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Differential effect of landscape structure on the large-scale dispersal of co-occurring bird-dispersed trees

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Abstract

Seed dispersal enables plants to reach favorable sites for population renewal or expansion far from conspecifics. However, the ability of plants to respond to habitat heterogeneity at large spatial scale is strongly mediated by seed dispersal vectors, e.g. animals, which usually restrict seed deposition to sites with specific environmental conditions, and at short distances from source plants. This spatial constraint, together with the technical difficulties of following the movement of seeds in the wild, makes the estimation of plant response to large-scale heterogeneity a challenge. Here, we applied an isotope-based technique to track bird-mediated seed dispersal of two co-occurring tree species in eight replicated landscapes in the Cantabrian Range (N Spain): the hawthorn *Crataegus monogyna* and the holly *Ilex aquifolium*. These species bear very similar fruits, partially overlap in the timing of fruit production, and their seeds are dispersed by the same species of frugivorous birds. Thus we expected that landscape structure, as represented by the amount of forest cover in the landscape, would affect the large-scale seed dispersal of neighboring individuals of *C. monogyna* and *I. aquifolium* in a similar fashion. Contrary to our expectation though, the effects of forest cover on the dispersal patterns of co-occurring hawthorn and holly were opposite: high forest cover in the landscape decreased large-scale dispersal for hawthorn, but enhanced it for holly. Our results suggest that small differences in the traits of plant and frugivore species, such as phenology patterns, can interact with the distribution of adult plants to generate strong differences in the response to landscape structure through seed dispersal, even for neighboring trees belonging to different species.

Zusammenfassung

Die Samenausbreitung erlaubt es Pflanzen, günstige Standorte zu erreichen, um Populationen zu erneuern oder weitab von Artgenossen zu siedeln. Die Fähigkeit von Pflanzen, auf die Habitatheterogenität auf großen räumlichen Skalen zu reagieren, wird entscheidend durch die Vektoren der Samenausbreitung vermittelt, die die Samenablage normalerweise auf Orte beschränken, die nahe der Samenquelle gelegen sind und spezifische Umweltbedingungen aufweisen. Diese räumliche Beschränkung macht zusammen mit der Schwierigkeit, die Bewegung der Samen in der Natur zu verfolgen, die Bestimmung der Reaktion der

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Pflanze auf großräumige Heterogenität zu einer Herausforderung. Wir setzten Isotope ein, um die Samenausbreitung durch Vögel in acht replizierten Landschaften im Kantabrischen Gebirge (Nord-Spanien) zu untersuchen. Die beiden Baumarten, Weißdorn (*Crataegus monogyna*) und Europäische Stechpalme (*Ilex aquifolium*) tragen sehr ähnliche Früchte, die Zeiträume der Fruchtbildung überlappen teilweise, und die Samen werden von denselben frugivoren Vogelarten ausgebreitet. Wir erwarteten deshalb, dass die Landschaftsstruktur, repräsentiert durch den Anteil der bewaldeten Flächen, die großräumige Ausbreitung der Samen von benachbarten Individuen von Weißdorn und Stechpalme in ähnlicher Weise beeinflussen würde. Tatsächlich waren aber die Einflüsse des Waldanteils auf die Ausbreitungsmuster der beiden Arten entgegengesetzt: Ein hoher Waldanteil in der Landschaft verringerte die großräumige Ausbreitung von Weißdornsamen, während die von Stechpalmensamen verstärkt wurde. Unsere Ergebnisse legen nahe, dass geringe Unterschiede in den Merkmalen der Pflanzen- und Vogelarten (z.B. in der Phänologie) so mit der Verteilung der adulten Pflanzen interagieren können, dass große Unterschiede bei der Samenausbreitung als Reaktion auf die Landschaftsstruktur hervorgebracht werden. Und dies gilt sogar für benachbarte Bäume unterschiedlicher Arten.

Keywords: *Crataegus monogyna*; Forest cover; Habitat loss; *Ilex aquifolium*; Large-scale seed dispersal; Northern Spain; Stable isotopes; *Turdus* sp.

Introduction

Habitat selection in plants depends on individual or population responses to the environmental heterogeneity in space or time (Bazzaz 1991). Among these responses, seed dispersal (i.e. the movement of seeds far from source plants to establishment sites) enables plants to find favorable conditions for population renewal or expansion (Ronce 2007; Cousens, Dytham, & Law 2008). Seed dispersal is, however, a non-random spatial process that narrows the actual range of environmental heterogeneity experienced by plants, as certain sites, with specific local conditions, are never reached by seeds (Gómez, Valladares, & Puerta-Piñero 2004; Robledo-Arnuncio, Klein, Muller-Landau, & Santamaría 2014). More importantly, seed dispersal is strongly restricted by distance as most of the seeds move at short distances from source plants and only a very small proportion of the seeds arrive at far sites (Schupp, Milleron, & Russo 2002; Cousens et al. 2008). Thus, large-scale dispersal – defined as a landscape-level, bi-dimensional process of seed deposition at far sites over large spatial extents – is inherently extremely limited. Large-scale dispersal is not only relevant for the long-term maintenance, expansion and evolution of plant populations (Clark 1998; Clark, Silman, Kern, Macklin, & HilleRisLambers 1999), but is also becoming crucial in the short term in the context of large-scale and fast moving anthropogenic changes in ecosystems (Pearson & Dawson 2005; McConkey et al. 2012). However, the potential of plants to respond to landscape-scale heterogeneity is expected to be low, even for plants with adaptations for long-distance dispersal mediated by animal vectors (Cousens et al. 2008; Côrtes & Uriarte 2013).

Despite its theoretical and applied relevance, the relationship between large-scale seed dispersal and landscape characteristics (e.g. the amount and spatial distribution of habitat cover classes) still remains poorly studied or understood (McConkey et al. 2012). This is because of the technical difficulties that accompany the empirical measurement of the movement of seeds in the field, which makes the estimation of large-scale dispersal a big challenge for ecologists (Nathan 2006; Robledo-Arnuncio et al. 2014). Studies relating seed arrival (inferred from the occurrence of dispersed seeds) with the characteristics of the neighborhood around deposition sites have revealed significant effects of habitat cover or patch isolation on dispersal (e.g. Hewitt & Kellman 2002; Koh, Reineking, Park, & Lee 2015) as well as different effects of habitat features depending on, for example, the seed dispersal syndrome (e.g. McEuen & Curran 2004; Cramer, Mesquita, & Williamson 2007; Carlo & Tewksbury 2014). Another series of studies that infer seed movement indirectly using inverse or mechanistic modeling (e.g. Soons, Messelink, Jongejans, & Heil 2005; Schurr, Steinitz, & Nathan 2008) have suggested that dispersal is also partially controlled by habitat structure around source plants, and that these effects may vary depending on plant dispersal traits (e.g. animal vs. wind dispersal). Only a few studies have managed to measure directly the large-scale movement of seeds, showing how movement is conditioned by landscape properties such as connectivity (e.g. Tewksbury et al. 2002; Damschen, Haddad, Orrock, Tewksbury, & Levey 2006). However, studies explicitly examining the movement of seeds in relation to landscape structure, while controlling for plant species traits, are still lacking. This is an important gap to fill, because general trait-based knowledge would facilitate a proper scaling-up, from individual species to communities, of the responses to landscape heterogeneity, and would improve the understanding of landscape filtering effects on species assemblages (Damschen et al. 2008).

Here, we apply a novel technique, based on ^{15}N isotopic labeling (Carlo, Tewksbury, & Martínez del Rio 2009), to empirically track the dispersal of seeds from source plants at a large spatial scale, and to relate dispersal to the landscape structure where the seed movements take place. We focus on two fleshy-fruited tree species that co-inhabit fragmented forests in the Cantabrian Range (N Spain) and that share a guild of frugivorous birds as principal dispersal agents. In order to interpret large-scale seed dispersal, we focused on an area between the immediate neighborhoods around source trees – where most seed dispersal events occur – and further sites – only reached by infrequent long-distance dispersal (Carlo, García, Martínez, Gleditsch, & Morales 2013). Our objective was thus to evaluate, across a regional extent, the relationship between large-scale seed dispersal and forest cover in landscapes where the two tree species grow alongside each other within the same forest patches. We predicted a similar seed dispersal response for both species given the common landscape structure.

Materials and methods

Study system

Our study species were the fleshy-fruited trees *Crataegus monogyna* Jacq. (hawthorn hereafter) and *Ilex aquifolium* L. (holly hereafter). These two species are dominant co-occurring tree species in the highly-fragmented, montane secondary forests found in Northern Spain. In autumn, both species produce sugar-rich red berries, 10–14 mm in diameter, which contain 1 (hawthorn, 6–7 mm) or 1–3 (holly, 4–5 mm) seeds. Six species of frugivorous thrushes are the main seed dispersal agents of both hawthorn and holly in the Cantabrian Range: blackbird *Turdus merula*, fieldfare *Turdus pilaris*, mistle thrush *Turdus viscivorus*, redwing *Turdus iliacus*, song thrush *Turdus philomelos*, and ring-ouzel *Turdus torquatus* (Martínez, García, & Obeso 2008). *T. pilaris, T. iliacus* and *T. torquatus* are over-wintering species in northern Spain, whereas *T. merula, T. viscivorus* and *T. philomelos* are species with resident populations that are joined by overwintering migrant individuals. These species show territoriality and a mostly insectivorous diet through spring and summer, but in autumn and winter they aggregate and flock, relying mostly on fleshy fruits for food (Snow & Snow 1988). All thrushes swallow fruits whole and defecate seeds intact, thereby acting as legitimate seed dispersers (Jordano 2000).

Study sites

We studied eight forest landscapes, two in each of four mid-elevation (ca. 1100 masl) sites (Sierra de Peña Mayor, Puertos de Marabio, Sierra del Aramo, Puerto de San Lorenzo) of the Cantabrian Range in Asturias, northern Spain (Fig. 1A). All landscapes were composed of forest patches of varying sizes and scattered trees, embedded in a dominant open matrix of pastures and heathlands. Forest mostly comprised secondary-growth patches, dominated by fleshy-fruited trees (holly, hawthorn, yew *Taxus baccata* L., and rowan *Sorbus aucuparia* L.), and hazel *Corylus avellana* L., but also some mature stands of beech *Fagus sylvatica* L. where the same fleshy-fruited species occur scattered in the understory. Each study landscape was delimited within a circular 150-m-radius plot. These landscapes were arbitrarily chosen to represent, in each site and relative to the local forest availability, one landscape of high forest cover and one landscape of low cover, around a group of co-occurring hawthorn and holly trees (i.e. source trees; Fig. 1B). Forest cover within each 150-m-radius plot, i.e. percentage of area covered, was estimated with a geographic information system (GIS, ArcGIS9.3, ESRI, Redland, CA, US) based on a 1:5000-scale orthophotograph, from which a layer of forest cover was digitized from the vertical projection of the whole tree canopy. This forest layer included mostly secondary forest patches, where fleshy fruit production is typically high, but also some patches of mature forest where fruit density is usually lower. Nevertheless, both types of forest patches are known to be used by frugivorous birds (García, Zamora, & Amico 2011). We thus considered that the percentage of forest cover in the whole area of each study plot (150-m-radius area) was the best parameter – and scale extent – for representing the surrounding habitat perceived by frugivorous birds, both when foraging on fruits at source trees and when taking decisions in terms of flying away from source trees after feeding (i.e. post-foraging movements).

Marking of seeds from source trees with stable isotopes

In May of 2009 we marked hawthorn and holly trees at the center of each 150-m-radius plot with ^{15}N. In each 150-m-radius plot, we sprayed between 1 and 7 flowering trees of each species (depending on availability) within a 15 m radius of its center point. We used a portable 10 L hand spray pump to apply a solution of ^{15}N-urea ($(^{15}NH_2)_2CO$ (98.9% ^{15}N, Cambridge Isotopes, Massachusetts, USA) on inflorescences and leaves at a concentration of 0.5 g L^{-1}. Spraying was concentrated on flowering structures since it is the most direct route to enrich seeds (Carlo & Norris 2012). The spray stream of the pump was adjusted to easily reach the canopy of most trees (3–5 m average height), but for taller trees we used a ladder to reach the top of the canopy. We added one drop of Tween 20 (Uniqema Americas LLC, New Jersey, USA) per liter, a non-ionic detergent to make the solution stick to the plant surface. As estimated by direct fruit counts on sprayed trees in October 2009, the total crop size of all ^{15}N-labeled trees in each plot averaged 10,089 (±2261SE) fruits for hawthorn, and 47,525 (±10,924SE) for holly (see Carlo et al. 2013 for further details).

Seed dispersal sampling

In October 2009, we set up a standardized design for sampling hawthorn and holly seed deposition by frugivorous birds

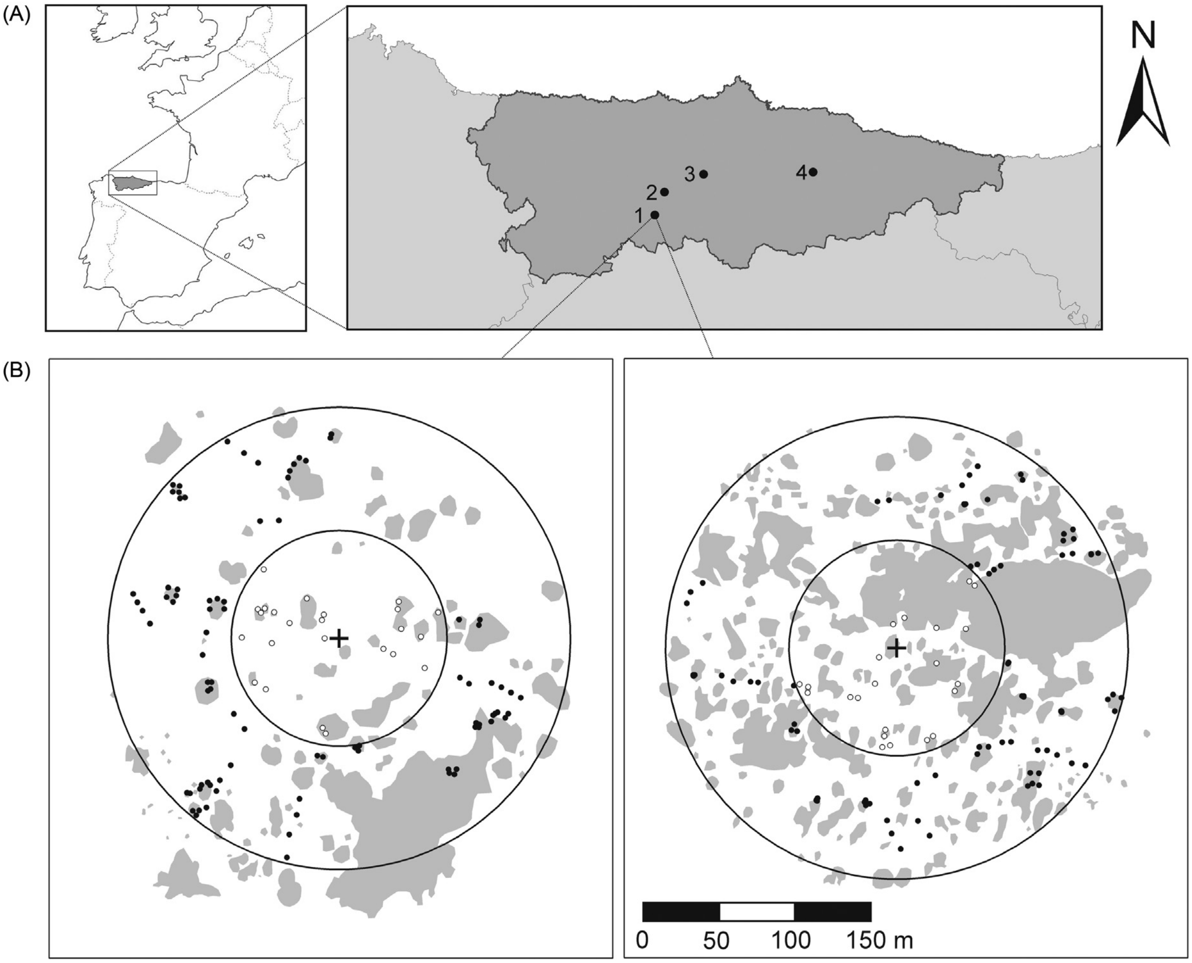

Fig. 1. (A) Geographical location of the study sites in the Asturias region of N Spain (1: Puerto de San Lorenzo; 2: Puertos de Marabio; 3: Sierra del Aramo; 4: Sierra de Peña Mayor). (B) Spatial structure of seed sampling design, representing the position of ^{15}N-marked source trees (central cross), the surrounding area used for sampling of Landscape Scale Dispersal (LSD area, ring between 70 and 150 m radii), and the distribution of seed sampling stations (dots, those at LSD area in black). Gray area represents the extent of forest cover. As an example, the two plots of the San Lorenzo site are represented (left, low forest cover; right, high forest cover).

across the study plots. Early in the fall of 2009 we established ground areas of 0.5 × 0.5 m, marked with staked small flags, as stations in which to sample seeds. Originally, 108 stations were arranged in concentric bands radiating out from each plot center, with the number of stations increasing proportionally with distance from the center, and with the stations being equally distributed among different types of microhabitat (Fig. 1B; see Carlo et al. 2013 for details). All ^{15}N-marked trees and sampling stations were geo-referenced with GPS, and the distance of each sampling station to the nearest ^{15}N-marked tree within the center patch was determined using GIS.

All bird-dispersed hawthorn and holly seeds were collected from sampling stations in November 2009, and again in February 2010. Dispersed seeds are easily distinguished from non-dispersed fruits fallen beneath trees because they are clean of pulp remains. In the lab we tallied both intact seeds and seed fragments in the batches of each sampling station, then oven-dried them at 60 °C and cleaned the seeds and fragments to remove soil and other non-seed material. Any contact between seed materials belonging to the different seed batches was avoided at all times.

The seeds corresponding to each tree species in each seed batch (i.e. sampling station) were separately ground in a Retsch MM-200 ball grinder, reducing them to fragments averaging 10–40 μm. We then weighed ≈10.0 mg (avg. = 9.85 ± 0.44 SD) of the ground seed material from each separate seed batch for mass spectrometry. All samples were analyzed in an elemental analyzer interfaced with a continuous flow isotope ratio mass spectrometer (see Carlo et al. 2013 for a detailed description of isotopic analysis). Finally, we inferred the number of ^{15}N-marked seeds of each tree species from each sampling station by using a mixing model based on a homogeneous mixture of *N* seeds. The mixing model 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 (see Carlo et al. 2013 for a full description of mixing model).

Estimating seed dispersal at large scale

In order to define an area to represent seed dispersal exclusively at the large scale (i.e. excluding short-distance events occurring in the immediate neighborhood of source trees), we focused on the ring-shaped section between 70 m and 150 m from the center with the ^{15}N-marked trees in each study plot, containing thus $n = 84$ sampling stations per plot (Fig. 1B). This section, hereafter referred to as LSD (Large-Scale Dispersal) area, accounted for 78.8% of the surface of the study plot. We considered that seed deposition in the LSD area best estimated the tail of seed dispersal kernels of the two tree species. In other words, LSD areas were far from source trees but still received a relevant proportion of seed deposition. Indeed, previous studies explicitly modeling seed dispersal kernels of the same tree species in the same study sites, have described a kernel tail approximately at the same distance range (Herrera, Morales, & García 2011; Carlo et al. 2013).

We sought to represent, for each tree species, the large-scale dispersal within each study landscape, relative to the quantity of seeds that had been marked in source trees. For this, we first estimated the *LSD arrival rate* as the number of LSD sampling stations per plot receiving at least one ^{15}N-marked seed, weighted by the number of fruits that were present in the source trees of each plot at the beginning of the fruiting season (in order to avoid the biases in arrival probability associated to the differences between plots in number of marked fruits, and in the concomitant number of marked seeds potentially leaving source trees). For representation purposes, this variable was multiplied by 1000. Second, as a comparative measure of the magnitude of seed dispersal far from sources in each plot, we estimated the *Proportion of seeds at LSD*, as the quotient between the number of marked seeds collected in the LSD sampling stations and the total number of marked seeds collected in the whole 150 m radius plot. We considered that values of the Proportion of seeds at LSD under 0.78 indicated limitation in large-scale dispersal, given that 78% of sampling stations (84 from 108) were located in the LSD area (that is, with no limitation to dispersal, one would expect to find a percentage of dispersed seeds in the LSD area stations proportional to their spatial coverage).

Statistical analysis

Our goal was to test the effect of the landscape structure on the ability of both hawthorn and holly to achieve effective large-scale seed dispersal, using the availability of forest cover as a major predictor variable, and both LSD arrival rate and the proportion of seeds at LSD as different response variables. As we approached variability in the seed dispersal process from a landscape-scale perspective, we considered each individual landscape (i.e. plot) to be a sampling unit and thus a replicate. Given that there was one high and one low forest cover plot at each of the four sites (Fig. 1B), our design thus had four replicates per forest cover category (High, Low), and only two replicates per study site. This small-sized design was unbalanced and precluded the use of generalized linear models that could estimate the effect of forest cover in seed dispersal by simultaneously controlling for paired site variability by, for example, considering site as a random or a fixed factor (Crawley 2002). We therefore used non-parametric Wilcoxon paired-sample tests (Zar 1996) to estimate the effects of forest cover level in each site (high vs. low) on both LSD arrival rate and the proportion of seeds at LSD. This led to a comparison of four pairs of replicates to test whether each of these measures of large-scale dispersal was consistently increased or reduced (one-sided test) in high/low forest cover landscapes. This sort of straightforward analytical procedure takes into account the logistical difficulties of achieving high replication in large-scale studies (e.g. Rodríguez-Cabal, Aizen, & Novaro 2007). Throughout the text, averages are reported with error bars representing the data range (i.e. minimum-maximum values).

Results

Forest cover in the study plots ranged from 6.7% to 59.9%, with landscapes classified as high cover averaging 37.6% (13.3–58.9), and low cover landscapes averaging 14.6% (6.2–27.0). The average percentages of forest cover in the LSD areas (i.e. the ring at 70–150 m radius surrounding the central area) for high and low forest cover landscapes, respectively, were 46.6% (15.1–75.0) and 16.6% (7.4–31.3). Forest cover in LSD areas was highly correlated with forest cover in the whole plots across sites (Spearman correlation: $r = 0.99$, $P < 0.0001$, $n = 8$), and accounted for between 87.6 and 99.5% of such forest cover. Therefore, all paired plots classified as high and low cover landscapes showed, respectively, paired high and low percentages of forest cover in LSD area.

The total number of ^{15}N-marked seeds collected within the study plots varied substantially across both species and sites, with the average number of seeds per site being 12.5 (1–29) for hawthorn and 116.6 (34–290) for holly. Nevertheless, the two tree species did not differ in the average seed dispersal farther away from source trees, as judged by LSD arrival rate (hawthorn: 0.51, 0–1.45; holly: 0.42, 0.11–0.76; Wilcoxon test: $W = 15$, $P = 0.726$) and the proportion of seeds at LSD (hawthorn: 0.37, 0.0–0.75; holly: 0.56, 0.11–0.86; Wilcoxon test: $W = 11$, $P = 0.362$). Arrival rate was positively correlated with the proportion of seeds at LSD (Spearman correlation: $r = 0.72$, $P < 0.001$, $n = 16$). That is, the higher the proportion of dispersed seeds reaching the LSD area from source trees, the more spatially spread LSD dispersal was within the landscape.

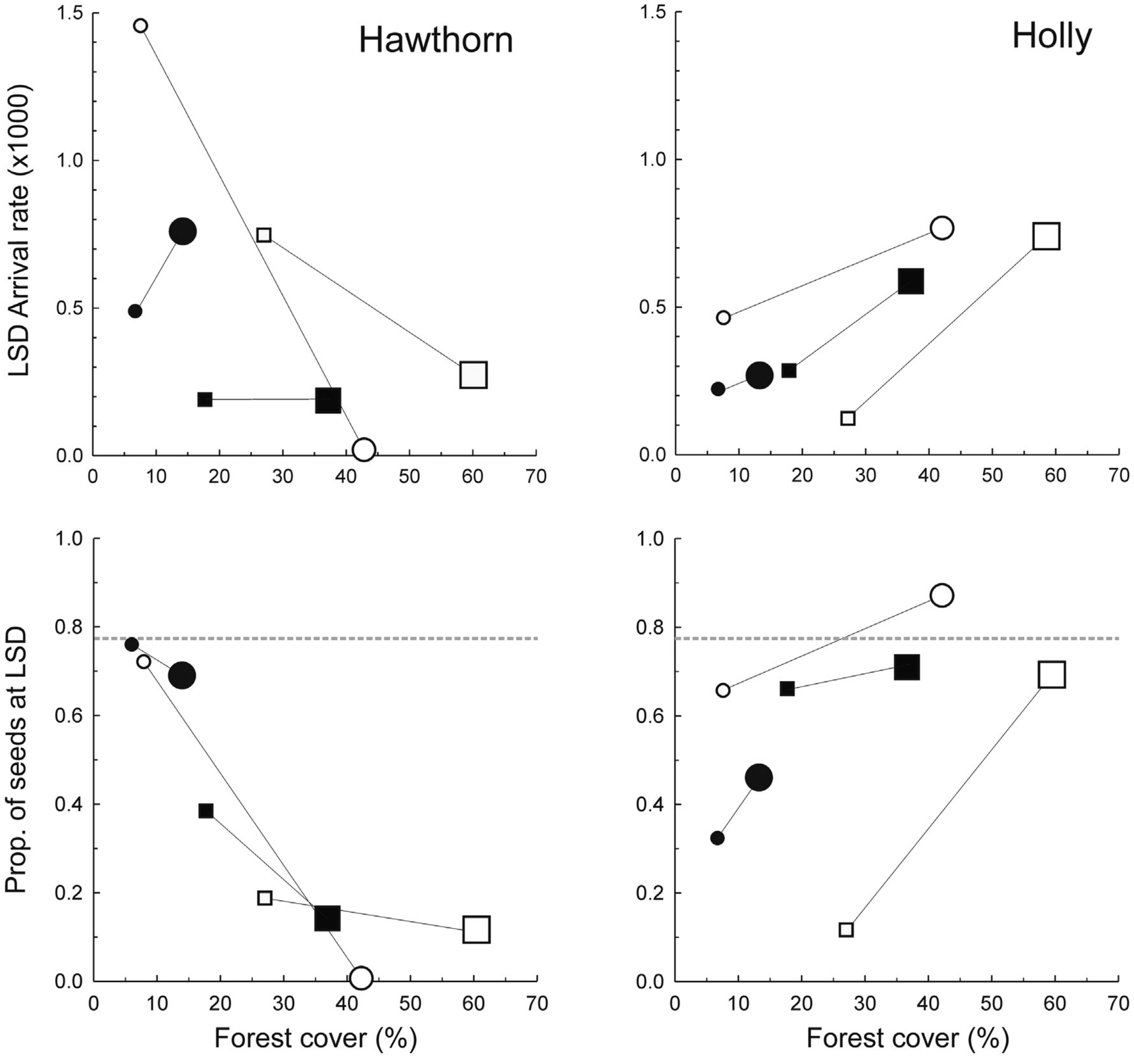

Fig. 2. Values for LSD Arrival rate (number of LSD sampling stations per plot receiving at least one ^{15}N-marked seed, weighted by the number of fruits marked in the plot center, multiplied by 1000) and Proportion of seeds at LSD (ratio between the number of marked seeds collected in the LSD area and the total number of marked seeds collected in the whole plot) of the two tree species studied, in relation to forest cover at the different study landscapes (black dots, Sierra de Peña Mayor; white dots, Puertos de Marabio; black squares, Puerto de San Lorenzo; white squares, Sierra del Aramo). Big and small symbols representing, respectively, values of landscapes with high and low forest cover values at each site. Symbols of the same site are linked by a line. The gray dashed line in bottom panels indicates the threshold value of the Proportion of seeds at LSD (0.78) under which limitation in large-scale dispersal would occur.

Large-scale seed dispersal was significantly affected by the amount of forest cover in the landscapes, but forest cover had differential effects on the dispersal of each tree species (Fig. 2). In the case of holly, the values of both LSD arrival rate and the proportion of seeds at LSD were consistently higher in high forest cover landscapes than in low cover landscapes across all sites (Wilcoxon test: $W = 10$, $P = 0.050$; for both response variables). In other words, comparatively more dispersed seeds reached a larger proportion of sites in the LSD area of high forest cover landscapes. Interestingly, only in these high forest cover landscapes holly seed dispersal reached the threshold value of large-scale limitation (0.78; Fig. 2). In the case of hawthorn, there were no global differences between landscape types in LSD arrival rates (Wilcoxon test: $W = 3$, $P = 0.292$), although this seed dispersal parameter did decrease with increasing forest cover in two of the four sites (Puertos de Marabio and Sierra del Aramo; Fig. 2). Nevertheless, in terms of the proportion of seeds at LSD, dispersal from hawthorn trees was consistently weaker in high forest cover landscapes than in low cover landscapes across sites (Wilcoxon test: $W = 0$, $P = 0.050$). That is, even when the probability of finding hawthorn dispersed seeds in the LSD area was independent of forest cover, after leaving source trees, the probability of a hawthorn seed reaching the LSD area decreased with increasing forest cover in the landscape. Indeed, hawthorn seeds suffered stronger limitation to large-scale dispersal in high cover landscapes than in low cover ones (Fig. 2).

Discussion

Here we estimate the movement of bird-dispersed seeds, quantifying the large-scale dispersal from source trees of two species in landscapes representing a gradient of forest cover across a wide geographic region. We empirically demonstrate that the seed dispersal patterns produced by shared frugivore species for two tree species growing side-by-side can differ depending upon the structure of the surrounding landscape. Contrary to what would be expected from their sharing of a dispersal syndrome (similar fruits, partially overlapped fruiting phenologies, and shared frugivore species) and a common origin point for dispersal, we found that hawthorn and holly showed opposite patterns of response to landscape structure: the same high forest-cover landscapes led to weaker large-scale seed dispersal in hawthorn but favored it in holly.

This main finding builds upon previous studies in the system. For example, earlier studies have evidenced the occurrence of long-distance dispersal in the tree species studied, highlighting that this sort of dispersal is directed to specific microhabitats such as fleshy-fruited trees (Carlo et al. 2013). Also, other studies have found that the seed dispersal kernel may depend on the structure of the neighborhood around source trees (Herrera et al. 2011), and have evidenced different shapes for the kernels of different tree species occupying different sectors of the same landscape (Martínez & González-Taboada 2009). The present results thus qualitatively improve the previous findings by showing explicitly how different tree species respond differentially to large-scale habitat heterogeneity through the seed dispersal process. Our findings also evidence how these tree species may be differentially affected by large-scale dispersal limitation depending on landscape structure.

In this work, we used a ^{15}N-marking technique that enabled us to easily label thousands of seeds on source trees and to track their dispersal using batch-processing procedures. This method allows for finding a needle (i.e. a marked seed) in a haystack (i.e. all seeds deposited in a sampling station) by sampling entire haystacks. This technique has been previously tested on herbaceous plants and shrubs (Carlo et al. 2009; Morales, Rivarola, Amico, & Carlo 2012), but this is the first time that it has been used on large woody trees to examine dispersal at large scales. The cost of the isotope salts used (urea 99.8% ^{15}N) and the mass spectrometry for working in eight landscapes and processing nearly 167,000 seeds reached ~30,000 USD. A drawback of working with trees was that the per-capita enrichment level of seeds was lower and more variable than has been previously reported with smaller plants (Carlo et al. 2009, Morales et al. 2012), which reduced our capacity to find "the needle in the haystack". We thus recommend that future studies using this method with trees should apply approximately double the amount of ^{15}N volume used here to ensure stronger signatures, and thus strengthen the methodology's ability to detect dispersal events.

Several processes may underlie the differences between tree species in seed dispersal patterns evidenced here, as suggested by complementary information collected at the same study sites over the same time period. First, bearing in mind that different species of frugivorous thrushes may show different patterns of habitat use in the same locality (García, Martínez, Herrera, & Morales 2013; Morales, García, Martínez, Rodríguez-Pérez, & Herrera 2013), one could argue for frugivore-plant specialization (e.g. Poulsen, Clark, Connor, & Smith 2002; Clark, Poulsen, Bolker, Connor, & Parker 2005) explaining the differences in dispersal patterns between tree species (see also Cramer et al. 2007). In this sense, although it has been suggested that the diet of the different thrushes depends more on the relative abundance of fruiting species each year than on intrinsic fruit preferences (García et al. 2013), some bias in the use of tree species by specific frugivores may occur. Namely, there is a biased use of holly by redwing (Martínez et al. 2008), apparently due to a temporal partitioning of interactions caused by the phenology of the tree species and the timing of bird wintering: holly fruits ripen later in the autumn than those of hawthorn, and migrant redwings arrive in the Cantabrian Range later than the other thrushes (many of which have resident populations). Data from the same year in the Sierra de Peña Mayor study site show some temporal segregation in the frugivore-plant interactions (Appendix A: Fig. 1). On the one hand, all species of thrushes feed on all trees during autumn (October-November, with hawthorn receiving a relatively higher consumption rate by a diverse array of thrushes), but in winter (December–January), thrushes feed primarily on holly fruits (with redwing being the main frugivore) even while hawthorn fruits are still available. Furthermore, data from bird abundance in the four study sites in 2009 shows that redwing increased their relative abundance from autumn to winter (D. Martínez and D. García, unpublished data; Appendix A: Fig. 2). As, compared to other thrushes, redwing is especially prone to concentrating its foraging and seed dispersal activity in high forest cover areas (García et al. 2013; Morales et al. 2013), holly seeds would be thus expected to have a higher probability of being dispersed where forest cover is high, even at distances far from source trees, as indeed is shown in this work.

Second, a distinct landscape-scale distribution of tree species may also underpin the differences in seed dispersal response to habitat structure. If, besides different fruiting phenologies, co-occurring tree species have different patterns of global spatial distribution, one would expect frugivores to cope with different fruiting landscapes for each tree species across the season, which would predict changes in plant dispersal kernels (Morales & Carlo 2006). This was probably the case in the study year and sites, where holly fruit production was 7-fold that of hawthorn, and holly accounted for ca. 70% of the individual trees of all fleshy-fruited species across forests (Appendix A: Fig. 3). Furthermore, there was a positive correlation between the abundance of holly fruits and forest cover in all sites (Appendix A: Fig. 4), probably resulting from the dominance of holly in larger forest patches (García et al. 2013). Conversely, weaker correlations between forest cover and fruit abundance were found for hawthorn, derived from the occurrence of this species in both large forests and in small patches, and even as remnant trees isolated in the open matrix (see also Herrera & García 2009). Thus, from the perceptual perspective of thrushes searching for fruits, high forest cover implies more holly fruits, but not necessarily more hawthorn fruits.

In sum, when birds fed mostly on hawthorn early in the fruiting season, they were exploiting a less abundant and less predictable fruit resource in the landscape. In this context, birds could be improving fruit foraging by concentrating their activity in small-extent neighborhoods when inhabiting high forest cover landscapes (thus moving less seeds far from sources when these occur in those landscapes), although they are still able to track for fruits in farther, including isolated, patches in low-cover landscapes (thus favoring distant seed deposition in these areas; see also Herrera & García 2009). Such a behavior could finally lead to the negative relationship between hawthorn large-scale dispersal and forest cover found here. Conversely, at the peak of ripe holly fruit abundance later in the season, birds (mostly redwing) would find a predictable landscape of high connectivity with abundant fruit resources in most forest patches, and they could use the habitat depending mostly on forest cover (see also García et al. 2011; Martínez & García 2015). In this context, more bird movement between forest patches, even when patches are far from each other, would be expected in high forest cover landscapes, leading to a positive effect of forest cover on holly large-scale seed dispersal.

Concluding remarks

This study suggests that the landscape distribution of fruiting plants, plant phenology and frugivore behavior interact to affect seed dispersal in contrasting ways for different plant species in the same landscapes. This is important because it is assumed that plant species with different dispersal syndromes (i.e. wind vs animal) would respond differentially, but plants from the same functional group would present unified dispersal responses to the same scenarios of landscape variability (e.g. habitat loss; McEuen & Curran 2004; Damschen et al. 2008). Our study shows that this type of generalization may not be appropriate in models which do not give consideration to the effects of phenology, plant distribution and frugivore responses. In the case of holly, seed dispersal is probably imposing a spatial positive feed-back, as large-scale dispersal is more frequent in more forested landscapes (already occupied by many adult plants), and a negative demographic effect of habitat loss is expected (as suggested at a geographical scale for this species; Montoya, Alburquerque, Rueda, & Rodríguez 2010). Conversely, in the case of hawthorn, large-scale dispersal was promoted in low covered landscapes (see also Herrera et al. 2011, for an inverse modeling approach, and Carlo & Morales 2008, for theoretical model), a fact that could endow this species with a greater ability to colonize the deforested matrix (i.e. a higher resilience to habitat loss and fragmentation; García et al. 2013). Clearly, animal-mediated seed dispersal must be interpreted not only as a mechanism of plants to respond to large-scale environmental heterogeneity, but also as a process driving, for different plant species, the probability of disappearing from current communities due to the filtering effects of environmental change.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.baae.2016.01.003.

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