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Research article

Effects of habitat alteration on the effectiveness of plant-avian seed dispersal mutualisms: Consequences for plant regeneration

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ABSTRACT

Anthropogenic habitat alteration may affect the dispersal service provided by avian seed dispersers, ultimately causing regeneration collapse, through a decay in both the quantitative (seed removal) and qualitative (seed arrival to safe sites) components of seed dispersal effectiveness. However, despite its implications for management in real-world landscapes, few studies have investigated the shifts in components of seed dispersal effectiveness resulting from habitat alteration. We advocate the use of stage-specific transition probabilities, combined with data on seed shadows and bird abundance and mobility, for a mechanistic inference of the consequences for recruitment of the disruption of plant-frugivore mutualism in altered habitats. Such an approach allows the identification of regeneration bottlenecks, evaluates the differential contribution to recruitment of quantitative and qualitative components of seed dispersal, and provides the means to compare seed dispersal limitation. We exemplify our conceptual approach with studies of seed dispersal and recruitment in the wild olive tree in unaltered and severely altered adjacent sites. We show that simplification of the habitat substantially affected bird abundance, diversity and mobility, which caused a reduction in fruit removal and a concomitant simplification of the seed shadows compared to the unaltered site. Linked to these shifts, postdispersal seed survival and seedling emergence and survival were affected. The final outcome of habitat alteration was the collapse of the regeneration dynamics with very few seeds escaping the influence of maternal plants and reaching the safest sites for recruitment (dispersal limitation). As predicted, the collapse in the regeneration dynamics resulted from severe decays in the quantitative but especially in the qualitative components of seed dispersal effectiveness. Management of fleshy-fruited plant populations in altered habitats should thus pay attention to landscape elements that promote frugivore abundance, diversity and mobility and that alleviate the dispersal limitation.

Introduction

Seed dispersal effectiveness (revised in Schupp et al., 2010) assesses the overall effectiveness of dispersal that a plant receives from its assemblages of dispersal agents. It states that an effective seed dispersal requires not only that the seeds are being dispersed but seed dispersal is resulting in successful establishment of new individuals. This idea stems from the seed disperser effectiveness framework of Schupp (1993), and separates quantitative and qualitative components on the seed dispersal. Influenced by this idea, it has been proposed that the plant-avian seed dispersal mutualism has cascading effects on plant population recruitment (Herrera et al., 1994; Jordano and Herrera, 1995). Through selecting fruits and differentially moving across the landscape, frugivores may filter the seeds that enter into the regeneration cycle of plant populations (e.g., Alcántara and Rey, 2003; Martinez et al., 2007; Lázaro and Traveset, 2009) and generate the spatial template for subsequent processes of plant recruitment, like postdispersal seed survival, seed germination and seedling emergence and survival (Herrera et al., 1994; Schupp and Fuentes, 1995; Alcántara et al., 2000a; García et al., 2005). Under this view, Herrera et al. (1994) developed a framework of stage-specific transition probabilities for plant recruitment which has been used with many species to evaluate the contribution of frugivore seed dispersal to plant population recruitment in natural and/or semi-natural habitats (Rey and Alcántara, 2000; García, 2001; Traveset et al., 2003; Rodríguez-Pérez and Traveset, 2007; Rother et al., 2013, among others). These studies have shown that fruit removal and seed arrival to different

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microhabitats are frugivore-related processes of fundamental relevance in the quantitative estimation of overall probabilities of recruitment, as well as for determining the net contribution of different microhabitats to recruitment.

Habitat loss, fragmentation and alteration by anthropogenic causes are currently an issue of major concern for ecologists and conservation biologists (Fahrig, 2003). Anthropogenic habitat alteration (for example, by agricultural practices, hunting, selective logging, livestock management, wild fire or urbanization) affects the abundance, diversity and/or activity of avian seed dispersers (Alcántara et al., 2000b; García et al., 2010; García and Martínez, 2012; Markl et al., 2012). A decay in effectiveness of seed dispersal mutualisms with implications for plant recruitment and population regeneration (i.e. seed dispersal service) is thus expected under anthropogenic habitat alteration through modification of both the quantitative (seed removal) and qualitative (seed arrival to safe sites) components of seed dispersal (García and Martínez, 2012). Despite their important implications for plant population management in real-world landscapes, few studies have integrated the shifts resulting from habitat alteration in the demographic processes involved in plant recruitment (but see Kolb et al., 2010; González-Varo et al., 2012). Just recently, shifts in several frugivore-related components of the recruitment process have begun to be investigated in fragmented landscapes, highlighting that in such landscapes plant–animal mutualisms may be seriously disrupted (e.g., García and Chacoff, 2007; Rodríguez-Cabal et al., 2007; Cordeiro and Howe, 2003; Cordeiro et al., 2009; González-Varo et al., 2012). It remains unclear whether such disruption affects recruitment by safe site limitation or seed dispersal limitation (Cordeiro et al., 2009; Herrera and García, 2010; González-Varo et al., 2012). However, habitat loss and fragmentation are just part of the gradient of habitat alteration (McIntyre and Hobbs, 1999), and many minimally fragmented habitats are nevertheless substantially modified in species composition, diversity and cover in comparison with non-altered habitats (i.e. they are affected by structural fragmentation *sensu* Lord and Norton, 1990).

Here we combine the ‘seed dispersal effectiveness’ (Schupp et al., 2010) and ‘stage-specific transition probabilities for plant recruitment’ (Herrera et al., 1994; Rey and Alcántara, 2000) frameworks for assessing the demographic effects of habitat alteration in animal-dispersed plants. We apply an integrative approach to recruitment (from seed dispersal to juvenile survival). We advocate the use of stage-specific transition probabilities, combined with data on seed shadows around maternal plants, and bird abundance and mobility through the habitat, to develop a mechanistic inference of the consequences for recruitment of the disruption of plant-frugivore mutualisms in altered habitats. Such an approach allows the identification of population regeneration bottlenecks, evaluates the differential contribution to recruitment of quantitative and qualitative components of seed dispersal, and provides insights to comparatively assess seed dispersal limitation among habitats. We hypothesize that under habitat alteration, the regeneration of bird-dispersed plant populations will be limited compared to natural and semi-natural habitats because of the modification of seed distribution patterns that have cascading effects on recruitment. We predict that habitat alteration changes the abundance, diversity and/or activity of avian seed dispersers (e.g., Markl et al., 2012), affecting not only seed removal rates (quantitative component), but also the number of seeds that escape the influence of maternal plants and the number and proportion of seeds being deposited in the safest sites for the recruitment of new individuals (qualitative component of the effectiveness of seed dispersal). A final consequence of such shifts may be a collapse in population regeneration. We will exemplify our conceptual approach and test these predictions using seed dispersal studies of the wild olive tree (*Olea europaea*) as a case study.

Methods

Study system and sites

The wild olive (*Olea europaea*, Oleaceae) is a small tree widely distributed through the Mediterranean Basin which produces winter-ripening fleshy fruits highly attractive to birds because of their high lipid content. It is one of the most representative species of mature Mediterranean scrublands and forests under thermo-mediterranean and infra-mediterranean bioclimates. Specifically, it dominates certain communities in these bioclimates and together with its companion species forms a habitat that has been cataloged as of special interest for conservation by European Union directives (Rey et al., 2009). This habitat constitutes an important Mediterranean wintering habitat for many insectivorous and frugivorous birds in the Western Paleartic. Details on the natural history of this species may be found in Jordano (1987), Alcántara et al. (1997a,b, 2000a,b), Rey and Alcántara (2000), and Rey et al. (1997, 2004). The fruit of the wild olive tree is a drupe that contains a single dispersal unit formed by a seed (embryo plus endosperm) wrapped in a hard endocarp (the whole unit hereafter referred as a seed). Small- to medium-sized frugivorous birds, mainly species of the genera *Turdus* and *Sylvia*, act as seed dispersers for this species. Seeds are dormant for around 20 months during which time they may be consumed by small rodents (e.g., genus *Apodemus*). Seed germination occurs during the second winter after dispersal. The emerged seedling can be harmed by water stress, physical damage (e.g., trampling, fallen branches), generalist vertebrate and invertebrate herbivores, sap-feeding insects (mainly *Euphyllura olivina*, Homoptera), and fungal attack. Approximately one year after germination, seedlings acquire adult vegetative traits (woody stems and wax-covered leaves) and become a sapling. Reproductive age is achieved after 7 or 8 years under garden conditions, but much later in the field. Adult plants can live for hundreds of years.

Data presented here come from the Sierra Sur de Jaén (37° 40′ N, 3° 45′ W; Jaén province, southern Spain). In this area we selected two adjacent sites where *O. europaea* is one of the dominant woody plants. Sillón del Rey (4.5 ha) is a highly disturbed scrubland site on a plateau dedicated to livestock grazing which has been subjected to this type of anthropogenic disturbance for more than 50 years. The vegetation is composed of an herbaceous layer with scattered *O. europaea* (9 trees/ha) and *Pistacia terebinthus*, which confers a savannah-like appearance to the site. In contrast to this site, La Parrilla (2.5 ha) is a well-preserved scrubland site on a ravine with dense and large patches composed of tall scrubs, small trees, and vines, separated by small open interspaces. It is dominated by *O. europaea* (17 ha^{-1}), *P. terebinthus*, *Phillyrea latifolia*, and *Quercus coccifera*. This site has remained largely unaltered for the last 50 years. Apart from the very different level of anthropogenic alteration there are some altitudinal and aspect differences between sites: ca. 80 m lower altitude in the unaltered site, which has a NW oriented slope. Ortho-photographs of these two sites for 2008 and 1954 are shown in Appendix 1.

Data collection

Data used to illustrate our conceptual approach have been partially published elsewhere. The published information comes from Alcántara et al. (1997a, 2000a,b) and Rey and Alcántara (2000). New unpublished information, specifically concerning seed shadows, seed arrival to different microhabitats, and seed predation,