



# Fragmentation, habitat composition and the dispersal/predation balance in interactions between the Mediterranean myrtle and avian frugivores

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Human-induced fragmentation and disturbance of natural habitats can shift abundance and composition of frugivore assemblages, which may alter patterns of frugivory and seed dispersal. However, despite their relevance to the functioning of ecosystems, plant-frugivore interactions in fragmented areas have been to date poorly studied. I investigated spatial variation of avian frugivore assemblages and fruit removal by dispersers and predators from Mediterranean myrtle shrubs (*Myrtus communis*) in relation to the degree of fragmentation and habitat features of nine woodland patches (72 plants). The study was conducted within the chronically fragmented landscape of the Guadalquivir Valley (SW Spain), characterized by ~1% of woodland cover. Results showed that the abundance and composition of the disperser guild was not affected by fragmentation, habitat features or geographical location. However, individual species and groups of resident/migrant birds responded differently: whereas resident dispersers were more abundant in large patches, wintering dispersers were more abundant in fruit-rich patches. Predator abundances were similar between patches, although the guild composition shifted with fragmentation. The proportion of myrtle fruits consumed by dispersers and predators varied greatly between patches, but did not depend on bird abundances. The geographical location of patches determined the presence or absence of interactions between myrtles and seed predators (six predated and three non-predated patches), a fact that greatly influenced fruit dispersal success. Moreover, predation rates were lower (and dispersal rates higher) in large patches with fruit-poor heterospecific environments (i.e. dominated by myrtle). Predator satiation and a higher preference for heterospecific fruits by dispersers may explain these patterns. These results show that 1) the frugivore assemblage in warm Mediterranean lowlands is mostly composed of fragmentation-tolerant species that respond differently to landscape changes; and 2) that the feeding behaviour of both dispersers and predators influenced by local fruit availability may be of great importance for interpreting patterns of frugivory throughout the study area.

Frugivory represents one of the most outstanding ecological interactions between plants and animals. Fleshy fruits encourage animal-mediated seed dispersal, whereas for animals fruits represent a source of food (Snow and Snow 1988, Jordano 1992, Herrera 2002). This conflict of interests may result in a diverse array of plant-animal interactions, since frugivorous animals, notably birds and mammals, can process fruits in several ways, typically by either 1) swallowing entire fruits and dispersing their seeds (legitimate seed dispersers) or 2) pecking/biting fruits for their pulp or seeds (pulp or seed predators; Jordano and Schupp 2000). Hence, plant fitness can be strongly influenced by the relative frequency of each type of interaction with frugivores (Jordano 1992). For instance, fruit predation may override other pre-dispersal processes such as flowering or fecundity (Traveset 1994, Wang and Smith 2002) and the spatial pattern of seed dispersal may shape post-dispersal processes such as seed survival or seedling establishment (Jordano and Schupp 2000, García et al. 2005).

Human-induced fragmentation of natural or semi-natural habitats may alter the patterns of abundance and distribution in both plant and animal populations and species, and thus affect species assemblages (Lindenmayer and Fischer 2006). Frugivory interactions may be spatially structured in accordance with variation in local frugivore assemblages (Gutián et al. 1992, Jordano 1994, Githiru et al. 2002). Consequently, seed dispersal in endozoochorous plants may decline in fragmented areas if seed dispersers are scarce (Santos et al. 1999, Cordeiro and Howe 2003, Rodríguez-Cabal et al. 2007, Kirika et al. 2008, Moran et al. 2009) or if seed predators become more abundant (Santos and Tellería 1994). However, despite their demographic relevance and potential vulnerability, the effects of habitat fragmentation on plant-frugivore interactions have received much less attention than either pre-dispersal processes in plant life cycles or the assessment of the genetic consequences of habitat fragmentation on plant populations (Hobbs and Yates 2003, Aguilar et al. 2006, but see Wright

2007). Moreover, most of studies that empirically evaluated this question have focused on the outcome of mutualistic interactions with legitimate dispersers, while antagonistic interactions with fruit or seed predators have often been overlooked (but see Santos and Tellería 1994). Information on plant-frugivore interactions and seed dispersal is key to understanding the functioning of ecosystems in fragmented areas, in particular when the plant species involved are either important components of the natural vegetation (Tellería et al. 2005, Herrera and García 2009) or keystone species (Rodríguez-Cabal et al. 2007, Kirika et al. 2008).

In the Mediterranean Basin over the last millennia, humans have directly or indirectly caused the transformation, destruction and fragmentation of natural habitats (Grove and Rackham 2001). The chronic fragmentation and disturbance of Mediterranean forests in fertile lowlands has created extensively cultivated areas where only remnant vegetation patches remain. Due to past and present land uses, such patches differ greatly not only in size and spatial arrangement, but also in habitat structure and species composition (Aparicio 2008, see also McIntyre and Hobbs 1999). Such intense habitat change may have a serious impact on plant-frugivore interactions because in warm Mediterranean habitats fleshy-fruited plant assemblages are mainly composed of late-successional species that are typically dispersed by birds (Herrera 1995). Fleshy-fruited plants may account for up to 57% of local woody species richness and 72% of woody plant cover in well-preserved woodlands (Herrera 1984, Jordano 1985). Since many bird species are strongly selective in terms of habitat and vegetation (Cody 1985), the frugivore assemblage in a given patch may be determined not only by its degree of fragmentation (Cordeiro and Howe 2003), but also by other habitat features related to local disturbances (Kirika et al. 2008) such as the abundance of fleshy-fruited plants (Tellería et al. 2005). In plants, habitat features and connectivity, along with frugivore abundance, should all influence seed dispersal success in the patch.

In this paper I investigate spatial variation in avian frugivore assemblages and their interactions with a fleshy-fruited shrub in the Guadalquivir Valley (SW Spain), a chronically fragmented and extremely deforested area that has long been intensively cultivated (Aparicio 2008). The studied plant was the Mediterranean myrtle *Myrtus communis* (Myrtaceae), a widespread Mediterranean species and one of the main components of woodland understoreys

and late successional shrublands in the area. I studied frugivore assemblages and fruit consumption by seed dispersers and predators over a whole fruiting season in relation to the degree of fragmentation and habitat features of different woodland patches in order to determine the most relevant aspect of fragmentation influencing this plant-frugivore system. Specifically, I addressed two main issues: 1) whether variation between patches in their degree of fragmentation and their habitat features determine changes in the abundance and composition of avian dispersers and predators of *Myrtus communis* seeds; and 2) whether variation between patches in frugivore assemblages, together with their degree of fragmentation and their habitat features, translate into different dispersal/predation balances for *Myrtus communis* and, therefore, in variable seed dispersal success between populations.

## Methods

### The plant-frugivore system

Myrtle *Myrtus communis* (Myrtaceae) is a sclerophyllous shrub and the sole representative of the Myrtaceae in the flora of the Mediterranean Basin. It grows to 4-m high and inhabits warm lowlands. Myrtle is hermaphrodite and insect-pollinated, and produces ellipsoidal berries  $8.2 \pm 1.2$  mm (mean  $\pm$  SD) in diameter (González-Varo et al. 2009). The berries, which are dark blue when they ripen (Fig. 1), have a sugar- and water-rich pulp (Traveset et al. 2001) that contains  $5.2 \pm 2.7$  seeds weighing  $10.8 \pm 4.1$  mg each ( $n = 2320$  fruits and seeds from 89 plants). Reproductive individuals may bear thousands of berries (mean  $\pm$  SD  $\approx 23\,000 \pm 15\,000$  fruits,  $n = 72$  plants). These ripen from mid-October until late November, at the same time as most other co-occurring fleshy-fruited species such as *Pistacia lentiscus* and *Olea europaea* var. *sylvestris* (Herrera 1984).

Myrtle seeds are mostly dispersed by passerine birds (Herrera 1984, Traveset et al. 2001). In southern Spain, myrtle shares its frugivore assemblage with almost all co-occurring bird-dispersed plant species (Herrera 1984). Most legitimate seed dispersers are either resident or wintering migrants belonging to Sylviidae and Turdidae, which typically swallow entire fruits and then defecate or regurgitate undamaged seeds (Herrera 1984). Seed predators are granivorous passerines (Fringillidae and Passeridae) and



Figure 1. Intact mature fruit of Mediterranean myrtle *Myrtus communis* (left) and avian-predated fruit (seedless) (right).

peck at fruits for seeds, but ignore the pulp. After seed predation by birds, seedless fruits usually persist on branches and can be recognised by the characteristic beak marks left by predators (Fig. 1). The pecking of pieces of pulp (discarding the seeds) by pulp eaters was rare in all myrtle populations studied

(<1% of the total fruits monitored showed pulp predation), and thus I focused on pre-dispersal and dispersal interactions with seed dispersers and seed predators.

Carnivorous mammals (red fox *Vulpes vulpes* and martens *Martes* spp.) have been reported to ingest myrtle fruits and act as legitimate dispersers (Aronne and Russo 1997, Traveset et al. 2001); nevertheless, although some of these animals are common in the patches studied, I never found any myrtle seeds in carnivore faeces. Rodents, such as the wood mice *Apodemus sylvaticus*, may feed on fallen fruits (i.e. post-dispersal predation) and consume their seeds (e.g. García et al. 2001), and seedless fruits, laterally gnawed and with teeth marks can be found beneath the shrub canopy, along with scattered seed fragments (González-Varo unpubl.).

### Study area and selected patches

The study was conducted in the Guadalquivir Valley (western Andalusia, southern Spain), a large (21 000 km<sup>2</sup>), fertile and intensively cultivated area, in which the historical transformation of natural habitats has left just ~1% of Mediterranean woodland cover in over 530 forest patches (Fig. 2a; for a detailed description see Aparicio 2008). The climate is typically Mediterranean, with warm dry summers and cool humid winters. Mean annual precipitation is ~550 mm. January and July temperatures average 10 and 26°C, respectively. Originally, the dominant vegetation in the area was sclerophyllous

Mediterranean maquis, mostly represented by vertebrate-dispersed plants associated with cork-oak *Quercus suber* and holm-oak *Q. ilex* subsp. *ballota* forests. Nowadays, the landscape in this area can be considered to be “relictual” (sensu McIntyre and Hobbs 1999), in which the overall patch area is reduced and spatial connectivity between patches is almost lacking (Aparicio 2008).

Of the 162 patches where myrtle is known to occur in this area (Albaladejo et al. 2009), I selected nine to conduct the present study: four large (87–1737 ha) and five small patches (2–32 ha; Fig. 2a). I used this distinction because large and small patches also support large (>2000 individuals) and small (≤120) myrtle populations, respectively (Table 1). Mean ±SD distance between selected patches was 80.8 ±47.1 km. The tree layer of these patches is mainly represented by holm-oaks, cork-oaks and/or planted stone pines *Pinus pinea*. The shrub layer is composed of low (<1 m) dry-fruited (Cistaceae, Labiatae and Leguminosae) and tall (>1 m) fleshy-fruited shrubs, among which *Pistacia lentiscus* (Anacardiaceae), *Myrtus communis* (Myrtaceae), *Olea europaea* var. *sylvestris* (Oleaceae), *Phillyrea angustifolia* (Oleaceae) and *Rhamnus lycioides* (Rhamnaceae) are the dominant species (Supplementary material Table S1). Due to patch management and successional processes (Aparicio 2008), understorey conditions vary greatly between patches, both in terms of cover and species composition.

### Characteristics of the patches and the myrtle populations

#### Degree of fragmentation

Using digital cartography of the study area (Aparicio 2008), I obtained (using GIS package ArcMap) the patch size (area) and percentage of woodland cover within a 5-km radius (R5 cover) around the patch centroid (Fig. 2b). This

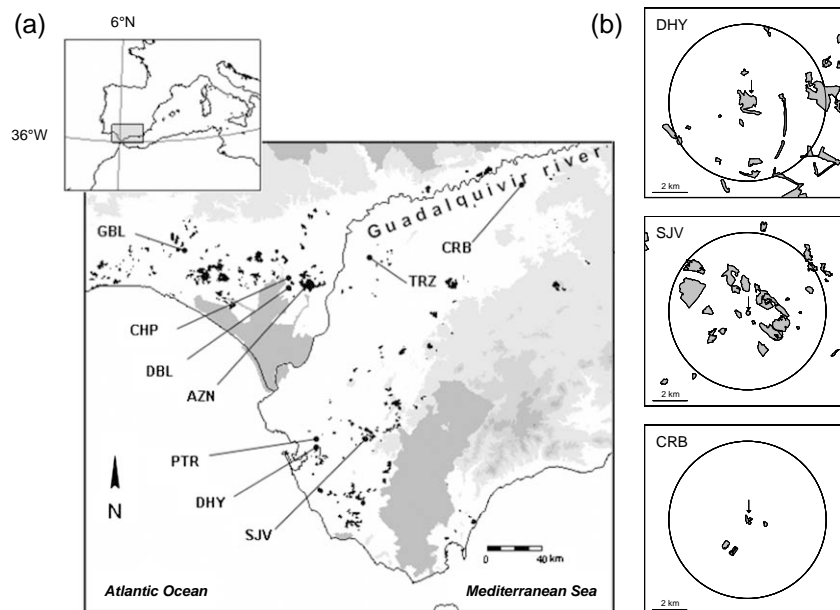


Figure 2. (a) Map of the Guadalquivir Valley (southern Spain) showing the location of the nine patches selected for study. The unshaded area represents lowland areas (below 200 m in altitude), where the remaining woodland patches are shown in black; higher elevations and legally protected areas are shown in light and dark grey, respectively. (b) Illustration of a large patch (DHY) and two small patches (SJV and CRB) with different degrees of isolation, showing the 5-km radius circle used to estimate the forest cover surrounding the patch.

Table 1. Characteristics of the nine studied woodland patches and myrtle *Myrtus communis* populations. The generic name of the main bird-dispersed plant species (BDP: *Crataegus monogyna*, *Myrtus communis*, *Olea europaea* var. *sylvestris*, *Phillyrea angustifolia*, *Pistacia lentiscus* and *Rhamnus lycioides*) is given.

| Patch name (code)                       | Large patches (>87 ha)                          |                                  |                                  |                                  | Small patches (<32 ha)         |                                     |                                   |  |   |
|---|---|----------------------------------|----------------------------------|----------------------------------|--------------------------------|-------------------------------------|-----------------------------------|--|---|
|   | Aznalcázar (AZN)                                | Dehesa Boyal (DBL)               | El Chaparral (CHP)               | Dehesa Yeguas (DHY)              | Gibraleón (GBL)                | Córdoba (CRB)                       | San José del Valle (SJV)          | Puerto Real (PTR)                                  | Tarazona (TRZ)                                  |
| Degree of fragmentation                 |   |                                  |                                  |                                  |                                |                                     |                                   |  |   |
| Patch size (ha)                         | 1737  | 244                              | 87                               | 90                               | 32                             | 10                                  | 5                                 | 2  | 2*  |
| R5 cover (%)                            | 30.5  | 4.6                              | 7.5                              | 2.7                              | 6.4                            | 0.5                                 | 7.9                               | 1.7  | 0.1   |
| Main matrix types                       | Cereal fields                                   | Olive groves                     | Olive groves                     | Cereal fields                    | Cereal fields                  | Cereal fields                       | Vegetable orchards                | Cereal fields                                      | Cereal fields                                   |
|   | Olive groves                                    | Oak savanna                      | Oak savanna                      | Cotton fields                    | Oak savanna                    | Olive groves                        | Oak savanna                       | Cotton fields                                      | Orange groves                                   |
| Habitat features                        |   |                                  |                                  |                                  |                                |                                     |                                   |  |   |
| Tree species                            | Pines   | Mixed                            | Mixed                            | Pines                            | Mixed                          | Oaks                                | Oaks                              | Pines  | Olives  |
| Main bird-dispersed plant species (BDP) | <i>Olea</i><br><i>Pistacia</i><br><i>Myrtus</i> | <i>Myrtus</i><br><i>Pistacia</i> | <i>Myrtus</i><br><i>Pistacia</i> | <i>Pistacia</i><br><i>Myrtus</i> | <i>Pistacia</i><br><i>Olea</i> | <i>Pistacia</i><br><i>Crataegus</i> | <i>Phillyrea</i><br><i>Myrtus</i> | <i>Pistacia</i><br><i>Myrtus</i><br><i>Rhamnus</i> | <i>Olea</i><br><i>Pistacia</i><br><i>Myrtus</i> |
| Tree cover (%)                          | 26.1  | 34.7                             | 29.2                             | 39.9                             | 32.0                           | 13.2                                | 28.7                              | 28.5   | 15.1  |
| Shrub cover (%)                         | 48.5  | 23.5                             | 25.3                             | 49.5                             | 18.4                           | 38.0                                | 47.4                              | 37.6   | 38.2  |
| BDP cover (%)                           | 21.5  | 11.5                             | 5.0                              | 19.8                             | 17.1                           | 14.3                                | 22.6                              | 10.0   | 37.4  |
| Myrtle population                       |   |                                  |                                  |                                  |                                |                                     |                                   |  |   |
| Myrtle pop. size                        | 85 100  | 8900                             | 2100                             | 3400                             | 50                             | 70                                  | 120                               | 30   | 30  |
| Myrtle cover (%)                        | 7.9   | 8.0                              | 3.1                              | 8.1                              | 0.8                            | 0.7                                 | 6.4                               | 3.0  | 12.2  |
| Myrtle/BDP ratio                        | 0.37  | 0.69                             | 0.63                             | 0.41                             | 0.05                           | 0.05                                | 0.28                              | 0.20   | 0.33  |

\*Hedgerows on both sides of a path (ca 50 × 450 m).

metric (R5 cover) can be considered as an inverse estimate of forest fragmentation at a broad landscape scale (Steffan-Dewenter et al. 2002). The total area sampled was 7854 ha (~80 km<sup>2</sup>). Patch size and R5 were positively, yet non-significantly correlated (Spearman's  $r_s = 0.550$ ,  $p = 0.125$ ,  $n = 9$ ).

### Habitat features

I characterized the vegetation structure and plant composition of each patch by means of interception of woody species along 50-m long linear transects ( $n = 6$ –12 depending upon patch size). Along with overall tree and shrub cover in each patch, I estimated the mean cover of each bird-dispersed plant species and the total cover of all bird-dispersed plants (hereinafter, “BDP cover”; Supplementary material Table S1). During the study, fruits were abundant in all patches, with most myrtle plants (>90%) and other fleshy-fruited species (e.g. *Pistacia*, *Olea* and *Phillyrea*) bearing fruits; thus, the BDP cover can be considered as an estimate of the fruit abundance available for birds. The dwarf palms *Chamaerops humilis* (Palmae), whose drupes are consumed by carnivorous mammals (Revilla and Palomares 2002) and the non-fruited plants (males) of dioecious (e.g. *Pistacia lentiscus*) or androdioecious plants (e.g. *Phillyrea angustifolia*), were not considered when obtaining the BDP covers.

I calculated the ratio between the myrtle cover and that of bird-dispersed plants (Myrtle/BDP ratio) in order to quantify the relative importance of myrtle within the whole assemblage of bird-dispersed plants in each patch; thus, the Myrtle/BDP is the inverse of the heterospecific fruiting environment. Myrtle population sizes were obtained by counting all plants in small patches, whereas in large patches, population sizes were estimated by counting all adult plants along 10 linear transects ( $500 \times 20 \text{ m} = 1 \text{ ha}$ ) randomly located within each patch and then extrapolating the myrtle density to the corresponding patch area. Population size was highly positively correlated with patch size ( $r_s = 0.933$ ,  $p < 0.001$ ,  $n = 9$ ).

The characteristics and variables measured in the nine studied patches are summarized in Table 1.

### Frugivore censuses

To obtain the composition and abundance of frugivores in each of the nine studied patches, I performed bird censuses between early November 2007 and late February 2008. This sampling period coincided with the peak fruiting period in myrtles. One 300-m fixed-line transect was established within small patches and two such transects within large patches. Censuses were repeated every 2–3 weeks, each consisting of the noting of all contacted birds – either audibly or visually – along each transect. Only frugivorous birds were counted. In total, 65 censuses were carried out during the study period (5 and 10 censuses per patch in small and large patches, respectively). Censuses were performed between 09.00 h and 12.00 h, on sunny or slightly cloudy days with low wind speed ( $< 20 \text{ km h}^{-1}$ ). Bird abundance was expressed as the number of birds contacted per 300 m. On the basis of published studies (Herrera 1984, Jordano 1987, 1994, Traveset 1994)

and personal observations, I classified each fruit-eating species according to its type of frugivory (seed disperser or seed predator). Given that the disperser guild in the study area is composed of resident and wintering species (both co-occurring during the fruiting period), I also classified each species according to its residency status (Jordano 1985). I distinguished resident and wintering dispersers because they behave differently in terms of their use of space (territorial and vagrant, respectively) during the fruiting period and thus may be affected in different ways by landscape and/or habitat features (Rey 1995, Tellería et al. 2008).

### Avian frugivory

I examined fruit consumption by dispersers and predators in the nine myrtle populations during the fruiting season 2007–2008. In September 2007, I selected and marked 5–10 fruiting plants per patch ( $n = 72$  plants). Fruit consumption was monitored throughout the whole fruiting season (October to April, 189 d in total) using two complementary methods: 1) monitoring fruits on branches (branch observations) and 2) monitoring fruits on the ground beneath the plant canopies (ground observations). The estimates derived from the branch counts may overestimate dispersal and underestimate predation because desiccated fruits or pecked fruits may drop to the ground after being attacked by frugivores. The use of two methods thus aimed to correct these sampling errors (for similar procedures see Alcántara et al. 1997, Jordano and Schupp 2000).

#### Branch observations

Before the fruit ripened in the first week of October 2007, I marked four branches per plant and counted all their fruits twice. Mean  $\pm$  SD number of fruits recorded per plant was  $106 \pm 14$ , totalling 619–1095 fruits per patch (total = 7843 fruits). I monitored fruit removal every 2–3 weeks throughout the fruiting season until early April 2008, when most berries had either been removed or were dried on the branches (total = 11 surveys including fruit recording). I initially considered any missing fruit (i.e. disappeared from the branch) between two consecutive surveys as removed by legitimate dispersers. Among the fraction of fruits that remained on the branches, desiccated and avian-predated fruits (Fig. 1) were counted as not dispersed and predated, respectively (Alcántara et al. 1997, Jordano and Schupp 2000). In each survey, all the studied patches were visited during the same week.

#### Ground observations

I estimated the initial canopy fruit density (fruits  $\text{m}^{-2}$ ) for each marked plant by counting the number of fruits within ten  $15 \times 15 \text{ cm}$  quadrats randomly placed throughout the plant canopy ( $0.225 \text{ m}^2$  sampled per plant) (see García et al. 2001 for a similar procedure). Then, I placed two permanent  $30 \times 30 \text{ cm}$  sampling quadrats beneath the canopy of each selected plant to sample fallen fruits. The fact that fruit density is very homogeneous over the whole myrtle canopy enhances the reliability of this sampling

method. Data from the two quadrats were pooled for each individual plant. Every 2–3 weeks, I collected all fruits within the quadrats and classified them as intact, desiccated or predated, differentiating between predated fruits as either predated by birds (showing a characteristic beak mark and lacking seeds; Fig. 1) or predated by rodents (gnawed pulp with teeth marks). As rodents usually consume myrtle fruits in situ (i.e. beneath the canopy) and no consumption by carnivores was detected in the patches studied, fruit losses from the sampling quadrats were considered to be negligible. At the end of the experiment, I estimated the total proportion of fallen fruits ( $Ft_i$ ) from each plant  $i$  by dividing the accumulated fruit density in the quadrats (all pooled, predated and non-predated fruits) by the fruit crop density in the projected canopy (see above), both expressed as fruits  $m^{-2}$ . Similarly, I estimated the proportion of avian-predated fruits that fell to the ground ( $Fp_i$ ) considering only the accumulated density of avian-predated fruits in the quadrats. I calculated the corrected dispersal rates at plant level as:  $D'_i = D_i - (D_i \times Ft_i)$ , where  $D_i$  is the dispersal rate (proportion of the crop consumed by avian dispersers) as originally estimated from the branch observations (see above) and  $Ft_i$  the estimated proportion of the plant crop that fell to the ground. Hence, the correction factor ( $D_i \times Ft_i$ ) represents the proportion of the observed dispersal ( $D_i$ ) that was overestimated by fallen fruits ( $Ft_i$ ). Similarly, I calculated the corrected predation rates at plant level as:  $P'_i = P_i + (P_i \times Fp_i)$ , where  $P_i$  is the predation rate observed on branches and  $Fp_i$  the proportion of avian-predated fruits that fell to the ground (see also Alcántara et al. 1997, Jordano and Schupp 2000).

## Data analyses

I used repeated-measures ANOVAs to test differences in the abundance of frugivore guilds (dispersers and predators) between patches, considering each fixed-transect as the subject and each census as the within-subject factor. Relationships between frugivore abundance and patch characteristics (degree of fragmentation and habitat features) were examined using Spearman's rank correlations. Correlations were performed separately for 1) each guild (dispersers and predators), 2) resident and wintering species within the disperser guild and 3) the most important bird species within each guild (all predator species and the main disperser species; Results).

To quantify the similarity between pairs of patches in terms of the composition of frugivores and bird-dispersed plants I used a proportional similarity index (PS; Hurlbert 1978), calculated as  $PS = \sum_{i=1}^n \min(p_{ia}, p_{ib})$ , where for  $n$  species,  $p_{ia}$  is the relative abundance of the species  $i$  at site  $a$ , and  $p_{ib}$  is the relative abundance of the species  $i$  at site  $b$ . Hence, the PS ranged from 0 (no overlap between assemblages) to 1 (complete overlap) (Jordano 1994, Githiru et al. 2002). Seed predators were excluded since, with the probable exception of greenfinches *Carduelis chloris* (Jordano 1990), fruits are not an important food source for most of these species in the region (Herrera 1984). I created two matrices of PS values for all possible pairs of patches ( $n = 36$  pairs), one for disperser frugivores and another for plants. I also created a matrix for inter-patch distances, and

two further matrices for the differences between patches in the degree of fragmentation (i.e. |patch  $a$  – patch  $b$ |) with the variables patch size and R5 cover). I used Mantel tests to assess whether the local composition of seed dispersers was significantly related to the composition of bird-dispersed plants, the degree of fragmentation and/or geographical location. Mantel tests were performed with the software PASSAGE 1.1 (Rosenberg 2004) and statistical significance was determined by setting 1000 permutations for each test.

I used one-way ANOVAs to test for differences between patches in final dispersal rates. I used Kruskal-Wallis tests for predation rates, as data could not be normalized with any transformation. For these analyses, I used only corrected estimates, because, as expected, branch observations overestimated dispersal rates and underestimated predation rates (Wilcoxon tests:  $Z > 5.9$ ,  $p < 0.001$ ,  $n = 72$ ; Fig. 4). Thus, I assumed that the corrected estimates were more realistic and are used throughout this paper (unless otherwise stated). Relationships between patch characteristics and each type of frugivory (dispersal and predation) were tested with Spearman's rank correlation.

When necessary, data were log- or angular-transformed to improve normality. I used the type III sum of squares for parametric tests because of unequal sample sizes (censuses and plants). All analyses were performed with the software STATISTICA v.6 (StatSoft 2001).

## Results

### Variation in frugivore assemblages

#### Variation in frugivore abundance

A total of 3037 birds belonging to 14 frugivore species (10 seed dispersers and four seed predators) were recorded from the nine patches between November 2007 and February 2008 (Supplementary material Table S2). Seed dispersers made up 67.2–86.9% of the frugivorous birds recorded in each patch, while seed predators accounted for 13.1–32.8%. Of the disperser guild, five species were present in all patches and accounted for >90% of records (Fig. 3): robin *Eriothacus rubecola*, blackcap *Sylvia atricapilla*, Sardinian warbler *Sylvia melanocephala*, song thrush *Turdus philomelos* and blackbird *Turdus merula*. The abundances of some disperser species were very similar between patches (e.g. robin:  $CV_{\text{patches}} = 15\%$ ), but varied greatly for other species (e.g. song thrush:  $CV_{\text{patches}} = 73\%$ ; Supplementary material Table S2). The seed predator guild consisted of four species (Fig. 3): greenfinch *Carduelis chloris*, chaffinch *Fringilla coelebs* and two sparrow species *Passer domesticus* and *P. hispaniolensis*.

The nine patches differed significantly in terms of the abundance of dispersers ( $F_{8, 4} = 22.31$ ,  $p = 0.005$ ), but not of predators ( $F_{8, 4} = 3.86$ ,  $p = 0.104$ ; Fig. 3). Disperser abundance was not significantly correlated ( $p > 0.05$ ) with any of the patch characteristics considered here (degree of fragmentation or habitat feature) (Table 2). Only shrub cover was positively and near-significantly ( $p \leq 0.1$ ) associated with the abundance of seed dispersers. While resident dispersers were more abundant in larger patches, wintering dispersers were more abundant in patches with the greatest BDP cover (Table 2). Song thrush *T. philomelos* abundance

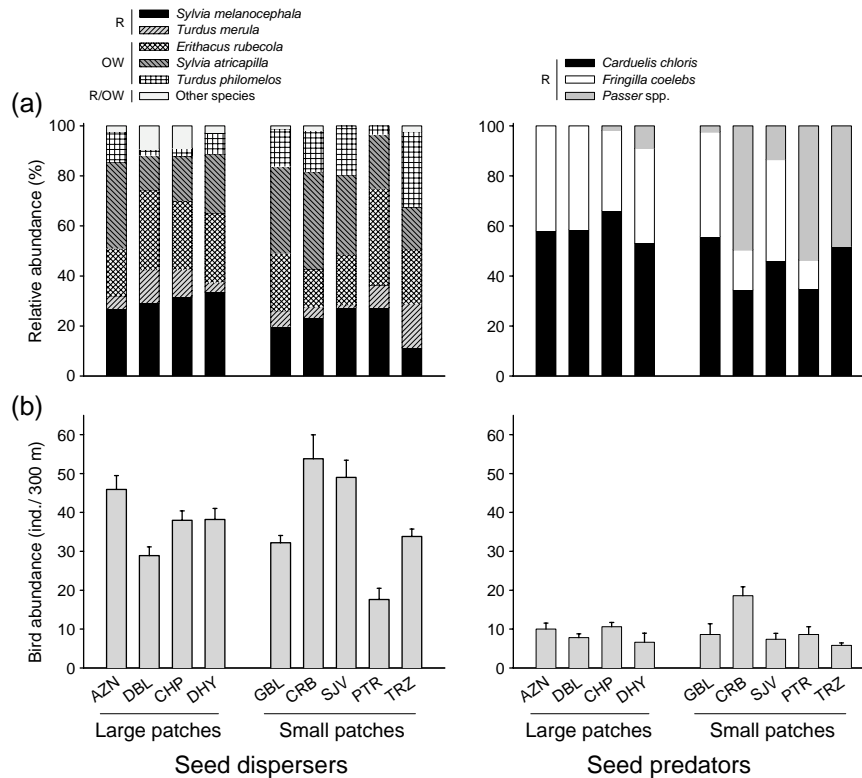


Figure 3. Composition and abundance of the avian frugivore assemblages (seed dispersers and predators) in the nine patches studied during the 2007–2008 fruiting season; (a) relative frequencies (%) of the different species and (b) absolute abundances (mean  $\pm$  SE) of each guild. “R” denotes year-round resident species, “OW” overwintering species.

was positively and significantly correlated with BDP cover, being the only disperser species influenced by habitat features. Predator abundance was not significantly correlated ( $p > 0.05$ ) with any of the patch characteristics, although it was negatively associated with BDP cover (near-significant correlation, Table 2). This lack of association could arise from contrasting correlations between species: for example, at species level, chaffinches *F. coelebs* were significantly more abundant at large/connected

patches, unlike sparrows (*Passer spp.*), which were more abundant at the most fragmented sites (Table 2, Fig. 3).

#### Similarity in the composition of avian dispersers

Mean  $\pm$  SD proportional similarity (PS) between patches for avian dispersers was  $0.76 \pm 0.10$  ( $n = 36$  pairs of patches), indicating a high overlap ( $\sim 76\%$ ) in the composition of this guild (Fig. 3) (all PS values are given

Table 2. Spearman’s coefficient ( $r_s$ ) values for the characteristics of the nine studied patches and abundances of different avian frugivores (guilds, groups and the most important species within each guild) during autumn–winter 2007–2008. R5 cover is the percentage of woodland cover within a 5-km radius around the patch centroid; BDP cover is the cover of bird-dispersed plants in the patch. In bold,  $p < 0.1$ ; \*,  $p < 0.05$ ; \*\*,  $p < 0.01$ .

| Frugivore guilds and species | Degree of fragmentation |                 | Habitat features |              |                |
|------------------------------|-------------------------|-----------------|------------------|--------------|----------------|
|                              | Area                    | R5 cover        | Tree cover       | Shrub cover  | BDP cover      |
| All dispersers               | 0.142                   | 0.233           | −0.367           | <b>0.600</b> | 0.400          |
| Resident dispersers          | <b>0.664</b>            | 0.393           | −0.042           | 0.226        | −0.192         |
| <i>Sylvia melanocephala</i>  | 0.360                   | 0.450           | 0.167            | 0.550        | 0.167          |
| <i>Turdus merula</i>         | 0.092                   | −0.260          | −0.301           | −0.343       | −0.142         |
| Wintering dispersers         | −0.075                  | 0.100           | −0.567           | 0.433        | <b>0.633</b>   |
| <i>Erithacus rubecola</i>    | 0.567                   | 0.444           | 0.544            | 0.377        | −0.017         |
| <i>Sylvia atricapilla</i>    | 0.251                   | 0.350           | −0.333           | 0.367        | 0.367          |
| <i>Turdus philomelos</i>     | −0.285                  | −0.067          | −0.550           | 0.433        | <b>0.833**</b> |
| All predators                | 0.239                   | 0.243           | −0.326           | −0.326       | −0.611         |
| <i>Carduelis chloris</i>     | <b>0.597</b>            | 0.402           | 0.000            | −0.234       | −0.427         |
| <i>Fringilla coelebs</i>     | <b>0.723*</b>           | <b>0.787*</b>   | 0.201            | −0.284       | −0.201         |
| <i>Passer spp.</i> §         | − <b>0.835**</b>        | − <b>0.698*</b> | −0.555           | 0.168        | 0.067          |

§ Includes *P. domesticus* and *P. hispaniolensis*.

in Supplementary material Table S3). For bird-dispersed plants, the PS was  $0.57 \pm 0.15$ , indicating that the relative composition of this plant guild overlapped on average  $\sim 57\%$  between patches (Supplementary material Table S3). Similarity between patches in the disperser guild was not related to bird-dispersed plant assemblages, patch size, R5 cover or inter-patch distances (Mantel tests:  $r_m < |0.1|$ ,  $p > 0.3$  in all cases). Thus, neither the composition of bird-dispersed plants, the degree of fragmentation nor geographical location determined the local composition of seed dispersers. Inter-patch distances were negatively related to the similarity between patches in their composition of bird-dispersed plants (Mantel test:  $r_m = -0.399$ ,  $p = 0.017$ ), indicating that nearby patches had more similar fruiting-plant assemblages.

### Variation in frugivory at myrtle

Fruit consumption showed both geographical and temporal patterns (Fig. 4). In the southernmost myrtle populations (DHY, SJV and PTR; Fig. 2a) avian fruit predation was completely absent. In addition, in most populations, fruit consumption by dispersers and predators exhibited contrasting temporal trends (Fig. 4): whereas fruits were consumed by dispersers during the whole of the study period (albeit at a faster rate towards the end of the season), fruit predation ended rather earlier in the season. Mean 82.6% of initial fruit crops (range<sub>pop</sub> = 60.4–96.9%) was consumed by frugivores, the remaining fell to the ground or desiccated on the branches.

Final dispersal and predation rates varied greatly between populations (range<sub>dispersal</sub> = 20–81%; range<sub>predation</sub> = 0–77%). Dispersal ( $F_{8, 63} = 5.43$ ,  $p < 0.001$ ) and predation rates ( $H_8 = 51.24$ ,  $p < 0.001$ ) differed significantly between populations (Fig. 5), although they were not correlated with frugivore abundance (dispersers and predators, respectively), degree of fragmentation or habitat features ( $r_s < |0.5|$ ,  $p > 0.3$  in all cases,  $n = 9$ ). However, both dispersal and predation rates were highly negatively correlated ( $r_s = -0.966$ ,  $p < 0.001$ ,  $n = 9$ ; Fig. 6a), which shows that the final dispersal rates were mostly determined by the intensity of avian predation suffered by each population.

Because the lack of avian predation in southernmost populations may obscure other general patterns, I performed separate correlation analyses including only those populations that experienced avian predation ( $n = 6$ ). This analysis revealed significant correlations with the Myrtle/BDP ratio for both dispersal ( $r_s = 0.899$ ,  $p = 0.015$ ) and predation rates ( $r_s = -0.841$ ,  $p = 0.036$ ) (Fig. 6b). Moreover, predation rates were negatively related to patch size (correlation marginally significant,  $r_s = -0.771$ ,  $p = 0.072$ ). Therefore, predation rates were lower (favouring dispersal) in patches where myrtle was more abundant in relative (Myrtle/BDP) and absolute terms (population size) (Fig. 6b). It is worth noting that although the Myrtle/BDP ratio was positively associated with patch size, the correlation was not significant for this subset of patches ( $r_s = 0.638$ ,  $p = 0.173$ ,  $n = 6$ ).

## Discussion

Habitat fragmentation may affect plant-frugivore interactions by reducing abundance and/or shifting the composition of local frugivore assemblages (Githiru et al. 2002, Cordeiro and Howe 2003, Kirika et al. 2008, Moran et al. 2009). One of the most notable results of this study is that the frugivore assemblage in the study area (and, in particular the disperser guild) can tolerate extreme habitat fragmentation, both in terms of abundance and composition. Another result of interest is that frugivory patterns at myrtle shrubs were not influenced by the abundances of either dispersers or predators.

### Fragmentation, habitat composition and variation in avian frugivore assemblages

I found that the abundance of seed predators was very similar between patches, but varied greatly for dispersers. However, such variation was not related to the degree of fragmentation, but to shrub cover (near-significant). Within each guild, individual species (song thrushes, chaffinches and sparrows) or groups of resident and wintering birds showed strong specificity in their response to patch characteristics. Probably, such intra-guild differences gave rise to the absence of clearly significant responses by whole guilds (Kirika et al. 2008).

Although habitat fragmentation may restrict the presence of forest-specialist bird species to large woodland patches (González-Varo et al. 2008), the frugivore assemblage in the study region seems to tolerate scenarios of severe fragmentation ( $< 0.1\%$  woodland cover within a 5-km radius, i.e.  $\sim 80 \text{ km}^2$ ). The five main disperser species, which also dominate the disperser assemblages in well preserved areas (Jordano 1985, Tellería et al. 2005), were recorded in all patches. As a result, the patches studied showed a high overlap in their composition of seed dispersers ( $\sim 76\%$ ). Other studies have also reported high similarity in frugivore assemblages between different habitat types despite important differences in plant composition (Jordano 1985, Ortiz-Pulido et al. 2000, Githiru et al. 2002). High similarity in frugivore assemblages between patches within a fragmented landscape is to be expected if frugivores are able to 1) move easily across the anthropogenic matrices (Rey 1995, Pizo 2004), 2) stay and/or persist at least temporally in a given patch (Herrera and García 2009 and references therein) and 3) feed on the different fruit species available in patches with different plant composition (generalist frugivory; Herrera 1984). Such traits identify most frugivorous birds considered here (Herrera 1995) and may be responsible for the fact that the similarity in disperser assemblages was not related either to the composition of bird-dispersed plants, the degree of fragmentation or geographical distance.

In northern latitudes, most extant bird assemblages and their current migratory routes arose during last five million years, influenced by global fluctuations in climate and vegetation distribution (Steadman 2005). Rey (1995) has suggested that Mediterranean frugivorous birds may have a relatively high tolerance of anthropogenic disturbance given

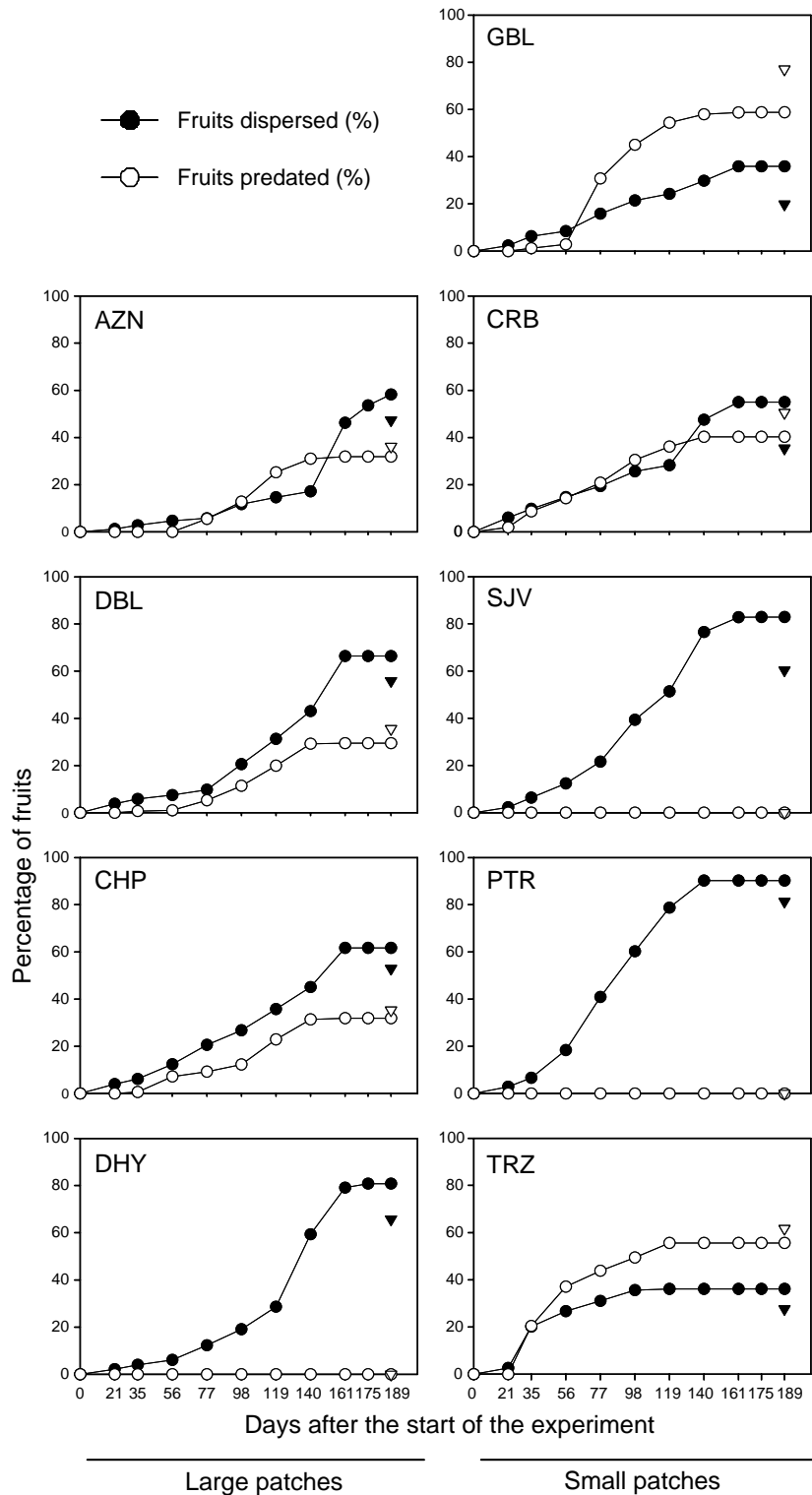


Figure 4. Temporal dynamics of myrtle *Myrtus communis* fruit consumption by avian seed dispersers and predators in the nine patches studied during the 2007–2008 fruiting season. Note that data are from branch counts (i.e. uncorrected estimates) because correction was only applicable to final accumulated estimates (see Methods for details). Black triangles represent the final corrected dispersal estimates; white triangles corrected predation estimates.

the nomadic behaviour of over-wintering species and their capacity for tracking rich-fruited wintering quarters across large geographical areas (see also Jordano 1985, Herrera 1995, Tellería et al. 2008). These birds represented in

average ca 65% in the number of dispersers in the studied patches. Although resident dispersers were more abundant in larger patches, a single wintering species (song thrush *T. philomelos*) and the whole group of wintering dispersers

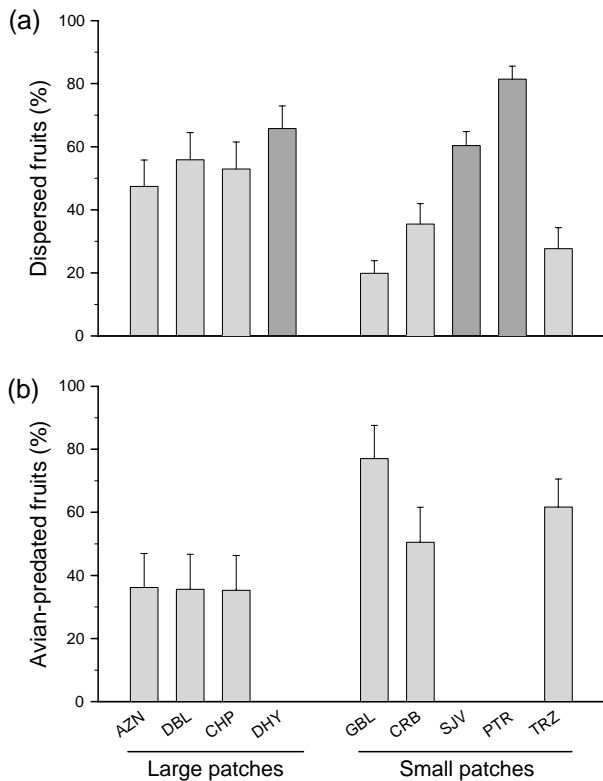


Figure 5. Final percentage (mean  $\pm$  SE) of (a) dispersed fruits (dispersal rates) and (b) avian-predated fruits (predation rates) in the nine myrtle *Myrtus communis* populations studied during the 2007–2008 fruiting season. Dark-grey bars represent the southernmost patches, where avian fruit predation was completely absent.

were more abundant in patches with greater cover of bird-dispersed plants. These findings highlight that “patch quality” (fruit abundance) rather than “patch quantity” (woodland cover) may be more important for wintering dispersers (Tellería et al. 2005, 2008; see also the “continuum model” in Fischer and Lindenmayer 2006).

### Fragmentation, habitat composition and the dispersal/predation balance in myrtle: the importance of frugivore feeding behaviour

Pooling all populations, the proportion of myrtle fruits removed by legitimate dispersers was 49.6%, which is among the lowest values ever reported for Mediterranean fleshy-fruited species (reviewed in Herrera 1995). Such low dispersal success was caused by severe interactions with avian predators in most of the studied patches. I found great spatial variation in frugivory interactions, as shown by the great differences in dispersal and predation rates between patches. However, these differences did not appear to be related to frugivore abundance. Thus, it could be argued that differences in dispersal and predation between patches were more influenced by the feeding behaviour of groups of birds than by shifts in their abundance or composition. For instance, an alternative food source at a broad landscape scale could explain why predators did not feed on myrtle fruits in the southernmost patches. I visited the nine studied

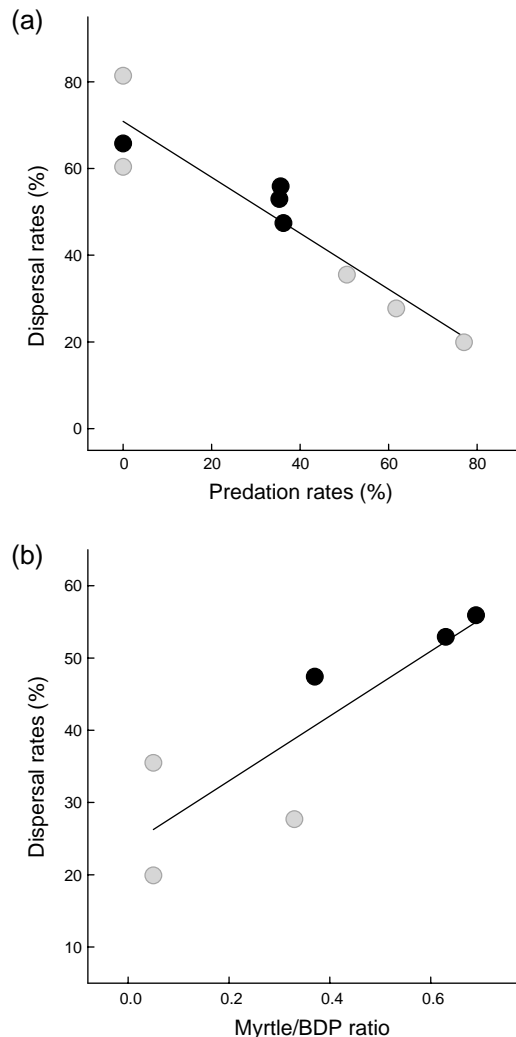


Figure 6. (a) Relationships between avian seed dispersal and predation rates in the nine myrtle *Myrtus communis* populations studied during the 2007–2008 fruiting season; and (b) relationship between dispersal rates and relative cover of myrtle in relation to the total cover of bird-dispersed plants (Myrtle/BDP ratio) for those populations that suffered from avian-predation ( $n = 6$ ; see text for details). Black circles represent large patches (>87 ha); grey circles small patches (<32 ha).

patches in the 2008–2009 fruiting season (during January 2009) finding the same pattern: fruit predation was completely absent from the southernmost myrtle populations. A possible explanation is the co-existence of the fruiting shrub *Pistacia lentiscus*, whose seeds are also commonly consumed by predators (Jordano 1990); this plant grows more densely in southern than northern areas (mean cover = 9 vs 19% in predated and non-predated patches, respectively; Supplementary material Table S1) and also produces better crops there than in other areas of the valley (González-Varo unpubl.). Indeed, it was noticeable that predators in the southernmost patches always fed on *P. lentiscus*.

The fact that most of the fruit crops remained on the branches until they were consumed either by dispersers or predators determined an almost perfect correlation between

dispersal and predation rates (Fig. 6). The monitoring of fruit removal over the whole fruiting season provided valuable information regarding the temporal patterns of frugivore activity that affect both the dispersal and predation of myrtle fruits. Seed predators generally ceased myrtle fruit consumption by the middle of the fruiting season (in February, around day 140 of monitoring), although fruits continued to be abundant (Fig. 4). This probably reflects a shift to an insect-based diet in preparation for the breeding season (Cramp and Perrins 1994). Because in most patches significant fruit removal by dispersers did not begin until late (the second half) in the fruiting season, predators greatly conditioned the crop fraction available to dispersers. Therefore, both types of frugivory generate complex patterns at population level, making the disentangling of causal relationships a particular challenge.

Among the “predated” myrtle populations, dispersal and predation rates were significantly related to the hetero-specific fruiting environment (Myrtle/BDP ratio) and near-significantly to patch size. Predation rates were lower (and dispersal rates higher) in patches where myrtle “dominated” the bird-dispersed plant assemblage and in larger patches (Fig. 6). Although the Myrtle/BDP ratio and patch size were positively associated (but not significantly), some evidences suggest that these two factors operate in combination. I propose two alternative non mutually-exclusive mechanisms to explain the effects of Myrtle/BDP ratio and patch size on frugivory patterns. Firstly, predators may become more satiated in large and/or myrtle-dominated patches. In fact, large patches harboured more fruits but supported similar predator densities to those of small patches. Further evidence is that early predation rates were higher in smaller patches (Fig. 4). The sparrow flocks that were frequently observed in the vicinity of the smaller myrtle populations are another possible factor that should be taken into account if – as seems likely – they occasionally predate on myrtle fruits (Supplementary material Table S2).

Secondly, the lower myrtle dispersal rates at patches with a high heterospecific fruiting environment (i.e. low Myrtle/BDP ratio) suggests that interspecific competition for dispersers might be occurring and myrtle thus might compete poorly with other fruiting plants when trying to attract dispersers. In contrast to the lipid-rich fruit of typical Mediterranean bird-dispersed plants such as *Olea*, *Pistacia* and *Phillyrea* (Herrera 1995), myrtle fruits are sugar- and water-rich (Traveset et al. 2001). A preference in dispersers for lipid-rich fruits, which are an essential part of their diets in autumn and winter (Herrera 1995), might explain why myrtle dispersal rates were lower in patches with a higher availability of heterospecific fruits (see the “nutritional-content hypothesis” in Izhaki [2002]). This mechanism may also explain why in such patches significant fruit removal by dispersers did not start until late in the fruiting season (second half), despite ripe myrtle fruits being available for several weeks (e.g. AZN, DHY, CRB in Fig. 4). Thus, dispersers turn to myrtle at the end of its long fruiting season when heterospecific fruits become scarce. This pattern was less apparent in small patches, which could also be related to a lower disperser satiation there (discussed above).

## Concluding remarks

This paper improves our understanding of plant-frugivore interactions in long-term fragmented areas, in particular, in warm Mediterranean lowlands. The results show that patterns of variation in frugivore assemblages and frugivory in heavily fragmented habitats may be more complex than previously reported (Santos and Tellería 1994, Cordeiro and Howe 2003, Rodríguez-Cabal et al. 2007, Wright 2007). I found that most frugivores, particularly seed dispersers, can tolerate extreme habitat fragmentation. Moreover, patterns of frugivory did not depend on frugivore abundance, but rather on the feeding behaviour of both dispersers and predators under the influence of local fruit availability. This caused geographical and between-patch differences in the dispersal/predation balance in myrtles, some of which may not be directly interpretable as fragmentation effects, but as effects of local abundance and diversity of fruits. Hence, we could expect that local patterns of frugivory may be different in those years with marked inter-species differences in fruit production.

Warm Mediterranean lowlands are important wintering quarters for European frugivorous birds (Jordano 1985, Rey 1995, Tellería et al. 2005). An interesting finding is that “patch quality” (fruit abundance) is more important than “patch quantity” (woodland cover) in determining the abundance of wintering dispersers. In a conservation context, this finding reveals that it may be possible to sustain frugivore numbers by managing the availability of fruiting plants (Tellería et al. 2005, 2008), that is, by promoting succession within extant forest patches rather than increasing woodland cover at landscape level, which, given current types of land uses, may not be feasible.

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