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Spatial and temporal variation in the avian-frugivore assemblage of Prunus mahaleb: patterns and consequences

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The patterns of spatial and temporal variation in the species richness and relative abundance of frugivorous birds that consume fruits and disperse seeds of *Prunus mahaleb* (Rosaceae) were studied in two Southeastern Spain populations and compared with previous information from 4 sites, 3 of them in Northwestern Spain. Data for 8 study years in one population are used to assess temporal variation in this frugivore assemblage. Species richness of local bird assemblages ranged between 6 and 26 species. Thrushes, redstarts, and warblers were the main seed dispersers among a total of 31 species recorded for all sites pooled, and together account for 82% of the feeding records. Chaffinches and tits, acting as pulp consumers, were also important in at least two highland assemblages. The proportional similarities for pairwise comparisons among assemblages averaged 0.31 ± 0.16, indicative of significant local variation in assemblage composition. However, most differences were between assemblages from the two geographic regions, with pairwise similarities between assemblages within a given region being significant. The relative importance of legitimate seed dispersers, pulp consumers, and seed predators varied significantly among sites, this variation being more pronounced than variability among years within a site. The matrix of proportional similarity among sites showed a structured pattern and was strongly correlated with a matrix of geographic distance among them. The frugivorous birds visiting *P. mahaleb* showed significant similarity and constancy among sites within a region and among years within a site, but subtle variations in the relative importance of legitimate seed dispersers versus non-disperser species had measurable effects on seed dispersal. Average fruit removal and seed dispersal efficiency for individual trees increased in sites or years with greater relative importance of legitimate seed dispersers in the frugivore assemblages. These variations and their potential effects could be very difficult to detect in short-term studies but may have demographic and evolutionary implications in this plant-frugivore interaction.

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The study of temporal and spatial variation is central to our understanding of the evolution of mutualistic interactions in general, because the evolutionary change of traits involved in the interaction depends on the degree of spatial and temporal constancy of the selection pressures derived from the interaction itself (Janzen 1980, Schemske and Horvitz 1984, Herrera 1988a, Horvitz and Schemske 1990, Jordano 1993a). Studies of plant-seed disperser mutualisms conducted in the last five years have started to show that both the mode and pattern of interaction between fleshy-fruited plants and animal frugivores varies considerably at different temporal and spatial scales. Significant variation occurs among habitat patches within a given site, or among populations within a region and, in addition, these spatial patterns might vary considerably between years (see Herrera 1988a, Katusic-Malmborg and Willson 1988, Keeler-Wolf 1988, Guitián et al. 1992, Howe 1993, Jordano 1993a, Willson and

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Whelan 1993, Herrera et al. 1994, Traveset 1994). However, the scarcity of information available about how disperser assemblages differ among plant populations and individuals is surprising, given their potential significance from a demographic perspective (but see Bronstein and Hoffmann 1987, Snow and Snow 1988, Sargent 1990). Moreover, this major gap in our knowledge of variation in plant/disperser mutualism is exacerbated by the dearth of studies addressing how variation in the size and composition of disperser assemblages influences seed removal and realized fecundity (Willson and Whelan 1993, Herrera et al. 1994).

Variation in disperser assemblage composition may have two major potential effects depending on whether it affects the abundance of frugivores or the relative importance of different frugivore types (e.g., legitimate seed dispersers, pulp consumers and/or seed predators) in the assemblage. First, fruit removal efficiency might be limited by a scarcity of frugivores, the fruit supply exceeding the potential demand of the animal population (i.e., a situation of frugivore 'satiation'). Frugivore satiation has been documented, either explicitly or implicitly, in a number of studies of fleshy-fruited plants during good crop years (see, e.g., Jordano 1987a, Herrera et al. 1994). Fruit removal efficiency in these years is expected to be impaired for individual plants, resulting in desiccation of ripe fruits on branches, and/or increased loss of fruits to pathogens and predators due to increased fruit retention times.

Second, the visitation rate or intensity of fruit removal by legitimate seed dispersers relative to frugivores that damage pulp and seeds might vary among populations or among habitat types within a given area (Snow and Snow 1988, Guitián et al. 1992, Traveset 1993) and have a lasting effect on seed dispersal and seedling recruitment (Herrera et al. 1994). In addition, the overall negative effect of these frugivores might vary for individual plants at a given locality in different years, depending on variations in their relative abundance at the site among fruiting events. To sum up, as frugivore coteries frequently include a varied assortment of legitimate seed dispersers, pulp consumers, and/or seed predators, we might expect seed removal success for individual plants to vary according to the relative importance of each frugivore group. However, I am not aware of long-term studies addressing the implications of this variation for seed dispersal and, moreover, studies characterizing long-term patterns of variation are scarce (Herrera 1988b, Jordano 1993a, and references therein).

Given that the disperser assemblages of a particular plant population are inherently variable in time, do these temporal variations affect predictably the efficiency of fruit removal? Does variation in fruit removal mirror the changes in composition of the frugivore community among different sites? Is there any evidence for measurable effects of this type of variation on fruit removal and seed dispersal? In this paper I address these questions for *Prunus mahaleb*, a deciduous rosaceous tree (Herrera and Jordano 1981, Jordano 1993b; P. Jordano and E. W. Schupp, unpubl., for descriptions of its reproductive biology including dispersal). A central objective is to examine the ecological consequences of variation in the composition and size of the avian disperser assemblage in terms of changes in fruit removal and seed dispersal success for individual plants.

Methods

Study area

This study was carried out during 1986–1993 in the Reserva de Navahondona-Guadahornillos (Parque Natural de las Sierras de Cazorla, Segura y las Villas, Jaén province, Southeastern Spain). I carried out the study at two sites in the highlands of this area. Additional data, reported by Herrera and Jordano (1981; and P. Jordano, pers. obs.), refer to a third, mid-elevation site.

Long-term intensive study is being conducted in Nava de las Correhuelas (N. Correhuelas, hereafter), a site in the highlands of the park, at 1615 m elevation. The site extends over ca 100 ha and includes both poldje deep cool soils and rocky, exposed slopes. Deciduous vegetation, including *Crataegus monogyna*, *Prunus mahaleb*, *Lonicera arborea*, *Berberis hispanica*, *Daphne laureola*, *Rosa canina* and *Acer monspessulanus*, occupies the deep soils. Adjacent rocky slopes are dominated by open pine forest (*Pinus nigra*, subsp. *salzmannii*) with *Juniperus communis*, *J. phoenicea*, *J. sabina* and scattered *Taxus baccata* (Valle et al. 1989). The climate is of Mediterranean montane type. Precipitation averages 1527 mm and concentrates in autumn-winter. Only 9% of total annual precipitation falls during June-September, the main ripening season for *P. mahaleb* fruits. Average temperatures for coldest and hottest months are 2.9°C and 22.5°C, respectively. Snowfalls are frequent from November to March.

Additional observations were conducted on a second *P. mahaleb* population located in Nava Noguera (N. Noguera, hereafter), 17 km southeast of the main site (1550 m elevation). Vegetation composition and habitat structure are very similar to the N. Correhuelas site. The data from the N. Correhuelas and N. Noguera sites were combined with information provided by Herrera and Jordano (1981) (Roblehondo, 2 km west, 1300 m elevation) to analyze among-site variation in frugivore assemblage composition within this Southeastern Spain region. At the Roblehondo site, *P. mahaleb* trees grow scattered on rocky soil in a mosaic of dense *P. nigra* forest, open areas with variously sized patches of deciduous shrubs (*Crataegus monogyna*, *Berberis hispanica*, *Rosa* sp.) and tracts with *Quercus rotundifolia*, *Phillyrea latifolia*, *Sorbus torminalis*, and *Juniperus oxycedrus* (Herrera and Jordano 1981).

For comparisons with the Southeastern Spanish, Cazorla region, I analyze here data provided by Guitián et al. (1992, and pers. comm.). They studied three sites located at the limits of the Orense and León provinces (Northwestern Spain, 600 m elevation). The sites include a sparse scrubland on rocky slopes, dominated by *C. monogyna*, *P. mahaleb*, and *Q. ilex*; a woodland clearing with *Q. suber*, *P. mahaleb*, and *Q. ilex*, on deep soil substrate; and a mixture of abandoned agricultural land, trails, and hedges dominated by *Q. ilex*. *P. mahaleb* is among the three dominant species in each of the sites (see Guitián et al. 1992 for further description).

Plant natural history

P. mahaleb, the Saint Lucy's or Mahoma's cherry, is a small tree (2–10 m height) that grows scattered at mid-elevation altitude (1250–1900 m) in Southeastern Spanish mountains, Pyrenees, and extends to the Ukraine, central and eastern Europe, Morocco, Syria, and west-central Asia (Webb 1968, Ceballos and Ruiz de la Torre 1979). Detailed information on the pollination biology has been published elsewhere (Jordano 1993b; see also Guitián et al. 1993). Fruits are drupes, black when ripe, 8.0 ± 4.4 mm long and 8.3 ± 0.5 mm wide ($N = 20$) with a sugary, water-rich pulp (Herrera and Jordano 1981). Chemical analyses of the fruit pulp reported by these authors yielded 3.2% crude fat, 2.8% crude protein, 6.3% ash, and 5.7% fiber, with 82.0% soluble carbohydrates. Fruit crops of individual trees usually range between 700–30 000 fruits.

Herrera and Jordano (1981), Herrera (1989), and Guitián et al. (1992) present information on interactions of *P. mahaleb* with frugivorous animals that consume fruits and disperse seeds. At least 28 bird species, four mammals, and one lizard have been recorded feeding on the fruits in the Southeastern sites (P. Jordano and E. W. Schupp, pers. obs.).

Bird censuses and feeding records

Line transects of fixed width (120 m) were censused 3 d/wk during the fruiting seasons each year (mostly late-July – early September) to determine the relative abundance of birds (number of birds/km census) and to obtain feeding records on fruits (1 feeding record = consumption of 1 fruit). Feeding records were obtained also during timed watches at individual trees. Both the N. Correhuelas and N. Noguera sites were studied in this way. Transect counts of birds and feeding observations at Nava Noguera included 15 censuses with 11.2 km walked, and 354 feeding records during 1986 and 1988. Sampled years at N. Correhuelas included 1986–1989 and 1992–1993 for census data, and the whole 8-yr period (1986–1993) for feeding records. Total sampling effort for the years 1986–1989 was 3.4 km, 2.1 km, 4.3 km and 6.2 km census, respectively, and 8.2 km and 10.4 km census for 1992 and 1993, respectively. The number of individual birds censused in these years were 754, 344, 562, 673, 988, and 875, respectively, with a total effort of 43 censuses and 66.4 km census distance. The number of feeding records was 5259 for the 8 yr pooled, 1986–1993. See Jordano (1993a) for details of the sampling methods.

Fruit removal

Removal efficiency will be referred to as the percentage of fruits taken by frugivores relative to the total fruit crop. Only a fraction of this fruit consumption potentially results in seeds being removed from the plant; thus, dispersal efficiency will refer to the percentage of seeds estimated to leave the tree.

Nava de las Correhuelas site

Fruit removal was assessed in 21 trees (1988 and 1989) and in 60 trees (1992 and 1993, including those 21 trees sampled in the previous years) growing in the Nava de las Correhuelas study site. Crop sizes of final-sized fruits were estimated by complete count on all marked plants during the last two weeks of July, when fruits start to ripe, just prior to massive fruit consumption. I used a hand counter to tally the number of fruits in different branches within a 'sector' of the canopy, then moving to a different sector until the total crown volume had been scanned. To check for accuracy I made periodic recounts for a large branch or group of branches. The count was repeated if the difference between successive counts exceeded 5% (crops $< 10^3$ fruits) or 10% (crop sizes $> 10^3$ fruits). I assumed exact counts for crop sizes < 2000 fruits.

I used two different methods to estimate fruit removal levels. First, weekly counts of fruits at marked branches were used in 1988 and 1989 to estimate standing crops of unripe, ripe, and damaged fruits, as well as pre-dispersal loss of fruits (Jordano 1987a, Herrera 1988c, Jordano 1989). At least 5 branches were marked per tree, totaling 3560 and 3780 fruits in 1988 and 1989, respectively. This sampling was used to estimate the fraction of the fruit crop ripened, consumed by frugivores, and dispersed. In addition, just after the 1988 fruiting season, I carried out counts of the fruit and seed remains on the ground beneath the canopy of sampled trees. Between 3 and 8 quadrats (0.50 m × 0.50 m) were sampled per tree depending on canopy area, and all fruit and/or seed remains were recorded and counted within the first week after $> 95\%$ of the initial fruit crop was removed; I also carried out a complete count of the fruits remaining on the branches. Fruit and seed consumption by rodents and/or ants is scarce during this period and during the first ten d after fruiting (P. Jordano, pers. obs.), so that fruit and seed counts in unprotected ground may provide adequate estimates of seed loss and the fraction of the fruit crop removed by frugivores. Removal of ripe fruits by carnivorous mammals might also account for a fraction of fruit loss on the ground. Unfortunately I have no available estimates of this removal, but comparisons of fruit and seed density in protected seed traps and open ground, together with counts of mammal scats and tracks in the site, suggest a small contribution of mammalian fruit removal compared to bird consumption. However, the relative importance of mammals might vary among populations (J. Guitián, pers. comm.). Fruit loss estimates for each tree were derived by dividing the number of ripe desiccated, ripe damaged, unripe fruits, and dropped seeds (with pulp remains attached) found in these samples by the fraction of canopy area sampled under the tree. This sampling was used to assess the consistency between the estimates of fruit loss and seed removal derived from branch counts and those from quadrat samples, and the two figures were found to be highly correlated ($r=0.895$, $N=21$, $P=0.003$).

Second, fruit consumption levels in 1992 and 1993 were assessed by sampling with seed traps beneath the trees. Traps consisted of 0.17-m^2 plastic trays covered with 1.23-cm-mesh wire to prevent fruit and seed consumption by rodents. Between 2 and 5 traps were placed per tree, depending on canopy size, so that the average sampling area per tree was 7.4 ± 0.7% (mean ± 1 SE, $N=60$) of the canopy area. As with the ground quadrats sampled in 1989, the estimates of fruit loss for each tree were obtained by dividing the number of ripe desiccated, ripe damaged, unripe fruits, and dropped seeds (with pulp remains attached) found in the seed traps by the fraction of canopy area sampled under the tree (see Howe and Vande Kerckhove 1981 for a similar method).

Comparisons among sites

Data on fruit removal levels for individual plants, relative to initial fruit crop sizes (removal efficiency), are available only for the N. Correhuelas and Roblehondo sites. Guitián et al. (1992, Table 1) report both the proportions of feeding visits by individual bird species and the fraction of seeds handled that are removed from the vicinity of the trees or dropped beneath the canopy of the parent plant. They studied 10, 8 and 7 trees at each of these sites. In a similar way, for the three Cazorla sites, I computed the proportions of seeds actually removed from the trees relative to the total handled by each bird species. I combined data on the proportion of feeding records and data on feeding rates (P. Jordano and E. W. Schupp, unpubl., Herrera and Jordano 1981). I thus compared among regions the relative effectiveness of the assemblages at each site, measured as the proportions of seeds estimated to leave the parent canopies relative to the total fruits handled by birds. For a given level of overall fruit removal by frugivores, these values are indicative of variation in dispersal efficiency among tree populations.

Statistical analyses

To characterize the patterns of variation in composition of frugivore assemblages, both among years at single localities, and among sites in different geographic areas, I used the proportional similarity index (PS; also known as the Renkonen index),

$$\sum_{i=1}^{n} \min\,(p_{ai}, p_{bi}),$$

where, for n species, p_{ai} is the relative abundance of species i in site or year a, and p_{bi} is the relative abundance of species i in site or year b (see, e.g., Krebs 1989, Horvitz and Schemske 1990). PS ranges from 0 (no taxa in common) to 1 (identical taxonomic composition). I tested the null hypothesis of dissimilar assemblage composition (PS = 0), and assessed significance by a bootstrap procedure (Crowley 1992) using normal approximation (Noreen 1989). Observed PS values were compared to a distribution of randomly generated PS values calculated for each of 10000 paired draws with replacement from the samples being compared. Randomization tests were used also for most correlation analyses. Again, I used 10000 replicated shuffles of the data and tested the null hypothesis of $r=0$ with significance estimated by normal approximation (Noreen 1989). For these analyses, I used the routine templates provided by Noreen (1989) and Press et al. (1992) subroutines for random number generation and other functions.

To characterize the pattern and amount of variation across sites or years I used the coefficient of variation ($\mathrm{CV}=100 \cdot \mathrm{SD}/\bar{X}$) of the relative bird abundance (birds·km^{-1}) or proportion of feeding records by each frugivore species.

Results

The frugivore assemblage

Four main types of frugivorous birds visit *P. mahaleb* trees, differing in foraging mode and immediate consequences for seed removal. Seed dispersers (SD hereafter) swallow the fruits whole and defecate and/or regurgitate the seeds, usually after leaving the tree. Pulp consumers (PC, hereafter) peck the fruit to obtain pulp pieces either without detaching it from the peduncle or, after plucking, by tearing off the pulp while holding the fruit in the bill or against a perch. In both cases, the seed is dropped to the ground. On occasions, PC species (*Parus ater*, *Garrulus glandarius*, and *Sitta europaea*) were observed to pluck some fruits and exit from the tree to another perch to eat the pulp; in those instances, the seeds are therefore 'dispersed' away from the parent plant without ingestion (pulp consumers-dispersers, PCSD hereafter). *G. glandarius* regularly behaves as a PC species, but some individuals also disperse seeds, as they swallow the stone after having detached, and ingested, the pulp. *Parus ater* and *Sitta europaea* were the only species observed to cache fruits or seeds after leaving the tree. Finally, only *Coc-*

Table 1. Proportional similarity (PS), above diagonal, among assemblages of frugivorous birds feeding at *P. mahaleb* in different Spanish geographic regions and sites.

Area and site[*]	Similarity[†]					
	NCOR	NNOG	ROBL	COBA	PORT	VILA
A. N. Correhuelas (NCOR)	–	**0.7560**	**0.3036**	0.1899	0.3382	0.1590
A. N. Noguera (NNOG)			**0.3987**	0.3343	**0.2677**	0.1803
A. Roblehondo (ROBL)			–	0.3982	0.4775	0.1324
B. Cobas (COBA)					**0.2264**	**0.1965**
B. Portela (PORT)					–	**0.2594**
B. Vilardesilva (VILA)						–

[*] A. Southeastern Spain. Sierra de Cazorla mountains; B. Northwestern Spain (data from Guitián et al. 1992).

[†] Significant PS values ($P \leq 0.05$) are shown in bold type. A bootstrap resampling procedure was used to estimate significance levels (see Methods).

cothraustes coccothraustes has been recorded to feed on the seed contents and thus act as a seed predator (SP hereafter).

Variation in space

A total of 26 and 19 bird species were recorded feeding on *P. mahaleb* fruits at the N. Correhuelas and N. Noguera highland sites, respectively, with 73.1% of the species being present in the two assemblages. The composition of the two Cazorla-highland frugivore avifauna, derived from census counts (Appendix 1 and 2), was significantly similar (PS = 0.688, $P = 0.0002$; data for all years combined for each site). Both assemblages are dominated by thrushes, *Turdus* sp., and redstarts, *Phoenicurus* spp., among SD species, and chaffinches, *Fringilla coelebs*, and tits, *Parus* spp., among PC and PCSD species. Not unexpectedly, the overall similarity in the avifauna at these sites is high, given their similar elevation, vegetational composition and landscape. For both sites, the proportion of feeding records by individual frugivore species was closely related to its average abundance (birds·km^{-1}, all years pooled)($r = 0.969$, $P < 0.01$ and $r = 0.918$, $P < 0.01$, for the N. Correhuelas and N. Noguera sites, respectively; randomization tests with 10000 iterations).

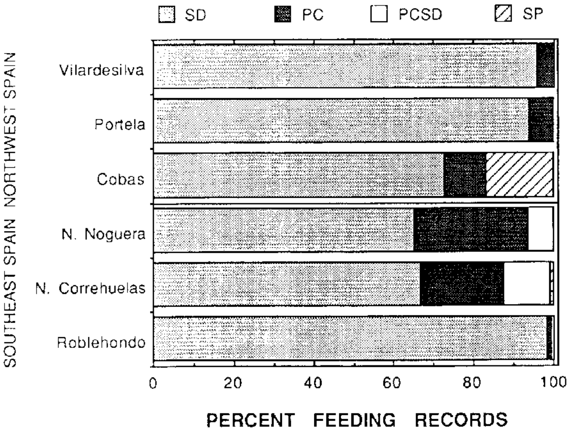

Fig. 1. Variation in the percentage of feeding observations of frugivorous birds visiting *Prunus mahaleb* plants in Northwestern (Vilardesilva, Portela, and Cobas sites; Guitián et al. 1992) and Southeastern (Nava Noguera and Nava de las Correhuelas, present study; and Roblehondo, Herrera and Jordano 1991) Spain sites. Frugivory types: SD, seed dispersers that swallow and defecate/regurgitate the seeds; PC, consumers of pulp, that bite pulp pieces and drop the seeds; PCSD, same as PC but infrequently leaving the tree with fruits in the bill; SP, seed predators.

The species richness of these two frugivore assemblages is well above the 8, 8, 6, and 11 species recorded for Roblehondo and the three Northwestern Spain sites (Cobas, Portela, and Vilardesilva), respectively (Herrera and Jordano 1981, Guitián et al. 1992). All them share thrushes, warblers, and redstarts as the main visitors to the plants, but the overall similarity, obtained from feeding records, across these sites is relatively low and not significant (PS = 0.31 ± 0.16; Table 1). Seven out of the 15 pairwise similarities among sites are significantly different from zero, and these roughly correspond to sites within the same geographic area. I tested the hypothesis that similarity of species compositions in these assemblages was associated to their overall 'closeness', estimated by their geographic proximity. A significant Mantel's test (Mantel 1967; see also Manly 1991) ($r = -0.391$, $P = 0.024$; 5000 permutations) indicated a close negative association between similarity and distance (i.e., pairwise similarities decreased with increasing geographic distance between the sites).

Frugivores visiting *P. mahaleb* plants in the two regions are mostly seed dispersers (SD plus PCSD species, i.e., those able to remove some seeds away from feeding trees; Fig. 1), which account for 82% of the feeding records in both Northwestern and Southeastern sites. However, the relative representation of the four frugivory types differs significantly across regions and sites (Fig. 1) ($\chi^2 = 9.5$, df = 3, $P = 0.02$, and $\chi^2 = 263$, df = 12, $P < 0.0001$, respectively, for the logistic model incorporating area and site within area as effects; CATMOD procedure, SAS 1988). First, feeding records of PC spe-

Table 2. Coefficients of variation in the relative abundance of different frugivore types, estimated as the proportions of feeding records, visiting *Prunus mahaleb* plants. Values were averaged for species in each frugivore category, either across sites or years within the main study area. Figures are the CV (100·SD/mean) for the proportions of feeding records contributed by each frugivory type computed across sites ($N = 6$) and years ($N = 8$), expressed as percentages of the mean. See Results for definition of frugivory types.

Frugivory type	Among sites*		Among years†	
	Mean	Range	Mean	Range
Seed dispersers	170.9	72.7–244.9	122.2	29.3–282.8
Pulp consumers	168.4	103.5–244.9	105.8	50.1–208.1
Pulp consumers-dispersers	172.6	158.6–192.2	74.1	37.3– 97.8
Seed predators‡	245.0	–	223.6	–

* data for 6 study sites, see Methods: Study area. Different years sampled.

† data for 8 yr (1986–1993), Nava de las Correhuelas study site, Sierra de Cazorla, Jaén province, Spain.

‡ Only one species recorded.

cies are relatively more frequent in Cazorla sites, while those of PCSD and SP are more common in Northwestern Spain sites. Second, trees of the two highland Cazorla sites are visited more frequently by PC and PCSD species than those at lower elevation sites in the two geographic areas (Fig. 1).

The degree of spatial variability in visitation by individual frugivore species was assessed by computing the coefficients of variation of the proportion of feeding records across the 6 sites (CV_{sites} hereafter). CV_{sites} values were remarkably similar among the 4 frugivory groups, and most species were highly variable, with $CV_{sites} > 110\%$ (Table 2). For all species pooled, mean CV_{sites} did not differ significantly between northwestern ($CV_{sites} = 115.8\%$) and Southeastern ($CV_{sites} = 112.4\%$) sites. For the 8 species present in the two areas there was a significant trend for greater spatial variability among northwestern sites ($\chi^2 = 6.39$, df = 7, $P = 0.01$; Wilcoxon test).

Frugivore groups did not differ in the average number of sites occupied (Kruskal-Wallis test, $\chi^2 = 3.93$, df = 3, $P = 0.27$). If all sites are combined in a single sample characterizing the assemblage of *P. mahaleb* frugivores, the proportion of feeding records by a given bird species was not correlated with the number of sites where the species was recorded visiting *P. mahaleb* ($r = 0.529$, $P > 0.15$; randomization test with 10000 replications). However, the CV_{sites} for the proportion of feeding records were negatively correlated with the number of sites where the species was recorded ($r = -0.579$, $P < 0.001$; randomization test with 10000 replications), suggesting that spa-

Table 3. Feeding records of frugivorous birds visiting *Prunus mahaleb* trees in the eight study years, Nava de las Correhuelas site. Figures are the percentage of feeding records relative to the annual total.

Species	Frugivory type*	1986	1987	1988	1989	1990	1991	1992	1993	Total
Columba palumbus	SD	4.61	1.69	0.07	1.27	0.28	1.20	0.95	1.03	1.21
Corvus corone	SD	0.46	1.52	–	0.76	–	–	0.42	0.77	0.42
Dendrocopos major	SD	0.15	2.36	0.29	–	0.83	1.20	0.21	0.65	0.46
Erithacus rubecula	SD	1.08	2.20	5.19	6.09	4.42	3.59	6.33	7.61	3.84
Ficedula hypoleuca	SD	–	–	–	–	–	–	–	0.13	–
Muscicapa striata	SD	–	–	–	–	–	–	–	0.39	–
Phoenicurus ochruros	SD	6.45	15.88	21.95	17.26	14.09	22.16	23.52	27.61	20.65
Phoenicurus phoenicurus	SD	3.84	1.69	1.17	6.85	4.14	1.80	2.11	1.68	2.44
Sylvia atricapilla	SD	0.31	0.34	1.32	3.30	1.93	1.80	2.00	1.03	1.36
Sylvia borin	SD	–	–	0.22	–	–	–	0.32	0.26	0.18
Sylvia cantillans	SD	–	0.34	1.10	3.30	2.49	1.20	–	0.26	0.70
Sylvia communis	SD	–	0.84	3.66	9.90	4.42	–	4.96	5.29	3.99
Sylvia conspicillata	SD	–	–	0.15	–	–	–	–	–	0.04
Sylvia melanocephala	SD	–	–	0.59	2.28	0.28	–	–	2.32	0.77
Turdus merula	SD	29.49	13.18	8.78	13.45	12.71	15.57	7.17	9.29	12.79
Turdus viscivorus	SD	26.42	16.72	15.00	13.20	19.06	13.17	22.05	11.87	18.19
Garrulus glandarius	PCSD	4.76	10.64	2.19	–	2.76	8.98	1.16	1.29	2.96
Parus ater	PCSD	4.45	11.32	4.61	6.60	11.60	11.38	13.08	10.58	8.58
Sitta europaea	PCSD	–	0.34	0.37	2.79	2.21	1.80	0.53	1.29	0.72
Fringilla coelebs	PC	16.44	17.91	31.53	7.36	16.85	10.18	11.29	10.06	17.12
Parus caeruleus	PC	0.61	1.35	0.80	3.81	1.66	2.40	0.95	1.81	1.34
Parus cristatus	PC	0.31	0.34	0.80	0.51	–	0.60	0.74	1.68	0.81
Parus major	PC	0.61	1.35	0.22	0.76	0.28	–	1.37	1.29	0.90
Serinus citrinella	PC	–	–	–	0.25	–	–	–	0.65	0.13
Serinus serinus	PC	–	–	–	0.25	–	2.99	0.84	1.16	0.39
Coccothraustes coccothraustes	SP	0.15	0.34	–	–	–	–	–	–	0.07
Number of records		652	594	1367	394	362	167	948	775	5259

* SD, seed disperser; PC, pulp consumer; PCSD, pulp consumer-seed disperser; SP, seed predator. See Results for definitions.

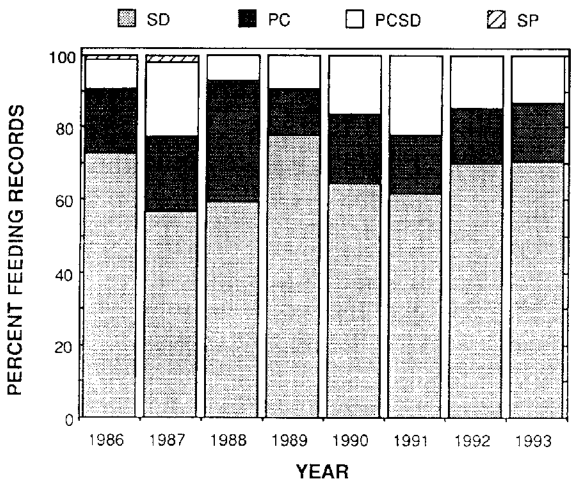

Fig. 2. Long-term variation in the percentage of feeding observations contributed by four types of frugivorous birds visiting *Prunus mahaleb* plants at the Nava de las Correhuelas study site. Legends for frugivore categories as in Fig. 1.

tially 'consistent' frugivores (recorded at most sites) tend to be consistent visitors to the plant.

Temporal variation

The temporal variation of the *P. mahaleb* assemblage was studied with both census data (Appendix 1) and feeding records (Table 3) for the years 1986–1993 at the N. Correhuelas site. For most years, SD species were the most abundant in this site, with *Phoenicurus ochruros*, *Turdus* spp., and *Erithacus rubecula* as the main species, and accounted for >50% of the frugivorous birds censused in any year. Abundant species in the PC and PCSD groups were *F. coelebs* and *Parus* spp., but both categories rarely accounted together for >40% of the frugivores censused. The long-term data on feeding records matched the pattern found in census information (Table 3). For all years with census and feeding records data, the proportion of records for a given species was significantly correlated with its relative abundance (proportion of birds censused) ($r_s > 0.766$, $P < 0.001$ in all cases). Across species, and for all the years pooled, the proportion of feeding records for each species was positively correlated with the number of years the species was recorded feeding at *P. mahaleb* ($r = 0.495$, $N = 26$, $P < 0.01$; randomization test with 10000 replications).

SD species accounted for >50% of the total feeding records in any year, and PC and PCSD showed important increases only in 1986, 1987, and 1991; SP was recorded only in 1986 and 1987. Between-year variation in the composition of the frugivore assemblage was evident, and the proportions of records for each frugivory group varied significantly during the 8-yr period (Fig. 2; $\chi^2 = 264.8$, df = 21, $P < 0.0001$).

The temporal variability in abundance was assessed by computing the coefficients of variation (CV_{years} hereafter) on either the census data for each species ($birds \cdot km^{-1}$; Appendix 1) or the proportion of feeding records (Table 3). The abundance of frugivorous birds in the study area was less variable (mean $CV_{years} \pm 1$ SE for $birds \cdot km^{-1}$ throughout the 1986–1993 period: 88.1 ± 10.6%, $N = 26$ species) than the proportion of feeding records contributed by each species (115.9 ± 15.2%). Both the CV_{years} analysis for census and feeding records data yielded similar results regarding temporal patterns of variation, and I will omit here presentation of the census results. CV_{years} for the proportion of feeding records did not differ significantly among frugivore groups ($\chi^2 = 0.79$, df = 2, $P = 0.67$; Kruskal-Wallis test; Table 2). Across species, CV_{years} showed a significant negative correlation with the number of years the species was recorded at *P. mahaleb* ($r = -0.956$, $N = 26$, $P < 0.01$; randomization test with 10000 replications). More reliable frugivores (recorded more years and contributing a greater proportion of records) showed a trend for more damped variations in the proportion of feeding records.

The PS analysis of between-year variation in assemblage composition (Table 4) revealed a consistently high similarity throughout the 8-yr period at the N. Correhuelas site, with significantly high PS values for both the census and feeding records data. It is important to note here that these PS values imply both similar species composition and proportions contributed by individual species. Slight variations in the identity or relative importance of species in a given year might cause significant variations in the relative importance of SD, PC, and PCSD groups, as explained above. The PS matrix for census data also revealed a significant similarity in the composition of the frugivore avifauna in the study period; 'census' and 'records' matrices were strongly correlated ($r = 0.769$, $P = 0.01$; Mantel's test with 1000 permutations; Table 4). This supports the earlier finding of a close positive relationship, across species, between abundance in the area and proportion of feeding records at *P. mahaleb*.

Table 4. Proportional similarity (PS), above diagonal, among assemblages of frugivorous birds feeding at *Prunus mahaleb* in different years, estimated from feeding records at the main study site, Nava de las Correhuelas. Below diagonal, between-year similarities (PS) derived from census data at the same site. All PS values are significant ($P \leq 0.005$).

Year*	1986	1987	1988	1989	1990	1991	1992	1993
1986	–	0.691	0.572	0.534	0.684	0.600	0.591	0.496
1987	0.642	–	0.713	0.664	0.829	0.817	0.732	0.701
1988	0.626	0.688	–	0.662	0.752	0.702	0.751	0.732
1989	0.645	0.693	0.687	–	0.761	0.724	0.711	0.757
1990	–	–	–	–	–	0.772	0.795	0.734
1991	–	–	–	–	–	–	0.765	0.783
1992	0.639	0.694	0.648	0.768	–	–	–	0.845
1993	0.566	0.693	0.653	0.753	–	–	0.783	–

* Census data were not available for 1990 and 1991.

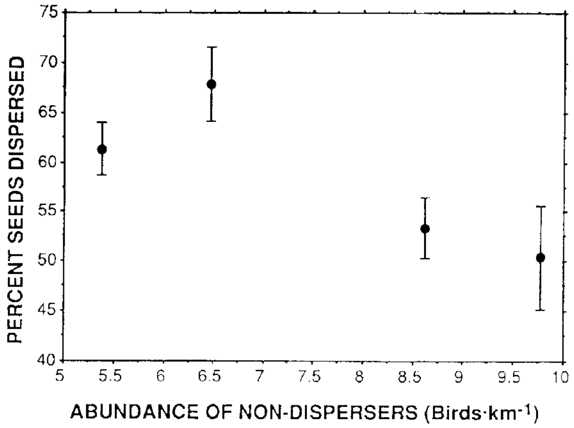

Fig. 3. Relationship between the abundance of non-disperser species (frugivory types PC, PCSD, and SP pooled; see Results for description) and variation in mean seed dispersal efficiency (± 1 SE), the proportion of the initial seed crop removed away from the parent tree. Data are for years 1988, 1989, 1992, and 1993, Nava de las Correhuelas study site.

Spatio-temporal variation

The available data for the 3 Sierra de Cazorla sites made possible a simultaneous analysis of CV_{sites} and CV_{years} across species. CV values here are an inverse indication of the predictability of each frugivore species at spatial and temporal scales (see Herrera 1988a). Spatial and temporal CV values were positively and significantly correlated across species ($r = 0.795$, $P < 0.001$; Pearson product-moment correlation). There is a set of predictable frugivores, visiting *P. mahaleb* at most sites and years and contributing a sizable proportion of fruit removal and seed dispersal (*T. merula*, *Ph. ochruros*, *Sylvia* spp.), and a number of scarce and unpredictable species recorded occasionally in a few sites.

Consequences for fruit removal

Between-site variation in fruit removal

I differentiate between removal of fruits from the parent plant, performed by either SD, PC or PCSD species, and removal resulting in potential seed dispersal, performed only by SD and, to a lesser extent, PCSD species. As a result, dispersal efficiency for individual trees might be low, even with high levels of fruit consumption and removal (high removal efficiency) if PC, PCSD, and SP species are relatively abundant in local assemblages.

The mean percentage of seeds dispersed relative to the initial fruit crop of ripe fruits was only 58.2% at the N. Correhuelas site, where visitation by PC and PCSD species is frequent (36.6% of feeding records). This contrasts with 83.0% for the Roblehondo site, where visitation by non-SD species is extremely infrequent (<2% of feeding records; Herrera and Jordano 1981; P. Jordano, pers. obs. for additional years). Data on removal and dispersal efficiency are not available either for the N. Noguera site or the 3 Northwestern sites. However, the effectiveness of the local assemblages at the six sites can be compared by calculating the proportions of seeds potentially dispersed relative to the total number of fruits handled (see Methods). Not unexpectedly, the overall assemblage effectiveness was positively correlated with the proportion of records for SD species ($r = 0.989$, $P < 0.01$; randomization test with 10000 replications). The effectiveness for the two high-elevation Cazorla sites (N. Correhuelas and N. Noguera)(65.1% and 63.4%, respectively) was slightly below the Cobas and Portela Northwestern sites (69.6% and 75.9%, respectively). These values are contrasted with 96.3% for the Roblehondo site, with an assemblage dominated by SD species, and the Vilardesilva assemblage (19.9%), dominated by *Sylvia cantillans*, a SD species that drops a large proportion of the fruits handled (Guitián et al. 1992, P. Jordano, pers. obs.). Therefore, most variation in dispersal effectiveness among assemblages was caused by changes in the relative abundance and visitation frequency of SD and PC species, as visitation by the SP group was infrequent (see Fig. 1).

Between-year variation in fruit removal

Data on fruit removal and dispersal efficiency are available for 1988, 1989, 1992, and 1993 for the N. Correhuelas site. Between-year variation in dispersal efficiency was correlated significantly only with the abundance of non-disperser (NONSD) species (PC, PCSD, and SP groups pooled)(Fig. 3). The average seed dispersal efficiency was impaired in those years with greater abundance of non-disperser species. Mean dispersal efficiency for *P. mahaleb* trees at the N. Correhuelas decreased in years with increased abundance of NONSD species ($r = -0.804$, $P < 0.06$; randomization test with 10000 replications). This result was not unexpected, as greater abundance of NONSD species in the area translated into a greater proportion of feeding records for these species.

Discussion

The frugivore assemblage: variations in space

The set of frugivores that consumes fruit, and disperses seed, of a particular plant species can vary along different scales, both spatially and temporally. Spatial scales of variation include changes in both species composition and numbers that occur among different geographic regions within the range of a species, among sites within a region, or among individual plants growing in different habitat types within a site. A number of previous studies have documented patterns of variation at each of these scales (Howe and Vande Kerckhove 1981, Bronstein and Hoffmann 1987, Keeler-Wolf 1988, Snow and Snow 1988, Guitián et al. 1992, Jordano 1993a, Traveset 1994).

The frugivore assemblage of *P. mahaleb* showed important variation among sites within the main Sierra de

Cazorla study area and between this area and Northwest Spanish sites (Guitián et al. 1992). Plants in the Cazorla highlands received more visits by PC and PCSD species, a trend caused by the greater relative abundance of tits and chaffinches in mixed pine-oak woodlands in this area relative to the sites with oak-dominated vegetation at lower elevations (Herrera 1984, Obeso 1987a, Herrera et al. 1994). The most predictable *P. mahaleb* visitors, *T. merula* and *Ph. ochruros*, are characteristic of woodland edges and open rocky areas with sparse thickets, typical growing sites for *P. mahaleb* at highland sites. Small warblers increase in importance as visitors in more forested landscapes, a trend expected from their habitat preference patterns (Prodon and Lebreton 1981). In addition, some of the main PCSD and PC species might show pronounced changes in diet composition among sites. For example, Obeso (1987b) reported marginal consumption of fleshy fruits by *P. ater* at 1300–1400 m elevation (<7% volume) during summer, and certainly consumption of *P. mahaleb* fruits by this species is much more pronounced at 1550–1700 m during this period (P. Jordano, pers. obs.). Non-disperser frugivore species for which fruits are not a central dietary component may show marked increase in fruit consumption closely tracking local and temporal peaks in fruit availability (see, e.g. Jordano 1987b, Snow and Snow 1988). Spatial and temporal predictability were positively related across frugivores visiting *P. mahaleb*, but we lack information for other species to evaluate the generality of this result. To my knowledge, no other study has examined concurrently the spatial and temporal variability of a frugivore assemblage with an adequate number of study sites and years (see Herrera 1988a and Horvitz and Schemske 1990 for pollination assemblages).

Most variation between regions (Northwestern and Southeastern Spain) was caused by changes in: 1) species richness of the assemblages; and 2) identity of the main visitors. But the overall proportions of feeding records by legitimate dispersers and non-dispersers (pulp consumers and seed predators) were nearly identical. Most visitors to *P. mahaleb* plants (>60% feeding records) were warblers, thrushes, or redstarts. Variation among Northwestern sites was much greater than variation among Cazorla sites, a difference probably related to the greater intrinsic heterogeneity of the former sites (Guitián et al. 1992) in vegetation composition, successional stage, and substrate type. It is interesting to note that the Northwestern site (Portela) with the greatest PS with the two Cazorla highland sites is the most similar physiognomically to these Southeastern sites. Redstarts (*Ph. ochruros*), a warbler (*S. atricapilla* or *S. communis*), and a thrush (*T. merula*) are the commonest visitors in these exposed rocky sites with sparse thickets of rosaceous treelets and shrubs. In contrast, redstarts are secondary dispersers in more forested sites such as Roblehondo and Cobas. Thus, regional patterns of spatial variation in assemblage composition can be interpreted in connection with habitat preferences by the birds and changes of avifauna along successional gradients (Prodon and Lebreton 1981, Herrera 1985, Guitián et al. 1992). But differences between regions are most likely the result of broader biogeographic variation in bird species richness and composition. Thus, a gradient of impoverishment of bird species richness towards the Northwestern Iberian Peninsula explains reductions in the number of congeners for the main frugivore genera (e.g., *Phoenicurus*, *Turdus*, *Sylvia*, and *Parus*). In addition, the greater disturbance of habitats in this region relative to the well preserved Southeastern sites studied here might have an added effect.

Fuentes (1990) and Guitián et al. (1992) tentatively suggested that among-habitat variation in avian fruit consumers of Western European plants could be comparable to, and as large as, geographic variation. Results of the present study indicate that for *P. mahaleb*, among-habitat variation in the frugivore assemblage is smaller than variation among geographic areas. The PS similarity matrix among sites showed a structured pattern, strongly correlated (Mantel's test) with a matrix of geographic distance among them. This result can be expected if the frugivore assemblages visiting plants in different sites (habitats) within a given geographic region are 'extracted' from a common species pool that might vary among geographic regions. In other words, as we proceed down along different 'biogeographic scales', from regions, sites within regions, habitats within sites, and microhabitats within habitats, I would expect a nested pattern of increasing similarity. Nestedness in species distributions is a frequent pattern in species assemblages of insular habitats (Patterson and Atmar 1986, Patterson 1987, Wright and Reeves 1992); however, as far as I know, we lack information on nested patterns in frugivore assemblages or in mutualistic assemblages in general. A nested pattern (i.e., any frugivore species is recorded in any assemblage with greater species richness than the one with lowest species richness where it is recorded) is evident in the frugivores visiting the three *P. mahaleb* populations of the Cazorla area (present study) and among *Turdus* species interacting with junipers in Southeastern Spanish mountains (Jordano 1993a and pers. obs.). This point deserves further consideration, which is beyond the scope of the present study, because spatially nested subsets of mutualists would imply more predictable patterns of interaction than expected from consideration of extensive variation in the identity and numbers of participant species.

The frugivore assemblage: variations in time

Few previous studies have documented long-term variation in assemblage composition at a single site, but most report important changes that take place in the usual 2–3 consecutive yr of their temporal span (but see Herrera 1988a, Jordano 1993a, Willson and Whelan 1993, and references therein). The results of the present, eight-yr study confirm these findings and point out that the relative importance of major frugivore types visiting a plant species can show marked annual changes, but the overall variability is similar among them. This key point emphasizes the need for long-term data in studies assessing the potential consequences of interactions with frugivores (Wheelwright 1986, Willson and Whelan 1993).

Even with extensive annual variation in the relative representation of different frugivore groups in the assemblage, the overall temporal variability (measured as CV_{years}) was less pronounced than variability among sites (CV_{sites}). This situation contrasts with variability patterns documented for fruit production and frugivore abundance in Southeastern Spanish high-elevation scrublands (Jordano 1993a). In these systems, between-year changes are much more pronounced than spatial variation; a result not unexpected as junipers exhibit mast fruiting (e.g., Jordano 1991, 1993a). In addition, frugivore populations are dominated by migratory thrushes, with important local and regional movements that track local fruit availability. Previous analyses from assemblages dominated by migratory frugivorous species, both in the Mediterranean Basin (Santos 1982, Debussche et al. 1985, Jordano 1985, 1993a, Herrera 1988b, Debussche and Isenmann 1992) and other areas (Burger 1987, Katusic-Malmborg and Willson 1988, Levey 1988, Willson and Whelan 1993; see Howe 1983) also suggest greater temporal unpredictability. Studies on other non-symbiotic mutualisms (Barton 1986, Herrera 1988a, Horvitz and Schemske 1990) however, reported greater spatial variability when compared with the extent of temporal variation.

Despite significant variation in the relative composition of major frugivore groups between years, results of the similarity analyses revealed an overall significant similarity among years in assemblage composition. The fact that annual variation in feeding records for the different species was strongly correlated with their relative abundance in the area suggests that between-year changes in assemblage composition mirrored the annual population fluctuations of the frugivore species. Variations in bird abundance during the ripening period of *P. mahaleb* (late July-early September) are probably indicative of changes in breeding densities and reproductive success of resident species, as the relative importance of long-distance migratory species at this time is small. The high similarity in assemblage composition between years could be attributed therefore to relatively stable breeding populations of the main species, at least if compared with the extreme between-year variations in the abundance of non-resident frugivores. Thus, CV_{years} for abundance values (birds·km^{-1}) were <60% for the main SD species (*Turdus* spp., *Ph. ochruros* and *S. communis*). These values for CV are well below those reported for assemblages composed of wintering frugivores (Jordano 1993a, see also Herrera 1988b, Willson and Whelan 1993, and references therein).

Long-term patterns of variation in fruit removal and dispersal success

Few previous studies have addressed the consequences of spatial and temporal variation in frugivore assemblages from the perspective of the plants (but see Herrera et al. 1994). The existing information is mostly limited to between-site or between-year differences in fruit removal, not analyzed explicitly in connection with variation in the frugivore assemblage. In this study I combined the information available on frugivores visiting *P. mahaleb* plants in different Spanish areas with long-term data from Southeastern Spain highland habitats to assess both the patterns and consequences of spatial and temporal variation in assemblage composition.

We might expect important effects of variation in the relative composition of frugivore assemblages on fruit removal and seed dispersal efficiency for fleshy-fruited plant species such as *P. mahaleb*, whose fruits are consumed by a variety of frugivore types (SD, PC, PCSD, etc.). Even with high intensity of fruit removal by frugivores (i.e., low proportion of the crop lost through desiccation on the tree or damaged by pathogens), actual dispersal success might be low if a large fraction of removed fruits are handled by PC or PCSD species (see e.g., Traveset 1994). Most PC species partly consume the pulp and induce a high risk of infection by pathogens (Sallabanks and Courtney 1992). In addition, the seeds with pulp pieces adhered or completely clean are usually dropped beneath the parent's canopy (Levey 1987). The average fraction of seeds handled by frugivores which are expected to be removed from the vicinity of parent trees differed among sites and was positively correlated with the relative importance of SD species in fruit removal (measured as % feeding records). A marked contrast in dispersal efficiency is evident between the highland (Nava de las Correhuelas) and mid-elevation (Roblehondo) Cazorla sites; fruit removal by SD species is much lower in the highlands (58.2% vs 83.0%, respectively), where fruit removal by PC and PCSD species is frequent. Therefore, variation in dispersal success should be strongly associated to variation in the relative representation of legitimate SD species in the assemblages.

Although most variation in dispersal efficiency across sites was explained by changes in the relative importance of the SD group, differences may also arise due to variations in visit frequency by SD species that differ in dispersal effectiveness (Schupp 1993). Thus, legitimate SD species show ample variation in the proportions of fruits dropped during feeding bouts (range = 0.0 – 75%, with an average of 5.9%; P. Jordano and E. W. Schupp, unpubl.). Guitián et al. (1993) reported very frequent visits by *S. cantillans* in the Vilardesilva population, resulting in a very low fraction of the seeds handled actually being removed from the trees (19.9%) despite significant levels of fruit consumption. *S. cantillans* is the smallest warbler species visiting *P. mahaleb* and drops a sizable fraction of the fruits it handles during foraging bouts (88.5%, reported to be pecked by Guitián et al. 1993; 27.2%, P. Jordano and E. W. Schupp, unpubl.). Similar patterns of variation have been reported previously (e.g. Howe and Vande Kerckhove 1979). Variation in assemblage composition is expected to have minor effects on dispersal efficiency for those plants with relatively homogeneous assemblages of highly efficient, legitimate SD species. Thus, the high fruit removal figures reported by Herrera (1984, 1988c) and Jordano (1984, 1987a, 1989) for a number of Mediterranean lowland shrub species are probably caused by most fruit removal effected by a relatively homogeneous SD set, mainly *Sylvia*, *E. rubecula*, and *Turdus* spp., with very low incidence of PC and PCSD taxa.

The data available for the Cazorla highland site reveals that average annual dispersal efficiency is also predictably associated to parallel changes in the relative importance of non-SD species in the assemblage. Realized seed dispersal was impaired in years with greater visitation by PC and PCSD species, resulting in increased fractions of the fruits being pecked and dropped directly beneath the plants. Although annual changes in the composition of the assemblage were relatively small (i.e., SD species accounted in any year for >60% of the feeding records), subtle variations in the abundance of PC and PCSD species caused measurable changes in seed dispersal efficiency. These non-SD species peaked in abundance in the assemblage, especially in years with good fruit crops (1987, 1988, and 1991). Annual variation in *P. mahaleb* crop size in the N. Correhuelas population is largely caused by variation in pollination success (Jordano 1993b) and strongly influences fruit availability. Tits and chaffinches, the main PC species in the area, may exhibit important annual changes in dietary composition that track this variation in fruit availability (Obeso 1987b), having a variable impact on seed dispersal efficiency. These results reinforce the idea (Willson and Whelan 1993) that relatively long series of study years are necessary to document subtle changes in plant/frugivore interactions with dramatic effects on fruit removal and seed dispersal. Future studies need to address whether these patterns of population- and year-differences in the numbers and species richness of frugivores visiting the plants translate into differences in selection regimes on fruit traits and potential for both demographic effects and evolutionary differentiation.

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Appendix 1. Relative abundance (percentage of birds censused) and abundance index (birds·km^{-1}, BKM) of avian frugivores visiting *Prunus mahaleb* trees, Nava de las Correhuelas site, during 6 yr.

Frugivory type Species	1986		1987		1988		1989		1992		1993	
	%	BKM	%	BKM	%	BKM	%	BKM	%	BKM	%	BKM
Seed dispersers												
Columba palumbus	0.53	1.18	1.45	2.38	0.18	0.24	0.59	0.65	0.91	1.10	0.91	0.77
Corvus corone	1.06	2.35	–	–	–	–	1.19	1.29	0.40	0.49	0.69	0.58
Dendrocopos major	0.40	0.88				–	0.15	0.16	0.20	0.24	0.57	0.48
Erithacus rubecula	1.59	3.53	4.07	6.67	4.27	5.65	5.94	6.45	6.07	7.32	6.74	5.70
Ficedula hypoleuca	–	–	–	–	0.18	0.24	0.15	0.16	–	–	0.11	0.10
Muscicapa striata	–	–	–	–	–	–	0.15	0.16	–	–	0.34	0.29
Phoenicurus ochruros	12.47	27.65	20.35	33.33	19.22	25.41	19.91	21.61	22.57	27.20	24.46	20.68
Phoenicurus phoenicurus	6.90	15.29	2.33	3.81	1.25	1.65	4.90	5.32	2.02	2.44	1.49	1.26
Sylvia atricapilla	0.66	1.47	0.87	1.43	1.60	2.12	1.34	1.45	1.92	2.32	0.91	0.77
Sylvia borin	–	–	–	–	–	–	0.30	0.32	0.30	0.37	0.23	0.19
Sylvia cantillans	–	–	0.58	0.95	0.89	1.18	0.59	0.65	–	–	0.23	0.19
Sylvia communis	–	–	3.49	5.71	5.69	7.53	8.02	8.71	4.76	5.73	4.69	3.96
Sylvia conspicillata			–	–	0.18	0.24	–	–			–	–
Sylvia melanocephala	–	–	–	–	0.89	1.18	1.19	1.29	–	–	2.06	1.74
Turdus merula	14.85	32.94	5.23	8.57	8.36	11.06	8.17	8.87	6.88	8.29	8.23	6.96
Turdus viscivorus	18.44	40.88	7.56	12.38	8.01	10.59	13.82	15.00	21.15	25.49	10.51	8.89
Pulp consumers-dispersers												
Garrulus glandarius	1.59	3.53	3.49	5.71	0.53	0.71	3.42	3.71	1.11	1.34	1.14	0.97
Parus ater	4.51	10.00	8.72	14.29	4.63	6.12	6.24	6.77	12.55	15.12	9.37	7.92
Sitta europaea	1.33	2.94	2.03	3.33	0.71	0.94	1.19	1.29	0.51	0.61	1.14	0.97
Pulp consumers												
Fringilla coelebs	22.15	49.12	18.31	30.00	30.07	39.76	11.00	11.94	10.83	13.05	8.91	7.54
Parus caeruleus	4.91	10.88	7.56	12.38	0.89	1.18	1.78	1.94	0.91	1.10	1.60	1.35
Parus cristatus	0.80	1.76	1.45	2.38	0.53	0.71	0.45	0.48	0.71	0.85	1.49	1.26
Parus major	1.46	3.24	3.20	5.24	0.71	0.94	0.45	0.48	1.32	1.59	1.14	0.97
Serinus citrinella	–	–	–	–	0.36	0.47	0.30	0.32	–	–	0.57	0.48
Serinus serinus	0.80	1.76	1.74	2.86	–	–	0.15	0.16	0.81	0.98	1.03	0.87
Seed predators												
Coccothraustes coccothraustes	0.13	0.29	0.29	0.48	–	–	–	–	–	–	–	–

Appendix 2. Relative abundance (perecentage of birds censused) and abundance index (birds·km^{-} . BKM) of avian frugivores visiting *Prunus mahaleb* trees, Nava Noguera site, during 2 yr.

Frugivory type Species	1986		1988		Frugivory type Species	1986		1988	
	%	BKM	%	BKM		%	BKM	%	BKM
Seed dispersers					Pulp consumers-dispersers				
Columba palumbus	2.50	0.88	2.11	1.17	*Garrulus glandarius*	3.33	1.18	0.90	0.73
Corvus corone	5.83	2.06	2.26	1.83	*Parus ater*	8.33	2.49	5.26	4.27
Dendrocopos major	–	–	0.30	0.24	*Sitta europaea*	2.50	0.88	1.35	1.10
Erithacus rubecula	–	–	5.71	4.63					
Phoenicurus ochruros	10.83	3.82	7.52	6.10	Pulp consumers				
Phoenicurus phoenicurus	0.83	0.29	3.16	2.56	*Fringilla coelebs*	26.67	9.41	25.41	20.61
Sylvia atricapilla	1.67	0.59	1.05	0.85	*Parus caeruleus*	5.00	1.76	6.02	4.88
Sylvia cantillans	1.67	0.59	0.60	0.49	*Parus cristatus*	4.17	1.47	1.35	1.10
Sylvia communis	–	–	1.35	1.10	*Parus major*	–	–	1.05	0.85
Sylvia melanocephala	–	–	0.30	0.24	*Serinus citrinella*	–	–	0.45	0.37
Turdus merula	9.17	3.24	12.78	10.37	*Serinus serinus*	–	–	2.41	1.95
Turdus viscivorus	1.67	0.59	14.29	11.59					