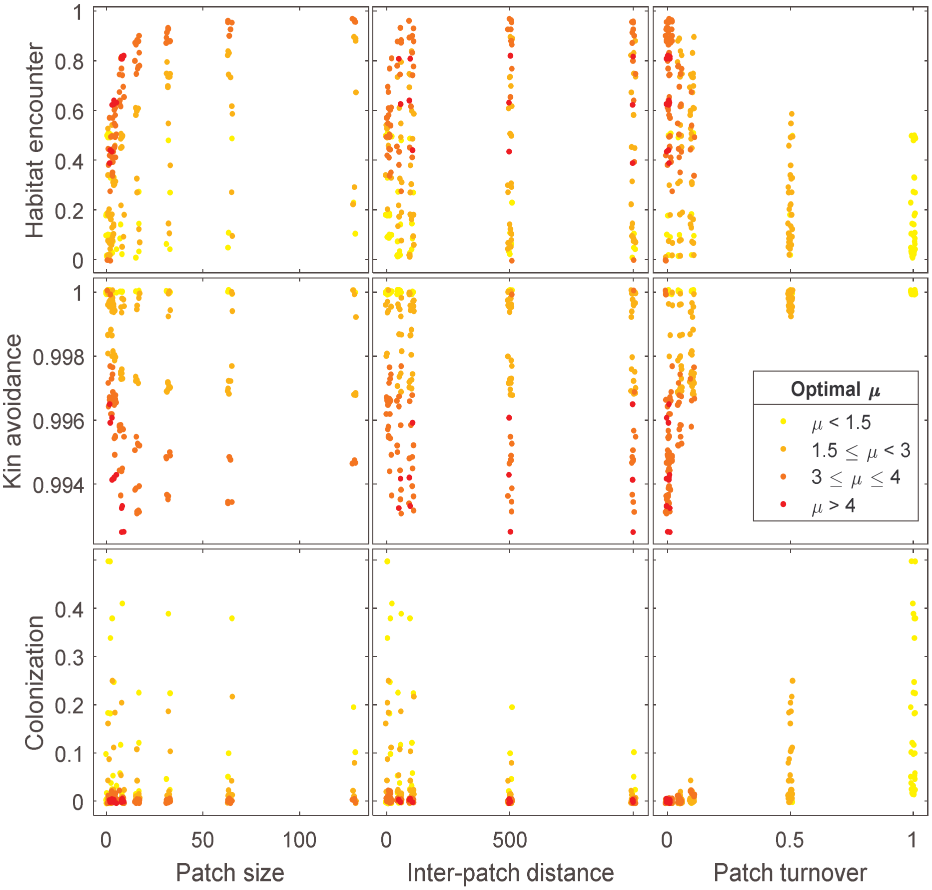

Figure 2.4. Scatterplots showing the dispersal metrics shaping the dispersal kernel ('Habitat encounter', 'Kin avoidance', and 'Colonization') as a function of landscape parameters ('Patch size', 'Inter-patch distance', and 'Patch turnover'). The dots in the scatterplots represent the optimal dispersal kernels.

patch turnover rates (Fig. 2.4, 2.5, Appendix S2.4), which very strongly increase the need to colonize new patches. Higher patch turnover rates correspond to lower optimal values for μ, with $\mu \sim 2$ for a wide range of landscapes with patch turnover rates between 0.1 and 1 (Fig. 2.5). Secondarily, optimal 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. 2.4, Appendix S2.4). Under low dynamic conditions, this translates to

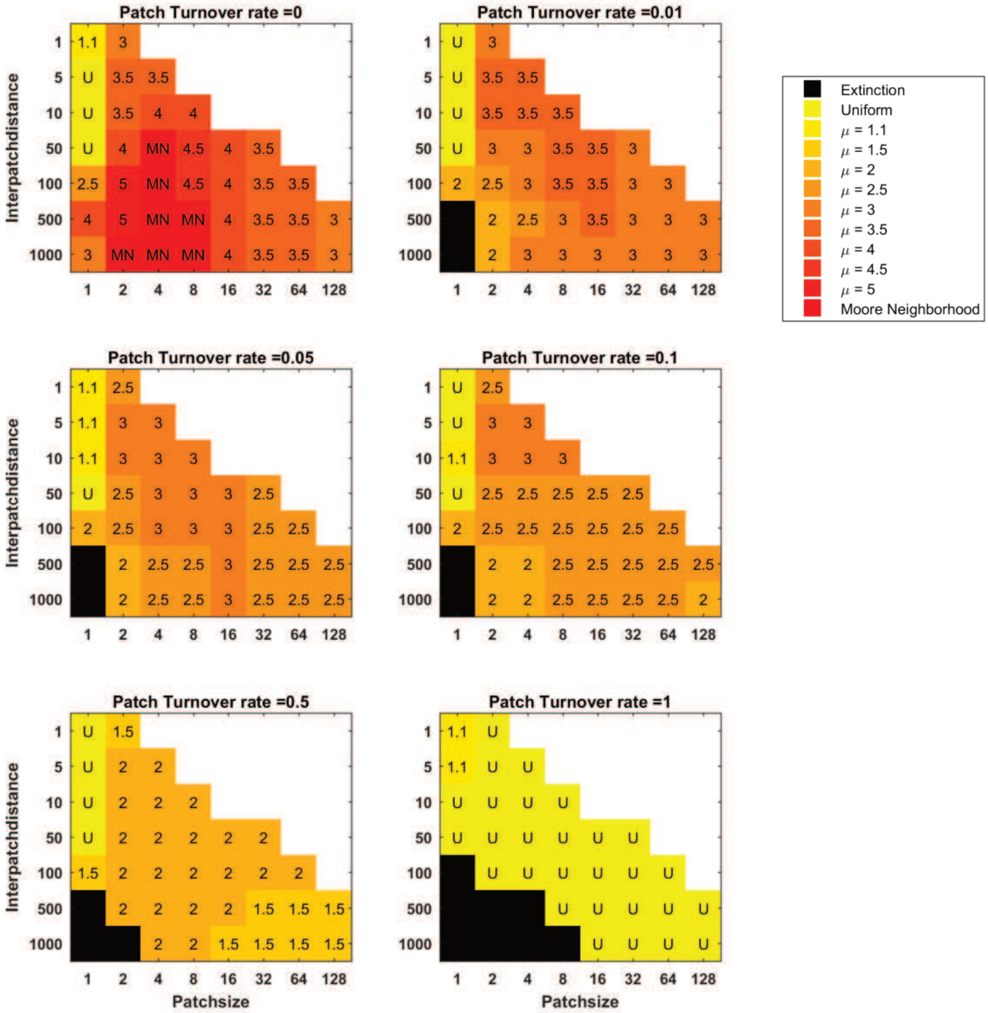

Figure 2.5. Heat maps showing the evolutionary stable dispersal strategies of all possible pairwise invasibility plots for landscapes with increasing patch turnover rates (from 0, top left, to 1, bottom right), as a function of both patch size and inter-patch distance.

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. 2.4, S2.4). The short-distance dominated dispersal strategies that we found to be optimal 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, implications and opportunities

Studies of animal movement behaviour have been able to identify general optimal movement strategies based upon the spatial distribution of resource availability. Using a similar analytical approach, we show that general optimal dispersal strategies can be identified for plants based purely on the shape of the seed dispersal kernel in relation to the spatiotemporal distribution of the plant habitat. 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. We therefore suggest that multi-scale dispersal patterns, flexible enough to adapt dispersal to landscape dynamics, are a key driver in the evolution of plant dispersal strategies. 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 reference 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. The reference framework following from our results is visualised conceptually in Figure 2.6. 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. (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 μ 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 (~ 2 to 100 times the plant size), intermediate inter-patch distances (~ 5 to 100 times the plant size) and relatively high patch turnover rates of around 50% per generation.

Some aspects of our findings make intuitive sense and are in line with well-known patterns observed in plant communities: Plant species found 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

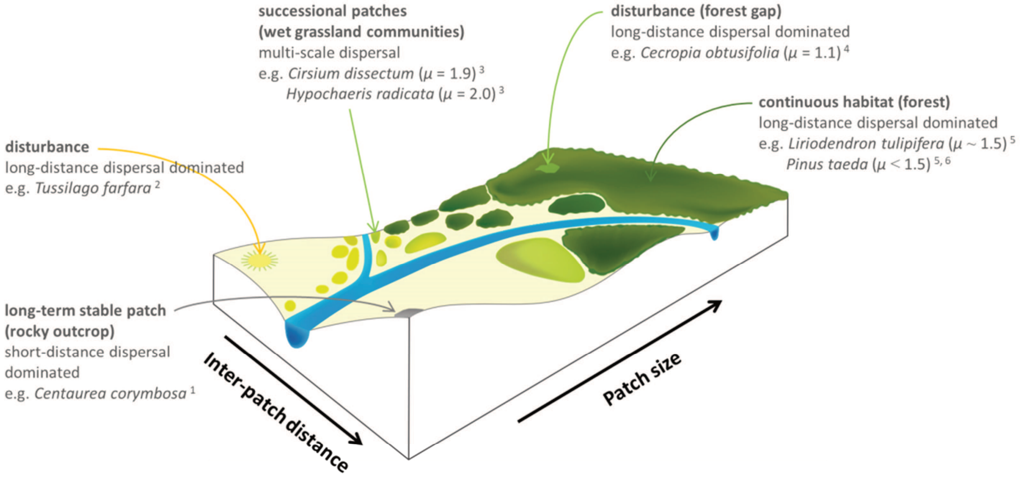

Figure 2.6. Conceptual diagram showing a range of dynamic (disturbances, successional grassland, forest gaps) and static (rocky outcrops, forests) habitats across gradients in inter-patch distance and patch size. In static, but patchy habitats, short-distance dispersal ($\mu > 3$) dominates dispersal 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 μ correlated to average patch size, inter-patch distance and, most importantly, patch turnover rate. Species examples are given; data from [1]Colas et al. 1997, [2]Bakker 1961, [3]Soons et al. 2005, [4]Alvarez -Buylla & Martinez-Ramos 1990, [5]Katul et al. 2005, [6]Nathan et al. 2002.

predominantly short-distance dispersal that promotes the chance of success in ‘winning the home patch’ (Tilman 1994; Kisdi & Geritz 2003; Levin *et al.* 2003a; Muller-Landau 2010). Yet, such hypotheses are not trivial. For example, in static but patchy landscapes short-distance dispersal strategies may rapidly evolve to be optimal. Indeed, there is support for such evolution in plants on islands, were colonization is followed by rapid loss of long-distance dispersal over only a few generations (Cody & Overton 1996; Kavanagh & Burns 2014). Such species are extremely vulnerable to habitat loss and fragmentation, as their dispersal strategy is not adapted to colonizing new areas. With ongoing global change, such dispersal-limited species may be 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 (Colas *et al.* 1997).

Some hypotheses generated within our study may appear somewhat 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 (Nathan *et al.* 2002) and heathlands (Bullock & Clarke 2000), 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 (Howe & Smallwood 1982; Hille Ris Lambers *et al.* 2002; Bell *et al.* 2006), but this would not explain dispersal over more than a few tens of m (the decay rate of pest-induced mortality, Comita *et al.* 2014). 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 leads 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 help to reveal whether these hypotheses indeed reflect the reality. Indeed, published data on plant dispersal kernels provide the first support for our hypothesis. It is difficult to obtain complete dispersal kernels from field measurements, as long-distance dispersal events are extremely difficult to measure but 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, Soons *et al.* 2004; and WALD, Katul *et al.* 2005). 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, theoretically could have tails with power laws of $\mu \sim 1.5$ (Katul *et al.* 2005a) and species such as *Pinus taeda* are likely to have even fatter tails (Nathan *et al*. 2002). 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 (Soons *et al.* 2004; data from Soons *et al.* 2005) 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 notion of multi-scale (broadly heterogeneous and heavy tailed) dispersal kernels (e.g. Lévy-like Pareto distributions) 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 (Bakker 1961), with a roughly estimated negative exponential tail of 0.59 (Willson 1993). 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 Alvarez-Buylla & Martinez-Ramos 1990). We summarize these first lines of evidence in Figure 2.6.

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 only a single aspect of plant dispersal kernels: either only the tail, or only the modal distance. With methodological hurdles to the study of long-distance dispersal being overcome (Nathan *et al.* 2002; Jones & Muller-Landau 2008; Carlo *et al.* 2009; González-Varo *et al*. 2014), much research has focused on quantifying the tail of the dispersal kernel (Nathan *et al.* 2008b; Jones & Muller-Landau 2008; Carlo *et al*. 2013; Gillespie *et al.* 2012), in some cases even trying to identify 'maximum dispersal distances' (Tamme *et al.* 2014). This has resulted in rapid progress in our understanding of, and ability to predict, the connectivity of plant populations in fragmented landscapes (Herrmann *et al.* 2016; Auffret *et al.* 2017) and has helped to explain species' abilities to track climate change (Nathan *et al.* 2011a; Kremer *et al.* 2012) or become invasive (Wilson *et al.* 2009). At the same time, other studies have focused on the mode of the dispersal distribution to facilitate cross-species comparisons (Thomson et al. 2011), 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. Our analyses show how changes in the dispersal kernel affect species fitness and survival across landscapes while considering that changes in one end of the distribution (e.g. an increase in long-distance dispersal) must also affect other aspects of the distribution (e.g. corresponding decrease in short-distance dispersal). Such an integrated approach to plant dispersal has also been advocated in the general 'movement ecology paradigm' (Nathan *et al.* 2008a), and an important first step in making large cross-species comparisons of entire dispersal kernels has recently been taken (Bullock *et al.* 2017).

Our approach moves beyond descriptive studies that attempt to identify statistical functions that best fit plant seed dispersal kernels. Such studies, including the classic work by Willson (1993) and Clark *et al*. (1999) and the recent study by Bullock *et al*. (2017), have provided important insights into the nature of plant dispersal distributions. However, they do not facilitate simple comparisons between large numbers of species or link these distributions to the underlying evolutionary drivers. In a recent theoretical study on seed dispersal kernels, Reynolds (2013) hypothesized that plants maximize the likelihood of finding the nearest unoccupied site by adopting a Lévy flight-shaped inverse power-law seed dispersal kernel. We consider his hypothesis as a major conceptual advance, as it is the first study considering plant dispersal as a search strategy comparable to animal search behaviour. We extend this notion as we state that the plant's seed dispersal distribution is a search for suitable habitat, dependent on the spatiotemporal distribution of *all* habitat, independent of whether this habitat is 'nearest' or not. We find that this search strategy can have different shapes as it is optimized for the spatiotemporal distribution of a species' habitat across the landscape. The simplicity of the approach, which uses a flexible dispersal function parameterized by a single parameter, μ, facilitates 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 current and future 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 promoting long-distance dispersal) modify the optimal search strategy (cf. Humphries & Sims 2014, Chapter 3 of this thesis) and examining plant dispersal kernels for the existence of 'composite walks', which combine multiple movement types into one dispersal strategy (cf. Morales *et al.* 2004). The latter would be relevant in species with dispersal dimorphisms or species using multiple dispersal vectors. Another particularly interesting future direction would be to explore to what extent plant searches can be considered as ‘informed searches’. In our model, we examined the relation between the optimal dispersal strategy and the spatiotemporal distribution of habitat in the landscape in terms of a ‘random search’, where the organism has no cues to guide its’ movement. This situation probably best describes the situation for many plant species. However, there is a growing body of evidence that plants dispersed by animals, water, and wind can also 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 (Spiegel & Nathan 2012; Fraaije *et al.* 2015b; Soons *et al.* 2017). In a recent study, ‘informed dispersal’ has been suggested as a strategy to escape competition and environmental stress (Martorell & Martínez-López 2014). Thus, a particularly exciting avenue for future research would be to 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. Clobert *et al.* 2009). 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.

Acknowledgements

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Supporting Information

Appendix S2.1: Derivation of the 2D-Pareto kernel

To derive a truncated 2-D probability density function (PDF) from a 1-D Pareto distribution, the function is normalized by a normalization constant (c). Starting with a 1-D probability density function

Eq. S2.1.1

$$p(l) = cl^{-\mu},$$

where *l* is distance and μ the scaling exponent, the normalization constant can be derived by taking the integral of equation S2.1.1 over 360 degrees and from the minimum to the maximum distance. This integral, multiplied with the normalization constant should equal 1;

Eq. S2.1.2

$$c \int_0^{2\pi} d\theta \int_{l_{min}}^{L_{max}} p(l)\, dl = 1$$

where L_{max} is the maximum (or truncation) distance and l_{min} is the minimum distance. Integration of equation S2.1.2 over 360 degrees and from l_{min} to L_{max} yields:

Eq. S2.1.3

$$2\pi c \left[\frac{L^{-\mu+2}}{-\mu+2} - \frac{{l_{min}}^{-\mu+2}}{-\mu+2}\right] = 1$$

Rewriting for c:

Eq. S2.1.4

$$c = \frac{1}{2\pi}\left[\frac{-\mu+2}{L^{-\mu+2} - {l_{min}}^{-\mu+2}}\right]$$

The 2D Pareto kernel is then obtained by combining equation S2.1.1 and S2.1.3:

Eq. S2.1.5

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

Equation S2.1.5 does not exist when μ equals 2. Therefore 2.0001 is used instead of 2.

Appendix S2.2: Sensitivity analysis on seed number

We tested the sensitivity of our simulation results to the parameter 'number of seeds produced per individual' by running simulations for 10 landscapes with large variation in fragmentation and dynamics (Table S2.2). We varied seed number by several orders of magnitude (10, 1000, and 10000) and compared the results to the results of the main simulations, where 100 seeds were produced per individual. In general, observed patterns were very similar when comparing pairwise invisibility plots from runs with different seed numbers (Fig. S2.2). In highly dynamic landscapes and for certain dispersal strategies, low seed numbers resulted in extinction (Table S2.2). In landscapes with low patch turnover dynamics, optimal μ increased slightly with seed number, suggesting slightly stronger selection for habitat encounter.

Table S2.2. Sensitivity analysis, based on 10 selected landscape scenarios, of optimal μ (μ_{opt}) for different values of the parameter 'number of seeds produced per individual'.

Patch size	**Inter-patch distance**	**Patch turnover rate**	**μ_{opt} #10**	**μ_{opt} #100**	**μ_{opt} #1000**	**μ_{opt} #10000**
8	50	0.1	2.5	2.5	3	3
2	5	0.5	2	2	2	2
1	50	1	X	1	1	1
1	10	0	3	1	1	1
128	500	0	3	3	3	3
2	100	0	4.5	4.5	4	4
4	500	0.01	2.5	2.5	3	3
32	50	0.05	2.5	2.5	3	3
16	500	0.5	2	2	2	2
2	5	0.01	3	3.5	3.5	3.5

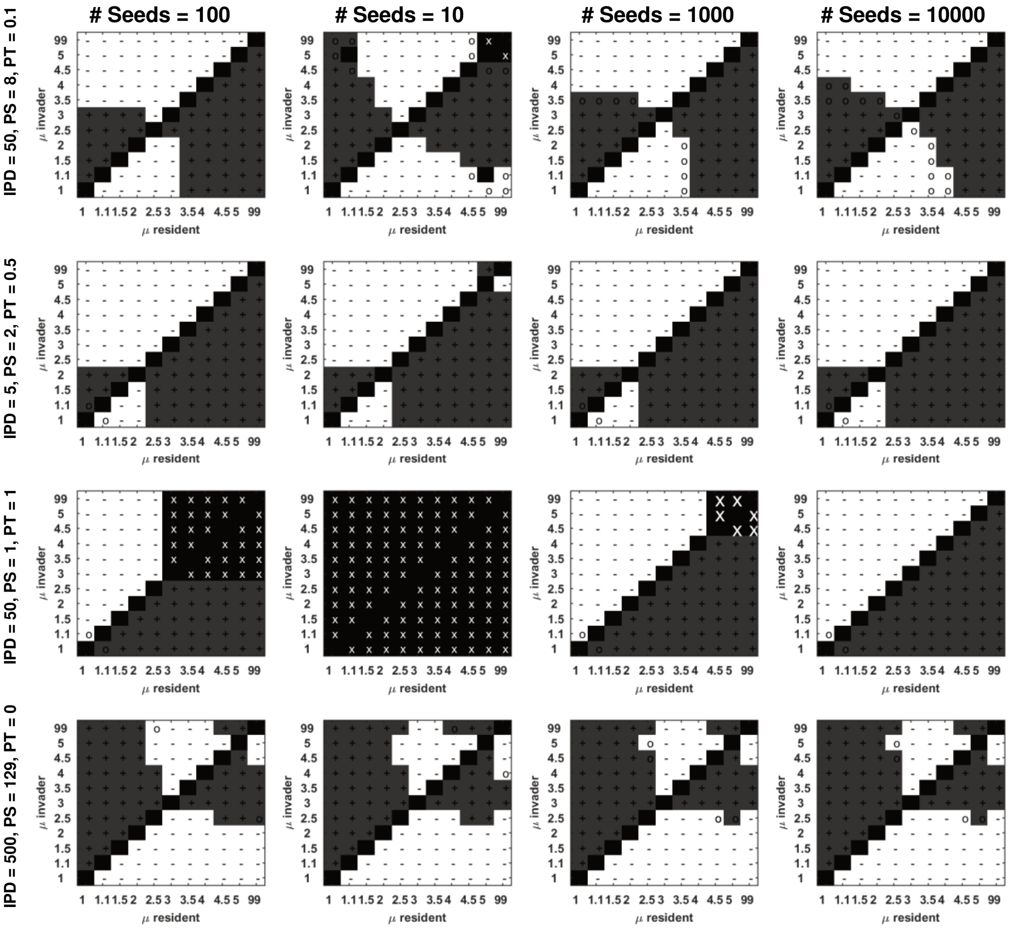

Figure S2.2. Pairwise invasibility plots for 4 out of 10 landscape scenarios that were run in the sensitivity analysis of optimal μ (μ_{opt}) for different values of the parameter 'number of seeds produced per individual'. Grey shading indicates the resident-invader combinations where the invasive population outcompetes the resident population 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 populations. IPD stands for inter-patch distance, PS for patch size and PT for patch turnover rate.

Appendix S2.3: Simulations using discrete dispersal events

To improve computational efficiency, we used convolution via Fast Fourier Transformation to calculate dispersal for all individuals simultaneously, thereby neglecting some of the stochasticity that is involved in discrete dispersal events. To test whether this simplification affected the competition dynamics considerably, we ran model simulations using discrete dispersal events for 2 landscapes and compared them to the model simulations using FFT. We found only small differences when comparing the results of the two models (Fig. S2.3). Stochasticity that is present in both models is likely to have caused the slight deviations that are seen around μ = 2.5 and μ = 3 in the top row.

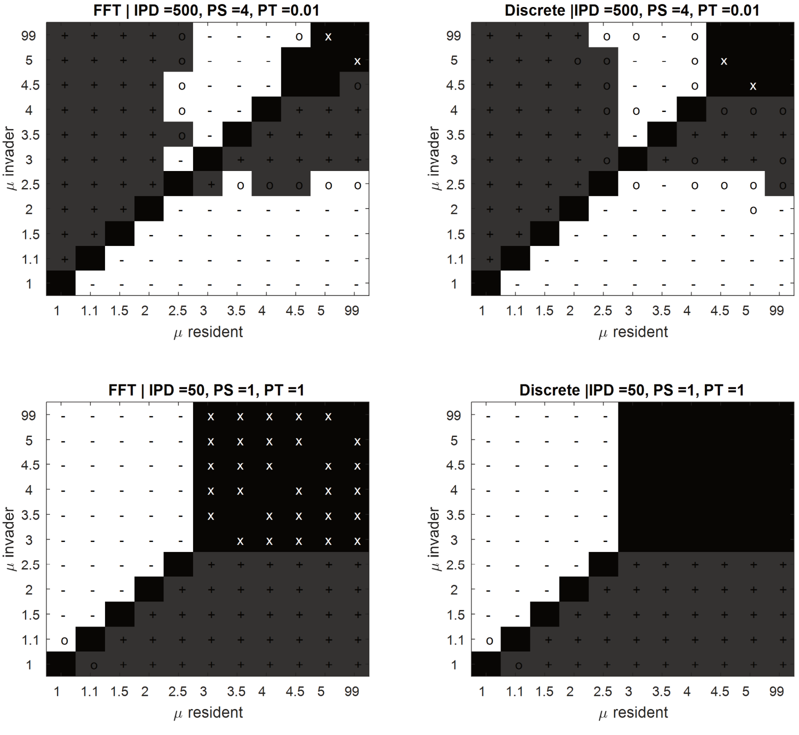

Figure S2.3. Pairwise invasibility plots for 2 landscape scenarios for the main model using FFT (left panels) compared with a model with discrete dispersal events (right panels). Grey shading indicates the resident-invader combinations where the invasive population outcompetes the resident population 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 populations. IPD stands for inter-patch distance, PS for patch size and PT for patch turnover rate.

Appendix S2.4: Contributions of habitat encounter, kin avoidance and colonization to determining optimal dispersal strategies

The absolute rates of habitat encounter, kin avoidance, and colonization that are achieved in the optimal dispersal strategies correlate strongly with habitat patch size and patch turnover (and to a lesser extent inter-patch distance, not shown here) (Fig. S2.4a). With increasing patch size, more habitat can be found close to the parent plant, which increases habitat encounter and decreases kin avoidance. With increasing patch turnover rate, habitat is less predictable which decreases habitat encounter and increases kin avoidance. As more new patches are formed, colonization rate also strongly increases with patch turnover rate. However, these absolute rates are not fully comparable and so do not fully clarify the importance of each of the forces in determining optimal strategies. By normalization of the absolute rates, we obtain better insight into whether the optimal strategy is driven by habitat encounter, kin avoidance, and/or colonization. This normalization is obtained for each landscape separately by:

$$P_{norm} = (P_{opt}-P_{min})/(P_{max}-P_{min}), \qquad \text{Eq. S2.4.1}$$

where P represents the dispersal metric in question (habitat encounter, kin avoidance or colonization). A value of 1 means that the highest value is selected in the optimal strategy, and 0 means the lowest value is selected. A high value can thus be interpreted as the dispersal metric being a very important factor for that landscape scenario, and 0 as relatively unimportant (e.g. due to a very narrow range). Normalized rates of habitat encounter, kin avoidance, and colonization show that static landscapes (no patch turnover) select for a maximization of habitat encounter, whereas highly fragmented (patch size = 1) and highly dynamic (patch turnover = 1) landscapes select for a maximization of kin avoidance. In all other landscapes a complex trade-off balances habitat encounter, kin avoidance and colonization. Here, all three factors play a role and colonization becomes increasingly important with increasing patch turnover and decreasing patch size.

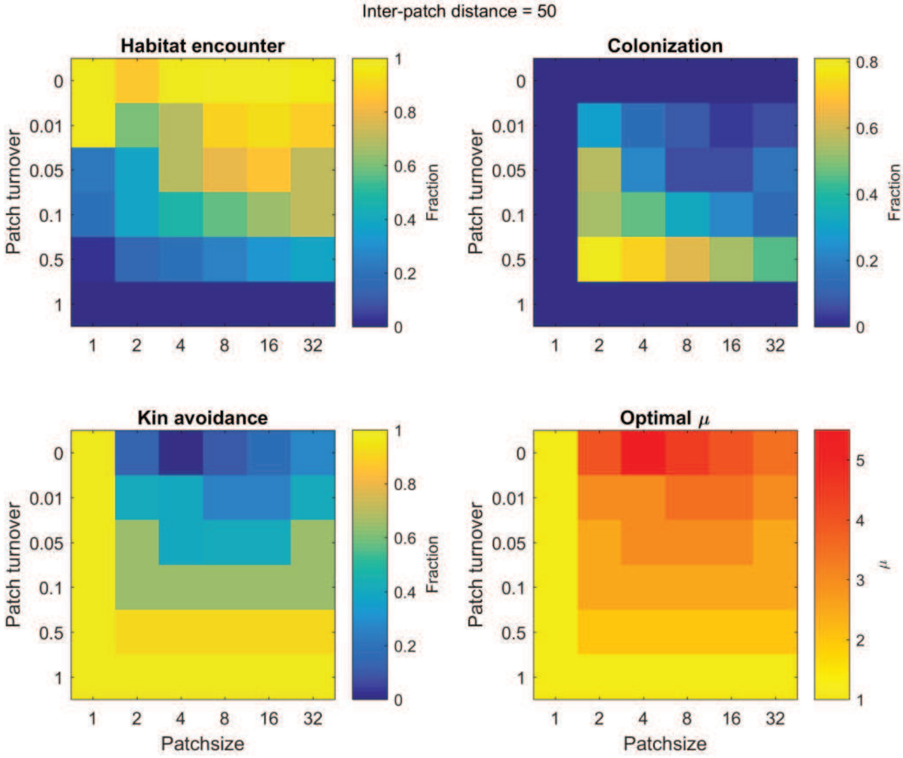

Figure S2.4a. Relations between absolute fractions of habitat encounter, kin avoidance, and colonization (at optimal dispersal strategies) and landscape parameters patch size and patch turnover. The optimal values of μ for these landscapes, derived from pairwise invasibility plots are shown in the bottom right panel.

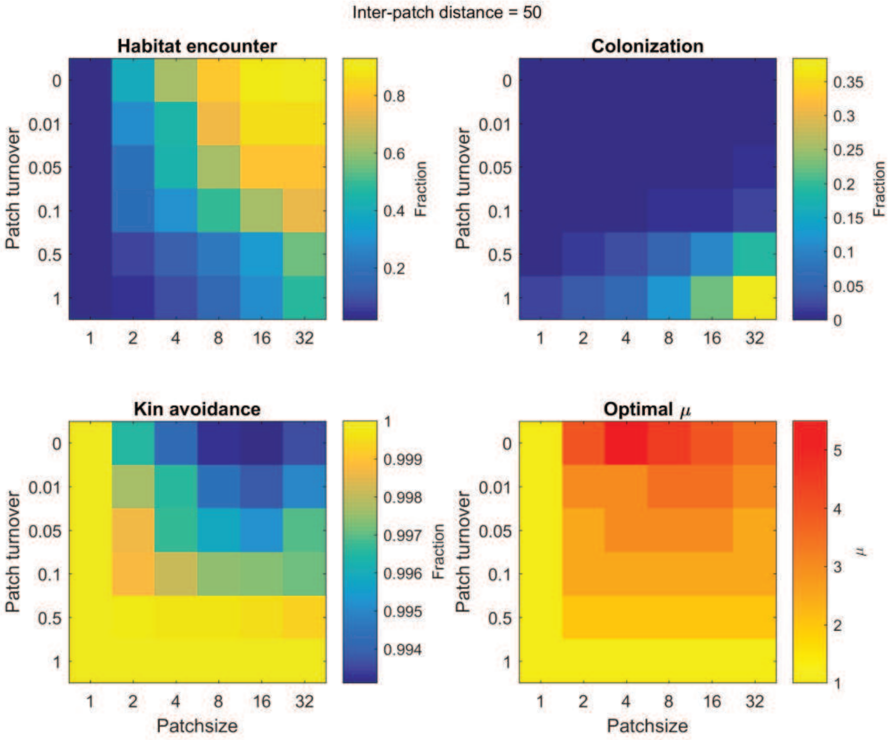

Figure S2.4b. Relations between normalized fractions of habitat encounter, kin avoidance, and colonization (at optimal dispersal strategies) and landscape parameters patch size and patch turnover. The optimal values of μ for these landscapes, derived from pairwise invasibility plots are shown in the bottom right panel.

3

Costs and benefits of non-random seed release for long-distance dispersal in wind-dispersed plant species

Jelle Treep, Monique de Jager, Leandra S. Kuiper, Tomer Duman, Gabriel G. Katul and Merel B. Soons

Abstract

Plant species dispersal ability is a major factor driving ecological responses to global change. In wind-dispersed plant species, non-random seed release in relation to wind speeds has been identified as a major determinant of dispersal distances. However, little information is available about the costs and benefits of non-random abscission and the consequences of timing for dispersal distances.

We asked: 1) To what extent is non-random seed abscission able to promote long-distance dispersal? 2) What is the effect of potentially increased pre-dispersal risk costs? 3) Which meteorological factors and respective timescales are important for maximizing dispersal? These questions were addressed by combining a mechanistic modelling approach and field data collection for herbaceous wind-dispersed species.

Model optimization with a dynamic dispersal approach using measured hourly wind speed showed that plants can increase long-distance dispersal by developing a hard wind speed threshold below which no seeds are released. At the same time, increased risk costs limit the possibilities for dispersal distance gain and reduce the optimum level of the wind speed threshold, in our case (under representative Dutch meteorological conditions) to a threshold of 5-6 m s^{-1}. The frequency and predictability (auto-correlation in time) of pre-dispersal seed-loss had a major impact on optimal non-random abscission functions and resulting dispersal distances.

We observed a similar, but more gradual bias towards higher wind speeds in six out of seven wind-dispersed species under natural conditions. This confirmed that non-random abscission exists in many species and that, under local Dutch meteorological conditions, abscission was biased towards winds exceeding 5-6 m s^{-1}.

We conclude that timing of seed release can vastly enhance dispersal distances in wind-dispersed species, but increased risk costs may greatly limit the benefits of selecting wind conditions for long-distance dispersal, leading to moderate seed abscission thresholds, depending on local meteorological conditions and disturbances.

Introduction

Seed dispersal in plants enables gene flow between existing populations and colonization of new habitat sites, and is therefore fundamental to species survival in a changing world (Howe & Smallwood 1982; Levin *et al.* 2003a; Renton *et al.* 2012). To predict plant species survival and potential range shifts in response to global changes, we need to be able to estimate species dispersal distances across wide-ranging environmental conditions (Brooker *et al.* 2007). Wind is one of the most common dispersal vectors of plant seeds (Van der Pijl 1982; Willson *et al.* 1990) and mechanistic models have been developed for this vector to estimate dispersal kernels from species-specific plant traits (Nathan *et al.* 2011b). However, even the most advanced and realistic mechanistic wind dispersal models tend to underestimate the tail of measured dispersal kernels when compared to field data (Soons *et al.* 2004a; Katul *et al.* 2005a; Soons & Bullock 2008). This is problematic, as the tail is of disproportionate importance since it contains long-distance dispersal (LDD) events. It has also been suggested that non-random seed release during specific meteorological conditions significantly enhances dispersal distance, partly explaining this underestimation (Greene 2005; Skarpaas & Shea 2007; Bohrer *et al.* 2008; Soons & Bullock 2008; Greene & Quesada 2011; Maurer *et al.* 2013; Pazos *et al.* 2013).

Over the past decade, several studies have shown a direct relation between meteorological variables (such as wind speed, turbulence and humidity) and seed release (hereafter termed 'abscission'). Most studies have focused on wind speed, reporting a rapid or exponential increase of abscission probability with increasing wind speed (Greene 2005; Skarpaas *et al.* 2006; Jongejans *et al.* 2007; Soons & Bullock 2008; Greene & Quesada 2011; Pazos *et al.* 2013). This is an intuitive result, as the motive force required to break the connection between a seed and its parent plant is drag, which is proportional to the square of wind speed (Greene 2005; Pazos *et al.* 2013). At the same time, abscission during stronger wind speeds increases dispersal distances (Soons *et al.* 2004a, b; Schippers & Jongejans 2005; Soons 2006; Soons & Bullock 2008; Pazos *et al.* 2013; Savage *et al.* 2014), which may result in selective pressures on non-random abscission mechanisms with a bias towards high wind speeds in plant species for which LDD is beneficial (Chapter 2). While we acknowledge that not all plants optimize their dispersal by maximizing LDD specifically (Chapter 2) and LDD may even be disadvantageous for many species (Gilman *et al.* 2010; North *et al.* 2011; Soliveres *et al.* 2014), non-random abscission has been shown to be a potentially effective way to increase the tail of the dispersal kernel.

Turbulence and updrafts due to mechanical shear or convection also promote LDD (Nathan *et al.* 2002, 2011b; Tackenberg 2003; Soons *et al.* 2004a; Wright *et al.* 2008; Maurer *et al.* 2013; Savage *et al.* 2014), and some plants release more seeds during turbulent conditions or updrafts (Skarpaas *et al.* 2006; Greene & Quesada 2011; Borger *et al.* 2012; Maurer *et al.* 2013). Furthermore, solar radiation, temperature and humidity may affect seed ripening processes and the drying of the tissue between seed and parent plant (Greene *et al.* 2008; Marchetto *et al.* 2012). Radiation, temperature and humidity are correlated with convective updrafts (Stull 1988) and could also act as a trigger for abscission during periods of convective conditions. However, the relative importance of convective updrafts for LDD in comparison to that of mean horizontal wind speed varies strongly between plant species (Tackenberg 2003; Soons *et al.* 2004a; Maurer *et al.* 2013).

The timing of abscission in relation to local meteorological conditions is thus likely to play an important role in determining dispersal distances in wind-dispersed plant species. However, a comprehensive mechanistic understanding of which traits determine abscission timing, and how these traits interact with the environment, remains lacking. Abscission is an instantaneous process that occurs when a drag force exceeding a certain threshold breaks the connecting tissue between seed and plant (Greene & Quesada 2011; Pazos *et al.* 2013; Thompson & Katul 2013). This threshold, therefore, is a strong determinant of which meteorological conditions predominate during dispersal. The threshold may be dynamic in time through processes of material fatigue (Pazos *et al.* 2013; Thompson & Katul 2013), drying (Borger *et al.* 2012; Marchetto *et al.* 2012) and processes at the cell level such as degradation of an abscission layer (Liljegren *et al.* 2000; Thurber *et al.* 2011), which act on timescales ranging from minutes (material fatigue and drying) to days (drying and plant-regulated processes) (Savage *et al.* 2014). Phenology determines the flowering and fruiting periods of plants at monthly, seasonal, to yearly timescales (Chuine 2010). As meteorology fluctuates across a range of timescales, from turbulence (millisecond-second), to diurnal variation (hour), synoptic weather systems (day), and seasonal variation (month; Stull 1988), selective pressures may act across a range of timescales in order to optimize the dispersal kernel by non-random abscission.

However, non-random abscission also comes with risk costs (Bonte *et al.* 2012). In many regions around the world, mean wind-speed variability is approximated by strongly right-skewed distributions (e.g. Weibull, Fig. S8) and high wind speeds remain rarities (Stull 1988). Hence, a high abscission threshold would result in a potentially long seed exposure time, entailing an increased risk of pre-dispersal seed loss by e.g. damage or predation (Moles *et al.* 2003; Bonte *et al.* 2012).

The effects of these risks can play an important role in shaping non-random abscission patterns and, hence, dispersal kernels.

Here, we examine how different mechanisms, operating across a wide range of timescales, shape non-random abscission and, hence, dispersal kernels. We conducted a modelling and a field study to answer the following questions: 1) To what extent is non-random abscission able to promote LDD? 2) What is the effect of potentially increased risk costs on non-random abscission strategies and dispersal kernels? 2) Which meteorological factors and respective timescales are important for maximizing LDD? The combined modelling and field study allowed us to explore the theoretical effects of different abscission strategies on LDD. These different abscission strategies were then compared to actual abscission strategies for seven wind-dispersed herbaceous plant species under natural conditions.

Methods

We used a mechanistic modelling framework to evaluate the extent to which abscission timing is able to promote LDD and how increased risk costs affect abscission strategies and dispersal kernels. As a second step, we used this framework to examine timing mechanisms across timescales and quantify the consequences for LDD. Finally, we carried out a field study to determine to what degree non-random abscission mechanisms exist in selected wind-dispersed plant species and to evaluate whether the mechanistic model-based predictions regarding abscission timing are plausible.

Model Description

In our modelling framework, we combined a mechanistic dispersal model with an abscission submodel (a schematic overview of the modelling framework is provided in Supplementary material Appendix S3.1 Fig. S3.1). We selected the Coupled Eulerian-Lagrangian Closure model (CELC; Katul and Albertson 1998, Nathan et al. 2002, 2011, Soons et al. 2004a, b) as the seed dispersal model to compute dispersal kernels for a range of wind speeds and plant species and used these kernels as input for the abscission submodel. CELC, relative to Large Eddy Simulations, offers a computationally cheap approach to quantify seed dispersal kernels as a function of prescribed atmospheric profiles of wind and turbulent statistics (Nathan *et al.* 2002, 2011b, Soons *et al.* 2004a, b). CELC randomly generates auto-correlated time series of turbulence velocity fluctuations around a profile of mean wind speed within and above vegetated canopies, which can be used to model entire seed dispersal trajectories. Additional details and settings are provided in Appendix 1. By simulating the trajectories of 50,000 seeds, we estimated the dispersal kernel for a plant species at a given wind speed. We repeated this procedure for 20 wind speeds (ranging from 1 to 20 m s^{-1} at a reference altitude of 10 m) for the seven plant species that were examined in the field study. Note that wind speed typically increases with altitude and the actual wind speeds experienced by the seeds are typically lower than the reference wind speed at 10 m altitude. An overview of these species and the required model parameters (1) seed release height and (2) terminal fall velocity of the seed are given in table 3.1. For parameterisation of the canopy profile, we assumed a homogeneous field with a maximum vegetation height of 1 m and a leaf area index (LAI) profile similar to a fen-meadow characterized in Fliervoet (1984) (Supplementary material Appendix 1 Fig. S3.2). For each species, we used the resulting dispersal kernels (20 in total, belonging to mean hourly wind speeds of 1 to 20 m s^{-1}) as input for the abscission submodel.

The abscission submodel simulates a seed dispersal kernel (K_y) for an individual plant (represented by a combination of seed terminal velocity and seed release height) for a full calendar year. The yearly dispersal kernel is calculated as a cumulative sum of all the hourly seed dispersal distances distributions (D_t), divided by the total seeds produced over the entire year;

$$K_y = (\sum P_t)^{-1} \sum D_t \qquad \textit{Eq. 3.1}$$

where P_t is the number of seeds produced at time step t (one time step equals one hour). In the main simulations the plant is assumed to produce an equal number of seeds every hour throughout the year. We also performed tests with variable seed production, which are presented in appendix Fig. A6. Each hour, the probability of abscission, pA_t, is calculated as a function of wind speed. The released seeds disperse according to the dispersal kernel (K_u, from the CELC model). The hourly distributions of seed dispersal distances (D_t) are then calculated as;

$$D_t = K_u(S_t + P_t)\, pA_t, \qquad \textit{Eq. 3.2}$$

where S_t is the number of seeds on the plant at time step t and pA_t is the probability of seed abscission at time step t.

For each hour, the remaining seeds from the end of previous hour are available for dispersal:

$$S_t = (S_{t-1} + P_{t-1})(1 - pA_{t-1}) \qquad \textit{Eq. 3.3}$$

At any specific instant in time, an individual seed requires a drag force exceeding a threshold to break its connection to the plant. This threshold can vary between seeds on an inflorescence. We assume that a sigmoid function is a reasonable descriptor of abscission when exploring full inflorescences instead of individual seeds (Thompson & Katul 2013). The logistic function of the hourly mean wind speed (u_t) is intuitive as the midpoint and the slope of the curve can be defined with parameter α (slope, s m^{-1}) and β (midpoint, m s^{-1});

$$p(A_t) = \left(1 + e^{-\alpha(u-\beta)}\right)^{-1} \qquad \textit{Eq. 3.4}$$

u_t (in m s^{-1}) used here to characterize the flow is the measured value at 10 m altitude. By varying the α and β parameters in parallel model runs, we examined the effects of non-random abscission relative to wind speed on a yearly dispersal kernel.

To simulate realistic meteorological scenarios, measured time series of hourly wind speed, precipitation, temperature and relative humidity from the KNMI (Royal Netherland Meteorological Institute) station in De Bilt (www.knmi.nl/nederland-nu/klimatologie/uurgegevens) were used as model input in the abscission submodel. To explore potential effects of variation in humidity, we also performed model runs using vapour pressure deficit (VPD) as predictor for non-random abscission probability (Appendix S3.1; Fig. S3.6). VPD was estimated from temperature and relative humidity measurements from the same KNMI time series (Tetens 1930). We selected a period of 32 years from the years 1962 to 1993, during which wind speed measurements were taken using a uniform method at 10 m altitude. A 30-year period is considered long enough to represent normal climatic variation. All our simulation results refer to measured wind speeds at a reference height of 10 m, although wind speed at the height of seed release is actually lower. The CELC model resolves actual wind speed at the height of seed release, but to facilitate comparisons we present wind speeds at reference height.

Simulations

Aim 1: Non-random abscission

We examined the effects of different abscission functions on LDD in the yearly dispersal kernel by running the model for 10x10 combinations of the slope (α) and midpoint (β) parameters of the sigmoid abscission function (Eq. 3.4). With these parameter combinations, the slope parameter ranged from very steep to smooth; $\alpha = 4 / i$ where $i = 1, 2, \ldots, 10$. The midpoint of the sigmoid function on the x-axis (hourly mean wind speed) ranged from 1 to 10; $\beta = j$ where $j = 1, 2, \ldots, 10$. We compared the effects of these non-random abscission functions by comparing the distances of the 99-percentiles of the resulting dispersal kernels K_y.

We then examined the effect of potentially increased pre-dispersal risk costs on the effects of different shapes of the abscission function on yearly LDD, by adding a general disturbance event that eliminates all seeds that are attached on the plant. For a simple and quantifiable scenario, we used a rain event as a proxy for a general disturbance. In some wind-dispersed species (such as *Sonchus* and *Cirsium* species), rain events indeed destroy the disc-shaped configuration of the *pappi*. Other species have adaptations to avoid such damage (e.g. *Taraxacum* and *Tragopogon* species), for instance by closing their infructurescences in response to increasing air humidity and re-opening them again after the rain event. For simplicity, we assumed elimination of all exposed seeds across all species (seeds neither disperse nor germinate and are considered lost). We included fraction of seed loss in the calculation of each yearly 99-percentile dispersal distance.

We then tested the robustness of the above results to variation in meteorological conditions by repeating the simulations for the meteorological time series sampled over the 32 different years.

Finally, we explored how much the effect of abscission and the optimal shape of the sigmoid abscission function for LDD vary between species. To this end, we quantified the dependence of the midpoint parameter β and resulting dispersal kernels on species characteristics, by running the model for 100 combinations of seed release height ($H = 0.2, 0.4, \ldots, 2.0$) and terminal velocity of the seed ($v_t = 0.2, 0.4, \ldots, 2.0$). We kept α constant at a high value as this was the optimal parameter setting from all previous simulations.

Aim 2: Potential risks

To determine how different pre-dispersal mortality risks shape the abscission strategies and dispersal kernels, we explored the effects of five disturbance scenarios: 1) Rain as a disturbance (described above), 2) No disturbance, 3) Constant probability of disturbance for each time step set at a probability of 0.05, 4) Constant probability of 0.22, and 5) Constant probability of 0.33. The frequency of rain was 0.22 in the KNMI data, however, in contrast to disturbance scenarios 3, 4 and 5, rain is typically auto-correlated over time. Comparison of scenarios 1 and 4 thus facilitates the comparison between an auto-correlated and a constant risk over time, with equal magnitude, while scenario 3 and 5 represent lowered and increased risks. We ran scenario 1 for all seven study species (see above) and the other scenarios for *Hieracium aurantiacum* and *Leontodon hispidus*, since the differences between species were qualitatively similar (Fig. 3.2).

Aim 3: Timing mechanisms across different timescales

To evaluate how plant physiological processes acting at different timescales may determine abscission timing and LDD, we modelled the effects of abscission timing at each of the following timescales: second – hour – day – season – year.

Second. Abscission timing is dependent on the turbulent fluctuations, happening at (milli)second timescales, around hourly mean wind speeds, which together determine the instantaneous wind speed that may break the seed-plant connection. In CELC, acceleration is generated by a deterministic drift term that varies with the flow statistics and randomly from a normal distribution with a standard deviation that is correlated with mean wind speed at a given hour. By setting a wind speed threshold of three standard deviations above the mean wind speed we examined the effect of dispersal only during turbulent gusts. We performed this exercise for hourly wind speeds of 2, 4, 6 and 8 m s^{-1} and compared dispersal kernels from abscission during gusts with dispersal kernels from normal random seed abscission. Note that in this case, only the mechanistic dispersal model CELC was used (Fig. S3.1).

Hour. We examined the effects of non-random abscission at hourly timescales on dispersal kernels by optimizing the non-random abscission function (Eq. 3.4) as discussed in the sections above (Simulations: 1. Non-random abscission).

Day. Non-random seed ripening and exposure may be traits that influence dispersal on a timescale of days, either by selecting beneficial dispersal conditions or lowering probabilities of disturbance. In the model we experimented with variable seed production based on VPD. A high VDP represents dry conditions which may decrease the probability of a rain disturbance. We tested two strategies: 1) seeds are only exposed when VPD exceeds 1500 Pa and 2) seeds are only exposed when VPD crosses a threshold of 1000 Pa.

Season. Phenology determines in which season(s) plants disperse. Here, we assessed whether seasonality in meteorology has an effect on optimal seed abscission functions and dispersal distances by running the model for 3-month periods (seasons) instead of a full year. Each run therefore utilized different meteorological input data for the model. For this, we divided the year into four seasons; winter (Dec., Jan. and

Feb.), spring (Mar., Apr. and May), summer (Jun., Jul. and Aug.) and autumn (Sep., Oct. and Nov.).

Year. To test how inter-annual variability in meteorological time series affects optimal seed abscission functions, which may determine if non-random abscission strategies are evolutionarily stable, we ran the model for each of the 32 years separately (1962 – 1993) and compared the optima across the years.

Field study

We examined abscission under field conditions for seven wind-dispersed plant species native to North-Western Europe: *Cirsium arvense, Hieracium aurantiacum, Leontodon hispidus, Sonchus asper, Taraxacum officinale* and *Tussilago farfara* (Asteraceae) and *Alopecurus pratensis* (Poaceae) (Table 1). The seeds of the six Asteraceae species all have plume-like structures (*pappi*), to reduce the terminal velocity of the seeds. The Poaceae species has seeds surrounded by glumes with long, feathery hairs that also reduce terminal velocity of the seed. We collected approximately 30 pre-flowering for each species from wild plant breeders or from parks in or close to Utrecht, the Netherlands, and potted them in the Utrecht University Botanical Gardens. The pots were placed outdoors where they were subjected to natural meteorological conditions, except for the fact that they were watered during particularly dry periods.

During an entire growing season, we examined the development of the plants and the timing of abscission in detail. Each day between 9:00 am and 16:00 pm (GMT+1), the percentage of seeds on each produced inflorescence was scored visually every hour. By dividing the decline of seeds per hourly interval by the total number of seeds at the beginning of the hour, we determined the probability of abscission per observed hour. These data were merged with hourly meteorological records from the KNMI station at De Bilt (see above), which is located at ~1 km from the experimental setup. The meteorological station, as well as our experiment in the botanical gardens, was located in a field with no major wind obstructions in the near surroundings (< 50 m distance). However, some bushes and an open greenhouse were located within 20 metres from our experiment, which may have caused local deviations from the measured wind conditions at the KNMI weather station. We used hourly mean wind speed as predictor variable. During the field study, hourly mean wind speed was recorded at 20 m altitude (note that the input data for the model was recorded at 10 m; the altitude of the wind sensor changed to 20 m after 1993). Although abscission is an instantaneous process dependent on wind-induced drag that fluctuates at very fine

Table 3.1. Overview of the species examined during the field study and their most important characteristics. Individuals were collected from wild plant breeders or dug out from nearby fields ('in situ'). Species characteristics are based on the LEDA traitbase (Kleyer *et al.* 2008)

	Cirsium arvense	***Sonchus asper***	***Hieracium aurantiacum***	***Tussilago farfara***	***Taraxacum officinale***	***Leontodon hispidus***	***Alopecurus pratensis***
Location	De Uithof, Utrecht	De Uithof, Utrecht	De Heliant, Wapserveen	De Uithof, Utrecht	De Uithof, Utrecht	De Heliant, Wapserveen	De Uithof, Utrecht
Method	In situ	In situ	Breeder	In situ	In situ	Breeder	In situ
Collection dates	16-19 May 2014	16 May 2014	23 May 2014	17-22 April 2014	24-25 April 2014	23 May 2014	1 May 2014
Observation period	June 20 - August 25	May 26 - July 19	June 10 - October 3	April 23 - May 23	April 28 - May 9	May 26 - October 3	May 7 - July 25
Seed terminal velocity in m s^{-1}	0.3	0.6	0.3	0.2	0.6	0.9	2.2
Seed release height in m	0.75	0.75	0.35	0.17	0.35	0.4	0.6
Number of seeds per inflorescence	200	198	50	313	155	77	100
Number of plants	25	7	24	25	23	34	30
Number of inflorescences	96	329	278	56	64	312	172
Number of observations	1368	876	2633	1087	873	6427	16481
Flower							

timescales (ms to s), hourly mean wind speed was significantly correlated to the maximum wind gust per hour (R = 0.94, p < 0.005, Fig. A3) and we used this as an approximation.

We estimated the shape of the abscission function for each plant species by non-linear least squares fitting procedures with a sigmoid function through the data. With 4 non-fixed parameters, this function retained the flexibility to select a linear or exponential shape (besides a sigmoid). In addition, we applied Generalized Linear Models to quantify the effect of wind, VPD and timing mechanisms at longer (than hourly) timescales; for example a decreasing seed release threshold (time since opening) and non-random seed release depending on time of day. We used a logit-link function to cope with the binomial structure of the abscission probability data. All analyses were performed in Matlab R2014b.

Results

Model results

Aim 1: Non-random abscission

Our model runs confirmed that non-random abscission with bias towards high wind speeds increases LDD. In the absence of any risk, the optimal (simulated) non-random abscission strategies resulted in a major increase in LDD across the entire tail of the dispersal kernel in comparison to random abscission (Fig. 3.1a,b). At the 99-percentile dispersal distance (1 percent of the seeds exceed this distance), this increase was by a factor of 20-40 for the two species presented. However, because some seeds were not released at the end of the simulation period (as the high wind speed threshold was not exceeded after the production of these seeds) this came with the cost of seed loss. When considering the simple case of risk of seed loss by rain events only, model calculations showed that non-random abscission increases LDD as expressed by 99-percentile distances only by a factor of 1.13-1.49 across all seven species (Fig. 3.2a-g). This increase extends across the entire tail of the dispersal kernel (Fig. 1c,d), although, in line with the 99 percentile, the increase was much smaller than for the scenarios without any disturbance (Fig. 1a,b). In all species and all scenarios, the longest dispersal distances were reached at abscission strategies with a steep sigmoid function (slope parameter α = 4), which more closely resembles a 'hard-threshold' function than a sigmoid (Fig. 2 & 3). The location of this threshold (midpoint parameter β) is very similar across species, but differs between disturbance scenarios (see next subsection). In the rain disturbance scenario, the longest dispersal distances

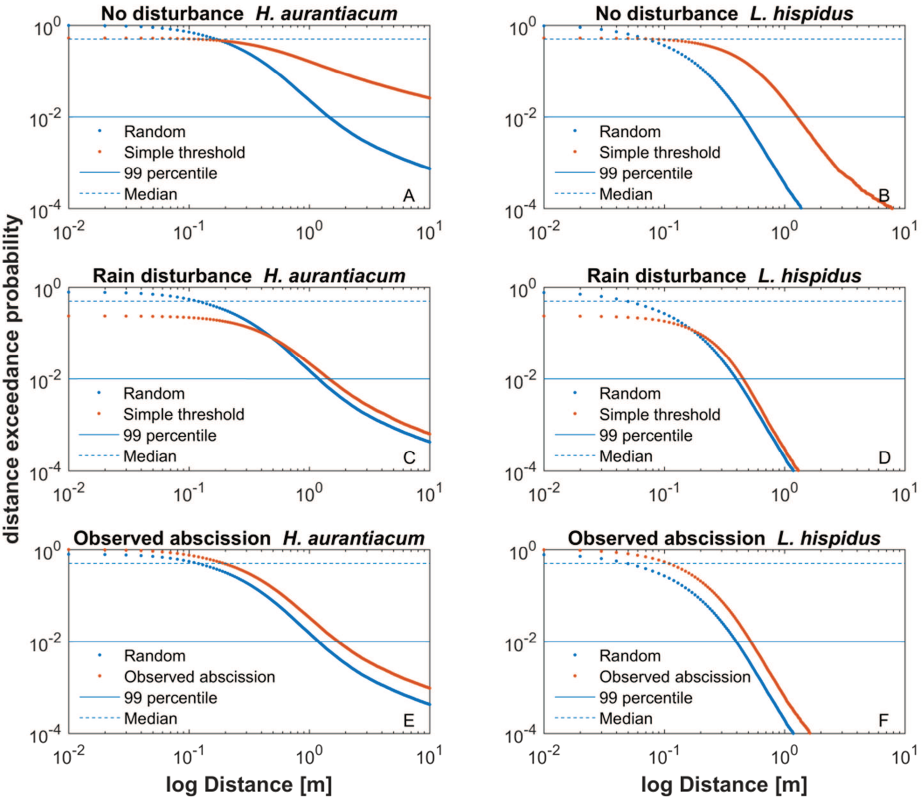

Figure 3.1. Consequences of abscission strategies for plant dispersal kernels, for *Hieracium aurantiacum* (left panels) and *Leontodon hispidus* (right panels). Top row: dispersal kernels (distance exceedance probabilities) for random seed abscission and for the optimal non-random abscission strategy with no risk included. Middle row: dispersal kernels for random seed abscission and for the optimal non-random abscission strategy with a realistic rain-disturbance scenario. Bottom row: dispersal kernels for random seed abscission and for the abscission function fitted to the field data.

were reached at a threshold wind speed of 5-6 m s^{-1} (midpoint parameter β = 5-6). Higher thresholds resulted in less LDD as more seeds were lost to rain disturbances (Fig. 3.2h).

Despite the similarities in abscission strategies for maximizing LDD between the species, several small but consistent differences were also observed. In all cases, the slope parameter remained maximal, but the optimal threshold wind speed increased with species' seed terminal velocity and seed release height (Supplementary material Appendix S3.1 Fig. S3.4a). Parameter β ranged from 5 to 6 m s^{-1} within our study species, to potentially > 7 m s^{-1} in species with high seed release height and relatively heavy seeds. Heavier seeds are more dependent on high wind speeds to achieve LDD. The optimal threshold also increased with species' seed release height (Fig. S3.4a), as wind speeds increase logarithmically with height above the ground surface (at least for near-neutral conditions) and taller species benefit more from the higher wind speeds. However, according to our model calculations, plant species with very low seed terminal velocity (0.2 m s^{-1}) benefitted the most from non-random abscission (Fig. S3.4b), as their seeds have the greatest probabilities of being uplifted and transported over long distances under high mean wind speed, high turbulence conditions.

Aim 2: Potential risks

The effect of potential risks on non-random abscission strategies and dispersal kernels was large. When no disturbances resulting in seed loss were considered, the optimal abscission function for LDD resembled a threshold function (very steep slope, α = 4) but the threshold wind speed was very high, at 12 m s^{-1} (Fig. 3.3a,b). The resulting dispersal kernels had fatter tails and much more LDD than reference kernels for random abscission (Fig. 3.1a,b), with 99-percentile dispersal distances for *H.*

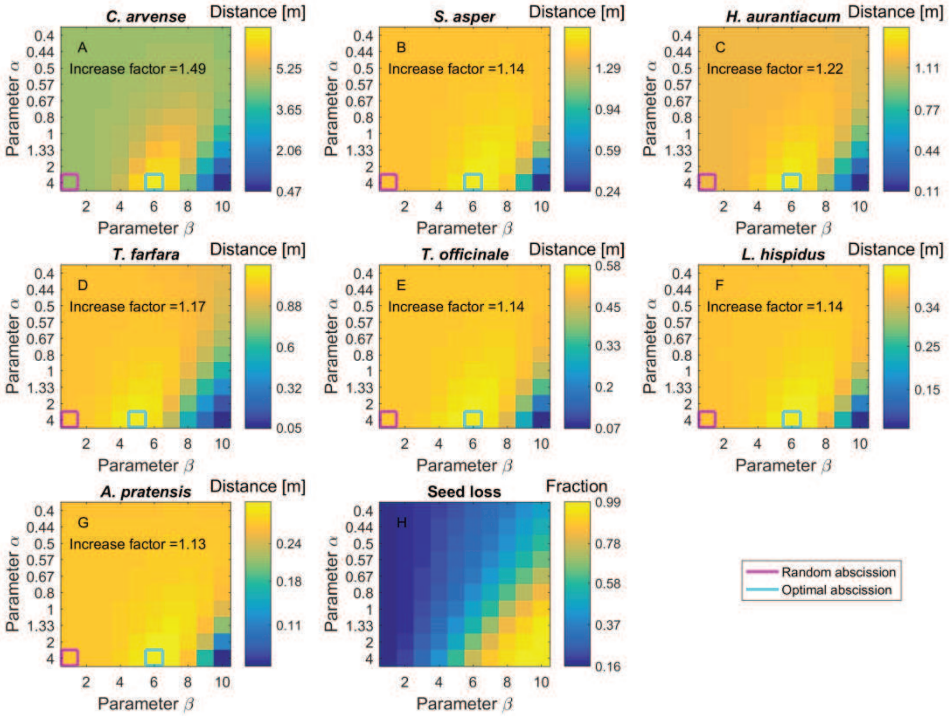

Figure 3.2. Panel A-G: Plant species' 99-percentile dispersal distances as a function of the slope (α) and midpoint (β) parameters of the abscission function (Eq.3.4). Presented dispersal distances are 30-year means. The lower-left cell in each panel represents the dispersal distance for random abscission (α = 4 and β = 1). Panel H: Seed mortality as a function of the slope and midpoint parameter of the abscission function.

aurantiacum and *L. hispidus* increasing by a factor of 40 and 20, respectively. Interestingly, given the meteorological time series used, the threshold did not increase beyond 12 m s^{-1}; even without any risk costs there appeared to be a limit to the value of this threshold, determined by the local wind speed frequency distribution.

In contrast, addition of a potential risk in the form of a disturbance resulting in seed loss yielded much lower wind speed threshold values. Inclusion of a realistic disturbance in the form of actual rain events resulted in parameters as discussed above (Fig. 3.2a-g), with threshold values of 5-6 m s^{-1}. When comparing the latter scenario to scenarios with disturbances that are not auto-correlated over time, it became clear that a probability of disturbance of 0.05 yielded very similar results (Fig. 3.3d,e). Although the probability of actual rain disturbance is 0.22, the auto-correlation and regularity of actual rain events resulted in an impact of a similar magnitude to random disturbance with a probability of 0.05. Increasing levels of random disturbances to 0.22 (the equivalent of rain but now random) and 0.33 resulted in greatly reduced threshold wind speeds, around 2 m s^{-1} (Fig. 3.3g,h,j,k).

Under such conditions, hardly any benefit can be gained from non-random seed abscission in terms of increasing the 99-percentile dispersal distance.

Aim 3: Timing mechanisms across different timescales

The model results presented above clearly stressed the relevance of mean horizontal wind speeds and short, hourly timescales in determining abscission and its consequences for LDD. Across species, the abscission threshold of individual seeds above wind speeds of ca. 5-6 m s^{-1} resulted in most LDD.

At shorter timescales, abscission during turbulent gusts increased median dispersal distances but hardly affected the tail of the dispersal kernels (Supplementary material Appendix S3.1 Fig. S3.5). A plausible explanation is that if the conditions achieve sufficient seed uplifting and subsequent LDD, the influence of the instantaneous turbulent gust at take-off becomes less relevant for long-distance dispersing seeds. The tail of the kernel appeared mainly sensitive to the 'background' mean wind speed, i.e. the hourly means used in the remaining model studies.

On diurnal timescales, we found no evidence supporting an effect of abscission in relation to VPD on LDD (Supplementary material Appendix S3.1 Fig. S3.6), probably because high wind speeds occur less often during high VPD conditions in the meteorological dataset considered.

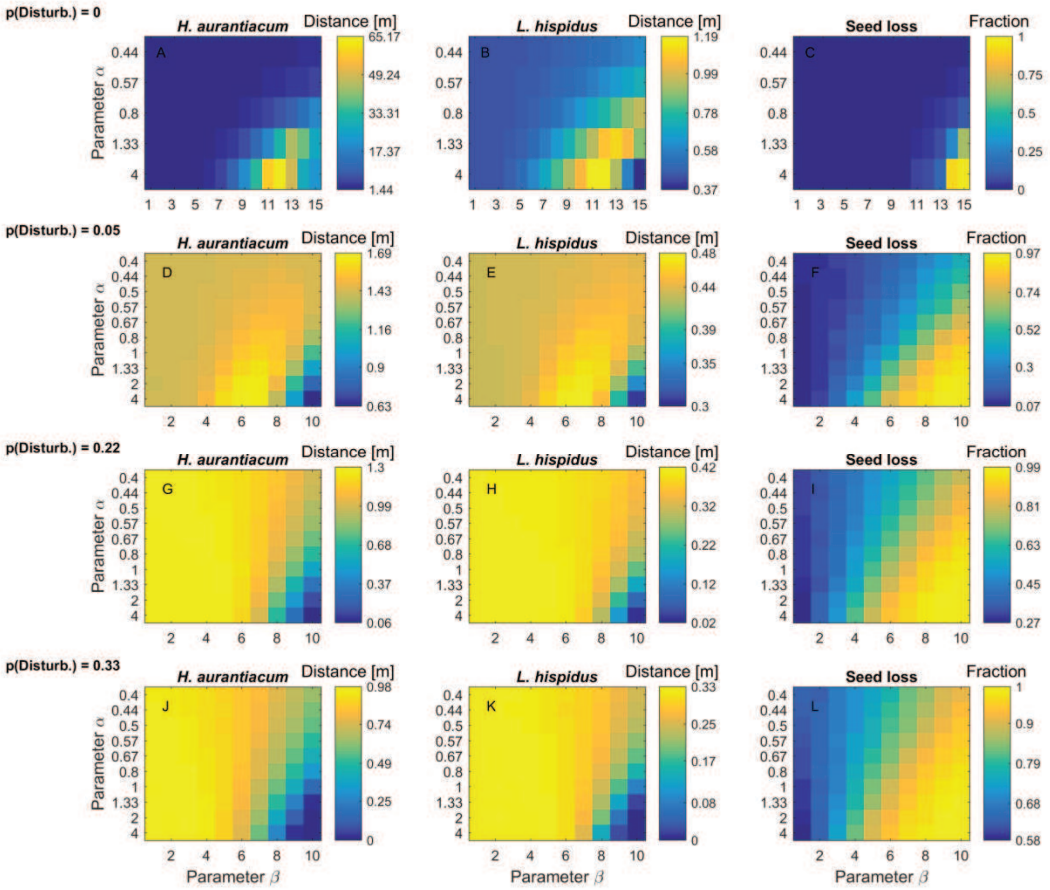

Figure 3.3. Plant species' 99-percentile dispersal distances and seed mortality as a function of the slope (α) and midpoint (β) parameters of the abscission function (Eq.3.4), for different potential risk scenarios: No disturbance (panels A-C), random disturbance with probability 0.05 (panels D-F), random disturbance with probability 0.22 (probability equal to rain disturbance in Fig.2, but without temporal auto-correlation; panels G-I) and random disturbance with probability 0.33 (panels J-L). Each disturbance event is assumed to result in loss of the exposed seeds. Presented dispersal distances are 30-year means. The lower-left cell in each panel represents the dispersal distance for random abscission (α = 4 and β = 1).

Considering longer timescales, significant differences were observed when comparing different seasons (Fig. 3.4). During winter and, particularly, spring the release threshold (optimal midpoint parameter β, given that α was maximal) of the non-random abscission function was significantly higher than during summer and autumn, suggesting that during winter and spring in the Netherlands non-random abscission may result in more LDD than during summer and autumn. At even longer timescales, across years, the variation in optimal abscission strategies for LDD was no

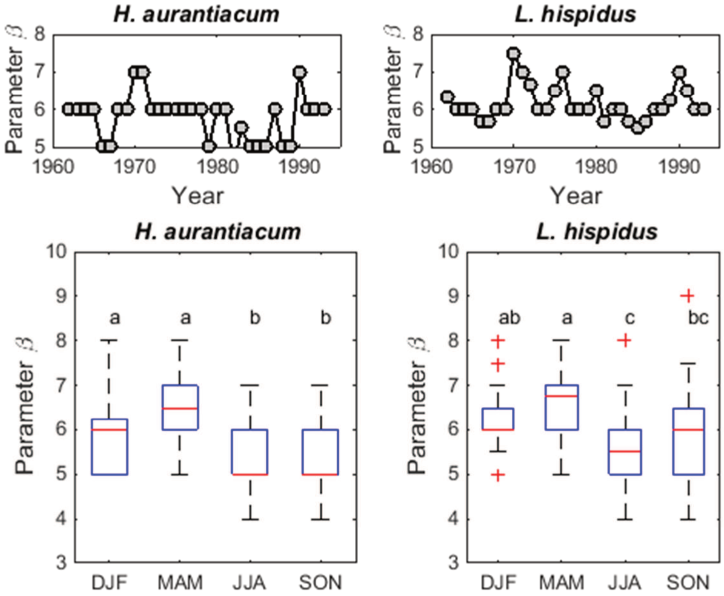

Figure 3.4. Variation in optimal midpoint parameter (β) values for LDD over a period of 32 years (upper panels) and across the four seasons (lower panels) for *Hieracium aurantiacum* and *Leontodon hispidus.*

larger than observed for seasonal variation (Fig. 3.4 and Supplementary material Appendix S3.1 S3.7), suggesting that climatic stability was sufficient for non-random abscission strategy to develop and be effective over multiple generations.

Field study results

In the Asteraceae species, seeds typically dispersed within a few days' time after first exposure. In *S. asper,* 95% of the seeds of an infructurescence dispersed within 1.55 hours (mean), with a standard deviation (sd) of 0.79 hours for 168 observed infructescences (n). In *C. arvense* (mean = 15.21; sd = 39.00; n = 14) and *H. aurantiacum* (mean = 17.26; sd = 26.55; n = 113), this happened within 24 hours, and in *T. farfara* (mean = 36.17; sd = 33.83; n=6), *T. officinale* (mean = 49.40; sd = 81.55; n = 5) and *L. hispidus* (mean = 48.04; sd = 45.37; n = 88) in around 2 days. In *A. pratensis* (Poaceae), it generally took very long before seeds dispersed and none of the infructurescences released all seeds.

The field data showed a very clear bias of abscission towards high winds in all species except *T. farfara* (Fig. 3.5). A sigmoid abscission function provided a good fit to the abscission measurements in *A. pratensis*, *H. aurantiacum*, *S. asper* and *T. officinale*.

In *C. arvense* and *L. hispidus* the shape of the abscission function only showed an exponential increase without the characteristic levelling off of a sigmoid function. In contrast to the theoretical abscission functions, the measured functions have a maximum abscission probability lower than 1. In reality the seeds within an infructurescence span a range of ripeness stages with many seeds not fully ripe or being sheltered behind neighbouring seeds at the moment of our observations. We calculated the potential consequences of the observed abscission functions in our model to show how the observed non-random abscission increases the tail of the dispersal kernel (Fig. 3.1e,f).

As a result of the non-random abscission, the frequency distributions of wind speeds sampled by dispersing seeds were shifted to the right compared to the background wind speed distribution in *C. arvense, H. aurantiacum, L. hispidus and S. asper* (Fig. 5). In these species, the positive bias of seed abscission started at wind speeds of 5-6 m s^{-1}, except for *T. officinale* where it was lower (4 m s^{-1}) and *A. pratensis* where it was higher (7 m s^{-1}; Fig. 5). These wind speeds are similar to the optimal model threshold, although the model predicted a sharp threshold rather than the gradual relation observed in the field. In *T. farfara*, no clear abscission pattern was found.

Abscission was not only non-random in relation to hourly mean wind speed. On longer timescales, more seeds dispersed during midday ((12-)13-14 o'clock) compared to morning and late afternoon across the Asteraceae species (but not in *A. pratensis*; Fig. A8). In the two species for which the most data were available, *H. aurantiacum* and *L. hispidus*, the predictor variables wind speed, time since opening, time of day and VPD all significantly contributed to explaining abscission probability (Table S3.1), together explaining 25 and 10%, respectively, of the variation in abscission. These analyses show that on longer timescales, more seeds dispersed when it was warmer.

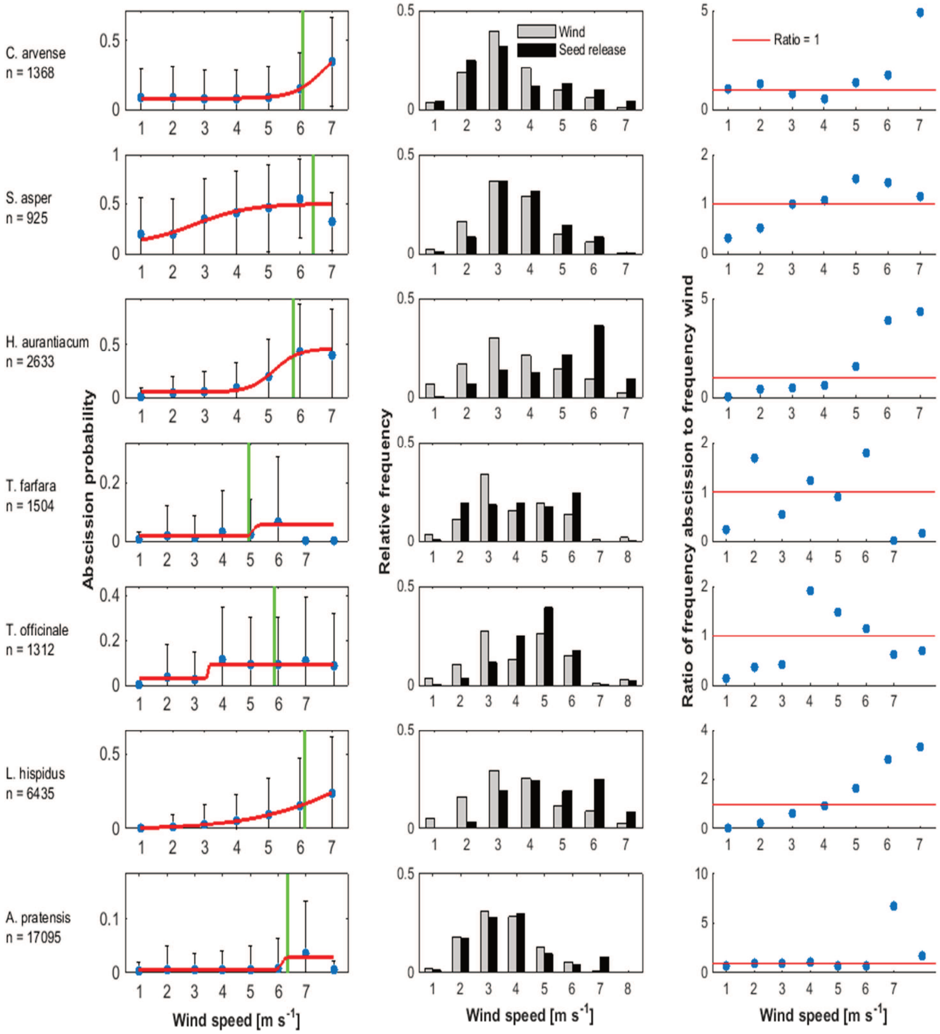

Figure 3.5. Left column: Mean abscission probabilities (blue dots, ± sd), measured hourly throughout an entire growing season, as a function of hourly mean wind speed measured at 20 m altitude at KNMI station De Bilt. The red lines are fitted sigmoid functions. The green lines indicate the optimal value of parameter β from the model simulations (scenario with auto-correlated rain disturbance). Middle column: Relative frequencies of mean wind speed (gray bars) and seed release (black bars) measured hourly throughout an entire growing season. Right column panels: Ratios of the relative frequency of seed abscission to relative frequency of occurrence, per wind speed (blue dots). The red lines represent a ratio of one; ratios higher than one indicate seed abscission biased towards the respective wind speeds. 'n' Is the number of observations.

Discussion

Our model runs showed that non-random abscission thresholds can maximize LDD by releasing seeds during strong winds only. However, potential pre-dispersal risk costs may result in seed loss while seeds are exposed during periods of low wind speeds, which greatly reduced LDD potential in our model. Under the climatic conditions for De Bilt, central Netherlands, non-random abscission with a per-seed threshold wind speed of around 5-6 m s^{-1} provides an optimal strategy maximizing LDD by wind, balancing maximal gain in dispersal distances *versus* minimal loss of seeds due to natural (rain) disturbances. Strikingly, this threshold was much lower than would be expected when potential risk costs are not considered (the 'no disturbance scenarios', which resulted in threshold wind speeds of around 12 m s^{-1}). Also, the threshold was much higher than would be expected when potential risks would be much higher than purely from rain (or a similar disturbance of equal size, like a random disturbance occurring with a probability of 0.22, which resulted in threshold wind speeds < 3 m s^{-1}). The field study data showed that in reality, for central Netherlands meteorological conditions, non-random abscission occurs in six out of the seven studied wind-dispersed plant species, at wind speeds above *ca*. 5-6 m s^{-1}. The field study also clarified that abscission on a per-infructurescence basis is less like a threshold (and more like a sigmoid) than the simulated abscission on a per-seed basis.

To what extent is non-random abscission able to promote LDD?

Non-random abscission with a per-seed threshold wind speed of 5-6 m s^{-1} was shown to enhance LDD (increase of 99-percentile distance by a factor of 1.13-1.49). Earlier studies already showed that increases in abscission with wind speed or updrafts may increase LDD by a factor of 1.2 (Savage *et al.* 2014), 1.3-2.6 (Soons & Bullock 2008) or even 2-3 (Maurer *et al.* 2013; Pazos *et al.* 2013).

In previous studies, as well as in our field data, a more exponential or sigmoid-shaped abscission function in relation to wind speed was found than the steep threshold-like function in our modelling study (Greene 2005; Skarpaas *et al.* 2006; Jongejans *et al.* 2007; Soons & Bullock 2008; Greene & Quesada 2011; Pazos *et al.* 2013). This is likely caused by natural variation in 'ripeness' of the seeds and/or material fatigue in the tissue connecting seeds to the plant (Pazos *et al.* 2013), resulting in a combined function of many different thresholds for an entire infructurescence (the typical unit of measurement in seed abscission studies; Greene 2005, Skarpaas et al. 2006, Jongejans et al. 2007, Soons and Bullock 2008, Greene and

Quesada 2011, Maurer et al. 2013, Pazos et al. 2013). This combined function may serve as a safe bet-hedging strategy to limit the risk of losing all seeds through a major disturbance or a lack of wind. In contrast, maximizing LDD is achieved by a single and constant hard-threshold wind speed for abscission according to the model. This strategy allows the midpoint/threshold wind speed to be higher and closer to the minimum caused by seed loss at even higher wind speeds (Fig. 3.2).

What is the effect of potentially increased risks on non-random abscission strategies and dispersal kernels?

Non-random abscission reduces the probability of dispersal during low wind speeds and therefore causes seeds to remain attached to the plant longer during low wind speed conditions. This strategy comes at increased risk costs (Bonte *et al.* 2012). Potential risks include seed predation and damage of the seeds or *pappus* by rain or other weather extremes (Jongejans *et al.* 2007; Bonte *et al.* 2012). These risks have a stochastic nature, but when the frequency of such events remains constant on evolutionary timescales, plants may evolve non-random abscission strategies that increase LDD while minimizing seed loss. We found clear optima of the slope and the midpoint that are quite stable over a 32-year period. Such stability may indicate that plant species have time to evolve non-random seed abscission mechanisms over multiple generations.

We have assumed that rain destroys all seeds, which may be a crude assumption. For some wind-dispersed species, rain makes the pappi of different seeds stick together, as in *S. asper* among our study species, but other species have mechanisms that cause the *pappus* to close and wait for reopening until all water has disappeared (Casseau *et al.* 2015). Our computed optimal wind speed thresholds were highly similar to the measured bias in wind speeds sampled by released seeds in the field study indicating the presence of a disturbance with similar magnitude. However, we cannot tell whether this was because the assumption of rain events being fatal was realistic, or whether another fatal disturbance, with a lower probability of around 0.05 but uncorrelated over time (i.e., probability of seeds being predated) was limiting the threshold to around 5-6 m s^{-1}. Another option is that pre-dispersal risk costs are much lower than our model results suggest and selection may favour reducing seed loss over maximizing LDD. Furthermore, shorter dispersal distances may even be favoured e.g. in patchy and relatively stable habitats (Chapter 2).

For all species, the frequency of disturbance has a major impact on the effect of abscission functions on dispersal kernels; under increasingly high disturbance regimes plants are better off dispersing seeds as soon as possible.

Which meteorological factors and respective timescales are important for maximizing LDD?

A summary of our findings across timescales is conceptualized in Figure 3.6. Abscission is an instantaneous process and occurs when a threshold force is exceeded. Wind gusts play an important role in producing this drag as instantaneous wind speed is composed of mean wind and a turbulent fluctuation around this mean. However, mean wind speed is also a major determinant in shaping the seed trajectories of seeds that travel longer than a few seconds and LDD may therefore be more sensitive to mean wind speed than turbulent gusts at take-off. On short timescales, for a mechanistic modelling approach, one may need to incorporate dynamic material strength that determines the seed release threshold, which may change over time (Borger *et al.* 2012) due to processes at the cell level (Liljegren *et al.* 2000) or material fatigue from drying and or wear-and-tear (Thompson & Katul 2013). In addition, ripening and exposing seeds during periods of low disturbance periods, for example dry and windy periods, could result in a better exploitation of a non-random abscission strategy. However, we found no evidence of variable seed production based on vapour pressure deficit increasing LDD or reducing seed loss.

On longer timescales, variation over the years was small but variation across the seasons resulted in significant differences in modelled optimal release thresholds, with optimal thresholds being higher in winter and spring. This is mainly caused by more frequently occurring strong winds in winter and spring (Supplementary material Appendix Fig. S3.9). Interestingly, the only species in our study that produces ripe seeds in spring, *T. farfara*, did not show such a higher release threshold - in fact it was the only species not exhibiting any relation between abscission probability and mean wind speed. The total number of infructurescenses of this species included in our study was the lowest compared to the other species (n=56), however, and it is not known whether the data on this species are representative of spring-dispersing species.

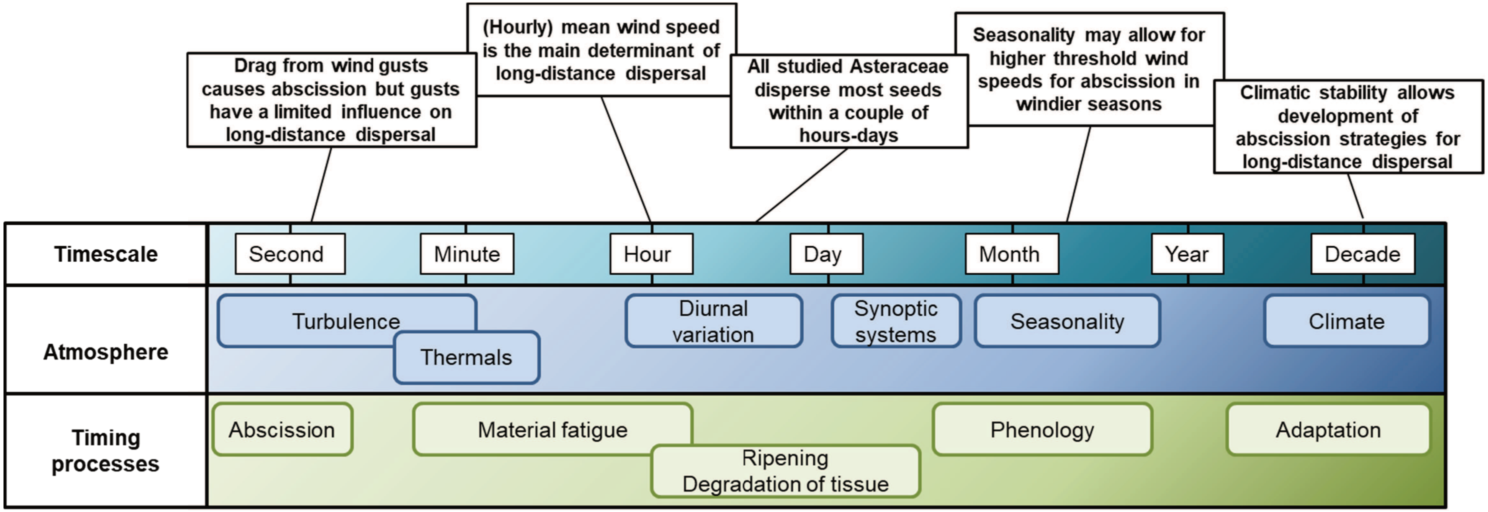

Figure 3.6. Timescales of the relevant biotic and abiotic factors relevant for the timing of abscission and a summary of the most important results across these timescales.

Conclusions and implications

Based on our results and the existing literature, we conclude that most species aiming to maximize seed dispersal distances by wind have some form of non-random abscission mechanism. Non-random abscission has the potential to increase LDD by wind and may help close the gap between modelled and measured frequencies of LDD events in the tail of the dispersal kernels. However, non-random abscission comes at a cost. Exploring both costs and benefits of non-random abscission over an entire growing season using realistic meteorological data shows that, under realistic risk costs (such as rain), potential positive effects of non-random abscission are much smaller than when such risks are ignored. Inclusion of the costs of non-random abscission will contribute to more realistic estimates of seed dispersal distances and predictions of seed dispersal under global change. Mechanistic dispersal models with non-random abscission functions will improve predictions of migration, invasion or colonization processes.

Acknowledgements

This project was funded by the Netherlands Organization for Scientific Research (NWO-ALW; VIDI grant 864.10.006 to M.B.S.).

Supporting information

Appendix S3.1: Model description

The Coupled Eulerian-Lagrangian Closure model (CELC; Katul & Albertson 1998; Nathan *et al.* 2002, 2011; Soons *et al.* 2004a; b) randomly generates auto-correlated time series of turbulence fluctuations around a profile of mean wind speeds within and above vegetated canopies. Trajectories of individual seeds are simulated, and a dispersal kernel is later computed based on the landing locations of the seeds.

CELC uses a second order closure model to create the vertical profiles of wind statistics (Wilson & Shaw 1977, in this work), and Thomson's simplest solution for solving a 3D Lagrangian stochastic Langevin equation to calculate the seeds trajectories (Thomson 1987; Rodean 1996).

To include the effects of heavy seeds in the Lagrangian component, a constant terminal velocity was imposed in the vertical direction. There are more complex ways to incorporate particle inertia, such as solving a momentum balance equation for the seed's velocity (Nathan *et al.* 2011b; Thompson & Katul 2013; Duman *et al.* 2016), however, the Asteraceae species typically produce seeds with a pappus that are tightly coupled to flow, so that the use of constant terminal velocity is sufficient. We also included the crossing trajectories' effect, which considers the seeds crossing trajectories of fluid elements under the influence of gravity (Csanady 1963; Wilson 2000). The universal constant (C_0) was set to 4.9 (Duman *et al.* 2016).

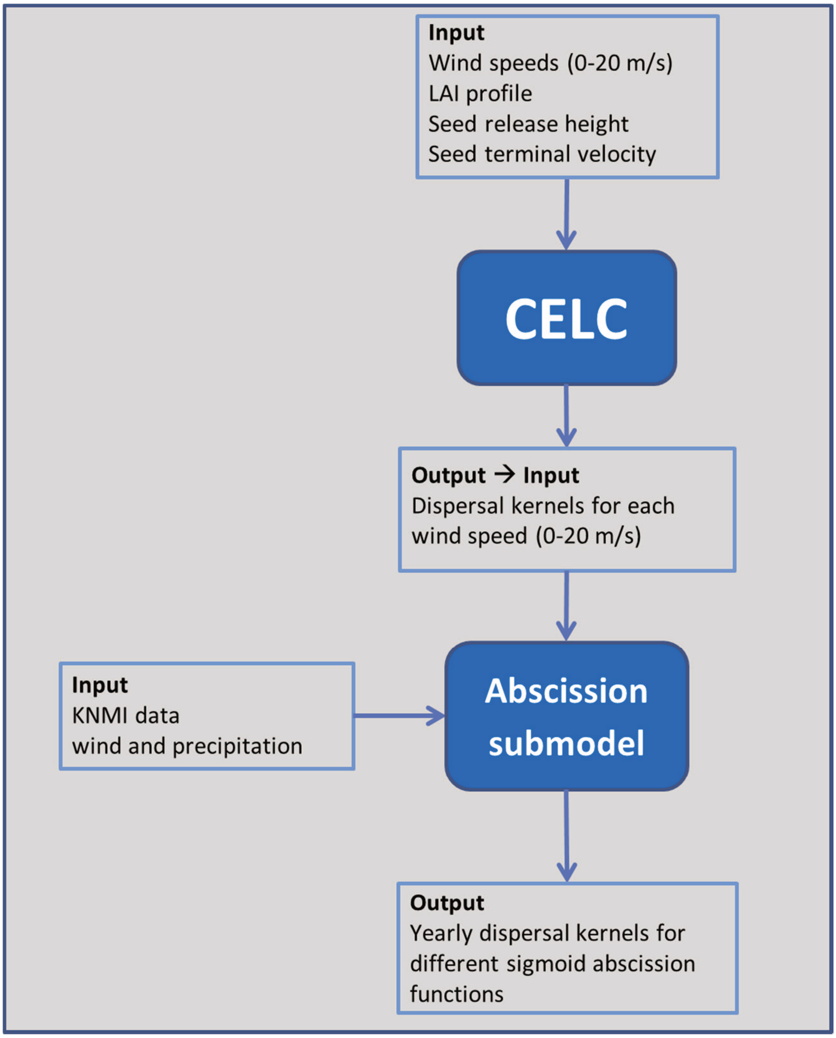

Figure S3.1. Schematic view of the model framework. Blue rounded rectangles represent the two models that are coupled. The transparent rectangles represent input and output variables.

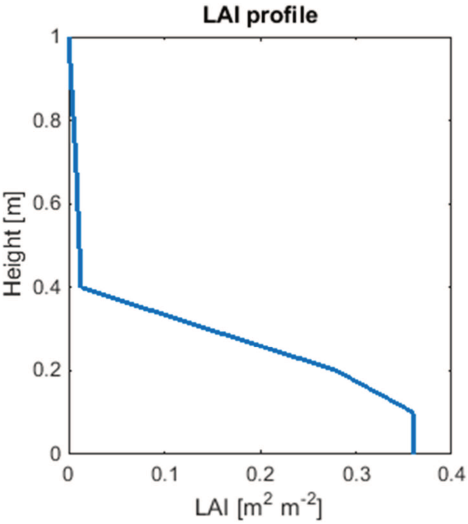

Figure S3.2. Leaf area index profile in a Cirsio-molinietum stand (Fliervoet 1984). This LAI profile is used as input for the closure model that generates wind profiles for the CELC model.

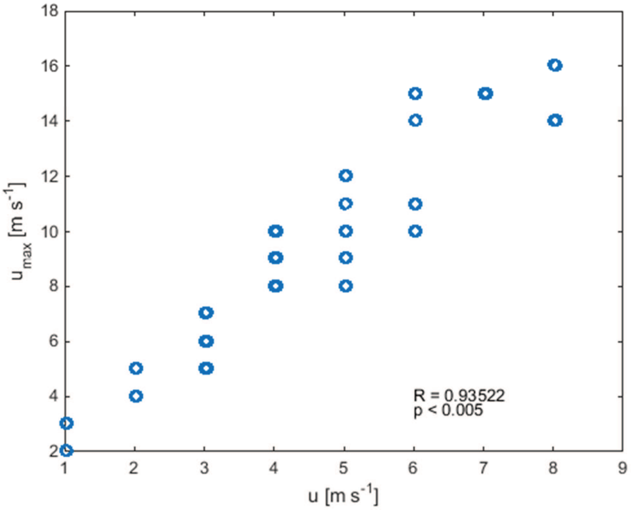

Figure S3.3. Correlation between hourly wind speed (u) and maximum wind gust (U_{max}, 3 seconds averaged) in this hour. Data obtained from the KNMI station over the same period as the field observations.

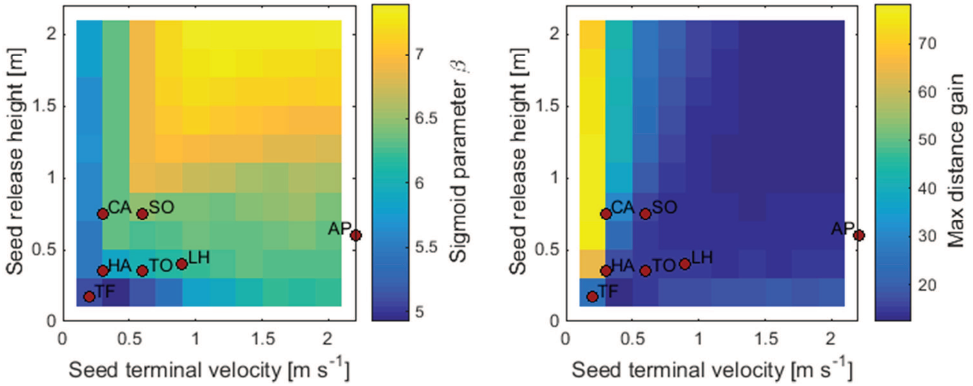

Figure S3.4. Left panel: Optimal value of the midpoint parameter (β) of a sigmoid abscission function as a function of seed terminal velocity and seed release height. Right panel: The distance gain of the 99 percentile dispersal distance that is obtained compared to random dispersal when adopting the optimal sigmoid abscission function. Red dots are the studied species.

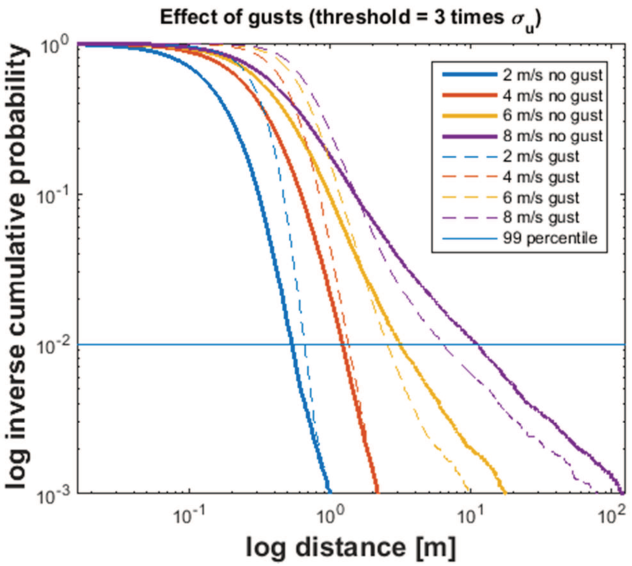

Figure S3.5. Effects of seed release during gusts on a dispersal kernel (exceedance probability) compared to effect of mean wind speed. The seed release threshold for dispersal during gusts is three standard deviations above mean wind speed (μ = 2, 3σ = 0.874; μ = 4, 3σ = 1.748; μ = 6, 3σ = 2.622; μ = 8, 3σ = 3.496).

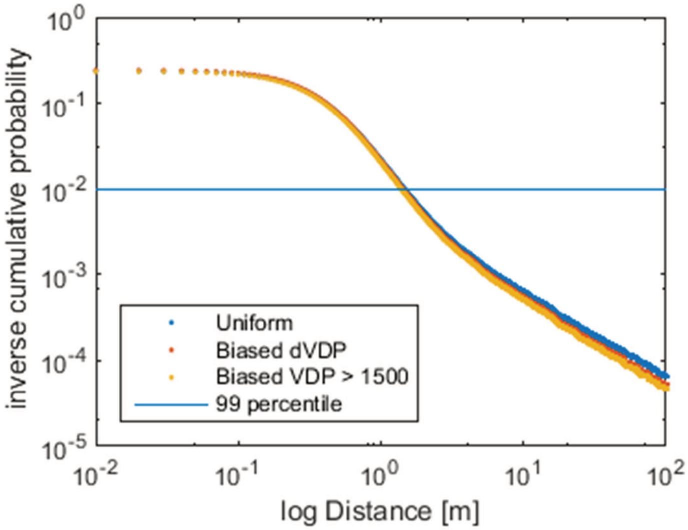

Figure S3.6. Effects of non-uniform seed production as a function of vapour pressure deficit on the dispersal kernels. Biased dVDP means: *if* VPD_{t-1} =< 1000 pascal AND VPD_t > 1000 *then* seed production = 1000, *else* seed production = 0. Biased VDP means: *if* VPD < 1500 pascal *then* seed production = 0, *else* seed production = 1000.

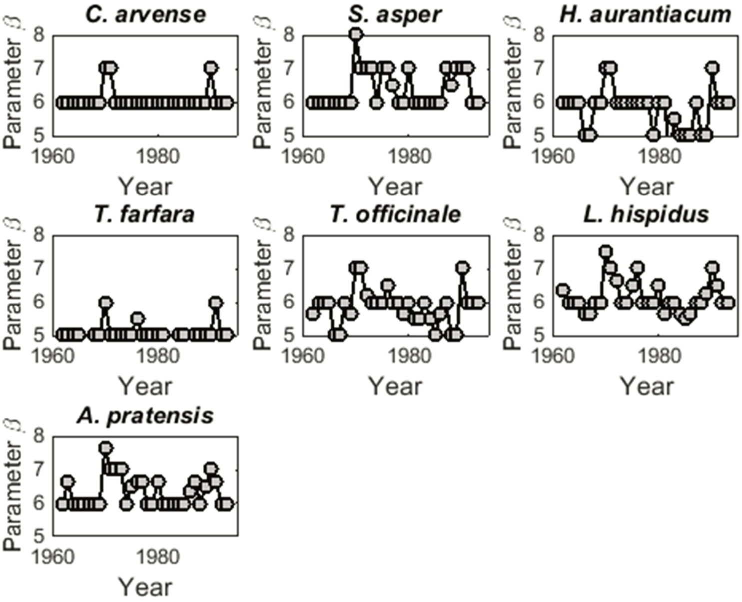

Figure S3.7. Variation in optimal midpoint parameter (β) values for LDD over a period of 32 years for all study species.

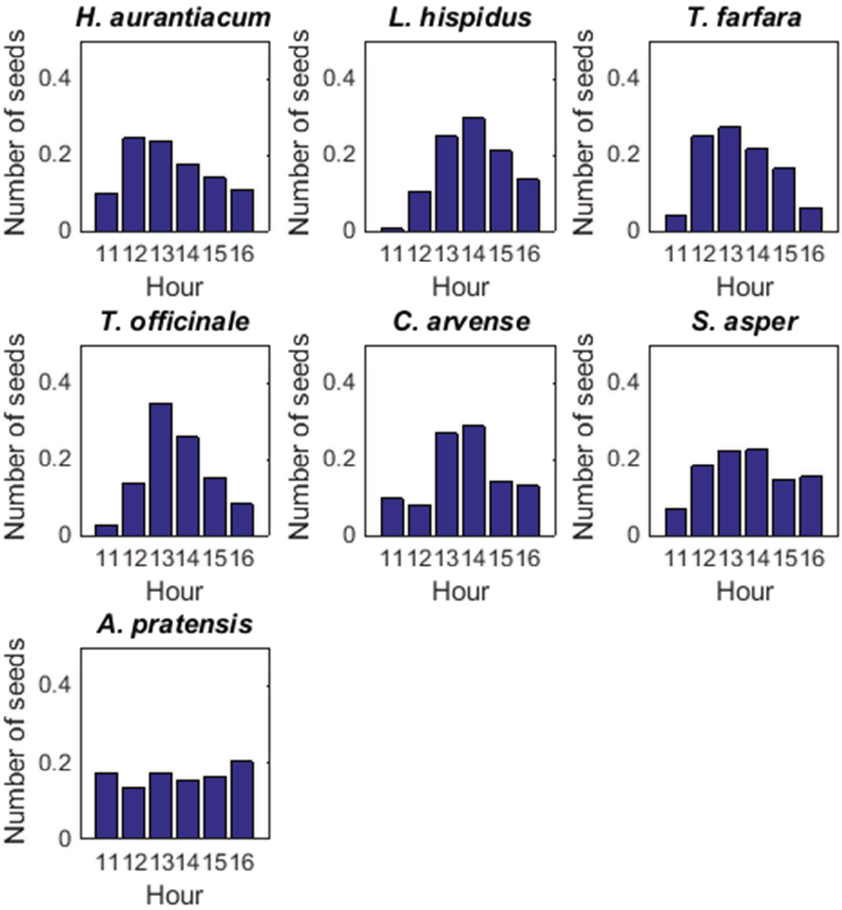

Figure S3.8. Fraction of seeds that are dispersed during each hour of the day for all studied species.

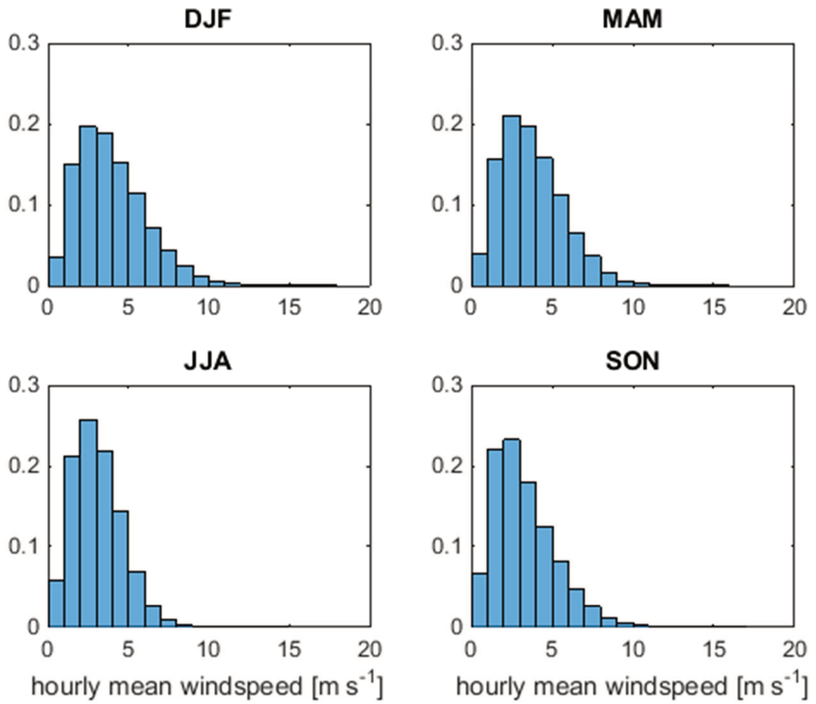

Figure S3.9. Frequency distribution of the hourly mean wind speed per season from 1961-1992. Distributions are Weibull shaped but have different tails. Seasons are defined as DJF (December, January and February), MAM (March, April and May), JJA (June, July and August) and SON (September, October and December).

Table S3.1. General linear model (GLM) results of abscission as a function of wind speed (U), time since opening (Time), time of day (H), and vapour pressure deficit (VPD). P values of all coefficients are < 0.005. Models are compared in terms of the adjusted coefficient of determination (R^2) and Akaike Information Criterion (AIC).

Hieracium aurantiacum

GLM	R^2	AIC	Intercept	U	Time	H	H^2	VPD
A = U	0,19	64101,56	-5,8	0,88	x	X	x	x
A = U + t	0,21	62999,27	-5,4	0,85	-0,014	X	x	x
A = U + t + H	0,22	62819,01	-7,0	0,88	-0,014	0,11	x	x
A = U + t + H + H^2	0,23	61841,14	-46,7	0,89	-0,014	5,82	-0,20	x
A = U + t + H + H^2 + VPD	0,25	60488,86	-43,4	0,72	-0,013	5,32	-0,19	0,00074

Leontodon hispidus

GLM	R^2	AIC	Intercept	U	Time	H	H^2	VPD
A = U	0,08	90635,58	-5,7	0,68	x	X	x	x
A = U + t	0,08	90634,66	-5,7	0,68	0,00043	X	x	x
A = U + t + H	0,09	90290,74	-7,6	0,72	0,00062	0,12	x	x
A = U + t + H + H^2	0,09	90269,26	-12,5	0,72	0,00061	0,84	-0,03	x
A = U + t + H + H^2 + VPD	0,10	89231,03	-11,7	0,69	0,00098	0,65	-0,02	0,00050

4

Seed dispersal distributions resulting from landscape-dependent daily movement behaviour of a key vector species, *Anas platyrhynchos*

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Abstract

Dispersal via animals (zoochory) is a primary mechanism for seed exchange between habitat patches. Recent studies have established that many plant species can survive waterbird gut passage. To quantify the patterns and consequences of waterbird-mediated dispersal, information on ingestion and gut passage must be combined with bird movement data. Such analysis has recently revealed seed dispersal kernels by migrating waterbirds. However, since many waterbird populations are largely resident, and migrating populations spend only a minor part of the main dispersal season (autumn-winter) on migration, daily regional scale movements probably cause more frequent dispersal.

We synthesized high resolution empirical data on landscape scale movements and seed gut passage times in a key disperser species, the mallard (*Anas platyrhynchos*), using a spatially explicit, mechanistic model to quantify dispersal distributions resulting from daily autumn-winter movements. We evaluated how landscape composition and seed traits affect these dispersal patterns.

The model indicates that mallards generate highly clumped seed deposition patterns, dispersing seeds primarily between core areas used for foraging and resting. Approximately 34% of all dispersed seeds are transported to communal roost areas, which may function as reservoirs for mallard-dispersed species, and 7% are transported between foraging areas. Landscape-dependent movement patterns strongly affect the dispersal distributions, resulting in multimodal dispersal kernels, with dispersal distances increasing with fragmentation of freshwater foraging habitat. Seed size-related gut retention times determine the proportion of seeds being dispersed away from the ingestion area, with larger seeds (20 mm^3) having a 8-10% higher potential for long-distance dispersal than smaller seeds (0.2 mm^3), if surviving gut passage. However, twice as many small seeds will finally accomplish long-distance dispersal due to their higher gut passage survival.

Synthesis: Firstly, this study reveals how seed dispersal patterns resulting from daily waterfowl movements are shaped by landscape-dependent differences in movement patterns. Secondly, seed survival appears more important than retention time in determining the scale of long-distance dispersal by non-migrating mallards. We conclude that the frequent flights of staging waterbirds result in directed dispersal over distances inversely related to wetland availability, indicating that they maintain landscape connectivity across a range from wet to increasingly dry landscapes.

Introduction

The spatial pattern of seed deposition after dispersal forms a template for plant recruitment and subsequent ecological and evolutionary processes (Nathan & Muller-Landau 2000; Fraaije *et al.* 2015a, b) and is therefore of critical importance for plants. Seed transportation by animals (zoochory) that use the same habitat types as the adult plants may be expected to be an effective dispersal strategy, increasing the success rate of recruitment (Howe & Smallwood 1982; Schupp 1993; Wenny 2001). However, the extent to which this occurs in the field is difficult to assess, because dispersal by animals is notoriously difficult to quantify. Firstly, animal behaviour is often quite variable and involves long-distance movements (Swingland & Greenwood 1983; Patterson *et al.* 2008). Secondly, the transport of seeds depends strongly on seed traits and is therefore highly variable (Howe & Smallwood 1982). If ingested, seeds have to pass the animal's digestive tract, which affects their survival and duration of transportation (retention time), depending on traits like seed volume and seed coat thickness (Janzen 1984; Soons *et al.* 2008; Reynolds & Cumming 2016). Therefore, mechanistic models are increasingly being used to predict seed dispersal distributions and to evaluate the consequences of zoochorous dispersal, despite the challenging implementation of the complex interplay between plant and animal traits that need to be obtained from field studies and lab experiments (Russo *et al.* 2006; Will & Tackenberg 2008; Kleyheeg 2015).

Waterbirds have long been assumed to be important dispersal vectors for wetland plants (Darwin 1859; van Leeuwen *et al.* 2012), and recently also for more terrestrial plant species (Kleyheeg *et al.* 2016; Soons *et al.* 2016). Internal (endozoochorous) dispersal by waterbirds has been identified as an important mechanism for dispersal between isolated wetland areas (Amezaga *et al.* 2002; Green *et al.* 2002). Particularly mallards (*Anas platyrhynchos*), the most abundant duck species worldwide with a large geographic distribution (del Hoyo *et al.* 1992), are likely to significantly shape the dispersal distributions of plant species. Seeds are an important component of the mallard diet, including a wide range of species (Brochet *et al.* 2012; Kleyheeg *et al.* 2016; Soons *et al.* 2016), most of which have the potential to survive digestive tract passage (Charalambidou & Santamaría 2005; van Leeuwen *et al.* 2012). At the same time, mallards are highly mobile on the landscape scale (Sauter *et al.* 2012; Bengtsson *et al.* 2014; Kleyheeg 2015) and capable of migrating over long distances (Krementz *et al.* 2012), providing ample opportunity for long-distance seed dispersal (Viana *et al.* 2013a). However, their opportunistic habitat use, nocturnal activity and rapid displacements have made it difficult to empirically quantify their contribution to seed dispersal in the field.

Mechanistic seed dispersal models have been applied to obtain a better understanding of the role of mallards in plant ecology. Current estimations of dispersal distances following transportation by mallards and other waterbirds are based on simple models, often identifying only maximum dispersal distances as estimated from gut retention time and flight speed during non-stop unidirectional flights directly after seed ingestion (e.g. Charalambidou *et al.* 2003; Soons *et al.* 2008; Kleyheeg *et al.* 2015; but see Viana *et al.* 2013). Indeed, long-distance dispersal (LDD) is of disproportional importance for spatial plant population dynamics (Cain *et al.* 2000; Nathan 2006), and migratory mallards and teal (*A. crecca*) were shown able to contribute substantially to LDD by transporting seeds over distances up to 1582 km (Viana *et al.* 2013b). However, during the period that ripe plant seeds are available to waterbirds (autumn-winter) migratory flights are relatively rare events, typically undertaken on less than ten days per autumn (Gaidet *et al.* 2010), and successful LDD events following migration are probably exceedingly rare (Clausen *et al.* 2002; Viana *et al.* 2016a). Daily, non-migratory waterbird movements in autumn and winter result in shorter, but much more frequent dispersal events and may have a higher probability of dispersal towards suitable sites with similar environmental (e.g. climatic) conditions.

Here, we quantify the dispersal patterns of seeds transported internally by mallards during their frequent daily movements in the autumn-winter period, taking advantage of the detailed information which has recently become available on all essential components of this dispersal mechanism: 1) the range of seed species ingested (Kleyheeg *et al.* 2016; Soons *et al.* 2016), 2) empirically-determined gut passage times and survival rates across a range of seed traits (Soons *et al.* 2008; van Leeuwen *et al.* 2012; Kleyheeg *et al.* 2015), and 3) mallard movement data from high resolution GPS tracks across a range of landscapes (Kleyheeg 2015). We combined these components in a single, mechanistic, spatially explicit model to analyse seed dispersal patterns. We specifically evaluated the relative contributions of landscape-dependent mallard movement behaviour and of seed volume, the latter being consistently reported as one of the most relevant seed traits determining gut passage time and survival (Figuerola & Green 2002; Soons *et al.* 2008; van Leeuwen *et al.* 2012; Kleyheeg *et al.* 2015), in establishing these patterns.

Materials and methods

We developed a spatially-explicit, mechanistic model to identify seed deposition patterns following endozoochorous seed dispersal by mallards. This model combines information on all components of the endozoochorous dispersal process (ingestion, gut passage and movement) to simulate the spatial dispersal patterns. Using these model simulations, we explored the effects of variability in landscape configuration and seed volume on the resulting seed dispersal distributions. The model consists of two parts: 1) a seed part, simulating the ingestion, gut passage and excretion of plant seeds, and 2) a bird part, describing mallard movements across landscapes. These two parts were integrated to obtain spatiotemporal patterns in seed dispersal distributions by coupling the time steps of the seed part of the model to the time and corresponding location of the GPS fixes of the mallard tracks.

Study system

Mallards are the world's most abundant dabbling duck species, with an estimated 19 million individuals spread over most of the Northern Hemisphere (del Hoyo *et al.* 1992; Wetlands International 2016). As opportunistic habitat generalists, they occupy a wide range of habitats from large natural wetlands to dry landscapes with few patches of open water, to cities and urban parks (del Hoyo *et al.* 1992; Snow *et al.* 1998). They also feed highly opportunistically, seasonally shifting their diet from animal-based in spring and summer to seed-based diet in autumn and winter, when ripe seeds are most abundantly available (Snow *et al.* 1998). Through GPS telemetry, we collected data on the daily movements of mallard at four localities in the Netherlands (Oud Alblas, Terra Nova, Juliusput and Enterveen; Kleyheeg *et al.* 2017a). The landscapes surrounding these localities varied in their availability of freshwater habitat from very high to relatively low, representative for the range of conditions commonly found across the temperate zone. Oud Alblas is a wet peat area with a year-round high water table and many interconnected ponds and ditches, representative for semi-natural and partly-drained areas with high connectivity of aquatic habitat. Enterveen is the other extreme, a sandy area with few, isolated ponds and canals, representative for relatively dry, fragmented landscapes. Terra Nova and Juliusput are intermediate sites, with the former resembling Oud Alblas but including a large lake, and the latter having more scattered water bodies. The spatial scale of mallard movements (flight distances and home range size) was strongly inversely related to the availability of freshwater habitat in the landscape, with implications for their role in biotic connectivity of fragmented habitats (Kleyheeg *et al.* 2017a). More details on the localities, their relation to other European wetlands, and the effects of their configuration on mallard movements can be found in Kleyheeg *et al.* (2017a).

The model: seed part (ingestion and gut passage)

Mallards have a clear circadian activity pattern, consisting of mainly resting during the day at a roost site and foraging primarily during the night at one or several foraging areas (Bengtsson *et al.* 2014; Kleyheeg *et al.* 2017a). In the model, we assumed that seed intake occurred only during the night and only when mallards were away from the day roost and not in flight (*i.e.*, only when present at foraging areas). During these periods, we assumed that the mallards were continuously foraging. Although some information is available on seed intake rates under lab conditions (Klaassen *et al.* 2006; van Dijk *et al.* 2012), it is difficult to estimate the number of seeds actually consumed by mallards in the field (and thus how many seeds are potentially dispersed). We therefore designed the model to estimate the spatial probability distribution of seed deposition rather than the absolute numbers, and assumed a constant intake rate of 1000 seeds per hour during foraging periods to facilitate interpretation of the results. The number of ingested seeds was multiplied by an empirically identified size-dependent seed survival probability (Eq. 4.2) to take into account relative differences in the proportion of dispersed seeds between differently sized seed species, following:

$$I = c \cdot s(V) \cdot dt \qquad \textit{Eq. 4.1}$$

where I is the number of ingested seeds per time step that will eventually survive digestion and be excreted, c is the constant intake rate (seeds per hour), $s(V)$ is a seed volume-dependent survival probability, and dt is the time step (0.25 hour, which equals the GPS interval, see below). The relation between survival (the proportion of seeds passing through the digestive tract intact) and seed volume was based on a logarithmic function fitted on seed retrieval data from a feeding experiment with 20 differently-sized seed species fed to mallards (Soons *et al.* 2008; see Fig. S1 in Supporting Information):

$$s(V) = 0.2121 - 0.039 \cdot \log V \qquad \textit{Eq. 4.2}$$

where V is the volume of an individual seed in mm^3. This results in survival probabilities between approximately 30% for small seeds and 3% for very large seeds within the range of seed volumes that have been found in the mallard diet (Soons *et al.* 2016). Seed excretion (E) per time step was calculated based on the 48-hour history of seed intake and an excretion probability as a function of time after intake:

$$E = \int_{-48}^{0} \big(I(t) \cdot \Gamma(|t|; k, \theta(V))\big)\, dt \qquad \textit{Eq. 4.3}$$

where $I(t)$ is the rate of intake of seeds (that will eventually pass the digestive tract intact) during time step t and $\Gamma(|t|; k, \theta(V))$ is the gut passage time drawn from a gamma distribution. The gamma distribution sums to one and we assumed that all surviving seeds passed the digestive tract within 48 hours, so that in our model the surviving seeds were excreted in the subsequent time steps after intake (up to 48 h) in proportions determined by the gamma distribution. The 48-hour integral was approximated using discrete time steps equal to the time interval between the GPS positions. The temporal pattern of gut passage is variable between seed species, between and within individual waterbirds, and between studies (van Leeuwen *et al.* 2012), but generally, the first seeds are excreted shortly after ingestion, with peak excretion within a few hours and a fat tail. We used a gamma distribution because it is one of the most frequently used probability distributions to characterize retention times and fits at least as accurately as lognormal and Weibull distributions (Viana *et al.* 2016b). The two parameters of the gamma distribution (shape k and rate θ) were estimated from cumulative empirical distributions of differently sized seeds of 18 plant species passing mallard guts (extracted from Soons *et al.* 2008; Fig. S2). Since seeds in Soons *et al.* were retrieved at discrete time intervals, we fitted the distributions while explicitly accounting for the interval-censored nature of the data using the R-package *fitdistrplus* (Delignette-Muller & Dutang 2015). Gut passage time showed a positive correlation with seed volume, which was best estimated by a constant shape parameter (k = 2.7, computed by minimizing the mean D-statistic of Kolmogorov-Smirnov tests for the 18 species, see Fig. S2) and a varying rate parameter following a logarithmic function of seed volume (linear regression: p = 0.022, R^2 = 0.29):

$$\theta(V) = 0.5646 - 0.042 \cdot \log V \qquad \textit{Eq. 4.4}$$

Increasing the rate parameter relative to the shape parameter results in a more peaked curve at a shorter retention time. This translates to peak excretion of very small seeds at around 2 h after ingestion and around 7 h after ingestion for the largest seeds in the mallard diet.

The model: bird part (mallard movements)

To best approach a realistic spatial pattern of seed deposition, we used high resolution movement trajectories of mallards from a GPS tracking study at the localities described above during autumn-winter 2012-2013 (Kleyheeg *et al.* 2017a). We used GPS tracks of five individual mallards in each of the four landscapes. We restricted the twenty individual trajectories to nine days, corresponding to the length of the shortest track. GPS positions had been recorded at a 15 minute interval (± GPS logger inaccuracy). We assumed there were no seeds inside the mallard's digestive tract at the start of the simulation, as we did not have GPS positions of the 48 h history from all mallards prior to the nine day simulation period. This means that excretion started one time step after the first arrival of an individual at a foraging site. Similarly, seeds that were still inside the mallard at the end of the simulation were not taken into account in the calculation of the dispersal distances.

To create spatial maps of seed deposition patterns, the probability of mallard presence between GPS fixes was estimated using Brownian bridges, an interpolation technique for estimating the movement path of an animal based on the properties of a conditional random walk between successive locations (Horne *et al.* 2007). Establishing a Brownian bridge between two locations requires a mean GPS error and a Brownian motion variance. The GPS error was estimated at 10 m (based on 24.081 positions of three loggers fixed to a pole). The Brownian motion variance was estimated dynamically for different behaviours (Kranstauber *et al.* 2012, 2014). We separated the data into flight (distance between GPS fixes >100 m) and non-flight (<100 m) behaviour and assigned a constant Brownian motion variance to each. For non-flight data, the Brownian motion variance was estimated using the classical leave-one-out approach assuming a purely Brownian random walk and homogeneous movement between two locations, as described in Horne *et al.* (2007). This way, the motion variance was found by using a window of three consecutive GPS fixes and estimating the second GPS fix based on the first and last GPS fix and a Brownian random walk between these points with a motion variance that is to be optimized. This optimization was done for all possible windows of three consecutive GPS fixes and maximizing the likelihood of predicting the left out GPS fixes correctly. This Brownian motion variance yielded 55 m^2 at Oud Alblas, 56 m^2 at Terra Nova and Juliusput, and 52 m^2 at Enterveen. For flight data, we selected all flights where one location was sampled during the flight from one core area to another. In this way sequences of three GPS points were created (*i.e.*, core area A, flight and core area B) from which a single Brownian motion variance was estimated using the leave-one-out approach (Horne *et al.* 2007). The Brownian motion variance during flight was 200 m^2 at Oud Alblas, 260 m^2 at Terra Nova, 280 m^2 at Juliusput, and 330 m^2 at Enterveen. We also calculated seed dispersal kernels using the measured GPS tracks. As opposed to the seed deposition probability maps, we based the dispersal kernels on actual dispersal distances (without Brownian Bridges). This was done to keep it mathematically feasible to track the ingestion and excretion locations of all individual seeds.

Simulations: landscape and seed volume effects

To assess the effect of landscape configuration on seed deposition patterns, we ran dispersal simulations for all four study landscapes. We linked the spatial behaviour of mallards (bird part) to seed deposition (seed part) by calculating the number of excreted seeds for each recorded GPS position of a mallard based on its history of seed ingestion in the previous 48 h (Eq. 4.3). For all seeds excreted at any time step, we calculated the distance to the site of their ingestion to establish seed dispersal distributions.

To assess the effect of seed volume on seed deposition patterns, we performed model runs for three seed volumes: V = 0.2 mm^3, V = 2 mm^3 and V = 20 mm^3, corresponding to the lower, median and higher ranges of the volume distribution of seeds in the mallard diet (Soons *et al.* 2016). We described differences in seed dispersal distributions (deposition patterns and dispersal distances) and specifically analysed the proportion of seeds dispersed away from the site of ingestion using chi-square tests.

All model simulations were run in Matlab version R2014b.

Results

Seed dispersal patterns

The mallards foraged in distinct patches in all landscapes, resulting in highly spatially concentrated seed intake, centred around shorelines of waterbodies and some agricultural fields (Fig. 4.1 and Fig. S4.3). Seed survival, retention times and movement activity of mallards together determined the subsequent seed deposition patterns. Most seed excretion occurred within foraging and roosting areas across the entire home range

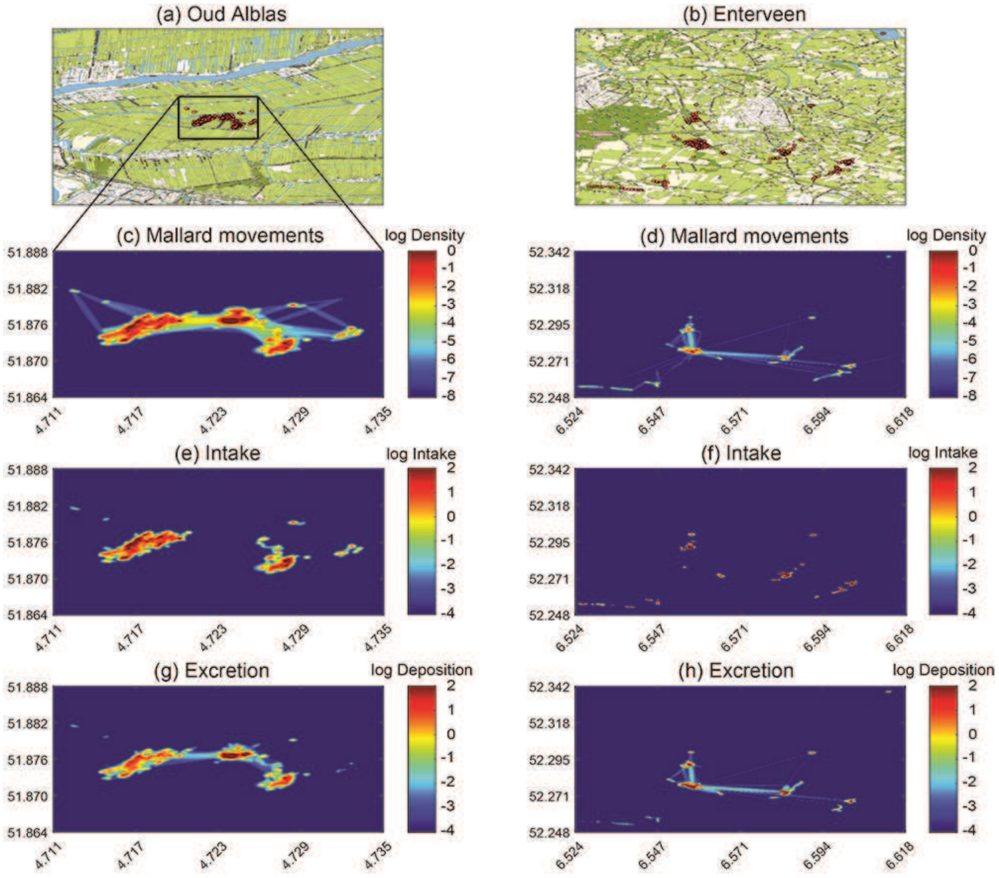

Figure 4.1 Landscape use by mallards (based on the density of GPS positions with Brownian bridges) and corresponding spatial patterns of seed ingestion and excretion at Oud Alblas (left; homogeneous, wet landscape) and Enterveen (right; fragmented, dry landscape). Graphs are based on 9-day tracks of five mallards in each area, feeding on seeds at the foraging sites at night and spending the day at a communal roost. Upper panels (maps) are of the same scale. Plots for the intermediate landscapes of Terra Nova and Juliusput are in Fig. S4.3 in the Supporting Information.

of the mallards, and several orders of magnitude less between core areas (Fig. 4.1 and Fig. S4.3). Due to the rapid gut passage and relatively long time spent in each foraging area, seeds excreted in the foraging areas had usually been ingested in the same area several hours earlier (Fig. 4.2). On average, *ca*. 40% of the ingested seeds were excreted in another core area than where they were ingested, depending on seed volume. Model simulations for seed volumes ranging from 0.2 to 20 mm^3 showed that this 'long-distance dispersal' (dispersal between core areas) occurred on average in 35.6% (range 33.0-40.9%) of the smallest surviving seeds, compared to 44.9% (range 41.8-51.2%) of the largest surviving seeds. However, due to the lower gut passage survival of large seeds, a much lower proportion of large seeds initially ingested (including those that do not pass the digestive tract intact) is dispersed away from the area of ingestion than small seeds. The absolute number decreased exponentially with volume, ultimately resulting in 2.3 times less long-distance dispersal for seeds of 20 mm^3 than for seeds of 0.2 mm^3, with little variation between landscapes (range 2.2-2.4). Most of the seeds dispersed away from the site of ingestion were dispersed to the roost: 22.4-35.0% (small seeds) and 28.4-44.3% (large seeds) were excreted at the main roost (Fig. 4.2). The seed size most ingested by mallards is around 2 mm^3, and for surviving seeds of this size class, long-distance dispersal occurred in 39.8% on average. Between 25.1% and 39.2% were excreted at the main roost. The highest percentage of excreted seeds of 2 mm^3 that were transported to another foraging area was found at Juliusput (12.3%), while this percentage was the lowest at Oud Alblas (3.1%, Fig. 4.2). However, the proportion of seeds dispersed within or outside the areas of ingestion did not differ significantly between seed volumes ($p > 0.71$ for each locality) or between localities ($p > 0.52$ for each of the three tested seed volumes).

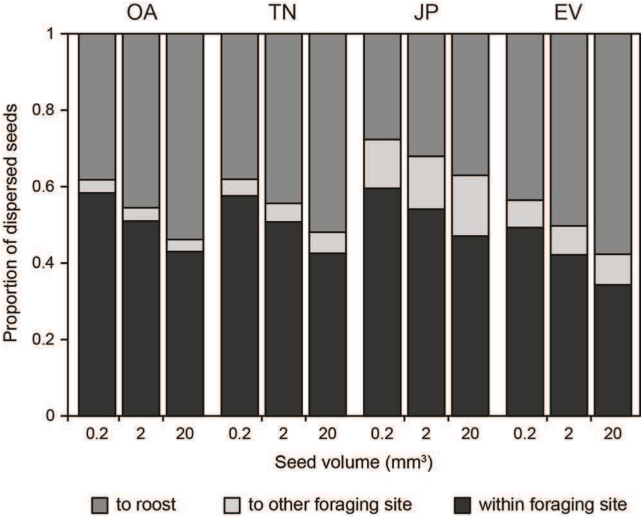

Figure 4.2. The proportion of seeds dispersed by five mallards per landscape over nine days, towards either the roost area (grey), another foraging area (light grey), or to the same foraging area as where the seeds were ingested (dark grey). The proportions are based on model runs for differently sized seeds (0.2, 2 and 20 mm^3) at Oud Alblas (OA), Terra Nova (TN), Juliusput (JP) and Enterveen (EV), ordered from homogeneous (wet) to fragmented landscapes. The proportion of seeds excreted during flight is very low (Fig. 4.1) and not shown here.

Dispersal distance distributions

Since most seeds were deposited at the foraging and roost core areas (Fig. 4.2), and rarely *en route* (Fig. 4.1), the distances between these areas strongly affected the dispersal kernels (Fig. 4.3). Accordingly, dispersal distances were longest in the driest landscape where wetland areas were most scattered (up to *ca*. 8000 m at Enterveen) and lowest in the wettest landscape where wetland habitat was most abundant (up to *ca*. 1600 m at Oud Alblas; Fig. 4.3). The dispersal distances were clearly related to the home range sizes of the mallards across the varying landscapes (Fig. 4.4). The higher probability of larger seeds to be dispersed away from their original patch resulted in marginally longer mean dispersal distances of large seeds (Table 4.1, Fig. S4.4).

Table 4.1. Modelled mean dispersal distance (D_{mean}) and the proportion of seeds dispersed away from the site of ingestion (P_{ldd}) for five plant species commonly found in mallard diets. The frequency of occurrence is calculated as the number of individual mallards carrying seeds of the species based on a review of diet studies in Europe (Soons *et al.* 2016). Model output for mallard-mediated dispersal is provided for the landscape types of Oud Alblas (relatively wet) and Enterveen (relatively dry). Note the contrasting effects of seed volume and location on the dispersal parameters.

Species	Freq. occur	Vol. (mm^3)	D_{mean}	P_{ldd}	D_{mean}	P_{ldd}
Carex aquatilis	0.438	1.77	479 ± 339	0.372	1973 ± 1873	0.454
Eleocharis palustris	0.212	2.20	481 ± 339	0.377	1976 ± 1874	0.459
Scirpus lacustris	0.222	5.34	487 ± 338	0.396	1990 ± 1880	0.479
Carex rostrata	0.290	6.69	489 ± 337	0.402	1994 ± 1882	0.485
Empetrum nigrum	0.477	9.94	491 ± 337	0.412	2001 ± 1885	0.495

To evaluate how gut passage time affects dispersal distances at the landscape-scale, we analysed the net displacement of mallards over time and compared this with realized dispersal distances over gut passage time (Fig. 4.3). The spatial behaviour of mallards showed a clear diel pattern with repeated visits to the same core areas for foraging and roosting. Therefore, at any time of the day, mallards were likely to be at the same area as where they were 24 hours earlier (either at the foraging or roosting site). Conversely, at twelve hour intervals, mallards had most likely switched between areas, from foraging to roosting or vice versa. Therefore, potential dispersal distances increased only for gut passage times up to twelve hours. The median dispersal distance of seeds retained in the guts for 12 hours was between 600 m (Oud Alblas) and 3000 m (Enterveen). Gut passage times from 12 to 24 hours led to decreasing dispersal distances and an increasing probability for seeds to be dispersed back to the area where they had been ingested. From 24 to 48 hours after ingestion this pattern repeated itself (Fig. 4.3).

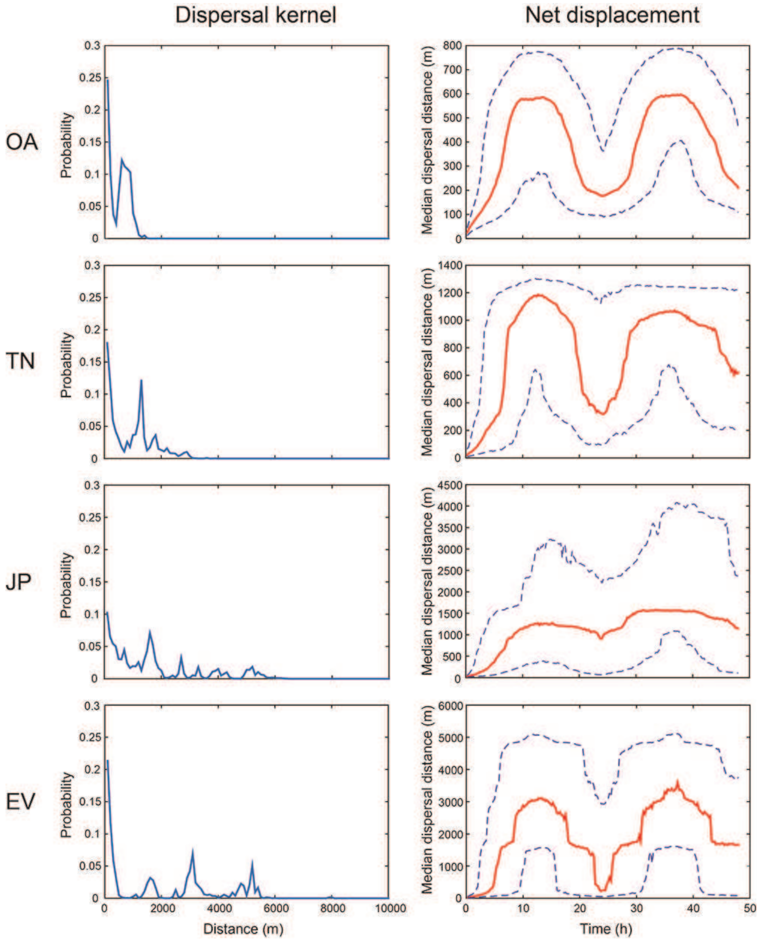

Figure 4.3. The left panels shown seed dispersal kernels (deposition probability over realized dispersal distance) for seeds of 2 mm³ (kernels for 0.2 and 20 mm³ in Fig. S4) in all four study landscapes: Oud Alblas (OA), Terra Nova (TN), Juliusput (JP) and Enterveen (EV), based on 5 mallards tracked for 9 days in each landscape. Dispersal distances increase and kernels show more peaks towards the drier landscapes where wetland areas are scarcer. The right panels present net dispersal distance over retention time up to 48 hours (median ± 5th and 95th percentiles).

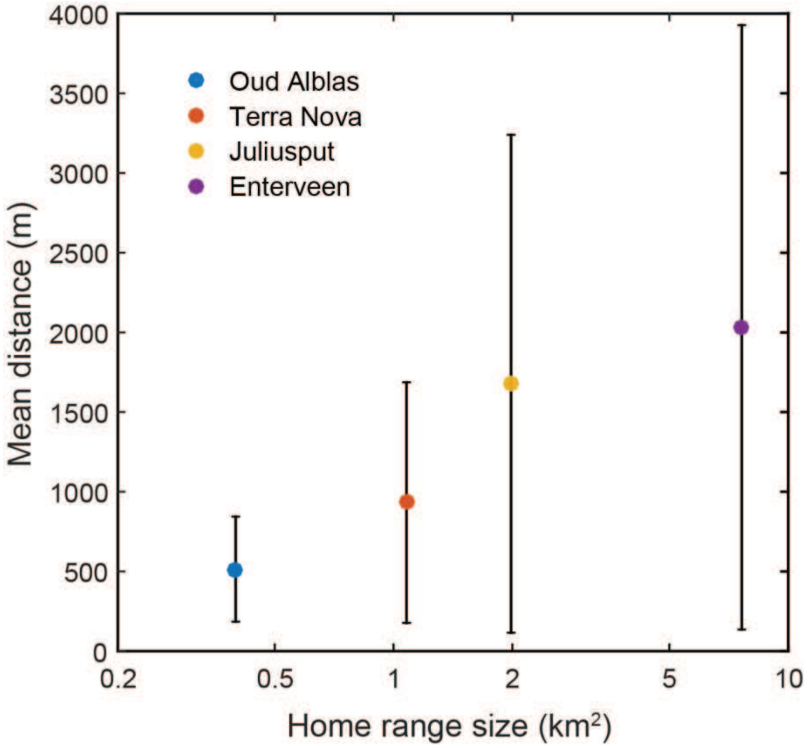

Figure 4.4. Relation between mean dispersal distance (± SD) of 2.0 mm^3 seeds and the mean home range size of individual mallards expressed as the area of the minimum convex polygon (MCP) around 100% of the GPS positions of individual mallards. MCPs were calculated using the adehabitatHR package (Calenge 2006) in R and shown earlier to depend on landscape configuration (Kleyheeg *et al.* 2017a).

Discussion

Our results show that the daily movement behaviour of mallards during the seed dispersal period, which is governed by landscape configuration, and the generally regular circadian pattern of core area use by mallards, strongly determine the spatial deposition patterns of the seeds they disperse. While seed volume is a main determinant of gut passage survival and hence of the numbers of viable seeds dispersed, it has little effect on the shape of the seed dispersal kernels. Through its effect on gut retention time, and considering only seeds that survived gut passage, larger seeds have a slightly higher probability to be dispersed away from the area of ingestion.

Dispersal patterns and distributions

The dispersal kernels resulting from mallard-mediated dispersal do not have the typical shapes known from hydrochory or anemochory, or from estimations of long-distance dispersal by migratory waterbirds, which are characterized by a monotonically decreasing dispersal probability over distance. Instead, the kernels are multimodal, connecting a number of frequently visited core areas and the in-between matrix within the extent of the mallard's home range. During autumn-winter, the home range size of mallards varies greatly between individuals, from less than 0.1 km^2 to more than 30 km^2 (Legagneux *et al.* 2009; Sauter *et al.* 2012; Kleyheeg *et al.* 2017a), suggesting that mallards maintain the connectivity between such core areas over large distances, depending on the landscape.

The consistency in the use of these relatively well-defined core areas results in highly clumped seed deposition in and around wetland habitat. Earlier studies on mallard habitat use show that mallards have a preference for shoreline habitat, both aquatic and terrestrial (Sauter *et al.* 2012; Bengtsson *et al.* 2014; Kleyheeg *et al.* 2017a). This indicates a high potential for directed dispersal for a wide range of plant species typical for aquatic, open water as well as shoreline and more terrestrial habitats (such as riparian zones, terrestrialising fens, banks, *etc.*). Indeed, this habitat range is also reflected by the species composition of plant seeds found in the mallard diet (Soons *et al.* 2016). Mallards may thus play an equally important role in connecting plant populations of aquatic and wetland habitats, as of more terrestrial systems, such as the dispersal-limited successional stages following colonization of open water (e.g. species-rich floating fens; Sarneel *et al.* 2011).

Mallards and many other waterbird species use communal roost sites (e.g. Tamisier 1978). Assuming that mallards ingest seeds only (or mainly) at the foraging sites, combined with few switches between foraging sites during the night, our model predicts that mallards disperse seeds disproportionally towards the daytime roost. This particularly applies to large seeds. The resulting asymmetric gene flow may result in spatial population dynamics of the dispersed species which resemble a 'mainland-island' system more closely than a network of equal patches (such as the traditional metapopulation; Hanski 1999). This suggests that waterbird roosts may function as a dead end for the dispersed species if habitat conditions at the roost are unfavourable for establishment. In contrast, if species dispersed to the roost encounter suitable conditions, roosts may serve as a 'reservoir' for the population dynamics and biodiversity in the surrounding landscape. From there, mallards sharing foraging areas but using a different roost (and *vice versa*) create a network of dispersal pathways across the landscape. Importantly, such networks may connect foraging and roost sites in different catchments (without hydrological connection), so that in many cases the seeds are dispersed to habitat patches that would be unreachable by hydrochory, and unlikely reached by anemochory. In this way, mallard-mediated dispersal complements other (directed) dispersal modes (Soons *et al.* 2017). Secondary dispersal by other mechanisms after seed excretion, e.g. by water, may lead to even further extension of the final seed shadow.

Interactions between dispersal and gut passage time

If seeds are dispersed outside of the area of ingestion, dispersal distances are often relatively high: at Oud Alblas and Enterveen 50% of these seeds were dispersed over more than 600 m and 3000 m, respectively. Since plant seeds normally end up close to the mother plant, landscape scale dispersal by mallards should be considered long-distance dispersal (*i.e.*, exceeding the threshold of 100 m as suggested by Cain *et al.* 2000, or 250 m as suggested by Traveset *et al.* 2013). Due to the typical fat-tailed dispersal kernels traditionally associated with zoochory (Nathan *et al.* 2008b), longer retention times of seeds within animals are often associated with longer dispersal distances. This may be the case for instance for grazing mammals, moving continuously through the landscape (Will & Tackenberg 2008), or for other animals heading in a dominant direction. Similarly, waterbird-mediated dispersal distances during migration, estimated based on an assumed unidirectional flight, range up to few thousands of kilometres for seeds retained in the digestive tract for >24 hours (e.g. Soons *et al.* 2008; Viana *et al.* 2013a). By contrast, the cyclic daily movement patterns of non-migratory mallards (Sauter *et al.* 2012; Bengtsson *et al.* 2014; Kleyheeg *et al.* 2017a) result in dispersal kernels with the highest median dispersal distances after gut retention of twelve hours and decreasing distances for seeds retained longer. Since retention times in mallard guts rarely exceed twelve hours (van Leeuwen *et al.* 2012), the positive relation between time and dispersal distance remains for most seeds. However, very long retention times, which are often emphasized as particularly important for extremely long-distance dispersal during migration (Cain *et al.* 2000; Nathan 2006; Nathan *et al.* 2008b), may actually result in relatively short dispersal distances in the majority of dispersal events, when mallards are not migrating.

The peaks of retention curves for large seeds approach 12 hours, which appears the optimal retention time for dispersal away from the original site of ingestion (Fig. 4.3). However, such long retention comes with the cost that survival is generally very low (<5% according to van Leeuwen *et al.* 2012). To optimize dispersal by waterbirds, plants need to adopt a strategy within the trade-off between retention time and survival by producing seeds that are small enough and with a tough enough seed coat to survive (Kleyheeg 2015; Reynolds & Cumming 2016), but large enough to optimize their retention time. *Sparganium erectum* might represent an example of such an adaptation, as it produces seeds with a seed coat so thick that it even requires damaging (for instance by digestive forces) to germinate (Soons *et al.* 2008), while the thick seed coat also makes the seeds large enough for relatively long retention (Kleyheeg 2015). It should be noted, however, that the 8-10% lower probability of small seeds (0.2 mm^3) to be dispersed away from the site of ingestion compared to large seeds (20 mm^3) is more than compensated by their 2.9 times higher gut passage survival probability (Eq. 4.2).

Future directions

We here aimed to identify the dispersal distributions of seeds dispersed by mallards in realistic landscapes, using dispersal probability distributions. The next step will be to translate these to actual numbers of seeds dispersed and to estimate the quantitative role of mallards in seed dispersal. This especially requires additional information on seed intake, particularly intake rates and foraging times under natural foraging conditions. Seed intake rates by mallards have been quantified under artificial, controlled conditions (e.g. van Dijk *et al.* 2012) and shown to be seed size-dependent (Fritz *et al.* 2001). However, for realistic quantification of seed intake in the field, this should be studied using natural seed densities provided to the animals in a way they also encounter seeds in the field. Therefore, natural seed densities, seed size distributions and mallard microhabitat use should be assessed in the field (Arzel & Elmberg 2004). In our model, we assumed that mallards were continuously foraging when present at foraging sites at night, which is a very generalized and simplified representation of reality (Jorde *et al.* 1983; Guillemain *et al.* 2002). The use of accelerometry in combination with GPS tracking would be a suitable method for estimation of when and where mallards forage, as accelerometry provides detailed long term data series of activity patterns (Wilson *et al.* 2006) and can be used to distinguish different types of behaviour, including foraging (e.g. Shamoun-Baranes *et al.* 2012; Kölzsch *et al.* 2016).

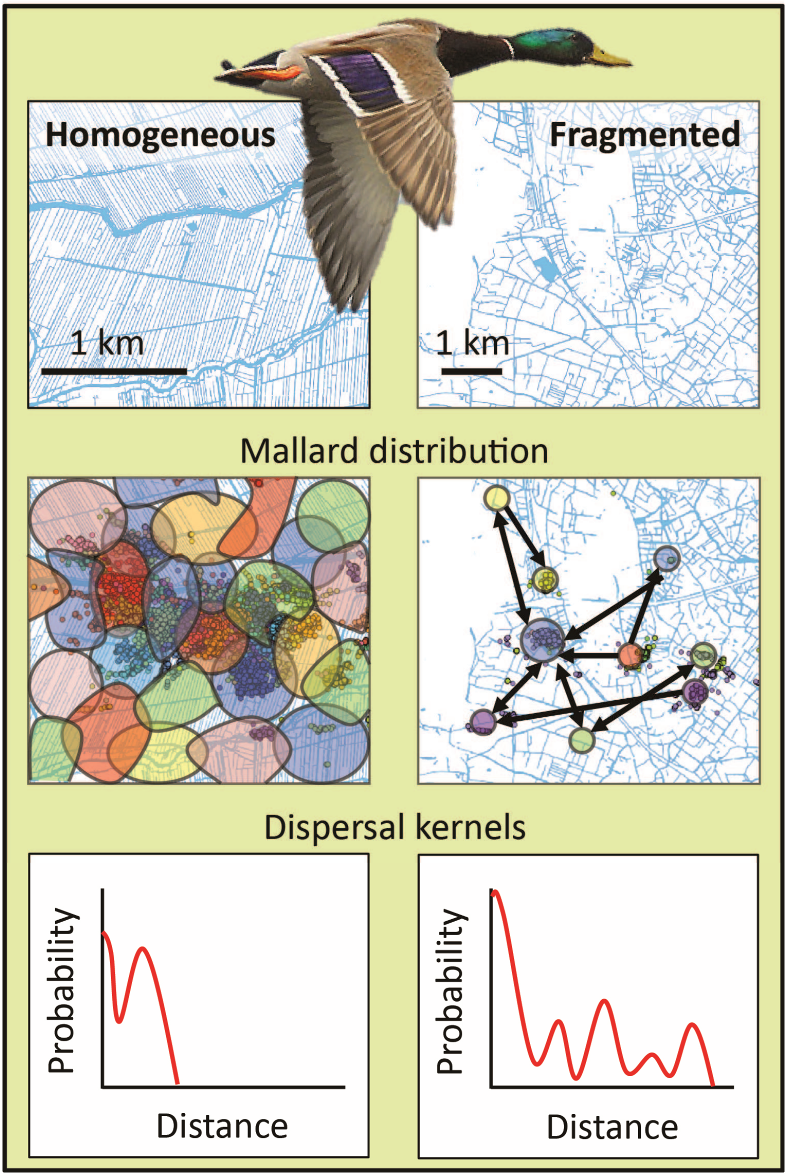

Figure 4.5. Conceptual diagram of how mallard movement behaviour and landscape configuration translate into connectivity and seed dispersal distributions across landscapes. In homogeneous landscapes with high wetland availability, mallard abundances are high but home ranges of individual mallards are small, resulting in a 'patchwork' of interconnected areas covering the entire landscape. In fragmented landscapes where wetlands are widely scattered, mallard abundances are lower but home ranges larger, resulting in a 'network' of few but tightly connected areas and strongly multi-modal dispersal distributions.

Conclusions and implications

This study provides the first spatially explicit identification of seed dispersal patterns generated by waterbird-mediated dispersal, and reveals important characteristics of waterbird daily movement behaviour and landscape configuration. During the autumn and winter season, when most plant seeds are available in the environment, mallard movements result in frequent long-distance seed dispersal with highly clumped deposition patterns at relatively well-defined, discrete areas within individual's home ranges used for foraging and/or roosting. Resulting seed dispersal kernels are clearly multi-modal, as typical for directed dispersal, and reveal dispersal distances at the scale of kilometres. In landscapes with decreasing availability of typical wetland foraging and roosting areas, dispersal distances between core areas increase and mallards maintain the connectivity between these areas for their associated species (Fig. 4.5). Seed volume largely determines the probability of viable seed dispersal (as it determines viable gut passage), but in contrast to their important role in wind dispersal and water dispersal, seed traits play a very limited role in determining dispersal distributions following mallard dispersal. However, by modulating retention time, seed volume does co-determine the proportion of seeds that are dispersed away from the area of ingestion. Most seeds are dispersed towards the communal roost site of the mallards, suggesting such areas play a key role in regional plant population dynamics and biodiversity. Yet, a significant proportion of dispersed seeds also ends up in other foraging areas which are likely to consist of similar suitable habitat for establishment for a wide range of plant species. The long-distance, directional dispersal between wetland areas emphasizes the important role of mallards - and potentially other waterbirds - in maintaining regional plant species persistence and biodiversity in a world facing ongoing habitat fragmentation.

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Supporting information: Dispersal model parameters, output and scripts.

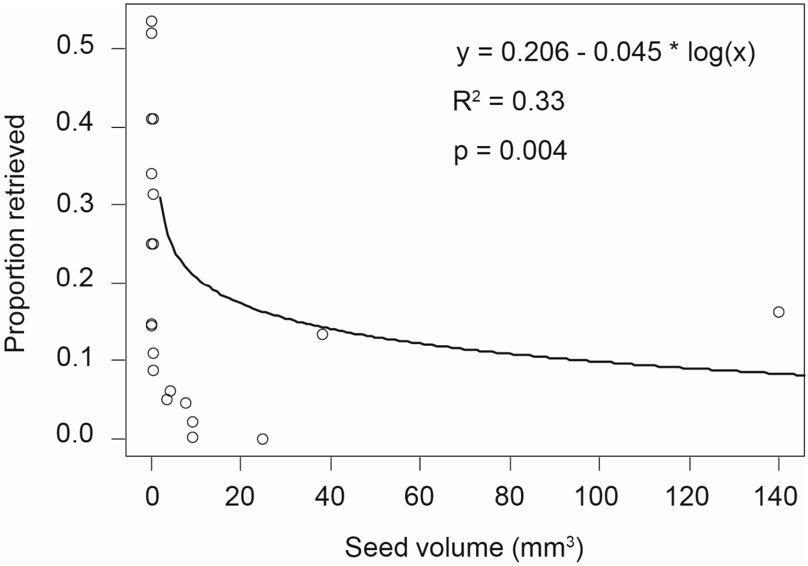

Figure S4.1. The exponential relation between seed volume and the proportion of seeds passing through the mallard digestive tract intact based on a feeding trial study with 24 plant species by Soons *et al.* (2008). Note that the variation in gut passage survival is high and other seed traits besides volume also play a role.

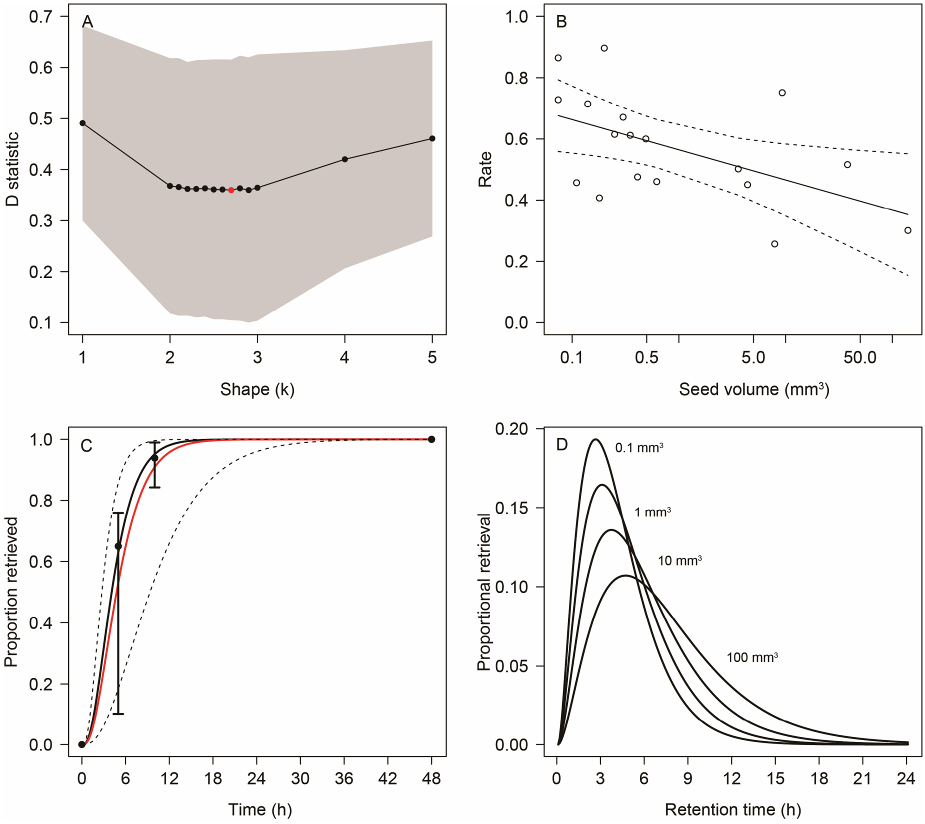

Figure S4.2. Parameter selection for gamma distribution of size-dependent seed retention times in the mallard's digestive system. After fitting the gamma distribution to the empirical retrieval data from Soons *et al.* 2008, we selected the best fitting shape parameter (k) giving the lowest mean D statistic for all plant species combined (depicted in red in panel A, with the grey area depicting the standard deviation around the mean). The corresponding rate parameter for each species was significantly related with (log-transformed) seed volume. Panel B gives the regression line and the 95% confidence intervals. The corresponding cumulative gamma distributions for seed sizes 0.2 and 20 mm^3, which are used in the manuscript, are shown with black and red lines, respectively, in panel C. The dotted lines represent the curves for the smallest and largest seeds used in Soons *et al.* 2008. The points and error bars depict the median proportion of retrieved seeds at the respective sampling times (5, 10 and 48 hrs) with 5th and 95th percentiles. Based on the same definition of retention curves, panel D gives an overview of the modelled retrieval patterns over time of plant seeds varying in size between 0.1 to 100 mm^3.

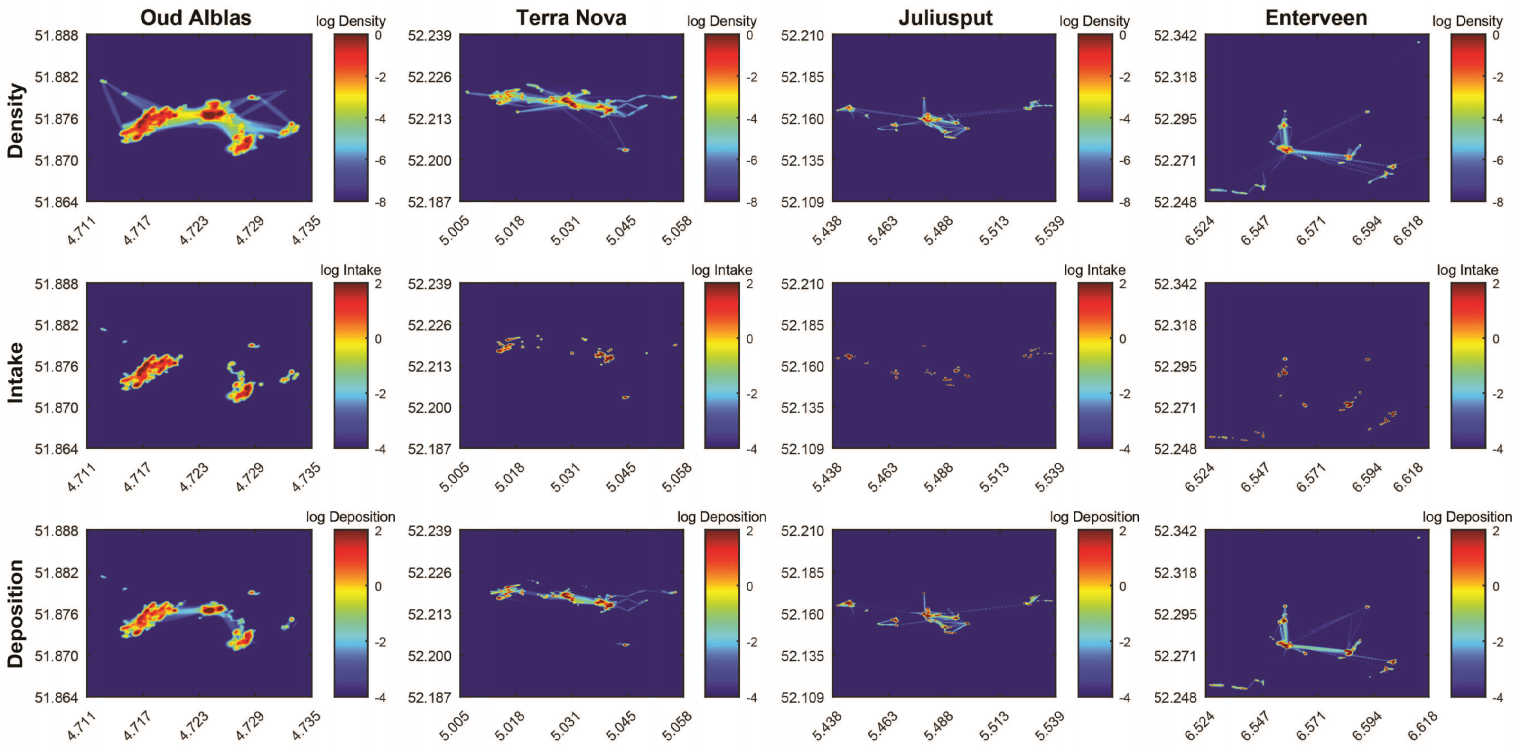

Figure S4.3. Habitat use and movement patterns of mallards (panels upper row), locations of seed intake (panels middle row), and pattern of seed excretion after digestive tract passage (panels lower row) in four landscapes differing in their degree of wetland fragmentation. Axes present decimal degrees. Note that the spatial scales differ between landscapes.

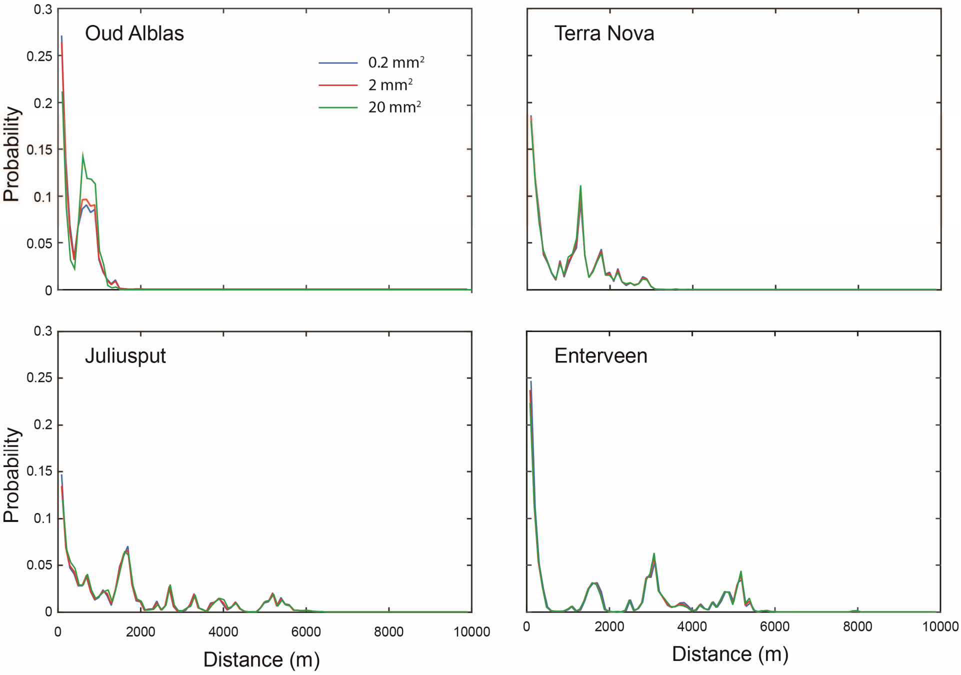

Figure S4.4. Dispersal kernels following mallard-mediated seed dispersal in four different landscapes in the Netherlands for seeds of three different volumes. Blue, red and green lines represent dispersal kernels for seeds of 0.2, 2 and 20 mm^3 respectively.

5

Using high resolution GPS tracking data of bird flight for meteorological observations.

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Abstract

Bird flight is strongly influenced by local meteorological conditions. With increasing amounts of high-frequency GPS data of bird movement becoming available, as tags become cheaper and lighter, opportunities are created to obtain large datasets of quantitative meteorological information from observations conducted by bird-borne tags. In this article we propose a method to estimate wind velocity and convective velocity scale from tag-based high-frequency GPS data of soaring birds in flight.

The flight patterns of soaring birds are strongly influenced by the interactions between atmospheric boundary layer processes and the morphology of the bird; climb rates depend on vertical air motion, flight altitude depends on boundary layer height, and drift off the bird's flight path depends on wind speed and direction. We combine aerodynamic theory of soaring bird flight, the bird's morphological properties and three-dimensional GPS measurements at 3-seconds intervals to estimate the convective velocity scale and horizontal wind velocity at the locations and times of flight.

We use wind speed and direction observations from meteorological ground stations and estimates of convective velocity from the Ocean-Land-Atmosphere Model (OLAM) to evaluate our findings. Although not co-located, our wind velocity estimates are consistent with ground station data, and convective velocity scale estimates are consistent with the meteorological model. Our work demonstrates that biologging offers a novel alternative approach for estimating atmospheric conditions on a spatial and temporal scale that complement existing meteorological measurement systems.

Introduction

Biologging is being used increasingly to track moving organisms in space and time (Ropert-Coudert & Wilson 2005; Rutz & Hays 2009; Bouten *et al.* 2013; Dodge *et al.* 2013). As tags become lighter, cheaper and more efficient, there is a rapidly growing amount of fine resolution data collected. Besides increasing data volumes, further sophistication of the GPS tags also yields different types of data in addition to location (e.g. acceleration, compass direction, temperature, pressure). Many studies have investigated the influence of meteorology, ocean currents and distribution of food on foraging and migration movement patterns (e.g. Dragon *et al.* 2010; Sapir *et al.* 2011; Shamoun-Baranes *et al.* 2011; Bohrer *et al.* 2012; Safi *et al.* 2013; Dodge *et al.* 2014). This is done by annotating remote sensing, ground station and reanalysis datasets to the observed locations of the animals from biologging following the track annotation approach (Mandel *et al.* 2011). Knowledge of the environmental conditions during movement is needed to improve the understanding of the animals' movement ecology and to develop predictive models of their movement (Nathan *et al.* 2008a).

Beyond providing richer and more accurate information about the animals' locations during movement, the wealth of available high resolution information offers new possibilities of estimating environmental conditions directly from the data collected on the tag (Charrassin *et al.* 2008). This can be fruitful for determining the values of environmental variables that are otherwise hard to measure. For example, measurements of boundary layer properties, such as thermal structures, are scarce especially in remote and mountainous locations. In this paper we demonstrate an approach for using GPS data of soaring birds to observe atmospheric boundary layer properties.

Bird flight is strongly related to meteorological conditions

Many large birds use soaring and gliding flight because flapping flight is energetically more costly (Hedenstrom 1993; Sakamoto *et al.* 2013; Duriez *et al.* 2014). Birds that use thermal convection for soaring use the energy in buoyant warm air to gain altitude and then use the potential energy to glide to the next thermal (Van Loon *et al.* 2011) (Fig. 5.1; a dynamic visualization can be found at www.doarama.com/view/433747). This type of flight will therefore be affected by the intensity of surface sensible heat flux and the atmospheric boundary layer depth which determine the strength and altitude range of available thermal uplift (Shannon *et al.* 2002a; Shamoun-Baranes *et al.* 2003; Mandel *et al.* 2008). Several species use orographic uplift instead, thereby gliding for kilometres along mountain ridges (Shepard *et al.* 2011; Bohrer *et al.* 2012). Due to a low wing loading soaring birds can be extremely effective when making use of thermals (Pennycuick 1971; Spaar & Bruderer 1996), lowering their sink rate relative to air to velocities on the order of 1 m s^{-1} (Pennycuick 1971).

In addition to vertical wind, horizontal wind speed and direction also influences the flight patterns of soaring birds (Shamoun-Baranes *et al.* 2003; Mandel *et al.* 2008; Lanzone *et al.* 2012; Vansteelant *et al.* 2015). Wind can displace birds while they are gliding as well as during the climbing phase as thermals are horizontally advected by wind (Kerlinger & Gauthreaux 1984; Kerlinger 1989).

Birds' flight patterns have been used for gathering qualitative information about thermals for a long period of time (Huffaker & Langley 1898; Woodcock 1940). However, obtaining quantitative information remained difficult until the invention of small altimeters and GPS devices. Shannon *et al.* (2002b) showed that bird-borne data can be used for obtaining quantitative meteorological observations. In their study, White Pelicans (*Pelecanus erythrorhynchos*) were equipped with altimeters and tracked from the ground during cross country flight. They demonstrated that the altimeter data could be used to estimate thermal updraft intensities over both valleys and mountainous areas. With the miniaturization of GPS devices that are available nowadays, with a temporal sampling frequency that can be set to higher than 1 Hz, both the quantity and accuracy of data points have greatly improved (Lanzone *et al.* 2012; Bouten *et al.* 2013) and opportunities are created to obtain more extensive meteorological information from bird-flight data.

Measurements of microscale meteorological processes are mostly obtained from static in situ or remote sensors, such as anemometers, temperature, pressure and humidity sensors which provide time series at one point in space. Multiple sensors are needed to capture the horizontal and vertical heterogeneity in the boundary layer. Platforms such as towers and radiosondes with static sensors, or remote methods such as LIDAR, can be used to obtain vertical profiles. Horizontal heterogeneity can best be captured with flying platforms, such as aircrafts, balloons or Unmanned Aerial Vehicles (UAV) (Stull 1988).

UAVs have improved greatly in size and efficiency in recent times; however, they are still costly to operate, both in funds and labour. Recent papers have highlighted the potential of using smartphone and vehicle-based pressure and temperature observations for improved high resolution weather analysis and prediction (Mahoney III & O'Sullivan 2013; Mass & Madaus 2014). We propose that airborne data from birds could be complementary to these data sources, particularly in remote areas and mountainous regions, where UAV access is difficult and smartphones and vehicles are not abundant.

By now, billions of GPS data points have been collected from bird-borne tags worldwide. A substantial amount of such data is available in online databases, such as Movebank (www.movebank.org) and UvA-BiTS (www.uva-bits.nl), and the type of data ranges from very local foraging flights to global scale migratory movements. In this study we explore the potential of using 3D location data of griffon vultures (*Gyps fulvus*) for estimating wind velocity and the convective velocity scale. The convective velocity scale is used in convective mixed layer similarity theories (Stull 1988) and is rarely observed by meteorological ground stations.

Estimation of wind velocity and convective velocity scale from 3-dimensional GPS location data

During soaring flight a bird typically circles upward in a thermal (climbing phase) and then glides and loses altitude to make horizontal progress in a particular direction (Fig. 5.1). During the climbing phase a bird may drift from the main flight bearing. This drift is caused by the horizontal displacement of thermals by advection with the horizontal wind (Kerlinger & Gauthreaux 1984; Stull 1988). In our study, we use this horizontal displacement of the thermal over time to estimate wind velocity. We developed an algorithm to automatically classify circling bouts (periods of consecutive circling behaviour), which can handle the large datasets of high resolution GPS locations over hours, days, or even years of flight. Periods of circling and gliding can be distinguished because they show different characteristic combinations of climb rate, ground speed and flight direction variation (Fig. 5.2). Further details about the classification algorithm can be found in the appendix. We estimated the horizontal displacement of each thermal with linear regression through all GPS points in each circling bout. The net horizontal displacement of the bird divided by the time span of each circling bout yields an estimate for wind speed. The direction of the horizontal displacement yields an estimate for wind direction. Estimates of wind velocity from longer periods of circling suffer less from uncertainty that is introduced by variation in horizontal position due to the circling movement. Therefore, we selected only circling bouts that took at least 72 seconds for our analyses.

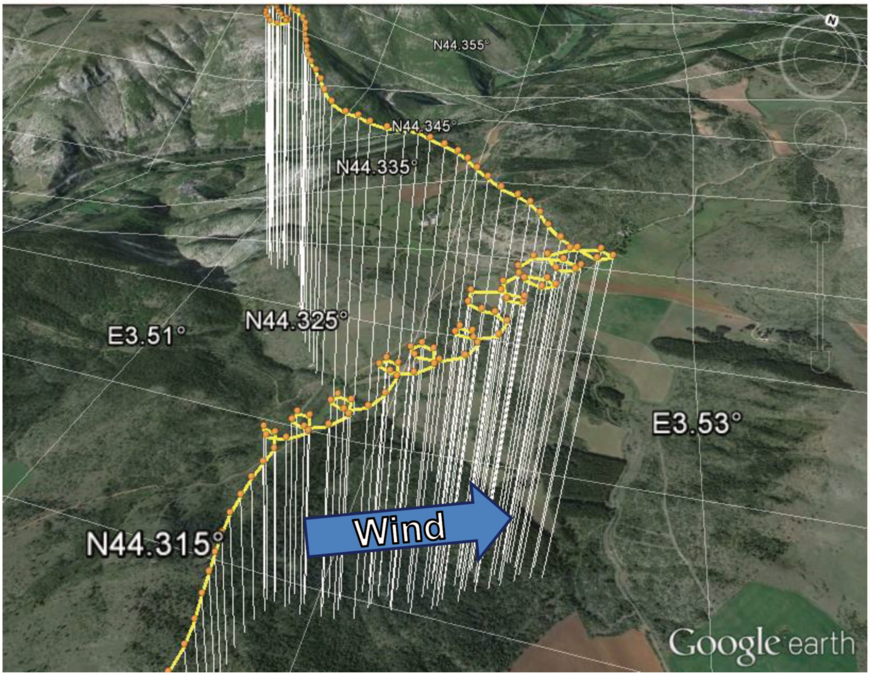

Figure 5.1. GPS sequences of a griffon vulture on 2 Aug, displayed in Google Earth. With circling flight, the vulture gains altitude in a thermal without flapping, after which it continues gliding toward its intended destination. During circling, there is a net horizontal drift that is caused by horizontal advection of the thermal due to wind. The blue arrow indicates the estimated wind direction based on this horizontal drift.

For estimations of vertical wind velocities in a thermal we used data from the same circling bouts. Circling flight is particularly suitable for estimating vertical air velocity because birds try to minimize sink rate relative to the upward moving air in order to gain altitude. Thus average sink rate estimations are more accurate when predicted from circling flight than from gliding flight. The sink rate of a bird relative to the air can be estimated using the theoretical formulation of aerodynamics of soaring birds, which has been established based on wind tunnel experiments and field observations (Pennycuick 1971; Tucker 1987). The sink rate is mainly dependent on morphological characteristics and the horizontal airspeed of the bird. We estimated airspeed of the vultures from its ground speed vector by subtracting the wind velocity. For this wind velocity we used the estimates from the horizontal displacement of thermals. As we explained earlier, these estimates for the horizontal wind speed from the GPS locations are independent of sink rate. The vertical wind velocity is estimated from the sink rate added to the measured climb rate between two GPS fixes (Shannon *et al.* 2002b). All equations can be found in the appendix to this paper.

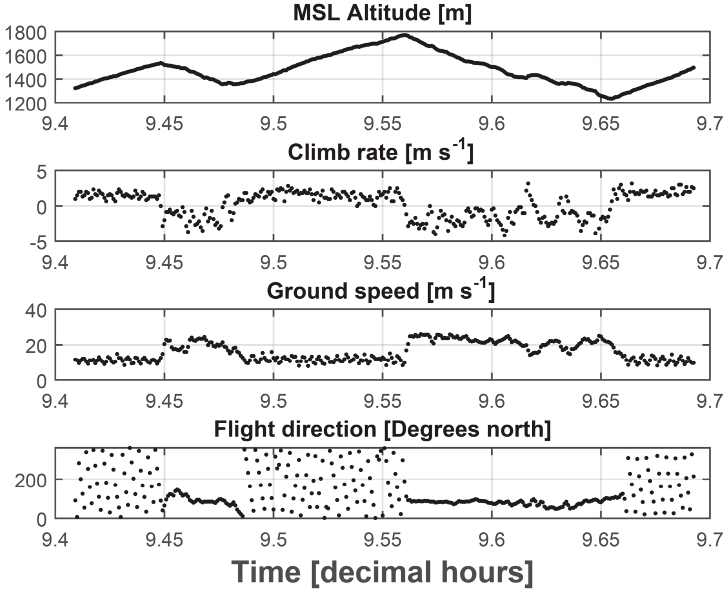

Figure 5.2. Time series of altitude (m MSL), climb rate (m s^{-1}), ground speed (m s^{-1}), and flight direction of a griffon vulture between 0924 and 0942 UTC 2 Aug 2012. Two distinct types of behaviour can be distinguished in all variables, namely circling flight and gliding flight. During circling flight, the vulture is gaining altitude; thus, the climb rate is positive, the horizontal speed is relatively low (between 10 and 15 m s^{-1}), and the direction is continuously changing. During gliding, the vulture is mainly losing altitude, the climb rate is mainly negative, the horizontal speed is relatively high, and the direction constant or gradually changing.

Case study: Griffon vultures in Grands Causses

Since 2010, 22 griffon vultures from a colony in the Grand Causses area, southern France, were equipped with GPS tags from the University of Amsterdam Bird Tracking System (UvA-BiTS; Bouten *et al.* 2013) in order to study their foraging behaviour (see additional details in Monsarrat *et al.* 2013). The solar-powered GPS tags weigh about 45 grams and contain a tri-axial accelerometer, rechargeable battery, data logger and a two-way communication system, which makes it possible to remotely download data and change the measurement interval (Bouten *et al.* 2013). The position- and altitude errors of the UvA-BiTS devices have been shown to be in line with other GPS systems. In a stationary position, and with a measurement interval of 6 s, the mean position error is 1.13 m (90% CI [0.2, 2.33]) and the mean altitude error is 1.42 m (90% CI [0.25, 3.75]).

The Grand Causses area is characterized by deep canyons (of approximately 400 m deep) along the rivers Tarn and Jonte in between limestone plateaus (Fig. 5.3). The nests of the griffon vultures are located on steep cliffs along the canyons. The land is mainly used for extensive sheep farming (grazing in steppe meadows) and for forestry (*Pinus sylvestris*). The area has a dry and sunny Mediterranean climate. The home range of this resident griffon vulture population is located with a radius of roughly 50 km around the main colonies (global home range area used by all birds approaches 10,000 km^2) (Monsarrat *et al.* 2013). According to accelerometer data, griffon vultures almost exclusively use circling and gliding flight and flap only very rarely, typically at take-off (Shepard *et al.* 2011; Duriez *et al.* 2014). They fly mostly during sunny days, when convection in the atmospheric boundary layer provides abundant thermal uplift.

For this case study the measurement interval of four loggers was set to 3 seconds. Data was collected on 2 August 2012 from four birds tracked simultaneously. Three of the four vultures were mainly active in the morning making long flights. All four vultures made a few shorter flights in the afternoon (see table 5.1 for further flight details). During that day, we recorded 79 circling bouts which were longer than 72 seconds and hence 79 estimates of wind velocity. 2 August 2012 was a warm and sunny day with a maximum temperature of 28.3 °C. The wind increased from around

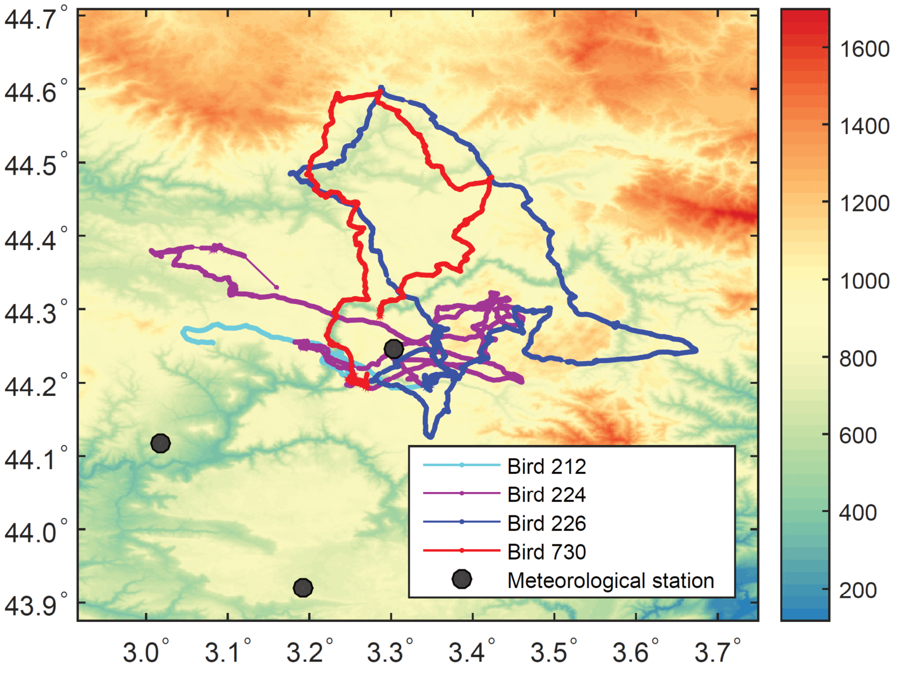

Figure 5.3. Topographic map of the area combined with GPS tracks of four griffon vultures on 2 Aug 2012 (lines) and the locations of three meteorological stations.

3 m s^{-1} in the morning from various directions to 7 m s^{-1} from the northwest (ground station data).

For evaluation of our GPS estimates of wind speed and direction we used hourly data obtained from three meteorological stations (owned by Météo-France), located on high vantage points within the home ranges of the griffon vultures (Millau-Soulobres (3.018 E, 44.118 N – 714 m), Saint-Pierre-des-Tripiers (3.303 E, 44.245 N - 929 m), La Cavalerie (3.192 E, 43.921 N - 718 m)). The sensors for wind are located at 10 m above the surface. Figure 5.3 shows a topographic map of the region, the locations of the meteorological stations and the GPS tracks of the four vultures on 2 August 2012. We interpolated the ground station data in space and time to the

Table 5.1. Flight characteristics for four individual vultures (Id) that have been tracked with high resolution GPS on 2 Aug 2012. Standard deviations are given in parentheses.

Id	Flight times (UTC)	Distance covered (km)	No. of circling sequences (>72 s)	Avg climb rate (m s^{-1})	Avg sink rate (m s^{-1})	Avg Circling radius (m)	Max altitude in a thermal (km MSL)
212	1200-1230	26.4	3	2.4 (0.89)	1.33 (0.65)	21.3 (3.84)	1.27 (0.04)
	1420-1445	13.0					
	1700-1720	15.5					
224	0730-1145	189.3	27	1.3 (0.74)	1.10 (0.79)	23.4 (4.47)	1.38 (0.26)
	1425-1630	95.7					
	1745-1800	8.3					
226	0800-1230	245.9	29	2.0 (1.06)	1.06 (0.32)	21.7 (5.80)	1.57 (0.28)
	1500-1620	58.1					
730	0825-1140	157.4	20	1.8 (0.77)	0.91 (0.14)	25.5 (4.13)	1.32 (0.24)

latitude, longitude and timestamps of the GPS measurements. For spatial interpolation to the location of the bird we used weighted distance interpolation. We compared wind speed estimates with ground station data using Pearson's correlation and for wind direction we used a correlation coefficient for directional data (ρ_{cc}) (Berens 2009).

The global Ocean-Land-Atmosphere Model (OLAM) (Walko & Avissar 2008) was used to evaluate the GPS estimates of vertical velocity of air. In any atmospheric model, the vertical wind speed averages to zero at a spatial scale that is larger than a few hundreds of metres, or in observations over a time period longer than about 30 minutes. Meteorological stations, which report hourly averages, therefore do not report mean vertical wind speed. Similarly, regional meteorological models that use a resolution coarser than hundreds of metres (typically, several kilometres) cannot resolve vertical wind that is associated with thermal convection, while thermals are very complex structures, where turbulent fluctuations can be larger than the mean uplift strength (Lenschow & Stephens 1980). Instead they use different parameterizations to estimate the convective tendencies in the atmospheric boundary layer, such as the convective velocity scale. If the bird-born GPS estimates of vertical velocity would provide a random sample from the thermal column, the average of all points in a thermal would be a direct estimate of the mean uplift strength in a thermal, which scales with w_*.

However, as the birds try to optimize their climb rate by mainly flying in the fast rising sections of the thermal, but are constrained to flying in circles in order to minimize their banking angle and sink rate (Shepard *et al.* 2013), and potentially also by selecting the larger thermals, bird-born observations cannot be treated as an unbiased random sample of mean uplift strength. Therefore, the two variables (observed vertical wind and modelled w_*) may have a different mean value range. Nonetheless, despite the relative bias of the means, they are expected to strongly correlate in space and time.

OLAM was initialized with weather reanalysis data from the European Centre for Medium Range Weather Forecasting (ECMWF) interim reanalysis dataset (Dee *et al.* 2011; data available online at http://apps.ecmwf.int/datasets/). A geodesic atmospheric grid is built from spherical hexagonal elements. The atmospheric grid is gradually refined around the area of interest, producing a fine grid resolution of 300 m over a circular area of 30 km in diameter. The vertical grid extends upward, from the surface to 25 km in height. The vertical resolution is 30 m near the surface and becomes gradually coarser with altitude to 1600 m for the uppermost layer. Fine resolution maps of surface elevation (SRTM 90; NASA 2012) and land cover (CORINE

Land cover facility; EEA 2006) data are used as model input. Output is generated every 30 minutes. The convective velocity scale (w_*) is calculated from the sensible heat flux (H), boundary layer height (z_i) and boundary layer average potential temperature ($\bar{\theta}$),

$$w_* = \left[\frac{g z_i H}{\rho c_p \bar{\theta}}\right]^{1/3} \qquad \textit{Eq. 5.1}$$

where ρ is air density and c_p is specific heat at constant pressure. The contribution of water-vapor flux to w_*, which is typically small in convective boundary layers, is neglected. Sensible heat flux and potential temperature are resolved by OLAM, and boundary layer height is parameterized in OLAM.

Results

GPS estimates of wind speed and direction are significantly and positively correlated with ground station data (Pearson's $r = 0.78$; $p < 0.001$ for wind speed and $\rho_{cc} = 0.67$; $p < 0.001$ for wind direction). Wind speed measurements from ground station data have higher values than the estimates from the GPS tracking data (Fig. 5.4). In the lower wind speed ranges (2.5-4 m s^{-1} on the x axis), there is larger variation in the wind speed estimates from GPS than in the ground station data. A main reason for this variation could be that our GPS estimates provide 79 independent observations of wind speed from a range of altitudes (Fig. 5.7), compared to 12 hourly observations from the ground stations from which 79 data points are derived by interpolation. The overall distribution of wind directions from GPS and ground station data is similar with winds coming from a west to northwest direction (Fig. 5.5), however there is a systematic bias: The ground station observations of wind direction ranges from west to north whereas the GPS data ranges from southwest to northwest. This turning in wind direction with height is consistent with the Ekman wind profile (Stull 1988).

The estimated mean vertical wind speed in the convective updrafts where vultures circle is significantly correlated with the convective velocity scale (w_*) calculated from OLAM output (Pearson's $r = 0.69$; $p < 0.001$). To test if the individual vulture has a significant effect on our vertical wind speed estimates, we used a generalized linear mixed model with w as the response variable, w_* from OLAM as the predictor variable, and individual as a random factor. We found that individual random effects are not significant (all $p > 0.05$), and w is positively and significantly correlated with w_* ($R^2 = 0.46$; $\beta = 1.12$; $p < 0.001$). This suggests that vertical wind

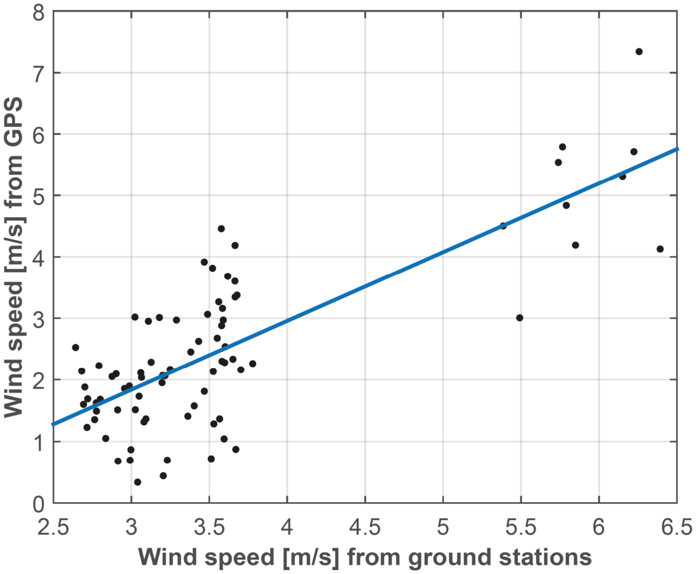

Figure 5.4. GPS estimates of wind speed as a function of ground station measurements of wind speed at 10 m AGL. Ground station measurements from three ground stations are interpolated in space and time to the location of the GPS estimates. Pearson's r is 0.78 (p < 0.001).

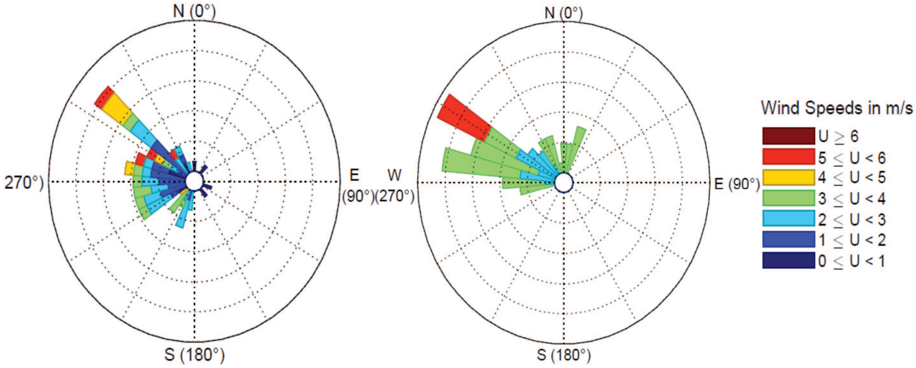

Figure 5.5. Wind roses on 2 Aug 2012 estimated from (left) GPS data of griffon vultures and (right) hourly ground station data at 10-m altitude linearly interpolated in time to the time stamps of the GPS estimates. The directional correlation between the GPS estimates of wind direction and ground station measurements is ρcc = 0.67 (p < 0.001).

estimates are consistent among individuals. While direct measurements of vertical wind from other sources are not available, the high correlation between our vertical wind estimates and the model's w_* indicates that GPS data can be used to estimate vertical wind velocity (Fig. 5.6). Mean vertical wind, as estimated from the flight tracks, increases during midday and follows a temporal diurnal pattern that agrees with boundary layer theory of increasing updraft intensities and growth of the boundary layer starting with solar radiation in the morning and intensifying during the day followed by decline in the late afternoon and toward the evening (Fig. 5.7). Similarly, in the first hours after sunrise the maximum flight altitudes increase which agrees with the diurnal pattern of boundary layer height, however, the increase does not continue until midday (Fig. 5.7). Around midday the three vultures that were flying stopped for feeding or resting (Table 5.1), which is a possible explanation for the vultures not climbing to the maximal potential elevation.

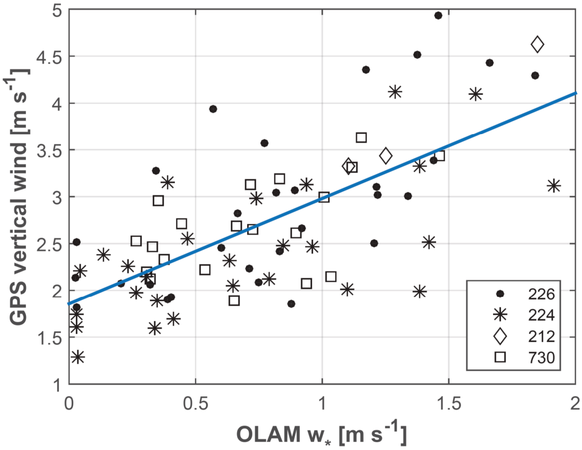

Figure 5.6. Average vertical wind in circling bouts as a function of convective velocity scale calculated from OLAM model output. Half-hourly OLAM output is interpolated in space and time to the locations of the GPS estimates. Pearson's r is 0.69 ($p < 0.001$).

Conclusions

Integrating meteorological and biological expertise has great potential for both communities (Charrassin *et al.* 2008; Shamoun-Baranes *et al.* 2010; Shepard *et al.* 2011). This study shows that high resolution GPS measurements of avian flight behaviour can be used to collect information about meteorological conditions at a fine scale and in areas where sensors are not available. Soaring birds, such as griffon vultures, are very efficient when circling in thermals (Pennycuick 1971; Shannon *et al.* 2002b) and therefore provide unique measurements of vertical velocities in thermals. The strong correlation of the mean vertical velocity in a thermal with model-resolved convective velocity scale is not surprising given mixed-layer similarity theory (Stull 1988). The correlation shows that the bird-born observations provide useful information of updraft intensities at the temporal and spatial scale of the model

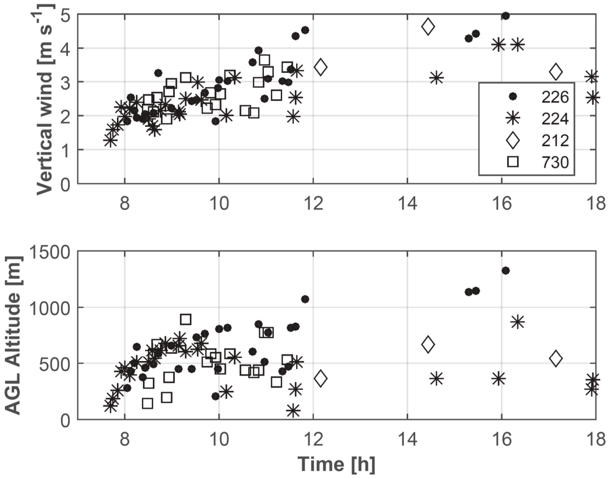

Figure 5.7. (top) Mean vertical wind in a thermal estimated from GPS data of griffon vultures as a function of time of day and (bottom) maximum flight altitude (m AGL) reached in each thermal as a function of time of day. Altitude is determined by subtracting the ground-level elevation (extracted from the SRTM 90 elevation dataset) from the altitude of the bird (m MSL), measured by the GPS. Different symbols represent different individuals. On the day of data collection, the griffon vultures were mainly active in the morning.

output. Since we compare the estimates with model data at half hourly time interval and spatial averages over grid cells of 300 m it is hard to evaluate accuracy of individual observations. The variation in GPS estimates could be caused by uncertainties in our method or the GPS estimates might be more informative than the model data. The same is true for estimates of wind velocities, which correlate well with ground stations data both when it comes to speed and direction. No co-located data is available to test the accuracy in detail, so we can only speculate about the causes of the different velocity ranges and the increased variation in the GPS estimates compared to ground station data. A better validation may be done by extrapolating the ground station data to the altitude of the bird using radix layer similarity theory (Santoso & Stull 2001) and accounting for the effects of mechanical stress and thermal wind on the variation of wind direction with altitude. For this, reliable data-sources of convective velocity scale, boundary layer height, geostrophic winds and temperature gradients are needed at fine resolution. The lack of fine scale weather data for evaluation makes it difficult to validate our measurements. Individual estimates of climb rate are fairly consistent which suggest that they can be used individually to map thermals at even finer temporal and spatial scales. However, until the development of an observation platform that could obtain direct measurements of uplift and wind speed over a full-thermal volume, rather than at a point, we could not know for certain in which part of the thermal the bird is located; we can only compare relative differences in climb rates.

A good understanding of the relations between bird movements and meteorology is crucial to enhance meteorological information content. These interactions can be very specific for different species, but also could depend on flight objective of the bird, for example whether a bird is searching for food, commuting between roosts or travelling to migrate (Shepard *et al.* 2011). When soaring birds travel large distances, they can reduce energy expenditure by circling in the stronger updrafts of the middle part of the boundary layer (Shannon *et al.* 2002a; Shamoun-Baranes *et al.* 2003; Sapir *et al.* 2011). When searching for food or commuting between roosts altitude plays a less prominent role since prey may be harder to detect at higher altitudes or climbing to high altitudes is not necessary if nearby targets are within gliding range.

Further miniaturization of GPS tags, batteries and sensors in the future will likely yield an exponential growth of high resolution data in the coming years. If knowledge of relations between bird flight and fine scale meteorology will be improved, more and more accurate information can be obtained. High resolution GPS data from birds can therefore become a promising complementary data source, filling gaps of conventional observation systems (Charrassin *et al.* 2008). Potential products can be used by glider pilots, in air quality forecasting and in emergency management in the case of chemical releases. By contributing data and expertise, biologists can help improve meteorological products which in turn can be used to help understand how birds respond to dynamic atmospheric conditions at these fine scales. The key perhaps is beginning an open dialogue between these communities and we hope that the current study will help stimulate future collaboration.

Acknowledgments

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Supporting information S1: Methods for deriving information from GPS tracks

Classification of circling bouts

In order to classify circling bouts in the data we use ground speed, the flight direction and the climb rate of the bird. We estimate the ground speed (V_i in m s^{-2}) at a location (P_i) by averaging the speed of the trajectory that ends at this location (P_{i-1} till P_i) and the trajectory that starts at this location P_i till P_{i+1});

$$V_i = \frac{\frac{P_i - P_{i-1}}{t_i - t_{i-1}} + \frac{P_{i+1} - P_i}{t_{i+1} - t_i}}{2} \qquad \textit{Eq. S5.1}$$

Where t_i is timestamp of GPS data point t.

The horizontal flight direction at a location is the average of the bearing of two lines connecting the trajectory that ends at this location and the trajectory that starts at this location.

The climb rate V_c in m s^{-1}) is obtained in the same manner as ground speed. First the climb rates in between the locations are calculated by dividing the altitude (z in m) difference by the time interval. Then the climb rate at a location is obtained by averaging the climb rate of the trajectory that ends at this location and the trajectory that starts at this location;

$$V_c = \frac{\frac{z_i - z_{i-1}}{t_i - t_{i-1}} + \frac{z_{i+1} - z_i}{t_{i+1} - t_i}}{2} \qquad \textit{Eq. S5.2}$$

A set of rules is developed to automatically classify circling flight. For the classification of each location, 5 consecutive estimates of climb rate and flight direction are used; the estimates on the location itself (P_i), the two previous locations P_{i-1} and P_{i-2}) and the two next locations (P_{i+1} and P_{i+2}). Three criteria are used for the classification of circling flight. 1) The change between the different flight directions at the 5 locations must be larger than 180 °. 2) The average climb rate at the five locations must be positive. 3) The ground speed of the bird must be larger than 5 m s^{-1}. If the sequence of 5 locations satisfies all three criteria, location P_i is classified as circling flight.

Estimation of sink rate

The sink rate of a soaring bird relative to air can be estimated based on an equation by (Pennycuick 1971), where sink rate is a function of horizontal airspeed and morphological characteristics;

$$V_s = \frac{2kW}{\pi \rho_0 b^2 V} + \frac{C_{D_0} \rho_0 S V^3}{2W} \qquad \textit{Eq. S5.3}$$

where W is the weight (N) of the individual, b is wing span (m) and S is wing area (m^2). ρ_0 is the air density at sea level (kg m^{-3} and k and C_{D_0} are species dependent coefficients. k is a drag coefficient related to the efficiency of the wings in producing lift and C_{D_0} is a zero-lift drag coefficient (Welch *et al.* 1977). V is the airspeed of the bird (m s^{-1}). In the current study V is estimated by subtracting the drift velocity of a thermal, as an estimate of the wind speed, from the groundspeed of the bird during the climb phase as measured by the GPS.

The turning motion, that is needed to stay in a thermal column, causes an inclined position of the birds' wings relative to the horizontal. The angle depends on the radius of the circles and the horizontal velocity and is typically between 20 and 40 degrees (Pennycuick 1971). This influences the sink rate of a circling bird V_{sc}, which is a little bit higher than the sink rate in straight gliding flight. This difference is estimated with

$$V_{sc} = \frac{V_s}{\sqrt{\cos^3 \varphi}} \qquad \textit{Eq. S5.4}$$

where φ is the bank angle (Shannon *et al.* 2002b). The bank angle is estimated with

$$\varphi = \sin^{-1} \frac{V^3}{rg} \qquad \textit{Eq. S5.5}$$

where r is the turning radius (m) and g is the gravitational acceleration 9.81 m s^{-1}.

The sink rate is mainly sensitive to variations in airspeed of the bird. Estimates for white-backed vultures, which are very similar to griffon vultures, yield k is 1 and C_{D_0} is 0.0232 (Pennycuick 1971).

The mass of a griffon vulture is highly variable as it is able to fast for long periods and can eat up to 1.5 kilogrammes of meat in one feed. Average body mass is estimated per individual from measured head and beak sizes, which are correlated to body mass.

The wing span and wing area of the griffon vultures have not been measured directly, however the folded wing has been measured. On another set of captive griffon vultures measurements are done of wing span, wing area and folded wing, where these variables are found to be highly correlated. This makes it possible to roughly estimate wing span and wing area from the folded wing measurements. An overview of the characteristics of the four vultures used in this research is shown in table S5.1.

Table S5.1. Characteristics of four griffon vultures from the population in the Grands Causses area. GPS data from these vultures was collected on 2 Aug 2012. The parameters mass, wing span, and wing area are used to estimate the sink rate of the vulture relative to air.

Individual	Sex	Age (yr)	Mass (kg)	Wing span (m)	Wing area (m^2)
212	Female	17	7.99	2.54	0.972
224	Female	5	8.27	2.52	0.953
226	Female	6	8.92	2.56	0.986
730	Female	16	7.86	2.59	1.012

6

General Discussion

Jelle Treep

Summary

Understanding movement of organisms is of crucial importance for management and restoration of natural areas. Firstly, movement of plants and animals facilitates re-colonization of habitat and gene flow between populations. Moreover, movement also has consequences for other taxa: moving animals can transport plant seeds and a wide range of other organisms (van Leeuwen *et al.* 2012; Soons *et al.* 2016), and plant seeds carry microbial communities (Barret *et al.* 2015), thereby providing connectivity between distant habitats in heterogeneous landscapes. For this reason, movement plays a central role in spatial species dynamics and species interactions (Nathan *et al.* 2008a). Recent advances in tools for modelling and monitoring movement paths have provided high resolution movement tracks of individual organisms and improved our detailed understanding of movement mechanisms (Cagnacci *et al.* 2010; Börger 2016; Hays *et al.* 2016). Further advances in monitoring environmental variables create new opportunities to study the relation between movement and the abiotic environment in greater detail (Shamoun-Baranes *et al.* 2010; Hays *et al.* 2016). However, the wide range of spatiotemporal scales of the processes involved in movement poses a great challenge in linking individual movements to population and ecosystem dynamics. This thesis demonstrates how mechanistic models can be used to link movement paths to endogenous and external drivers at various spatiotemporal scales.

The general movement ecology framework ('the movement ecology paradigm'; Nathan et al. 2008) is a powerful conceptual framework that can be used to map links between movement, internal drivers and external factors (Fig. 1.1). In **chapter 1** of this thesis, I discuss how this framework applies to bird movement and seed dispersal in plants, and the combination of the two (seed dispersal by moving birds). I also explain how the following chapters (2-5) examine specific parts of this movement framework. In these chapters spatiotemporal models and large environmental and movement datasets are used to study interactions between plants, birds and their environment. New hypotheses are developed regarding dispersal of plant seeds (**chapter 2**), important mechanisms in the seed dispersal process are identified (**chapter 3 and 4**), and high resolution movement data is demonstrated to be a useful means to measure environmental factors (**chapter 5**). In this general discussion (**chapter 6**), the most important conclusions from each chapter are summarized in light of the general movement ecology framework, and these chapters are used to generate a final synthesis of the key findings and dictate future perspectives.

In **chapter 2**, we develop a framework for the identification and analysis of plant movement strategies based on the assumption that plant and animal movements are driven by similar factors. In animal movement ecology, theoretical research and experiments have identified optimal movement patterns in random searches that optimize encounter of unknown targets (De Jager *et al.* 2011; Humphries & Sims 2014; Kölzsch *et al.* 2015). We suggest that seed dispersal can also be viewed as a random search, where the shape of the entire seed distribution (dispersal kernel) is evolved to optimize finding empty habitat and depends strongly on the spatiotemporal distribution of habitat. Using model simulations, we demonstrate that dispersal strategies optimize trade-offs between habitat encounter, avoiding kin competition and colonizing new patches. These trade-offs result in multi-scale dispersal strategies being optimal across a wide range of dynamic patchy landscapes. In static patchy landscapes short-distance dominated dispersal strategies are selected, whereas in uniform or highly unpredictable landscapes long-distance dominated dispersal strategies are selected. The shape of the optimal dispersal kernel is most sensitive to patch turnover rates. These theoretical results provide new hypotheses within the 'Where to move?' part of the movement ecology framework (Fig. 1.1), which can be used as null-model in plant dispersal research.

Based on our results, we propose that the entire shape of the dispersal kernel plays a role in optimizing a trade-off between local and non-local habitat search. The entire kernel should therefore be considered in studies where dispersal ecology plays a role. In many ecological studies, a clear distinction between colonizers (with high dispersal capacities) and competitors (with low dispersal capacities) is made. This is a helpful model, but colonizers and competitors should be regarded as extreme cases with many possible strategies in-between that are all tightly linked to the spatiotemporal distribution of habitat. Our theoretical framework provides exciting opportunities to further explore analogies between animal movement and plant movement. Interesting examples include: composite search behaviour that combines multiple movement types into one dispersal strategy (cf. Morales *et al.* 2004) in species with dispersal dimorphisms or species using multiple dispersal vectors, and 'informed searches' as a strategy to escape competition and environmental stress (Martorell & Martínez-López 2014) in plant species with directed dispersal.

In **chapter 3,** we address the 'motion capacity' of wind-dispersed plants in relation to wind dynamics ('external factors'), and thereby study how plant and seeds traits may be relevant in optimizing dispersal. Using model simulations, with measured time-series of wind speed as input, we show that plants can increase dispersal distances by releasing seeds above a certain wind speed threshold. The higher this threshold is, the higher the probability of long-distance dispersal events, which may allow the development of long-distance dispersal strategies. However, observations show that plants release seeds non-randomly with a bias towards wind speeds exceeding 5-6 m s^{-1}. Thus, the observed plants are clearly not utilizing the wind speed extremes that would maximize long-distance dispersal events. There are two important possible explanations for this: 1) potential risks involved in retaining seeds on the plant until high wind speeds are reached, such as seed predation or damage by other disturbances, are a limiting factor in driving the evolution of wind speed thresholds in seed abscission. In our model simulations, we find that the frequency of disturbances has a strong influence on long-distance dispersal probability and abscission thresholds maximizing this long-distance dispersal probability. 2) The dispersal kernels do not aim to maximize long-distance dispersal, but rather aim for an optimal dispersal distance distribution. Our study in **Chapter 2** provides theoretical support for this explanation. In conclusion, we identified the cost and benefits of non-random seed abscission in several wind-dispersed plant species, which improves quantitative understanding of dispersal and may help to improve estimates of dispersal in studies of colonization in fragmented landscapes, plant invasions and range shifts under global change.

In **chapter 4**, the movement of birds is linked to the movement of ingested plant seeds; the movement path of the birds is an external source of energy for the movement of plant seeds. Using a model of seed digestion by mallards and GPS data of mallard movement, we quantify the spatiotemporal patterns of seed dispersal in landscapes that differ in their degree of fragmentation. Daily foraging flights of mallards result in frequent transport of seeds between distant waterbodies, thereby maintaining habitat connectivity for plants in fragmented wetlands. Furthermore, landscape (spatial distribution of foraging sites) is shown to be a major determinant of mallard movements, and thereby indirectly a major determinant of seed dispersal distributions. The motion capacity of seeds, given the available external energy source, is determined mainly by one trait: seed size. Seed size-related gut retention times determine the proportion of seeds dispersed away from the ingestion area. Large seeds have relatively longer gut retention times and thereby a higher probability of long-distance transportation. However, larger seeds have a lower probability of surviving gut passage. Seed size-mediated survival appears to be more important than retention time, and, accordingly, more small seeds will finally accomplish long-distance dispersal. The frequent long-distance transport of seeds makes Mallards, and possibly many other granivorous birds, important seed dispersal vectors that play a crucial role in regulating plant diversity under ongoing habitat fragmentation.

In **chapter 5**, we use the relation between movement and external factors in the opposite direction: biologging data of soaring bird movement is used in combination with knowledge about the bird's motion capacity to obtain information about external factors. Because griffon vultures use thermal convection to gain altitude and glide in between thermals to cover horizontal distances, their flight patterns are strongly related to meteorological phenomena. We use aerodynamic theory of griffon vultures to estimate vertical wind speed in convective updrafts based on vulture climb rates that as measured by GPS. While the vultures are circling in thermals, the thermals drift horizontally due to wind, thereby allowing us to estimate wind speed and wind direction from the GPS data as well. We used the atmospheric model OLAM to evaluate vertical wind speed estimates and ground station measurements to evaluate wind speed and wind direction estimates. We found strong correlations between estimates based on GPS data and high resolution wind speed and wind direction observations and modelled convective updraft velocities, demonstrating that biologging offers a novel alternative approach for estimating atmospheric conditions on a spatial and temporal scale that complements existing meteorological measurement systems. This is particularly interesting for obtaining information about thermal structures that are difficult to observe with regular sensors and in remote areas where high resolution wind speed and direction observations are sparse.

The role of models in movement research

The general movement ecology framework (Nathan *et al.* 2008a) is a conceptual model that promotes our understanding of how four components - internal state, navigation capacity, motion capacity and external factors - together shape movement patterns. However, it is not straightforward to obtain quantitative understanding of the interplay between the different components because of the wide range of scales that are involved (Nathan *et al.* 2008a). Each component comprises multiple traits and/or processes that may be relevant from the individual level to population levels and at very short to evolutionary timescales. In order to obtain fundamental mechanistic understanding of how different traits and processes together shape movement paths, integration of many spatiotemporal scales is required.

Models can integrate processes acting at different spatiotemporal scales and thereby connect different components of the movement framework. By making these connections, models provide a way to study consequences of individual behaviour on (eco)system dynamics in complex systems that mimic the complexity of natural systems (Grimm *et al.* 2005; Jeltsch *et al.* 2013). A drawback of complex models is that evaluation of model output, assumptions and structure is often impractical. For such evaluations, data would be required that are in practice (nearly) impossible to obtain. For example, in **chapter 3** it would be extremely difficult to record all actual seed abscission events and resulting dispersal distances for an entire growing season. In **chapter 4**, it would not be possible to monitor gut passage of seeds during normal daily mallard behaviour, nor measure actual dispersal distances, as both intake and deposition are difficult to observe. Thus, only parts of the models are tested under experimental settings. Therefore, uncertainty remains concerning the assumptions related to parameter values and model structure. However, despite this limitation, mechanistic models do provide important new insights concerning the interplay between dispersal traits and external factors at fine spatiotemporal scales, and how these together can shape broad scale patterns, such as the evolution of dispersal traits and dispersal kernels.

Furthermore, models can act as virtual laboratories where sensitivity 'experiments' can be carried out to identify important variables or processes (Oreskes *et al.* 1994). Such experiments can be done by comparing model outcomes while varying model parameters and/or model inputs. In this way, one can determine which parameters or mechanisms have a large effect on model outcomes and are potentially important factors in natural systems. Examples of sensitivity experiments are presented in **chapters 2, 3 and 4** of this thesis. In these chapters, we examined the sensitivity of I) optimal dispersal kernels to spatiotemporal landscape structure (**chapter 2**), II) non-random abscission and dispersal kernels to seed traits and disturbance frequency (**chapter 3**), and III) mallard-mediated seed dispersal distributions to landscape structure and seed size (**chapter 4**). The factors that are identified as having a large effect on model outcomes are potentially important in natural systems and are hereby highlighted as topics of specific interest for further investigation.

Models can take many forms depending on the system under investigation and research aim. Spatiotemporal simulation models are flexible tools that can incorporate many sub-models without using very complex mathematics. Deciding which mechanisms or sub-models to include and exclude in the model can be a difficult task. Adding more mechanisms may lead to more 'realistic' models, but can hamper thorough understanding of the modelled system. Furthermore, adding mechanisms may require additional assumptions and increase uncertainty. Setting boundaries on model complexity is therefore very much dependent upon the aim of the modeller (Grimm *et al.* 2005; Evans *et al.* 2013). Since **understanding** of the key mechanisms driving dispersal patterns of plants seeds is a main aim in the studies of **chapter 2-4**, models were kept as simple as possible and only used mechanisms within the specific research focus. In **chapter 5,** a model is used to make the connection between movement data and air flow estimates. Here, we tried to estimate wind speed and convection as accurately as possible to prove the potential of movement data for the quantification of meteorological variables. Since the aim is clearly different, we chose to implement Pennycuick's aerodynamic theory of soaring bird flight (Pennycuick 1971) in full, although simplification is possible in this formulation.

Models can help advance our understanding of movement ecology of plants and birds by filling knowledge gaps in the movement framework. Different internal and external drivers of the movement framework should be understood in coherence, however it is often not possible to physically observe all drivers of movement. In wind- dispersed plant seeds, for instance, observations of seed dispersal traits and their effect on aerodynamics are numerous and can be used for understanding the mechanisms of their 'motion capacity', whereas selective pressures on dispersal traits remain unknown, with dispersal objectives often remaining unclear. These objectives can be identified and mapped using models (**chapter 2**; Phillips *et al.* 2008; Dytham 2009) or tested in specific situations such as range expansions (Cody & Overton 1996). Progress in understanding potential dispersal objectives through models could improve understanding of (evolution of) observable dispersal traits and mechanisms. This could also work for other species and taxa and different combinations of movement drivers.

Future perspectives

The aim of this thesis is to connect movement theory, movement data and environmental data to help improve our understanding of movement patterns of birds and plants. Organismal movement is a key process in ecosystem dynamics as movements facilitate colonization and gene flow, and also has consequences for other taxa that are carried internally or externally during movement (van Leeuwen *et al.* 2012; Barret *et al.* 2015; Soons *et al.* 2016). The ongoing worldwide decline of biodiversity due to increasing pressures of climate change, in combination with habitat fragmentation resulting from urbanisation and intensive agriculture (Vitousek *et al.* 1997; Butchart *et al.* 2010), highlights the importance of movement ecology research (Damschen *et al.* 2008; Allen & Singh 2016). Great challenges in movement ecology include bridging the gap between theory and observations (Kays *et al.* 2015) and linking individual behaviour to population and ecosystem dynamics (Börger 2016). We have shown how mechanistic models can be used to integrate theory and data and processes acting at various spatiotemporal scales. The general movement framework supports integration of scales in terms of separating endogenous and external drivers of movement into different components and mapping the relations between these components (Nathan *et al.* 2008a). We used models to quantify several of these relations. Although birds and plants have different mechanisms for movement and very different life-histories, the movement ecology framework is applicable to both birds and plants.

The improvement of understanding of individual bird movement in recent decades has for a large part been driven by miniaturization of sensors that can monitor the movement of individual birds in great detail (Cagnacci *et al.* 2010). Further miniaturization of measurement devices in the future will make it possible to equip birds with additional sensors (e.g. heart rate monitor, accelerometer) to further elucidate the interplay between internal state dynamics, motion capacity and individual movements. A major challenge that remains is the translation of individual decisions and differences between individuals to population and eco-evolutionary dynamics (Shamoun-Baranes *et al.* 2017). Broad scale population level patterns are increasingly being observed in radar studies (Dokter *et al.* 2013; Kemp *et al.* 2013). Individual-based models inspired by GPS data of individual movements can be used to simulate population level patterns that are observed by radar, thereby integrating the individual and population levels.

Much progress has been made in understanding the relation between flight behaviour and meteorology, driven by the development of methods for annotating of environmental data to movement data (Mandel *et al.* 2011; Kemp *et al.* 2012; Dodge *et al.* 2013). However, understanding of the relation between endogenous drivers of individual bird movement and meteorological phenomena at fine scales is hampered by the lack of fine scale meteorological data (Shamoun-Baranes *et al.* 2017). An increasing sampling effort of various meteorological sensors, and new measurement platforms such as unmanned aerial vehicles (Stull 1988), together with increasing computational power for modelling, will refine the resolution of meteorological datasets in the future. Meanwhile, high resolution GPS data of bird flight movement can help to quantify atmospheric flows, as demonstrated in **chapter 5**. Quantifying flows based on movement data has the potential to be used in many other taxa and environments (Hays *et al.* 2016). An exciting future direction for this method would be the integration of wind and convection estimates based on radar tracking of bird movements. Similar approaches have been used for quantifying wind speeds based on insect tracking with radar (Rennie *et al.* 2010). Integration of the abovementioned methods using models can further advance the study of interactions between bird movements, endogenous and external factors across the full range of spatiotemporal scales, thereby providing more accurate predictions of population dynamics and biodiversity in the light of global change.

Although the movement ecology of plants and animals follow similar principles, advances in the field of plant seed dispersal are hampered by specific challenges. In order to study consequences of habitat fragmentation and global change for plant populations and biodiversity, it is necessary to quantify dispersal in biodiversity models (Pearson & Dawson 2005). However, measuring dispersal of plant seeds is laborious and the tracking of entire trajectories of tiny seeds remains extremely difficult (Nathan *et al.* 2005). Mechanistic models can be used to estimate dispersal kernels of animal-dispersed (Will & Tackenberg 2008) as well as wind-dispersed species (Soons *et al.* 2004a; Katul *et al.* 2005b; Bohrer *et al.* 2008) and could be further improved through enhanced understanding of interactions between internal and external drivers of movement. Evaluation of model output can be done using several potential sources of observations. Firstly, DNA analyses of seedlings and potential parent plants are expected to become very efficient in the near future. This will facilitate the allocation of seedlings to parents (parental analysis), which can be used to obtain large datasets of dispersal distance distributions for a wide range of species (Ashley 2010), although it should be noted that the distribution of seedlings is a result of two processes: dispersal and recruitment. Furthermore, tracking of seed mimics can be performed in various environments to study potential trajectories of seeds in heterogeneous landscapes.

Given that sensor development will lead to possibilities for collecting large volumes of data for smaller birds, such as mallards, new opportunities will become available to further improve our understanding of seed dispersal potential by waterbirds. High resolution GPS and accelerometer data can be used to classify behaviour and temporal foraging patterns (Shamoun-Baranes *et al.* 2012), which is still an uncertainty in our model presented in **chapter 4**. High resolution GPS data can also result in better estimates of dispersal kernels, including insights into directed seed deposition in water bodies, shorelines and terrestrial surfaces. When seed diet and digestion can be quantified for other bird species, dispersal can be estimated for a wide range of plants and systems. This is necessary because animal-mediated dispersal is an important vector providing long-distance directed dispersal to distant habitats (Carlo *et al.* 2013). For projections of plant population dynamics of animal-dispersed plants, it should be noted that this vector is not free of risk: long-distance dispersal frequency is highly dependent on the number of moves and, hence, the abundance of the vector species. Declining populations of vector species could result in greatly reduced dispersal potential and, therefore, reduced colonization and gene flow in plant populations.

Quantification of seed dispersal by wind is also very much dependent on the integration of mechanistic models with observations of specific dispersal mechanisms. Non-random seed release is a major uncertainty in current wind-dispersal models, as we have shown in **chapter 3**. Particle image velocimetry (PIV) is a promising way to obtain insights into seed release and transport in great detail (Marchetto *et al.* 2010). Previously, important insights about particle dispersion have been obtained from various studies combining models with field observations or flume tank experiments (Bullock & Clarke 2000; Soons *et al.* 2004a; Duman *et al.* 2016). However, much of this work has been performed in spatially homogeneous settings, while many landscapes are heterogeneous. This spatial heterogeneity greatly affects atmospheric flows (Dupont *et al.* 2011) and likely has a large effect on dispersal kernels. Large eddy simulation models can resolve turbulence and land atmosphere interactions in heterogeneous landscapes at very fine spatial resolutions (< 1 m). These models can be used to simulate the effect of flow alterations, generated by canopy heterogeneities, on seed trajectories and dispersal kernels (Bohrer *et al.* 2008; Damschen *et al.* 2014). Detailed observations of the effects of landscape heterogeneity on trajectories of dispersing seeds are still generally lacking, but this knowledge gap could be filled by appropriate seed mimic experiments.

A major gap in our current knowledge of seed dispersal in general is the lack of understanding regarding the evolution of dispersal. Evolution of dispersal is mainly studied in specific situations where the dispersal objective is relatively clear, such as island systems or during range expansions (Cody & Overton 1996; Williams *et al.* 2016; Lustenhouwer *et al.* 2017). In **chapter 2**, we have developed general hypotheses that suggest that optimal dispersal kernels are dependent on the spatiotemporal distribution of habitat. The hypotheses that we formulated in **chapter 2** need to be evaluated with empirical data to further elucidate the relation between spatiotemporal landscape structure and evolution of dispersal. This could be done in a broad investigation of available dispersal data. Dispersal traits that optimize dispersal may evolve when a certain dispersal strategy remains optimal over evolutionary timescales, i.e. when biotic interactions and abiotic spatiotemporal landscape characteristics are stable through time. Insights in how environmental factors shape the evolution of dispersal strategies, and progress in knowledge of dispersal mechanisms should mutually inspire each other, thereby improving the understanding and quantification of dispersal in plants.

In order to improve forecasts of biodiversity dynamics in a changing world, movement ecology should be incorporated in biodiversity models. Species distribution models are commonly used tools to identify biodiversity hotspots and predict future species distributions. Species distribution models often rely on correlations between species occurrence and abiotic variables. However, there is autocorrelation in many spatial species abundance datasets which can be partly attributed to movement, and this effect is rarely incorporated into species distributions models (Guisan & Thuiller 2005; Wisz *et al.* 2013). Bridging the gap between mechanistic movement models and species distributions models could greatly improve predictions of biodiversity dynamics in the near future (Jeltsch *et al.* 2013). Increased monitoring has allowed detailed mapping of movements of plants and birds (Kays *et al.* 2015; Börger 2016), but movement data alone is not enough to determine best management practices since movement patterns will change due to future environmental changes. For accurate estimates of future movement patterns, we require quantitative understanding of how internal and external drivers shape movement patterns, to determine how future change of these drivers will affect movements (Nathan *et al.* 2008a) and ultimately diversity (Jeltsch *et al.* 2013). Mechanistic models play a key role in integrating the drivers of movement that act at various spatiotemporal scales, thereby improving understanding of movement and helping in the development of strategies to maintain diversity in our changing world.

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Nederlandse samenvatting

Het begrijpen van bewegingen van organismen is cruciaal om natuurlijke dynamiek in het landschap te herstellen en te beheren. Ten eerste maakt beweging het voor dieren en planten mogelijk om nieuwe leefgebieden te koloniseren en om genen uit te wisselen met andere populaties. Maar daarnaast hebben bewegingen van dieren en planten ook consequenties voor andere organismen: dieren dragen dikwijls plantenzaden en andere kleine organismen met zich mee en plantenzaden kunnen op hun beurt weer microben meedragen. Op die manier zorgen de bewegingen van dieren en plantenzaden voor verbindingen tussen natuurgebieden in versnipperde landschappen. Bewegingen spelen dus een belangrijke rol voor ruimtelijke soortendynamiek en interacties tussen soorten.

De afgelopen tientallen jaren is er een enorme vooruitgang geweest in technologie om bewegingen van organismen te monitoren en te modelleren. Hierdoor is het nu mogelijk om bewegingen van individuen met een hoge resolutie in kaart te brengen en is ons begrip van bewegingsmechanismen enorm vooruit gegaan. Daarnaast heeft technologie voor een enorme vooruitgang gezorgd in het in kaart brengen van omgevingsvariabelen, waardoor we relaties tussen bewegingen en de abiotische omgeving in detail kunnen bestuderen. De processen die een rol spelen bij bewegingen van organismen bestrijken uiteenlopende ruimte- en tijdschalen. Daarom is het nog steeds moeilijk om verbanden te leggen tussen de bewegingen van individuele organismen en de dynamiek van populaties en ecosystemen. Dit proefschrift laat zien hoe mechanistische modellen gebruikt kunnen worden om de link te leggen tussen bewegingen van zowel plantenzaden als vogels en interne en externe (omgevings-) factoren op verschillende ruimte- en tijdschalen.

Planten verplaatsen zich normaal gesproken maar één keer in hun leven, als zaadje. Bij hun zaadverspreiding maken zij gebruik van externe energiebronnen zoals: water, wind of dieren. Vogels daarentegen verbruiken zelf energie om zich te verplaatsen door middel van vliegen, lopen of zwemmen. Hoewel er grote verschillen zijn tussen deze levensvormen kunnen bewegingspatronen van vogels en planten uitgelegd worden met behulp van een vergelijkbaar theoretisch kader (hoofdstuk 1). Bewegingspatronen van zowel plantenzaden als vogels worden gevormd door een complexe samenhang tussen factoren die in te delen zijn in 4 categorieën: 1) Waarom bewegen?, 2) Waarheen bewegen?, 3) Hoe bewegen?, en 4) Externe factoren. Allereerst is er een motivatie om te bewegen (Waarom bewegen?), bijvoorbeeld het vinden van nieuw voedsel of leefgebied. Organismen gebruiken informatie over waarheen ze moeten bewegen (Waarheen bewegen?), bijvoorbeeld door direct waarnemen, ervaring of intrinsieke drijfveren (genetisch geheugen). Afhankelijk van de motivatie en informatie gebruiken organismen bepaalde mechanismen om naar een specifiek doel te bewegen (Hoe bewegen?). Deze interne factoren hangen allemaal nauw samen met externe factoren zoals de ruimtelijke verspreiding van leefgebied, aanwezigheid van predatoren en de abiotische omgeving. De hoofdstukken in dit proefschrift beschrijven interacties tussen bewegingspatronen en verschillende factoren binnen dit theoretische kader en gebruiken ruimtelijke modellen en/of grote datasets om de betreffende interacties te onderzoeken.

Er is de afgelopen decennia veel onderzoek gedaan naar efficiënte zoekstrategieën voor uiteenlopende diersoorten, waarbij zowel experimenten als modellen hebben aangetoond dat bepaalde stochastische zoekpatronen de kans op het vinden van onbekende doelen optimaliseren. **Hoofdstuk 2** laat zien dat ditzelfde principe ook voor de verspreiding van plantenzaden zou kunnen gelden, waarbij de vorm van de totale verspreidingscurve van plantenzaden afkomstig van één plant geëvolueerd is om de kans op het terechtkomen in geschikt leefgebied te optimaliseren. Modelsimulaties laten zien dat de optimale vorm van de verspreidingscurve sterk samenhangt met de beschikbaarheid van leefgebied in ruimte en tijd. Vooral het ontstaan en verdwijnen van leefgebieden door de tijd speelt hierbij een belangrijke rol. De optimale strategie in een groot deel van de landschappen is een ‘multi-schaal’ verspreidingsstrategie waarbij een optimale balans wordt gevonden tussen lokale en niet-lokale verspreiding. Een strategie met focus op lokale verspreiding is alleen optimaal in versnipperde landschappen zonder dynamiek in het ontstaan en verdwijnen van leefgebied. Een strategie met focus op niet-lokale verspreiding is optimaal in uniforme landschappen of landschappen waar continu leefgebied ontstaat en verdwijnt. Deze verspreidingsstrategieën vormen de basis voor het formuleren van hypothesen binnen het ‘Waarheen bewegen?’ deel van het theoretisch kader. Deze hypothesen kunnen dienen als nul-modellen in onderzoek naar plantenverspreiding.

De resultaten suggereren bovendien dat de complete verspreidingscurve van zaden, bij de beste strategie, een optimale balans weergeeft tussen lokale en niet-lokale verspreiding. Dat betekent dat de hele verspreidingscurve beschouwd moet worden in populatieonderzoek waar verspreiding een rol speelt. Vaak wordt echter uitgegaan van een tweedeling tussen pioniersoorten (goede verspreiders) en climaxsoorten (slechte verspreiders). Dit is een nuttig model, maar pionier- en climaxsoorten zijn twee uitersten waartussen veel andere strategieën mogelijk zijn die sterk samenhangen met de verdeling van leefgebied in ruimte en tijd. Dit nieuwe referentiekader levert veel interessante mogelijkheden op om verspreidingsstrategieën van planten verder te analyseren, onder andere op het gebied van samengestelde zoekstrategieën en 'geïnformeerde zoekopdrachten' bij plantensoorten met heel gerichte zaadverspreiding.

Wind is een belangrijke externe energiebron voor de verspreiding van plantenzaden. Windverspreide planten hebben drie belangrijke eigenschappen die de verspreiding van zaden beïnvloeden: valsnelheid van het zaadje, de hoogte waarop het zaadje losgelaten wordt en het moment waarop het zaadje losgelaten wordt ('Hoe bewegen?'). Deze eigenschappen bepalen in samenhang met windstromen waar de zaden terecht komen en hoe de totale verspreidingscurve eruitziet. Planten kunnen verspreidingsafstanden enorm vergroten door zaden alleen los te laten als de windsnelheid een bepaalde drempelwaarde overschrijdt (**hoofdstuk 3**). Model-simulaties, met een atmosfeermodel en werkelijk gemeten windsnelheden als invoer, laten zien dat naarmate deze drempelwaarde hoger ligt, zaden steeds verder verspreiden. Observaties bij planten die in potten zijn gekweekt in de buitenlucht, laten echter zien dat planten hun zaden voornamelijk loslaten bij windsnelheden hoger dan 5 à 6 m s^{-1}. Deze planten gebruiken dus vooral hoge windsnelheden maar niet de extreem hoge windsnelheden die de kans op lange-afstandsverspreiding zo groot mogelijk zouden maken.

Er zijn twee aannemelijke verklaringen voor dit verschil: 1) Het vasthouden van zaden om te wachten op hogere windsnelheden voor lange-afstandsverspreiding brengt risico's met zich mee. Mogelijke risico's zijn bijvoorbeeld zaadpredatie of schade door extreme weersomstandigheden. Deze risico's zijn wellicht een beperkende factor bij het evolueren van een drempelwaarde voor het loslaten van zaden. Modelsimulaties bevestigen dat het risico op verstoringen een sterk effect kan hebben op lange-afstandsverspreiding en op de optimale drempelwaardes om lange-afstandsverspreiding te maximaliseren. 2) Verspreidingscurves van zaden hebben niet als doel lange-afstandsverspreiding te maximaliseren, maar hebben een ander doel. Een mogelijk doel is het vergroten van de kans om in geschikte habitat te landen, zoals voorgesteld in hoofdstuk 2. Hierbij wordt niet uitsluitend de kans op lange-afstandsverspreiding gemaximaliseerd, maar de verspreidingscurve in zijn geheel geoptimaliseerd ten opzichte van de beschikbaarheid van leefgebieden. Hoofdstuk 3 laat zien welke kosten en baten er te verwachten zijn voor planten bij het evolueren van strategieën in samenhang met windsnelheid. Door deze kosten en baten mee te nemen in toekomstige modellen kunnen schattingen van zaadverspreiding beter opgenomen worden in voorspellingen van kolonisatie in versnipperde landschappen, invasieve soorten en het verschuiven van biomen als gevolg van klimaatverandering.

Dikwijls eten vogels zaden die het spijsverteringsstelsel kunnen overleven. Door zaden op de ene plek op te eten en op een andere plek weer uit te poepen zijn vogels een belangrijk transportmiddel voor de verspreiding van plantenzaden. Modelsimulaties tonen aan dat dagelijkse vliegbewegingen van wilde eenden zorgen voor veelvuldig transport van plantenzaden tussen versnipperde aquatische ecosystemen (**hoofdstuk 4**). Hiervoor is een model ontwikkeld voor de vertering van zaden door eenden en een koppeling gemaakt met gemeten GPS gegevens van foerageergedrag van wilde eenden. Dit model is gebruikt om de ruimtelijke patronen van zaadverspreiding te quantificeren in landschappen die verschillen in de mate van versnippering van natte natuurgebieden. De mate van versnippering van natte natuur in een landschap heeft een grote invloed op de afstanden die eenden vliegen om te foerageren en daarmee een grote invloed op verspreidingsafstanden van meeliftende zaden. Zaadgrootte heeft invloed op de tijd die zaden erover doen om de weg door het spijsverteringssstelsel van een wilde eend af te leggen en op de overlevingskansen van de zaden. Grote zaden doen langer over de weg door het spijsverteringsstelsel, waardoor deze zaden een grotere kans hebben op lange-afstandsverspreiding, maar ook een lagere kans op overleven. De eigenschap zaadgrootte beïnvloedt daarmee de verspreidingspatronen van zaden ('Hoe bewegen?'). De veelvuldige lange-afstandsverspreiding van zaden door wilde eenden tijdens foerageervluchten, maakt dat wilde eenden, en mogelijk veel andere zaadetende vogels, belangrijke verspreiders van plantzaden zijn. Wilde eenden zorgen ervoor dat aquatische ecosystemen in versnipperde landschappen met elkaar in contact blijven en spelen daarmee een belangrijke rol in het bepalen van de plantendiversiteit.

Vogels maken zelf ook gebruik van externe energiebronnen om zich efficiënt te verplaatsen, bijvoorbeeld door te cirkelen in een thermiekbel om hoogte te winnen. De relatie tussen vlieggedrag van vogels en de atmosfeer wordt in **hoofdstuk 5** gebruikt in de omgekeerde richting: niet om vogelgedragingen te begrijpen in relatie tot externe factoren, maar om externe factoren te meten met gegevens van vogelvluchten. Dit is mogelijk omdat er uit onderzoek al veel bekend is over hoe vogels thermiek gebruiken om te vliegen ('Hoe bewegen?'). Vale gieren klappen zelden met hun vleugels, omdat dit hen veel energie kost. Tijdens het vliegen gebruiken ze thermiek om hoogte te winnen en zweven ze vervolgens om horizontale afstand af te leggen totdat ze een nieuwe thermiekbel tegenkomen. Hierdoor worden de vliegpatronen van vale gieren in grote mate bepaald door luchtstromen. In hoofdstuk 5 wordt theorie over aerodynamica van vale gieren gebruikt om de opwaartse snelheid van lucht in thermiekbellen te schatten met behulp van GPS gegevens van vluchten van vale gieren. Het meteorologische model OLAM wordt gebruikt om deze schattingen te evalueren. Daarnaast worden schattingen gemaakt van windsnelheid en windrichting op basis van de horizontale verplaatsing van de gieren tijdens het cirkelen in een thermiekbel. Deze schattingen worden vergeleken met windsnelheden en windrichtingen gemeten door meetstations op de grond. Sterke correlaties tussen de geschatte waarden en de gemodelleerde- en gemeten waarden laten zien dat het mogelijk is om hoge resolutie informatie te verzamelen over wind en thermiek met behulp van GPS data van vogelvluchten. Deze informatie kan dienen als uitbreiding op de gebruikelijke methoden om luchtstromen in kaart te brengen, met name in regio’s waar metingen schaars zijn.

Mechanistische modellen hebben een belangrijke rol gespeeld in het onderzoek dat beschreven wordt in dit proefscrift. Modellen zijn gebruikt om quantitatieve verbindingen te leggen tussen verschillende interne en externe factoren die bewegingen van organismen bepalen. Hierbij hebben modellen verschillende ruimte- en/of tijdschalen verbonden. Omdat ecosystemen gekenmerkt worden door een complexe samenhang van factoren die op uiteenlopende ruimte- en tijdschalen relevant zijn, is het soms onmogelijk om deze samenhang te begrijpen zonder modellen. Verder zijn met behulp van modellen gevoeligheidsexperimenten uitgevoerd om belangrijke onderliggende mechanismen te identificeren. Dankzij het gebruik van mechanistische modellen was het mogelijk om ons begrip van de passieve bewegingen van planten en dieren door de lucht in belangrijke mate te vergroten.

Bewegingen van planten en dieren zijn van cruciaal belang voor de toekomstige biodiversiteit in deze wereld, die in een snel tempo verandert door klimaatverandering en versnippering van natuurgebieden. Om verwachtingen over bewegingen van planten en dieren op te kunnen stellen, moeten de interne en externe factoren die verantwoordelijk zijn voor bewegingen in samenhang begrepen worden. De kennis uit dit proefschrift draagt hier aan bij. In de komende jaren zal de snelle ontwikkeling van verbeterde meetmethoden van dierbewegingen helpen om bewegingen en hun onderliggende interne en externe factoren beter te begrijpen. Daarop gebaseerde mechanistische modellen kunnen worden gebruikt om deze bij elkaar te brengen en te komen tot gedetailleerde verwachtingen over toekomstige bewegingspatronen en de consequenties voor biodiversiteit.

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Curriculum Vitae

I was born in Heemstede, the Netherlands, on 14 November 1985 and received my secondary education at the Stedelijk Gymnasium Haarlem. After a ‘gap year’ in Australia, I started studying Earth Sciences at the University of Amsterdam in 2006 and completed a half-year minor in Geology at Mount Royal College in Calgary, Canada. Afterwards I obtained my master’s degree in Earth Sciences at the University of Amsterdam, during which I followed courses in atmospheric science at the Institute for Marine and Atmospheric Research in Utrecht. During my studies I became fascinated by concept driven and data driven models as tools for understanding geo-ecological systems and forecasting. I carried out research projects on the modelling of land-atmosphere interactions and relating these models to soaring bird flight data collected by miniature GPS loggers (supervised by Prof. dr. ir. Willem Bouten). I carried out part of my master thesis research in the lab of Dr. Gil Bohrer at the Ohio State University. After completing my masters in 2013 I started a PhD under supervision of Dr. Merel Soons in her VIDI project: “Flying, floating or hitching a ride: the dispersal of plants in heterogeneous landscapes”. The results of this work are published in this book. Besides my education and research activities I worked as a teaching assistant in several modelling, statistics and field courses at the University of Amsterdam and Utrecht University. I also was a member of the PhD council of the graduate school PE&RC and was involved in organizing the annual PE&RC symposium. I submitted the manuscript of this PhD thesis in December 2017.