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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.
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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

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