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Dispersal limitation at the expanding range margin of an evergreen tree in urban habitats?

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ABSTRACT

Dispersal limitations contribute to shaping plant distribution patterns and thus are significant for biodiversity conservation and urban ecology. In fleshy-fruited plants, for example, any preference of frugivorous birds affects dispersal capacities of certain fruit species. We conducted a removal experiment with fruits of *Ilex aquifolium*, a species that is currently expanding its range margin in northern Europe in response to climate change. The species is also a popular ornamental tree and naturalization has been observed in many parts of its range. Fruits of native *I. aquifolium* and of three cultivars were offered to birds at the expanding range margin in urban habitats in eastern Denmark. The four fruit types were removed at different rates and red fruits were preferred over a yellow cultivar. Small fruit diameter was positively related to fruit removal, and removal was faster under tree canopies compared with open habitats. The preference for red cultivars compared with native *I. aquifolium* may contribute to naturalization and potential invasion of garden escapes. Preferential foraging under closed canopies indicates trees and shrubs as recruitment foci for fleshy-fruited plants in urban landscapes. The results should be included in urban forestry and planting of potentially invasive ornamental species.

Introduction

Dispersal is a key element in shaping plant distributions, and dispersal limitation can exclude a species from suitable sites (Gaston, 2009). During the past decade, 'bioenvelope' models based on abiotic requirements have been used to predict species distributions (Huntley et al., 1995; Bakkenes et al., 2002; Berry et al., 2002). However, most distribution models rely on the assumption of unlimited dispersal, which is unrealistic given the lack of mobility in many plant species (Carey, 1996; Engler and Guisan, 2009). Dispersal limitation is receiving increased attention in recent years, and it is crucial to improve our understanding of this topic to predict future plant distributions under climate change (Engler and Guisan, 2009).

Anthropogenic activities such as trade, travel and disturbance of ecosystems are assisting to overcome spatio-temporal dispersal barriers of many species. The dispersal pathways created by these activities must be incorporated within advanced models of plant dispersal, especially in urban landscapes. One of these pathways involves deliberate spread of cultivated species (Hodkinson and Thompson, 1997), and trade of ornamentals, often with attractive fleshy fruits, is a significant factor for the spread of potentially invasive species (Li et al., 2004). Of 199 representative invasive species listed, 25% are known to have fleshy fruits dispersed by birds (Cronk and Fuller, 1995). This seed dispersal mutualism is general and diffuse but very effective (Richardson et al., 2000), as most fleshy-fruited plants are dispersed by several bird species in the introduced range. Birds facilitate naturalization of ornamentals from gardens to near-by ecosystems, and thus assist overcoming an important barrier to invasion, i.e. seed dispersal (Milton et al., 2007).

Patterns in fruit removal, and hence dispersal by frugivorous birds, have been examined at different spatial scales (Kollmann, 2000), and increased fruit removal from isolated and scattered fruit displays compared to forest interiors and aggregated fruit displays have been observed (Denslow, 1987; Malmborg and Willson, 1988; Herrera et al., 1994). However, the observations from natural landscapes may not apply to urban habitats (Aronson et al., 2007), and the effect of bird foraging on dispersal of fleshy-fruited species in cities is still largely unknown. The strong preferences of frugivorous passerines for closed canopies, for example, might be relaxed because of reduced predator pressure in urban habitats.

Differential selection of fruits by birds affects the dispersal of seeds and eventually the local composition of vegetation, but generalizations about what traits underlie bird choices remain elusive

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Table 1
Fruit traits and total removal of four *Ilex aquifolium* types used for the field experiment. Fruit diameter was measured at the beginning of the experiment (Ba, *I. aquifolium* 'Bacciflava'; Cg, *I. aquifolium* 'Crinkle Green'; Na, native *Ilex aquifolium*; Py, *I. aquifolium* 'Pyramidalis').

Plant abbreviation	Fruit diameter (mm)	Pyrenes per fruit	Pulp dry mass per fruit (mg)	Pulp-to-seed ratio	Removal after 72 days (%)
Ba	8.21	4.0	82.4	0.87	35
Na	8.02	4.1	63.2	0.64	91
Py	8.02	3.6	100.3	1.67	92
Cg	7.62	3.4	64.9	0.63	95

(Levey and Del Rio, 2001; Gosper et al., 2005). Due to the excellent color vision of birds, visual signaling may play an important role in preferences of frugivorous birds (Siitari et al., 1999). The global prevalence of red and black fruits is often explained by avian preference for these colors (Willson and Whelan, 1990), but the evidence for this preference can be different in controlled experiments or natural populations (McPherson, 1988; Traveset et al., 2001; Tsujita et al., 2008). Experiments on fruit color preferences are often designed to exclude the effects of other fruit traits, although bird selection is influenced by fruit diameter, seed size, and pulp-to-seed ratio (Denslow, 1987; Sallabanks, 1993; Wheelwright, 1993).

The holly *Ilex aquifolium* L. is a fleshy-fruited evergreen tree with an expanding range in northern Europe due to climate change (Banuelos et al., 2004; Walther et al., 2005). The main seed dispersers of this species are birds (Peterken and Lloyd, 1967), while mammals play only a minor role (Snow and Snow, 1988). Holly is also a common urban ornamental, and numerous cultivars exist with differences in frost hardiness, height, fruit abundance, fruit size, and color (Galle, 1997). Little is known about how these traits affect the preference of frugivorous birds and hence the dispersal capacities of the cultivars at the expanding range margin. Thus, fruit removal of three common cultivars and a native provenance of *I. aquifolium* was investigated in contrasting urban sites in eastern Denmark. In this study, we address the following questions: (1) Do frugivorous birds differentially select between fruits from cultivated and native *I. aquifolium*? (2) Is fruit color of *I. aquifolium* the primary trait selected for by frugivorous birds? (3) Does habitat type influence fruit removal from *I. aquifolium* by frugivorous birds in an urban environment?

Materials and methods

Study species and areas

I. aquifolium L. (Aquifoliaceae) is a small tree or shrub up to 23 m in height. It has evergreen, usually spiny leaves varying between 2.5 and 7.5 cm in length (Peterken and Lloyd, 1967). The species is dioecious with flowers clumped in axils of branches produced in the previous year. Flowering occurs in May–June and the fruit is a drupe containing up to four pyrenes which are typically dispersed by passerine birds, mainly thrushes which remove the fruits during winter (Snow and Snow, 1988). The natural range extends throughout north-western, central and southern Europe, and the species reaches its north-eastern limit within Denmark (Peterken and Lloyd, 1967). It has been used as a classical example for a relatively sharp range margin due to more severe winter frost in subcontinental regions (Iversen, 1944; Gaston, 2003), but more recently the species has expanded its north-eastern range margin by about 100–200 km (Banuelos et al., 2004; Walther et al., 2005; Skou et al., 2011).

Cultivars

The removal study was done with fruit branches of three common cultivars and one native provenance (Table 1). The following cultivars were used: (1) *I. aquifolium* 'Bacciflava' with dark olive-green leaves, 6–8 cm long, 3–5 spines on each side, green stems, fruits brilliant greenish-yellow, 8 mm diameter, and 3–5 in clusters; (2) *I. aquifolium* 'Crinkle Green' with dark olive-green leaves 5–7 cm, 4–8 spines on each leaf margin, stem green to brownish, fruits vivid red with 7–9 mm diameter, and 1–3 in clusters; (3) *I. aquifolium* 'Pyramidalis' with dark olive-green leaves, 6–8 cm long, margins usually entire, rarely 1–2 spines often only on one side, green stem, fruits vivid red, 8–10 mm diameter, and 1–4 in clusters (Galle, 1997). Fruit branches of the three cultivars were obtained from the nursery 'Vornaes' on the island of Funen in central Denmark.

The fruit branches of the native *I. aquifolium* originated from a natural population on the island Als in southeastern Jutland, but the plants had been cultivated for more than a decade in a common garden in southern Zealand ('Rosenfeldt Gods') and thus had comparable growing conditions to the cultivars.

Removal experiment

The experiment was carried out in six urban sites with >2 km distance within greater Copenhagen, i.e. at the expanding range margin of the species in eastern Denmark (latitude 55.40–55.45, longitude 12.30–12.35; 10–30 m a.s.l.). Three locations were cemeteries ('Holmens Cemetery', 'Solbjerg Cemetery', 'Vestre Cemetery'), and three were botanical gardens ('Botanical Garden at Frederiksberg', 'Charlottenlund Botanical Garden', 'University of Copenhagen Botanical Garden').

To focus on differences between fruit types, the branches used for the removal experiment were standardized so each branch had between 10–20 leaves and 10–20 fruits (average 17.2 fruits per branch). One branch of each plant type was randomly fixed on corners of wooden boards 20 cm × 20 cm, so that the fruiting parts of the branches (10–15 cm) were freely exposed. These experimental units were placed on a 1.6 m stick to restrict accessibility to frugivorous birds.

In each of the six sites, five feeding stations were randomly placed in open areas with low vegetation (<0.5 m) more than 5 m away from trees >3 m, and five other stations were placed nearby under closed canopy with tall shrubs or trees (>3 m). For all sites except Solberg Cemetery, they were placed under *Taxus baccata* trees that had a particularly close canopy and were not fruiting in the experimental period. The feeding stations were spaced by 5–15 m.

At every site, one additional station was covered by net chicken wire to control for losses of fruits from the *I. aquifolium* branches without bird interference. In addition, in four sites one red-fruited *I. aquifolium* tree was haphazardly chosen as control for possible deviation of bird response to experimental set-up compared with natural fruit displays. Here ten branches with 15 fruits were randomly selected 1–2 m above ground and the number of fruits was counted at every visit.

All sites were revisited 15 times from 7th December 2009 till 17th February 2010 (after 1, 2, 4, 8, 16, 30, 44, 46, 49, 52, 56, 59, 63, 66, and 72 days). Temperatures during the experiment were colder than in the previous two winters (L.A. Møller, unpubl. data), but close to long-term average (1890–2001). Fortunately, no