

## FACTORS SHAPING THE SEEDFALL PATTERN OF A BIRD-DISPERSED PLANT

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**Abstract.** The spatial distribution of seeds can influence several parameters of the natural regeneration of plant populations. Factors shaping seedfall patterns have been typically explored from the tree perspective (seed shadow) or from the population perspective (seed rain). However, the seed rain is actually composed of multiple seed shadows. In this paper, we use this framework to explore the variables shaping the seedfall pattern of the wild olive tree (*Olea europaea* var. *sylvestris*), a fleshy-fruited tree of the Mediterranean scrublands. We monitored the movement patterns of avian seed dispersers and the seedfall around each fruit-bearing *O. europaea* tree in two contrasting sites, differing in the degree of human management and abundance of scrub cover.

None of the seed dispersers moved between microhabitats (different shrub species and open interspaces) as a function of microhabitat relative abundance. All dispersers foraged preferentially at *O. europaea*; only the smaller species visited open interspaces, and these only sporadically.

Avoidance of open sites by frugivores, especially larger species, and their attraction to source trees were the major determinants of the seedfall pattern. Regarding seed size distribution among microhabitats, we found that only small seeds were significantly overrepresented in open interspaces. From the seed shadow perspective, seed density under trees was similar in the two study sites, but it decreased with distance at a higher rate in the disturbed scrubland. From the seed rain perspective, seed density was significantly different among microhabitats, with open interspaces collecting few, if any, seeds, and places under source trees receiving the highest densities.

Results from seed shadow and seed rain analyses were integrated to construct a path model to explore the relative contribution of spatial, microhabitat, and individual tree features to the seedfall pattern. Factors related to microhabitat were identified as having a major role in shaping seedfall pattern. Open interspaces collected few seeds, points under shrub species with sparse foliage collected moderate seed densities, and points under shrubs with dense foliage collected the highest seed densities. The comparison between sites suggests that habitat alteration (a reduction of the scrub layer) can lead to contrasting seedfall patterns. The occurrence of an abundant scrub layer in the well-preserved scrubland allowed a complex pattern of seed rain. In contrast, the sparse scrub cover in the disturbed scrubland yielded a seedfall pattern composed of multiple seed shadows constrained to the vicinity of tree crowns. Thus, our sampling design and analytical approach have proved useful in describing the relative importance of the set of variables that shapes the complex seedfall pattern of a bird-dispersed plant. This seedfall pattern, in turn, is central to the understanding of the spatial patterns of plant recruitment and the efficiency of the dispersal mutualism.

**Key words:** *bird-dispersed plants; habitat alteration; Mediterranean scrubland; microhabitats; Olea europaea* var. *sylvestris*; *seed dispersal; seed rain; seed shadow; seed size; wild olive.*

### INTRODUCTION

Seed dispersal is a spatial process ultimately aimed to enhance the probability that seeds will reach suitable sites for their future development (Howe and Smallwood 1982, Willson 1992). Many plant species are dispersed by vertebrate frugivores (Howe 1986, Jordano

1992, Stiles 1992) that, through their fruit selection and foraging patterns, determine the identity of the dispersed seeds and where the seeds are delivered (Levey 1986, Hoppes 1987, Murray 1988). Thus, to some extent, frugivores can determine the spatial distribution of plant recruitment (Herrera et al. 1994, Schupp 1995, Schupp and Fuentes 1995)

The spatial distribution of dispersed seeds typically has been analyzed either from the individual's perspective or from the population's perspective (Willson 1992). Usually, these contrasting approaches have

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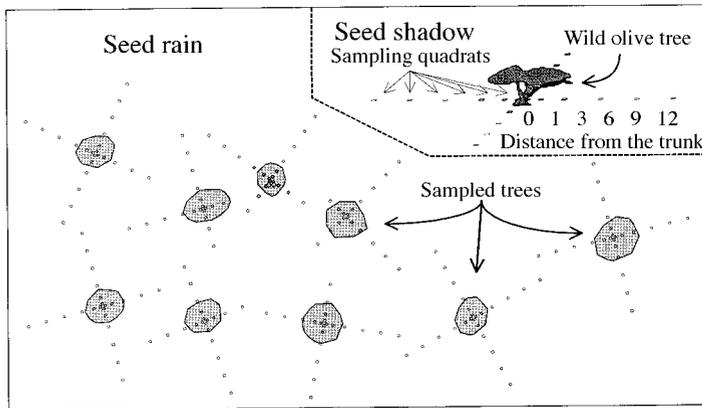


FIG. 1. Sampling design for seed shadow and seed rain. Seed density was monitored around each fruiting tree along four transects of  $50 \times 50$  cm quadrats at six distances (0, 1, 3, 6, 9, and 12 m) from the trunk (= seed shadow). The adjacent trees allow analysis of the overall distribution of seeds within the study sites (= seed rain).

adopted two different terms to describe seed distributions. "Seed shadow," which refers to the spatial distribution of seeds dispersed from a plant as a function of distance from the mother plant (e.g., Augspurger 1983, Augspurger and Hogan 1983), is frequently used to assess evolutionary aspects of seed dispersal (Portnoy and Willson 1993, Willson 1993). "Seed rain," which describes the distribution of seeds within the habitat occupied by the population (usually neglecting tree sources or distance to potential tree sources), focuses on a more demographic view of seed dispersal (e.g., Izhaki et al. 1991, Debussche and Isenmann 1994, Masaki et al. 1994).

In the case of many tropical fleshy-fruited tree species, the rarity and relative isolation from conspecific adults may allow a clear separation of single-tree seed shadows (Janzen et al. 1976, Burbidge and Whelan 1982, Howe et al. 1985, Dalling et al. 1998). In contrast, the usually higher densities and shorter distances among conspecific trees in temperate plant communities often lead to overlapped seed shadows, so that the individual perspective is more difficult to address (Hoppes 1988) and has been attempted only for subdominant species (Debussche and Isenmann 1994) or in highly disturbed habitats (Debussche et al. 1985, Holthuijzen and Sharik 1985a, b). The short distance between conspecifics is not the only reason for overlapping seed shadows. The attraction of seeds from conspecifics, which can be as important in tropical as in temperate systems, also contributes.

However, the dichotomy between the individual and population perspectives is partly an artifact, because the population seed rain is actually composed of multiple seed shadows (Fig. 1). Thus, it seems appropriate to link both individual and population perspectives to better understand the shaping of the spatial distribution of seeds. This linkage may be facilitated by a slightly different conceptualization of the seed shadow as "the spatial distribution of seeds generated around a tree." This conceptualization retains from the original definition its dependence on distance from a tree, but makes

room for overlapping as it discards the origin of the seeds, which is beyond the reach of the techniques available in seed dispersal studies. Furthermore, not only the distance to source trees, but also the complex movements of different frugivores within a structurally heterogeneous habitat, should be taken into account to accomplish the linkage (Herrera and Jordano 1981, Hoppes 1987, Malmborg and Willson 1988, Murray 1988, Izhaki et al. 1991, Chavez-Ramírez and Slack 1994). Recent efforts have considered both the distribution of source trees and parameters of habitat structure to explain the population-level seedfall pattern (Hoppes 1988, Masaki et al. 1994, Russell and Schupp 1998). However, comparison of the relative importance of these multiple parameters remains largely unexplored. Further, the relative importance of these factors could be different in contrasting habitats, leading to contrasting patterns of recruitment.

We used the wild olive (*Olea europaea* var. *sylvestris*, Brot. Oleaceae), a frequent small tree in scrublands along the northern Mediterranean Basin, to explore factors shaping the seedfall pattern in disturbed and well-preserved scrublands. Specifically, we addressed two main objectives. First, we analyzed the possible effect of seed size, as proposed by Schupp (1995), on seed distribution among microhabitats. In Mediterranean communities, seeds of different size can be dispersed by different frugivore species (Jordano 1984, Rey et al. 1997), which may have contrasting foraging patterns (Cuadrado 1988). Thus, the possibility exists for seeds of different size to arrive preferentially into certain microhabitats (Schupp 1995). The wide range of seed sizes produced by our study species (Alcántara et al. 1997a) allowed us to explore this possibility from an intraspecific perspective. Secondly, we explored the contribution of parameters influencing seed shadow and seed rain to the overall seedfall pattern. To address this objective, we analyzed the shape of the seed shadow and the distribution of seeds among different microhabitats (the seed rain). Results from these analyses were integrated to construct a path model that explores

the relative contribution of spatial, microhabitat, and individual tree features to the seedfall pattern.

## METHODS

### *Study species and study sites*

Different aspects of the natural history of *O. europaea* are described in Jordano (1987) and Alcántara et al. (1997a, b, c). Mean individual crop size varies greatly between years, ranging in our study sites from 0 to  $9999 \pm 5988$  fruits over four years (all data are reported as mean  $\pm$  1 SD unless otherwise stated). Fruits are single-seeded drupes that ripen throughout the autumn and winter. The seed is enclosed in a hard endocarp  $1.20 \pm 0.23$  mm thick. The whole propagule (seed plus endocarp; seed hereafter) is  $10.61 \pm 1.80$  mm long and  $6.22 \pm 0.77$  mm wide, with seed mass of  $226.0 \pm 75.0$  mg. Seeds are dispersed by small- to medium-sized frugivorous birds, primarily species of the genera *Turdus* and *Sylvia*.

The study was conducted at Sierra Sur de Jaén ( $37^{\circ}40'$  N,  $3^{\circ}45'$  W; Jaén province, southern Spain). In this area, we selected two sites where *O. europaea* is one of the dominant woody plants. Sillón del Rey (4.5 ha) is a highly disturbed scrubland dedicated to live-stock grazing. The vegetation is composed of a herbaceous layer and scattered *O. europaea* (9 trees/ha) and *Pistacia terebinthus*, which confers a savannah-like appearance to the site. In contrast to this site, La Parrilla (2.5 ha) is a well-preserved scrubland with dense and large patches composed of tall scrubs, small trees, and vines, separated by open interspaces. It is dominated by *O. europaea* (17 trees/ha), *P. terebinthus*, *Phillyrea latifolia*, and *Quercus coccifera*.

### *Movement patterns of dispersers*

The major dispersers of *O. europaea* seeds in our study area (Alcántara et al. 1997c) are Song Thrush (*Turdus philomelos*), Blackcap (*Sylvia atricapilla*), Sardinian Warbler (*S. melanocephala*), and European Robin (*Erithacus rubecula*). At La Parrilla, we determined the microhabitat preferences of each bird species, using four observation points evenly distributed across the site, from which all microhabitats considered could be observed. In order to quantify microhabitat availability, we estimated the relative cover of each microhabitat along five randomly placed line transects ( $2 \times 50$  m) at each observation point (see Izhaki et al. [1991] for a similar observation method). We then monitored the use of microhabitats by birds monthly from October 1996, when the first ripe fruits were present, to March 1997, when most of the frugivores had already migrated. During 30-min observation periods, we watched each frugivore arriving at the observation area and recorded the microhabitat(s) where it foraged, considering a maximum of five contacts (movements between individual plants or between microhabitats). This method has been recommended by several authors

(Hertz et al. 1976, Wagner 1981). Morrison (1984) suggested a minimum sample size of 30 birds to obtain good estimates of the foraging pattern. We achieved this sample size for *S. atricapilla* ( $N = 90$ ) and *E. rubecula* ( $N = 48$ ), but not for *S. melanocephala* ( $N = 24$ ) and *T. philomelos* ( $N = 26$ ). Thus, to obtain better estimates of the frequency of microhabitat use, we computed bootstrap estimates (Potvin and Roff 1993) from 1000 random combinations (with replacement) of  $N$  individuals for each bird species  $\times$  microhabitat combination. These bootstrap estimates have been included in the analyses of avian foraging patterns.

### *Dispersal pattern in relation to seed size*

During winter 1993–1994, we estimated ripe fruit crop size and the seed size frequency distribution (see Alcántara et al. 1997b for details) for all of the *O. europaea* trees fruiting in both study sites. The frequency distribution of seed sizes produced in each study site is the expected distribution in the seed rain, if avian frugivores do not select for seed size. Therefore, any significant departure in the seed rain from this distribution would indicate a relationship between seed size and dispersal probability.

To study the size distribution of seeds arriving at different microhabitats, we pooled into three size classes the seeds collected from seedfall sampling: large ( $>0.2$  g), medium (0.1 to 0.2 g), and small seeds ( $<0.1$  g). These classes are related to the sizes that the main frugivores can disperse: the large ones can only be dispersed by *T. philomelos*, the medium ones by this species and *S. atricapilla*, and the small seeds can be dispersed by all the frugivores (Rey et al. 1997). This classification of seed sizes allowed us to potentially link specific groups of bird species to size-specific patterns of seed arrival across microhabitats.

### *Seedfall sampling*

Sampling was conducted in April 1994, just after the end of the seed dispersal period (Alcántara et al. 1997a). Seed density was sampled along four radial transects around each fruiting *O. europaea* tree in the two study sites ( $N = 39$  trees at La Parrilla and  $N = 17$  trees at Sillón del Rey; Fig. 1). Transects consisted of six  $0.5 \times 0.5$  m quadrats placed at 0.25, 1.5, 3.5, 6.5, 9.5, and 12.5 m from the trunk, the maximum distance being greater than the mean distance to the nearest conspecific ( $9.73 \pm 13.41$  m). Frequently, transects from two adjacent trees overlapped. In such cases, sampling was stopped just before reaching the point where transects converged (Fig. 1). In each quadrat, all seeds (undamaged, broken, or gnawed) were collected and subsequently counted. The fresh mass, maximum length, and maximum width of undamaged seeds were measured. Nondispersed seeds eventually fall beneath the tree within the fruit, which impedes their germination because the high lipid content of the pulp pre-

vents water imbibition. Therefore, only seeds dispersed during the study year (easily distinguishable from older seeds by their fresh endocarp) were counted. Overall, 863 seeds were collected at Sillón del Rey and 3137 seeds at La Parrilla. Each quadrat was additionally classified according to the percentage of scrub cover above it (0, 20, 40, 60, 80, 100%) and according to the following microhabitat types: *O. europaea*, *Pistacia terebinthus*, *Pistacia lentiscus*, *Q. coccifera*, *Rhamnus lycioides*, *Phillyrea latifolia*, *Crataegus monogyna*, *Rosa canina*, or open interspace. Each quadrat was assigned to only one microhabitat type according to the dominant shrub species, i.e., the species that occupied the largest area or volume above the quadrat.

Seed dispersal began in early November 1993 (Alcántara et al. 1997a). Between then and early April 1994 (our sampling date), rodents could have removed an undetermined number of seeds. Thus, our sampling method might underestimate the quantity of seeds fallen within the sampling plots. To minimize this bias, we considered gnawed seeds, but we were not able to account for seed caching. However, during the dispersal season (November 1993–April 1994), most seeds were dispersed from late February through March (>50% at Sillón del Rey and 80% at La Parrilla; Alcántara et al. 1997a), suggesting that a large percentage of seeds was not exposed to rodents for a long time before sampling took place. Therefore, our data may describe the spatial distribution of the majority of dispersed seeds.

To further analyze the adequacy of the quadrat method, during a subsequent fruiting season we compared seed density estimates obtained by the quadrat method and by seedfall traps. Ten seedfall traps (26 × 33 × 5 cm aluminum pans, with a wire mesh over the top to exclude rodents) were set up in November 1996 in each of five microhabitats (*O. europaea*, *P. latifolia*, *P. terebinthus*, *Q. coccifera*, and open interspaces). Traps were monitored every two weeks until April 1997. At this time, we sampled one 50 × 50 cm quadrat adjacent to each trap. Seed densities (standardized for the same area) obtained by both sampling techniques did not differ (Wilcoxon matched pairs:  $Z = 0.40$ ,  $P = 0.40$ ,  $N = 40$ ). Quadrats sampled in open interspaces received no seeds, so they were excluded from this analysis. Furthermore, seed density was highly correlated across sampling points between methods ( $r_s = 0.88$ ,  $P < 0.0001$ ,  $N = 40$ ). Thus, the quadrat sampling method produced adequate estimates of the actual seed density occurring at each point.

#### Data analyses

To analyze seed size distributions in different microhabitats, we computed for each the frequency of small, medium, and large seeds. This generated a contingency table (three size classes × seven microhabitats) with the null hypothesis that the frequencies of the different size classes do not vary across microhabitats.

Seed density was not normally distributed, even after transformation. Therefore, analyses involving seed density were performed with Poisson error distribution and logarithmic link function using the GENMOD procedure of SAS (SAS Institute 1993, 1994). The log-link function also allowed us to linearize the nonlinear relationship between distance and seed density, because the exponential function becomes a linear function by taking natural logarithms.

In order to test simultaneously the effects of all factors involved in the spatial distribution of seeds, we designed a path model to be analyzed by means of a structural equation model (see Mitchell 1993 for an example). The path structure proposed (Fig. 2) is built upon factors found by Alcántara et al. (1997a, b, c) to influence *O. europaea* seed dispersal success for the same study season and sites used in the present study, and upon the relationships described in this paper.

*Path model.*—Our target variable was seed density, the number of seeds per quadrat (Fig. 2). The model is structured in three sections. The first (left side) includes variables related to the identity of the source tree nearest to a given quadrat. These variables (ripening phenology, fruit width, and crop size) are characteristics of individual trees and influence the number of seeds dispersed by each (Alcántara et al. 1997c). The second section (right side) is related to microhabitat characteristics (cover type and percent cover of shrubs in the quadrat). Following the results of the seed rain analysis (see *Seed rain* in *Results*), cover type was categorized in three classes: species with dense foliage, species with sparse foliage, or open interspaces. Due to its qualitative nature, cover type was effect-coded using two dummy variables (the number of character states – 1; Pedhazur 1982), and was incorporated in the model as a latent construct of these dummy variables. For quadrats in open interspaces, dummy 1 = 1 and dummy 2 = 0; for sparse-foliage quadrats, both dummy 1 and dummy 2 = 0; and for dense-foliage quadrats, dummy 1 = 0 and dummy 2 = 1. A latent construct is a new variable (not actually measured) generated in the model from other variables (Pedhazur 1982, StatSoft 1995). The unmeasured “cover type” factor was thus used as a quantitative surrogate for the qualitatively defined types of foliage. Finally, the third section included only the effect of distance from the nearest source tree. All of the manifest variables (except those generating cover type) were allowed to directly affect seed density. Indirect effects on seed density were also allowed for tree parameters through their independent effect on the number of seeds dispersed, and for cover type through percent cover.

The model was fitted separately for the two study sites to assess the consistency of the causal pattern across populations. The matrix of Pearson correlation coefficients among the variables included in the model (Table 1) was analyzed with the SEPATH module of STATISTICA (StatSoft 1995). This program correctly

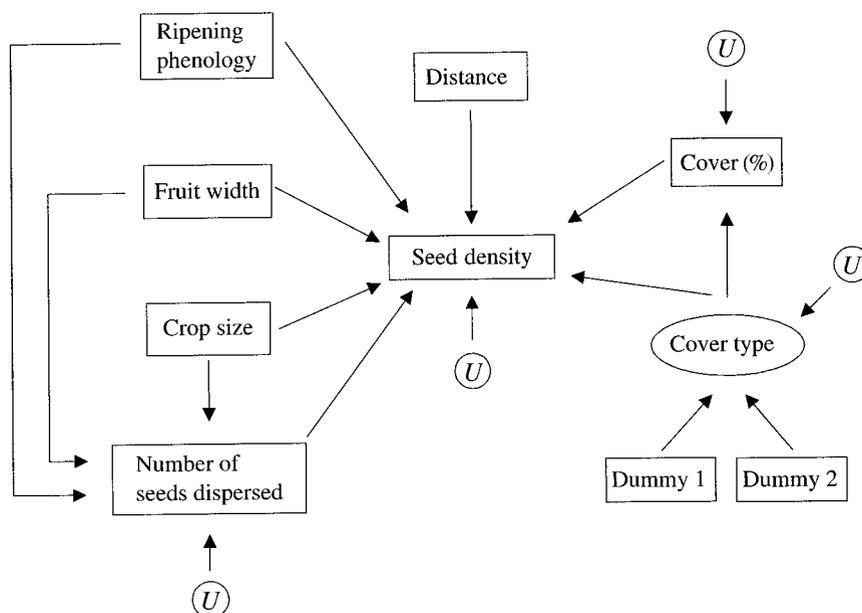


FIG. 2. Structure of the path model. The model depicts the effects on no. seeds/quadrat (seed density) of dispersal-related traits of the nearest source tree (left column of variables), microhabitat characteristics (right column of variables), and distance to the nearest source tree. Residual variables ( $U$ ) indicate unmeasured factors affecting a given variable. Rectangles contain manifest endogenous variables. Cover type (oval) is a latent variable incorporating three levels of foliage density coded with two dummy variables (see *Methods: Data analyses* for details).

estimates standard errors of path coefficients from the correlation matrix, and estimates a completely standardized path model, in which both manifest and latent variables have unit variances. Multivariate normality is required for this type of analysis. When it is not achieved (as in the case of our target variable, seed density) and a large sample size is available, the use of an Asymptotically Distribution Free Discrepancy Function (Browne 1984, Muthén and Kaplan 1992) is preferable. Therefore, we chose the ADFG option in SEPATH to perform the fitting of the model. Finally, another requisite for this type of analysis is a linear relationship between the variables. To promote this linearity, some variables were transformed. Seed density, crop size, and distance from the tree were transformed to their natural logarithm, and the percentage of scrub cover was transformed to its arcsine-square root.

## RESULTS

### *Microhabitat use by the main seed dispersers*

Birds visited microhabitats differently from their availability ( $G$  test for goodness-of-fit:  $P < 0.01$  for each bird species; Table 2). Microhabitats differed in the proportion of the total visits by the set of frugivores (Kruskal-Wallis  $H = 22.83$ ,  $df = 6$ ,  $N = 28$ ,  $P < 0.001$ ). Overall, the most preferred microhabitat was *Olea europaea*, whereas open interspaces were least visited. Within microhabitats, open interspaces were only used by *Sylvia melanocephala* and especially by *Erithacus rubecula*, the smallest dispersers. For shrub species,

there were no significant differences in use of a given microhabitat among bird species (*O. europaea*:  $\chi^2 = 4.9$ ,  $df = 3$ ,  $P > 0.1$ ; *Pistacia terebinthus*:  $\chi^2 = 2.5$ ,  $df = 3$ ,  $P > 0.1$ ; *Phillyrea latifolia*:  $\chi^2 = 4.0$ ,  $df = 3$ ,  $P > 0.1$ ; *Quercus coccifera*:  $\chi^2 = 3.7$ ,  $df = 3$ ,  $P > 0.1$ ). Although the small sample size precluded analysis, *Rhamnus lycioides* was mainly visited by *S. melanocephala*, and *P. lentiscus* by *Turdus philomelos*.

### *Dispersal patterns in relation to seed size*

Seed size frequency distribution in the seed rain was significantly different from that produced by the trees in both sites (Kolmogorov-Smirnov test of goodness-of-fit; Sillón del Rey:  $d_{\max} = 36.17$ ,  $N = 420$ ,  $k = 8$ ,  $P < 0.001$ ; La Parrilla:  $d_{\max} = 359.19$ ,  $N = 2657$ ,  $k = 11$ ,  $P < 0.001$ ). The largest size classes tended to be underrepresented in the seed rain, especially at Sillón del Rey (Fig. 3).

Overall, seed size frequency distribution differed among microhabitats (Table 3). Considering individual microhabitats, however, the distribution was significantly different from that in the seed rain only in open interspaces, with large seeds underrepresented and small seeds overrepresented. Size distribution under *Q. coccifera* and *R. lycioides* was marginally different from that expected ( $0.05 < P < 0.10$ ). In the first case, small seeds tended to be underrepresented; in the second, medium-sized seeds were underrepresented. Despite a lack of significance in individual microhabitats, there was a trend toward overrepresentation of large seeds in most microhabitats with woody cover.

TABLE 1. Correlation matrices for the variables included in the path models; boldface indicates significance at  $P < 0.05$ . Data for Sillón del Rey are above the diagonal ( $N = 373$  sampling points); those below the diagonal are for La Parrilla ( $N = 527$  sampling points).

Variables	DIST	DENS	%COV	NDISP	CROP	PHEN	FWIDTH	OPEN	DFOL
Distance (DIST)		<b>-0.696</b>	<b>-0.714</b>	0.003	0.001	-0.014	-0.007	<b>0.659</b>	<b>-0.764</b>
Seed density (DENS)	<b>-0.515</b>		<b>0.840</b>	0.023	0.045	-0.015	0.015	<b>-0.803</b>	<b>0.838</b>
Percentage of shrub cover (%COV)	<b>-0.477</b>	<b>0.652</b>		0.008	0.013	0.019	0.011	<b>-0.927</b>	<b>0.916</b>
No. seeds dispersed (NDISP)	0.035	0.085	-0.000		<b>0.815</b>	<b>-0.475</b>	<b>0.613</b>	-0.008	-0.026
Crop size (CROP)	0.041	<b>0.089</b>	0.039	<b>0.613</b>		<b>-0.239</b>	<b>0.230</b>	-0.027	-0.031
Ripening phenology (PHEN)	-0.042	-0.077	0.021	<b>-0.322</b>	<b>-0.482</b>		<b>-0.434</b>	-0.028	0.004
Mean fruit width (FWIDTH)	<b>0.093</b>	0.038	0.031	<b>0.417</b>	<b>0.322</b>	<b>-0.538</b>		0.009	-0.012
Open sites (OPEN)	<b>0.473</b>	<b>-0.579</b>	<b>-0.862</b>	0.009	-0.028	-0.022	-0.026		<b>-0.799</b>
Shrub species with dense foliage (DFOL)	<b>-0.523</b>	<b>0.582</b>	<b>0.668</b>	-0.056	-0.042	-0.017	-0.007	<b>-0.559</b>	

Notes: Variables related to the nearest source tree are: DIST, distance from the tree (m); NDISP, number of seeds dispersed; CROP, crop size; PHEN, number of fortnight (starting in the first of October) when the first fruits ripened; FWIDTH, mean fruit width. Variables related with the microhabitat on each sampling point are: %COV, percentage of woody cover above the sampling point; OPEN, no woody vegetation above the sampling point; DFOL, presence of shrubs with dense foliage above the sampling point: wild olive (*Olea europaea* var. *sylvestris*), *Phillyrea latifolia*, *Quercus coccifera*, or *Pistacia lentiscus*. The main target variable is: DENS, number of seeds in each sampling point.

### Seed shadows

In both study sites, the mean seed density decreased with distance from a maximum at the trunk and followed a negative exponential curve (Table 4). Although the intercept of this curve was similar for both sites, the slope was clearly steeper at Sillón del Rey (Fig. 4).

When considering each tree separately, and using only those trees for which we sampled at least two quadrats per distance (i.e., at least two complete transects), all seed shadows tested from Sillón del Rey (14 trees) significantly fit a negative exponential function. At La Parrilla, however, only 16 out of 27 (59.26%) seed shadows fit this function. In Sillón del Rey, the intercept (mean  $\pm$  1 SE) was  $4.00 \pm 0.25$  (range 2.38–5.70) and the slope was  $-1.06 \pm 0.16$  (range -0.46 to -2.62). The values for the intercept did not differ from those at La Parrilla ( $3.81 \pm 0.18$ ; range 1.84–6.64; Mann-Whitney  $Z = -0.64$ ,  $P = 0.52$ ), but the slopes did differ (La Parrilla:  $-0.44 \pm 0.10$ ; range 0.13 to -2.59; Mann-Whitney  $Z = -3.91$ ,  $P < 0.001$ ).

Thus, seed density under trees was similar at both sites, but decreased more quickly with distance in Sillón del Rey. This trend was consistent if we compared

individual seed shadows or mean seed shadows at a site.

### Seed rain

Seed density differed significantly among microhabitats at both study sites (Table 5). Open interspaces collected few, if any, seeds, whereas quadrats under *O. europaea* received the highest densities. However, are these differences due only to the effect of microhabitat, or do they depend, to some extent, on the location of each sampling point within the plot?

The number of seeds reaching a point depends on at least three parameters: (1) the distance to source trees, (2) the quality or attractiveness of such trees for frugivores, and (3) microhabitat characteristics of the point promoting the arrival of frugivores. To analyze the net effect of microhabitat on seed density, independent of the distance and quality of a source tree, we conducted the following analyses. We first analyzed seed density per quadrat using a Poisson regression with tree identity as grouping variable to control for quality of source trees, and distance to the tree as a covariate to control for the effect of distance. The re-

TABLE 2. Bootstrap estimates of percentage of contacts by the main frugivores in each microhabitat, and percentage of area covered by these microhabitats in the sampling stations.

Microhabitat	Contacts by frugivore species (%)†				Area covered by microhabitat (%)
	<i>S.m.</i> ( $n = 37$ )	<i>S.a.</i> ( $n = 142$ )	<i>E.r.</i> ( $n = 76$ )	<i>T.p.</i> ( $n = 39$ )	
<i>Olea europaea</i>	35.14	43.66	40.79	25.64	24.72
<i>Pistacia lentiscus</i>	2.70	0.70	1.32	7.69	2.75
<i>Pistacia terebinthus</i>	27.03	18.31	26.32	23.08	19.78
<i>Quercus coccifera</i>	5.41	14.08	7.89	15.38	6.59
<i>Phillyrea latifolia</i>	21.62	21.13	11.84	25.64	4.94
<i>Rhamnus lycioides</i>	5.41	2.11	1.32	2.56	4.94
Open interspaces	2.70	0.00	10.53	0.00	36.26

† Abbreviations: *S.m.*, *Sylvia melanocephala*; *S.a.*, *Sylvia atricapilla*; *E.r.*, *Erithacus rubecula*; *T.p.*, *Turdus philomelos*. The total number of contacts ( $n$ ) for each species is given in parentheses.

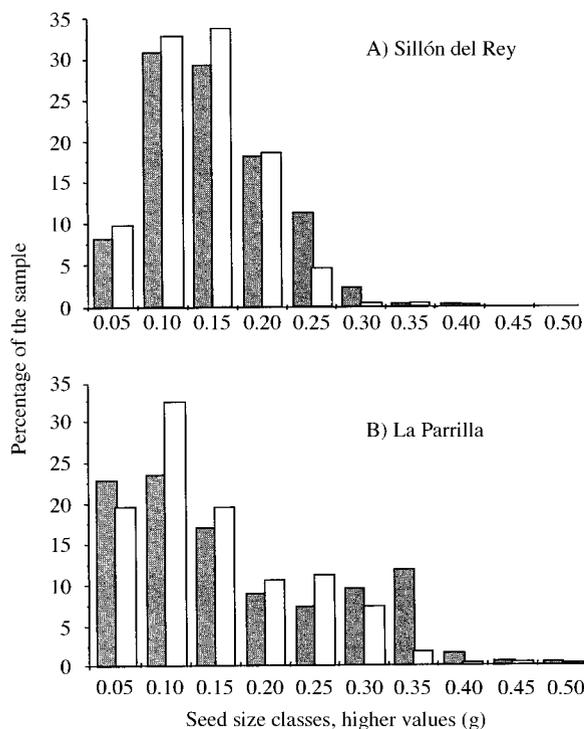


FIG. 3. Seed size distribution in the seed rain (open bars) compared to that expected from the total seed production (shaded bars) at (A) Sillón del Rey site and (B) La Parrilla site.

siduals generated by this analysis can be interpreted as the seed density in a quadrat that was independent of its position in the plot (i.e., independent of how far from which tree the sampling point was placed). Finally, we analyzed differences between microhabitats using these residuals, rather than seed numbers, to assess the net microhabitat effect on seed density, independent of the location of the sampled points in the plot.

This procedure was conducted independently for each site (Table 6). In both cases, the Poisson regression yielded significant effects of tree identity and distance, as expected from the analysis of the seed shad-

ows. However, the residuals did not differ significantly among microhabitats at Sillón del Rey. Thus, in this site, seed rain can be described as a collection of individual seed shadows, determined only by distance to, and identity of, the nearest tree.

In contrast, the residuals for La Parrilla differed significantly among microhabitats. Nonparametric multiple comparisons (Zar 1984:199) between all pairs of microhabitats showed that *O. europaea* differed from *R. lycioides*, *P. terebinthus*, and open interspaces, and *R. lycioides* differed from open interspaces. This suggests that these microhabitats comprise three groups regarding their ability to attract seeds: (1) species with dense and evergreen foliage, such as *O. europaea*, *P. latifolia*, and *Q. coccifera*, which were the major attractors (i.e., they had the largest positive residuals:  $1.19 \pm 7.61$ ,  $1.68 \pm 4.31$ , and  $1.33 \pm 3.45$ , respectively); (2) species with sparse foliage, such as *R. lycioides* and *P. terebinthus* (residuals:  $-0.68 \pm 3.56$  and  $-0.99 \pm 4.55$ , respectively); and (3) open interspaces, which were the minor attractors (i.e., with the lowest values for the residuals:  $-2.54 \pm 3.43$ ). In short, seed rain at La Parrilla was modeled not only by the distribution of trees (= seed shadows), but also by parameters related to habitat composition and structure.

*General model of seedfall*

As previously shown, the density of seeds reaching a point in space depends on parameters related to the seed shadow, tree identity, and microhabitat. The seed shadow effect is clearly related to distance, but the effects due to tree identity and microhabitat can be more complex. The critical point is what determines or controls the seedfall patterns. Is it only the seed shadow around specific trees, or is it more complex, with distance, identity, and microhabitat all contributing? We evaluated these effects by means of a Structural Equation Model for each site (Fig. 5 and Table 7).

*Sillón del Rey.*—The proposed path model significantly fit our data ( $\chi^2 = 4.941$ ,  $df = 9$ ,  $P = 0.839$ ,  $N = 373$ ) and explained 76.6% of the variance in seed density. Seed density was mainly influenced by the microhabitat side of the model because of the strong

TABLE 3. Distribution of seeds within microhabitats according to size, as a percentage of the total seeds collected in each microhabitat (*n*). Seed size classes are: large (>0.2 g), medium (0.1–0.2 g), and small (<0.1 g). Results of the three size classes  $\times$  seven microhabitats contingency table are also shown.

Microhabitat	<i>n</i>	Seed size classes			Contingency analysis	
		Large (%)	Medium (%)	Small (%)	Partial $\chi^2$	<i>P</i>
<i>O. europaea</i>	2191	18.9	35.7	45.4	0.45	0.80
<i>P. lentiscus</i>	14	28.6	14.3	57.1	2.77	0.25
<i>P. terebinthus</i>	199	22.1	33.2	40.7	2.25	0.32
<i>Q. coccifera</i>	44	31.8	36.4	31.8	5.56	0.06
<i>P. latifolia</i>	48	29.2	22.9	47.9	4.59	0.10
<i>R. lycioides</i>	82	20.7	23.2	56.1	5.35	0.07
Open interspaces	76	5.7	33.3	60.9	12.63	0.002
Total seed rain	2654	19.2	35.1	45.7	33.58	<0.001

TABLE 4. Exponential fitting of seed density (the dependent variable) by distance from the trunk (the independent variable).

Site	$\ln(a) \pm 1 \text{ SE}$	$b \pm 1 \text{ SE}$	$F$ (df)	$P$
Sillón del Rey	$4.31 \pm 0.14$	$-1.00 \pm 0.10$	415.37 (1389)	<0.001
La Parrilla	$3.78 \pm 0.07$	$-0.21 \pm 0.02$	130.07 (1529)	<0.001

Notes: Simple linear regression models were computed by Poisson regression with log-link function and an overdispersion parameter, estimated as the deviance divided by the degrees of freedom. The exponential model is  $y = ae^{bx}$ ; the linearized function is  $\ln(Y) = \ln(a) + bX$ .

total effect of cover type (0.767), a variable that had positive values for species with dense foliage (dummy 2) and negative values for uncovered places (dummy 1). Among the tree characteristics, crop size and mean fruit width had positive direct effects but negative indirect ones, resulting in a small total effect on seed density (0.035 and  $-0.030$ , respectively). Ripening phenology had small and negative direct and indirect effects, yielding a total negative effect ( $-0.048$ ). Finally, the number of seeds dispersed from the tree was the second largest effect on seed density ( $-0.120$ ), even larger than the effect of distance ( $-0.087$ ). In short, the spatial distribution of seed density responded primarily to the cover type, which, in this site, corresponds mainly to the dichotomy of *O. europaea* vs. open interspaces, and secondarily to the different dispersal success of different trees.

*La Parrilla*.—The path model significantly fit our data ( $\chi^2 = 16.675$ ,  $df = 9$ ,  $P = 0.054$ ,  $N = 527$ ) and explained 52.4% of the variance in seed density. None of the parameters describing the nearest tree or its dispersal success had a significant effect on seed density. The effects of the two microhabitat variables (percent cover and cover type) and distance were more evenly partitioned than at Sillón del Rey. The percentage of shrub cover had the strongest direct effect on seed density, but its total effect (0.391) was exceeded by that of cover type (0.545), a variable that had positive values for species with dense foliage (dummy 2) and negative values for open interspaces (dummy 1). These microhabitat effects were stronger than the significant effect of distance ( $-0.229$ ).

## DISCUSSION

### *Spatial distribution of seed size*

Frugivores select different fruit sizes to consume (Hedge et al. 1991, Sallabanks 1992, Jordano 1995, Alcántara et al. 1997c, Rey et al. 1997). Because the size of single-seeded fruits usually correlates with seed size (Jordano 1987, 1995, Wheelwright 1993, Herrera et al. 1994) frugivores can favor the dispersal of certain seed sizes. Fig. 3 indicates that seeds heavier than 0.2 g (our large seed size class) were less consumed (= dispersed) than expected from their availability. This contrasts with the significant positive relationship in our path model between fruit width and the number of seeds dispersed from the tree (Fig. 5). Such discrepancy suggests that the positive effect of size has a maximum limit beyond which seeds are contained in fruits too large to be swallowed by the frugivore species present in our study site. In fact, trees with mean seed size beyond 0.21 g ( $N = 1$  and  $N = 4$  in Sillón del Rey and La Parrilla, respectively) dispersed very low amounts of seeds. However, as there were only a few such trees in the populations, the overall trend of fruit size was still positive (Fig. 5).

As suggested by Schupp (1995), differences among frugivores in sizes of seeds dispersed and in foraging movements among shrub species resulted in the different microhabitats receiving different distributions of seed sizes. For most microhabitats, the seed size distribution resembled the general distribution found in the seed rain. Nonetheless, under *Quercus coccifera* there was a marginally significant bias toward medium

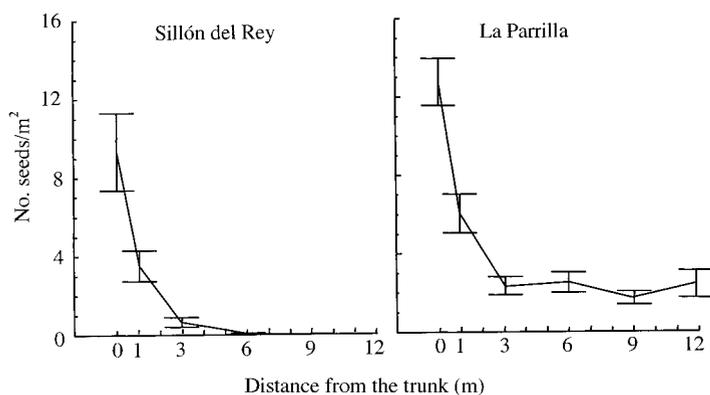


FIG. 4. Seed density as a function of distance from the nearest source tree (= seed shadow). Figures show mean density ( $\pm 1 \text{ SD}$ ) at each distance in the two study sites.

TABLE 5. Mean ( $\pm 1$  SD) seed density (no. seeds/m<sup>2</sup>) in each microhabitat at the two sites. In parentheses are the number of quadrats sampled.

Microhabitat	Sillón del Rey 1994	La Parrilla	
		1994	1997
A) No seeds/m <sup>2</sup>			
<i>O. europaea</i> , dense foliage	31.27 $\pm$ 51.08 (199)	37.17 $\pm$ 49.62 (285)	108.82 $\pm$ 111.68 (10)
<i>P. terebinthus</i> , sparse foliage	0 $\pm$ 0 (18)	9.26 $\pm$ 17.58 (89)	4.71 $\pm$ 6.53 (10)
<i>R. lycioides</i> , sparse foliage	ns	17.26 $\pm$ 40.86 (19)	ns
<i>Q. coccifera</i> , dense foliage	np	15.60 $\pm$ 10.74 (10)	31.65 $\pm$ 41.99 (10)
<i>P. latifolia</i> , dense foliage	np	20.66 $\pm$ 23.81 (12)	16.74 $\pm$ 16.66 (10)
Open interspaces	0.16 $\pm$ 1.39 (271)	3.15 $\pm$ 10.32 (117)	0 $\pm$ 0 (10)
B) Kruskal-Wallis comparison among microhabitats			
<i>H</i>	296.01	203.81	54.92
<i>df</i>	4	8	4
<i>n</i>	391	540	100
<i>P</i>	<0.001	<0.001	<0.001

Notes: Abbreviations include "ns," indicating that the microhabitat was not sampled (<10 quadrats sampled), and "np," indicating that the microhabitat was not present in the plot.

and large seeds. Although our analyses do not clearly attribute this bias to the dominance of a specific frugivore species, it must be noted that large seeds could only be dispersed by *Turdus philomelos*. A clearer pattern occurred in open interspaces, which were only visited by small frugivores, and where the seed size distribution was significantly biased toward the smallest seeds. As with many other species (e.g., Tripathi and Khan 1990, Westoby et al. 1992, Leishman and Westoby 1994, Moegenburg 1996, Saverimuttu and Westoby 1996), seed size positively affects *Olea europaea* seedling development (J. M. Alcántara, P. J. Rey, F. Valera, and A. M. Sánchez-Lafuente, unpublished data). Consequently, this size-dependent pattern of dispersal could make successful recruitment more likely under *Q. coccifera* and less likely in open interspaces than would be expected based only on microhabitat suitability.

TABLE 6. Poisson regression of the effects of tree and distance from tree on seed density per quadrat.

Site and factors	df	<i>F</i>	<i>P</i>
Sillón del Rey			
Tree	16 371	14.59	<0.001
Distance	1371	687.15	<0.001
La Parrilla			
Tree	36 498	3.63	<0.001
Distance	1498	145.49	<0.001

Notes: The residuals from these comparisons were tested at two sites for differences among microhabitats by means of Kruskal-Wallis chi-square tests: Sillón del Rey,  $\chi^2_3 = 7.26$ , *P* = 0.20; La Parrilla,  $\chi^2_3 = 53.47$ , *P* < 0.001.

† Comparison of residuals among microhabitats.

#### Factors shaping the seedfall pattern

The spatial distribution of seeds in bird-dispersed plants is the result of complex movements of different frugivorous-insectivorous bird species within a structurally heterogeneous habitat (Herrera and Jordano 1981, Hoppes 1987, Malmborg and Willson 1988, Murray 1988, Izhaki et al. 1991, Chavez-Ramírez and Slack 1994). Our study shows that, for one tree species, these movements can be controlled by three main factors: traits of individual source trees that attract frugivores, distance to the source tree, and microhabitat structure. This dependence has been shown separately for bird-dispersed seeds in a wide range of habitats, including tropical forests (Murray 1988, Willson and Crome 1989, Alvarez-Buylla and Martínez-Ramos 1990), temperate forests (Hoppes 1988, Masaki et al. 1994), and Mediterranean scrublands (Herrera 1984a, Izhaki et al. 1991, Debussche and Issenmann 1994, Herrera et al. 1994). However, few studies have analyzed such factors in an integrative way (Hoppes 1988, Masaki et al. 1994), and none has studied the relative importance of variables related to them.

Masaki et al. (1994) proposed that a single mathematical model, including effects such as spacing of conspecific trees, heterospecific fruiting trees, gaps, perching trees, or crop size, would explain a high percentage of the variance in seed density and would highlight the relative importance of each factor. Our study has demonstrated that such an integrative view is feasible in a path model. In our case, this approach had three major merits. First, it allowed us to explain a large percentage of the variance in the spatial distribution of seeds in two contrasting habitats (>50% within the structurally complex scrubland of La Parrilla and

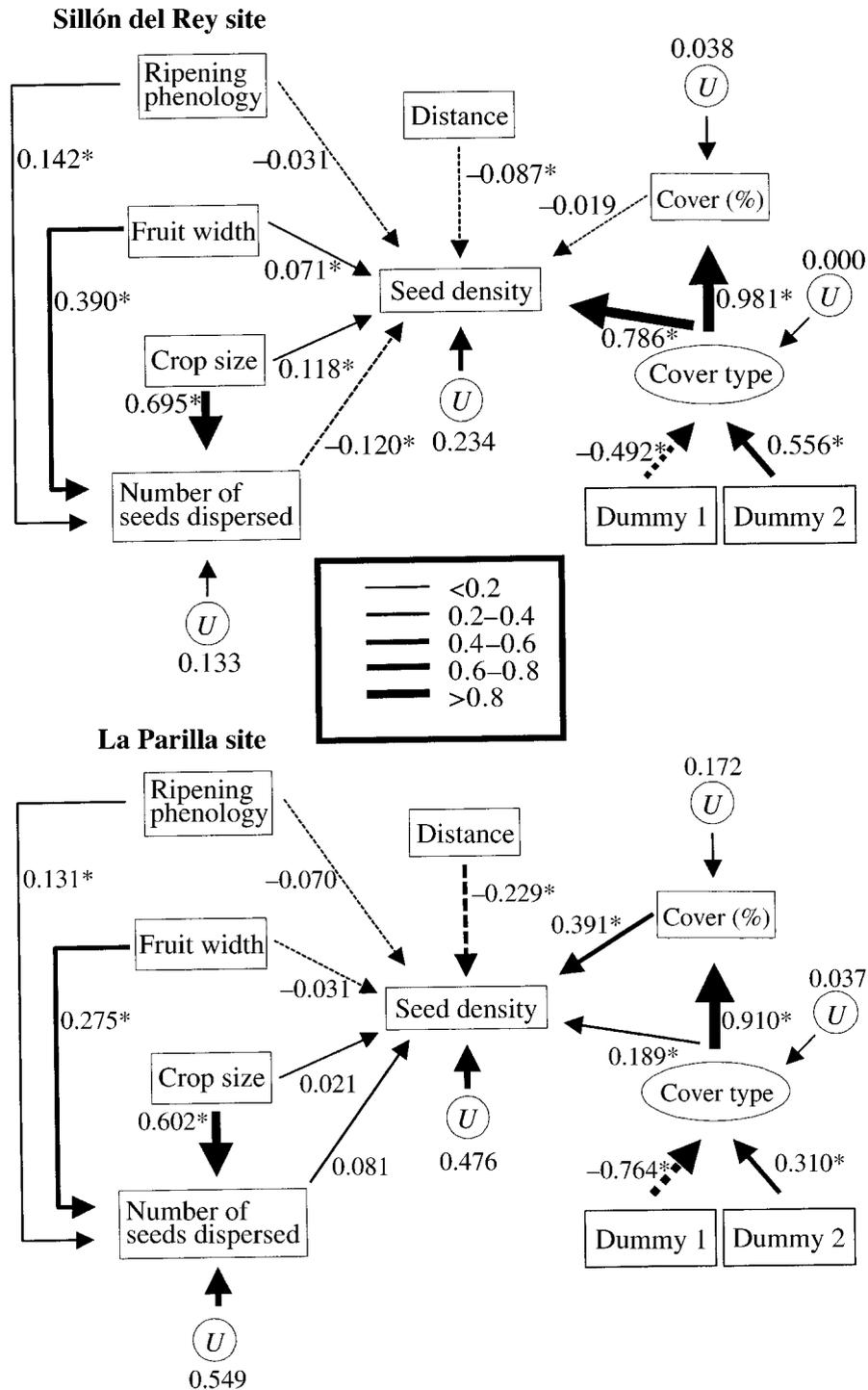


FIG. 5. Results of the analysis of the path model for the two study sites (see *Methods* for a detailed explanation). Dashed lines indicate negative effects; solid lines are positive effects. Figures associated with arrows are the standardized path coefficients (line widths according to the symbol key; single asterisks indicate that path coefficients are significantly different from zero at  $P < 0.05$ ), except for values above (U), which indicate the unexplained variance of dependent variables.

TABLE 7. Summary of the direct (D), indirect (I), and total effect (T) of each variable on seed density.

Variable	Sillón del Rey			La Parrilla		
	D†	I‡	T§	D	I	T
Variables related to nearest <i>O. europaea</i>						
Ripening phenology	-0.031	-0.017	-0.048	-0.070	0.011	-0.059
Mean fruit width	0.071	-0.047	0.024	-0.031	0.022	-0.009
Crop size	0.118	-0.083	0.035	0.021	0.049	0.067
No. seeds dispersed	-0.120		<b>-0.120</b>	0.081		0.081
Distance	-0.087		-0.087	-0.229		<b>-0.229</b>
Other variables						
Percent cover	-0.019		-0.019	0.391		<b>0.391</b>
Cover type	0.786	-0.019	<b>0.767</b>	0.189	0.356	<b>0.545</b>
Dummy 1		-0.396	<b>-0.396</b>		-0.128	<b>-0.406</b>
Dummy 2		0.427	<b>0.427</b>		0.169	<b>0.169</b>

† Direct effects are path coefficients (see Fig. 5).

‡ Indirect effects are computed as the sum of products of the coefficients along all of the possible routes from the variable to seed density.

§ Total effects are the sum of direct and indirect effects (boldface indicates total-effects values >0.1).

|| See *Methods: Data analyses* for an explanation of the variables.

>75% in the disturbed Sillón del Rey). Secondly, it allowed us to clarify the relative importance of different significant effects. Third, it allowed us to compare the relative importance of these effects between two contrasting sites, thus explaining why very different seedfall patterns may be found for the same plant species. However, even more interesting than the high percentage of variance explained is the comparison among effects within and between sites.

*Microhabitat*.—The spatial distribution of seeds within each site primarily reflected the effect of cover type, both directly or indirectly through its effect on percent cover. In our study sites, shrub species with dense foliage (*O. europaea*, *P. latifolia*, *P. lentiscus*, and *Q. coccifera*) form dense scrub patches and also received the highest seed densities. Species with sparse foliage (*P. terebinthus* and *R. lycioides*) are scattered in open areas and accumulated small or highly variable seed densities, whereas open interspaces seldom received any seeds. Mean seed density in the five main microhabitats of La Parrilla (see Table 5) was correlated between years ( $r_s = 0.90$ ,  $P < 0.05$ ,  $N = 5$ ), so their relative importance was consistent.

The avoidance of open interspaces by most Mediterranean frugivores is well known (Herrera and Jordano 1981, Izhaki et al. 1991). The effect of foliage density can be related to protection against predators (Howe 1979, Guitián et al. 1994) or to structural requirements of foraging birds (Levey et al. 1984, Robinson and Holmes 1984). Another important plant feature attracting frugivores, and thereby seeds, is the production of fleshy fruits (Herrera 1984a, Debussche et al. 1985, Murray 1988, Izhaki et al. 1991, Debussche and Issenmann 1994, Herrera et al. 1994, Masaki et al. 1994), but it does not seem to be important in our study site. Seed density under *P. latifolia* (the only shrub fruiting simultaneously with *O. europaea*) was close to that under *Q. coccifera*, which produces acorns, or

under *R. lycioides*, which fruits during summer; furthermore, unlike *P. latifolia*, both species have thorny structures offering protection for small birds.

The final result of the occurrence of an abundant scrub layer and the preferences of frugivores for certain shrub species is a complex seed rain that spreads out seeds very efficiently. This occurred at La Parrilla, where half of the quadrats sampled beyond the crowns of source trees received one or more seeds. Similar efficiency was achieved by *P. latifolia* (53% of the sampling points) in other southern Spanish scrublands (Herrera et al. 1994), and a higher value was described for *Cornus controversa* (83.75%) in a Japanese temperate forest (Masaki et al. 1994). In contrast, the scarcity of scrub cover around source trees in Sillón del Rey resulted in <1% of the quadrats sampled beyond the crowns receiving one or more seeds.

This last feature can explain the apparently opposite results obtained for the microhabitat effect at Sillón del Rey. Although we concluded from the study of the seed rain that microhabitat did not affect seed density, the path model suggested the opposite. This can arise from the strong relationship between distance and microhabitat in this site, where short distances (0–3 m) are overwhelmingly dominated by *O. europaea*, whereas farther distances (3–12 m) are invariably open interspaces. Therefore, the significant effect of microhabitat in the path model would parallel that of distance, reflecting the dichotomy between a high concentration of seeds under *O. europaea* (the only shrub with dense foliage in this site) and their absence from open interspaces. When we analyzed these effects in a stepwise fashion (see *Seed rain*), distance accounted for most of their shared influence on seed density and left the microhabitat without effect. However, when considered simultaneously in the path model, it became clear that the effect of cover type (conspecific vs. open) was much stronger than the distance effect.

*Distance.*—When comparing the distance effect between sites, we again obtained apparently opposite results from the seed shadow perspective vs. the path model. In the first case, distance had a much stronger negative effect at the Sillón del Rey than at La Parrilla, but the opposite was shown by the path analyses. The different meanings of both analyses may account for this apparent contradiction. The slopes of the distance–density relationship in the study of seed shadows indicate that seed density declined more quickly with distance at Sillón del Rey. This is clearly shown in Fig. 4, which also suggests that once outside the tree crown, seed density in this site was almost constant at nearly zero. Thus, the relationship practically holds under the tree crown, and is absent farther away. In fact, this is suggested by the small path coefficient from distance to seed density: two points under the same cover type, with similar percent cover, and located around the same source tree, would have very similar seed densities even if one were closer to the tree. This is not the case in La Parrilla, where the continuous scrub cover allowed a longer tail of the seed shadows (shallower slopes) and, thus, a more consistent distance effect.

*Traits of the nearest source tree.*—The characteristics and seed dispersal success of the nearest source tree had a significant effect on seed density at Sillón del Rey, but not at La Parrilla. Thus, points under the same cover type, with similar percent cover and at the same distance from different source trees, would have a similar seed density at La Parrilla, but not at Sillón del Rey. In the latter site, the path model indicated a positive effect of crop size and a negative effect of the number of seeds dispersed on seed density. This agrees with our use of the term “seed shadow” (trees are not only seed sources but also seed sinks): (1) a large crop size attracts frugivores (Howe and Estabrook 1977, Davidar and Morton 1986, Denslow 1987, Murray 1987, Sargent 1990), which increases the arrival of seeds around the tree; and (2) a high seed dispersal away from the source trees decreases seed concentration (“nucleation”) beneath them.

In summary, the spatial distribution of wild olive seeds was primarily influenced by cover type. This latent variable reflects different situations in the two sites (conspecifics vs. open interspaces at Sillón del Rey, and a gradient of open interspaces to shrubs with sparse foliage to shrubs with dense foliage at La Parrilla). Consequently, the two sites had distinctive seedfall patterns. At Sillón del Rey, the final distribution of seeds was shaped as multiple seed shadows concentrated near the tree crowns. At La Parrilla, although nucleation around source trees also took place, the presence of large scrub patches promoted the mixing of seed shadows and the establishment of a more evenly spread seed rain.

#### *Implications of distinctive seedfall patterns for population recruitment*

The interactions between seed dispersers and microhabitat parameters shape the seed distribution patterns,

which, in turn, can largely determine the spatial dynamics of population recruitment (Schupp and Fuentes 1995). Both our results on the movements of the main dispersers and similar studies of Mediterranean seed dispersers (Herrera and Jordano 1981, Herrera 1984b, Izhaki et al. 1991, Kollmann and Pirl 1995, Rey et al. 1996, Alcántara et al. 1997a, c) indicate that these birds seldom visit open interspaces. The avoidance of open areas could explain the scarcity of seeds outside the tree canopies in the disturbed Sillón del Rey, where new individuals could only emerge under conspecifics. However, adult individuals of many woody species prevent the establishment of conspecifics under their canopy (Augspurger 1983, Howe et al. 1985, Schupp 1988a, b, 1990, Herrera et al. 1994; but see Horvitz and Schemske 1986, Augspurger and Kitajima 1992). As this is the case for *O. europaea* (J. M. Alcántara, P. J. Rey, F. Valera, and A. M. Sánchez-Lafuente, unpublished data), recruitment in this site may be null or low, and the population may be condemned to extinction in the long term. In contrast, in the well-preserved scrubland of La Parrilla, in addition to nucleation under conspecifics, the growth of new individuals scattered within the scrubland is likely.

Thus, the spatial distribution of *O. europaea* seeds reflects a double pattern of nucleation around conspecifics and avoidance of open sites. This pattern seems to be widespread in bird-dispersed plants around the Mediterranean basin (Izhaki et al. 1991, Debussche and Issenmann 1994, Herrera et al. 1994, Verdú and García-Fayos 1996). When conspecifics, or source trees, are scattered in an open landscape, nucleation is the most likely seedfall pattern, and many difficulties are expected for recruitment. The occurrence of simple perches without any foliage (e.g., deciduous trees like *P. terebinthus*) may moderately facilitate seed arrival; however, when perches also offer protection such as a dense foliage or thorns, seed arrival increases and the concentration around source trees becomes a less dominant characteristic of the pattern. This pattern agrees with the habitat requirements of most of the Mediterranean fleshy-fruited plants, which colonize the plant community during late successional stages (Houssard et al. 1980, Escarré et al. 1983, Herrera 1984c, Guitián and Sánchez 1992; but see Ne'eman and Izhaki 1996). In such cases, *O. europaea* benefits from its disperser assemblage because its seeds are disseminated preferentially under shrubs and are seldom deposited in open sites. However, the final spatial distribution of its recruitment may not necessarily resemble the pattern created by the frugivores, as it can be influenced by the spatial heterogeneity of postdispersal processes within the scrubland (e.g., Herrera et al. 1994).

The sampling scheme and analytical approach proposed here have proved to be useful to describe and analyze, in a directly comparable way, the relative importance of the set of variables shaping the complex seedfall pattern of a bird-dispersed plant. Dissecting

the relative effect of such factors is central to understanding the spatial dynamics of recruitment and the final consequences of the mutualistic interaction between birds and plants.

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