DISPERSAL SPECIAL FEATURE

Modelling long-distance seed dispersal in heterogeneous landscapes

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Summary

1. Long-distance seed dispersal is difficult to measure, yet key to understanding plant population dynamics and community composition.

2. We used a spatially explicit model to predict the distribution of seeds dispersed long distances by birds into habitat patches of different shapes. All patches were the same type of habitat and size, but varied in shape. They occurred in eight experimental landscapes, each with five patches of four different shapes, 150 m apart in a matrix of mature forest. The model was parameterized with small-scale movement data collected from field observations of birds. In a previous study we validated the model by testing its predictions against observed patterns of seed dispersal in real landscapes with the same types and spatial configuration of patches as in the model.

3. Here we apply the model more broadly, examining how patch shape influences the probability of seed deposition by birds into patches, how dispersal kernels (distributions of dispersal distances) vary with patch shape and starting location, and how movement of seeds between patches is affected by patch shape.

4. The model predicts that patches with corridors or other narrow extensions receive higher numbers of seeds than patches without corridors or extensions. This pattern is explained by edge-following behaviour of birds. Dispersal distances are generally shorter in heterogeneous landscapes (containing patchy habitat) than in homogeneous landscapes, suggesting that patches divert the movement of seed dispersers, 'holding' them long enough to increase the probability of seed defecation in the patches. Dispersal kernels for seeds in homogeneous landscapes were smooth, whereas those in heterogenous landscapes were irregular. In both cases, long-distance (> 150 m) dispersal was surprisingly common, usually comprising approximately 50% of all dispersal events.

5. *Synthesis*. Landscape heterogeneity has a large influence on patterns of long-distance seed dispersal. Our results suggest that long-distance dispersal events can be predicted using spatially explicit modelling to scale-up local movements, placing them in a landscape context. Similar techniques are commonly used by landscape ecologists to model other types of movement; they offer much promise to the study of seed dispersal.

Key-words: dispersal kernels, edge, habitat corridor, landscape ecology, long-distance seed dispersal, patch shape, seed dispersal, seed rain, spatially explicit model

Introduction

Seed dispersal sets the template on which recruitment occurs, thereby influencing the spatial structure of plant populations (Jordano & Herrera 1995; Schupp & Fuentes 1995; Wang & Smith 2002). Seed dispersal can also determine which species are able to establish and coexist (Hurtt & Pacala 1995; Harms

et al. 2000; Nathan & Muller-Landau 2000; Levin *et al*. 2003). Although seed dispersal takes place across a wide range of scales, long-distance seed dispersal is increasingly recognized as both important and overlooked (Nathan 2006). Part of the reason long-distance seed dispersal has been neglected is that it is fundamentally a landscape-level process and the field of landscape ecology has traditionally focused on animal, not plant, movement. This emphasis is understandable – animals move, whereas adult plants are generally rooted in

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place. Plants do move, however, when they disperse as pollen and seeds (Silvertown 2004). Because many plant species rely on animals for seed dispersal, landscape ecology's emphasis on animal movement has much to offer plant ecologists interested in long-distance seed dispersal.

Ecologists typically measure long-distance dispersal in two ways: by marking and recapturing individuals at mapped locations and by using genetic markers that link dispersed individuals to the location of a parent (Nathan *et al.* 2003; Bullock *et al.* 2006; Jordano *et al.* 2007). A disadvantage of these techniques is that their results are difficult to generalize to different landscapes and across spatial scales. Modelling the movements of seed-dispersing animals provides an alternative approach (Murray 1988; Holbrook & Smith 2000; Westcott & Graham 2000). Although models require more assumptions than empirical measures of dispersal, they can more easily be applied to larger scales and to different landscape configurations (Turchin 1998). An approach that combines empirical measures of dispersal with modelling can provide the advantages of both techniques while overcoming some of the disadvantages (Nathan *et al.* 2002; Levey *et al.* 2005; Russo *et al.* 2006). Still, a common constraint often remains for plant ecologists: landscapes are either too small to have direct application to the scale at which seed dispersal occurs (Gonzalez *et al.* 1998; Holyoak 2000; Hoyle 2007) or too large to be well replicated or to allow experimental manipulation (Debinski & Holt 2000).

We present a model of seed dispersal by frugivorous birds moving through patchy landscapes. The model is parameterized through field observations of small-scale (*c.* 20 m) movements, which are scaled up by an order of magnitude to predict patterns of long-distance dispersal into discrete habitat patches that vary in connectivity and shape. Our study system is unique because the model is derived and tested on real landscapes that were created *de novo*, allowing us to randomly assign patch types and to replicate the landscapes. We describe the model and experimental landscapes and then explore how the presence, shape, and connectivity of patches influence spatial patterns of seed dispersal. More specific objectives are described in the following section, after our experimental landscapes, model, and previous results are more fully described.

Methods

TERMINOLOGY, STUDY SYSTEM, MODEL, AND PREVIOUS RESULTS

We define 'long-distance' dispersal as displacement of a seed by at least 150 m. This threshold is similar in magnitude to arbitrary thresholds of long-distance dispersal used by others (Cain *et al.* 2000; Russo *et al.* 2006), but is objectively linked to the spatial scale of our study system. In particular, 150 m is the minimum distance seeds must travel to be dispersed into a patch of habitat other than the one in which they originated; it represents non-local dispersal.

We conduct landscape-level analyses, meaning that we take into account not only the conditions at particular locations (e.g. habitat type and plant cover) but also the landscape context of those locations (e.g. connectivity and distance to edge). By 'edge' we mean the boundary between the habitat of our patches and the habitat of the surrounding matrix.

Our study system consists of eight experimental landscapes, each consisting of five patches (Fig. 1a). All landscapes contain a central patch (100 × 100 m) and four peripheral patches. The peripheral patches are located 150 m from each of the four sides of the central patch. There are three types of peripheral patches: connected, winged, and rectangular. Connected patches have a 150 × 25 m-wide corridor of the same habitat type that joins them to the central patch. Winged patches have two blind-end corridors (75 × 25 m) projecting from opposite sides of the patch in a direction parallel to the nearest edge of the central patch. Rectangular patches have an area the size of the corridor added to the side of the patch furthest from the central patch, creating a rectangle (137.5 × 100 m). Because patch types were randomly assigned and all have the same total area (1.375 ha), any differences among them in seed dispersal can be solely attributed to differences in patch shape and connectivity. All experimental landscapes contain all four patch types. In four of the landscapes the fifth patch is a second winged patch and in the remaining four landscapes the fifth patch is a second rectangular patch. Randomization of patch types within a given experimental landscape resulted in three configurations of patch types: two winged patches on opposite sides of the central patch (*n* = 2), two winged patches adjacent to each other (*n* = 2), and two rectangular patches on opposite sides of the central patch (*n* = 4; see Fig. 1).

Our study site is the Savannah River Site (33.20′°N, 81.40′°W), a National Environmental Research Park near Aiken, South Carolina. Habitat patches were created in the winter of 1999–2000 by harvesting trees in a mature forest dominated by loblolly (*Pinus taeda*) and slash pine (*P. elliotii*), with some oaks (*Quercus* spp.). Timber and other debris were removed and the sites burned several months later. After burning, we erected a grid of 3 m-tall polyvinyl chloride poles, 25 m apart and at least 12.5 m from the nearest edge. From the top of all poles, we suspended seed traps made from 25 cm-diameter flowerpots.

Our study species was the eastern bluebird, *Sialia sialis* (Turdidae). It is highly frugivorous and prefers the open habitat of our patches over the forested matrix between the patches, although it readily enters the forest and tends to move along the forested side of edges. It also prefers to sit on high and exposed perches, such as our pole tops. Of 90 independent observations of fruit-eating birds perched on pole tops, the vast majority (80%) were of bluebirds. Thus, we are confident that patterns of seed rain described from the seed trap data resulted mostly from the movement of bluebirds across our experimental landscapes.

Details of our model are provided in Levey *et al.* (2005) and in the Appendix. We summarize the model's general structure and our previous results because they form the basis of the current study. In brief, we used empirical measures of perching time, move length, and move direction to simulate movements of a bluebird from the centre of the central patch, where it had consumed fruit. We first described the distributions of perch time, move length, and move direction as functions of the habitat the bird was occupying (patch or matrix), its distance to edge, whether it was near a single edge or two edges (e.g. if it were near a patch corner), and for move direction, the direction of the nearest edge and the bird's previous move. Perch time was best described by an exponential distribution and move lengths by a lognormal distribution. Perch time was dependent on habitat (patch vs. matrix) and distance from edge. Move length was dependent on habitat. Movement direction was described by a mixture of von Mises distributions, one focused in the previous movement direction (this component alone would lead to a correlated

(a) aerial view of one landscape

(b) dispersal isoclines of 3 landscapes
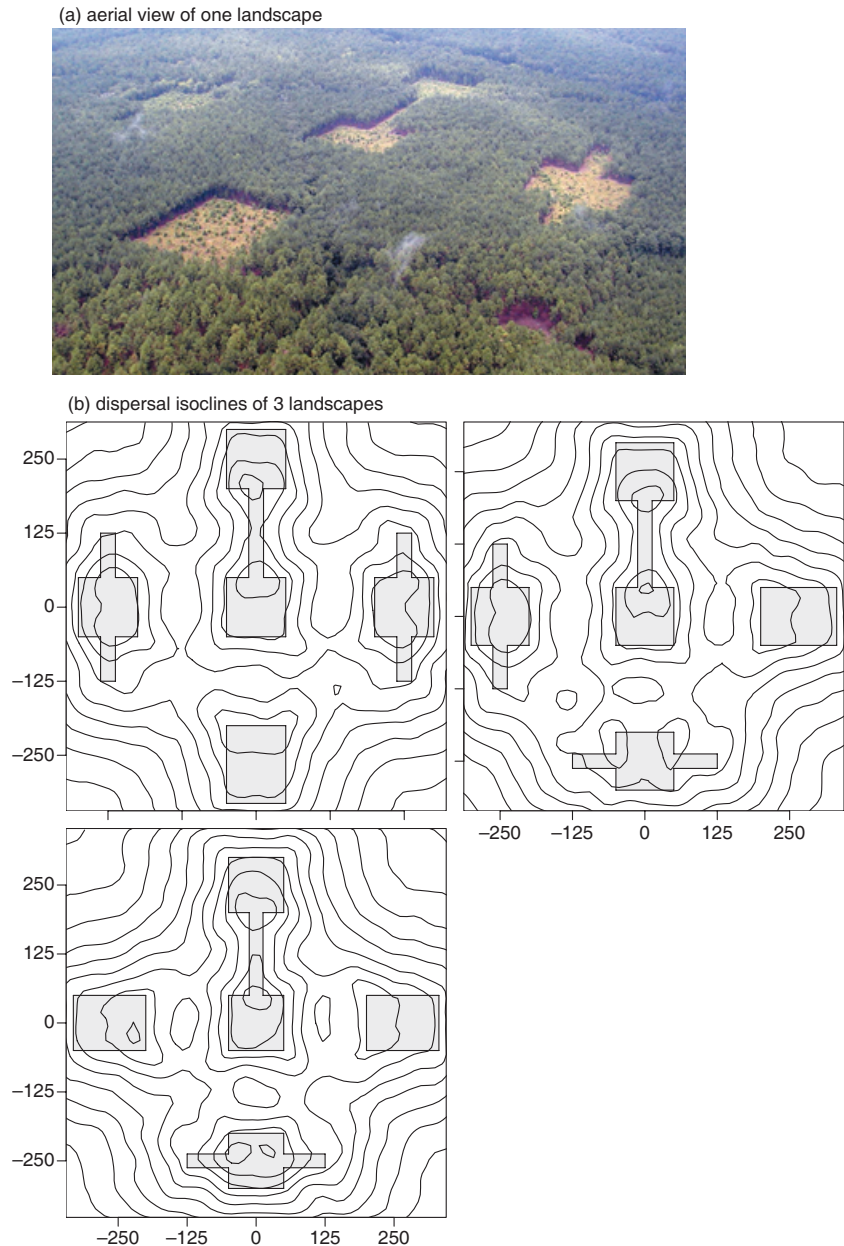
Fig. 1. (a) Aerial photograph of one of eight experimental landscapes; this one has two winged patches on opposite sides of the central patch, a connected patch at the top of the landscape and a rectangular patch at the bottom. It matches the schematic in the upper left of panel b. There were two other arrangements of patches, as illustrated in panel b. (b) Isoclines of occupancy density, 45 min after starting from random locations within each of the three types of landscapes. Contours represent predicted seed rain densities, with the highest densities in and around patches. Each landscape had 750 000 simulated dispersal events, of which approximately 500 000 end points were within the illustrated region. Numbers show distance in metres.

random walk) and one focused in a direction parallel to the nearest patch edge. We simulated movements by randomly picking a perch time based on the observed distribution of perch times in the occupied habitat and distance from edge, then randomly picking a move direction based on habitat, orientation and distance from edge, and direction of previous move, and then randomly picking a move length based on habitat. The bird then moved from one point to the next. In our original model, this process was repeated for 45 min of simulated movements to match the approximate average gut passage time for seeds in bluebirds. The landscapes are unbounded and not modelled as a torus; birds are neither reflected off nor absorbed by artificial borders when they move away from the patches. The model was programmed in R, versions 2.5.0–2.6.1 (R Development Core Team 2007).

To test the model's results in the field, we placed branches of fruiting wax myrtle (*Myrica cerifera*) in the centre of the central patches and sprayed the fruits with a dilute solution of fluorescent powder (Levey & Sargent 2000). Bluebirds readily consumed these fruits and defecated the seeds into our pole-top seed traps. Observed seed rain agreed closely with the model's predicted distribution of seeds among connected, winged, and rectangular patches (Levey *et al.* 2005). For both observed and predicted results, seed inputs from the central patch into winged and rectangular patches were nearly identical. Also, connected patches received 31–37% more *M. cerifera* seeds from the central patch than did winged and rectangular patches. The model revealed that the effect of corridors on seed dispersal was driven by edge-following behaviour – bluebirds frequently followed the corridor edges, preferentially staying in matrix habitat as they moved between habitat patches. Upon arriving at a patch edge, they often entered the patch to forage.

The objective of this article is to apply the model more broadly, using it to predict how landscape heterogeneity (i.e. the occurrence of patches in matrix habitat) and patch shape affect the distribution of dispersal distances ('dispersal kernels'). Our previous study focused on corridor use, examining bird movement that always

started in the centre of the central patch and ended in the peripheral patches. Here we treat the same study system as a set of five habitat patches in an unbounded landscape, with birds and seeds originating within all patches or from random locations, not solely from the central patch.

We use the model to address five questions. (i) Given that bluebirds preferentially follow edges and that winged patches have proportionally more edge than rectangular patches, why was there no difference in the observed number of seeds deposited in winged and rectangular patches when birds started in the centre of the central patch? This question surfaced as paradox in our previous study (Levey *et al.* 2005). Intuitively, winged patches should act as 'drift fences' to edge-following birds – the wings should intercept individuals dispersing through the matrix and redirect them towards the patch (Anderson & Danielson 1997; Haddad & Baum 1999). We use the model to explain why this phenomenon was not apparent in observed patterns of seed rain. (ii) How do connected, rectangular, and winged patches differ in their ability to attract dispersers and 'catch' seeds that originate anywhere in the landscapes? This question focuses on the model's ability to discern spatial differences in seed rain across heterogeneous landscapes; unlike the next two questions, it does not explicitly consider dispersal distances. (iii) How does landscape heterogeneity affect dispersal kernels? This question is motivated by the difficulty of empirically measuring long-distance dispersal events. The model, which accurately predicts long-distance dispersal in our landscapes (Levey *et al.* 2005), can provide dispersal kernels. By comparing dispersal distances in our experimental landscapes to those in homogeneous landscapes, we show that habitat patches influence the pattern of long-distance dispersal of seeds, thereby setting the stage for the following two questions. (iv) How do dispersal kernels differ for seeds that originate in patches of different shape and how do they differ for seeds that originate in one patch and are deposited in another patch? We are most interested in the dispersal of seeds between patches because such events represent long-distance dispersal into favourable habitats. (v) Where are seeds that originate in different types of patches most likely to be dispersed? This question takes us from the perspective of dispersal kernels, which are one-dimensional representations of dispersal (i.e. single probability distributions), to two-dimensional landscapes, allowing us to visualize exactly where seeds go.

MODEL MODIFICATION AND APPLICATION

To explore why edge-following behaviour does not result in greater seed dispersal into winged than rectangular patches (question i), we parameterized and ran the model as previously (Levey *et al.* 2005). All birds started in the centre of the central patch. We focused on two metrics of bird behaviour: how often birds dispersing from the central patch visit each peripheral patch type and once in a patch, how long they spend there. A visit is defined as entry into a patch from the matrix or from the end of the corridor. Our rationale is that seed rain is determined by the total time a bird with seeds in its gut spends in a patch. Because the total time in a patch is a product of number of visits and average visit time, a higher rate of visitation by birds following edges into patches may be countered by a shorter duration of visit, as birds follow edges out of patches. The net result might be no difference in total time spent (and number of seeds dispersed) in winged and rectangular patches.

To assess how patch shape may affect spatial patterns of seed rain (question ii), we again ran the model as previously, except that simulated birds were started in random locations throughout the landscapes. Although fruiting plants do not occur in random locations

and hence seed dispersal does not originate from random locations, for this exercise we were more interested in where seeds go than where they originate. Randomization of starting points allowed us to eliminate any effects of starting location on ending location. We completed 750 000 simulated dispersal events for each of the three types of landscapes at the study site.

To determine how the presence and shape of patches affect dispersal kernels (questions iii and iv), we modified our simulations in two ways. First, we started birds in the centres of all patch types. We did so to better reflect true dispersal events; seeds are most likely to originate from within patches because fruiting plants are relatively rare in the matrix. For this exercise we were more interested in dispersal distances (displacement) than actual coordinates of dispersed seeds. Second, we used a shifted gamma distribution based on gut retention times in a related species, American robins (*Turdus migratorius*; Turdidae; Levey & Karasov 1992), to determine when each simulated bluebird defecated the seed it consumed at time = 0 (see Appendix S1 in Supplementary material). This modification yielded a gut passage time distribution ranging from 16 to 145 min with a mean of 45 min and a median of 41 min. To the extent that robins and bluebirds are similar in their movement patterns and digestive physiology, it provides a more realistic estimate of dispersal kernels than the fixed time of defecation (45 min) we had used previously. For each of the three landscape types, we ran approximately 122 000 simulated dispersal events (*c.* 24 500 starts in each patch), recorded starting and ending points, and calculated dispersal distances. We compared dispersal kernels of seeds dispersed within our landscapes to an identical landscape without patches (i.e. all matrix habitat; question iii). We plotted dispersal kernels for seeds originating in the three patch types and for seeds that landed in each patch type but that had originated in another patch (question iv).

To visualize the spatial distribution of seeds dispersed from patches of different shapes (question v), we used the same runs that provided the dispersal kernels (questions iii and iv) and constructed probability density isoclines around one patch of each type (rectangular, winged, and connected).

Results

QUESTION (I): SEED RAIN AND THE DRIFT FENCE EFFECT

When birds start in the central patch, the model predicts they will visit connected patches approximately 17% more than winged patches and visit winged patches approximately 15% more than rectangular patches (Fig. 2a). The higher number of visits to winged than rectangular patches demonstrates that the 'blind' corridors on winged patches indeed function as drift fences. However, the more frequent visitation to winged than rectangular patches is offset by longer visits to rectangular patches; birds stayed in rectangular patches approximately 10% longer than in winged patches (Fig. 2b). The net result is that total time spent in winged and rectangular patches is nearly equal (Fig. 2c). Thus, although the edge configuration of winged patches causes edge-following bluebirds to move into winged patches more frequently, it also leads the same birds out of the patches more quickly, thereby explaining why observed seed rain in winged patches and rectangular patches is similar, despite the drift fence effect in winged patches.
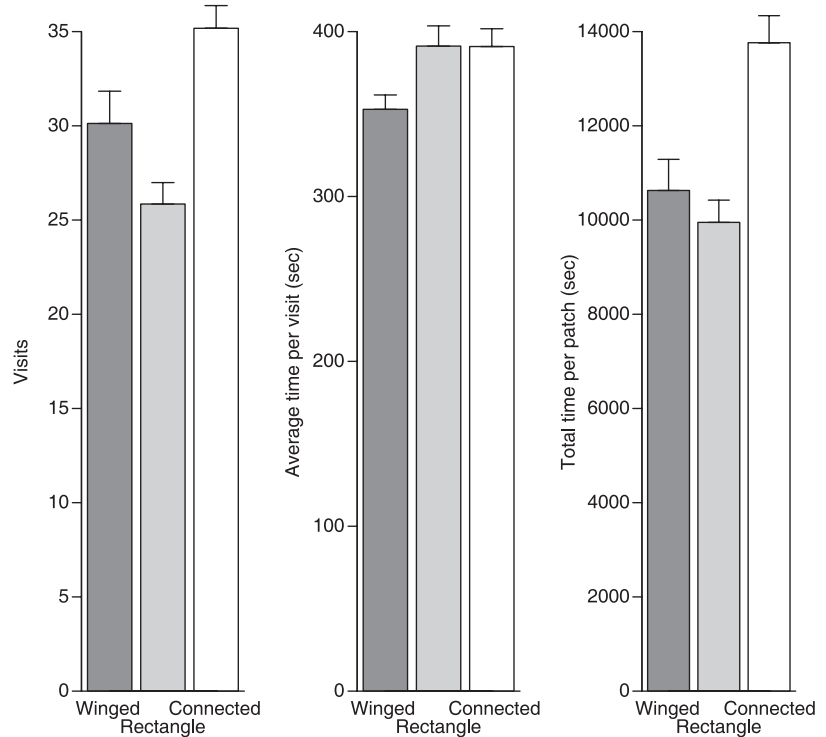
Fig. 2. Average numbers of visits, time spent per visit, and total occupancy time (number of visits × time/visit) of simulated bluebirds. All movements started in the centre of the central patch and were recorded from 15 to 90 min after the start.

QUESTION (II): ISOCLINES OF SEED RAIN IN AND AROUND PATCHES

Probability density isoclines generated from birds starting at random locations reveal the highest probabilities for seed deposition occur in winged, central and connected patches (Fig. 1b). More specifically, six of six central and connected patches contain the highest densities of seed rain in their respective landscapes, whereas four of four rectangular patches have seed densities as low as ($n = 1$) or lower than ($n = 3$) other patch types in their landscapes. Also, birds are more likely to end in or near patches of any type than elsewhere in the landscapes. These results illustrate that bluebirds are attracted to edges and the open habitat of patches (Fig. 1b). Less obvious, landscape context definitely matters: while all patches are symmetric north-to-south and east-to-west, the sides of patches near the centre of each landscape consistently have higher occupancy, despite the unbounded nature of the simulated landscapes and the birds' random starting locations. In short, seed rain is influenced both by patch characteristics (e.g. corridors and wings) and by landscape characteristics (e.g. location and type of nearby patches).

QUESTIONS (III) AND (IV): DISPERSAL KERNELS

Dispersal kernels generated by birds starting in all patches and travelling through our landscapes differ from those of birds starting in the same locations but travelling through a completely homogeneous landscape (i.e. all matrix habitat; Fig. 3). The most obvious difference is a longer and fatter tail
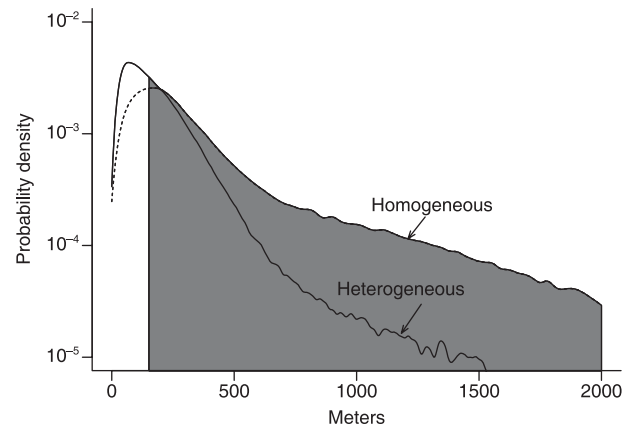
Fig. 3. Dispersal kernels for bluebirds starting in patch centres and dispersing seeds during simulated trips through two types of landscapes. Heterogeneous landscapes (122 000 total simulations) contain patches of second growth in a matrix of forest as in Fig. 1. Homogeneous landscapes (50 000 total simulations) contain only matrix habitat. The shaded areas represent long-distance dispersal events; note that they are common in both types of landscape.

in the distribution of distances in homogeneous landscapes; predicted dispersal distances in our five-patch experimental landscapes are generally shorter. This difference is almost certainly due to bluebirds being attracted to the edge habitat of patches and consequently not moving as far from their point of origin. The mode for the heterogeneous landscape (*c.* 70 m) was also shorter than that for the homogeneous landscape (*c.* 170 m). Accordingly, long-distance dispersal

(a) Dispersal kernels by starting location

(b) Dispersal kernels by ending location
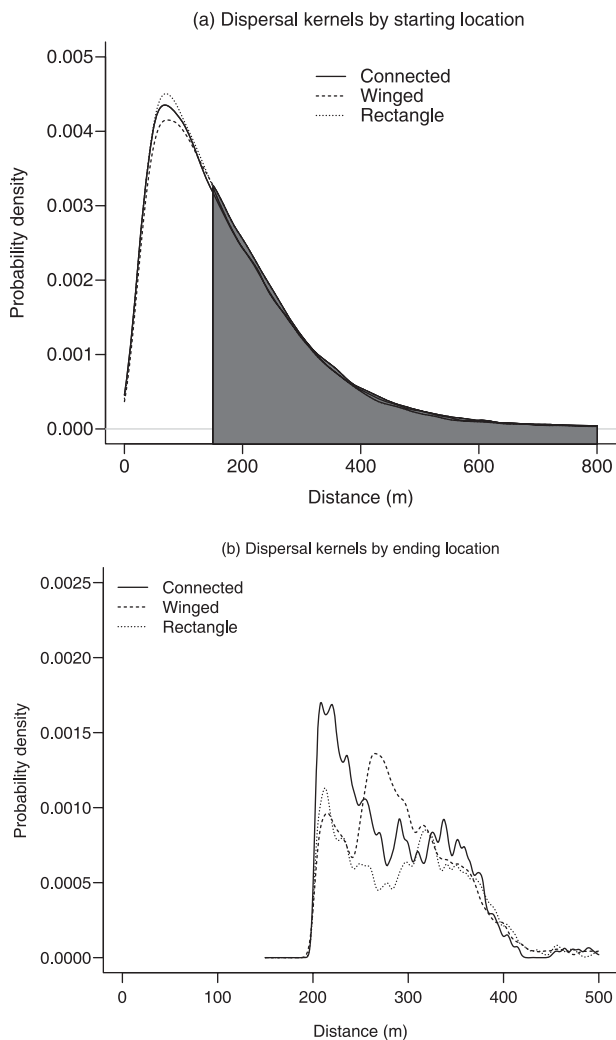
Fig. 4. (a) Dispersal kernels for bluebirds starting in connected, rectangular, and winged patches and dispersing seeds (122 000 total). Shaded areas represent long-distance dispersal events. (b) Dispersal kernels of seeds dispersed into patches of each type by bluebirds that started in different patches.

was more common in homogeneous than in heterogeneous landscapes (73.5% vs. 48.7% of dispersal events, respectively).

When birds started in the centre of connected, rectangular, and winged patches and ended anywhere, the resulting dispersal kernels were nearly identical, except for a relatively high peak for birds originating in rectangular patches and a relatively low peak for birds originating in winged patches (Fig. 4a). Importantly, long-distance dispersal was a uniformly common event. Seeds originating in connected patches were dispersed long distances ($\geq$ 150 m) in 47.9% of cases, whereas those originating in winged and rectangular patches were dispersed long distances in 49.8% and 47.1% of cases, respectively.

When birds started in the centre of a patch and ended in another patch (i.e. long-distance dispersal only), dispersal kernels differed by the type of patch receiving the seeds (Fig. 4b). In agreement with our previous study (Levey *et al.*

2005), the most frequent type of movement was along corridors between connected patches. The modal dispersal distance for connected patches was approximately 200 m, the distance between the centres of adjoining connected patches. Winged and rectangular patches often received seeds from immediately adjacent patches, illustrated by peaks for each of these patch types near 200 m. Winged patches, however, showed an even larger peak between 250 and 300 m, illustrating that they attract dispersers from further away than do rectangular patches.

QUESTION (V): DISPERSAL OF SEEDS FROM PATCHES OF DIFFERENT SHAPES

The shape of a patch clearly influences the density isocline of seeds originating from the patch's centre (Fig. 5). Isoclines bulge outwards around wings and corridors, confirming the pattern observed when seeds originate in random locations of the landscapes (Fig. 1). This effect is most obvious within approximately 50 m of the patch edge, reflecting bluebirds' attraction to the boundary between patch and matrix habitats. As the isoclines approach neighbouring patches, they often flatten (i.e. become more linear) along edges, especially edges associated with wings.

Discussion

The seed dispersal literature contains many descriptive studies of frugivore behaviour, empirical data on seed rain, and phenomenological models that together provide rich detail about the quality and quantity of animal-mediated seed dispersal (Schupp & Fuentes 1995; Herrera 2002; Levey *et al.* 2002; Jordano *et al.* 2007; Carlo & Morales 2008). Nonetheless, it remains extraordinarily difficult to predict the probability of a given seed landing in a given place, especially for long-distance dispersal events (Nathan 2006). The difficulty extends beyond constructing dispersal kernels – they are a starting point, describing seed dispersal that is both isotropic (independent of dispersal direction) and homogeneous (independent of starting point and dispersal path). The Holy Grail of seed dispersal is to accurately predict the probability distributions of seed density from a particular configuration of parents and then to relate those distributions to seedling demography (Schupp & Fuentes 1995; Wenny & Levey 1998; Jordano *et al.* 2007; Hampe *et al.* 2008).

Spatially explicit, mechanistic models provide a means of predicting the locations of dispersed seeds (Levin *et al.* 2003; Levey *et al.* 2005; Bullock *et al.* 2006; Russo *et al.* 2006). When seeds are dispersed abiotically, as by wind, parameterizing mechanistic seed dispersal models requires detailed knowledge of the seed, the plant, and the wind (Nathan *et al.* 2002). When seeds are dispersed biotically, the focus must shift to understanding the factors controlling animal behaviour (e.g. Carlo & Morales 2008). It is here that the field of landscape ecology has great potential for providing the needed tools.
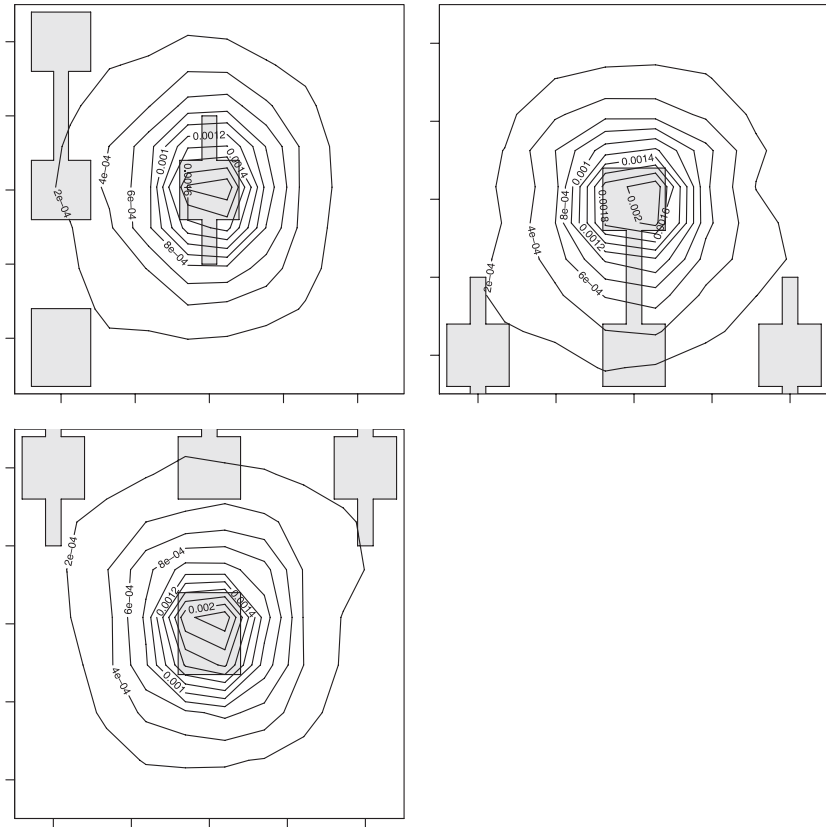
Fig. 5. Seed density isoclines of seeds dispersed from the centre of a winged patch (upper left), connected patch (upper right), and rectangular patch (lower right) during simulated dispersal by a bluebird (24 500 simulations each).

A particularly useful approach is to quantify how an animal's movement trajectory changes when it encounters different landscape elements, then to use such 'decision rules' to predict the animal's eventual occurrence elsewhere (Haddad 1999; Schultz & Crone 2001; Revilla *et al.* 2004; Haynes & Cronin 2006; Noonburg *et al.* 2007). The goal of these types of studies is to describe the processes that underlie patterns of animal distribution across the landscape in exactly the same way that seed dispersal biologists strive to understand the mechanisms by which seeds arrive in particular sites. The underlying principle is that where an animal moves and settles in a heterogeneous landscape is determined by how it perceives the landscape, not by physical features of the landscape *per se* (Lima & Zollner 1996; Chetkiewicz *et al.* 2006). The interaction of how an animal senses the landscape and how it reacts to particular features (e.g. edges) results in unequal occupancy of areas and, in the case of frugivores, clumped distributions of defecated seeds (Russo *et al.* 2006). Indeed, essentially all empirical studies that have documented spatial patterns of animal-dispersed seeds have found this expected pattern of 'contagious' dispersal (Fragoso 1997; Wenny & Levey 1998; Wenny 2001; Kwit *et al.* 2004; Russo *et al.* 2006; Jordano *et al.* 2007; Hampe *et al.* 2008). In contrast, spatially implicit models of seed dispersal (i.e. those that neglect the landscape context) often do not consider frugivore behaviour, are based on single probability distributions (e.g. lognormal), and predict smooth dispersal kernels. Thus, a take-home message of our study is that understanding

animal-mediated seed dispersal requires understanding how and why fruit-eating animals move as they do, not simply where they go (Carlo & Morales 2008).

Using spatially explicit models to predict seed dispersal has a major advantage over the use of similar models by landscape ecologists to predict animal movement. When a frugivore defecates a seed at a location away from the parent plant the seed has been dispersed, whereas when an animal moves between two areas, the animal may or may not have dispersed (Belisle 2005; Van Dyck & Baguette 2005; Conradt & Roper 2006; Schtickzelle *et al.* 2007). This distinction between dispersal and movement is important, since population consequences of permanent occupancy (i.e. dispersal) are much larger than those of temporary occupancy (i.e. movement). A related advantage of spatially explicit models in studies of seed dispersal is that the relevant scale of seed dispersal is clearly defined by the movement rates and gut retention times of frugivores, whereas the relevant scale for animal movement and dispersal is often unclear.

Although we measured movement for a single species of seed-dispersing bird, we are confident that our technique for estimating long-distance dispersal is more broadly applicable. Many species whose local movements have been previously studied respond strongly to landscape elements in much the same way as bluebirds. Parids, for example, follow forest edges (Desrochers & Fortin 2000) and many other bird species tend to follow corridors or avoid crossing open areas (Belisle *et al.* 2001; Belisle & Desrochers 2002; Harris & Reed

2002; Robichaud *et al.* 2002; Castellon & Sieving 2006). Our model is also relevant to many species of bird-dispersed plants that depend on long-distance dispersal into patches of open habitat for recruitment and long-term population viability (Cipollini *et al.* 1994).

LANDSCAPE PATTERNS OF SEED DISPERSAL

The model uncovered a mechanism by which edge-following behaviour does not necessarily lead to increased seed rain in patches with large amounts of edge. When birds started in the centre of the central patch, they visited winged patches more frequently than rectangular patches, as expected from edge-following behaviour, but also left winged patches more quickly than rectangular patches, thereby offsetting the high visitation frequency in winged patches and leading to equivalent amounts of seed rain in the two patch types. This balance between patch visitation frequency and duration shows that within-patch processes are important in determining between patch differences in a landscape (Orrock & Danielson 2005).

More generally, the model's results illustrate how landscape heterogeneity can change the shape of dispersal kernels. When landscapes are comprised of a single type of habitat, dispersal kernels are smooth, with long tails. When landscapes are comprised of different habitat types as in our study system, the behaviour of seed dispersers is modified upon encountering habitat boundaries and dispersal kernels become irregular and have shorter tails. This difference is likely to have been caused by dispersers being attracted to patches and spending more time in them than in matrix, thereby reducing the distance seeds are dispersed.

The model revealed a surprising result: approximately 50% of seed dispersal by bluebirds in our landscapes qualifies as long-distance dispersal. Although other studies have concluded that long-distance seed dispersal is not uncommon (Jones *et al.* 2005; Westcott *et al.* 2005; Hardesty *et al.* 2006; Russo *et al.* 2006), the general consensus remains that it is rare (Nathan 2006). Of course, much of this discrepancy in perception hinges on the definition of 'long-distance', which is notoriously arbitrary. In our study system, long-distance dispersal can be objectively defined because inter-patch movement is a discrete event that occurs at a standardized and biologically meaningful distance (i.e. well beyond the bounds of the parent population). The frequency of long-distance dispersal will remain uncertain and controversial until similarly objective and biologically based definitions of 'long-distance' are widely applied (Nathan 2005).

It remains unclear whether the dispersal kernels we have described are typical of other bird-dispersed seeds at other times of year. We note that bluebirds in the winter at our site are not territorial and probably move over longer distances in a typical 45 min period than when they are territorial.

Finally, the model shows how a particular component of landscape structure, patch shape, affects spatial patterns of seed dispersal. Because patch edges tend to 'hold' dispersers such as bluebirds, seed rain is generally concentrated along edges, and patches with more edge have high density isoclines that encompass larger areas than isoclines in patches with less edge. Likewise, corridors tend to direct seed rain from one patch to another via edge-following behaviour of bluebirds. These effects are most apparent for seeds being dispersed from the centre of a given patch type (Fig. 5). Other factors such as bird and plant density will also influence the spatial pattern of seed dispersal (Carlo & Morales 2008).

Taken together, these results demonstrate how bird behaviour and long-distance seed dispersal depend on landscape context. Edges, for example, do not exist in isolation; they are an inherent feature of patches and, especially, corridors. Likewise, patches do not exist in isolation; one patch can influence seed rain into an adjacent patch by diverting or intercepting dispersers that might otherwise arrive in the adjacent patch. An important lesson is that narrowly defined metrics of landscape structure and local measures of patch shape will not be sufficient to accurately predict long-distance seed dispersal. Disperser behaviours need to be integrated with landscape features at multiple scales – a challenge that is already being met by landscape ecologists studying the movements of other animals (Haddad 1999; Schultz & Crone 2001; Revilla *et al.* 2004; Urban 2005; Cushman *et al.* 2006; Haynes & Cronin 2006; Russo *et al.* 2006). Applying their techniques to the field of seed dispersal will help the field of landscape ecology broaden to include movement of plants and will help the field of seed dispersal uncover where seeds go when they leave the immediate vicinity of their parent.

Acknowledgements

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Supplementary material

The following supplemental material is available for this article:

Appendix S1. Tracking and modelling methods.

This material is available as part of the online article from:
http://www.blackwell-synergy.com/doi/full/10.1111/
j.1365-2745.2008.01401.x
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Appendix

Portions of this appendix are reproduced from Levey, D.J., Bolker, B.M., Tewksbury, J.J., Sargent, S., & Haddad, N.M. (2005) Effects of landscape corridors on seed dispersal by birds. *Science*, **309**, 146-148, *with permission of the American Academy for the Advancement of Science*.

Bluebird Tracking

Birds were relatively easy to track, given their tendency to sit on high perches in the habitat patches and along edges or in the subcanopy of the forest, where the open understory facilitated viewing. They were not obviously influenced by human presence; in the patches they were approachable to 15m and in the forest they would fly directly overhead. At each point where the bird changed direction of travel or perched, we placed a numbered flag and recorded the time. After the bird was lost from view, we mapped the location of flags in relation to a grid system of markers, pinpointing the location of each independently to avoid compounding error.

Model Construction

We divided data on movement into three independent metrics of consecutive moves: perching time between moves, move length, and move direction. Our goal was to describe these metrics as a simple function incorporating only a few variables: the habitat the bird was occupying (patch or matrix); its distance to the nearest edge; and (for move direction) the orientation of the nearest edge and the direction of the bird's previous move. Throughout, we used likelihood ratio tests for nested models and Akaike's Information Criterion (AIC) for non-nested models to choose the best fitting (and

appropriately parsimonious) model, including null models of random movement, $\kappa = 0$ (see *Move Dispersion,* below). All parameter estimation and simulation was done in the R language (http://www.R-project.org).

Perch time. Perch times were exponentially distributed ($P(t) = \lambda \exp(-\lambda t) dt$), where λ is the per-capita probability of leaving a perch per second. We used survival analysis (the `survival` package in R) to test for a dependence of λ on habitat (patch or matrix), distance from the nearest edge, and habitat by distance interaction. Both habitat and distance to the nearest edge influenced the time interval between moves. Because the two predictor variables were correlated (birds inside the patch tended to be closer to edges), the best single model included only one of them, distance from edge, with the average residence time decreasing linearly (albeit weakly) with $\log(\text{distance} + 0.1)$: $\lambda = 5.03 - 0.078 \log(d+0.1)$ (Table A1). The model assumes that flights between perches are instantaneous.

Move length. Lengths of moves between consecutive perches were well described by a log-normal distribution, with the standard deviation of log move length the same in both habitats (0.693) but mean move length slightly different (2.974 in forest, 2.780 in patch; all distance units in the model are in the 12.5 m grid units used to mark out the experimental landscapes). Distance from edge did not have a statistically significant effect on move length.

<u>Move direction</u>. Move direction used the most complicated models. We used

mixtures of von Mises distributions, a standard distribution from circular statistics

(Preisler and Akers 1995), to describe the probability distribution of move directions

for a bird located at a particular point. The basic von Mises distribution is controlled

by two parameters, μ (ranging from zero to 360°), which controls the modal or

primary move direction, and κ, which controls "dispersion" (increasing values of κ

increase probability of movement in the preferred direction).

Primary move direction

The primary move direction (μ) may depend on the direction of the nearest edge and/or

the direction of the bird's previous move. Specifically, we explored three models for

primary move direction: (1) in the same direction as the previous move [a correlated

random walk], (2) parallel to the nearest edge, in the direction consistent with the

previous move (i.e., in the same 180° arc), (3) in a direction representing a weighted

average between #1 and #2, with a parameter β determining the weighting ($\beta=0$

corresponds to model #1, $\beta=1$ represents model #2, and $0<\beta<1$ represents a mixture

(Preisler & Akers, 1995; Schultz & Crone, 2001). Because it was difficult to define edge

movement when a bird was equidistant from two differently oriented edges, we

considered edge-following behavior (models #2-3) only when birds were unambiguously

located near a single edge (52% of the time in patches and 61% of the time in matrix).

When two edges were equidistant, we fitted model #1, which allows only for correlation

with the previous move. In the matrix single-edge habitat, model #2 (β=1, edge-following) fit best; in the patch single-edge habitat, model #3 fit best with β=0.74.

Mixture probabilities

We allowed for mixtures of von Mises distributions, either a binary mixture with modal directions in opposite directions (180° apart) or a four-part mixture in left, backward, or right directions relative to the primary direction (0°, 90°, 180°, and 270° relative to the primary direction). In the binary case the probability of going forward, in the primary direction, was $p_{forward}$, with a probability (1-$p_{forward}$) of moving backward (180° from the primary direction); we evaluated separately the special cases $p_{forward}$=0.5 (random movement backward or forward along the primary direction vector) and $p_{forward}$=1 (pure forward movement). Pure forward movement fit best in the multiple-edge case (either patch or matrix habitat), and random forward-backward movement fit best in the patch single-edge case. In the four-part mixture (which was the best-fit model in the matrix single-edge case) the probabilities of going forward, left, backward, or right were estimated as (0.39, 0.03, 0.12, 0.08) and the probability of taking a random (undirected) move with κ=0 was 0.38.

Move dispersion

The von Mises dispersion parameter (κ) determines the strength of movement in the primary direction (κ=0 represents a random walk, with 12.5% of moves in the forward octant; $\kappa \rightarrow \infty$ leads to all moves in the primary direction, or 100% in the forward octant; and κ=1 gives 26% of moves in the forward octant). Our model uses two parameters to

determine κ: one to describe the baseline (intercept) value of κ when a bird is sitting right

on an edge and one to define the exponential distance-dependence of κ when birds are

farther away from the edge: κ=exp(log(κ) intercept + d·log(κ) slope). In general, log(κ)

slope is either zero (no distance-dependence) or negative (move direction becomes more

variable/less focused with distance). Movement was more focused along the primary

direction in the patch single-edge case (log(κ)= 0.47) than in matrix multiple-edge case

(log(κ)= -0.084). Movement in the patch multiple-edge case, which was the only

situation where edge-dependence was statistically significant, was strongly focused at an

edge but rapidly became more variable away from an edge (log(κ) intercept= 0.809,

log(κ) slope= -0.595). In the matrix single-edge case, dispersion parameters were fitted

separately for the four directions (log(κ): forward=0.975, left=5.98, backward=5.11,

right=5.14).

The movement model is illustrated in Fig. A1.

Gut retention time

To estimate a distribution of gut passage times, we used data from Levey and Karasov

(1992) on the passage times of liquid markers through the guts of American Robins

(*Turdus migratorius*). We suspect these data likely over estimate passage times of seeds.

We used the summary statistics of the distribution: mean (48 minutes), median (37

minutes), mode (33 minutes), and minimum passage time (i.e., time for the first 2.5% of

marker to be defecated: 20 minutes). We used a shifted gamma distribution, that is

$\text{Prob}(x<T) = 0$

$\text{Prob}(x>T) = \text{Gamma}(x-T,\text{shape},\text{scale})$

We estimated the parameters of the shifted gamma (shape, scale, T) by minimizing the squared deviation between the observed metrics (mean, median, mode, minimum) and the theoretical values for the shifted gamma distribution with the specified shape and scale parameters. The obtained metrics for the best distribution (T=15.9, shape=2.17, scale=13.5) matched the observed values closely:

	observed	theoretical
min	20	19.9
mode	33	31.7
mean	48	45.3
median	40.9	37

Available Code for Use by Others

Code (in R language) for the model is available for download and use at
http://www.zoo.ufl.edu/bolker/corridor/

Table A1. Parameters for movement model. Parameters described in text. CRW = correlated random walk.

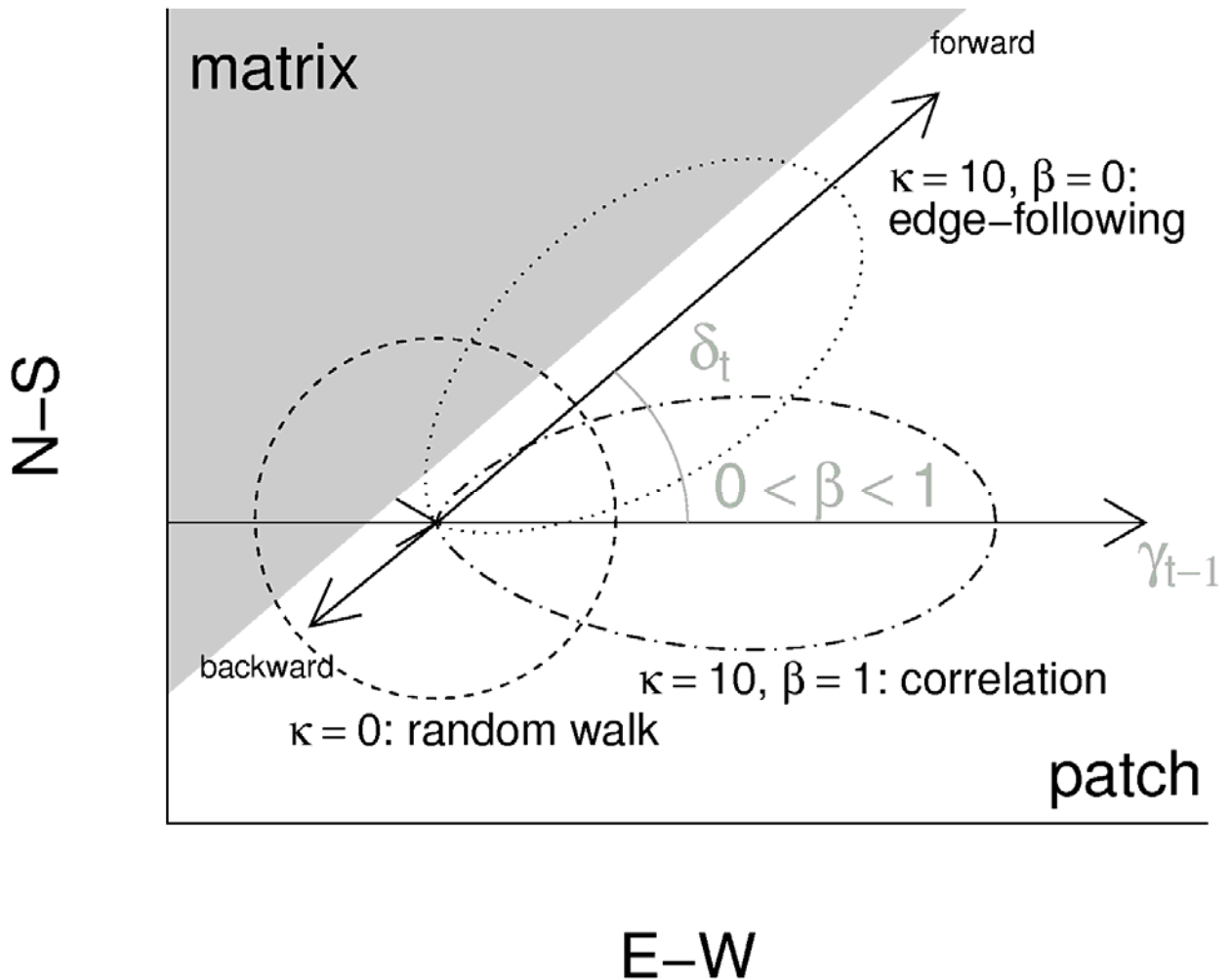| habitat	# of edges	perch time (s): exponential	move length (12.5 m): log-normal	move direction: von Mises mixture			
				dispersion parameter ($\log(\kappa)$)		weighting parameter (β)	forward/ backward probability ($p_{forward}$)
				intercept	slope $(12.5 \text{ m})^{-1}$		
matrix	single	$\log(\lambda) =$ 5.0327 − 0.0784(d+0.1)	μ (log) = 2.974, σ (log) = 0.693	$0°$=0.975, $90°$=5.98, $180°$=5.11, $270°$=5.14	0	1	$0°$=0.39, $90°$=0.03, $180°$=0.12, $270°$=0.08, random=0.38
	multiple			-0.084	0	0 (CRW)	1
patch/ corridor	single		μ (log) = 2.780, σ (log) = 0.693	0.447	0	0.744	0.5
	multiple			0.809	-0.595	0 (CRW)	1

Figure A1. Illustration of the movement model. Y-axis is north-south dimension (N-S); X-axis is east-west (E-W). Shaded area denotes matrix habitat (forest) and white area denotes patch habitat (second-growth). For a bird whose previous move was directly from left to right ($\gamma_{t-1}=0$) and that is located near an edge ($\delta_t = 45^{\circ}$), a correlated random walk ($\beta=0$) would tend to move it in the same direction while consistent edge-following ($\beta=1$) would have it move along the edge in the direction closest to its previous direction. The parameter $p_{forward}$ controls whether a bird is

likely to move opposite to the consistent direction, or to its previous direction of travel. Several extreme cases are illustrated: random walk (κ=0, arbitrary β and $p_{forward}$), strong consistent edge-following (κ=10, β=0, $p_{forward}$=1), and strong correlated random walk (κ=10, β=1, $p_{forward}$=1). If the bird had been traveling right-to-left, then the consistent edge direction ("forward") would be flipped 180°.

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