Acta Oecologica 71 (2016) 73–79

Contents lists available at ScienceDirect

Acta Oecologica

journal homepage: www.elsevier.com/locate/actoec

Original article

Introducing cultivated trees into the wild: Wood pigeons as dispersers of domestic olive seeds

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ARTICLE INFO

Article history:
Received 8 July 2015
Received in revised form
15 September 2015
Accepted 17 September 2015
Available online 26 September 2015

Keywords:
Columba palumbus
Frugivory
Olea europaea
Seed dispersal
Seed size

ABSTRACT

Animals may disperse cultivated trees outside the agricultural land, favoring the naturalization or, even, the invasiveness of domestic plants. However, the ecological and conservation implications of new or unexplored mutualisms between cultivated trees and wild animals are still far from clear. Here, we examine the possible role of an expanding and, locally, overabundant pigeon species (*Columba palumbus*) as an effective disperser of domestic olive trees (*Olea europaea*), a widespread cultivated tree, considered a naturalized and invasive species in many areas of the world. By analyzing crop and gizzard content we found that olive fruits were an important food item for pigeons in late winter and spring. A proportion of 40.3% pigeons consumed olive seeds, with an average consumption of 7.8 seeds per pigeon and day. Additionally, most seed sizes (up to 0.7 g) passed undamaged through the gut and were dispersed from cultivated olive orchards to areas covered by protected Mediterranean vegetation, recording minimal dispersal distances of 1.8–7.4 km. Greenhouse experiments showed that seeds dispersed by pigeons significantly favored the germination and establishment in comparison to non-ingested seeds. The ability of pigeons to effectively disperse domestic olive seeds may facilitate the introduction of cultivated olive trees into natural systems, including highly-protected wild olive woodlands. We recommend harvesting ornamental olive trees to reduce both pigeon overpopulation and the spread of artificially selected trees into the natural environment.

1. Introduction

Seed dispersal by animals is crucial for the dynamics and regeneration of many ecosystems (Willson and Traveset, 2000; Wang and Smith, 2002). Animals that consume fruits can inadvertently contribute to the colonization of new environments by facilitating long-distance dispersal (Jordano et al., 2011). In fact, long-distance dispersal has a critical impact in ecology and conservation because it influences many key aspects of plant biology, including population dynamics, biogeographic patterns and biological invasions (Sauer, 1988; Cain et al., 2000; Clobert et al., 2012).

Today, intensive agriculture is considered a major anthropogenic driver that has strongly modified land-use patterns worldwide (Lambin and Meyfroidt, 2011). In addition, agricultural practices have favored the introduction of new cultivated genotypes and phenotypes, mostly based on artificial selection. However, these cultivated plants may have a short evolutionary history with the concurrent assemblage of possible seed dispersers. This is especially important for mosaic landscapes where animals may disperse cultivated plants to suitable microsites outside the agricultural land, favoring the naturalization, and sometimes, the invasiveness of cultivated plants. However, the effectiveness and ecological consequences of new or unexplored mutualisms between cultivated plants and long-distance seed dispersers are still far from clear (Delibes et al., 2012).

Domestic olive trees (*Olea europaea* L. subsp. *europaea* var. *europaea*) were domesticated about 6000 years ago in the Near East and in the Iberian Peninsula (Besnard et al., 2001; Terral et al., 2004). Today, they are cultivated worldwide and have a strong social and economic importance, especially in Mediterranean regions (Loumou and Giourga, 2003). However, olive tree is considered a naturalized or, even, an invasive species in many regions of the world (e.g. California, Hawaii, Chile, Australia, New Zealand), where it is usually treated as a pest (Spennemann and Allen, 2000a,b; Besnard et al., 2007; UICN, Invasive Species

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http://dx.doi.org/10.1016/j.actao.2015.09.005
1146-609X/

Specialist Group; www.issp.org). Olive orchards also have a significant impact on the landscape and may affect important ecological processes inside and outside the agricultural land (Ruano et al., 2004; Francia-Martínez et al., 2006; Rey, 2011). Wild olive seeds [*O. europaea* subsp. *europaea* var. *sylvestris* (Mill.) Lehr] are mostly dispersed by small frugivorous birds (mainly Turdidae and Sylviidae families), which enhance local seed dispersal and relatively long-distance colonizations (Rey and Alcántara, 2000; Spennemann and Allen, 2000a; Bass et al., 2006; Besnard et al., 2007). However, these birds are not able to swallow the large fruits of cultivated olive trees (Rey, 1993, 2011; Rey et al., 1997) since their artificial selection towards larger fruits for human consumption (mostly oil) make them largely exceed the gape size of most potential dispersers (Herrera, 1984; Rey et al., 1997; Delibes et al., 2012). Notwithstanding, recent genetic studies, based on maternally inherited DNA markers, have shown evidence of seed-mediated gene flow from cultivated olive farms to wild olive populations, suggesting long-distance seed dispersal events (Besnard et al., 2011, 2013).

Pigeons (Family Columbidae) occur worldwide and have developed a great adaptation to most ecosystems (Baptista et al., 1997). Some pigeon species have strongly benefited from human activities, with many taxa currently showing an increase in their natural ranges (Baptista et al., 1997). Some species are even able to exploit human-modified habitats, including intensive agriculture lands and urban areas where they commonly cause significant damage, not only to crops (Murton and Jones, 1973; Fazlul-Haque and Broom, 1984; Jiménez et al., 1994; Inglis et al., 1997) but to buildings, monuments and private properties (Coghlan, 1990; Haag-Wackernagel, 1995). However, despite the ecological and economic impact of both olive orchards and pigeons worldwide and their wide co-occurrence across many landscapes, the ecological and conservation implications of its possible interaction remains elusive. Here, we assess the possible role of an expanding and, locally, overabundant pigeon species, the wood pigeon (*Columba palumbus*), as a legitimate long-distance disperser of domestic olive trees. During the past decades wood pigeons populations have increased dramatically in many parts of its range (BirdLife International, 2014) and have been even introduced into areas where olive trees are considered invasive or naturalized, particularly in North America (Phillips, 1928; Long, 1981; Jeschke and Strayer, 2005). However, the effectiveness of pigeons as dispersers of domestic olive trees and its possible effect on the natural environment has not been evaluated so far.

We, specifically, assess the effectiveness of wood pigeons as dispersers of domestic olive trees by analyzing the following quantity and quality components of dispersal (*sensu* Schupp et al., 2010): (1) the proportion of pigeons consuming domestic olive fruits; (2) the number and size of seeds consumed per individual; (3) the size of undamaged seeds that passed through the gut; (4) the minimal dispersal distances; (5) the germination rate and time of pigeon-dispersed seeds in comparison to intact seeds, and (6) the proportion of germinated seeds that successfully turn into seedlings. For all these aspects, we also evaluate the effect of seed size to address whether artificial selection for larger fruits may have an effect on the sign and strength of the fruit–frugivore interaction. This integrative approach will allow us to assess the magnitude of this potential mutualism and to establish possible conservation practices to contain the increasing threat of domestic olive trees escaping from commercial orchards (Spennemann and Allen, 2000a,b; Besnard et al., 2007; Delibes et al., 2012) as well as to contain the overpopulation of pigeons in many urban areas (Luniak, 2004; Cannon et al., 2005; SEO/Birdlife, 2013).

2. Material and methods

2.1. Study area and species

This study was conducted in “Lugar Nuevo”, a State Property of 9335 ha, located in the Sierra de Andújar Natural Park, Southern Spain (38° 90′N, 4° 30′W; Jaén province). The elevation ranges from 200 to 680 m above the sea level, and the climate is Mediterranean with a highly variable precipitation (400–700 mm annual rainfall, average 535 mm) and a 3-month dry summer. Monthly mean temperatures are between 14.3 and 18.4 °C (Gómez-Manzaneque et al., 2002), with high temperatures in summer (usually above 35 °C) and very few frosts in winter. Soils are acid and poor in nutrients with a lithological substrate of quartzites, slates and sandstones. Vegetation is dominated by oak forests and woodlands (*Quercus ilex*, *Quercus suber*, *Quercus faginea*) together with planted pine forests (*Pinus pinaster*, *Pinus pinea*). Wild olive trees (*O. europaea* subsp. *europaea* var. *sylvestris*) and other evergreen shrubs (*Arbutus*, *Phillyrea*, *Pistacia*, *Cistus*) are common and can form large scrub patches. Wild olive woodlands occupy 1.5% of the study area, with stands that range from 20 to 90 ha although isolated individuals occur across great part of the territory. Agricultural land (mostly olive farming) is about 4–5 km from the Southern border of the study area (Fig. 1). Wild ungulates are very abundant (*Cervus elaphus*, *Sus scrofa*, *Dama dama*), with an estimated density that exceeds 36–39 deer km^{-2} (data only for *C. elaphus*; Nugent et al., 2011). The area is included in the NATURA 2000 Network, housing important populations of endangered wildlife species such as Iberian Imperial eagle (*Aquila adalberti*), Iberian lynx (*Lynx pardinus*) and Iberian wolf (*Canis lupus* subsp. *signatus*) as well as protected habitats considered in the European Commission Habitat Directive (92/43/EEC), including the wild olive woodlands (Habitat 9320).

Wood pigeons (*C. palumbus*) are common in the study area all year round. Population estimations varied from 5000 to 6000 reproductive pairs in the area, approximately 12 individuals per 10 ha (Notario et al., 2012). However, wintering population of wood pigeon are lower (Bea et al., 2003). Wood pigeon has been mostly considered an important seed predator (Purroy et al., 1984; Santos and Tellería, 1997; Bea et al., 2003; Perea et al., 2013, 2014) but also a significant seed disperser, especially of small drupes (Jordano, 1987; Jordano and Schupp, 2000; Deckers et al., 2008).

Domestic olive trees (olive orchards) belong to the variety Picual. This variety produces much larger seeds (Mean ± SE = 0.36 ± 0.02 g; Rial and Falqué, 2003) than wild olive trees (0.20 ± 0.005 g; Alcántara et al., 2000). Mean fruit width is 15.65 ± 1.47 mm in domestic olives, and 6.86 ± 1.39 mm in wild olives (Rey et al., 1997).

2.2. Seed and fruit collection

Between March and June 2012, we visited and monitored a total of 11 wood pigeon spring roosts across the study area (Fig. 1). Wood pigeons droppings are usually large (>10 cm in diameter when accumulated under roosts) and easy to recognize at this time of the year (purple color from the consumed olives). The number of wood pigeons in each roost varied from 2 to 8 individuals. In each roost we collected wood pigeon droppings containing large olive seeds (>0.20 g) to ensure that they belonged to domestic olive trees. In addition, to avoid possible size overlapping between domestic and wild olive seeds we only chose seeds with rough surface (with deep wrinkles), as opposed to those with smooth surface, which are characteristic of wild olive trees (Vargas and Talavera, 2012). Following these criteria, a total of 250 seeds were randomly selected from the wood pigeons droppings. Mean ± SE of pigeon-