

# Connectivity from a different perspective: comparing seed dispersal kernels in connected vs. unfragmented landscapes

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**Abstract.** Habitat fragmentation can create significant impediments to dispersal. A technique to increase dispersal between otherwise isolated fragments is the use of corridors. Although previous studies have compared dispersal between connected fragments to dispersal between unconnected fragments, it remains unknown how dispersal between fragments connected by a corridor compares to dispersal in unfragmented landscapes. To assess the extent to which corridors can restore dispersal in fragmented landscapes to levels observed in unfragmented landscapes, we employed a stable-isotope marking technique to track seeds within four unfragmented landscapes and eight experimental landscapes with fragments connected by corridors. We studied two wind- and two bird-dispersed plant species, because previous community-based research showed that dispersal mode explains how connectivity effects vary among species. We constructed dispersal kernels for these species in unfragmented landscapes and connected fragments by marking seeds in the center of each landscape with <sup>15</sup>N and then recovering marked seeds in seed traps at distances up to 200 m. For the two wind-dispersed plants, seed dispersal kernels were similar in unfragmented landscapes and connected fragments. In contrast, dispersal kernels of bird-dispersed seeds were both affected by fragmentation and differed in the direction of the impact: *Morella cerifera* experienced more and *Rhus copallina* experienced less long-distance dispersal in unfragmented than in connected landscapes. These results show that corridors can facilitate dispersal probabilities comparable to those observed in unfragmented landscapes. Although dispersal mode may provide useful broad predictions, we acknowledge that similar species may respond uniquely due to factors such as seasonality and disperser behavior. Our results further indicate that prior work has likely underestimated dispersal distances of wind-dispersed plants and that factors altering long-distance dispersal may have a greater impact on the spread of species than previously thought.

**Key words:** Anemochory; connectivity; dispersal kernel; habitat fragmentation; isotope marker; landscape ecology; longleaf pine savanna; seed dispersal; zoochory.

## INTRODUCTION

Dispersal, especially over long distances, is a key process influencing ecological and evolutionary dynamics (Clobert et al. 2001), the size and persistence of populations (Pulliam 1988), species interactions (Herrmann et al. 2012), and the capacity for adaptive evolution (Lenormand et al. 2009). Rates of dispersal in contemporary landscapes are altered by habitat loss and fragmentation, which can

pose a threat to populations by disrupting movement pathways (Collinge 2009, Ibáñez et al. 2014).

Assuring connectivity through maintenance or construction of landscape corridors is the most frequently used management technique to counter negative impacts of habitat fragmentation (Hilty et al. 2006). Studies spanning arthropods, small mammals, birds, and a variety of plants have shown that landscape corridors can increase movement of organisms between connected fragments, relative to unconnected fragments (Gilbert-Norton et al. 2010, Damschen et al. 2014, Haddad et al. 2015). For other species, such as wind-dispersed plants, mechanistic dispersal models predict increased dispersal in connected fragments through increased airflow and updrafts (Damschen et al. 2014). However, because previous studies have not compared dispersal between connected and unfragmented landscapes (Beier and Gregory 2012),

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it has not been possible to evaluate the extent to which corridors can restore landscape-level connectivity.

In habitat fragments, varying connectivity can cause changes in communities through altered immigration processes (Damschen and Brudvig 2012), and there is a growing need for frameworks that allow corridor effectiveness to be predicted across species (Haddad et al. 2003, Hudgens and Haddad 2003). Life-history theory may present such a framework by providing insight into tradeoffs that constrain movement abilities (Stearns 1976). For plants, it is known that dispersal ability is related to traits such as seed mass and shape, terminal velocity, seed release height, and mode of dispersal (Tamme et al. 2014). Whereas dispersal mode has been shown to provide an important way to generalize connectivity effects (Damschen et al. 2008, Montoya et al. 2008), it is unknown if this trait can be used to predict the degree to which corridors restore connectivity across species.

Previous studies in large-scale experimental landscapes have shown how landscape corridors can increase rates of dispersal for two bird-dispersed species, *Morella cerifera* and *Rhus copallina* (Tewksbury et al. 2002, Haddad et al. 2003). Here, we use a newly developed stable isotope technique (Carlo et al. 2009, Forster and Herrmann 2014) to mark seeds of the same bird-dispersed plant species within the same large-scale experimental landscapes to determine if corridors restore connectivity to levels observed in unfragmented landscapes. We further marked two previously untested wind-dispersed plant species to explore whether the degree to which corridors restore connectivity varies by dispersal mode. The efficiency of corridors was evaluated by comparing seed dispersal kernels in landscapes where fragments are connected by corridors to kernels in unfragmented landscapes.

## METHODS

### Site description

The study took place within 12 landscapes at the Savannah River Site (Fig. 1A), an 800 km<sup>2</sup> National

Environmental Research Park in South Carolina, USA (33.20° N, 81.40° W). Six experimental landscapes were established in 1999–2000 and two in 2007 to investigate the effectiveness of corridors in promoting dispersal in fragmented landscapes (Tewksbury et al. 2002, Fig. 2B). These landscapes were created by clearing mature plantation pine forest and followed by a low intensity, prescribed fire. The resulting clearings are undergoing restoration to longleaf pine savannas through continued implementation of prescribed fires on a 2–3 yr rotation, planting of low densities of longleaf pine (*Pinus palustris*), and removal of deciduous trees. Within each experimental landscape, we worked in two 100 × 100 m fragments connected by a 150 m long × 25 m wide habitat corridor. Four unfragmented landscapes (26–50 ha) were created between 2005 and 2010 by clearing mature pine forests, burning the clearings, and planting either longleaf or longleaf and loblolly (*Pinus taeda*) seedlings (Fig. 2A). Although generally younger than our connected landscapes, these unfragmented landscapes contain many of the same plant species and are structurally similar to the connected landscapes. All landscapes were separated by at least 1.5 km to minimize the chance of seeds dispersing between them (Fig. 1A).

### Species

We investigated seed dispersal in connected and unfragmented landscapes for two wind- and two bird-dispersed plant species that are native and common in our study sites (Radford et al. 1968, Kilgo and Blake 2005). The wind-dispersed species, *Eupatorium compositifolium* and *Eupatorium glaucescens* (formerly *Eupatorium cuneifolium*; Asteraceae), are herbaceous perennials that grow to approximately 1 m in height (Radford et al. 1968, nomenclature follows Weakly 2012). Seeds mature and are dispersed from September to November for *E. compositifolium*, and from July to October for *E. glaucescens* (Radford et al. 1968). The bird-dispersed species, *Morella cerifera* (formerly *Myrica*

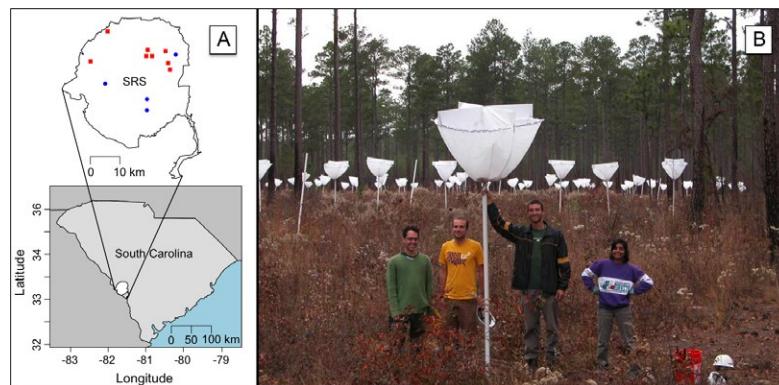


FIG. 1. (A) Unfragmented (circles) and connected landscapes (squares) at the Savannah River Site (SRS), South Carolina, USA. (B) Seed traps at different distances along the corridor and in the connected fragment. Photo credit: N. Haddad.

*cerifera*; Myricaceae) and *Rhus copallina* (Anacardiaceae), ripen fruits from August to October and from August to September, respectively (Radford et al. 1968). The fruits provide food mainly for wintering birds in the region, and are primarily dispersed by Eastern Bluebirds (*Sialia sialis*) and Eastern Phoebes (*Sayornis phoebe*) (McCarty et al. 2002, Levey et al. 2005). *Morella cerifera* is an evergreen shrub that typically grows to approximately 3 m tall at the study site. *Rhus copallina* is a deciduous shrub that rarely exceeds 2 m.

### Seed marking

We marked seeds of all species by spraying above-ground inflorescences of reproductive individuals with a solution of distilled water and  $^{15}\text{N}$  ammonium nitrate

(99.9 atom %; Icon Isotopes, Summit, New Jersey, USA). Bird-dispersed plants were sprayed with a solution of 0.125 g/L (Carlo et al. 2009); wind-dispersed plants were sprayed with a solution of 0.25 g/L. To lower surface tension and improve contact to plant tissue, one drop of Tween20 (Sigma-Aldrich, St. Louis, Missouri, USA) was added to each liter of solution. Plants were sprayed using a handheld pump sprayer equipped with a fine mist nozzle. Each plant was sprayed until all flower petals were moist. Flowers were sprayed in the mornings between 6:30 h and 10:00 h to minimize evaporation of the solution and ensure absorption before afternoon rains.

In connected landscapes, we sprayed all individuals in the center 80 m  $\times$  80 m of one of the two fragments (Fig. 2B). Near the center of unfragmented landscapes (Fig. 2B), we sprayed all individuals within a circle of

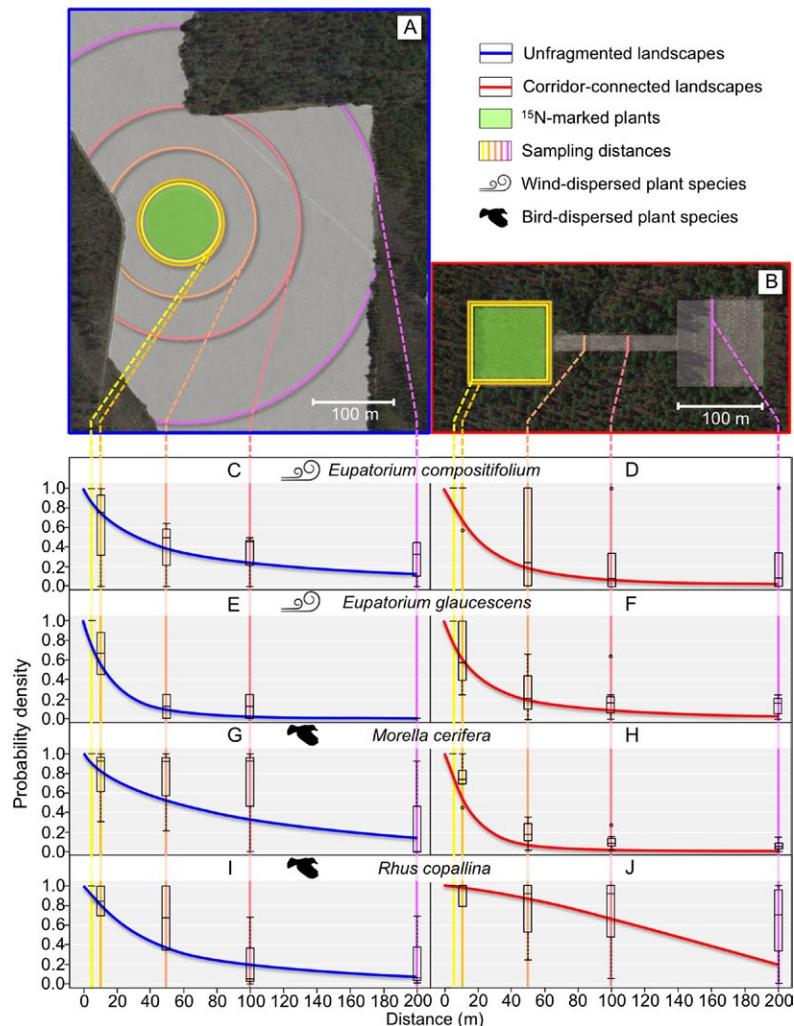


FIG. 2. (A) Unfragmented and (B) connected landscape with sampling distances (5 m, 10 m, 50 m, 100 m, 200 m) shown as differently colored lines. See Appendix S1:Table S1 for the number of seed traps at each distance. Fitted probability curves for unfragmented (C, E, G, I) and connected (D, F, H, J) landscapes of four different plant species, including box-plots of probability densities calculated for each sampling distance. C–F depict probability curves of two wind-dispersed species, and G–J depict probability curves of two bird-dispersed species.

equal area to the sprayed area in the connected fragments (45.14 m radius). *E. compositifolium* was sprayed eight times (September – November 2012), *E. glaucescens* was sprayed 14 times (August – September 2012), *M. cerifera* was sprayed six times (March – June 2012), and *R. copallina* was sprayed six times (September – October 2012). Species were sprayed different numbers of times because individuals varied in flowering phenology within populations of single species. Our goal was to ensure that all flowers on all individuals were sprayed at least three times.

Additional *M. cerifera* and *R. copallina* individuals were sprayed at remote locations (>1.8 km from the closest experimental landscape) to supplement naturally occurring populations in both types of landscapes. Branches of remote *M. cerifera* plants that bore isotope-marked fruits were cut in December 2012 and attached to PVC poles in the center of the sprayed areas. Each of the 12 landscapes was supplemented with ~36 000 *M. cerifera* fruits. Approximately 6,000 fruits were harvested from supplemental *R. copallina* plants in December 2012 and equally divided among one unfragmented landscape and three connected landscapes that had low numbers of naturally occurring *R. copallina* plants. At each of these four landscapes, the supplemental fruits were placed in feeders and attached to the same PVC poles as the branches with *M. cerifera* fruits.

#### Seed sampling

Dispersed seeds of all species were sampled with 1,788 seed traps, 125 in each connected landscape and 197 in each unfragmented landscape (Fig. 1B). Each seed trap consisted of two semi-circle fabric funnels with a total sampling area of 1 m<sup>2</sup>. The top opening was attached to a wire ring to keep the funnels open. Two plastic baffles were constructed in an “X” pattern across the opening and attached to the wire ring. The purpose of the baffles was to redirect wind into the funnel and to serve as perches for seed-dispersing birds. Each seed trap was mounted on top of a 3 m tall PVC pole, with the base of both funnels anchored to the pole to prevent wind from turning the funnels inside out.

In both landscape types, the PVC poles with seed traps were mounted on rebar at distances of 5 m, 10 m, 50 m, 100 m, and 200 m from the outside perimeter of the sprayed area (Fig. 2A,B). In connected landscapes, the seed traps at 5 m and 10 m distances were located in the sprayed fragments, and those at distances of 50 m and 100 m were located in the corridor. The farthest sampling distances in connected landscapes were represented by seed traps established along five parallel transects equally distributed at 160 m, 180 m, 200 m, 220 m, and 240 m in the connected fragments. We pooled samples from these five distances into a single distance category, 200 m, in our analyses, because the transect length available for traps at these distances was limited to 100 m (the width of a fragment) and the sampling effort within

a single 100 m transect proved to be insufficient for the low seed arrival probability at these distances. Seed traps were equidistant from each other within a distance category and deployment ended at forest edges. We increased the number of seed traps with increasing distance to maintain similar sampling effort at each distance (Nathan et al. 2003, Carlo et al. 2013; Appendix S1:Table S1). Seed traps were deployed from August 2012 until September 2012 and left in the field until March 2013. To minimize damage to seeds and accumulation of plant litter in traps, seed traps were emptied twice, in November 2012 and March 2013. A few (<1%) bird-dispersed seeds in traps showed minor signs of fungal infestation, but this did not influence our ability to identify them to species. Further, it cannot be ruled out that some wind-dispersed seeds lost their pappus in the traps and that those seeds and others may have been discarded with accumulated plant litter in the traps. This, however, should have equally affected both species of wind-dispersed seeds in our study. We found no evidence of granivorous animals such as birds and ants removing seeds from the traps.

#### Seed preparation and mass spectrometry analyses

Seeds collected from traps were sorted and identified to species. For each landscape, seeds of each species were combined by distance category. Only fully mature seeds were used in analyses.

Because it was impractical to test for presence of <sup>15</sup>N in thousands of individual seeds, we analyzed seeds in batches of up to 100 seeds of a single species collected from the same distance within a given landscape (Carlo et al. 2013). Seeds within a batch were thoroughly homogenized using a Wig-L-Bug grinder (Dentsply, Elgin, Illinois, USA) for wind-dispersed species and a Mixer Mill MM200 (Retsch, Haan, Germany) for bird-dispersed species. After grinding a batch, all equipment in contact with seed material was washed twice with distilled water and soap, rinsed a third time with distilled water, wiped, given a final rinse with acetone, and allowed to air dry.

We then weighed samples of each batch and wrapped them in tin cups (5 × 9 mm, CE Elantech, Lakewood, New Jersey, USA) for mass spectrometry. Whenever possible, sample masses of approximately 9 mg were used for each batch (Carlo et al. 2013). If the ground seed material was less than 9 mg, the maximum possible weight was used (0.4–9.0 mg). All samples were analyzed for <sup>15</sup>N atom % using an elemental analyzer (Costech ECS 4010 CHNSO Analyzer; Costech Analytical Technologies, Valencia, California, USA) connected to a Thermo Scientific ConFlo IV Universal interface (Thermo Fisher Scientific, Waltham, Massachusetts, USA), which served as an inlet to the continuous flow isotope ratio mass spectrometer (Thermo Delta V Advantage; Thermo Fisher). Analyses were performed at the Laboratory for Isotopes and Metals in the Environment at Pennsylvania State University (State College, Pennsylvania, USA).

### Statistical analyses

*Estimating number of  $^{15}\text{N}$ -marked seeds in traps.*—We estimated the number of marked seeds in a given batch using a two-source mixing model (Carlo et al. 2013), because the percentage of  $^{15}\text{N}$  atoms ( $^{15}\text{N}$  atom %) in a batch of marked and unmarked seeds depends on both the proportion of marked seeds in the batch and the  $^{15}\text{N}$  atom % of each seed. Thus the distribution of  $^{15}\text{N}$  values of a batch of  $n_m$  (marked) and  $n_u$  (unmarked) seeds is the convolution of a total of  $n_m + n_u$  distributions, with the distribution of marked values represented  $n_m$  times and that of unmarked values represented  $n_u$  times. To establish  $^{15}\text{N}$  atom % distributions for marked and unmarked seeds for each species, we analyzed seeds collected directly from marked plants in the sprayed areas of each landscape, and seeds collected from control plants in unsprayed areas of the experimental landscapes. For each species, we tried to fit a single Gaussian distribution to the  $^{15}\text{N}$  atom % data of marked and unmarked control seeds. In all instances, however, a simple distribution was not appropriate for the data and hence, a combination of two Gaussian distributions was fitted to the data. Depending on availability, 20–44 unmarked and 20–37 marked seeds were used to fit the distributions. To be conservative, we left-truncated the fitted distributions for marked seeds to a  $^{15}\text{N}$  atom % value 0.01 larger than the highest  $^{15}\text{N}$  atom % value of the corresponding unmarked seeds to avoid any overlap. For example, the range of  $^{15}\text{N}$  atom % found in unmarked seeds of *M. cerifera* varied from 0.357 to 0.371, so we truncated the distributions of marked seeds to have values larger than 0.372.

The model searched for the combination of marked and unmarked seeds that maximized the likelihood of observing a  $^{15}\text{N}$  atom % value similar to the one observed in the batch. The distribution of  $^{15}\text{N}$  atom % from a particular batch of marked and unmarked seeds was estimated by first simulating  $10^6$  seed mixtures by sampling from the combinations of distributions fitted to the marked and unmarked control seeds. An empirical cumulative distribution function was then computed from these simulated values, using the function `ecdf` in R 3.0.3 (R Development Core Team 2014). From this empirical cumulative distribution we computed the likelihood of the observed  $^{15}\text{N}$  atom %. The estimated number of marked seeds in a batch corresponds to the number of marked seeds that maximize the likelihood.

*Fitting dispersal kernels.*—For comparability of sampled marked seeds within and among sites, we standardized the estimated number of marked seeds for sampling days (number of traps  $\times$  days from deployment to seed collection) and for total area of the distance band (length of circumference  $\times$  diameter of seed trap [ $\sim 1$  m]) at each distance per site. To do so, we first divided the estimated number of marked seeds sampled at a distance by the number of sampling days at the distance, resulting in the number of marked seeds caught per  $\text{m}^2$  (i.e., per trap) per day, which represents the daily seed trap capture rate. We

multiplied this rate by the total area of the distance band, which accounts for the decreasing probability for seeds to land in a seed trap with increasing distance, creating a daily seed rain rate for each distance band. For example, in an unfragmented landscape, the daily seed trap capture rate of marked seeds from *M. cerifera* in the first ring of traps 5 m from the source plants was 0.02 seeds per day, and one seed trap sampled 0.32% of the total area within this 4.5–5.5 m band (see Appendix S1: Table S1). By multiplying the daily seed trap capture rate by the total area of the corresponding distance band, we determined the daily seed deposition rate to the distance band, which corresponds to seven seeds in the example above. This calculation provides the seed number for 100% of the area at each distance band and allows standardized comparison of dispersed marked seeds between distance bands.

Based on the standardized numbers of marked seeds at each distance, survival analyses were used to construct dispersal kernels (Jansen et al. 2012). Every marked seed was treated as an event and observed dispersal distances were treated as failure times. Kaplan–Meier survival analyses were used to calculate the survivorship function for each species and landscape (cf. Jansen et al. 2008, 2012, Hirsch et al. 2012) using the function `survfit` (Therneau 2014) in R 3.0.3 (R Development Core Team 2014). Dispersal data were pooled across landscapes of the same type because of low numbers of marked seeds in seed traps, especially at long distances. For each species, we tested if there was a difference between survival curves in the two landscapes with the function `survdiff` (Therneau 2014), which uses the *G*-rho family of tests (Harrington and Fleming 1982). We then fitted five commonly-used dispersal distance kernels in their one-dimensional form (i.e., probability density functions of the distribution of dispersal distances; Nathan et al. 2012) to the Kaplan–Meier survivorship functions: (1) exponential, (2) gamma, (3) Gompertz, (4) lognormal, and (5) Weibull. We used the function `flexsurvreg` (Jackson 2014) to search for parameter values in each of the five probability density functions that maximized the likelihood of the distance-to-observation data. We used relative likelihood, and the delta, and weights of Akaike information criteria (AIC; Akaike 1973) to determine which function best fit the observed data (Appendix S1: Table S2).

*Long-distance dispersal definition.*—Two general approaches are typically used to define LDD (Nathan 2005): (1) The proportional definition, in which LDD events include a small proportion (e.g., 1%) of all dispersed seeds that traveled the farthest, or (2) the absolute definition, in which dispersal events are considered LDD if they exceed a specified distance. In our study, we used the absolute definition because we were interested in movement between fragments that were specific distances apart. We defined LDD events as seeds sampled at 200 m distance from the source because it represents the distance that seeds must travel, to move between connected fragments.

## RESULTS

We analyzed a total of 6,016 seeds, of which 4,197 came from *Eupatorium compositifolium*, 491 from *Eupatorium glaucescens*, 412 from *Morella cerifera*, and 916 from *Rhus copallina*. Based on the  $^{15}\text{N}$  percentage of the analyzed seed batches, the two-source mixing model inferred the presence of 27 marked seeds for *E. compositifolium*, 37 marked seeds for *E. glaucescens*, 195 marked seeds for *M. cerifera*, and 85 marked seeds for *R. copallina*.

For the two wind-dispersed species, we found no evidence for differences in Kaplan-Meier estimates (i.e., fraction of seeds dispersing to each distance) between connected and unfragmented landscapes. Of the five dispersal kernel functions, the lognormal distribution fit all wind-dispersed Kaplan-Meier estimates best (Appendix S1:Table S3). The median dispersal distance for *E. compositifolium* was 10 m in connected landscapes and 30 m in unfragmented landscapes (Fig. 2C,D;  $G$ -rho  $P = 0.09$ ,  $df = 1$ ). For *E. glaucescens*, the median dispersal distance was 10 m for both connected and unfragmented landscapes (Fig. 2E,F;  $G$ -rho  $P = 0.54$ ,  $df = 1$ ).

Conversely, dispersal kernels differed significantly between connected and unfragmented landscapes for both of the bird-dispersed species. *M. cerifera* seeds dispersed further in unfragmented than connected landscapes (median dispersal of 10 m and 100 m, respectively; Fig. 2G,H,  $G$ -rho  $P < 0.01$ ). Accordingly, the best fits were the lognormal distribution for connected and the gamma distribution for the unfragmented landscapes (Appendix S1:Table S3).

For the second bird-dispersed species, *R. copallina*, seeds dispersed further in connected than unfragmented landscapes (median dispersal of 200 m and 50 m, respectively; Fig. 2I,J,  $G$ -rho  $P < 0.01$ ). The best fits for the Kaplan-Meier estimates were the Gompertz distribution for connected and the lognormal distribution for the unfragmented landscapes (Appendix S1:Table S3).

## DISCUSSION

Through a stable isotope seed-tracking technique, we constructed seed-dispersal kernels for four plant species in unfragmented and connected landscapes. Our results show that dispersal probabilities can be similar in connected and unfragmented landscapes, up to distances of 200 m. The consistency and magnitude of this effect varied among species, however, in a way associated with seed dispersal mode.

Despite the striking difference in landscape configuration, we found no difference in dispersal kernels for wind-dispersed plants between unfragmented and connected landscapes (Fig. 2C–F). For *E. compositifolium*, the median dispersal distance varied from 10 m in connected landscapes to 30 m in unfragmented landscapes, while the median dispersal distance was 10 m for *E. glaucescens* in both landscapes. The similarity of dispersal distances between the two types of landscapes is

surprising, as the forest matrix surrounding connected fragments is known to increase resistance to dispersal by wind (Greene and Johnson 1996, Ozinga et al. 2004, Schurr et al. 2008). Yet, it is also known that structurally complex landscapes can alter wind speeds and directions (Bohrer et al. 2008), which can result in positive effects of corridors on dispersal of wind-dispersed seeds (Damschen et al. 2014). By modeling airflow, Damschen et al. (2014) found that wind patterns within open, connected fragments increase the uplift probabilities of wind-dispersed seeds, and redirect and accelerate wind through corridors, promoting long-distance dispersal. Our results support this hypothesis and demonstrate that dispersal of wind-dispersed seeds in connected fragments is comparable to dispersal in unfragmented landscapes.

In contrast to wind-dispersed plants, dispersal differed significantly between unfragmented and connected landscapes for bird-dispersed plants. Even more strikingly, the impacts of corridors were reversed for the two species (Fig. 2G–J). For *M. cerifera*, the median dispersal distance in connected landscapes was reduced ten-fold when compared to the median dispersal distance measured in unfragmented landscapes. Conversely, for *R. copallina*, corridors increased the distance that seeds dispersed relative to unfragmented landscapes; median dispersal distance was four-times greater in connected than unfragmented landscapes. Hence, seed deposition in connected landscapes was either primarily limited to the sprayed fragment (84% of *M. cerifera* seeds) or to the connected fragment (70% of *R. copallina* seeds), ~200 m away (Fig. 2B). Our results, which indicate dispersal over primarily short or long distances, may be explained by bimodal dispersal patterns observed in fragmented woodland habitats, where birds either move short distances between the neighboring trees within a fragment or long distances between fragments (Gómez 2003, Lenz et al. 2011). Even though the two fragments in our experimental landscapes were connected, few marked seeds were dispersed into the corridor, supporting observations that at least some species of seed-dispersing birds in these landscapes travel mainly through the woodland matrix, alongside the corridor edges (Levey et al. 2005). Biotic factors, such as predators and competitors, and/or abiotic factors, such as climatic conditions, within the corridors may have limited its use for seed dispersers (Vasudev et al. 2015). In addition, intrinsic characteristics of dispersers, such as different bird species (Cramer et al. 2007), or seasonal effects (Evans et al. 2013) may have caused the divergent patterns observed for the two bird-dispersed plants.

Habitat isolation has been shown to alter plant dispersal in fragmented landscapes (Ibáñez et al. 2014) and corridors are the most frequently used management technique to counter isolation effects (Hilty et al. 2006). Previous studies in our experimental landscapes and elsewhere have shown how corridors can increase rates of dispersal relative to dispersal between unconnected fragments, including for our two bird-dispersed species *M. cerifera* and *R. copallina* (Tewksbury et al. 2002, Haddad et al.

2003, Gilbert-Norton et al. 2010); however, the question remained whether these increased rates of dispersal are sufficient to restore landscape connectivity to levels found in unfragmented landscapes. Our findings illustrate for the first time that corridors cannot only increase dispersal compared to fragmented landscapes, but in some cases can even raise long distance dispersal probabilities above levels measured in unfragmented landscapes (*R. copallina*).

Documenting long-distance dispersal poses a methodological challenge: recovering a fixed set of marked seeds within an increasing pool of individuals and a diminishing pool of dispersal events in an exponentially increasing area (Nathan and Muller-Landau 2000, Nathan 2006). A literature review of maximum dispersal distances for herbaceous, wind-dispersed plants revealed that documenting dispersal events greater than 100 m have only been achieved by following individual seeds across the landscape (Morse and Schmitt 1985). Using our isotope marking technique, we were able to simultaneously track large numbers of wind- and bird-dispersed seeds to distances up to 200 m from the parent plant (Fig. 2C–J). Such measures of dispersal are essential as we aim to predict the outcomes of ecological processes at a range of spatial scales (Bullock and Clarke 2000, Gilman et al. 2010). In conservation, our method can aid in predicting how organisms will respond to synergistic changes in habitat and climate (Coreau et al. 2009, Ibáñez et al. 2009). Further, it allows researchers to simultaneously mark multiple species – even entire communities.

Dispersal over long distances is rare (Cain et al. 2000, Nathan and Muller-Landau 2000), but perhaps not as rare as generally assumed (Horn et al. 2001, Levey et al. 2008, Carlo et al. 2013). On average, 15.1% of the wind-dispersed seeds we recaptured had dispersed ~200 m in unfragmented and connected landscapes. This is surprising because predictive models estimate a maximum dispersal distance of only 27.4 m for plants with growth forms and terminal velocities similar to our wind-dispersed species (Tamme et al. 2014). In other mechanistic models, only 1.4% of seeds from plants with terminal velocities similar to our wind-dispersed plants dispersed  $\geq 200$  m (Heydel et al. 2014). For bird-dispersed species, the proportion of seeds dispersing ~200 m was even higher; on average 27.7% of recaptured seeds were found at this distance. Although similar or greater distances have previously been reported for bird-dispersed plants (Lenz et al. 2011, Carlo et al. 2013), our results indicate that previous work has likely underestimated dispersal distances of wind-dispersed plants, likely due to limitations imposed by previous tracking methods.

A systematic underestimation of long distance dispersal would have far-reaching consequences. Whereas short-distance dispersal influences processes such as resource use and recruitment patterns, long-distance dispersal has impacts at larger scales, affecting processes such as spatial spread and colonization of new habitats (Nathan et al. 2003). Theoretical studies that incorporate realistic dispersal kernels show that model outcomes are

extremely sensitive to changes in the tail of the dispersal distribution (Kot et al. 1996, Chave et al. 2002), and our results suggest that factors that reduce (e.g., fragmentation, disperser loss) or increase (e.g., corridors) rates of long-distance dispersal (Tewksbury et al. 2002, Şekercioğlu et al. 2004) may have a greater impact on the spread and distribution of species than previously thought. The discrepancy between maximum dispersal distance and dispersal distances restricted by, for example, fragmentation takes on even more importance in light of climate change, during which populations may need to shift their ranges rapidly to keep up with changing climatic conditions (Corlett and Westcott 2013).

Nonetheless, long-distance dispersal is not universally beneficial to plants. Negative effects can arise for rare species that are restricted to a particular type of habitat that is very sparsely distributed. In the context of our study, all species were common and regularly occur in a variety of open habitats. Therefore, long-distance dispersal is considered beneficial for the persistence of these species.

Our findings also highlight new research directions. First, a broader sampling of species will allow for stronger testing of how seed dispersal mode and other traits related to dispersal, such as plant height (Thomson et al. 2011), predict how corridors affect dispersal. These efforts will help assess the generality of our finding that dispersal of wind-dispersed plants was similar between connected and unfragmented landscapes. Compared to plant species dispersed by animals (McEuen and Curran 2004), wind-dispersed plant species are rarely considered in reserve design planning, in spite of also being threatened by habitat fragmentation (Ouborg 1993). A broader consideration of how wind-dispersed species may integrate with reserve design is warranted.

Second, three-way comparisons among fragmented, connected, and unfragmented landscapes would provide further resolution of the extent to which corridors can restore dispersal. Again, this would be particularly important for wind-dispersed plants, given our more limited understanding of their responses to fragmentation and connectivity, relative to animal-dispersed species. For bird-dispersed plant species, factors other than physical connectivity, such as the availability of frugivores and the spatial distribution of fruit resources, strongly shape kernels (Morales and Carlo 2006) and thus could interact with corridor effects. Fruit resource availability and distribution could be expected to reduce the effects of corridors when fruits are found across the different components of the matrix (e.g., patches, edges, and the matrix) and create a type of connectivity that is non-structural (Carlo et al. 2013).

In summary, we have shown that seed dispersal between fragments connected by corridors can be similar or even enhanced relative to dispersal in unfragmented landscapes. Variation in dispersal kernels between species with different modes of dispersal as well as between bird-dispersed species was large, however. Restoration that takes into account different species is challenging, and

this study highlights that there is no one-size-fits-all solution. We also conclude that long-distance dispersal of seeds is more common than generally appreciated, perhaps because previous methods have poorly detected rare dispersal events. Resolving the intertwined impacts of habitat fragmentation and dispersal ability on population persistence remains a fundamental challenge of landscape ecology.

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