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Original article

Landscape effects on jay foraging behavior decrease acorn dispersal services in dehesas

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ABSTRACT

Dehesas are savanna-like, oak woodlands with a high conservation value that are threatened by chronic regeneration failure. Acorn dispersal by Eurasian jays (*Garrulus glandarius*) is vital for oak recruitment although jay preference for continuous forests may condition this mutualism in dehesas. In this study, we evaluated whether the acorn dispersal services provided by jays to oaks differed between both habitats and assessed factors that could potentially drive such differences. We (1) monitored acorn removal rates at feeders located close to focal trees in a holm oak (*Quercus ilex*) forest and in a nearby dehesa over a 6-year period; (2) measured the spatial traits of focal trees and their acorn production; and (3) monitored dispersal distances and microhabitat selection for acorn caching during 2012.

Our results indicated that jays were able to exploit dehesas located close to forest habitats, but did so infrequently and as a secondary food source (acorn removal rates were six times lower in dehesa than in nearby forests). This likely occurred because dehesas did not offer new or more abundant food sources on a landscape scale. In forests, tree choice was driven by crop traits while in dehesas it was driven by spatial location. Jays preferentially foraged at dehesa trees near forest patches and aggregated to other trees, regardless of crop traits. Acorns were mobilized four times closer in dehesas, and seeds were preferentially cached in unsuitable microhabitats for seedling establishment. Our results suggest that (i) distance to forest habitats and tree isolation effects on jay foraging behavior reduces their dispersal services in dehesas as compared to nearby forests, and (ii) practices designed to enhance acorn dispersal by jays in this habitat should focus on the maintenance or creation of forest patches interspersed within dehesa areas.

1. Introduction

Seed dispersal is a key factor in the maintenance of most plant populations (Farwig and Berens, 2012 and references therein), especially for large-seeded, dominant forest trees that depend on keystone animal-plant mutualisms (Herrera et al., 2011; Schupp et al., 2010). Many studies have highlighted the importance of seed dispersers for buffering the effects of environmental changes on plant regeneration potential (e.g. Hampe, 2011; Higgins and Richardson, 1999). However, mutualistic relationships are context-dependent and global change drivers may shift the outcomes of plant–animal interactions (Agrawal et al., 2007; McConkey et al., 2012). In particular, changes in land use may alter key environmental factors such as the food and habitat available for dispersers, local competition for sources, matrix permeability to their movement, or the perceived risk of predation. Under such new conditions, dispersers may modify their foraging behavior altering seed dispersal patterns, which set the template on which recruitment occurs (as reviewed in McConkey et al., 2012). Landscapes are changing in the world. Thus, detecting environmental factors that impact seed-dispersers foraging decisions and seed deposition patterns in anthropogenic habitats provides highly valuable information for the assessment of plant vulnerability to land use change, as well as the development of adequate conservation policies.

Natural-human systems with contrasting landscape configurations are largely distributed within the Mediterranean Basin (Blondel, 2010). Among them, savanna-like holm oak (*Quercus ilex*) woodlands (dehesas and montados) are of particular interest due to the wide areas they cover, the high biological diversity they host, and the great cultural heritage they hold (Campos et al., 2013; Diaz et al., 1997). Although holm oaks are often considered as resistant to global change due to their drought tolerance as adults (David et al., 2007; Tognetti et al., 1998), recent research indicates recruitment

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limitations in dehesas as a result of low seed dispersal to safe sites for seedling establishment (Pulido et al., 2010; Pulido and Diaz, 2005; Smit et al., 2008). The oak (*Quercus* spp.) - Eurasian jay (*Garrulus glandarius*) relationship is a typical example of a seed dispersal mutualism that may buffer management effects on oak regeneration potential (Bossema, 1979; Purves et al., 2007). Jays provide high-quality seed dispersal to oaks in forest habitats, where they nest and forage (Brotons et al., 2004; Santos et al., 2002), by mobilizing acorns to safe sites for oak recruitment, and have the potential to connect habitat mosaics (Gomez, 2003). Therefore, efficient dehesas exploitation by jays would result in the enhancement of seedling recruitment in these habitats and/or their connection with nearby forests.

The goals of this study were: (1) to determine if the dispersal services provided by jays in dehesas differed from those found in forest habitats, and (2) to assess which factors could drive such differences. In general, forest-dwelling animals are more prone to exploit non-forested areas if they offer different or more abundant food sources (e.g. DaSilva et al., 1996). However, the food source in dehesas and forests during autumn is the same (acorns). Therefore, the attractiveness of this habitat to jays may depend on higher acorn production at the landscape scale or on the higher crop quality of dehesa trees. In dehesas, tree thinning and pruning results in higher acorn production. However, low stand density (10–30 stems/ha) may counteract this effect, leading to similar acorn production at the landscape scale in both types of habitats, discouraging jays from exploiting dehesas. For such a case, low visitation rates would hamper acorn dispersal by jays in this habitat.

Between-habitat differences in visitation rates may be related to differences in the key environmental factors driving tree-choice by jays. Reaching trees in dehesas may imply a high cost for jays whose nesting territories are centered in forest patches (Pons and Pausas, 2008). For such conditions, we expected that the spatial location of trees (distance to forest habitats and isolation) would override crop trait effects on tree choice (see Luck and Daily, 2003; Pizo and dos Santos, 2011 for frugivorous forest-dependent birds). On the contrary, in forest habitats we expected jays to select trees based on crop traits that enhance foraging benefits (Blendinger et al., 2008; Sallabanks, 1993). In such case, practices designed to enhance the seed dispersal services of jays in dehesas should focus on managing landscape structure rather than enhancing crop quantity or quality of individual trees.

Jays may deposit acorns differently in forests and dehesas, as seed dispersal distances and their habitat selection for acorn caching largely depends on landscape composition and structure (Gomez, 2003; Pons and Pausas, 2007a). Since jays cache acorns for later consumption, their hoarding strategies facilitate seed retrieval and hamper cache pilferage by other granivores. In terms of mobilization distances, we hypothesized that jays would mobilize acorns collected in dehesas towards forest habitats (nesting sites) (Yahner, 2012). Such a practice would entail higher dispersal distances in dehesas and the maintenance of landscape connectivity between both habitats. Regarding microhabitat selection, we expected a strong negative selection by jays for tree canopies and shrubs in forests in order to avoid cache pilferage by rodents or wild boars (Gomez, 2003; Pons and Pausas, 2007a). However, lower mouse and wild boar abundances in dehesas (Díaz, 2014) would relax microhabitat selection for acorn caching. Since microhabitat-related, post-dispersal acorn predation and seedling dry-out are the main bottlenecks for oak early recruitment stages in Mediterranean areas, differences in microhabitat selection by jays could have important effects on final seed fate (Gomez, 2004; Pulido et al., 2010; Smit et al., 2008).

In summary, at the outset of the experiment, we expected a low use of dehesas by jays leading to limits for seed dispersal. We hypothesized that low dispersal services provided by jays in dehesas would be related to similar acorn production than forests at the landscape scale together with the increased costs associated with reaching dehesa trees. Therefore, we expected that jay foraging preferences in dehesas would be driven by the spatial location of trees rather than by crop quality, opposite to our expectations in forests. Finally, we expected that acorns collected in dehesas would be mobilized towards forests, entailing increased dispersal distances and promoting spatial connectivity between habitats.

2. Methods

The overall goals of determining whether and why dispersal services provided by jays in dehesas differ from those found in forests were divided into the following related aims.

(1) To determine how and why jays use the dehesas as a food source during the fall, we monitored acorn removal rates at feeders located close to focal trees in a forest and in nearby dehesa plots over a period of 6-years. We also simultaneously measured acorn production in both habitats in order to assess whether between-habitat differences in visitation rates were related to acorn production at the landscape scale or to differences in the crop quality of focal trees.
(2) To determine if key factors driving tree-choice by jays differed between the forest and dehesa, we tested the effects of crop quality and the spatial location of trees on acorn removal rates in each habitat.
(3) To test between-habitat differences on seed deposition patterns we monitored dispersal distances and microhabitat selection for seed caching during the winter of 2012 in both habitats. Specific expectations, methods, and sample sizes for each related analysis are provided in Table 1.

2.1. Study area and experimental design

We studied holm oaks and the behaviour of Eurasian jays (*G. glandarius*) in the National Park of Cabañeros (Ciudad Real province, central Spain, 30S 385450, UTM 4353479, see Díaz et al., 2011 for details and map). The climate is Mediterranean with hot dry summers and mild wet winters, has a characteristic period of summer drought, and strong among-year variability in temperature and rainfall. Mean annual rainfall was 636 mm for the period from 1985 to 2009 (range 291–920 mm) and the mean annual temperature was 15.0 °C (range 14.0–16.7 °C).

Two spatial configurations of oak woodlands are found in the park: forests and dehesas. Forests occupy hills and lower slopes. The tree density is 97 trees ha^{-1}, on average, and understory cover is well developed (>60% of shrub cover). Dehesas occupy plain lowlands and are savannah-like woodlands (12 trees ha^{-1}, on average). Scattered trees grow in an open grassland matrix with almost no shrub cover (<1%). To monitor acorn removal rates by jays, we selected 46 holm oak trees in 2005 (20 in two forest sites and 26 in two dehesa sites). We selected focal trees so that they spanned the range of spatial locations and tree characteristics that potentially influence jay foraging decisions (crop size, acorn size, infestation rates, isolation from nearby trees, and distance to forest habitats; Bossema, 1979; Dixon et al., 1997; Perea et al., 2011; Pons and Pausas, 2007b, Table 2). To facilitate use by different individual birds, we also selected focal trees as spaced as possible (within an area of 780 ha). In February 2012, we selected 16 trees from our original pool in order to video-record birds and radio-track acorns (eight trees per habitat). During this period, we divided the study area into two blocks. Trees within areas of 150 ha encompassing four video-monitored trees located in forests and four video-monitored trees