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RECRUITMENT OF A MAST-FRUITING, BIRD-DISPERSED TREE: BRIDGING FRUGIVORE ACTIVITY AND SEEDLING ESTABLISHMENT¹

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Abstract. The recruitment of *Phillyrea latifolia* L. (Oleaceae), a bird-dispersed tree of Mediterranean forest, is described. Fruit removal by birds, seed rain, post-dispersal seed predation, seed germination, and seedling emergence, survival, and establishment were studied. The main objective was testing whether seed dispersal by birds produced a predictable seedling shadow as a result of coupled patterns of seed rain, seedling emergence, and seedling establishment. *P. latifolia* is a mast-fruiting species and large fruit crops were produced in only 2 (1981 and 1989) out of 15 yr (1978-1992). We report here on the 1989 fruiting event at one scrubland and one forest site.

Ripe fruits were available from mid-September to early June. Extensive removal by birds started after fruit crops of other species were depleted. Seed dispersers were more abundant, and fruit predators more scarce, in scrubland than in forest. *P. latifolia* fruits were a major component in the diet of principal seed dispersers (*Sylvia atricapilla* and *Erithacus rubecula*) that depended almost exclusively on them for food late in the season. Fruit removal levels were higher, crops were depleted earlier, and individual plants dispersed more seeds in scrubland than in forest. Crop size was the best predictor of number of seeds dispersed by individual plants in scrubland, while fruit characteristics were more influential in forest. Seed dispersal was largely a within-population phenomenon, as no seed fall occurred in traps set beyond the distributional limits of *P. latifolia* in the study region. Frugivores produced a spatially predictable seed rain at the two sites. Seed rain was greatest beneath fleshy fruit-producing species (under female individuals in dioecious species) in scrubland and at forest-gap interfaces in forest. Post-dispersal seed predation was low at the two sites (39 and 54% after 1-yr exposure). In forest, seed survival was lower in gaps than in forest interior or forest edges. In scrubland, seed survival differed widely among microhabitats (defined by overlying plant species), ranging from 19% (open ground) to 61% (beneath *Rosmarinus officinalis*). In forest, density of emerging seedlings was unrelated to location in the habitat mosaic (gap, forest edge, interior). Seedling density did differ among microhabitats in scrubland, where emergence was greatest under fleshy fruit-producing species. Seedling survival was higher in forest than in scrubland, where seedlings incurred greater mortality due to desiccation. In both sites, seedling survival depended significantly on microhabitat and was depressed under adult conspecifics.

The activity of frugivores directly impacted seedling distribution in scrubland, as spatial patterns of seed deposition were not overshadowed by later-acting factors, such as rodent seed predation or variation in germination. In forest, there was spatial discordance between seed rain and seedling distribution, as a consequence of uncoupled seed rain and seedling emergence. Spatial patterns of seed deposition by birds may thus have a lasting impact on the population dynamics of *P. latifolia*, but this will vary among populations depending on the extent of coupling of the different stages in the recruitment process (dispersal-seed rain-germination and seedling establishment).

Key words: avian frugivory; fleshy fruits; mast fruiting; Mediterranean scrublands; mutualism; Oleaceae; plant demography; post-dispersal seed predation; recruitment; seed dispersal; seedling survivorship; Spain.

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INTRODUCTION

Seed dispersal is the last step in the reproductive cycle of plants, but also the starting point in the process of population renewal and recruitment. As an interface between the adult and seedling stages, the process of seed dispersal is thus a keystone demographic bridge (Harper 1977). Plant mortality is highest at the seed and early seedling stages (Harper 1977, Cook 1979, Cavers 1983) and thus there is ample opportunity for natural selection to favor those dispersal-related plant traits that predictably improve the survival probability of seeds and increase the chance of successful seedling establishment. This observation has traditionally provided a biologically sound justification for the claims that natural selection has shaped dispersal-related plant traits (Janzen 1970, Stebbins 1971, Harper 1977, Howe and Smallwood 1982). Nevertheless, even though the bridge nature of dispersal has provided the justification for the adaptationist emphasis prevailing in recent studies of seed dispersal by animals, these investigations have rarely walked over that bridge to look at both sides of the demographic interface. To use Howe's words (1989:417), "The implied marriage of animal foraging with plant demography is rarely consummated."

With relatively few exceptions (e.g., C. M. Herrera 1984b, Janzen 1985, Holthuijzen et al. 1987, Coates-Estrada and Estrada 1988, Reid 1989, Fleming and Williams 1990, Alvarez-Buylla and Garcia-Barrios 1991), the vast majority of studies on the ecology of seed dispersal by vertebrates conducted in the last two decades tend to fall into one of the following three major categories, each roughly corresponding to a consecutive stage in the recruitment process (dispersal-seed rain-germination-seedling establishment). The first and numerically most important group consists of studies focusing on the dissemination of seeds, or "sensu stricto dispersal" (identifying dispersal agents and quantifying patterns in time and space of fruit consumption), without collecting information on its consequences. A second, more reduced group consists of investigations dealing with patterns of seed rain in time and space (e.g., McDonnell and Stiles 1983, Debussche et al. 1985, Stiles and White 1986, Hoppes 1988, Willson and Crome 1989, Izhaki et al. 1991). Few among these, however, have directly related seed rain patterns to habitat use by seed dispersers (Hoppes 1987, Murray 1988). Investigations belonging to the third, most demographically oriented category of studies have examined patterns in time and space of seed and seedling survival and seedling performance. Most of these latter studies have been purely experimental and did not gather information on the dispersal and seed rain stages (e.g., Webb and Willson 1985, Schupp 1988a, b, Willson 1988, Schupp and Frost 1989, Streng et al. 1989, Willson and Whelan 1990, Whelan et al. 1991). In general, studies in each of these three categories have

dealt with different plant species. An outstanding exception is the series of contributions by Howe and co-workers on seed dispersal and its consequences in the tropical tree *Virola surinamensis* (Howe and Vande Kerckhove 1981, Howe and Richter 1982, Howe et al. 1985, Howe 1986, 1990, Fisher et al. 1991), although the various stages in the recruitment process were generally examined in different reproductive episodes.

An important sequel of studying different recruitment stages in different species or seasons is that detailed information on the patterns of dispersal, seed rain, and seed and seedling survival during a single reproductive event are not simultaneously available for any species of vertebrate-dispersed plant. The implications of this fact go beyond mere methodological considerations. The potential ecological and evolutionary significance of dispersal traits will depend on the degree of coupling between patterns of seed dispersal and subsequent patterns of seed rain and demographic processes at the seedling stage (Harper 1977, Dirzo and Domínguez 1986, Howe 1989). An accurate assessment of the degree of coupling (or predictability of consequences) requires information on the recruitment of individual species during single reproductive episodes. Undertaking an integrative approach of this sort requires simultaneous monitoring of frugivore abundance and fruit use (diet composition and reliance on the fruits of the studied species), assessing patterns of variation among individual plants in fruit crop removal by frugivores, and estimating absolute and relative numbers of seeds removed from the parent plants by seed dispersers. Furthermore, it is also necessary to assess the spatial and temporal patterns of seed rain generated by frugivores. To this end, microhabitat types potentially differing in seed or seedling survival should be identified and sampled to obtain relative probabilities of seed rain, germination patterns, and seed and seedling survival rates. By completing the preceding protocol, successive stages from seed dispersal through early seedling establishment may be bridged in a stepwise manner, and a series of consecutive transition probabilities between stages may then ideally be obtained. To our knowledge, such an approach has not been undertaken previously for any vertebrate-dispersed plant. This study was designed specifically to fill this conspicuous gap in the abundant literature on seed dispersal by frugivorous animals.

Objectives of the study

This paper presents the results of a 3.5-yr field study on the seed dispersal ecology of *Phillyrea latifolia* L. (Oleaceae), a bird-dispersed tree, in southeastern Spain. The investigation reported here was aimed primarily at obtaining accurate quantitative descriptions of recruitment in this species at both the population and individual plant levels. By simultaneously examining patterns of seed dispersal, seed rain, and seedling emergence and survival for a single reproductive event, we

address the following three major questions: (1) Does seed dispersal by birds result in predictable seed and seedling shadows? (2) Are spatial patterns of seedling emergence and establishment predictably related to patterns of seed rain? and (3) If they are not, what factors contribute to the uncoupling of seed rain and population recruitment?

This study also has two supplementary objectives. We describe here for the first time the dispersal ecology of a mast-seeding (*sensu* Janzen 1978), fleshy-fruited plant. *P. latifolia* is unique among bird-dispersed plants studied so far in exhibiting conspicuous, long-interval mast-fruiting behavior. Populations over large areas produce huge fruit crops synchronously at intervals of up to 8 yr (see *Plant natural history* below). Masting is common among wind- or scatterhoard-dispersed forest trees, but it seems to be relatively infrequent among fleshy-fruited woody plants (Silvertown 1980). The consequences of masting in dry-fruited plants have often been examined (e.g., Janzen 1976, Wästljung 1989, Kelly et al. 1992, Sork et al. 1993), but we are not aware of any previous investigation on fleshy-fruited species.

The second supplementary objective was to assess whether seed dispersal and its demographic consequences vary between populations. Recent studies on plant-animal mutualisms have revealed considerable spatiotemporal inconstancy in the interaction of plants and their animal counterparts (C. M. Herrera 1988a, Horvitz and Schemske 1990). This aspect remains largely unexplored for the interaction between plants and vertebrate dispersal agents (but see Jordano 1993). Patterns of fruit removal and seed dispersal have been shown to vary among separate populations of the same species (Howe and Vande Kerckhove 1979, Bronstein and Hoffman 1987, Guitián et al. 1992), but little is known about the consequences of this variation for seed rain and seedling recruitment.

PLANT NATURAL HISTORY

The genus *Phillyrea* comprises four species of evergreen trees or tall shrubs that are confined largely to the sclerophyllous forests and maquis of the Mediterranean Basin (Sébastien 1956, Mabberley 1987). The group belongs to an ancient lineage that originated prior to the initiation of the Mediterranean-type climate (the oldest fossils of *P. latifolia* date from the Upper Miocene; Pons 1981).

P. latifolia is a small tree (up to 7 m in height, usually 3–5 m) characteristic of relatively well-preserved Mediterranean habitats at middle elevations. In the Sierra de Cazorla (southeastern Spain), where this study was conducted (see *Study area* below), *P. latifolia* is a major component of the dense evergreen forests and tall shrublands found at elevations between 700 and 1200 m (J. Herrera 1984). In our study region, the species is functionally androdioecious. Male trees have perfect

flowers with nonfunctional pistils and do not produce fruits (C. M. Herrera and P. Jordano, *personal observation*; see also Campbell 1922, Armenise 1956, Lepart and Dommée 1992). Hermaphroditic individuals have perfect flowers with functional pollen and produce fruits. Flowering takes place in March–April. The small (1.5–2.5 mm diameter), greenish, nectarless flowers are wind-pollinated. The flower-eating larvae of the weevil *Cionellus gibbifrons* (Coleoptera: Curculionidae) are abundant in the inflorescences of *P. latifolia* in some years, causing extensive fruiting failure in heavily infested trees. A species of psyllid homopteran (*Euphyllura* sp.) attacks *P. latifolia* shoots, flower buds, and seedlings.

Fruits are black, single-seeded drupes that ripen in September–October. Ripe fruits are 7.1 ± 0.6 mm (mean \pm 1 SD) long and 7.5 ± 0.8 mm wide, and their average fresh mass is 259 ± 78 mg ($N = 20$). On a dry mass basis, the pulp of ripe fruits is made up of 86.8% soluble carbohydrates, 5.6% fiber, 3.1% lipids, 2.3% protein, and 2.2% ash (C. M. Herrera 1987). Spontaneous abscission of ripe fruits is usually negligible; fruits may persist on the plants until the next spring without any external sign of deterioration. In our Sierra de Cazorla study area, *P. latifolia* fruits are eaten and seeds dispersed exclusively by small- to medium-sized frugivorous birds (C. M. Herrera 1984a, 1989). Fruit consumption and seed dispersal takes place mainly in the period October–March. We do not have any record of invertebrate predation on ripe *P. latifolia* fruits. *P. latifolia* seeds show double dormancy and germination may occur up to 3 yr after dispersal (Catalán 1978, and present study). Germination and seedling emergence in the field take place from January through May.

In the Sierra de Cazorla region, *P. latifolia* exhibits dramatic annual fluctuations in fruit production at the population level. Abundance of ripe fruits was estimated during October–November 1978–1990 (the time of greatest ripe fruit abundance) at one locality (“Hoyos de Muñoz,” see *Study area* below; this is the “Cazorla” study site of C. M. Herrera 1984a). Fruits of *P. latifolia* were superabundant in two years (1981 and 1989; 24 and 33 fruits/m², respectively), very scarce in four years (1978, 1983, 1985, 1987; <3.5 fruits/m²), and completely absent in the remaining seven years (Table 1). Annual variation in the abundance of ripe fruits in the habitat was closely related to fluctuations in the proportion of individuals fruiting (Table 1).

The 1981 and 1989 massive fruiting events recorded at Hoyos de Muñoz occurred with remarkable supra-annual synchrony over most of the 2500-ha Guadahornillos valley in which that site is located (C. M. Herrera, *personal observation*). On each of these years, most trees in the area fruited massively and huge fruit crops were produced over vast expanses of habitat due to the dominant role of *P. latifolia* in the vegetation. The present study investigated the 1989 fruiting event (see C. M. Herrera [1984a] for supplementary data for 1981).

TABLE 1. Supra-annual fruiting pattern of *Phillyrea latifolia* at Hoyos de Muñoz, Sierra de Cazorla (see *Study area*) over a 15-yr period.*

Year	% individuals fruiting	Ripe fruit abundance (fruits/m ²)
1978	...†	1.12
1979	...	0
1980	...	0
1981	44.8	24.03
1982	0	0
1983	36.1	3.46
1984	0	0
1985	16.1	0.11
1986	0	0
1987	1.6	0.02
1988	0	0
1989	54.1	32.75
1990	0	0
1991	3.3	...
1992	19.7	...

* Proportions of fruiting individuals in the population are based on data from 70 individually marked plants. Average abundance of ripe fruit per area was estimated in October–November, the time of peak ripe fruit availability (see C. M. Herrera 1984a, 1988b for methods).

† ... = no data available.

STUDY AREA

The study was carried out in the Guadahornillos valley, a well-preserved 2500-ha tract of Mediterranean-type montane forest and tall shrubland located in the Sierra de Cazorla (Jaén province, southeastern Spain). Dominant trees are *Quercus rotundifolia*, *Phillyrea latifolia*, and *Arbutus unedo* (see J. Herrera [1984] and Valle et al. [1989] for descriptions of vegetation). Climate is of a Mediterranean type. Mean annual precipitation is 1527 mm, most of which falls in autumn–winter (66%) and spring (24%). Monthly average temperatures of the coldest (January) and hottest (July) months are 3.3°C and 23.2°C, respectively. Frosts occur commonly throughout the winter, but snowfalls are infrequent under 1300 m elevation.

Two main sites, Agracea and Hoyos de Muñoz, were selected for the study. The Hoyos de Muñoz site (hereafter referred to as “Hoyos” in the text) is a dense sclerophyllous scrub up to 4.5 m in height, at 1150 m elevation. Vegetation is dominated by *Q. rotundifolia*, *P. latifolia*, *Viburnum tinus*, and *A. unedo* (Appendix 1; see C. M. Herrera [1984a], Yela and Herrera [1993] for further details on the vegetation of this site). The Agracea site is 2 km away, at 1200 m elevation. Vegetation is a tall (height 5–18 m), dense evergreen forest dominated by *Q. rotundifolia*, *P. latifolia*, and *A. unedo* (Appendix 1). Species of fleshy-fruited, vertebrate-dispersed plants are much more abundant at Hoyos than at Agracea. In the latter site, fleshy fruits are extremely scarce in years of *P. latifolia* fruiting failure.

In Hoyos, observations and experiments were conducted in two 2.5-ha plots (250 m apart) of similar vegetational composition (plots A and B hereafter). Ten microhabitat categories were distinguished based

on the identity of the overlying tree or shrub species or lack thereof (“open ground” category). A total of 150 sampling stations (roughly evenly distributed among microhabitats) were permanently marked at the start of the study in September 1989 (see *Methods: Seed rain* below).

Distinct microhabitat categories based on plant cover composition were not discernible in the Agracea forest. Four 120 m long linear transects were set up there at the initiation of the study (transects A–D hereafter). Transects A and B were located on a northwest-facing slope and transects C and D on a contiguous, northeast-facing one. On each slope, the two transects ran parallel at a distance of 25 m. In each transect, 24 sampling stations (spaced at 5-m intervals) were permanently marked. Each station was characterized by three variables describing overlying vegetation (height and number of woody species) and its position relative to the habitat mosaic recognizable at the site (gap, edge, or forest interior). Furthermore, each station was scored for the presence of each of the five locally dominant woody species (*Arbutus unedo*, *Erica arborea*, *Juniperus oxycedrus*, *P. latifolia*, *Quercus rotundifolia*).

In both sites, most of the observations and experiments were performed at the permanently marked stations (or a subsample thereof). For the purpose of some analyses examining within-site variation, transects (Agracea) and plots (Hoyos) will both be referred to as “subsites.”

Additional field work (see *Methods: Seed rain* below) was carried out at eight other locations in the Guadahornillos valley encompassing an elevational gradient ranging from 750 to 1350 m elevation (see J. Herrera [1984] for description of vegetation).

METHODS

An observational and experimental approach was adopted to estimate the probabilities of successful transitions between consecutive stages in the recruitment process, including fruit removal by frugivorous birds, seed rain, seed survival in the soil, germination, and seedling establishment. Fruit production and characteristics were studied to assess their influence on fruit removal by birds. Avifaunal composition and food habits were also studied quantitatively. To characterize the events during dispersal and early post-dispersal stages, we evaluated seed rain in different microhabitats and the associated probabilities of germination and post-dispersal seed survival. Seed predation and germination were assessed at the same sites where frugivore abundance, fruit removal, and seed rain were studied. Seedling establishment was studied by following seedling emergence and early seedling survival during the first 3 yr after the dispersal event.

Predispersal events and fruit removal

A total of 87 fruiting *P. latifolia* individuals were monitored. The plants at Agracea ($N = 55$) were marked

in early September 1989 along transects A–D. Those at Hoyos ($N = 32$) were a subset of a larger group of plants marked in 1981 and surveyed every year since then (Table 1) and were distributed among plots A and B. Size of fruit crops was estimated for each plant by counting nearly ripe fruits in September 1989, before the start of fruit consumption by birds.

Seasonal patterns of fruit availability and levels of fruit removal were studied in a subsample of 52 plants. Fruits on marked branches were counted monthly from October 1989 to May 1990. The number of unripe, ripe, ripe desiccated, and missing fruits were determined on each occasion. Estimates of standing crops of ripe fruits and fruit removal by birds throughout the fruiting season were obtained from these counts. We monitored the fate of 6968 fruits at Agracea ($N = 32$ plants) and 4181 fruits at Hoyos ($N = 20$ plants). Two or three (depending on plant size) 35×35 cm plastic trays were placed directly underneath the canopies of plants with marked branches to sample falling fruits. These data were used to correct fruit removal estimates based on number of missing fruits between consecutive branch counts. No evidence was found of rodents or other animals removing fallen fruits from trays.

Ripe fruits were collected from marked trees, measured (maximum width), and weighed to the nearest 0.1 mg. Fresh seed mass was determined after separation of the pulp and fresh pulp mass was obtained by subtraction.

Bird abundance and fruit use

To determine relative densities of avian frugivores and assess temporal changes in the composition of the local avifauna, bird censuses were carried out at monthly intervals (October 1989–April 1990) at the two main sites using a circular-plot method (Reynolds et al. 1980, Desante 1986). We selected four census points along each of the four Agracea transects and six points in each of the two Hoyos plots. All individual birds seen or heard during a 20-min period within a 15-m radius from the census point were recorded. Species detected beyond the 15-m radius during the census period were noted as well. Census points along each transect (Agracea) or within each plot (Hoyos) were at least 25 m apart. Censuses were conducted within 3 h of sunrise during two consecutive days with favorable weather and were always performed simultaneously at the two sites.

Ten standard, 12.2-m long mist nets were operated monthly at Hoyos from October 1989 to March 1990. Mist-netting was not conducted at Agracea because of time restrictions. Total netting effort was 1327 net-hours, roughly evenly distributed among months. Trapped birds were weighed and marked individually using numbered aluminum bands. Fecal samples were obtained from captured birds to study diet composition. The method is described in detail in C. M. Herrera (1984a) and Jordano (1988). The relative contributions

in volume made up by animal and vegetable matter were estimated for each fecal sample to the nearest 10%. Fleshy fruits consumed were identified to species on the basis of seed characteristics or by comparison of fruit skin patterns (cell shape and size, presence of glands, trichomes, etc.) with a reference collection of fruit skin microphotographs. The percentage in volume made up by fruit remains other than seeds (fruit skin and pulp tissue) was also estimated. For each plant species identified in the sample, the minimum number (or fraction thereof) of fruits represented was estimated from the number of seeds and the amount of fruit skin, whichever was largest. Potential limitations of the method have been discussed elsewhere (C. M. Herrera 1984a, Jenni et al. 1990).

Seed rain

The post-dispersal distribution of *P. latifolia* seeds was studied at the among- and within-habitat levels by means of seed-collecting traps. Traps were in operation from September 1989 through April (sites along the elevational gradient) or June 1990 (Agracea and Hoyos). Seed traps ($35 \times 35 \times 10$ cm colorless plastic trays) were nailed to the ground, and checked at monthly intervals. On each occasion, the traps were emptied and collected seeds were counted and identified to species. All traps were numbered individually and separate records were kept for individual traps. No evidence was found of rodents or other animals removing seeds from traps.

For the among-habitat investigation, trap lines were set at eight sites along the Guadahornillos elevation gradient. This gradient encompassed the Agracea and Hoyos main sites and extreme locations were ≈ 6 km apart. Forty traps were placed in each site, arranged into two 50 m long parallel lines. In each line, 10 pairs of traps were spaced 5 m apart.

For the within-habitat study, seed traps were spread among microhabitat types (Hoyos) or along transects (Agracea). A total of 300 traps was used at Hoyos, evenly distributed among the 10 microhabitat categories recognized there. One pair of traps was placed in each of the 150 sampling stations. A total of 288 traps was used in Agracea. One triplet of traps was placed at each of the 96 stations at that site (24 triplets per transect).

Duration and survival of seeds in the soil

Dispersed seeds of *P. latifolia* either remained dormant, rotted in the soil, were eaten by rodents, or germinated. Determining simultaneously the proportion of seeds exiting the seed bank through each of these pathways was impractical. For this reason, separate experiments were conducted to assess the duration of viable seeds in the soil in the absence of rodent predation, and the magnitude and spatial patterns of seed predation by rodents.

The persistence of seeds in the soil in the absence of rodent predation was investigated at Agracea and Hoyos. Rodent-proof, fiberglass 1.5-mm mesh bags containing litter and *P. latifolia* seeds were placed in the top soil layer and nailed to the ground. Seeds for these experiments were collected in December 1989 at Hoyos from the ground beneath perches of *Erithacus rubecula*, one of the main bird dispersers of *P. latifolia*. In February 1990, a total of 50 and 48 bags, each containing 25 seeds, were evenly distributed among Hoyos microhabitat categories and Agracea transects, respectively. All bags were placed at sampling stations where seed traps were also located. Bags were recovered in April 1992. The number of ungerminated, unrotten seeds was recorded (seven and six bags were lost at Hoyos and Agracea, respectively) and their viability assessed by planting them outdoors.

The effect of microhabitat on the probability of seed predation by rodents was examined experimentally at Agracea and Hoyos. The experimental unit was a pair of seeds glued (using a small amount of high-strength glue) to a 30 × 10 mm piece of plastic mesh (the smaller seed of the pair at the proximal end, and the larger one at the distal end) which was held at ground level by a wire nailed to the ground. These units were arranged into groups of 10 and spread over a surface of ≈ 1 m² ("blocks" hereafter). A total of 50 (totaling 1000 seeds) and 48 (totaling 960 seeds) blocks were evenly distributed among microhabitat categories and transects in Hoyos and Agracea, respectively. At both sites, blocks were placed at sampling stations. Experiments were set up in February 1990 and rodent seed predation was checked periodically until February 1991. Rodents fed on seed contents by chewing through the coat of glued seeds and left unequivocal signs of their activity (seed coat remains attached to or beside the plastic mesh).

Seed germination experiments

The effects of light regime and mother plant on seed germination were examined in a field experiment at the Agracea site. A total of 320 seeds from eight mother plants were sown at two locations 40 m apart in February 1990 according to a balanced factorial design (mother and light regime as main effects). One site ("shade" treatment) was in dense forest, while the other was in a large gap with a sparse canopy ("light" treatment). Seeds were sown in 20 × 15 cm perforated aluminum flat pans (eight mother plants per site, 40 seeds per mother, with two 20-seed replicates per mother) placed on the ground and filled with local soil. Experimental pans were located within large-mammal enclosures at the two sites and covered with mesh wire to prevent interference from rodents. Seeds started to germinate in early spring of 1991; biweekly record was kept of all subsequent germinations until late May 1991, when seedlings ceased to emerge.

The influence of mother plant and seed size on seed germination and seedling size and survival were in-

vestigated in a separate experiment conducted outdoors in the Torre del Vinagre Botanical Garden (700 m elevation, ≈ 10 km from Hoyos). Climate of Torre del Vinagre is warmer and drier than that of Agracea; thus, overall seed germination levels and timing of seedling emergence in the experiments performed at the two sites are not strictly comparable. A total of 1370 seeds from 27 plants (11 from Hoyos, 16 from Agracea) were sown in early January 1990. Mother plants providing the seeds for the experiments were chosen among those marked for monitoring fruit removal (see *Predispersal events and fruit removal*). Seeds were sown in 20 × 15 cm perforated aluminum flat pans filled with standard peat moss. All experimental seeds were previously weighed (fresh mass) and kept identified individually until sowing. In each pan, seeds were regularly arranged into a rectangular grid and their position mapped. In this way, emerging seedlings could later be assigned to individual seeds of known mass. We harvested all seedlings surviving at the end of the experiment (mid-May 1991) and weighed the aerial parts after drying to constant mass.

Seedling emergence and survival

The effect of microhabitat on seedling emergence and survival were studied on naturally emerged seedlings at the two main study sites. All *P. latifolia* seedlings emerging in 1.5-m² areas at sampling stations were tagged individually (using numbered tape flags) in the spring of 1991 (Hoyos and Agracea) and 1992 (Agracea only). A random subsample was marked when the number of emerging seedlings was very large and the total number of seedlings was counted. In Hoyos, relatively few seedlings emerged at the sampling stations located in plot A in 1991. To increase sample sizes, we set up 15 supplementary areas in plot B (each ≈ 5 m² in size) in five different microhabitats and all emerging seedlings were marked there in 1991 and 1992. A total of 6170 seedlings were marked and subsequently monitored during the study (4316 and 1854 at Agracea and Hoyos, respectively). These include additional seedlings ($N = 721$) marked at Agracea outside the regular transects in 1991, which were used only in the analyses of temporal patterns of survival.

Seedlings marked on different dates were identified as different "cohorts" for the analyses. In 1991, four and three cohorts were marked at Agracea and Hoyos, respectively. In 1992, two cohorts were marked at each site. It must be noted that seedlings emerging in the spring of 1992 came also from seeds dispersed during the 1989–1990 season (see *Results: Seed germination and seedling emergence in the field*).

Seedling survival was studied by periodic surveys of marked seedlings conducted over intervals of 552 and 535 d after marking at Agracea and Hoyos, respectively. Seedling survival was recorded at each census, as well as signs of herbivory or other type of damage to cotyledons or leaves, and cause of death. Six causes

of seedling loss were considered: herbivory, desiccation, fungal attack, damage by psyllids, trampling by ungulates, and "unknown" (seedling missing, no remains left).

Data analysis

Procedures in the SAS statistical package (SAS 1988, 1989) were used for most analyses. Analyses of variance were done with procedure GLM, using Type III sums of squares due to the unbalanced nature of most data sets (Shaw and Mitchell-Olds 1993). Partitions of variance in fully random nested designs were performed with procedure NESTED and the significance of effects tested with procedure GLM. Linear models based on logistic regression (procedure CATMOD using maximum likelihood estimation) were applied in situations in which the dependent variable was categorical. Failure time analysis (Muenchow 1986, Pyke and Thompson 1986) was used in the analyses of seed germination experiments and seed and seedling survival data. Computations were performed using either SAS procedures LIFEREG and LIFETEST or program PTL in the BMDP statistical package (Benedetti et al. 1985).

Path analysis (Li 1975, Pedhazur 1982; see Schemske and Horvitz 1988 for a detailed description of path analysis in an ecological context) was used to examine the magnitude of direct and indirect effects of plant and fruit traits on the number of seeds dispersed by individual plants. SAS procedure CALIS was used for the computations (SAS 1989).

Data were tested for normality before parametric testing; either appropriate normalizing transformations or nonparametric alternatives were used in cases of non-normality. Throughout this paper, means are shown ± 1 SD unless otherwise indicated.

RESULTS

Plant size and fecundity

Agracea plants were significantly taller (average height = 3.6 ± 1.5 m, $N = 55$) than those at Hoyos (2.3 ± 1.9 m, $N = 32$) ($t = 5.17$, $P < 0.0001$). Other variables correlated with plant height, such as crown depth and area of canopy's vertical projection, were also significantly greater at Agracea (results not shown).

The number of ripe fruits produced per plant ("crop size" hereafter) was significantly greater in Agracea (median = 798 fruits) than in Hoyos (median = 530 fruits) (chi-square = 9.08, $P = 0.003$; median test). Crop size (log-transformed) was positively related to plant height ($R^2 = 0.287$, $F_{1,85} = 33.88$, $P < 0.0001$; the two sites pooled). The slope of the crop size-plant height regression did not differ between sites. After correcting for differences between sites in plant size, least-squares-adjusted means for crop sizes did not differ significantly between sites ($t = 0.424$, $P = 0.67$).

Between-sites variation in crop size was thus largely a consequence of differences in mean plant size.

Fruiting phenology

At the population level, availability of ripe *P. latifolia* fruits extended over nearly 8.5 mo, from mid-September 1989 to early June 1990. When branches first were marked for study in late September, >80% of fruits were ripe, and only 19 out of 52 plants still bore some unripe fruits. Only a negligible number of ripe fruits had been removed from marked branches when they were marked (as assessed by the occurrence of empty pedicels).

The mean proportion of fruit crops remaining on individual plants ranged between 70 and 90% during October-December and decreased markedly afterwards (Fig. 1). This seasonal pattern was similar at the two sites, but mean monthly values (across plants) of percent ripe fruit remaining were significantly greater at Agracea ($t = 2.97$, $df = 7$, $P = 0.021$; paired test). By early May, marked branches bore very few ripe fruits at Hoyos, while some plants still retained >10% of their initial crops at Agracea.

The duration of individual fruit crops was estimated as the interval from initial marking until disappearance of the last fruit. In those few plants at Agracea with ripe fruits remaining at the end of observations, the assigned duration was the whole observation period. Individual plant crops lasted significantly fewer days in Hoyos (126 ± 20 d, $N = 20$ plants) than in Agracea (174 ± 32 d, $N = 32$ plants) ($t = 3.42$, $P = 0.001$). Larger or more fecund plants tended to have longer fruit removal periods than smaller or less fecund conspecifics. For all plants combined ($N = 52$), fruit crop duration was positively correlated with plant height ($r_s = 0.392$, $P = 0.005$) and crop size ($r_s = 0.296$, $P = 0.034$).

Fruit characteristics

Characteristics of ripe *P. latifolia* fruits at the two study sites are summarized in Table 2. We examined variation between and within sites, and among individuals, in fruit diameter (DIAM), fresh fruit (FRUM) and seed (SEEM) mass, and pulp ratio (PR; fresh mass of pulp divided by fresh mass of whole fruit), using a fully random nested ANOVA. Plants were nested within subsites (plots in Hoyos, transects in Agracea) and subsites nested within sites. Although there was a trend for fruits to be larger and heavier in Hoyos than in Agracea (Table 2), differences between sites, or among subsites within sites, were not significant for any of the fruit traits examined ($P > 0.05$ in all cases).

There was significant variation among plants (within subsites) in fruit characteristics ($F_{45, 1176} \geq 20.7$, $P < 0.0001$, for all traits). Ranges and coefficients of variation of individual means (the two sites combined) for DIAM (5.1-8.4 mm, 10.9%), FRUM (86.4-351.6 mg, 28.4%), SEEM (43.9-105.2 mg, 20.5%), and PR (41.9-

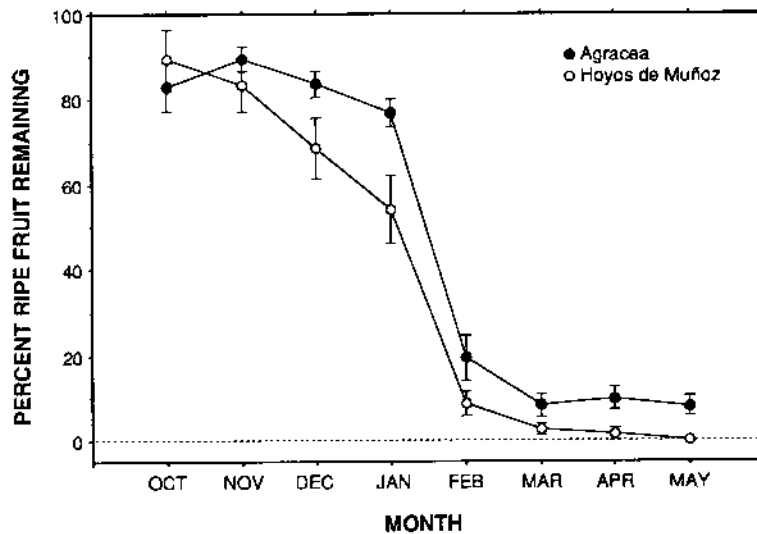


FIG. 1. Monthly variation in the percentage of *P. latifolia* fruit crops remaining on plants at the two main study sites, October 1989–May 1990 (means \pm 1 SE).

78.4%, 13.6%) indicate broad individual variation in fruit traits. DIAM, FRUM, and SEEM plant means were closely correlated among themselves ($r \geq 0.568$, $N = 51$ plants, $P < 0.0001$), denoting the existence of an underlying “fruit size” factor. The pulp ratio (PR) was positively correlated with DIAM and FRUM ($r \geq 0.718$, $P \ll 0.0001$) and unrelated to SEEM ($r = -0.130$, $P = 0.36$).

The bird assemblage

Two indices of bird abundance will be used in this section to describe the composition of bird assemblages at the Agracea and Hoyos sites: (1) the proportion of censuses in which a given species was recorded, regardless of distance to the census point (“Occurrence in censuses”); and (2) the mean number of distinct individuals recorded within a 15-m radius of the observation point (“Number of individuals per census”). Occurrence in censuses provides a more comprehensive view of the species composition of local bird assemblages, because large-bodied species were rare and only infrequently recorded within the 15-m radius used

in point censuses. The number of individuals per census, on the other hand, is a better index of relative abundance for the commoner species.

Bird species were classified into three frugivory classes based on data and criteria presented by C. M. Herrera (1984a, c) and information on their diets obtained during the present study (see *Diet of avian frugivores*). The “non-frugivores” class comprises species that have never been recorded feeding on fleshy fruits in the study region. “Fruit predators” include species that feed on the pulp, the seeds, or both, of fleshy fruits but without usually performing seed dispersal. “Seed dispersers” are species that feed on whole fleshy fruits and disperse seeds.

Composition and residence status.—A total of 29 bird species were recorded in censuses over the study period in the two sites combined (Table 3: Occurrence in censuses). Most species were frugivores, either fruit predators (37% of total) or seed dispersers (37%), while non-frugivores represented a relatively minor component of total species richness (26%). Fruit predators belonged almost exclusively to the genus *Parus* and several genera in the Fringillidae, while most species of seed dispersers belonged to the genera *Turdus* and *Sylvia*. The composition of local bird assemblages was fairly similar at the two study sites. Most species recorded in censuses (71%) were present at both sites and the proportions of non-frugivorous, fruit predatory, and seed disperser species did not differ between sites ($P = 0.82$, Fisher exact probability test).

About two-thirds of species (62%) were year-round residents in the region (Table 3). All the remaining species were winter visitors with the single exception of *Phylloscopus bonelli*, a summer immigrant recorded in early spring at Agracea (some of the winter immi-

TABLE 2. Summary of characteristics of ripe *P. latifolia* fruits (mean \pm 1 SD) at the two main study sites. N = number of fruits.

	Agracea ($N = 777$)	Hoyos de Muñoz ($N = 450$)
Fruit diameter (mm)	6.7 \pm 0.9	7.3 \pm 0.8
Fresh fruit mass (mg)	191.8 \pm 64.6	236.8 \pm 73.5
Fresh seed mass (mg)	66.3 \pm 17.5	70.4 \pm 24.1
Pulp ratio (%)*	63.3 \pm 10.4	69.5 \pm 8.5

* Fresh mass of pulp divided by fresh mass of whole fruit, $\times 100$.

TABLE 3. Composition of the bird communities at the Agracea and Hoyos de Muñoz sites during October 1989–April 1990, the main seed dispersal period for *P. latifolia*. * $N = 112$ and 84 censuses at Agracea and Hoyos de Muñoz, respectively.

Species and frugivory type*	Occurrence in censuses (%)		Mean number of individuals per census	
	Agracea	Hoyos de Muñoz	Agracea	Hoyos de Muñoz
Non-frugivores				
<i>Certhia brachydactyla</i> (R)	50.00	19.05	0.17	0.02
<i>Dendrocopos major</i> (R)	25.00	32.14	...†	...
<i>Picus viridis</i> (R)	6.25	7.14
<i>Phylloscopus collybita</i> (W)	13.39	1.19	0.07	...
<i>Phylloscopus bonelli</i> (S)	0.89
<i>Regulus ignicapillus</i> (R)	60.71	32.14	0.83	0.37
<i>Troglodytes troglodytes</i> (R)	...	1.19	...	0.01
Cumulative abundance			1.07	0.40
Fruit predators				
<i>Aegithalos caudatus</i> (R)	26.79	29.76	0.56	0.45
<i>Chloris chloris</i> (W)	...	1.19
<i>Coccothraustes coccothraustes</i> (W)	0.89	1.19
<i>Carduelis spinus</i> (W)	...	1.19
<i>Fringilla coelebs</i> (R)	44.64	34.52	0.06	0.12
<i>Parus ater</i> (R)	33.93	21.43	0.30	0.14
<i>Parus caeruleus</i> (R)	83.04	52.38	0.79	0.25
<i>Parus cristatus</i> (R)	23.21	25.00	0.11	0.08
<i>Parus major</i> (R)	42.86	41.67	0.31	0.23
<i>Sitta europaea</i> (R)	75.00	48.81	0.34	0.12
<i>Serinus serinus</i> (W)	...	3.57
Cumulative abundance			2.47	1.39
Seed dispersers				
<i>Corvus corone</i> (R)	2.68
<i>Columba palumbus</i> (R)	12.50	7.14	...	0.01
<i>Erithacus rubecula</i> (W)	87.50	94.05	1.00	1.40
<i>Garrulus glandarius</i> (R)	24.11	10.71	0.04	0.02
<i>Sylvia atricapilla</i> (W)	56.25	82.14	0.21	1.24
<i>Sylvia melanocephala</i> (R)	...	34.52	...	0.15
<i>Turdus iliacus</i> (W)	14.29	1.19	0.08	...
<i>Turdus merula</i> (R)	80.36	59.52	0.13	0.12
<i>Turdus philomelos</i> (W)	32.14	11.90	0.20	0.02
<i>Turdus torquatus</i> (W)	2.68
<i>Turdus viscivorus</i> (R)	29.46	11.90	0.09	...
Cumulative abundance			1.75	2.96

* Species are grouped into three different frugivory classes (see Results: The bird assemblage). Codes for local residence status are shown in parentheses: W, winter immigrant; R, year-round resident; S, summer immigrant. The prevailing residence status is shown for those species with mixed migratory regime in the study region.

† ... = not recorded.

grants, like *Sylvia atricapilla* and *Erithacus rubecula*, maintain small local breeding populations in the area. Forty-one percent of frugivorous species (fruit predators and seed dispersers combined) were winter visitors.

Abundance.—Monthly means of the number of individuals recorded per census within the 15-m detection radius are used in this section as an index of species abundance (Table 3: Individuals per census). Only 20 species (both sites combined) provided data amenable to this analysis.

There were important differences between sites in the relative numerical importance of the three frugivory classes ($P \ll 0.0001$, Fisher test). Seed dispersers were numerically much more important at Hoyos (62.3% of total individuals) than at Agracea (32.9%), while the reverse was true for species of fruit predators (29.2 and 46.8% of total individuals in Hoyos and Agracea, respectively). Non-frugivores represented

20.3% of individuals at Agracea and only 8.5% at Hoyos. In Hoyos, the two most abundant species were the dispersers *E. rubecula* and *S. atricapilla* (1.40 and 1.24 individuals per census on average, respectively; Table 3), which accounted together for 55% of all individuals recorded in the censuses. In Agracea the two dominant species were *E. rubecula* (1.00 individuals per census) and the fruit predator *Parus caeruleus* (0.79 individuals per census), which together accounted for only 34% of individuals (Table 3).

Within each site, the relative numerical importance of non-frugivores, fruit predators, and seed dispersers did not experience major changes during the autumn–winter period (Fig. 2). Seed dispersers represented between 81 and 85% of all individuals censused in Hoyos in the period November–January. Their relative importance declined slightly in February–April, paralleling an increase in the relative abundance of fruit predators. Fruit predators were numerically dominant in

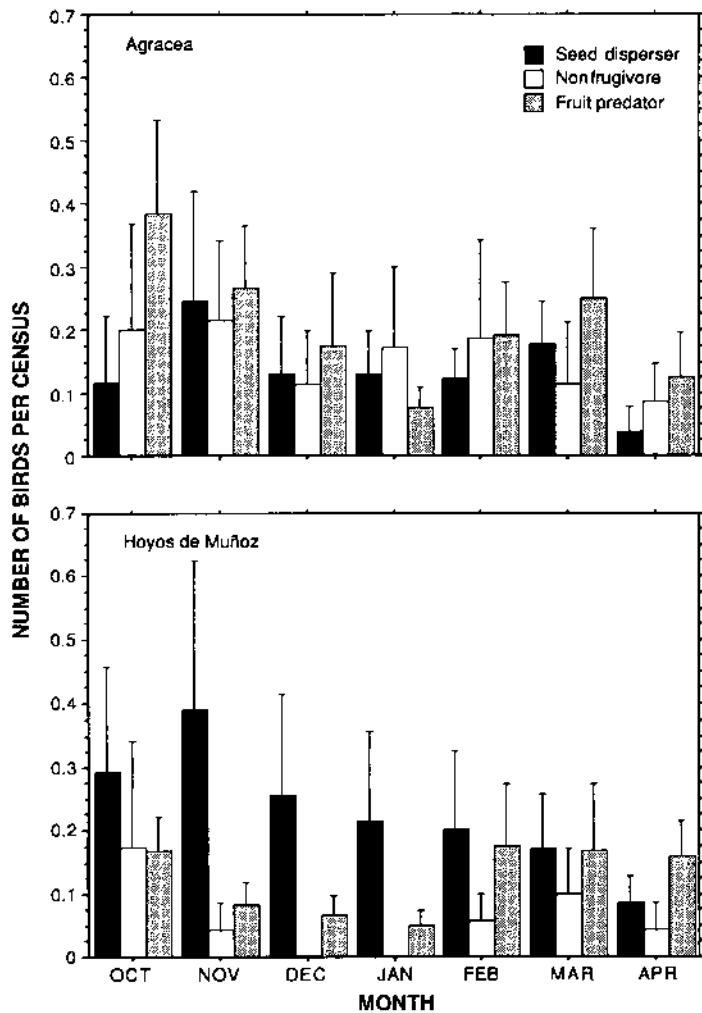


FIG. 2. Monthly variation in the abundance of seed disperser, fruit predatory, and non-frugivorous birds (all species combined) at the two study sites, October 1989–April 1990 (means and 1 SE). See *Results: The bird assemblage* for description of frugivory categories.

Agracea in all months except January, when they ranked third to seed dispersers and non-frugivores.

Diet of avian frugivores

At least 13 bird species fed on fleshy fruits at the Hoyos site in the period October 1989–March 1990 (Tables 4 and 5). Seven species were fruit predators that fed on pulp (*Aegithalos caudatus*, *Parus ater*, *P. caeruleus*, *P. cristatus*, *P. major*) or seeds (*Coccothraustes coccothraustes*, *Fringilla coelebs*) of fleshy fruits without performing seed dispersal. Six species (*Eriothacus rubecula*, *Sylvia atricapilla*, *S. melanocephala*, *Turdus iliacus*, *T. merula*, and *T. philomelos*) were legitimate seed dispersers that ingested whole fruits and defecated or regurgitated intact seeds.

Fruit predators.—Fruit remains appeared very often in the feces of fruit predators (range = 67–100%), but they generally accounted for a low proportion of fecal sample volume (Table 4). Fruits from a total of nine plant species were identified in the 91 feces examined. *P. latifolia* was the species eaten by the greatest number

of fruit predators (six out of seven species), its frequency of occurrence in feces ranging from 14% (*P. cristatus*) to 78% (*P. major*).

Seed dispersers.—Fleshy fruits were the dominant fraction in the diet of all species of legitimate seed dispersers. The frequency of occurrence of fruit remains in feces was 100% for all bird species; fruits represented, on average, between 75 and 99% of feces' volume (Table 5). A total of 13 fruit species were identified in the 276 feces from seed dispersers examined. *P. latifolia* was the only fruit species eaten by all six seed disperser species (Table 5).

Fruits of *P. latifolia* were the major component in the diet of all species except *S. melanocephala* (Table 5). The frequency of occurrence of *P. latifolia* fruits in feces ranged from 63% (*T. merula*) to 100% (*T. iliacus* and *T. philomelos*); they accounted for between 18% (*S. melanocephala*) and 99% (*T. iliacus*) of the total estimated number of fruits ingested. Despite the prominent role of *P. latifolia* fruits in the diet of seed dispersers, these birds regularly consumed other co-oc-

TABLE 4. Composition of the fruit diet of the major avian fruit predators at the Hoyos de Muñoz site, October 1989–March 1990. Figures are frequencies of occurrence (%) of fruit species in feces. The mean number of fruit species per sample was computed using only data from feces that contained some fruit. *N* = number of feces examined.

Plant species	"Seed predators"		"Pulp predators"				
	<i>Coccothraustes coccothraustes</i> (<i>N</i> = 2)	<i>Fringilla coelebs</i> (<i>N</i> = 9)	<i>Aegithalos caudatus</i> (<i>N</i> = 12)	<i>Parus ater</i> (<i>N</i> = 5)	<i>Parus caeruleus</i> (<i>N</i> = 40)	<i>Parus cristatus</i> (<i>N</i> = 14)	<i>Parus major</i> (<i>N</i> = 9)
<i>Arbutus unedo</i>	...†	...	33.3	20.0	20.0	28.6	33.3
<i>Hedera helix</i>	2.5
<i>Lonicera implexa</i>	...	11.1	...	20.0	...	7.1	...
<i>Phillyrea angustifolia</i>	2.5
<i>Phillyrea latifolia</i>	50.0	44.4	66.7	...	35.0	14.3	77.8
<i>Pistacia lentiscus</i>	100.0	66.6	70.0	35.7	55.6
<i>Pistacia terebinthus</i>	60.0	17.5	...	11.1
<i>Rubus ulmifolius</i>	...	11.1	2.5
<i>Smilax aspera</i>	2.5
% samples with fruit	100	66.7	75.0	80.0	90.0	71.4	100
% fruit volume per sample*	97.0 ± 3.5	15.8 ± 24.2	31.3 ± 32.4	5.1 ± 4.9	40.9 ± 32.0	10.5 ± 22.3	58.7 ± 33.4
Fruit species per sample*	1.5 ± 0.7	1.5 ± 0.6	1.4 ± 0.5	1.5 ± 1.0	1.8 ± 0.7	1.3 ± 0.5	1.8 ± 0.8

* Mean ± 1 SD.

† ... = not recorded.

TABLE 5. Composition of the fruit diet of the major avian seed dispersers at the Hoyos de Muñoz site, October 1989–March 1990. Figures are percentages with respect to the total number of fruits ingested, as estimated from the number present in the feces examined, and the frequencies of occurrence of fruit species in feces. *N* = number of feces examined.

Plant species	<i>Erithacus rubecula</i> (<i>N</i> = 125)		<i>Sylvia atricapilla</i> (<i>N</i> = 125)		<i>Sylvia melanocephala</i> (<i>N</i> = 7)		<i>Turdus iliacus</i> (<i>N</i> = 3)		<i>Turdus merula</i> (<i>N</i> = 8)		<i>Turdus philomelos</i> (<i>N</i> = 8)	
	% fruits ingested	% occurrence in feces	% fruits ingested	% occurrence in feces	% fruits ingested	% occurrence in feces	% fruits ingested	% occurrence in feces	% fruits ingested	% occurrence in feces	% fruits ingested	% occurrence in feces
<i>Arbutus unedo</i>	0.1	7.2	0.2	20.0	1.0	33.3	5.4	75.0
<i>Daphne gnidium</i>	1.5	3.2	5.2	14.3
<i>Hedera helix</i>	0.2	0.8
<i>Juniperus oxycedrus</i>	0.1	0.8
<i>Lonicera implexa</i>	0.1	0.8	1.5	8.0	7.8	14.3
<i>Phillyrea angustifolia</i>	0.5	1.6	5.2	14.3
<i>Phillyrea latifolia</i>	50.4	88.8	48.5	95.2	17.9	85.7	99.0	100	83.5	62.5	78.1	100
<i>Pistacia lentiscus</i>	37.9	56.8	37.0	55.2	57.6	100	18.6	37.5
<i>Pistacia terebinthus</i>	0.1	1.6	1.6	6.4	0.5	14.3
<i>Rubia peregrina</i>	1.6	5.6	1.8	8.0
<i>Rubus ulmifolius</i>	0.7	6.4	0.3	6.4	0.6	28.6
<i>Smilax aspera</i>	0.6	4.0	5.1	29.6	4.1	12.5
<i>Viburnum tinus</i>	8.3	16.0	1.9	5.6	5.2	14.3	6.9	12.5	3.3	12.5
% occurrence of fruit†	...	100	...	100	...	100	...	100	...	100	...	100
% fruit volume per sample‡	74.7 ± 28.4	...	96.2 ± 9.5	...	91.7 ± 10.8	...	98.0 ± 2.6	...	99.4 ± 1.8	...	98.9 ± 1.6	...
Fruit species per sample‡	1.9 ± 0.8	...	2.4 ± 1.0	...	2.9 ± 1.1	...	1.3 ± 0.6	...	1.6 ± 0.7	...	1.5 ± 0.8	...

* ... = not recorded.

† Percentage of feces containing fruit remains.

‡ Mean ± 1 SD.

TABLE 6. Monthly variation in body mass (mean \pm 1 SD) and relative importance of *P. latifolia* fruits in the diet for the two major avian seed dispersers at the Hoyos de Muñoz site, October 1989–March 1990. *N* = number of feces examined.

	Oct	Nov	Dec	Jan	Feb	Mar
<i>Erithacus rubecula</i>						
<i>N</i>	32	31	6	6	23	27
% occurrence*	78.1	80.7	100	83.3	100	100
% fruits†	23.7	23.1	29.9	22.0	74.6	87.2
% fruit volume per sample‡	46.9 \pm 32.8	68.9 \pm 25.2	88.8 \pm 10.8	94.0 \pm 5.7	93.9 \pm 4.1	90.7 \pm 8.8
Body mass (g)	15.4 \pm 1.2 (33 birds)	15.4 \pm 1.4 (35 birds)	16.2 \pm 0.8 (6 birds)	15.8 \pm 0.8 (7 birds)	17.3 \pm 1.2 (25 birds)	16.6 \pm 0.8 (27 birds)
<i>Sylvia atricapilla</i>						
<i>N</i>	26	29	22	21	17	10
% occurrence*	76.9	100	100	100	100	100
% fruits†	14.4	28.1	46.9	60.2	87.5	96.0
% fruit volume per sample‡	89.9 \pm 19.2	97.5 \pm 2.7	97.6 \pm 3.0	98.9 \pm 1.4	98.3 \pm 1.6	96.4 \pm 5.0
Body mass (g)	17.0 \pm 1.2 (26 birds)	17.1 \pm 0.8 (29 birds)	17.3 \pm 1.1 (22 birds)	17.2 \pm 1.1 (22 birds)	17.0 \pm 1.2 (17 birds)	17.2 \pm 0.7 (10 birds)

* Percentage of feces with *P. latifolia*.† Percentage of total fruits ingested contributed by *P. latifolia*.‡ Percent volume of fruit tissue per sample (mean \pm 1 SD).

curing fruits. The mean number of fruit species present in each fecal sample ranged between 1.3 (*T. iliacus*) and 2.9 (*S. melanocephala*) (Table 5).

Monthly variation in the importance of *P. latifolia* fruits in the diet was investigated for *E. rubecula* and *S. atricapilla*, the two major seed dispersers (Table 6). These species fed on *P. latifolia* fruits during the entire 6-mo study period. By the end of the winter, both *S. atricapilla* and *E. rubecula* relied almost exclusively on fruits and, within these, on those of *P. latifolia*. The latter occurred in 100% of *S. atricapilla* feces in all months except October. The proportion of total estimated number of fruits in the diet of this species contributed by *P. latifolia* increased steadily from October (14%) to a peak in March (96%). For *E. rubecula*, *P. latifolia* fruits occurred in 100% of feces in December, February, and March and in >75% of feces in the remaining months. The proportion of fruits contributed by *P. latifolia* remained between 22 and 30% in the period October–January and increased sharply in February and March (75–87%).

There was no evidence of detrimental consequences on body condition of the late-season monophagy on *P. latifolia* fruits exhibited by the two major dispersers. Mean monthly body mass of *S. atricapilla* remained remarkably constant during October–March (Table 6; $F_{5,120} = 0.36$, $P = 0.88$, for differences among months). *E. rubecula* exhibited a slight increase in mean body mass toward the end of the autumn–winter period (Table 6; $F_{5,127} = 11.05$, $P \ll 0.001$). Body mass data from individual birds that were mist-netted on >2 occasions during this study (13 *E. rubecula* individuals mist-netted on 28 occasions and 14 *S. atricapilla* individuals on 31 occasions) were also examined to look for relationships between body mass and consumption of *P. latifolia* fruits. Correlations between individual means for body mass and contribution of *P. latifolia* fruits to the diet were positive, although statistically

nonsignificant, for both *E. rubecula* ($r = 0.295$, $N = 13$, $P = 0.33$) and *S. atricapilla* ($r = 0.245$, $N = 14$, $P = 0.40$).

Fruit removal

Variation between and within populations.—Birds removed 77.5 \pm 21.4% ($N = 20$ plants) and 32.8 \pm 27.9% ($N = 32$ plants) of *P. latifolia* fruit crops in Hoyos and Agracea, respectively. The difference between sites ($F_{1,51} = 37.09$, $P < 0.0001$; arcsine transformed data) is in accordance with the greater abundance of seed dispersers in Hoyos (Table 3). Mean number of seeds removed per plant was also significantly greater ($F_{1,30} = 4.08$, $P = 0.048$; log-transformed data) in Hoyos (682 \pm 742 seeds per plant, $N = 20$) than in Agracea (387 \pm 557 seeds per plant, $N = 32$), despite the greater fecundity of plants at the latter site (Table 7).

Within sites, absolute and relative fruit removal levels were fairly homogeneous spatially (Table 7). The relative contribution of between- and within-site variation to total variance in fruit removal was examined using nested ANOVAs (subsites nested within sites). The site effect accounted for 58.8% of total variance in percent fruit removal, while subsites within sites accounted for only 2.4%. Plants located in different Agracea transects did not differ significantly in percent removal ($F_{3,28} = 0.99$, $P = 0.41$); those on different Hoyos plots exhibited only marginally significant differences ($F_{1,18} = 4.24$, $P = 0.06$). For the number of seeds dispersed (log-transformed), the site effect accounted for 7.6% of the total variance and subsites within sites for a further 9.9%.

Correlates of individual variation.—The potential influence of differences in fruit (mean diameter, mean seed mass) and plant (height, crop size) traits on individual variation in percent fruit removal was examined using multiple linear regression. Only fruit diameter (standard regression coefficient = 4.45, $t = 3.95$,

TABLE 7. Summary statistics for absolute fecundity of *P. latifolia* plants and absolute and relative seed removal figures for the two study sites and their subsites.*

Site and subsite	N†	Crop size		Number of seeds dispersed		Percentage of seeds dispersed	
		Mean ± 1 SE	Range	Mean ± 1 SE	Range	Mean ± 1 SE	Range
Agracea							
A	6	1356 ± 556	723–2066	360 ± 220	147–755	28.2 ± 16.7	14.3–58.3
B	9	851 ± 419	434–1507	181 ± 125	78–399	28.3 ± 27.4	6.7–87.7
C	10	1848 ± 1915	65–6215	708 ± 897	25–3085	45.0 ± 30.9	11.5–93.4
D	7	1073 ± 938	77–2902	217 ± 252	2–754	25.2 ± 31.5	2.6–91.7
Hoyos de Muñoz							
A	9	594 ± 854	100–2670	535 ± 780	86–2413	87.4 ± 12.0	61.5–95.6
B	11	1226 ± 840	100–2750	803 ± 724	77–2641	69.3 ± 24.3	24.2–96.0

* Crop size is the number of full-sized, ripe fruits produced per plant; number and percentage of seeds dispersed are the estimated number of seeds and percentage of the fruit crop that were removed from branches by avian frugivores.

† Number of plants.

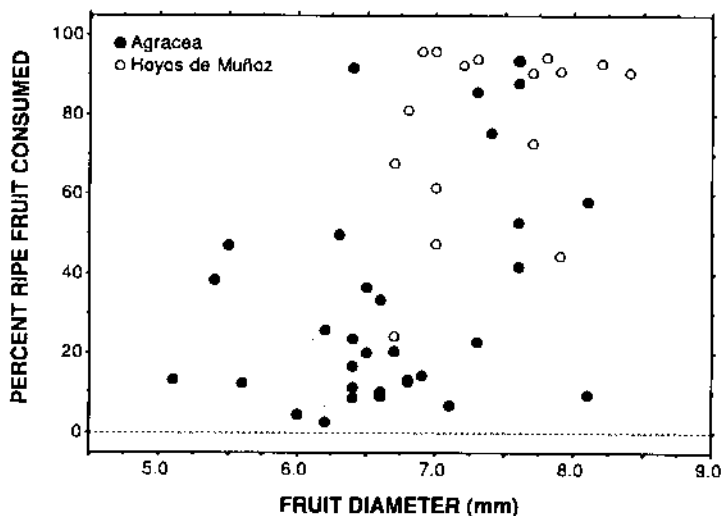
$P = 0.003$) had a significant effect on percent fruit removal. Percent fruit removal increased with increasing mean fruit diameter (Fig. 3). Individual variation in this variable explained 27.7% of among-plant variance in percent fruit removal (R^2 of regression). The slope of the percent removal–fruit diameter regression did not differ between sites ($F_{1,44} = 0.16$, $P = 0.69$; analysis of covariance).

A causal model for individual variation in dispersal success.—The direct and indirect effects of plant height, crop size, fruit characteristics, and percent fruit removal on the absolute number of dispersed seeds were examined using a path analytical model (Fig. 4A). An unmeasured, latent factor reflecting plant-related variables (e.g., vigor, microsite-related factors) also was included in the model. The model chosen was thought to account satisfactorily for the interrelationships and indirect effects of variables. The model was fitted separately for the two study sites in order to assess the consistency of the causal pattern across populations (correlation matrices used are shown in Appendix 2).

A large proportion of variation in the number of seeds dispersed per plant was explained by the path model, both at Agracea ($R^2 = 0.935$) and Hoyos ($R^2 = 0.994$). The model fitted the two datasets similarly well (goodness of fit index, GFI = 0.909 and 0.816 for Agracea and Hoyos, respectively; SAS 1989).

Indirect effects of mean seed mass (SEEM) and mean fruit diameter (DIAM) on the absolute number of seeds dispersed (DISP) by individual plants were higher in Agracea (0.152 and 0.270, respectively) than in Hoyos (0.072 and 0.121) (Fig. 4B). Sites differed also in the relative magnitude of the effects of percent removal (CONS) and crop size (CROP) on the number of seeds dispersed (DISP). The total effects (the sum of direct and indirect effects; Pedhazur 1982) of CROP and CONS on DISP were 0.623 and 0.664, respectively, at Agracea; and 0.957 and 0.320, respectively, at Hoyos. The total number of seeds dispersed by individual *P. latifolia* plants thus depended largely on plant fecundity in Hoyos (where fruit removal by birds was consistently high), while it depended equally on fecundity

FIG. 3. Percentage of ripe fruits removed from individual *P. latifolia* plants at the two main study sites plotted against mean fruit diameter. Each symbol corresponds to a different tree.



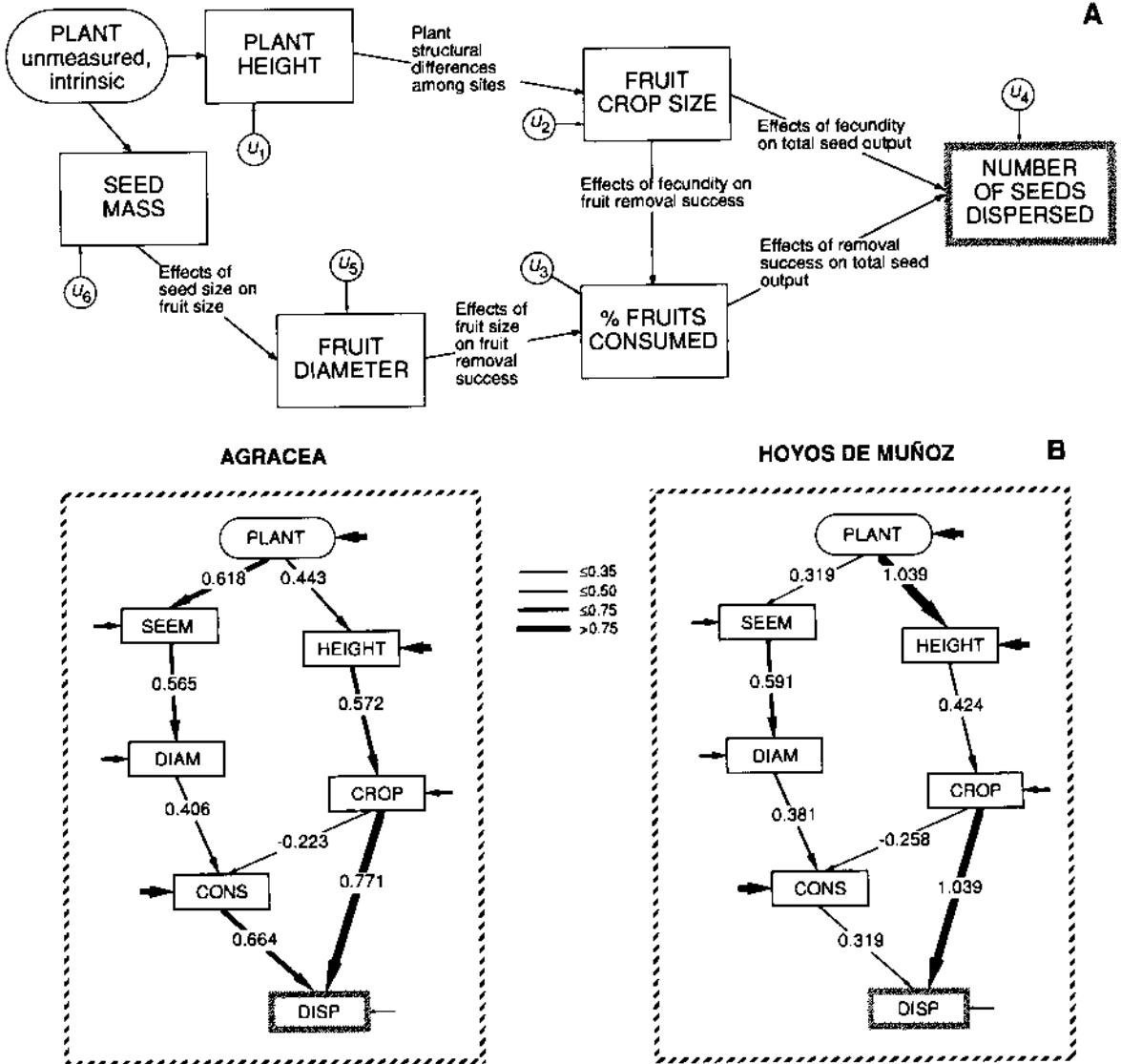


FIG. 4. (A) Path model for the effects of *P. latifolia* plant and fruit characteristics on relative fruit removal success (% fruits consumed) and the absolute number of seeds dispersed per plant. The model depicts the causal pattern as a series of directed arrows, labeled with a description of the hypothesized effect. Residual variables (U_i) indicate unmeasured factors affecting a given variable. Rectangles include manifest endogenous variables, and ovals include latent exogenous variables. (B) Path diagrams for the Agracea and Hoyos sites. Figures on arrows are the path coefficients (line widths coded according to the symbol key). Path coefficients are not shown for unmeasured effects. Models were fitted with CALIS procedure (SAS 1988) on the correlation matrices shown in Appendix 2, specifying the error variances of the manifest variables. HEIGHT, plant height; SEEM, fresh seed mass; DIAM, fruit diameter; CROP, crop size; CONS, proportion of fruits consumed by frugivores; DISP, number of seeds dispersed.

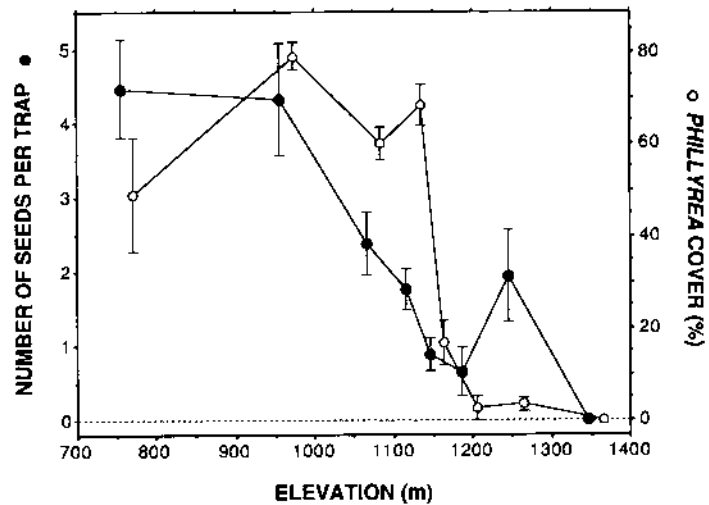
and percent removal in Agracea (where fruit removal by birds was considerably lower) (Table 7). CROP had similar negative (direct) effects on CONS at the two sites (Fig. 4B), but its indirect negative effect on DISP was greater at Agracea (-0.148) than at Hoyos (-0.083). This finding and the stronger direct effect of CROP on DISP in Hoyos indicate that among-plant variation in fruit removal success at Agracea obscured individual differences in absolute fecundity.

Seed rain: patterns in space

The total number of *P. latifolia* seeds collected by individual traps over the whole study period was used as a measure of seed rain. These figures were transformed using the Freeman-Tukey square-root transformation (Zar 1984) for all statistical analysis reported in this section.

Among-habitat patterns.—The massive fruiting of *P.*

FIG. 5. Altitudinal variation in *P. latifolia* seed rain per trap along the Guadahornillos valley (means \pm 1 SE). Seed traps were located along transects at each of the eight sampling stations along the elevational gradient. Percent cover (mean \pm 1 SE) is based on cumulative intercepts along four 20 m long transects at each station.



latifolia during the study season resulted in an abundant and widespread seed rain over most of the Guadahornillos valley. Fifty-three percent of the traps along the elevational gradient ($N = 320$) collected at least one *P. latifolia* seed during the study period. Out of a cumulative total of 816 seeds from 14 bird-dispersed species recovered from the traps, 656 (80.4%) were from *P. latifolia*.

The mean number of *P. latifolia* seeds collected by individual traps changed significantly with elevation (Fig. 5; $F_{7, 312} = 19.01$, $P < 0.0001$). Seed rain was greatest at the two lowermost sites and declined steadily with elevation (with only a minor anomaly at the 1250-m site). The cumulative seed rain recorded at the two lowermost sites (4.5 and 4.3 seeds per trap on average) was equivalent to nearly 36 seeds/m². Not a single *P. latifolia* seed was collected by traps located at the uppermost (1350 m) site.

Across sites, seed rain was correlated positively with the local percent cover of *P. latifolia* in the habitat ($r = 0.732$, $N = 8$, $P = 0.039$) and negatively with elevation ($r = -0.896$, $N = 8$, $P = 0.002$). Nevertheless, when the influence of these two variables on seed rain was examined simultaneously using multiple regression, only elevation had a significant effect on seed rain ($t = 2.95$, $P = 0.03$), and the effect of percent cover was no longer significant ($t = 0.90$, $P = 0.41$). The correlation between seed rain and percent cover was thus only an indirect consequence of the relationship between the latter variable and elevation (Fig. 5).

Within-habitat patterns: Agraceae. — During the 8-mo study period, traps collected a total of 1185 seeds from seven bird-dispersed species. Seeds from *P. latifolia* represented 93.0% of total seeds recovered.

A generalized linear model was fitted to the data to test for the effect of habitat descriptive variables (vegetation height and number of woody species at each station; position relative to the habitat mosaic; and

presence-absence of each of the five locally dominant woody species) on seed rain (number of seeds collected by individual traps), using individual traps as sampling units. The model was statistically significant ($F_{9, 278} = 3.82$, $P = 0.0001$), and differences among stations in structure of overlying vegetation accounted for 11.0% of among-trap variation in seed rain. Of the eight variables included in the model, only vegetation height ($F_{1, 278} = 7.74$, $P = 0.005$) and position relative to the habitat mosaic ($F_{2, 278} = 5.18$, $P = 0.006$) had significant effects on the seed rain ($P \geq 0.13$ for the other variables). Least-squares, model-adjusted means (\pm 1 SE) of seed rain indicate that seed rain tended to increase from gaps (1.10 ± 1.21 seeds per trap) through forest interior (3.66 ± 0.91 seeds per trap) to forest edges (4.05 ± 0.92 seeds per trap). The model-fitted parameter for vegetation height was -0.143 ± 0.051 (mean \pm 1 SE); when all other variables were held constant, seed rain tended to decrease with increasing height of overlying vegetation.

A fully random, nested ANOVA design was used to assess the spatial scale of patchiness in the post-dispersal distribution of seeds. Sampling stations were nested within transects and transects were nested within slopes. There were no significant differences between slopes ($F_{1, 2} = 1.23$, $P = 0.38$) or between transects within slopes ($F_{2, 92} = 3.02$, $P = 0.053$) in seed rain; these two spatial scales accounted together for only 5.9% of total variance. Differences among stations within transects were highly significant ($F_{92, 192} = 3.41$, $P < 0.0001$) and accounted for 42.0% of total variance in seed rain. Differences between adjacent traps in the same triplet accounted for 52.2% of variance. Patchiness in the post-dispersal distribution of *P. latifolia* at the Agraceae site was therefore extremely fine-grained. Most spatial variation in seed rain took place at a scale of 5 m (among stations) or less (among traps within triplets).

TABLE 8. Number of *P. latifolia* seeds collected per trap over the 8-mo study period in different microhabitat types, Hoyos de Muñoz (mean \pm 1 SD; $N = 30$ traps in each microhabitat type).

Microhabitat type	Seeds/trap
Open ground	0.20 \pm 0.41
<i>Arbutus unedo</i> *	0.63 \pm 1.03
<i>Juniperus oxycedrus</i> *	0.60 \pm 0.67
<i>Rosmarinus officinalis</i>	0.87 \pm 1.55
<i>Pistacia lentiscus</i> , males	1.27 \pm 1.76
<i>Quercus rotundifolia</i>	1.37 \pm 1.77
<i>Smilax aspera</i> *	2.00 \pm 2.48
<i>Phillyrea latifolia</i> *	2.17 \pm 2.89
<i>Viburnum tinus</i> *	2.67 \pm 2.35
<i>Pistacia lentiscus</i> , females*	3.43 \pm 5.88

* Fleshy-fruit-producing species.

Within-habitat patterns: Hoyos.—Seeds from seven bird-dispersed species ($N = 1634$ seeds) were recovered from the traps over the 8-mo study period. Seeds of *Viburnum tinus* were most abundant (36.5% of total), followed by those of *P. latifolia* (28.0%) and *Pistacia lentiscus* (26.6%).

Microhabitats differed significantly in the mean number of *P. latifolia* seeds collected by individual traps ($F_{9, 290} = 7.90$, $P \ll 0.0001$), from a minimum in the open ground (0.2 seeds per trap, or 1.2 seeds/m²) to a maximum beneath *Pistacia lentiscus* females (3.4 seeds per trap, or 21.5 seeds/m²) (Table 8). The four microhabitat types receiving the greatest seed rain (*S. aspera*, *P. latifolia*, *V. tinus*, female *P. lentiscus*; each > 2.0 seeds per trap on average) corresponded to species producing fleshy fruits. This pattern also occurred intraspecifically. Average seed rain was significantly higher under female (and thus fruit-producing) *P. lentiscus* plants than under conspecific, fruitless males ($F_{1, 58} = 6.78$, $P = 0.012$) (Table 8). A similar result was obtained when data from traps under *S. aspera* vines were split according to plant sex. Seed rain under females (2.4 \pm 2.6 seeds per trap, $N = 23$) was significantly greater than under males (0.6 \pm 1.5 seeds per trap, $N = 7$) ($F_{1, 28} = 6.05$, $P = 0.020$).

Patchiness in the post-dispersal distribution of *P. latifolia* seeds was not restricted to variation among microhabitat types, but also occurred within microhabitats. Variation among microhabitats explained 17.8% of total variance in seed rain (seeds per trap), while variation among stations within the same microhabitat accounted for 26.9% and was also statistically significant ($F_{146, 144} = 1.93$, $P < 0.0001$). Considerable patchiness occurred also at even smaller spatial scales. Variation among adjacent traps in the same station explained as much as 55.3% of total variance in seed rain.

Seed rain: patterns in time

Dispersal of *P. latifolia* seeds took place from late September through early June. On average, dispersal was significantly earlier at Hoyos than at Agracea (Table 9) ($P < 0.001$, Kolmogorov-Smirnov test).

There was considerable delay between the peak of ripe fruit availability and the peak of seed dispersal at both sites. While most fruits of *P. latifolia* were already ripe by October, peaks in seed rain took place in February and March at Hoyos and Agracea, respectively (Table 9), matching differences between sites in phenology of fruit removal (Fig. 1). As shown by the study of the diet of avian frugivores (see *Diet of avian frugivores*), *P. latifolia* at Hoyos shared the dispersal agents with other fleshy-fruited species. Among these, *P. lentiscus* and *V. tinus* ripened large fruit crops at about the same time as *P. latifolia*. In contrast to *P. latifolia*, however, their dispersal peaks occurred shortly after fruit ripening (October–November and November, for *P. lentiscus* and *V. tinus*, respectively; Table 9). The dispersal peak of *P. latifolia* at Hoyos, therefore, lagged behind those of other coexisting, simultaneously ripening species.

Duration of seeds in the soil

After a 2-yr burial, an average of 6.3 \pm 5.4 ($N = 42$ bags) and 8.5 \pm 4.9 ($N = 43$) *P. latifolia* seeds (out of the initial 25) remained viable per bag at Agracea and

TABLE 9. Seasonal variation in the intensity of the *P. latifolia* seed rain (seeds per trap per 30 d) at the two main study sites (shown as means \pm 1 SD).* For Hoyos de Muñoz, seed rain data are also shown for the other two major bird-dispersed species at the site.

Sampling period (1989–1990)	Agracea		Hoyos de Muñoz	
	<i>Phillyrea latifolia</i>	<i>Phillyrea latifolia</i>	<i>Viburnum tinus</i>	<i>Pistacia lentiscus</i>
28 Sep–31 Oct	0.14 \pm 0.43	0.08 \pm 0.32	0.02 \pm 0.15	0.41 \pm 1.12
31 Oct–04 Dec	0.29 \pm 0.96	0.12 \pm 0.36	0.20 \pm 2.03	0.42 \pm 1.04
04 Dec–02 Jan	0.39 \pm 1.06	0.28 \pm 0.87	0.19 \pm 0.74	0.29 \pm 0.96
02 Jan–07 Feb	0.69 \pm 1.51	0.31 \pm 0.71	0.98 \pm 1.80	0.15 \pm 0.51
07 Feb–06 Mar	0.71 \pm 1.52	0.40 \pm 1.10	0.41 \pm 1.25	0.06 \pm 0.31
06 Mar–10 Apr	1.05 \pm 2.79	0.26 \pm 0.73	0.02 \pm 0.12	0.01 \pm 0.16
10 Apr–11 Jun	0.16 \pm 0.46	0.01 \pm 0.99	0	0

* Figures shown are the estimated number of seeds collected by each trap in a 30-d period, obtained after correcting original seed trap catches for differences in the duration of sampling periods ($N = 288$ and 300 traps in each sampling period for Agracea and Hoyos de Muñoz, respectively).

TABLE 10. Analysis of variance table (logistic analysis, maximum likelihood estimation) for the effects of vegetation composition and structure, and seed size ("smaller" vs. "larger" in experimental pairs) on the probability of *P. latifolia* seed survival at the end of the 1-yr experimental period ($N = 960$ and 1000 seeds in Agracea and Hoyos de Muñoz, respectively).

Site and source of variation	df	χ^2	<i>P</i>
Agracea			
Intercept	1	0.05	0.81
Vegetation height	1	0.44	0.51
Seed size (SS)	1	1.02	0.31
Habitat category (HC)	2	7.93	0.018
HC \times SS	2	3.53	0.17
Number of species	1	0.00	0.97
<i>Arbutus unedo</i>	1	0.06	0.81
<i>Erica arborea</i>	1	0.54	0.46
<i>Juniperus oxycedrus</i>	1	0.06	0.81
<i>Phillyrea latifolia</i>	1	0.20	0.65
<i>Quercus rotundifolia</i>	1	0.49	0.48
Hoyos de Muñoz			
Intercept	1	8.44	0.004
Microhabitat	9	46.21	$\ll 0.0001$
Seed size	1	4.15	0.042
Microhabitat \times seed size	9	4.30	0.89

Hoyos, respectively ($F_{1,83} = 6.12$, $P = 0.015$, for the difference between sites). Seed persistence levels did not differ among microhabitat types in Hoyos ($F_{9,33} = 0.37$, $P = 0.93$) or among gaps, forest interior, and forest edges in Agracea ($F_{2,39} = 0.30$, $P = 0.74$).

Post-dispersal seed predation

Rodent predation levels on experimental seeds were low at both sites (39.5 and 54.2% cumulative predation over 1 yr in Agracea and Hoyos, respectively). To account for the existence of right-censored data (seeds still surviving at the end of the experimental period), the difference between sites in mean survival level was tested using failure time analysis. As estimated by the product-limit method, the expected survival time (mean ± 1 SE) of individual seeds at Hoyos (37.4 ± 0.7 wk) was ≈ 9 wk shorter than at Agracea (46.3 ± 0.4 wk). The difference between sites was statistically significant (chi-square = 230.8, df = 1, $P \ll 0.0001$; Mantel-Cox test).

Within-habitat patterns: Agracea.—The influence of habitat variables and seed size on seed survival was examined using logistic analysis. Individual seeds were the sampling units for the analysis and the response variable was the status (present or missing) of each seed by the end of the experimental period. Experimental blocks of seeds were located in a subset of the permanent stations and they were characterized by the same variables used in the analysis of spatial variation in seed rain (height of vegetation, number of woody species, position with respect to the habitat mosaic, and presence of the five dominant woody species; see *Seed rain: patterns in space, Within-habitat patterns:*

Agracea). Seed size (position in the experimental pair) was also included among independent variables.

The fitted model (Table 10) was statistically significant, as revealed by the nonsignificant likelihood ratio (chi-square = 89.20, df = 75, $P = 0.13$). Location of seeds in the habitat mosaic had a significant effect on survival. Survival was lowest in gaps (50.5%, $N = 200$ seeds) and higher in the forest interior (62.7%, $N = 440$ seeds) and at forest edges (63.8%, $N = 320$). None of the other variables examined had a significant influence on seed survival.

Within-habitat patterns: Hoyos.—There was a highly significant effect of microhabitat type and a barely significant effect of seed size on seed survival (Table 10). The smaller seed in a pair had a slightly higher probability of survival (48.8%) than the larger one (42.8%). Most microhabitat types had fairly similar seed survival rates, mostly between 40 and 50%, and only the open ground (19%) and *Rosmarinus officinalis* (61%) departed noticeably from this pattern (Table 11). The former microhabitat alone contributed 57% of the overall microhabitat \times survival chi-square result (Table 11).

Seed germination and seedling emergence in the field

Despite intensive field work, not a single newly emerged *P. latifolia* seedling was found in the study area during 1990. Seeds dispersed during the 1989–1990 autumn–winter period remained dormant in the soil until the spring of 1991, when massive and largely synchronous germination first occurred. Only a fraction of dormant seeds, however, germinated that year, and a second germination pulse took place in the spring of 1992. That seeds germinating in 1992 came also from the 1989 reproductive event is supported by the observation that the *P. latifolia* population did not fruit in the autumn of 1990 (Table 1) and by the results of the experiments to determine the persistence of viable seeds in the soil (see *Duration of seeds in the soil* above).

TABLE 11. Variation among microhabitats in the survival rate of experimental *P. latifolia* seeds, Hoyos de Muñoz ($N = 100$ seeds per microhabitat type). Also shown are the partial chi-squares contributed by each microhabitat type to the overall chi-square of the microhabitat \times survival contingency table ($\chi^2 = 50.66$).

Microhabitat type	Percent survival	Partial χ^2
Open ground	19.0	28.93
<i>Pistacia lentiscus</i> , females	39.0	1.86
<i>Viburnum tinus</i>	40.0	1.36
<i>Pistacia lentiscus</i> , males	43.0	0.32
<i>Juniperus oxycedrus</i>	46.0	0.002
<i>Phillyrea latifolia</i>	48.0	0.19
<i>Smilax aspera</i>	51.0	1.09
<i>Arbutus unedo</i>	55.0	3.41
<i>Quercus rotundifolia</i>	56.0	4.19
<i>Rosmarinus officinalis</i>	61.0	9.31

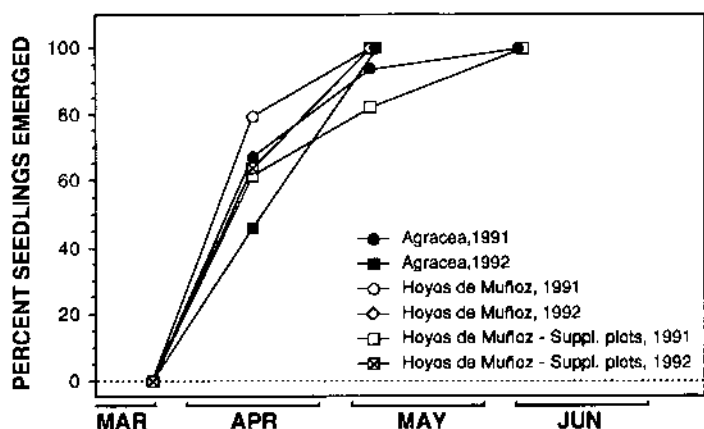


FIG. 6. Timing of emergence of *P. latifolia* seedlings. Shown are the cumulative emergence curves at Agraceca (1991 and 1992) and Hoyos de Muñoz (1991) for regular sampling points, along with those for the Hoyos de Muñoz supplementary plots (1991 and 1992).

The bulk of the information on marked seedlings will be used in a later section (see *Seedling survival*) to examine survival patterns. In this section, data on marked seedlings are used to examine the timing and within-habitat patterns of seedling emergence.

A total of 1374 and 2706 seedlings emerged at the 96 stations of the Agraceca site in 1991 and 1992, respectively. The mean seedling emergence was 14.3 ± 12.5 seedlings per station (10.7 seedlings/m²) and 28.2 ± 34.6 seedlings per station (22.9 seedlings/m²) in 1991 and 1992, respectively; the difference between years was statistically significant ($t = 4.43$, $N = 96$, $P < 0.0001$; paired t test). In Hoyos, only 260 seedlings emerged in the regular sampling stations in 1991 (stations were not surveyed in 1992), and 946 and 691 emerged at the supplementary areas in 1991 and 1992, respectively. Although there were slight differences between sites and years in the timing of seedling emergence, the vast majority of seedlings appeared synchronously during April regardless of year and site (Fig. 6).

In Agraceca, the mean number of seedlings emerging per station did not differ among gaps, forest interior, and forest edges ($F_{2,93} = 1.74, 0.71, \text{ and } 0.82$, $P \geq 0.20$, for 1991, 1992, and both years combined, respec-

tively). Similarly nonsignificant results (not shown) were obtained when seedling densities were used instead of absolute numbers per station or when the potential influence on seedling emergence of other habitat descriptive variables was examined.

In Hoyos, in contrast, there was a highly significant effect of microhabitat type on the mean number of seedlings emerging per station in 1991 ($F_{9,146} = 4.53$, $P < 0.001$; data log-transformed). Seedling emergence was greatest under *P. lentiscus* females, *V. tinus*, and *S. aspera*; 79.3% of all seedlings occurred in these microhabitats (Table 12). The lowest seedling emergence levels occurred in the open ground and under *P. latifolia* and *P. lentiscus* males.

Seed germination experiments

Agraceca experiments.—The percent of seeds that germinated during the 1st yr, all plants and sites combined, was 39.4% ($N = 320$ seeds). Germination data were analyzed using a saturated logistic model including the effects of mother plant, light regime, and their interaction. The light regime (gap vs. forest interior) had no significant effect on the probability of germination of individual seeds (chi-square = 1.47, $df = 1$, $P = 0.23$). Seeds from different individuals differed significantly in percent germination (range = 25.0–60.0%; chi-square = 19.25, $df = 7$, $P = 0.007$). Differences among plants remained consistent between light treatments, as revealed by the nonsignificance of the interaction term (chi-square = 10.76, $df = 7$, $P = 0.15$).

Torre del Vinagre experiments.—Germinations started in December 1990 and lasted until May 1991 (median date = 20 March 1991). The overall germination level, all plants combined, was 23.7%. Seeds from Agraceca and Hoyos did not differ significantly in percent germination (chi-square = 0.27, $df = 1$, $P = 0.60$). Individual plants did differ broadly (range = 8–44%) and significantly (chi-square = 70.80, $df = 26$, $P < 0.0001$). Among plants, percent seed germination

TABLE 12. Variation among microhabitats in the number of *P. latifolia* seedlings emerging per sampling point in the spring of 1991 at the Hoyos de Muñoz site. N = number of points in each microhabitat category.

Microhabitat type	N	Seedlings/point (mean \pm 1 SD)
Open ground	15	0.07 \pm 0.26
<i>Phillyrea latifolia</i>	15	0.20 \pm 0.56
<i>Pistacia lentiscus</i> , males	15	0.33 \pm 0.62
<i>Juniperus oxycedrus</i>	15	0.60 \pm 1.35
<i>Rosmarinus officinalis</i>	15	0.60 \pm 1.45
<i>Quercus rotundifolia</i>	15	0.60 \pm 0.74
<i>Arbutus unedo</i>	15	1.00 \pm 1.41
<i>Smilax aspera</i>	21	2.33 \pm 4.12
<i>Viburnum tinus</i>	15	4.87 \pm 9.38
<i>Pistacia lentiscus</i> , females	15	5.80 \pm 13.99

decreased significantly with increasing mean seed mass ($F_{1,25} = 4.38, P = 0.046$).

Early mortality was fairly low among experimental seedlings. Only 14.2% of the 325 seedlings that emerged died before the completion of the experiment. We found no significant effect of seed mass (chi-square = 3.32, $df = 1, P = 0.07$) or mother plant (chi-square = 29.63, $df = 26, P = 0.28$) on the probability of short-term seedling survival when the effects of the two variables were tested simultaneously using failure time analysis.

There was significant heterogeneity among plants in the mean dry mass of seedlings at final harvest ($F_{25, 228} = 5.41, P < 0.0001$; log-transformed data); plant means ranged between 13.0 and 31.2 mg. The mass of individual seedlings (SLM, in milligrams), all plants combined, was significantly related to the original seed's mass (SDM, in milligrams) (regression equation: $SLM = 10.63 + 0.17SDM, R^2 = 0.167; F_{1, 252} = 50.38, P < 0.0001$). Plant means for seed and seedling mass were also positively related ($F_{1,24} = 12.16, P = 0.002$).

Seedling survival

As noted in *Methods: Seedling emergence and survival*, few seedlings emerged in 1991 at the Hoyos site in the stations of plot A. In this section, results for the Hoyos site are presented separately for plot A (relatively few seedlings, marked in 1991 only) and plot B (a much larger sample, marked in 1991 and 1992).

Causes of seedling mortality.—Most seedlings died of desiccation, many of them during their first summer (Table 13). Desiccation was also probably responsible for the death of most seedlings without identifiable mortality causes. The "desiccation" and "unknown" categories accounted together for 68.1% of total seedling mortality.

The relative importance of mortality causes differed among sites (chi-square = 221.1, $df = 16, P < 0.0001$) (Table 13). Differences in the frequency of deaths from desiccation (partial chi-square = 15.2, $df = 2, P = 0.0005$) were attributable to the higher losses to desiccation at Hoyos plot A (54.6%), relative to Agracea and Hoyos plot B (39.0 and 39.6%, respectively; data for 1991 and 1992 combined). Damage by psyllid homopterans produced greater seedling mortality in Agracea (2.4%) than in the two Hoyos plots (0% and 1.3%; partial chi-square = 11.8, $df = 2, P = 0.003$). Herbivory caused greater mortality at Hoyos plot B (4.1%) than at plot A (0%) or Agracea (1.2%) (partial chi-square = 58.8, $df = 2, P < 0.0001$). The impact of trampling by ungulates did not differ among sites (partial chi-square = 4.9, $df = 2, P = 0.09$).

Among-habitat patterns.—A significantly greater proportion of seedlings survived (1991 and 1992 data combined) in Agracea (27.6%) than in either of the two Hoyos plots (18.8 and 14.9%) (chi-square = 71.4, $df = 2, P < 0.0001$), largely because of the lower mortality from desiccation in the former site (Table 13).

Seedling survival curves at Agracea and Hoyos sites

TABLE 13. Causes of mortality for *P. latifolia* seedlings at the two main study sites during 1991 and 1992. Figures are percentages with respect to the total number of seedlings monitored at each site and year (in parentheses). Data for Agracea include a supplementary sample of 721 seedlings marked outside the regular transects.

Fate	Agracea		Hoyos de Muñoz A	Hoyos de Muñoz B	
	1991 (2097)	1992 (2219)	1991 (260)	1991 (946)	1992 (648)
Survived*	19.6	35.1	18.8	7.6	25.5
Died					
Herbivory†	1.8	0.7	0	1.7	7.6
Fungus	1.2	0	0.8	2.6	0
Desiccation	52.0	26.6	54.6	50.5	23.8
Lost‡	0.9	0.2	0	0.5	0.3
Trampling§	2.4	1.2	0	2.2	1.4
Desiccation+					
Homoptera	0.2	4.4	0	0	3.2
Unknown¶	21.9	31.8	25.8	34.9	38.2

* Alive by the end of study and with no obvious signs of damage other than portions of leaf/cotyledon area removed.
 † Leaves/cotyledons totally consumed by herbivores.
 ‡ Seedling lost, missing tag.
 § Rooted out or trampled by large herbivores (mainly *Sus scrofa*).
 || Desiccated, showing evident signs of psyllid attack.
 ¶ Cause of death not determined, most likely due to desiccation.

(all cohorts pooled) are shown in Fig. 7. Mortality was highest shortly after seedling emergence and tended to become progressively less afterwards. Survival curves leveled off after the first summer (125–130 d after emergence) and mortality was relatively low subsequently. Temporal pattern of survival did not differ among sites (chi-square = 0.44, $df = 2, P = 0.80$; Gehan-Wilcoxon test, all cohorts and years pooled in each group). The expected survival time for Agracea seedlings was 22.3 ± 3.1 wk (mean ± 1 SE), and that for Hoyos plots A and B were 15.0 ± 3.4 wk and 21.6 ± 3.5 wk, respectively.

Differences in survival patterns between 1991 and 1992 seedling cohorts were barely significant in Agracea (chi-square = 3.52, $df = 1, P = 0.06$) and Hoyos plot B (chi-square = 2.90, $df = 2, P = 0.09$). In a given year, survival differences between cohorts within sites were not significant in any of the possible pairwise comparisons (chi-square $< 0.148, P > 0.70$); therefore, data for different cohorts will be pooled in subsequent analyses of within-habitat patterns.

Within-habitat patterns: Agracea.—The effects of habitat mosaic (forest edge, gap, forest interior), vegetation height, and composition and species richness of overlying vegetation on *P. latifolia* seedling survival were tested using logistic analysis. The fate of each seedling (alive or dead at the end of the study) was the response variable, while values of independent variables were those corresponding to the station where the seedling was located. Habitat type, plant species

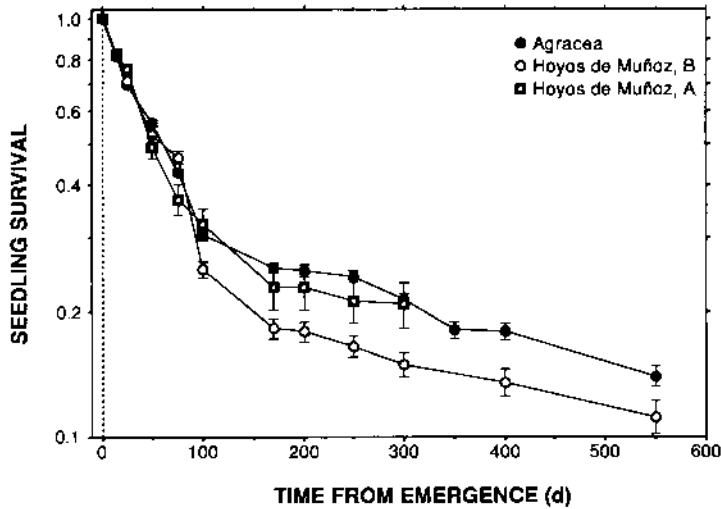


FIG. 7. Survival functions for *P. latifolia* seedlings. Shown are survival values (means ± 1 SE) resulting from product-limit (Kaplan-Meier) estimations using LIFETEST procedure (SAS 1988) (note logarithmic vertical scale). Except for Hoyos plot A (data were available only for 1991), curves for each site were obtained after pooling data for 1991 and 1992 (there was no significant heterogeneity in survival curves between years within sites or among cohorts within years; Gehan-Wilcoxon test, $P > 0.06$ for all comparisons).

TABLE 14. Variation in the survival of *P. latifolia* seedlings among habitat types in Agraceca (transects A-D pooled, $N = 3595$ seedlings) and Hoyos de Muñoz (plots A and B, $N = 1854$ seedlings). Hoyos de Muñoz microhabitats were defined only by the composition of plant species.

Site Effect and level	Percent survival	χ^2	P
Agraceca			
Habitat category*			
Edge	30.64	14.14	0.0003
Gap	23.72	1.01	0.32
Interior	23.34	4.21	0.037
Plant cover†			
<i>Arbutus unedo</i>	21.79	4.12	0.039
<i>Erica arborea</i>	28.04	6.52	0.010
<i>Juniperus oxycedrus</i>	25.38	0.01	0.92
<i>Phillyrea latifolia</i>	23.35	34.50	<0.0001
<i>Quercus rotundifolia</i>	24.49	1.57	0.21
Hoyos de Muñoz, A			
Microhabitat‡			
<i>Arbutus unedo</i>	20.00	0.01	0.92
Open ground	0.00	0.26	0.62
<i>Juniperus oxycedrus</i>	11.11	0.53	0.52
<i>Phillyrea latifolia</i>	0.00	0.79	0.62
<i>Pistacia lentiscus</i> , females	21.18	0.09	0.76
<i>Pistacia lentiscus</i> , males	28.57	0.01	0.92
<i>Quercus rotundifolia</i>	22.20	0.01	0.92
<i>Rosmarinus officinalis</i>	20.11	26.29	<0.0001
<i>Smilax aspera</i>	18.37	0.22	0.64
<i>Viburnum tinus</i>	15.07	2.00	0.15
Hoyos de Muñoz, B			
Microhabitat‡			
<i>Arbutus unedo</i>	18.79	8.71	0.003
<i>Phillyrea latifolia</i>	10.11	8.19	0.004
<i>Pistacia lentiscus</i> ‡	21.60	11.84	0.0007
<i>Quercus rotundifolia</i>	10.43	10.39	0.0014
<i>Rosmarinus officinalis</i>	40.74	61.27	<0.0001

* χ^2 values are partial contributions to the overall χ^2 of the habitat category \times survival contingency table.

† Significance values correspond to the χ^2 of the presence/absence of each species \times survival contingency table.

‡ Male and female plants combined.

richness, and composition of plant cover all had significant effects on seedling survival (chi-square ≥ 4.6 , $P < 0.03$). Survival was significantly improved under canopies of *E. arborea* and significantly impaired under *A. unedo* and *P. latifolia* (Table 14, Fig. 8). Seedlings emerging in forest edges, gaps, and forest interior differed in survival probability (chi-square = 19.3, $df = 2$, $P < 0.0001$). Survival in forest edges was greater than in gaps or the forest interior (Table 14).

Within-habitat patterns: Hoyos.—Microhabitat type significantly affected seedling survival at the two Hoyos plots (chi-square = 23.8, $df = 9$, $P = 0.005$ for plot A; chi-square = 81.2, $df = 4$, $P < 0.0001$ for plot B; Table 14). At plot A, only *R. officinalis* showed a significant effect, with increased survival beneath shrubs of this species. The result was similar in plot B, where survival in *R. officinalis* patches was disproportionately high relative to other microhabitats. All the microhabitats influenced survival significantly at this plot (Table 14), either positively (*A. unedo*, *P. lentiscus*, *R. officinalis*) or negatively (*P. latifolia* and *Q. rotundifolia*). The trend for increased seedling mortality under *P. latifolia* plants was similar to that found in Agraceca (Fig. 8).

DISCUSSION

Mast fruiting

Fruit production by *P. latifolia* exhibits all the characteristics of mast-fruiting plants, including drastic fluctuations in crop size, supra-annual synchrony, and irregular fruiting intervals (Janzen 1978, Silvertown 1980, Norton and Kelly 1988, Sork et al. 1993). We are aware of a single study where masting has been documented rigorously for a fleshy-fruited species (Norton and Kelly 1988). Wide annual fluctuations in fruit production have been described, however, for many fleshy-fruited, vertebrate-dispersed plants from tropical (Howe 1986, Wheelwright 1986, Schupp 1990) and extra-tropical (Laine 1978, Vander Kloet and Ca-

bilio 1984, C. M. Herrera 1988b, Jordano 1993) habitats. More detailed studies may eventually prove that masting is not so infrequent in this group of plants as commonly assumed.

Two main hypotheses have been proposed to explain mast fruiting (Janzen 1976, 1978, Silvertown 1980, Sork et al. 1993, and references therein). Masting may be associated with years in which resources are more available (the "resource matching" hypothesis) or it may represent an evolved response to seed predation ("predator satiation" hypothesis). The predator satiation hypothesis was considered by Norton and Kelly (1988) as a particular case of a more general "economies of scale" hypothesis, whereby large episodes of reproduction are more efficient than small ones due to, e.g., increased attraction of animal dispersers (the case of fleshy-fruited plants) or reduced seed predation (i.e., the classical satiation hypothesis). As discussed in the remainder of this section, the information available for *P. latifolia* does not seem to support either of these two "economies of scale" possibilities (although other possibilities, e.g., increased pollination, remain unexplored and cannot be ruled out).

Numerical responses of frugivorous birds to increases in the size of preferred fruit crops have been reported for some boreal (Tyrväinen 1975, Kolunen and Vikberg 1978) and high-mountain (Jordano 1993) habitats. In our study area, however, the size of frugivore populations did not increase significantly during *P. latifolia* mast years in response to increased fruit availability. In the Hoyos study site, annual variation in the abundance of *E. rubecula* and *S. atricapilla* (the main dispersers of *P. latifolia*) during autumn–winter of 1978–1987 was unrelated to the supply of *P. latifolia* fruits (C. M. Herrera 1988b). In the absence of numerical responses by disperser populations, the dramatic increase in *P. latifolia* fruit supply during mast years may lead to disperser satiation phenomena in localities where disperser populations are sparse and/or crop sizes are very large. The reduced fruit removal levels found at our Agraceca study site (see *Variation between habitats* below) most likely reflected the satiation of local avian dispersers. Increased mean crop duration and delayed dispersal caused by fruit superabundance in Agraceca did not increase fruit losses to predators, as found in other studies (Ballardie and Whelan 1986, Jordano 1987). The vast majority of fruits failing to disperse simply dried on the plants, without any sign of damage by vertebrate or invertebrate predators.

Comparative data on the survival of *P. latifolia* seeds in mast and non-mast years are not available, so the predator satiation hypothesis may be only indirectly evaluated. We have never recorded post-dispersal predation of *P. latifolia* seeds by invertebrates. Small-mammal populations are uniformly sparse in the montane Mediterranean forests and scrublands where this study was conducted (P. E. Hulme, *personal communication*). This scarcity may partially explain the low

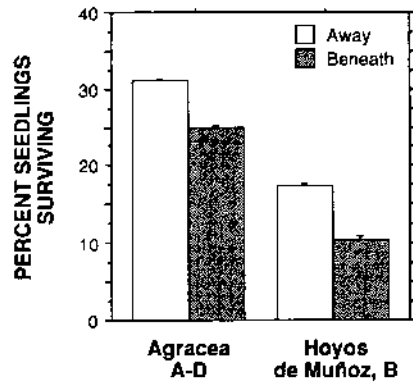


FIG. 8. Survival of *P. latifolia* seedlings under and away from adult conspecifics. Data were pooled across transects A–D for the Agraceca site. The number of seedlings was very small for Hoyos de Muñoz plot A; only data for plot B are shown. Vertical lines denote the upper binomial 95% confidence limits.

post-dispersal seed predation rates recorded in this study (39.5% and 54.2% seed predation after 1-yr exposure in Agraceca and Hoyos, respectively). These figures are about two orders of magnitude lower than those reported for nonfleshy-fruited masting trees during good crop years (e.g., Shaw 1968, Gashwiler 1970, Gardner 1977, Boucher 1981, Génard and Lescourret 1985) and about one order of magnitude lower than those found in experimental studies of post-dispersal seed predation of fleshy-fruited, vertebrate-dispersed plants (e.g., De Steven and Putz 1984, Schupp 1990, Whelan et al. 1991).

The Phyllyrea latifolia–fruit consumer system

The *P. latifolia*–fruit consumer system described in this study (see also C. M. Herrera 1984a) was similar in most respects to that of other bird-dispersed, western Mediterranean woody plants studied to date (e.g., C. M. Herrera 1984a, 1988d, Jordano 1987, 1989a). Fruits of *P. latifolia* ripened in autumn. Most seeds were dispersed during autumn–winter by a relatively reduced group of small-bodied, overwintering birds (*Sylvia*, *Erithacus*) subsisting on a predominantly frugivorous diet during an extended period. In the Hoyos site, *P. latifolia* fruits were a prominent component of the diet of these frugivores in the two masting events that occurred in the period 1978–1993 (1981 and 1989; C. M. Herrera [1984a: Table 5] and this study, respectively). The major dispersers of *P. latifolia* fed on several fruit species during most of the autumn–winter period, but eventually turned to a virtually monophagous diet of *P. latifolia* fruits by the end of the season. The shift to a *P. latifolia*-dominated diet by the major dispersers at Hoyos was simultaneous with a marked increase in the representation of *P. latifolia* seeds in seed traps and a sharp reduction in the number of ripe

fruits borne by marked plants (compare Table 6, Table 9, and Fig. 1).

The fruit species predominant in the diet of major dispersers changed from October through March (results not shown in this paper) and reflected the changing species composition of seed trap catches. Most-consumed fruit species formed an orderly temporal sequence of decreasing nutritional value of pulp (percent lipids plus protein content on a dry mass basis [in parentheses]; data from C. M. Herrera 1987), from *Pistacia lentiscus* (64.3%) through *Viburnum tinus* (25.3%) to, finally, *P. latifolia* (5.4%) (Table 9). The shift to *P. latifolia* monophagy thus was the last stage in a seasonal sequence and took place when local fruit crops of other abundant, nutritionally more rewarding, and apparently preferred species were exhausted. This interpretation is supported by data from the 1981 mast year. On that occasion, the combined abundance in the Hoyos site of fruits of other species (2.7 fruits/m² on average) was considerably lower than in 1989 (44.4 fruits/m²) (C. M. Herrera 1988b, and *personal observation*), and frugivores extensively consumed *P. latifolia* fruits immediately after ripening (C. M. Herrera, *personal observation*). Variation between mast years in the availability of other fruit species thus gave rise to contrasting feeding responses of frugivores to the superabundance of *P. latifolia* fruits that, most likely, resulted also in differences in the timing of fruit removal and seed deposition. Caution should thus be exerted when attempting certain generalizations from the present, single-season study. The importance of undertaking long-term studies of plant-frugivore interactions has recently been stressed by Willson and Whelan (1993). *P. latifolia*, however, with only two major reproductive events over a 15-yr period, certainly is not the best study subject to address that issue.

The late-season monophagy of major dispersers on *P. latifolia* fruits in 1989–1990, lasting for nearly 2 mo, was an interesting result of the present investigation. Previously reported instances of monospecific or nearly monospecific fruit diets by Mediterranean frugivores always involved lipid- and/or protein-rich fruit species (e.g., *Olea europaea*, *P. lentiscus*, *V. tinus*; C. M. Herrera 1981, 1984a, Jordano 1989b), but never a fruit species so poor in these major nutrients as *P. latifolia*. The prevalence of multi-species fruit diets among small-bodied Mediterranean frugivores often has been interpreted as a mechanism of obtaining a nutritionally balanced diet and avoiding secondary compounds (C. M. Herrera 1984a, Jordano 1988, Izhaki and Safriel 1989; but see Mack 1990, Izhaki 1992). Experimental studies by Izhaki and Safriel (1989) with Mediterranean frugivores showed that single-species fruit diets predictably resulted in loss of body mass. Their results contrast with our field data for *E. rubecula* and *S. atricapilla* (one of the species included in their investigation), which fed almost exclusively on *P. latifolia* fruits during nearly 2 mo without significant decrease in body mass. The

inclusion of only minor amounts of protein-rich, insect food in the diet apparently sufficed to prevent the decrease in body mass induced by a monophagous fruit diet (Jordano 1988, Simons and Bairlein 1990).

Variation between habitats in patterns of fruit removal

Individual *P. latifolia* plants at Hoyos had greater relative fruit removal success and had more seeds dispersed than their Agracea conspecifics, despite the greater fecundity of the latter. Fruit crops were only partly consumed in Agracea, while they were totally exhausted in Hoyos. These differences may be attributable, directly or indirectly, to the contrasting successional status of the two habitats. Crop size depended closely on plant size; thus the larger, presumably older plants of the Agracea mature forest produced larger fruit crops than those of the Hoyos scrubland. Furthermore, legitimate seed dispersers were scarcer and fruit predators and non-frugivores commoner in Agracea than in Hoyos, despite the close qualitative similarity in the species composition of their avifaunas. In the study region (see also Cody and Walter 1976, Massa 1981, Debussche and Isenmann 1992), overwintering populations of the two major *P. latifolia* dispersers (*E. rubecula* and *S. atricapilla*) are most dense in mid-successional, tall scrublands like those at Hoyos, while those of non-frugivores and fruit predators (mainly species of forest-dwelling Paridae) reach their highest densities in mature forests (C. M. Herrera 1984a, Obeso 1986, 1987).

Differences between our two main study sites in vegetational structure and associated avifaunal composition led not only to variation in fruit removal, as shown also by other studies (Bronstein and Hoffmann 1987, Denslow 1987, Guitián et al. 1992), but, more importantly, gave rise to subtle differences in the selective potential of frugivores on fruiting-related plant traits. Birds uniformly depleted *P. latifolia* crops in Hoyos (thus leading to small individual variance in percent fruit removal). Also the significant effect of fruit characteristics (fruit diameter, seed mass) on percent fruit removal did not have any important effect on individual variation in the absolute number of seeds dispersed. In Agracea, in contrast, fruit crops were less thoroughly depleted and individual differences in percent fruit removal and fruit characteristics were much more important in determining the number of seeds dispersed by individual plants. Plants of *P. latifolia* forming part of the mid-successional scrubland thus had virtually all their seeds dispersed, irrespective of differences in fruit traits, and crop size was the single most important factor determining individual variation in the number of dispersed seeds. In the mature forest, in contrast, a distinct potential existed for frugivores to exert selection on fruit traits, because fruit characteristics influenced the number of seeds dispersed by individual plants via their effect on percent fruit removal.

The Hoyos scrubland and Agracea forest exemplify two distinct seral stages of the plant succession typically occurring at 1000-1200 m elevation in the study region. The longevity of *P. latifolia* most likely exceeds 150 yr (C. M. Herrera, *personal observation*), and many individuals of this species becoming established at a site during early- or mid-successional stages will persist locally as the tall scrubland turns into mature forest. If differences between habitats in aspects of *P. latifolia* dispersal ecology found in this study are actually due to contrasting successional status, rather than site-specific, then *P. latifolia* trees would "experience" these differences as age-dependent variation in their seed dispersal regime. Age-dependent variation in the selective regime on dispersal-related traits would be an additional factor constraining the selective potential of vertebrate dispersal agents on long-lived vertebrate-dispersed plants (Howe 1984, C. M. Herrera 1985a, 1986, Willson and Whelan 1993).

Patterns of seed rain

At the among-habitat level, an unanticipated result of this study was the absence of measurable seed "export" beyond the upper distributional limit of *P. latifolia* in the Guadahornillos watershed, despite massive availability of fruits and intense mobilization of seeds by frugivores. Not a single *P. latifolia* seed hit the seed traps placed at the uppermost site (1350 m elevation), even though the nearest fruiting *P. latifolia* plants were <400 m away from trap lines. Failure to collect any seeds at that site could be due to insufficient sampling effort, but it indicates that seed rain, if it occurs at all, must be negligible. Tails of seed distribution curves have important consequences for the rates of colonization of new sites, yet little is known about them in endozoochorously dispersed, fleshy-fruited plants (only one study out of the 68 data sets reviewed by Portnoy and Willson 1993). Our results for *P. latifolia* show that the tail of the dispersal curve at the species' upper distributional limit is limited even when fruits are superabundant and colonization of areas beyond the regional distribution of the species may be seed-limited. Eriksson and Ehrlén (1992) documented seed-limited recruitment for several vertebrate-dispersed plants. These observations (see also Debussche et al. 1985, Holthuijzen and Sharik 1985a, b, Hoppes 1988, Willson and Crome 1989) suggest that seed dispersal by mobile animals often may not result in far-reaching dispersal of seeds at the regional or among-habitat levels.

The broad variation in *P. latifolia* seed rain along the Guadahornillos elevational gradient is probably attributable to among-habitat differences in disperser abundance. When the influence on seed rain of *P. latifolia* percent cover (an indirect estimate of local fruit abundance) and elevation were examined simultaneously, only the latter variable had a significant effect.

Seed rain decreased steadily with elevation, which is in accordance with the sharp elevational gradient in the autumn-winter abundance of *E. rubecula* and *S. atricapilla* in the Guadahornillos watershed (C. M. Herrera and P. Jordano, *personal observation*). These small-bodied species are rare in winter at elevations >1000 m (Obeso 1986, 1987), where frequent snowstorms and low temperatures probably limit their habitat use.

At the within-population level, mobilization of *P. latifolia* seeds by frugivorous birds resulted in a predictable seed shadow at the two study sites. As found in other studies of bird-dispersed plants (e.g., Hoppes 1987, Katusic-Malmborg and Willson 1988, Murray 1988, Izhaki et al. 1991), spatial heterogeneity in *P. latifolia* seed rain should be attributed to nonrandom foraging by frugivorous birds. In Agracea, seed rain at a given spot depended mainly on its position in the habitat and was unrelated to the composition of overlying vegetation. Seed rain was greatest in forest edges, the favored foraging place of the most abundant local disperser (*E. rubecula*; Lack 1948, da Prato and da Prato 1982, Guitián 1985). In Hoyos, seed rain did depend closely on composition of the plant cover. It was highest under fleshy fruit-bearing species and, within these, under fruit-bearing females of two dioecious species. The concentration of *P. latifolia* seeds under fruiting plants was clearly a consequence of the mixed fruit diet of the major dispersal agents, which fed simultaneously on several fruit species during most of the *P. latifolia* dispersal period. Microhabitats receiving the greatest seed rain corresponded precisely to plant species contributing most fruits to the diet of major dispersers (compare Tables 5 and 8). By acting as focal points for frugivores' foraging, fruiting plants thus were the most direct determinants of the *P. latifolia* seed shadow at the Hoyos site.

Our Hoyos results agree with those of previous studies that have documented the overwhelming influence of the spatial location of fruiting plants on the seed shadows of bird-dispersed plants in early- and mid-successional Mediterranean scrublands (e.g., Debussche et al. 1982, 1985, Izhaki et al. 1991, Debussche and Lepart 1992). They also provide further support to the notion of a diet-mediated, potential "habitat-shaping" ability of frugivorous birds proposed by C. M. Herrera (1985b, 1988c). Results for the Agracea forest, in contrast, are more similar to those reported from some North American temperate forests, where seed rain of bird-dispersed shrubs tends to be most intense in forest-gap interfaces (McDonnell and Stiles 1983, Hoppes 1988, Katusic-Malmborg and Willson 1988). The contrast between our two study sites confirms the notion that seed shadows generated by avian dispersers are strongly context-sensitive, particularly in relation to those horizontal and vertical components of habitat structure that influence the foraging behavior of dispersal agents (Janzen 1983).

Seedling emergence: combined effects of seed rain and seed survival

Post-dispersal seed predators often have been shown to affect spatial patterns of seedling emergence by differentially destroying seeds over one species' seed shadow (Andersen 1987, Harmon and Stamp 1992) or altering the spatial pattern of seedling recruitment (Augsburger and Kitajima 1992, Forget 1992). As discussed below, predators did not have this effect on *P. latifolia* during the reproductive episode studied here.

In the Hoyos site, variation among microhabitats in seedling density closely paralleled variation in seed rain. A significant correlation existed across microhabitats between seed rain intensity (Table 8) and seedling density (Table 12) ($r = 0.830$, $N = 10$, $P = 0.003$). Seedling emergence was consistently greater under fleshy-fruited species, with the outstanding exception of *P. latifolia*. Relatively few seedlings of this species emerged under conspecific plants, despite abundant seed rain. Seed predation levels were not disproportionately high in that microhabitat and other factors were probably involved (e.g., germination inhibitors found in conspecific leaf litter; Mayer and Poljakoff-Mayber 1975, Solomon 1983).

With the exception of the open ground, post-dispersal seed predation levels were similarly low in all microhabitat types, thus giving rise to the consistency between seed rain and seedling emergence across microhabitats in the Hoyos scrubland. Spatial consistency between seed rain and seedling emergence illustrates the direct influence of avian frugivores on the seedling shadow of *P. latifolia*. By depositing seeds preferentially beneath certain plant species, seed dispersers virtually constrained the emergence of seedlings to particular microhabitats. This long-lasting effect of frugivore activity should be expected whenever risk of seed predation and germination prospects are not so variable among microhabitat types as to obscure the spatial patterns of seed deposition originated by frugivores.

In contrast with the Hoyos site, seedling emergence in Agracea did not differ among the habitat types recognized there and was also unrelated to the composition of plant cover. Seed predation levels were lower in forest edges, the microhabitat receiving the greatest seed rain, than in either gap or forest interior sites. However, these differences did not translate into significant spatial variation in seedling density. The even distribution of seedling recruitment across microhabitat types in the Agracea site thus suggests that emergence was limited by factors other than post-dispersal seed predation.

Seed germination experiments revealed important differences among *P. latifolia* individuals in seed germination levels, seedling vigor (as measured by seedling mass), and probability of seedling establishment. As documented in other studies (Cideciyan and Mal-

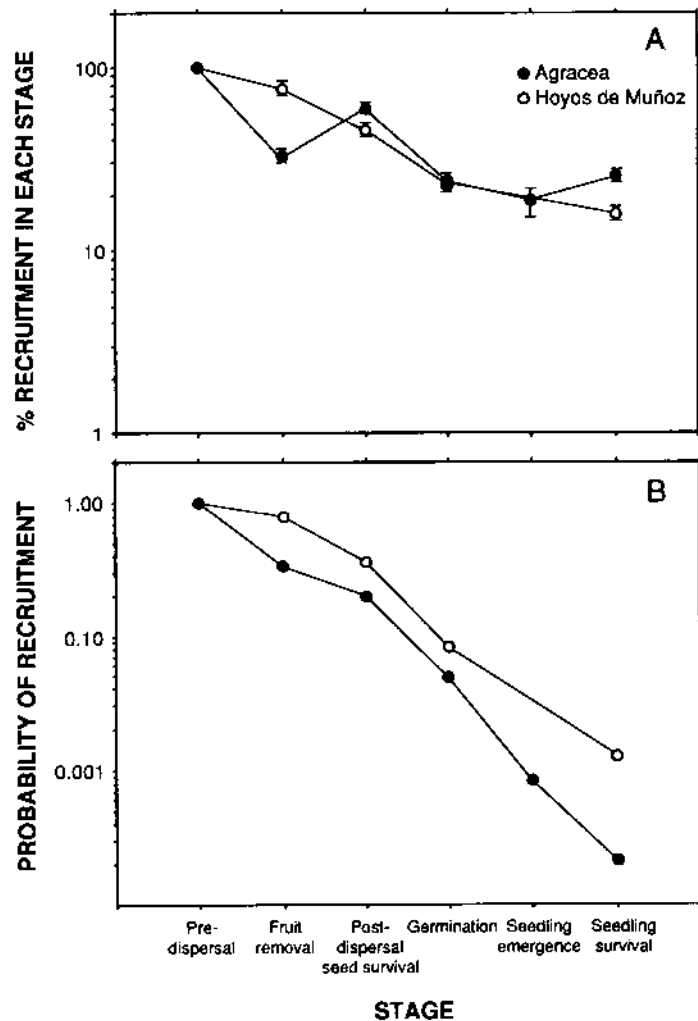
loch 1982, Howe and Richter 1982; see also Jurado and Westoby 1992), individual variation in seed mass had an important effect on both germination levels and seedling vigor, ultimately influencing seedling establishment. Germination levels of experimental seeds in the field did not differ between gap and forest interior microhabitats, but individual differences remained consistent between microhabitats. In this situation, the wide interplant variation in germination percentages (25–60%) has a potential impact on the composition of the seed bank and seedling cohorts. Furthermore, germination levels decreased and seedling vigor increased with increasing seed mass, thus adding complexity to the interaction between seed mass and the particular conditions of the microsite where individual seeds were delivered. These types of "intrinsic" individual plant effects might theoretically have implications for the spatial pattern of seedling establishment, if not overshadowed and compensated by "extrinsic" factors such as, for instance, differential seed rain or post-dispersal rodent predation.

Synthesis: recruitment as a multistep process

Recruitment probabilities during the fruit-to-seedling process.— Assuming that successive transition probabilities are independent, the probability of a seed in a ripe fruit becoming an established seedling may be estimated as the product of elemental transition probabilities between consecutive stages in the recruitment process (dispersal, seed rain, germination, and establishment) (e.g., Gill and Marks 1991). This simple demographic model may help to identify the possible compensatory effects of late-acting factors in the process, as well as key factors determining seedling establishment.

The probability of a seed in a ripe fruit becoming a 2nd-yr seedling was nearly 10 times greater in Hoyos than in Agracea (Fig. 9). The negative demographic impact of lower ripe fruit removal at Agracea relative to Hoyos was not compensated for by greater seed escape from rodent predation and increased seedling emergence and survival (Fig. 9). Our results illustrate a cascading effect of disperser activity on *P. latifolia* demography and suggest that differences between populations in fruit removal may have long-lasting consequences for seedling recruitment levels. Situations of disperser satiation, such as that occurring in Agracea, may have dramatic delayed effects on patterns of seedling recruitment by severely limiting fruit removal and imposing low recruitment not easily compensated for by later acting factors in the recruitment process. Previous studies have emphasized this limiting role for post-dispersal seed predators and pathogens (Harper 1977, Crawley 1990), but satiation of the disperser assemblage might also be frequent among fleshy-fruited species that show ample annual variation in fruiting levels.

FIG. 9. Synthesis of recruitment expectancies for *P. latifolia* seeds throughout the fruit removal—end of second growing season (2-yr seedlings) at the two main study sites (note logarithmic vertical scale). (A) Relative recruitment at each stage. Dots and bars indicate mean (± 1 SE) of fruits removed from individual crops (Fruit removal), the percentage of seeds surviving (Post-dispersal seed survival) and germinating (Germination) in experimental plots (with 95% binomial confidence intervals), and the percentage of seedlings emerging (Seedling emergence) and surviving by the end of the 2nd yr (Seedling survival) (with 95% binomial confidence intervals). (B) Probability of recruitment through the end of each stage (log scale). "Pre-dispersal" expectancies were arbitrarily set at 100% (A) and 1.0 (B).



Coupling of stages in the recruitment process.—The degree of coupling between different stages in the recruitment process influences the evolution of germination, seed bank, and seedling persistence strategies, and ultimately determines the persistence of species at the local and regional scales (Grubb 1988). Studies simultaneously monitoring seed rain and seedling survivorship have shown that early seedling recruitment may be spatially correlated with seed rain, although this concordance may vanish as seedlings age and establish as saplings (Hett 1971, Cook 1979, Collins 1990, Gill and Marks 1991, Houle 1992). Did the effects of sequentially acting factors through the *P. latifolia* recruitment process cause spatially correlated patterns of recruitment? This question may be addressed by examining whether seedling establishment 2 yr after dispersal was spatially correlated with the seed rain generated by frugivorous birds. An analysis of this sort is briefly illustrated here for the Agracea site.

For each sampling station, we computed the proportion of the total seed rain falling at the station, the proportion of seeds that survived post-dispersal pre-

dispersal relative to the total number of seeds surviving, the proportion of seedlings emerged relative to the total number emerged, and the proportion of seedlings surviving relative to the total surviving. Across stations, more seeds survived where seed rain had been greater ($r_s = 0.298$, $N = 48$, $P = 0.04$) and more seedlings became established where emergence had been greater ($r_s = 0.781$, $N = 48$, $P = 0.0001$), but the number of seedlings emerging was unrelated to the number of surviving seeds ($r_s = -0.087$, $N = 48$, $P = 0.55$). Seed rain and seedling establishment were thus spatially uncoupled despite the concordance existing between other stages, and the distortion occurred at the seed bank stage. Variable levels of seed germination, losses to pathogens, pre-emergence death of seedlings, and re-shuffling of dispersed seed through secondary dispersal (Augspurger 1983, Morris et al. 1986, Augspurger and Kitajima 1992, Houle 1992) are some of the factors that may have contributed to uncouple seed rain and seedling recruitment by erasing or distorting the variation among microsites in seed rain. Outdoor experiments revealed that differences among individual plants

in germination and seedling establishment were related to variation in seed mass. With as fine-grained a seed rain pattern as the one documented here, a given spot of the forest most likely received a random assortment of seeds with regard to parentage and size, and this would interact quite unpredictably with the particular abiotic conditions of the microsite.

CONCLUSION

Recruitment is a complex and multifarious process involving several sequentially connected stages. The importance of no stage should be either downplayed or overemphasized a priori. Consideration of recruitment as a continuous, multistep sequence of events is essential to our understanding of vegetation dynamics and of the evolution of individual traits affecting demographic patterns in plant populations (Grubb 1977, Schupp et al. 1989, Whelan et al. 1991). Furthermore, the demographic and evolutionary relevance of the interaction between fleshy-fruited plants and their dispersal agents will depend on the effectiveness of dispersal at influencing patterns of population recruitment (Howe 1989, Jordano 1992). Stages in the recruitment process have been most often examined one stage at a time, and although these detailed investigations have enhanced our knowledge of the factors involved in seed dispersal and population recruitment, we must be aware that these "zoom-in" approaches hardly allow a realistic reconstruction of the general outline of the overall process. The main contribution of this study lies precisely in its attempt at providing a comprehensive, sequential picture of the recruitment process of *P. latifolia*. The main conclusion of our investigation is that later acting factors in the recruitment process have a definite potential to obscure or even cancel the effects of earlier ones, thus leading to a serious disruption in the continuity of the process and a reduction in the overall predictability of its demographic consequences. The breakdown of overall predictability is a reflection of the uncoupling of separate stages, whose extent may vary broadly among habitats. From the viewpoint of the mother plant, the collapse of predictability at some point in the recruitment process entails an important "loss of control" over its final consequences. This conclusion is further supported by the considerable spatial randomness existing in virtually all stages of the recruitment process. Even though statistically significant spatial patterning was found, for instance, in seed rain and seedling emergence, most spatial variance was accounted for by variation at the lowermost levels of spatial resolution, on the order of a few metres or even centimetres. Patterns of fruit removal and seed rain generated by dispersal agents may be subsequently erased or distorted by factors acting later in the process or simply obscured by very fine-grained spatial randomness. The influence of frugivorous animals, however, will depend on the extent of coupling of the different stages in the recruitment process, which is largely

site- or population-specific. In recruitment, the whole is not the sum, but the product of parts, and as such, permanently susceptible to the overwhelming influence of some near-to-zero operand.

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APPENDIX 1

Relative importance (percent cover) of woody species at the two main study sites (based on cumulative intercepts along 20 m long transects).

Plant species	Percent cover	
	Agracea (<i>N</i> = 12 transects)	Hoyos de Muñoz (<i>N</i> = 10 transects)
<i>Arbutus unedo</i> *	7.9	15.1
<i>Daphne gnidium</i> *	0.2	1.2
<i>Erica arborea</i>	10.9	0.4
<i>Juniperus oxycedrus</i> *	11.2	0.8
<i>Lonicera implexa</i> *	0.1	1.0
<i>Phillyrea angustifolia</i> *	1.1	1.0
<i>Phillyrea latifolia</i>*	29.8	18.2
<i>Pinus pinaster</i>	0.9	0.6
<i>Pistacia lentiscus</i> *	...	2.2
<i>Pistacia terebinthus</i> *	0.1	1.9
<i>Quercus faginea</i>	0.6	0.7
<i>Quercus rotundifolia</i>	31.9	15.7
<i>Rosa canina</i>	...	1.3
<i>Rosmarinus officinalis</i>	0.7	5.5
<i>Rubia peregrina</i> *	...	2.0
<i>Rubus ulmifolius</i> *	...	7.3
<i>Smilax aspera</i> *	1.1	3.8
<i>Viburnum tinus</i> *	0.4	17.7
Open ground	3.2	3.3

* Fleshy fruit-producing species. Species recorded at only one site and with <1% cover are: *Cistus salviifolius*, *Jasminum fruticans**, *Pinus halepensis*, and *Quercus coccifera*.

APPENDIX 2

Correlation matrices (Pearson product-moment) for characteristics of individual *Phillyrea latifolia* plants and fruit removal estimated as the percentage of the fruit crop and the absolute number of fruits removed by birds. Correlations above the diagonal are for Agracea (*N* = 32 plants) and those below the diagonal are for Hoyos de Muñoz (*N* = 18 plants).

Character	HEIGHT	CROP	CONS	DIAM	SEEDWT	DISP
Plant height (HEIGHT)	...	0.572****	0.093	0.457**	0.234	0.483**
Fruit crop size (CROP)	0.424	...	-0.092	0.320	0.207	0.710****
Percent fruits consumed (CONS)	-0.099	-0.286	...	0.334	0.368*	0.592****
Fruit diameter (DIAM)	-0.039	-0.072	0.400	...	0.565****	0.444**
Seed mass (SEEDWT)	0.182	0.356	-0.058	0.591**	...	0.429**
Number of seeds dispersed (DISP)	0.418	0.949****	0.023	0.078	0.335	...

**** *P* < 0.0001, ** *P* < 0.01, * *P* < 0.05.