



Geographic consistency in the seed dispersal patterns of *Taxus baccata* L. in the Iberian Peninsula

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Abstract

Aim of the study: Seed dispersal is a crucial process in tree population dynamics. In the case of yew, *Taxus baccata* L., seeds are dispersed by birds and mammals in a non-random, microhabitat-dependent way, a pattern constraining population renewal and expansion. While skewed dispersal has been frequently found, we lack knowledge on how consistent are spatial restrictions across time and yew's geographical range. This sort of information is required for the development of trans-regional management tools for this species.

Area of study: Three *Taxus baccata* stands across Spain, namely Cantabrian Range, Sierra de Gredos and Sierra de Cazorla.

Material and methods: During two consecutive years, we have been studying the contribution of frugivorous animals to the seed dispersal patterns of *Taxus baccata* L., in three ecologically contrasted localities of the Iberian Peninsula.

Main results: The spatial distribution of the seeds in the landscape was very heterogeneous, with the majority of the seeds consistently dispersed into forested microhabitats and almost none outside the forest. The main seed dispersers were always frugivorous birds, particularly thrushes (*Turdus merula*, *T. viscivorus*, *T. philomelos* and *T. iliacus*).

Research highlights: The results highlighted the large-scale consistency of the seed dispersal system of *Taxus baccata*. We suggest that the generalized spatially-restricted dispersal contributes to the lack of regeneration and absence of population expansion of the species all over its range. As a trans-regional conservation strategy, we recommend measures aimed at maintaining as much as diverse assemblage of frugivores in order to provide complementary seed dispersal and therefore enhance population regeneration and expansion.

Keywords: English Yew; frugivory; seed rain; microhabitats; *Turdus* spp.; carnivorous mammals; spatially-restricted dispersal.

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Introduction

The English yew, *Taxus baccata* L., once widespread, is now a relict forest tree species in Europe (Thomas & Polwart, 2003). Over the past centuries, yew populations have been declining in number, size, and therefore in connectivity (Dovčiak, 2002; Linares, 2013), especially at the margins of its geographical range (Sanz, 2008; González-Martínez *et al.*, 2010). In the Iberian Peninsula, *T. baccata* is widespread, but most populations are small and suffer from lack of regeneration due to constrained recruitment (Abel *et al.*, 2007; Sanz *et al.*, 2009; Linares, 2013). Two

major causes have been evoked to explain recruitment limitations: either too few seeds are produced and dispersed (seed limitation) or, even if produced in great number, these seeds do not reach favorable microsites for establishment of new individuals (establishment limitation; Mendoza *et al.*, 2009). In yew populations, current empirical evidences showed that seed dispersal is strongly biased in space at a very fine scale, thus supporting the latter statement (Hulme, 1996; García & Obeso, 2003; Martínez *et al.*, 2008; Sanz *et al.*, 2009; Linares, 2013). Indeed, emergence and survival of *T. baccata* seedlings are highly sensitive to water availability (Sanz *et al.*, 2009), herbivory (García *et al.*,

2000; García & Obeso, 2003), light availability (Svenning & Magard, 1999; Devaney *et al.*, 2014), and conspecific density (Dovčiak, 2002; Devaney *et al.*, 2014). Given these restrictions, the fine-scale pattern of seed dispersal, by setting the initial template for establishment, is a crucial determinant of population renewal (Schupp & Jordano, 2011; Beckman & Rogers, 2013).

As many fleshy-fruited plants, yew relies on the interaction with frugivorous animals for efficient dispersal, therefore, for establishment and survival of new individuals (Howe & Smallwood, 1982; Jordano & Schupp, 2000; Schupp *et al.*, 2010). Both the number of dispersed seeds and the place where they are deposited strongly depend upon the identity and the behavior of the frugivorous animals (Jordano & Schupp, 2000; González-Varo *et al.*, 2014). In temperate ecosystems, the main seed dispersers of fleshy-fruited trees are carnivorous mammals and birds (Gutián & Munilla, 2010; García *et al.*, 2010; Peredo *et al.*, 2013). Birds typically account for a large proportion of dispersed seeds (Jordano, 1987; Herrera, 1998; Martínez *et al.*, 2008), depositing them at very short distances from mother trees (Godoy & Jordano, 2001; Jordano *et al.*, 2007; Martínez *et al.*, 2008), and usually under tree canopies as a result of their active selection of forest habitats (Alcántara *et al.*, 2000; Jordano & Schupp, 2000; Martínez *et al.*, 2008; Martínez & García, 2015a). This is the case of yew in the Cantabrian mountains (N Spain), for which birds tend to disproportionately disperse the seeds beneath conspecific adult trees (García *et al.*, 2005b; Martínez *et al.*, 2008), a pattern that may hamper recruitment due to increase predation, pathogen attack, and competition in high-density seed or seedling clumps (Janzen-Connell effects; Janzen, 1970; Schupp & Jordano, 2011; Devaney *et al.*, 2014). In any case, birds also disperse some seeds underneath heterospecific trees or shrubs, both of which may provide suitable microsites for seedling survival (Giertych, 2000; García *et al.*, 2000; García & Obeso, 2003; García *et al.*, 2005b). Additionally, carnivorous mammals have been found to disperse a small fraction of seeds and contribute rather differently, as they frequently defecate the seeds in open areas such as trails or rocks, but generating very big clumps in faeces and latrines (Gutián & Munilla, 2010; Peredo *et al.*, 2013). Although germination rate and seedling survival after mammal deposition are likely to be low, mammal seed dispersal may still play a role in re-colonizing deforested and distant areas (Jordano *et al.*, 2007; Escribano-Avila *et al.*, 2012; Peredo *et al.*, 2013).

Besides the spatial components, an important feature of plant-frugivore interactions is their temporal

variability (Jordano, 1993). The amount of fruits available for frugivores usually varies within and between years (Herrera, 1998; Gutián & Munilla, 2010). Similarly, the abundance of frugivores also shows inter-annual fluctuations, especially when they belong to migrant species (e.g. *Turdus* spp., Jordano, 1993; Tellería *et al.*, 2014). Thus, the yearly patterns of yew seed dispersal are expected to change, as conditioned by both community-whole fruit availability and frugivore abundance (see Martínez & García, 2015a, for other tree species with similar dispersal syndrome).

The seed dispersal system of many fleshy-fruited trees have been found to display strong spatio-temporal variability (Jordano, 1993; Herrera, 1998; Perea *et al.*, 2013). However, few studies have actually assessed how consistent or inconsistent are those systems. On one hand, discerning whether the local, small-scale patterns of seed dispersal – with most of seeds being deposited under conspecific trees but very few out of forest – are generalized across yew distribution range is a prerequisite for the development of integrative and large-scale management plans (see also Sanz *et al.*, 2009). On the other hand, understanding the magnitude and the sense of inter-annual variability in yew seed dispersal patterns is key to assess the ability of the species to cope with rapid ecological changes, especially those derived from human impact (Hampe, 2011).

In this study, we have explored the variability in the seed dispersal system of *T. baccata* L. over a large geographic extent in the Iberian Peninsula and across different years. We selected yew populations encompassing contrasted biogeographical conditions (Euro-siberian vs Mediterranean), and studied the seed dispersal patterns during two consecutive years. Specifically, we i) quantified the small-scale spatial heterogeneity of the seed rain, ii) identified the assemblage of frugivorous animals interacting with *T. baccata*, assessing the relative contribution of different frugivore types to the seed rain, and iii) discussed the relevance of observed spatio-temporal consistencies, or inconsistencies, in terms of regeneration limitations in the context of yew large-scale conservation and management.

Material and methods

Study species, *Taxus baccata* L.

The evergreen, non-resinous gymnosperm *Taxus baccata* L., the common yew, is a dioecious wind-pollinated tree (Thomas & Polwart, 2003; Sanz *et al.*,

2009). It grows across Europe, in different soil types, taking part of primary and secondary forests, and even occurring as an isolated tree in cultural landscapes (Linares, 2013). Embryos are protected by pseudobayes, composed of a seed partially covered by a red and fleshy aril (fruit hereafter, for simplicity). Fruits ripen from late summer (August) to late autumn (November), and female trees usually have big crop sizes, with little variation between years (e.g. 5000 fruits on average in the Cantabrian mountains of N Spain; Valdés, 2006). Yew relies essentially on avian frugivores for seed dispersal, especially on thrushes, *Turdus* spp., that feed on fruits directly from branches (Snow & Snow, 1988).

Carnivorous mammals have also been found to have a complementary role on seed dispersal, after feeding on fruits fallen under female trees (e.g. Peredo *et al.*, 2013). Both thrushes and mammals swallow entire fruits, dropping intact seeds in their faeces (although regurgitation is also possible in birds; Martínez *et al.*, 2008), and are thus considered as legitimate dispersers (*sensu* Jordano, 2000).

Study sites

Our study system includes three different sites distributed from north to south of Spain (Figure 1A). The first study site is Sierra de Peña Mayor (43°17'N, 5°30'W; "Peña Mayor" hereafter) in Oviedo province, NW Spain, at 1000 m a.s.l. elevation. There, the forest habitat is highly fragmented and embedded in a dominant matrix of pasture and heathland. Forest is mostly composed of secondary-growth patches dominated by fleshy-fruited tree species (*Crataegus monogyna* Jacq., *Ilex aquifolium* L., and *Taxus baccata*), together with *Corylus avellana* L. Some mature, beech (*Fagus sylvatica* L.)-dominated stands, and many isolated remnant trees also compose the fragmented landscape. Yew is mostly present in mature stand fringes and in secondary stands, and rarely isolated in the deforested matrix. Our study stand was embedded in the forest continuum and comprised 70 yew adult trees, 40 females and 30 males.

The second site is Barrerón de Escobarejos in Sierra de Gredos (40°12'N, 5°60'W; "Escobarejos" hereafter) in Cáceres province, SW Spain, at 1350 m a.s.l. elevation. Yew population is located in the upper limit of a semideciduous oak forest (*Quercus pyrenaica* Willd.) on a north-facing slope. The vegetation is dominated by tall and medium-sized shrubs, mainly *Erica* spp., *Genista florida* L., and *Cytisus oromediteraneus* Rivas Martínez *et al.*, with a few clumped

fleshy-fruited trees (*Sorbus aucuparia* L., *Ilex aquifolium* L., and *Taxus baccata*) distributed along seasonal streams (Sanz, 2008; Lavabre *et al.*, 2014). Although present at a low density, yew is the dominant tree species at this site, and the population included 21 adult trees, 15 females and 6 males.

The third site is Nava de las Correhuelas (37°59'N, 2°54'W, Parque Natural de Sierra de Cazorla, Segura y las Villas; "Cazorla" hereafter) in Jaén province, SE Spain, at 1615 m a.s.l. elevation. The site vegetation is dominated by grassland with scattered woody deciduous patches, with gravelly soil or rocky outcrops covered by shrubs (e.g. *Juniperus* spp., *Rosa* spp.) or small isolated trees. Some pine stands (*Pinus nigra* subsp. *salzmannii* (Dunal) Franco) also occur on rocky slopes (Valle *et al.*, 1989; García, 2006). The site is protected by a fence for excluding large mammals, and thus grazing pressure is low. The protected yew stand included 26 adult trees, 20 females and 6 males.

The field study was conducted over two fruiting seasons, from August 2006 through December 2007 at the three study sites.

Seed sampling

We aimed to represent the fine-scale environmental variability of the microsites where yew seeds are deposited by birds. We thus defined different types of microhabitats in each study site based on both soil type and vegetation cover (see Figure 1B&C for an example in Peña Mayor): 1) "*T. baccata* female", beneath a female conspecific tree; 2) "*T. baccata* male", beneath a male conspecific tree; 3) "shrub", beneath an individual of a woody species <1.50 m in height (e.g. *Cytisus oromediteraneus*); 4) "fleshy-fruited tree", beneath a tree >1.50 m in height and belonging to one fleshy-fruited species other than yew (e.g. *Ilex aquifolium*); 5) "non fleshy-fruited tree", beneath a tree of a non fleshy-fruited species >1.50 m in height (e.g. *Corylus avellana*); 6) "open ground", deep soil with cover of non-woody vegetation (pasture) or barren soil with gravel under 25 cm²; 7) "rock", including stones on soil, boulders and rock substrates of at least 25 cm². We categorized types 1-5 as "covered" microhabitats and types 6-7 as "open" microhabitats. All microhabitats were present and sampled across sites, to the exception of "shrub", which was absent from Peña Mayor.

We studied the bird-generated seed rain with a microhabitat-based sampling of seed deposition. In each study site, we adapted the methodology to the local constraints (e.g. human activities, large mammals) to avoid damage of the sampling devices. In Cazorla, we collected the seeds deposited in seed traps that were

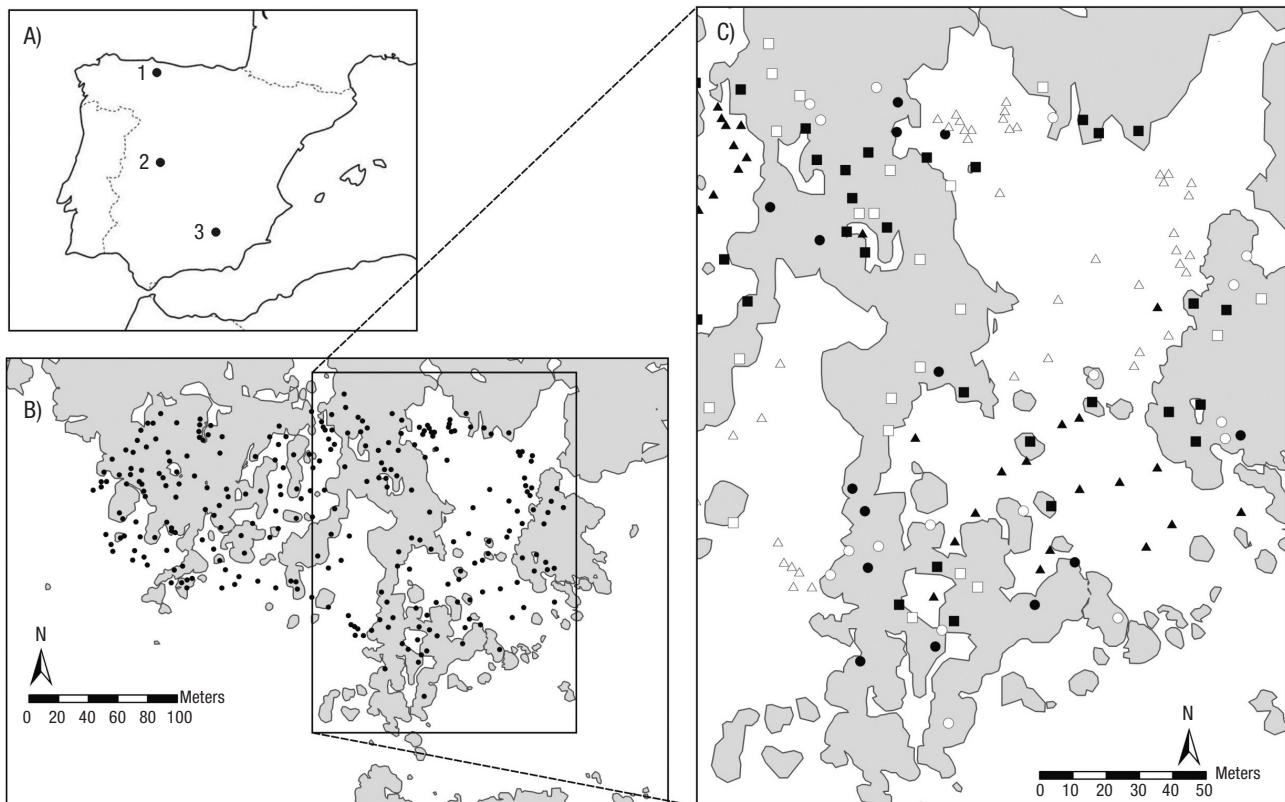


Figure 1: Geographical details of the study design. A) Location of the study sites (1: Peña Mayor; 2: Escobarejos; 3: Cazorla) in the Iberian Peninsula. B) Map of Peña Mayor with the location of the sampling stations (dots), and the distribution of forest cover (grey). C) A detail of sampling stations at Peña Mayor, illustrating the different types of microhabitats in which dispersed seeds were collected (black circle: *Taxus bacata* female trees; white circle: *Taxus bacata* male trees; black square: fleshy-fruited trees (excluding *Taxus bacata* trees); white square: non fleshy-fruited trees; black triangle: open ground; white triangle: rocks). See the “Material and methods” section for a detailed description of the microhabitats.

0.32×0.26×0.8 m trays, top-covered with a wire mesh to prevent seed consumption by post-dispersal seed predators (mostly rodents, see Jordano & Schupp, 2000, for a similar methodology). For the “rock” microhabitat, due to the difficulty to install seed traps and their conspicuousness to animals (including frugivores), we collected the seeds directly from open quadrats, permanently marked on the rock substrate, with the same surface than seed traps. Seed predation by rodents is usually low in open microhabitats and it mostly occurs in late winter (Hulme, 1997; García *et al.*, 2005a), and thus seed losses due to predation were considered negligible (see García *et al.*, 2011; Carlo *et al.*, 2013; Lavabre *et al.*, 2014, for validation of the methodology). In Peña Mayor and Escobarejos, we also sampled seed deposition in permanently labelled open quadrats of 0.5×0.5 m, as the presence of abundant free-ranging cattle and human activities in these two sites prevented the use of seed traps.

The sampling scheme consisted of an even number of sampling stations per microhabitat (when not constrained by microhabitat availability), with a total number of 353, 239, and 277 for Peña Mayor, Escobarejos, and Cazorla, respectively.

Each station consisted of two sampling surfaces – either open quadrats or seed traps – located at a maximum distance of 0.5 m from each other. Hereafter, and for simplicity, we will refer to each sampling station as a seed-plot. We checked seed-plots fortnightly, collecting and counting all yew seeds during the whole fruiting season in 2006 and 2007. Yew bird-dispersed seeds – smooth, and without aril – are easily distinguishable from non-dispersed seeds in fallen fruits – seeds with aril remains. We added some seeds collected in seed-plots but showing signs of rodent predation (open husks, gnawed coats) to the pool of dispersed seeds.

While surveying seed-plots, we systematically walked the whole extent of the study sites searching for carnivorous mammal scats. A similar surface was explored between sites, accounting for seed-plots and the 1.5-m wide paths between seed-plots. Scat collection was done at Peña Mayor and Escobarejos but not at Cazorla because the fence prevented carnivores like foxes and badgers from freely entering into the area (only a few scats, probably belonging to stone marten

Martes foina Erxleben, were occasionally found, but were considered not representative of the real activity and composition of the mammalian frugivore guild). When possible, scats were identified in the field at the species level following size and shape criteria. We identified at least three species: red fox (*Vulpes vulpes*), marten (*Martes* spp.), and badger (*Meles meles*) but we were not able to unambiguously assign many scats to one of these species. We have thus considered carnivorous mammals as a single functional group of seed dispersers. Every scat was collected individually in a paper bag and the microhabitat type where it had been dropped was recorded. Scats were oven-dried at 60°C for 5–10 days depending on the size prior to analysing seed content. For each scat, the faecal material and the seeds were carefully separated by hand and all yew seeds were counted.

For each year, we estimated the bird-generated seed rain from the total number of seeds collected in seed-plots over all surveys. At the microhabitat scale, we calculated the number of seeds per square meter in order to standardize the values between study sites. The mammal-generated seed rain was directly estimated from the counts of *T. baccata* seeds found in scats.

Frugivory by birds

In each study site, we conducted direct observations of birds feeding on fruits on 14, 11, and 9 focal female trees in Peña Mayor, Escobarejos, and Cazorla, respectively. Watching was done from prominent sites or hides under nearby trees, 40–50 m far from focal trees and with the help of 8×40 binoculars or a 13–25×50 spotting scope. One-hour observation sessions were performed during the activity range of frugivores (9:00 am to 18:00 pm) such that 55 (Peña Mayor), 68 (Escobarejos) and 70 (Cazorla) hours of observation cumulative time was allocated throughout the two study years. During observation, we focused on single individual birds, recording the bird species and the number of fruits swallowed per bird. We only considered here observations from legitimate seed dispersers (sensu Jordano, 2000), excluding seed- or pulp-predators (e.g. *Parus* spp.). As we were unable to properly assess the species of some individuals belonging to the *Turdus* genus, we finally grouped bird observations into three categories: blackbird, (*Turdus merula*), other thrush (all other *Turdus* spp. observations), and small birds (mostly robin *Erithacus rubecula* L. and blackcap *Sylvia atricapilla* L.). We considered that these frugivore groups represented different functional types of seed dispersers (Jordano *et al.*, 2007).

Frugivores' contribution

For each year and each study site, we estimated the contribution of each frugivore group to yew seed dispersal as:

$$C_i = \frac{N_i}{N_t} \quad (1)$$

where N_i is the number of yew seeds contributed by group i and N_t is the total number of dispersed seeds. For carnivorous mammals, N_i is the number of seeds collected in scats, and their contribution was only estimated for Peña Mayor and Escobarejos. For birds, we extrapolated the number of seeds dispersed by each functional groups from frugivory observations as it follows:

$$N_i = \frac{F_i}{F_t} N_b \quad (2)$$

where F_i is the number of fruits consumed by group i , F_t is the total number of fruits consumed by birds, and N_b is the total number of seeds dispersed by birds as estimated from seed-plots.

By combining in this way the numbers of seeds dispersed by birds and mammals, we have probably overestimated the relative weight of mammals on local seed deposition patterns, as the seeds of the different groups of dispersers were collected over different sampling surfaces. In any case, we considered that this method was still valid to compare the differential contribution of birds and mammals across sites and years, as sampling extents were similar between sites and years.

Statistical analyses

Spatial (between microhabitats) and temporal (between years) differences in seed deposition by birds were tested by means of generalized linear models (GLMs) considering microhabitat and year as fixed main factors and the number of dispersed seeds as the response variable. Models incorporated a negative-binomial error distribution and a *log* link function, after testing with different error distributions to find the best-fit model (by using residual deviance as a goodness-of-fit statistic; Quinn & Keough, 2002). Independent models were built for each study site.

We compared between years the fraction of the total seed rain allocated to a given microhabitat by means of a microhabitat×year contingency table. To identify which microhabitats were responsible for the observed overall significance, if any, partial significance of individual cell frequencies were tested using a *G*-exact

test (Sokal & Rohlf, 1995). All the analyses were carried out using the R package (R Core Team, 2014).

Results

Seed rain

Bird-generated seed rain

The spatial patterns of seed dispersal created by birds varied between study sites and years (Figure 2). At Peña Mayor 15796 and 2195 bird-dispersed seeds were collected in 2006 and 2007, respectively. At Escobarejos, 1114 seeds were found in 2006 and 4408 in 2007. At Cazorla, the number of bird-dispersed seeds was 1653 in 2006 and 757 in 2007. Despite quantitative differences between sites and years in total seed densities, the quali-

tative patterns of seed dispersal were, in general terms, consistent across sites. Namely, the microhabitats under conspecific trees, “*T. baccata* female” and “*T. baccata* male”, always received the highest densities of dispersed seeds, while open microhabitats (“open ground” and “rock”) received little, if no seeds (Figure 2A). After yew trees, “fleshy-fruited tree” was, more often, the most important microhabitat in terms of seed densities received, across sites and years. The differences in the relative importance of the microhabitats, with most of seeds being deposited under yew trees but seldom reaching open sites, were even stronger when expressed in terms of the percentage of seeds accumulated in each microhabitat, for every site each year (Figure 2B).

Besides these general patterns, GLM models revealed strong variability in seed density between microhabitats and years within each site, as judged by the significant effects of microhabitat type and year (Table 1). Year effect

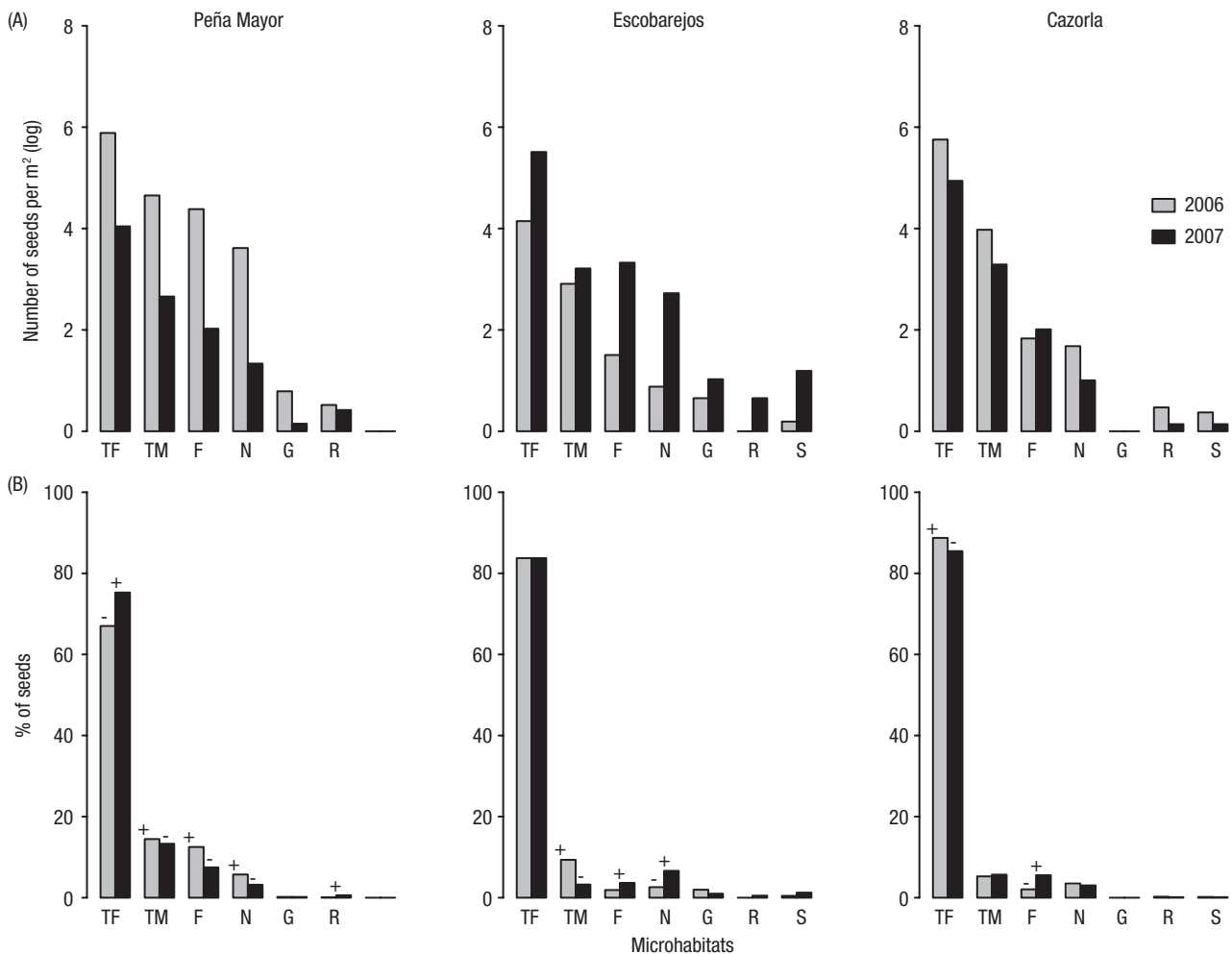


Figure 2. Variability in the bird-dispersed seed rain at the microhabitat scale. TF: *Taxus baccata* female tree; TM: *Taxus baccata* male tree; F: fleshy-fruited tree; N: non fleshy-fruited tree; G: open ground; R: rock; S: shrub. Unlabelled microhabitat signaled microhabitat S that was absent at Peña Mayor. A) Density of seeds per microhabitat in the three study sites calculated as the number of seeds per square meter. B) Percentage of seeds dispersed into each microhabitat type in 2006 and 2007 at the three study sites. The results from a microhabitat×year contingency table analysis are signaled using + (larger fraction of seeds) and – (smaller fraction of seeds) to indicate for which microhabitat, and in what direction, the fraction of seeds significantly varied between years.

Table 1. Effects of year and microhabitat factors on the number of avian-dispersed yew seeds. Independent GLMs with negative binomial errors were performed for each study site. Significance of the deviance quotients were tested with a Pearson's Chi-square test

Effect	Estimate (\pm SE)	z-value	P ($> z $)	Dev.	Res. d.f.	Res. Dev.	P ($>$ Chi)
Peña Mayor							
Intercept	3.68 \pm 0.17	21.84	< 0.0001	1989.11*	604		
Year (Y)				353.66	1	1635.45	< 0.0001
2007	-2.49 \pm 0.25	-9.97	< 0.0001				
Microhabitat (M) [§]				1025.31	5	610.14	< 0.0001
G	-4.19 \pm 0.3	-14.0	< 0.0001				
N	-0.78 \pm 0.24	-3.27	< 0.01				
R	-4.76 \pm 0.34	-14.02	< 0.0001				
TF	1.51 \pm 0.23	6.63	< 0.0001				
TM	0.27 \pm 0.25	1.11	0.27				
Y \times M				22.77	5	587.37	< 0.001
2007 \times G	0.47 \pm 0.63	0.75	0.454				
2007 \times N	-0.07 \pm 0.37	-0.19	0.849				
2007 \times R	2.22 \pm 0.5	4.41	< 0.0001				
2007 \times TF	0.65 \pm 0.33	1.95	0.051				
2007 \times TM	0.43 \pm 0.36	1.20	0.23				
Escobarejos							
Intercept	0.56 \pm 0.57	0.98	0.327	914.26*	477		
Year (Y)				60.90	1	853.36	< 0.0001
2007	2.04 \pm 0.78	2.61	0.009				
Microhabitat (M) [§]				499.71	6	353.65	< 0.001
G	-1.34 \pm 0.66	-2.02	0.044				
N	-0.91 \pm 0.67	-1.36	0.173				
R	-20.86 \pm 2243.27	-0.01	0.993				
S	-2.82 \pm 0.77	-3.66	< 0.001				
TF	2.88 \pm 0.66	4.34	< 0.0001				
TM	1.60 \pm 0.78	2.04	0.041				
Y \times M				18.23	6	335.42	0.006
2007 \times G	-1.37 \pm 0.91	-1.51	0.131				
2007 \times N	0.27 \pm 0.90	0.30	0.762				
2007 \times R	17.49 \pm 2243.28	0.01	0.994				
2007 \times S	0.36 \pm 0.98	0.37	0.714				
2007 \times TF	-0.66 \pm 0.91	-0.72	0.469				
2007 \times TM	-1.72 \pm 1.09	-1.58	0.114				
Cazorla							
Intercept	-0.16 \pm 0.33	-0.49	0.620	996.78*	559		
Year (Y)				24.67	1	971.13	< 0.0001
2007	0.21 \pm 0.46	0.46	0.644				
Microhabitat (M) [§]				685.32	6	285.81	< 0.0001
G	-20.14 \pm 2398.16	-0.01	0.993				
N	-0.16 \pm 0.4	-0.39	0.694				
R	-2.14 \pm 0.67	-3.24	0.001				
S	-2.43 \pm 0.72	-3.37	< 0.001				
TF	4.12 \pm 0.47	8.79	< 0.0001				
TM	2.33 \pm 0.66	3.54	< 0.001				
Y \times M				4.75	6	281.06	0.577
2007 \times G	-0.21 \pm 3391.51	0	1				
2007 \times N	-1.14 \pm 0.59	-1.93	0.054				
2007 \times R	-1.60 \pm 1.28	-1.26	0.209				
2007 \times S	-1.31 \pm 1.30	1.01	0.315				
2007 \times TF	-1.03 \pm 0.66	-1.56	0.12				
2007 \times TM	-0.92 \pm 0.93	-0.98	0.33				

* Null deviance of the model

§ TF: *Taxus baccata* female tree; TM: *Taxus baccata* male tree; F: fleshy-fruited tree; N: non fleshy-fruited tree; G: open ground; R: rock; S: shrub.

had different signs on different sites, with a decrease in the average seed density from 2006 to 2007 at Peña Mayor and Cazorla, but an increase in Escobarejos. Interestingly, the significant microhabitat×year interaction revealed that, at Peña Mayor and Escobarejos, the local differences in the relative role of microhabitats changed between years. For example, in Peña Mayor, the differences between covered and uncovered microhabitats were stronger in 2006 than in 2007, whereas in Escobarejos, microhabitats other than yew accumulated more seeds in 2007 than in 2006, relative to microhabitats under yew (Figure 2B).

The analysis of frequencies in the microhabitat×year contingency table also evidenced strong interannual variation in the fraction of seeds allocated to each microhabitat type (i.e., the cell combinations that exhibit large residual values, differed significantly from the expected values). For example, the relative role of microhabitat “*T. baccata* female” differed between years in Peña Mayor, but showed no difference in Escobarejos (Figure 2B). Each study site showed, in any case, some global variability ($G = 111.55$, $df = 5$, $P < 0.001$ for Peña Mayor; $G = 200.03$, $df = 6$, $P < 0.001$ for Escobarejos; $G = 19.96$, $df = 6$, $P < 0.01$ for Cazorla).

Mammals-generated seed rain

In Peña Mayor, we collected 54 and 15 scats in 2006 and 2007, respectively. Overall, 71% of the scats were found in open microhabitats, with 24 found on trails and 25 on meadows and rocks. The remaining 20 scats were encountered in forest patches, with 10 under *T. baccata* female trees. In Escobarejos, we found 21 scats in 2007 but none in 2006. There, scats occurred almost exclusively in open microhabitats on trails (5 scats) or under *T. baccata* female trees (15 scats).

Frugivore assemblage and contribution to seed dispersal

The frugivore assemblage dispersing *T. baccata* seeds was consistently composed of birds and carnivorous mammals, except in Cazorla where mammals were excluded (Figure 3). Comparing to birds, the role of carnivorous mammals as seed dispersers was marginal in most cases, and only in Peña Mayor had a bigger relative contribution in 2006 (Figure 3).

Among birds, thrushes, *Turdus* spp., contributed the most to the seed dispersal of *T. baccata*, accounting for more than 55% of dispersed seeds across sites and years (on average $83\% \pm 17\%$ SE). *Turdus viscivorus* and *T.*

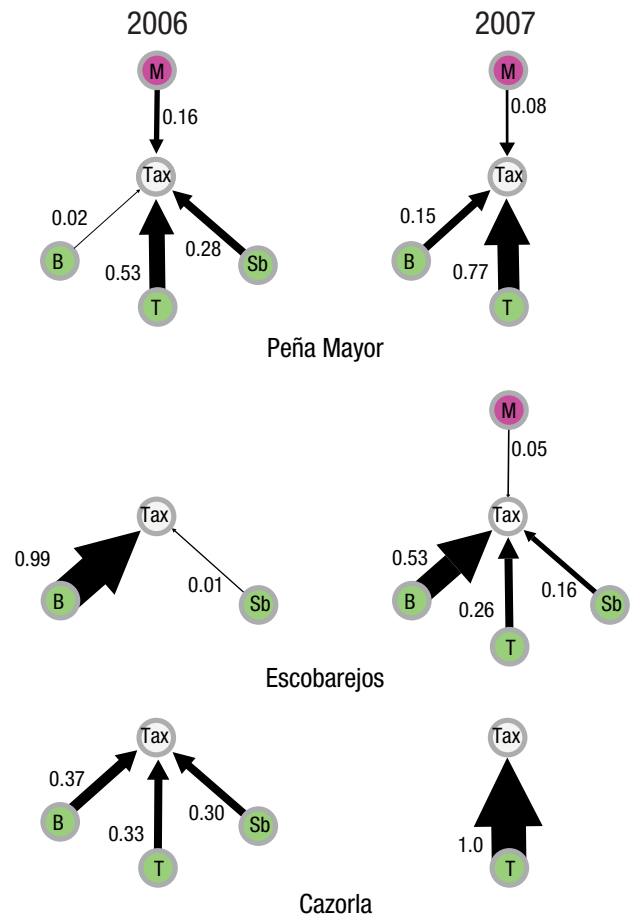


Figure 3. Contribution of different groups of frugivores to the seed dispersal of *Taxus baccata* in the three study sites. The arrows are directed from the seed dispersers to the plant (Tax) and their widths are proportional to the percentage of seeds that each group contributes to the overall seed rain (with exact values above arrows). Frugivore species were classified into carnivorous mammals (M, above) and birds (below), this latter comprising black-bird, *Turdus merula* (B), other thrush species, including *T. viscivorus*, *T. iliacus*, and *T. philomelos* (T), and small birds, including *Erithacus rubecula*, *Sylvia atricapilla*, and *Phoenicurus ochruros* (Sb). See text for further details on the species.

merula were the most frequently observed, representing 100% of the thrush species at Escobarejos and Cazorla in both years. A more diverse thrush community was present in Peña Mayor where we also observed *T. philomelos* and *T. iliacus*. Small-sized passerines – *Erithacus rubecula*, *Sylvia atricapilla*, and *Phoenicurus* spp. – had a variable contribution in all study sites and in both years, but they overall participate to seed dispersal to a lesser extent.

Discussion

For fleshy-fruited trees, the interaction with frugivorous species is key to prevent vulnerable populations

from collapsing (Farwig & Berens, 2012; Caughlin *et al.*, 2015). Due to a low population growth rate associated with reduced recruitment, *Taxus baccata* is highly vulnerable to landscape degradation and climate change (Dovčiak, 2002; Thomas & Polwart, 2003; Abel *et al.*, 2007). Therefore, comprehending its seed dispersal dynamics is of particular importance for the persistence, hence the conservation, of the species. In this study, we have analysed the spatial and temporal variability in the seed dispersal system of *T. baccata* along a large geographic gradient representing contrasted biogeographical (Eurosiberian vs Mediterranean), demographic (large vs relictual populations), and ecological (rich vs poor forest communities) conditions. Despite environmental variability, we found a consistent pattern in the three study sites, with the vast majority of the seeds dispersed beneath the canopy of conspecific trees, and very few in open areas. Also, we identified thrushes, *Turdus* spp., as the main, if not exclusive, seed dispersers.

Overall, our results showed that the bird-dispersed seeds were non-randomly distributed in the landscape, but were rather aggregated into a limited number of microhabitat types while many others received little or no seeds (Figure 2). Trees concentrated on average 98.8% of the bird-dispersed seeds, 80% being under yew females. Open microhabitats received virtually no seeds in all three study sites (Figure 2). These results were in agreement with previous studies at Peña Mayor study site (García *et al.*, 2005b; Martínez *et al.*, 2008) and in other study systems (Jordano *et al.*, 2007; González-Varo *et al.*, 2014), therefore suggesting temporal consistency over a longer time scale, but go beyond when scaling-up seed dispersal patterns from a local to a geographical extent.

Considering that the landscape itself was highly heterogeneous at the three study sites, the aggregated distribution of the seed rain could reflect the local patchiness of the microhabitats (Nathan & Muller-Landau, 2000). Nonetheless, some studies have shown that seed dispersal patterns do not necessarily match with microhabitat availability (Bartuszevige & Gorchov, 2006; Lavabre *et al.*, 2014). Actually, at Escobarejos, 84 % of the bird-dispersed seeds were found beneath female yews in both years when these barely cover 0.4% of the landscape (Lavabre *et al.*, 2014). This seems to be also the case for the other sites studied here, where the cover of yew canopies represents a small part of the local surface but the open habitat is dominant.

Our experimental design could have, to some extent, affected the observed seed rain heterogeneity – at Peña Mayor and Escobarejos study sites – because open quadrats are prone to seed losses due to either abiotic

(e.g. strong wind) or biotic (e.g. seed removal by rodents) factors. Nonetheless, if the losses are homogeneous among the seed-plots, we might have quantitatively, but not qualitatively, underestimated the number of dispersed seeds. Indeed, abiotic factors are not expected to unevenly affect the seed-plots. Rodents, on the contrary, are known to be selective, both for the species they feed on and the microhabitat where they forage (Hulme, 1997; García *et al.*, 2005a). Since we have counted the predated seeds as part of the dispersed seeds, we have accounted for a part of the potential bias due to rodent seed removal. In addition, the microhabitats usually showing the highest predation rate are those for which we found the highest seed densities, *i.e.* yew trees (Figure 2A; García *et al.*, 2005a). In the case that, in spite of accounting for predated seeds, we have still underestimated the number of seeds dispersed beneath yew trees, then it would suggest that these microhabitats received even higher seed densities than what we found, thus reinforcing the present differences between microhabitats.

In addition to the general spatial patterns in the bird-generated seed rain, we observed subtle interannual variations (Figure 2B). For example, at Peña Mayor, the relative importance of many microhabitats varied between years. In 2006, the year with the largest bird-generated seed rain, a smaller fraction of seeds was dispersed under yew females, but a bigger proportion of seeds reached yew males and other tree species canopies (fleshy-fruited or not), suggesting that more seeds escaped from maternal neighborhood in 2006 than in 2007.

The coarse composition of the frugivore assemblage was, in general terms, consistent between sites and years (Figure 3). The main seed dispersers of *T. baccata* were always frugivorous birds, especially thrushes (*Turdus merula*, *T. viscivorous*, *T. iliacus*, and *T. philomelos*) since they accounted, on average, for 83% of the seed rain. As a group, thrushes largely select forested habitats, or trees when forest fragments are scarce, and usually avoid open habitats (Jordano & Schupp, 2000; García *et al.*, 2010; Martínez & García, 2015a). In autumn, during the fruiting season of the fleshy-fruited species at our study sites, thrushes' behavior is principally driven by fruit resource-tracking and protection against predators (García *et al.*, 2011; Morales *et al.*, 2013; Martínez & García, 2015b). This spatial behavior would then explain the skewed spatial patterns of seed dispersal in yew across its Iberian distribution range.

In spite of this general behavior, the different thrushes displayed some specificities in their patterns of fruit resource-tracking which likely translates into the seed rain (Morales *et al.*, 2013). *Turdus merula* and *T. ili-*

acus preferentially forage around the focal trees, sometimes in big flocks (*T. iliacus*), and fly short distances towards the neighbouring microhabitats (Martínez *et al.*, 2008), thus most likely dispersing the seeds within forest patches. On the other hand, *Turdus viscivorus* tends to fly long distances and hence would disperse a substantial amount of seeds among forest patches (Jordano & Schupp, 2000; Martínez *et al.*, 2008; Morales *et al.*, 2013). Indeed, Morales *et al.* (2013) showed that *T. merula* generated a more locally aggregated seed rain than *T. viscivorus*, who produced a more homogeneous seed rain at the landscape scale. We observed similar patterns at our study sites. For example, at Escobarejos, *T. baccata* female trees are mainly surrounded by conspecific males and open areas (Sanz, 2008; Lavabre *et al.*, 2014). These were, indeed, the microhabitats receiving a greater fraction of bird-dispersed seeds in 2006, when *T. merula* was the dominant seed disperser. Similarly, in 2007, the increase in the percentage of seeds dispersed into microhabitats “non fleshy-fruited tree” and “fleshy-fruited tree” (Figure 2B) was consistent with the foraging behavior of *T. viscivorus*, who preferentially selects tall or fruit-bearing trees for perching or feeding, respectively.

The contribution of carnivorous mammals as seed dispersers was always low relative to birds’ role, even considering a potential overestimation due to differences in sampling structure. In any case, we found some inter-annual differences in some sites, such as in Peña Mayor, where their contribution in 2006 was twofold that in 2007. As judged from the differences in the density of dispersed seeds (18907 seeds in 2006 vs 2372 in 2007, Figure 2), we expect a yew fruit production bigger in 2006 than in 2007, to which mammals would have responded by increasing this species in their diet (see also Guitián & Munilla, 2010). Similarly at Escobarejos, the density of dispersed seeds in 2006 suggests a smaller fruit production than in 2007, which might explain the absence of mammal scats for this year. Despite their potential to disperse the seeds over long distances (Jordano *et al.*, 2007; Matías *et al.*, 2009), their role as efficient seed dispersers remain unclear. Indeed, Peredo *et al.* (2013) found that they deposited a large fraction of the seeds into unsuitable microhabitats for germination and seedling establishment, such as latrines in the case of badgers, a microsite where seeds are probably faced to overcrowding and recurrent disturbance (but see Escribano-Avila *et al.*, 2012).

In sum, our results showed a consistent pattern of spatially-restricted seed dispersal that would help to explain the constrained yew regeneration and null population expansion in all studied environmental settings. Most of seeds were deposited under yew adults,

likely suffering from the effects of density-dependent seed and seedling mortality (Janzen-Connell effects; Steinitz *et al.*, 2011; Devaney *et al.*, 2014), and few seeds were dispersed outside forest stands and far from established populations. Moreover, in the three study sites, regeneration was also probably establishment-limited since the availability of suitable sites for seedling recruitment was reduced. Indeed, open microhabitats were dominant but harmful for seedlings due to summer drought, in the Mediterranean region, or overbrowsing, in the Eurosiberian region (García & Obeso, 2003; Mendoza *et al.*, 2009). Only fleshy-fruited trees of other species and shrubs seem favorable sites for establishment (García *et al.*, 2000; García & Obeso, 2003), but these microhabitats are still scarce and received few seeds.

Such geographically consistent patterns have important consequences for the persistence of the species. A generalized spatially-restricted seed dispersal limits considerably the capacity of the species to cope with ecological disturbances such as fragmentation, habitat loss or human activities. On the long-term, ecological limitations – restricted dispersal and the concomitant recruitment bottleneck – translate to the genetic structure of the species, causing genetic erosion and elevated inbreeding (Hilfiker *et al.*, 2004b, 2004a; Dubreuil *et al.*, 2010; González-Martínez *et al.*, 2010).

Concluding Remarks

The seed-dispersal patterns of *Taxus baccata* were the result of complex interactions between the microhabitat mosaic within the landscape, the identity of the frugivore species and the combination of specific feeding behaviors within the frugivore assemblage. This study highlights the consistency of this mutualistic system and its derived ecological patterns across the species range in the Iberian Peninsula. Although a large proportion of the seeds lands underneath conspecifics, the fraction that escapes from the neighborhood of *T. baccata* trees is crucial for subsequent stages of the species’ population dynamics (González-Martínez *et al.*, 2010; Schupp & Jordano, 2011). As the main driver of seed flow, frugivorous birds play a pivotal role for yew populations, however carnivorous mammals should not be neglected since they contribute to the recolonization process through long distance dispersal (Escribano-Avila *et al.*, 2012). Conservation and management practices should focus on maintaining a frugivore assemblage as diverse as possible to allow for complementary seed dispersal (García & Martínez, 2012; Escribano-Avila *et al.*, 2014), thus increasing the chance for a seed to reach favourable conditions and

at some distance from the mother tree. Given the large-scale approach from which these recommendations emerge, we encourage to consider these guidelines in a trans-regional strategy for the conservation of yew populations in Southern Europe.

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