February 2013
esa
Volume 94 No. 2

ECOLOGY

A PUBLICATION OF THE ECOLOGICAL SOCIETY OF AMERICA



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Ecology, 94(2), 2013, pp. 301–307
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Where do seeds go when they go far? Distance and directionality of avian seed dispersal in heterogeneous landscapes

Tomás A. Carlo,[1,4] Daniel García,[2] Daniel Martínez,[2] Jason M. Gleditsch,[1] and Juan M. Morales[3]

[1]*Department of Biology and Intercollege Graduate Degree Program in Ecology, Pennsylvania State University, University Park, Pennsylvania 16802 USA*

[2]*Departamento de Biología de Organismos y Sistemas, Universidad de Oviedo, y Unidad Mixta de Investigación en Biodiversidad (CSIC-UO-PA), Oviedo 33071, Asturias, Spain*

[3]*Laboratorio Ecotono, INIBIOMA-CONICET, Universidad Nacional del Comahue, Quintral 1250, (8400) Bariloche, Argentina*

Abstract. Seed dispersal at large scales strongly influences plant population dynamics. Still, ecologists have rarely measured seed dispersal at relevant scales, and the role of habitat types in affecting seed dispersal at long distances remains unexplored. We studied seed dispersal of *Ilex aquifolium* and *Crataegus monogyna* in northern Spain, hypothesizing that seeds would be recovered at higher rates and at longer distances (LDD) at habitats with fleshy-fruited trees, compared to habitats with other tree types or at open habitats. We tracked seeds in eight landscapes by enriching trees with ^{15}N isotopes at the center of landscapes, and then detected ^{15}N-marked seeds by sampling at distances of up to 700 m. We found that seeds arrive in greater densities and at longer distances in habitats with trees, particularly fleshy-fruited types, producing different LDD probabilities for each habitat. Results also show a disproportional arrival of seeds in habitats similar to those of mother plants, which should affect seed establishment and the genetic diversity of plant neighborhoods. Findings reveal the strong dependence of seed dispersal on the existing templates that guide the movements of avian dispersers in heterogeneous landscapes and also suggest that LDD above tree lines and beyond hard habitat edges can be difficult.

Key words: avian dispersers; Cantabrian Range, northern Spain; Crataegus monogyna; *directed dispersal; dispersal kernel; European holly; frugivory; hawthorn;* Ilex aquifolium; *landscape connectivity; seed shadow; stable isotopes.*

Introduction

Seed dispersal is of central ecological importance because it modulates the tempo and pattern of plant range expansions, adaptation rates, metapopulation dynamics, and species' coexistence (Hurtt and Pacala 1995, Levine and Murrell 2003). Particularly critical is dispersal at long distances (i.e., LDD) because it should enable plant species and communities to cope better with climate change and habitat loss (Neilson et al. 2005, Nathan et al. 2008, Hampe 2011). Higher frequencies of LDD increase the speed with which plants can track shifting or novel habitats, which can lower the extinction threshold of populations, maintain gene flow, and affect their adaptability and evolution (Levine and Murrell 2003, Nathan et al. 2008). However, measuring seed dispersal, particularly LDD, from specific plant sources, has proven to be a challenge because field studies can easily determine where seeds arrive, but not from which sources (Nathan 2006). The LDD problem is equivalent to finding "a needle in a haystack," with the haystack becoming larger as longer distances are sampled. This limitation has hindered our understanding of the factors driving differences in the frequency, distance, and directionality of seed dispersal, limiting our ability to forecast LDD even in general ways (Nathan 2006).

Our goal in this study was to measure seed dispersal at landscape scales (25–700 m), and to evaluate dispersal directionality toward habitat types, of two major avian-dispersed tree species in the temperate forests of the Cantabrian Range (northern Spain): the European holly (*Ilex aquifolium* L.) and the hawthorn (*Crataegus monogyna* Jacq.). Directional dispersal refers to spatial biases that consistently clump seeds in some sites and not others, a typical characteristic of seed shadows made by frugivores (Schupp et al. 2002). A special case of directional dispersal is *directed* dispersal, which occurs when seeds arrive nonrandomly in the most favorable habitats for recruitment (Howe and Smallwood 1982, Wenny and Levey 1998). Spatially biased dispersal can be important to maintain community diversity because it can both create and regulate the spatial structure of seed shadows, which can create opportunities for species to coexist by reducing the extent of competitive exclusion (Howe and Smallwood 1982, Hurtt and Pacala 1995, Schupp et al. 2002).

The mechanisms responsible for spatial biases in frugivore-dispersed plants are well known, and include the active tracking of fruit resources (Hampe 2008,

Manuscript received 2 June 2012; revised 28 September 2012; accepted 18 October 2012. Corresponding Editor: B. J. Grewell.

[4] E-mail: tac17@psu.edu

García et al. 2011) and the social and territorial behavior of frugivores (Russo et al. 2006, Karubian et al. 2010). However, the scale of directional seed dispersal and how it relates to LDD and the arrival of seeds at specific habitats has been overlooked. Given the traditional difficulties in measuring seed dispersal directly (Nathan 2006), most of what we know about the mechanisms of large-scale dispersal by frugivores comes from simulation models (Morales and Carlo 2006, Uriarte et al. 2011), studies using experimental landscapes (Levey et al. 2005), or indirect measures of dispersal (Lenz et al. 2011, Spiegel and Nathan 2011).

Here we used a stable isotope seed-marking method (Carlo et al. 2009) to examine the distance and habitat-related directionality of the natural seed dispersal patterns of holly and hawthorn. Previous studies have shown that holly and hawthorn fruits are major food items of six species of overwintering thrushes (*Turdus* spp.; Martínez et al. 2008, García et al. 2012) in the Cantabrian Range of northern Spain. The thrushes commonly form flocks that track fruit resources at the landscape scale through long-distance flights (García et al. 2011, 2012). When foraging, thrushes perch on trees and rarely on open ground, generating a heterogeneous seed rain concentrated under trees, particularly those bearing fleshy fruits (García et al. 2005, Martínez et al. 2008). Thus, we predicted that seeds would be disproportionately dispersed at long distances more toward fleshy-fruited tree habitats (FF) than toward habitats of trees without fleshy fruit (NF), or into open habitats (O) composed of pastures and heathlands. Our rationale is that fleshy-fruited habitats strongly attract seed dispersers coming from near or far. Thus, in variegated and fragmented landscapes, LDDs should be more likely to be directed to patches with fruit resources, by "spatially contagious" processes among plants bearing fruit (Kwit et al. 2007).

Materials and Methods

Site description and marking of seeds with ^{15}N.—We used the aboveground isotopic spray method of Carlo et al. (2009) to mark seeds of holly and hawthorn by enriching reproductive trees with ^{15}N stable isotope. Trees were marked in May of 2009 (spring blooming) at the center of eight study landscapes in four sites (Sierra de Peña Mayor, Sierra del Aramo, Puertos de Marabio, Puerto de San Lorenzo) of the Cantabrian Range in Asturias, Spain (Fig. 1; Appendix A). Study sites were composed of forest patches of varying sizes and scattered trees on landscapes dominated by open pastures and heathlands. In each site, we marked with isotopes 1–7 flowering trees of each species (depending on availability) within a 15 m radius of each center point of two types of landscapes: one with high forest cover, and the other with low forest cover within a radius of 150 m (Appendix B). The spray applications in both species resulted in an average ^{15}N atom% content in seeds that was two orders of magnitude above the natural occurrence of the stable isotope in the site (see Appendices B and C for more details). The high ^{15}N content of seeds from marked trees allowed us to use continuous flow mass spectrometry and two-source mixing models to detect their presence in mixtures of seeds arriving at sampling stations from different source trees (i.e., ^{15}N-marked or normal).

Sampling seed dispersal.—The stations to sample seed dispersal consisted of permanently marked, open-ground 50 × 50 cm quadrats where all seeds dropped by birds during the fruiting season were collected. Studies in the same system show that the method provides reliable estimates of seed abundance, despite some predation by rodents (García et al. 2005, 2012). Stations were arranged in six concentric bands away from the eight center patches in the following manner (the number of sampling stations per band follows in parenthesis): 0–25 m (3 stations; center area containing ^{15}N-marked trees), 25–35 m (3 stations), 35–50 m (6), 50–70 m (12), 70–100 (24), and 100–150 m (60). At each band we placed equal numbers of sampling stations under trees bearing fleshy fruits (FF), under trees without fleshy fruits (NF), and in open pastures (O). Long-distance dispersal (i.e., LDD: 150–700 m) was sampled as an addition to the abovementioned radial sampling only in the four landscapes of Sierra de Peña Mayor and Puertos de Marabio. In total we allocated 108 LDD sampling stations in three blocks associated with each of the four landscapes in Sierra de Peña Mayor and Puertos de Marabio (Fig. 1). Up to 150 m, sampling stations per habitat represented 0.04 % of the area at each band, whereas in the 150–700 m band they accounted for 0.00002% of the surface area.

All ^{15}N-marked source trees and sampling stations were georeferenced with GPS, and the distance of each sampling station to the nearest marked tree at the center patch was determined using GIS. All bird-dispersed holly and hawthorn seeds arriving at sampling stations were collected in November 2009 and again in February 2010. Dispersed seeds are easily identifiable because, unlike seeds from non-dispersed fruits fallen beneath trees, they are clean of pulp remains (García et al. 2007). Seeds from the same sampling unit were stored in paper bags and maintained together as a batch. In the lab, we tallied and processed both intact seeds and those preyed upon by rodents (i.e., seed husks with teeth marks and fragments) in each batch. Seeds were then oven-dried at 60°C and cleaned to remove soil and other materials. Contact between seed materials belonging to different seed batches was strictly prevented at all times.

We found avian-dispersed seeds in a total of 1296 sampling stations, which provided 873 batches of holly seeds and 568 batches of hawthorn seeds (one seed batch = one sampling station). The seed batches contained anywhere between 1 and 3746 seeds (average batch size for holly = 125.4 ± 330.9 seeds, mean ± SD; batch size for hawthorn = 3.3 ± 8.9 seeds). We processed a total of 166 921 seeds in these batches, of which 97.45% were

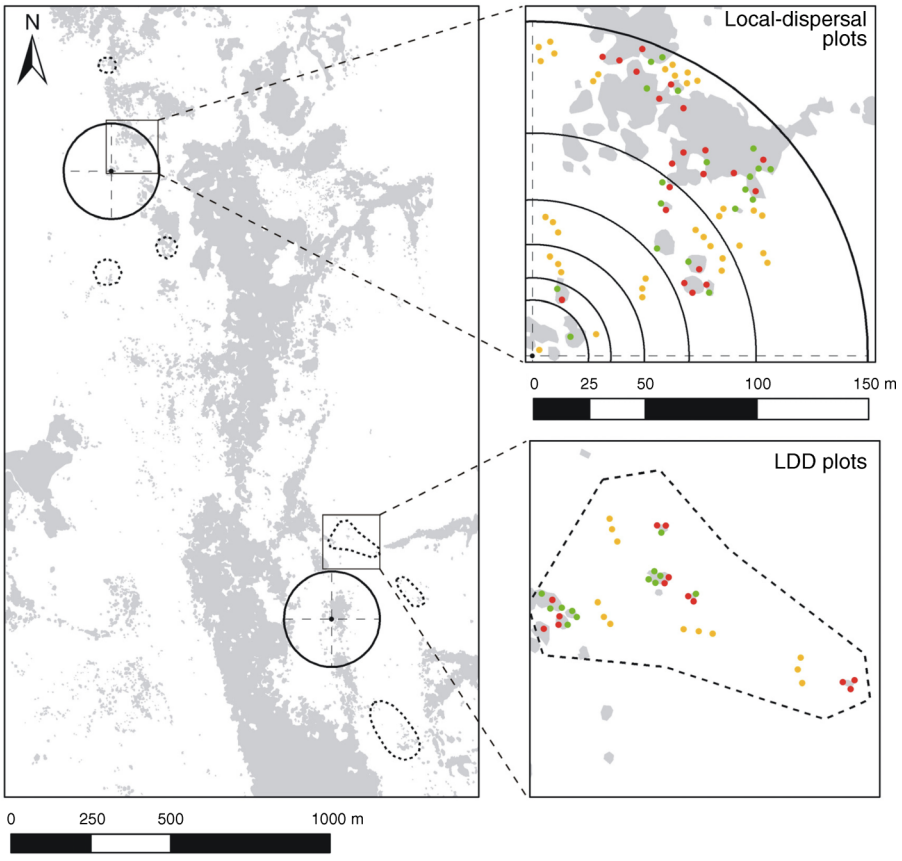


FIG. 1. (Left panel) Layout of a study site (Sierra de Peña Mayor in the Cantabrian Range, northern Spain) showing the paired design consisting of the two landscapes per site, one with low (top circle) and other with high (bottom circle) forest cover (gray) within 150 m of the centers where holly (*Ilex aquifolium*) and hawthorn (*Crataegus monogyna*) trees were marked with ^{15}N stable isotopes. Dots are sampling stations for seed dispersal, and gray areas represent forest patches. Sampling stations were distributed in proportion to the area of six distance bands from the centers with ^{15}N-marked trees (top right panel). Sampling of long-distance dispersal (LDD) was concentrated in "blocks" 150–700 m from centers. (bottom right panel). Sampling effort was equal by habitat type: under fleshy-fruited trees (red dots), under other trees (green), and in open pastures (yellow).

holly seeds and the rest were hawthorn. The majority of the seeds were from sampling stations within 150 m of the source trees, but 21.4% of the holly seeds and 25.4% of the hawthorn seeds were collected at distances between 150–700 m.

Sample preparation for mass spectrometry analyses.—All seeds from a sampling station were ground together as a single batch in order to thoroughly mix and reduce seeds to fragments of 10–40 μm. Batches of up to 20 seeds were ground using a Retsch Mixer Mill MM200 (Haan, Germany), and larger batches were ground in a Retsch Ultra Centrifugal ZM 200 mill (Haan, Germany) or with coffee grinders. After grinding a batch, all equipment in contact with seed material was thoroughly washed twice with clean water and soap, rinsed a third time with distilled water, wiped, and then given a final rinse with acetone and allowed to air dry under a hood. We then weighed ~10.0 mg (9.85 ± 0.44 mg, mean ± SD) of each seed batch material and wrapped it in a tin cup for mass spectrometry (5 × 9 mm, CE Elantech, Lakewood, New Jersey, USA). All samples were analyzed in an elemental analyzer (PDZ Europa ANCA-GSL, Sercon Ltd., Cheshire, UK) interfaced with a continuous flow isotope ratio mass spectrometer (PDZ Europa 20-20, Sercon Ltd., Cheshire, UK) at the Stable Isotope Facility of the University of California at Davis, California, USA.

Two-source mixing model.—Our goal was to infer the number of ^{15}N-marked seeds in a homogeneous mixture of n seeds. For this we estimated the probability (likelihood) of obtaining the observed atom% value of batches, from each of the distributions coming from every possible combination of marked and normal seeds. For example, to infer the number of marked seeds in a batch from $n = 10$ seeds, we computed the likelihood of the observed ^{15}N atom% value for each of the 11 (0, 1, 2, . . . , 10) possible combinations of seeds (Appendix C). See the Supplement for R code.

Statistical analyses.—We used a linear model (ANCOVA) to examine how seed dispersal of holly and hawthorn was affected by variables of habitat type, distance, amount of forest cover on the landscape, and

location (i.e., study site). For this, in each landscape, we calculated the average number of marked seeds at sampling stations within each distance class (Appendix C). We then converted the average dispersal values to rates by dividing each of those averages by the number of marked seeds that were present in the fruit crop of source trees at the respective center patch. This accounts for differences in the abundance of marked seeds at sources among sites, and thus allows the fair comparison of dispersal rates between plots with different fruit abundances. Then we applied an arcsine transformation to the square root of the dispersal rates, and used it as response variable in a fixed-effects linear model with habitat type (O, NF, FF), distance, landscape forest cover (low, high), and site (four sites) as factors, including the interactions habitat type × distance and distance × site. We also constructed seed dispersal kernels for holly and hawthorn where "movement space" (Schurr et al. 2008) depended on habitat type (FF, NF, O) by fitting 2Dt probability density functions (Clark et al. 1999) to the dispersal data pooled across sites and using maximum likelihood (Appendix C). For this analysis, we used the distance of sampling locations to the nearest source of ^{15}N seeds for each species.

Results

From the isotopic values of the seed batches, the two-source mixing model detected the presence of many ^{15}N-marked seeds: we inferred dispersal for 1053 holly seeds in 250 batches (i.e., 28.6% of holly batches had marked seeds), and for 128 hawthorn seeds in 96 batches (i.e., 16.9% of hawthorn batches had marked seeds). Although LDDs were sampled in only four landscapes, 11.4% of marked holly seeds and 21.9% of marked hawthorn seeds were detected at distances greater than 150 m, with 13 batches of holly and 16 batches of hawthorn showing marked seeds at distances greater than 300 m (see Appendix B: Fig. B1).

As predicted, the seed dispersal patterns were strongly biased toward patches of trees, especially toward trees bearing fleshy fruits (Fig. 2). In the absence of dispersal directionality, seed sampling stations would have received seeds in proportion to the habitat-balanced effort (i.e., each habitat type receiving ~33.3% of marked seeds). Instead, stations in open pastures (O) received 2.12% of marked seeds, those under non-fleshy-fruited tree cover (NF) accounted for 22.96% of seeds, and 70.62% of seeds arrived at stations under fleshy-fruited tree cover (FF) ($\chi^2 = 995.8$, df = 2, $P < 0.0001$). Even when considering that open habitat was by far the most abundant of the three habitats, seed deposition was disproportionately higher under trees (e.g., FF and NF together would account for 85% of marked holly seeds per hectare, assuming 75% landscape cover for O). Habitat directionality was also evident when looking only at the fraction of seeds reaching long dispersal distances (i.e., 150–700 m; Fig. 2). These biases result in habitat-specific seed dispersal kernels (i.e., 2Dt probability density functions, following Clark et al. [1999], Schurr et al. [2008]) where the probabilities for LDDs are higher for habitats with tree cover, especially FF locations (Fig. 2).

As determined by ANCOVA analyses, habitat type was the most important factor explaining the dispersal rates of both holly and hawthorn (Fig. 2 and Appendix D). There was no significant interaction between "dispersal distance" and "habitat type" for either species, but there was an interaction between "dispersal distance" and "site" (Appendix D) that was due to the fact that only half of the eight study landscapes had LDD plots (i.e., there was no significant interaction for either species when data from LDD plots were excluded from analyses). Additional factors that significantly affected the arrival of marked seeds at sampling stations were "site" and "forest cover" (Appendix D). A significant effect of "site" is expected, given local differences in the abundance of fruit, frugivore abundance, and the configuration of landscapes. For example, some sites such as Puertos de Marabio and Puerto de San Lorenzo had more than twice the dispersal rate as the other sites. Finally, dispersal rates for hawthorn decreased as forest cover increased in the surrounding landscape, but this effect was marginally significant for holly (Appendix D).

Discussion

Our study shows that the seed dispersal patterns of avian frugivores can be highly directional, and our results demonstrate that habitat heterogeneity across spatial scales can differentially influence dispersal rates at long distances. For example, habitat type, as determined by the presence/absence of the cover of trees bearing fleshy-fruits, accounted for 49.6% of the variance in dispersal rates of holly, which was more than twice the variance explained by dispersal distance, and 16.3% of the total variance in the dispersal rates. The behaviors of thrushes wintering in the Cantabrian Range explain these patterns: the selection of tree cover for foraging (i.e., fleshy fruits are their major resource), finding protection from predators, and the repeated use of favorite perching sites.

Directional dispersal at both short and long distances also presents a paradox: seeds are being dispersed, often hundreds of meters away from source trees, but most seeds ended up in the same type of habitat that they left behind. Holly seeds best illustrate this phenomenon, with 86% of detected dispersal events being toward sites with other fruiting *Ilex*, despite the fact that only 66.9% of all the FF stations were placed under fruiting holly (29.3% were under hawthorn, and the remainder 3.8% under *Taxus baccata* and *Hedera helix*). This may appear as "movement without movement" as dispersed seeds tend to arrive at similar sites to those they left behind (Kwit et al. 2007). Thus, directional dispersal appears to be an important mechanism limiting the dissemination of seeds (sensu Schupp et al. 2002), with

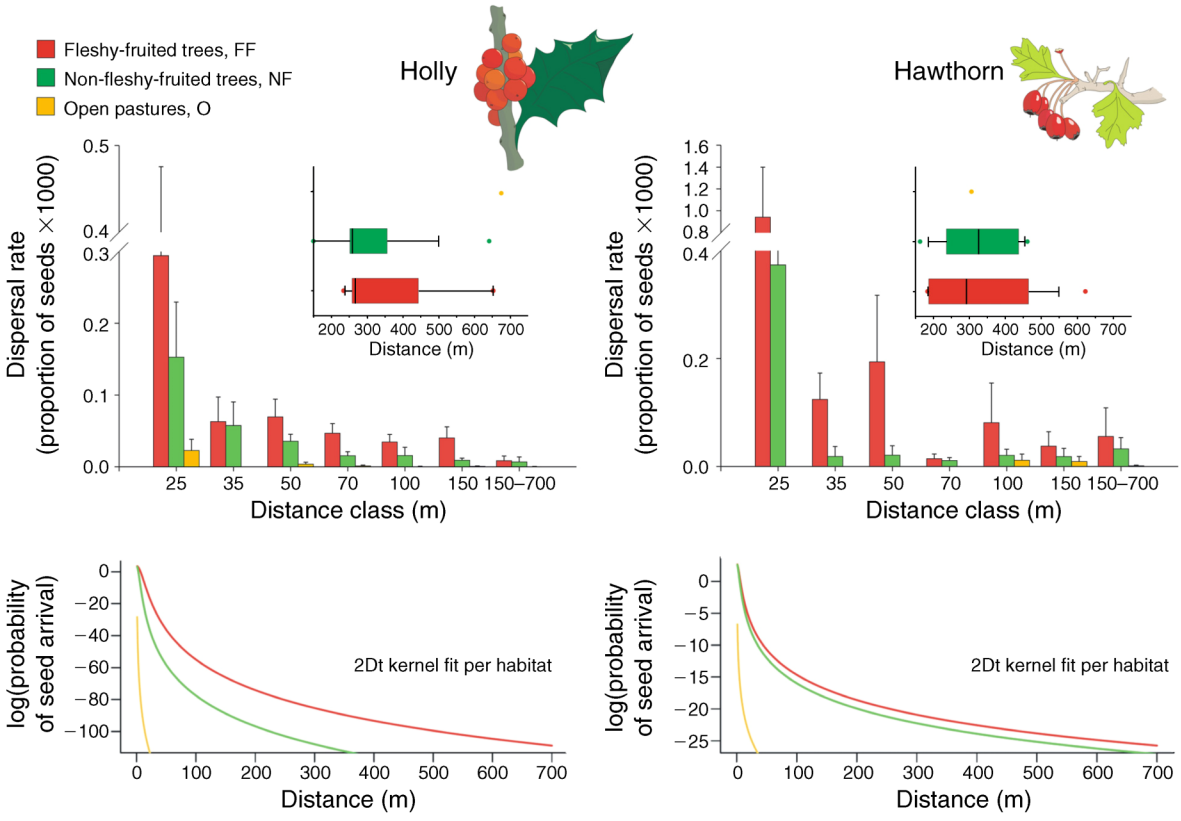


FIG. 2. A higher rate of seeds of holly (*Ilex aquifolium*) and hawthorn (*Crataegus monogyna*) arrived at sampling stations under tree cover bearing fleshy fruits (FF), than to stations under tree cover without fleshy fruits (NF) or in open pastures (O), across distance bands (top panels; bands under 150 m are labeled with their upper bound, e.g., 25 for 0–25 m). Dispersal rate (mean + SD) was calculated as a proportion: the number of dispersed ^{15}N-marked seeds relative to the ^{15}N-marked seed crop on source trees at the center patch of each study landscape. For purposes of scale, the values have been multiplied by 1000. Top insets show boxplots for LDD events (the box extends from the first to the third quartiles, with median, whiskers, and outliers). Directional seed deposition patterns resulted in a higher probability density of LDDs in FF and NF habitats than in O habitats (bottom panels). Dispersal 2Dt kernels (probability density functions) were fitted to data where "movement space" (Schurr et al. 2008) depended on habitat type. Results of an effects test (ANCOVA) for holly with dispersal rate as response variable and with "habitat" (three levels), "study site," "percent forest cover" (two levels), and "distance" as factors are: $r^2 = 0.33$, $F_{12, 137} = 5.58$, $P < 0.0001$; for the hawthorn effect test (ANCOVA, same parameters as *Ilex*), $r^2 = 0.29$, $F_{12, 137} = 4.75$, $P < 0.0001$. See Appendix D for ANCOVA tables and parameter estimates. Artwork credit: Daniel Martinez.

the less obvious consequence of promoting the formation of plant neighborhoods with higher genetic diversity than otherwise would be expected (see Karubian et al. 2010).

Still, it is important to determine whether the observed dispersal biases favor the establishment of holly and hawthorn, constituting an example of *directed* dispersal (Wenny and Levey 1998). Dispersal toward sites with high seed densities, such as those under fleshy-fruited trees, could easily lead to Janzen-Connell effects (i.e., negative density dependence) that increase seed and seedling mortality in such sites (Bell et al. 2006). However, previous studies and experiments conducted in some of the same sites (e.g., Sierra de Peña Mayor) found no density dependence in the predation rates of holly and hawthorn seeds (García et al. 2005, 2007). These studies report that regardless of habitat, seed arrival rates were positively correlated with recruitment at later life stages in holly and hawthorn (García et al. 2005). Furthermore, dense and sclerophyllous tree species such as holly facilitate recruitment by offering protection in the heavily grazed open areas (García and Obeso 2003), suggesting that seed dispersal may indeed be *directed* toward suitable recruitment sites.

Linking long-distance with directed seed dispersal.—It is key to understand and predict the capacity of plants to move on fragmented and degraded habitats to keep up with potentially rapid global and climatic changes, and to better assess and manage the ecological connectivity of landscapes. Clark (1998) concluded that trees could migrate fast and keep up with climate change, provided a "fat-tailed" kernel where LDDs are frequent. Still, fat-tailed kernels offer only part of the answer. An increasing probability of dispersing far is by no means a guarantee for seed survival and for the establishment of reproductive adults and viable populations. In fact, it

can be argued that, in many circumstances, moving far or experiencing biased dispersal can increase the chances of landing in a hostile environment (Nathan 2006, Spiegel and Nathan 2011). Further, survival rates are typically low for seeds and seedlings, even in suitable habitats, which suggests that, in general, multiple "hits" to suitable habitats will increase establishment probabilities. Nevertheless, multiple hits to the right kind of habitat can appear as highly improbable given the high heterogeneity of landscapes in which suitable recruitment sites can compose a tiny fraction of all possible arrival sites, especially at long distances. But as our results show, directed dispersal can solve this problem because frugivores, in addition to making LDDs sufficiently frequent (Fig. 2), also have the effect of concentrating seeds in relatively few locations. Such locations will often have attributes similar to those of the seed source when the frugivores display some level of habitat affinity. Thus, we argue that it is the combination of frequent LDDs *and* directed seed dispersal that, under the right circumstances, can allow plants to migrate rapidly.

The ability of plants to disperse seeds at long distances beyond their current geographic range is believed to be the single most important factor that will affect the future distribution of many species under climate change scenarios (reviewed by Hampe 2011). However, if LDD depends largely on directed dispersal toward existing woody vegetation, then our findings suggest that species can be predicted to advance easily and rapidly in some habitats, but slowly in others. For example, dispersal should be facilitated in landscapes containing woody vegetation that, prior to climate change, excluded species not by LDD limitation, but by other abiotic or biotic filters. Conversely, LDD will be difficult in areas that could turn into suitable habitat following climate changes, but are devoid of tree cover or are unattractive to avian vectors, such as habitats beyond tree lines and other hard vegetation edges.

Concluding remarks.—Our large-scale, field-based study shows that habitat heterogeneity, even when involving just differences in tree cover type, can strongly influence seed dispersal by frugivores, and can be used to predict the arrival of seeds at scales of hundreds of meters. Underscored is the fact that frugivore behavior adds a nonrandom dimension to the seed dispersal process that dramatically changes probabilities of seed arrival across distances and habitats. Understanding this dimension can prove useful for creating and managing connectivity in fragmented and degraded landscapes, as well as help to better parameterize plant community models by allowing LDD probabilities to be informed by landscape characteristics (Carlo and Morales 2008, Schurr et al. 2008, Morales et al. 2012). We believe that our results are representative of many landscapes worldwide, because fragmented landscapes with habitat types similar to the ones we studied, and frugivores with medium-sized home ranges like those of *Turdus* spp., are widespread in many temperate and tropical regions (McConkey et al. 2012). Our study has also demonstrated that stable-isotope marking can be used to track dispersal at large spatial scales, and if used in combination with population genetic data and models, could improve our understanding of dispersal ecology. Future studies should aim to examine LDD processes at the edge of species ranges and on "advancing/retreating fronts." Our findings also suggest the possibility that LDD could be manipulated by creating or maintaining vegetation patches that optimize the attraction of vectors from afar, at least for avian-dispersed woody species.

Acknowledgments

The Penn State Biology Department supported T. A. Carlo and J. M. Gleditsch. Daniel García was supported by the Spanish National Program of Research and Development (grants MICINN CGL2008-01275 and MINECO CGL2011-28430), and D. Martínez by the European Social Fund and MICINN through a FPI grant. Funding for J. M. Morales was provided by CONICET and PIP 114-200801-00276. Andrés Pagán, C. Guardado, J. Rodríguez, R. Pérez, A. W. Norris, and M. L. Flores-Mangual conducted fieldwork. Andrés Peredo, A. John, K. H. Kim, M. Shiles, S. Flecha, K. Thaker, R. Glenn, S. Verma, C. Wang, B. Russell, and A. Kejas prepared samples. Andy Stephenson, and D. J. Levey provided comments on the manuscript.

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Supplemental Material

Appendix A

View of study sites and seed sampling locations in northern Spain (*Ecological Archives* E094-024-A1).

Appendix B

Additional methods and results related to the marking of seeds with ^{15}N stable isotope in the field (*Ecological Archives* E094-024-A2).

Appendix C

Details of a two-source simulation mixing model used to detect presence of marked ^{15}N seeds in batches of seeds found in seed traps, and methods for fitting 2Dt kernels to seed dispersal data (*Ecological Archives* E094-024-A3).

Appendix D

Linear models (ANCOVA and parameter estimate tables) testing the effects of independent variables on seed dispersal rates of holly and hawthorn (*Ecological Archives* E094-024-A4).

Supplement

R source code for a two-source simulation mixing model that detects ^{15}N-enriched seed in seed batches composed of unknown quantities of ^{15}N-enriched (marked) and normal (unmarked) seeds (*Ecological Archives* E094-024-S1).