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Spatial patterns in long-distance dispersal of *Quercus ilex* acorns by jays in a heterogeneous landscape

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In this paper, I analyse the interaction between the holm-oak *Quercus ilex*, and one of its main dispersers, the European jay *Garrulus glandarius*, in an heterogeneous Mediterranean landscape. I quantify the spatial dispersal pattern of the seed shadow at two spatial scales, landscape (among patches) and microhabitat (within patches), by directly tracking the movement of seeds. Two main traits of the jay-mediated dispersal of holm-oak acorns across the landscape, the spatial pattern of dissemination and the distance from the source tree, are significantly and directly influenced by jay activity. Jays moved acorns nonrandomly, avoiding one main patch type of the study area to cache acorns, the shrubland-grasslands, and moving most of the acorns to pine stands, whether afforestation or open pinewoods. Within each patch type, jays had also a strong preference for caching acorns in some microhabitats, since >95% of the acorns dispersed by jays were cached beneath pines. The distance of holm-oak acorn dispersal was long in the study site, over 250 m, with some dispersals occurring up to 1 km from the source oaks. The shape of the dispersal kernel function fitted to the dispersal pattern produced by jays differed from those quantified for many other plant species. Jay-mediated dispersal had two components, one local and another produced by long-distance dispersal. Due to the heterogeneity of these Mediterranean environments, this difference in scale overlaps with a difference in habitat composition, short distances events resulting in dispersals within the same oak stands and long distance events resulting in dispersal outside of oak stands, usually to other vegetation units. Jay activity and movement pattern can have thus dramatic effects on both the local regeneration as well as the potential for regional spread of the holm-oak populations.

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Seed dispersal plays a pivotal role in the demography of plants, and thus is crucial for the maintenance of most plant populations (Clark et al. 1999a, Jordano 2001, Wenny 2001). Dispersal is, furthermore, a key process determining the spatial distribution of seeds and, thus, of the subsequent recruitment probabilities of individuals (Schupp 1995, Schupp and Fuentes 1995, Wenny 2000, Nathan et al. 2000). In animal-dispersed plants, the spatial arrangement of dispersed seeds, or the seed shadow, depends greatly on the disperser activity (Jordano and Godoy 2002, Schupp et al. 2002). Despite the large number of studies on a wide variety of aspects of seed dispersal by animals, the actual role of dispersers in creating seed shadows and the consequences of distinct seed shadows for plant recruitment are still poorly known (Wenny 2000, Jordano and Schupp 2000, Jordano and Godoy 2002). This lack of knowlegde is partially due to the difficulty of tracking the actual movements of seeds by dispersal agents (Overton 1994, Wenny and Levey 1998, Wenny 2000, Levey and Sargent 2000, Godoy and Jordano 2001).

Most landscapes are highly heterogeneous at several spatial scales (Turner et al. 2000), and studies of plant-animal interactions must take into account the roles of both the heterogeneity and the spatial scale in the putative outcomes of interactions. Specifically, dis-

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persers in heterogeneous environments can move seeds over a wide range of distances, with disparate consequences for plant populations (Clark et al. 1998, Rees et al. 2000, Eriksson and Ehrlén 2002). Whereas short movements primarily influence local regeneration, long movements affect the migration of individuals between different patches or populations and the population spread and colonization patterns across the landscape (Vander Wall 1990, Ehrlén and Eriksson 2000, Rees et al. 2000, Clark et al. 2001). Thus, not only the local population dynamics but also the regional distribution of some species can be limited by dispersal in heterogeneous environments (Willson 1993, Eriksson and Ehrlén 2002, Jordano and Godoy 2002, Schupp et al. 2002). Curiously, most studies on the role of dispersers on plant populations have traditionally focused on the dispersal events occurring at local scales, within the population limits (Wenny and Levey 1998, Wenny 2000, Jordano and Schupp 2000, Rey and Alcántara 2000, García 2002, and references therein), a process that, although necessary for local regeneration, cannot explain plant population expansion to other areas. Understanding colonization of unoccupied patches, by contrast, must be achieved not only determining local dispersals but mainly by carefully studying the dispersal events taking place outside the limits of existing populations as well as the ecological factors limiting recruitment in these potentially colonizable places (Johnson and Webb 1989, Schupp et al. 1997, Clark et al. 1998, Bossuyt et al. 1999, Cain et al. 2000). In this context, dispersal of trees to other forested or non-forested habitats, although an important ecological process for understanding the dynamics of forests at a larger spatial scale, has seldom been explored.

In this paper, I analyse the interaction occurring between a plant species, the holm-oak *Quercus ilex*, and one of its main dispersers, the European jay *Garrulus glandarius*, in a heterogeneous Mediterranean landscape. I quantify the spatial pattern of dispersal by directly tracking the movement of seeds. The specific goals are to determine 1) the effect of environmental heterogeneity on jay activity patterns and thus on the resulting acorn dispersal; 2) the dispersal pattern generated by jays, differentiating between local and long-distance movements of acorns; and 3) the difference between the spatial distribution pattern of acorns observed directly from jay flights and that estimated from dispersed seeds.

Methods

Study area

The study site (35 ha in total) is located in the head of the river Huenes valley (Sierra Nevada Protected Area, SE Spain), and altitudinally distributed between 1550 and 1900 m a.s.l. It was formerly a mixed forest dominated by autochthonous Scots pines (*Pinus sylvestris nevadensis*) in the wettest parts and by holm oaks in the driest parts, together with other tree species (*Acer opalus* ssp. *granatense*, *Taxus baccata* and *Sorbus aria*). Most of the holm oaks and autochthonous pines disappeared during the last century due to human activities (grazing, charcoal production, etc.). In the 1950s most of the surface of the entire area was afforested with allochthonous pines (mainly *Pinus sylvestris iberica*, and to a lesser extent *P. nigra* and *P. pinaster*) and only the steepest areas with poor soil escaped afforestation. Consequently, the landscape is now a mosaic of small patches of mixed oak-autochtonous pine woodlands coexisting with several to many afforestation stands.

Climate in the zone is continental Mediterranean, with cold winters and hot summers, with severe summer drought (July–August). The mean minimum temperature in the coldest month (January) is −0.9°C, the mean maximum of the hottest month (July) is 29.0°C, and the mean annual temperature is 11.5°C. Rainfall is concentrated mainly in autumn and spring, with an annual rainfall of 825 mm (mean 1990–1998; data from the climatic station located in the center of the study site at 1650 m a.s.l.).

Landscape and microhabitat structure

I defined four main patch types ocurring in the overall study zone, based on vegetation cover and on the species forming the canopy: 1) "oak-pine woodland", small fragments of oak woodlands composed of large oak trees and many reproductive resprouts, intermingled with isolated adult Scots pines *Pinus sylvestris*, Corsican pines *P. nigra* and cluster pines *P. pinaster*; 2) "afforestation", medium to large patches of old autochthonous Scots pine forests and oak woodlands which have been re-forested with non-native Scots and Corsican pines; 3) "open pinewood", remains of the original autochtonous pine woodlands with some scattered oaks and abundant understory cover of shrubs but without reforestation; and 4) "shrubland-grassland" patches without trees and occupied with many different species of shrubs, scrubs and/or herbaceous vegetation. I pooled all these different types of non-forested patches in a single category since they potentially represented an homogeneous physiognomic type for the jays.

By using abundant observation of the overal study zone acummulated during the last 6 yr, and an digitalized aerial photography (1:2000 from a 1:10 000 original photography taken in 1999), I determined the number of patches of the above-defined patch types. Patches were projected in the georeferenced topographic map as polygons, and the following structural traits of the landscape were quantified: 1) size of each patch, in ha; 2) the perimeter/area ratio of each patch; and 3) the shortest distance from the border of each oak-pine woodland to the border of any other type of patch (Turner et al. 2000).

To determine the microhabitat cover and to carry on the measurements on jay dispersal and caching behaviour, I marked during 1999 four plots of 100 × 100 m in oak-pine woodlands, each in a different patch, and 8 plots in afforestations, two 100 × 100 m plots in two patches and six 25 × 25 m plots in a different large patch. These latter plots were separated by > 100 m (Gómez et al. 2001a). In 2001 I established a 100 × 100 m plot in an open pinewood patch and a 70 × 50 m plot in each of two grassland-shrubland patches. The size of the plots were based on the size of the patches. These plots were haphazardly located to cover a representative area of each patch and to leave a buffer zone 5 m wide. I defined ten types of microhabitats based on both the type of soil and vegetation cover (Jordano and Schupp 2000): 1) "holm-oak", under the canopy of adults and juveniles holm oaks; 2) "pines", under the canopy of adult trees belonging to any of the three species of pines ocurring in the zone; 3) "tall shrubs", under the canopy of shrub species > 1.50 m tall, including *Juniperus oxycedrus*, *Crataegus granatensis*, *Prunus ramburii*, *Rosa* spp., *Amelanchier ovalis*, and juveniles of pine; 4) "low shrubs", under the canopy of shrubs < 1.50 m tall, including *Juniperus communis*, *Rhamnus myrtifolius*, *Berberis hispanica*, *Rubus ulmifolius* and *Arctostaphyllos uva-ursi*; 5) "brooms", beneath fabaceous tall shrubs including *Adenocarpus decorticans*, *Genista cinerea* and *Cytisus reverchonii*; 6) "spiny scrubs", beneath stunted spiny scrubs 50 cm high, including *Erinacea anthyllis*, *Echinospartium boissieri* and *Astragalus granatense*; 7) "non-spiny scrub", beneath stunted scrubs 50 cm high, including *Salvia lavandulifolia*, *Thymus mastichina*, *Artemisia campestris*, *Lavandula viridis*, *Ononis aragonensis*, *Santolina rosmarinifolia*, *Genista versicolor*; 8) "tussock", beneath perennial herbs > 50 cm tall including *Dactylis glomerata hispanica*, *Cynosurus echinatus* and *Brachipodium* sp.; 9) "rock", boulders and rock substrate; and 10) "open", which includes both bare soil with small gravel and cobble and with sparse herbaceous cover, mainly annuals and short-lived perennials, as well as deep soil with thick cover of herbs. The relative abundance of microhabitat types was estimated in each large plot by means of 5 linear 50-m transects running the length of each plot (Bullock 1996). At each meter of the tape the presence/absence and the identity of vegetation covering the ground were recorded at three points, the center and 1 m to each side at and perpendicular to the transect. In each 0.12-ha plot (those located in afforestations), the relative abundance of each microhabitat type was estimated by locating at random 100 point per plot (N = 600 points).

Movement pattern of acorns by jays

The movement pattern of acorns dispersed by jays was estimated during two years (2000–2001) by observing jays moving acorns during the dispersal period of holm oaks (October–November) in the four intensively studied oak-pine woodland plots. Observations were carried out from sunrise to sunset from three positions, recording: time, weather, and number of jays foraging on the observed patch. The location of these positions allowed me to track the flight paths of the jays after feeding on acorns, and determine in most cases the locations of the caches. To accurately determine the caching destination, I always watched from a vantage point from which I could see the entire study area, being careful not to disturb the normal behaviour of the birds. Visibility was good since birds flew above the trees. The observation points allowed scanning the whole study zone with the different patches of oaks and other vegetation types. When a foraging jay left an oak with an acorn in the bill, I followed it until it landed, noting the patch of the destination, the behaviour after landing, and when possible, the microhabitat where the jay cached the acorns. Microhabitats was mostly determined when dispersal distances were short and when stand destination was pine plantation, since no shrub grow in the understory of the dense pines in this type of stands, and thus the caching microhabitat was in these cases under pine (see Results). Nevertheless, these flights represented > 90% of the total. Dispersal distances were estimated by marking on an aerial photograph of the study site the departure and the burial points. Although jays usually move more than one acorn per flight and sometimes can transport acorns only in their distensible esophagus (Vander Wall 1990), I conservatively defined as dispersal flights only those carried out by jays transporting an acorn in their bills (Johnson et al. 1997). Dispersal distance was defined as the distance between the focal oak and the point in which the jay went down to the ground to bury the acorns (Johnson and Adkisson 1985). Many times the jays perched in tall trees located in the middle of the way, changing even the direction of the flights. In these cases, I still considered as dispersal distance the straight line between the focal oak and the final caching destination (Johnson and Adkisson 1985). In addition, in most cases I was able to observe only the caching of the first acorn, and thus my estimates of dispersal distance are underestimates. Nevertheless, when possible I followed the birds until they buried all acorns, considering in these cases the distances existing between the departure point and the points where each acorn was cached as different dispersal distances, each acorn contributing to a different dispersal distance.

To estimate the number of acorns moved per flight I used two complementary methods. First, I made direct observations of jays foraging in oaks located close to my observation points. In addition, to increase the number of observations, I artificially fed jays with acorns during two months to acclimate them to the food source and to our presence. After this, I observed during two weeks their behaviour from a hide situated 4 m away, noting the number of acorns taken into their distensible esophagus and the size of the acorn transported (using as comparison the bill length of the jays). The food supplementation point was visited by at least 10 different individuals, although I pooled the data since I was unable to mark all of them and to recognize every individual jay every time.

Characteristics of acorn caches

I looked for caches from November to June every year of study in the study plots, by recording recently-emerged seedlings, In addition, in some plots where seedlings were scarce, I also sampled the soil up to 5 cm depth in quadrats of 2 × 2 m randomly distributed. I defined a cache according to the spatial position with respect to adult oaks and to the location of the acorn within the soil. It was impossible to me to distinguish the jay-produced caches from cache made by wood-mice, and for this reason some caches used in this study could correspond to rodent dispersal. For each cache that I was able to recover, I recorded the following main traits: 1) microhabitat type as described above; 2) depth in cm of the buried acorn from the top of the acorn to the ground surface (including litter); 3) burial substrate, differentiating between soil, when the acorn was buried into the ground, and litter, when the acorn was deposited just beneath the litter layer but not buried into the soil; 4) distance to nearest adult oak; and 5) in those caches found in the microhabitat pine, the distance to the nearest pine trunk or any other landmark.

Fitting of the empirical dispersal curves

The empirical dispersal curves were first fit by using the first-degree (linear) polynomial of the response surface methodology (RSM) model as:

$$u^{\varepsilon} = \alpha + \beta r^{\theta}$$

where u is density or percentage of flights made by jays to a given distance r from the seed source and α, β and θ are constants indicating the shape of the curve (Turchin 1998). Depending on the number of parameters considered, this general model can convert to many widely used functions. I fit the overall dispersal curve produced by jays, and I then split the curve into two components, one describing the flights made within the same patch and the other describing the flights made to other patches. I considered the Portnoy and Willson (1993) full model:

$$u = ar^{\phi} \exp[-br^{\theta}]$$

as well as the special cases of the negative exponential (if $\phi = 0$ and $\theta = 1$), the negative power law ($\theta = 0$) and the gaussian ($\phi = 0$ and $\theta = 2$) submodels (Turchin 1998). In addition, to fit the flights carried out to other patch types, I extended the RSM models to incorporate the second-degree (quadratic) polynomials since visual inspection showes the existence of a optimum in the empirical curves. In this case I used both direct ($\varepsilon = 1$) and inverse models ($\varepsilon = -1$). Finally, the overall dispersal curve produced by the jays in the study site was fit by incorporating the third-degree (cubic) polynomial, as:

$$u^{-1} = a - b \log r + c(\log r)^2 - d(\log r)^3$$

The goodness of fit between theoretical models and empirical curves were analyzed in all cases by using an iterative method (Gauss-Newton method, Anon. 1997) to search for the least-square estimates of the parameter values. This method provides approximate standard errors of the estimates as well as profile confidence limits (Anon. 1997). To compare between models, I used the Schwarz Bayesian Criterion (SBC), computed as:

$$n \ln(SS(Res)_p) + \ln(n)p' - n \ln(n)$$

where n is sample size, p′ is number of parameter of each model and $SS(Res)_p$ is the residual sum of squared errors (Rawling et al. 1998). The model obtaining the minimum value is considered more appropriate (Rawling et al. 1998). I preferred this criterion over the Akaike Information Criterion (AIC) because it uses the multiplier ln(n), more heavily penalizing models with a large number of independent variables than does AIC (Rawling et al. 1998).

Results

Landscape and microhabitat structure

The main patch types in the study site are the oak-pine mixed woodlands (41.6% of the surface) and the pine afforestations (36.5%). By contrast, the shrubland-grasslands only occupy 15.7% of the surface, and the open pine woodland 3.1% of the surface. There were no differences in the sizes of the patches belonging to each patch type ($H = 0.37$, $DF = 3$, $p = 0.93$, Kruskal-Wallis test), due to large variance in size. Though not significantly different, it is instructive to note that the average estimated size was 1.64 ± 0.43 ha ($n = 9$ patches) for oak-pine woodlands, 2.16 ± 1.0 (n = 6 patches) for pine afforestations, 1.08 for the only open pinewood patches occurring in the study zone and 1.09 ± 0.35 (n = 5 patches) for shrublands-grasslands. There were significant among-patch type differences in the mean distance to the closest oak-pine woodland ($F_{3,140} = 5.17$, $p = 0.002$), however. Thus, the average estimated distance from an oak-pine patch to the closest shrubland-grassland was 227 ± 29 m, to an open pinewood was 397 ± 85 m, to the closest afforestation was 159 ± 20 m and to the closest oak-pine woodland was 199 ± 28 m.

In the afforestation plots there was almost 100% cover of the microhabitat pine (Table 1), > 80% of these being Scots pine *Pinus sylvestris*. A few scattered oaks survived among the pines and a small amount of open existed where pines have fallen collapsed creating a small gap (Table 1). In addition, > 95% of the ground surface under pine canopies was covered by open (without understory); only a very few individuals of *Rosa* sp. and *Crataegus granatensis* were found.

In the open pinewood the pine cover was 19%, of which ca 16% was *Pinus nigra* and 3% was *P. sylvestris nevadensis* (Table 1). In this patch type, there was a high proportion of surface covered by open (bare soil), tall shrubs (mainly *Amelanchier ovalis* and *Crataegus granatensis*), low shrubs (*Arctostaphyllos uva-ursi*) and spiny scrubs (mainly *Echinospartium boissieri*).

In the plots located in oak-pine woodlands, oaks covered ca 10% of the surface, whereas pines covered ca 13%, of which 10% was *P. sylvestris*, 2.5% was *P. nigra* and the remaining was *P. pinaster*. In these plots, bare soil and non-spiny scrubs (mainly *Salvia lavandulifolia*, *Santolina rosmarinifolia* and *Thymus mastichina*) covered a large proportion of the surface (Table 1). Finally, most of the surface of the shrubland-grassland plot was covered by tussock species (mainly *Dactylis glomerata* and *Cynosurus echinatus*), non-spiny scrubs (*Thymus mastichina* and *Artemisia campestris*) and open, in this case being deep soils with a thick cover of annuals, short-lived perennials or small perennials (e.g. *Festuca* sp.), which do not grow large enough to dramatically change microclimate conditions, and usually dry off during summertime.

Spatial pattern of acorn dispersal by jays

During the two years of study, I observed 412 flights made by jays transporting acorns (dispersal flights). The daily number of jays dispersing acorns per oak-pine woodland patch was 6 ± 0.3 individuals (n = 21 censuses, 4 patches), and they usually moves in pairs or in trios. On average, there were 13.02 ± 2.67 dispersal flights per hour in each oak-pine woodland patch, although the number of dispersal flights varied through the day, being highest between 10 and 12 am (23.8 ± 9.7 flights h^{-1}, n = 14 d). Each bird transported on average 2.8 ± 0.1 acorns per flight (n = 103, range: 1–4), one in the beak and the others in the distensible esophagus.

Jays moved acorns to three different patch types: within the same oak forest patch from which they gathered the acorns, to the pine afforestations and to the autochtochnous open pinewood. During the two years of study I did not observe dispersal flights to any shrubland-grassland patch or between different oak-pine woodland patches. Jays dispersed significantly more acorns into afforestations than expected based on the cover of this patch type in the study site ($\chi^2 = 51.69$, DF = 5, $p < 0.0001$). In fact, 80.1% of the dispersal

Table 1. Percentage of surface covered by microhabitat type in each of the four patch types (microhabitat cover) and percentage of flights made by jays to each microhabitat to cache acorns (jay dispersal). In bold are those microhabitats preferred by jays for caching acorns within each patch type (after contigency analyses with $\alpha = 0.05$). N = number of transects, P = number of plots, F = number of flights.

Patch types	Oak-pine woodland		Shrubland-grassland†	Afforestation		Open pinewood	
Microhabitat type	Microhabitat cover (N = 10, P = 2)	Jay dispersal (F = 53)	Microhabitat cover (N = 10, P = 2)	Microhabitat cover (N = 10, P = 8) #	Jay dispersal (F = 330)	Microhabitat cover (N = 5, P = 1)	Jay dispersal (F = 29)
Holm-oak	10.50 ± 3.29	3.8	0	0.004 ± 0.04	0	1.44 ± 1.61	0
Pines + open	12.48 ± 4.42	**60.4**	0	99.98 ± 0.02	100.0	19.08 ± 5.13	**76.2**
Tall shrubs	6.56 ± 3.48	**15.1**	9.70 ± 1.67	0	0	13.86 ± 2.43	14.3
Low shrubs	2.21 ± 0.53	3.8	0.12 ± 0.13	0	0	12.54 ± 4.18	0
Brooms	3.28 ± 1.65	0	0	0	0	0	
Spiny scrubs	3.38 ± 1.29	**9.4**	0.26 ± 0.29	0	0	14.54 ± 3.43	9.5
Non-spiny scrubs	15.27 ± 13.00	5.7	17.50 ± 5.02	0	0	1.34 ± 0.30	0
Tussock	7.66 ± 2.54	0	42.96 ± 11.3	0	0	3.68 ± 2.20	0
Rock	3.45 ± 1.68	1.9	0.12 ± 0.13	0	0	1.9 ± 0.77	0
Open	37.62 ± 5.19	0	29.28 ± 8.01	0.004 ± 0.04	0	31.54 ± 3.43	0

†No dispersal flight was observed into shrubland-grassland during the two years of study.
In the afforestation 0.12-ha plots there were also 600 additional random sampling points.

flights were to afforestations, while only 12.9% were within the same oak-pine woodland patch, and 7.0% were to open pinewood patches (n = 412 dispersal flights).

The dispersal of acorns was also markedly directed towards specific microhabitats within each patch type. Thus, there were statistical differences between the expected (according to the microhabitat structure determined for each patch type) and the observed between-microhabitat pattern of acorn dispersal both within oak woodlands ($\chi^2 = 84.81$, $p < 0.0001$) and within open pinewood ($\chi^2 = 87.20$, $p < 0.0001$). Most acorns were cached, in both of these patch types, under pines and to a less extent, under shrubs (Table 1). Furthermore, in afforestations all caches I could observe were placed under pines, although I did not compare statistically the two distributions (expected and observed), since this was basically the only microhabitat in this patch type. When pooling all observations, across all patch types, 94% of the caches made by jays were made under pines.

The shape of dispersal curves produced by jays

Jays moved acorns between 5 and 1000 m, with an average of 262.9 ± 195.1 m [200] (mean ± 1 SE [median]). The average dispersal distance differed among patch types of destination ($H = 112.67$, $p < 0.0001$, Kruskal-Wallis), being much greater when jays moved acorns into afforestations (402 ± 16 m [250]) and open pinewoods (375 ± 41 m [200]) than when jays moved within the same oak woodland (72 ± 26 m [20]). Jays did not move acorns to the nearest afforestation patch since every oak-pine woodland patch was located much closer to another afforestation patch than to the one of destination.

The shape of the dispersal kernel produced by jays had two peaks, one at a very short distance and the other at an intermediate distance (Fig. 1). For this reason, the three-degree inverse polynomial (Model 2: $u^{-1} = 0.14 + 2.17 \log r - 2.50(\log r)^2 + 0.70(\log r)^3$, $R^2 = 0.87$, $F = 74.43$, $p = 0.0001$) fit well to the data. When splitting the dispersal curve by patch type of destination, I found that each curve fit a different function. Thus, the frequency of dispersal flights within the same oak-pine woodland patch was a gradually decreasing function of the distance from the source oak (Fig. 1), generating a dispersal curve that, although significantly fitting all theoretical kernels tested, best fit the Portnoy and Wilson (1993) Full Model according to the Schwarz Bayesian Criterion (Table 2). In contrast, when jays moved acorns into afforestations or into the open pinewood, they produced a dispersal kernel with a maximum peak at intermediate distances from the source oak (Fig. 1), thereby significantly fitting only the quadratic polynomial function (Table 2). Consequently, the skewness of the density distributions was much higher for dispersal within oak-pine woodlands (1.049) than for dispersal to afforestations and open pinewoods (0.666 and 0.816).

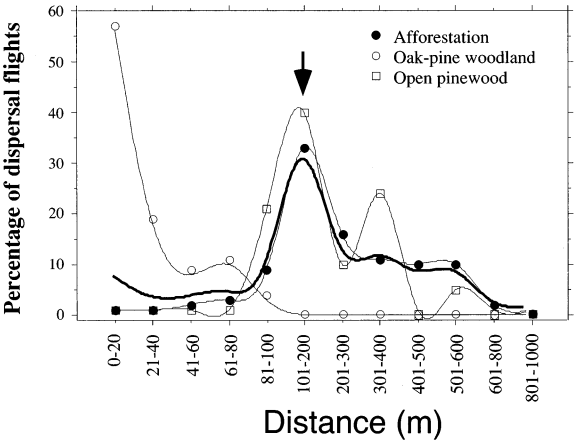

Fig. 1. Empirical dispersal curves produced by jays in the study site during the years 2000–2001 depending on the patch type where they deposited the acorns. The thick solid line refers to the overall dispersal curve without splitting by patch types. The arrow shows the average distance from oak-pine woodlands to the nearest afforestation patch. Curves were fit by Smoothing Spline Fits ($\lambda = 0.1$, Anon. 1997), with $R^2 = 0.92$ for the overall curve, $R^2 = 0.99$ for the oak-pine woodland curve, $R^2 = 0.94$ for the afforestation curve and $R^2 = 0.89$ for open pinewood curve.

Traits of acorn caches

All caches I found during 2001 (n = 210) had a single acorn, except for one cache with two acorns. The mean distance of acorn caches to the nearest adult oak was 14.3 ± 0.9 m (n = 210), although it differed among patch types ($F_{2,163} = 48.87$, $p < 0.0001$, Fig. 2), being greater for acorns cached outside oak-pine woodlands (Fig. 2). The distance to the closest adult oak differed among microhabitats both for those caches located in oak-pine woodlands ($F = 4.4$, $DF = 4{,}59$, $p < 0.0001$) as well as for those located in the open pinewood ($F = 11.5$, $DF = 3{,}6$, $p < 0.01$, Table 3). The largest oak-cache distance in oak-pine woodlands was 11.5 ± 4.9 m for caches located under spiny scrubs, whereas it was over 50 m in the open pinewood for caches located under non-spiny scrubs and tall shrubs (Table 3). As observed in Table 3, the distance from the caches to the nearest oak was always less than the distances flown by jays from the source oaks to these microhabitats. The distance from acorn caches to the nearest adult oak was much greater in afforestations (19.0 ± 1.0 m) than in oak-pine woodlands (8.2 ± 0.9 m).

Jays did not cache the acorns at random in the afforestations. Caches located in the afforestation plots (n = 134) were closer to pine trunks, rocks and other landmarks than expected based on a nearest neighbour analysis (86.7 ± 6.0 [70] cm vs 119.4 ± 3.4 [105], mean ± 1 SE [median]; $D = 0.23$, $\chi^2 = 23.59$, $p < 0.0001$, Kolmogorov-Smirnov test).

The average burial depth was 1.5 ± 0.1 cm, ranging between 0.5 and 4.0 cm. There were no among-patch type or among-microhabitat differences in burial depth ($p > 0.1$ all cases, one-way ANOVAs). Aproximately 52% of the acorns were cached just beneath the litter, the rest buried in the mineral soil. The percentage of acorns buried in mineral soil as opposed to between litter and soil varied between microhabitats in oak-pine woodlands ($\chi^2 = 15.99$, DF = 6, $p = 0.01$), being highest when the cache was in bare soil (100%) and spiny scrubs (100%), and lowest in low shrubs (0%) and holm-oak (36%). In contrast, 100% of the caches found in the open pinewood had the acorns buried into the mineral soil regardless of microhabitat (Table 3). Jays buried acorns in the mineral soils less frequently in afforestation (32.6%) than under pine in oak-pine woodlands ($\chi^2 = 17.75$, $p = 0.0001$).

Discussion

Two main traits of the dispersal of holm-oak acorns across the landscape, the pattern of dissemination between patches and microhabitats and the distance from the source tree, are greatly influenced by the activity of European jays in the study site.

Table 2. Fit of the dispersal curves produced by jays transporting acorns to each patch type to the main RSM models considered (see Methods). The estimate values of each parameter was obtained by using the non-linear iterative Gauss-Newton method (100 iterations). Figures are least-square estimates ± approximated standard errors [confidence limits] for the model parameters.

Patch type		RSM Models				
		Full Model $u = ar^{-\phi} \exp[-br^{\theta}]$	Inverse Power Law $u = ar^{-\phi}$	Negative Exponential $u = a \exp[-br]$	Gaussian $u = a \exp[-br^2]$	Inverse Polynomial $u^{-1} = a + br + cr^2$
Oak-pine woodland	a	56.90 ± 1.97 [49.03–64.8]	57.29 ± 2.24 [52.32–62.27]	136.70 ± 16.05 [104.18–188.75]	75.39 ± 7.63 [57.78–98.76]	−0.36 ± 0.23 [−1.29–0.52]
	b	0.001 ± 0.001 [−0.04–0.05]		0.89 ± 0.09 [0.70–1.17]	0.30 ± 0.05 [0.18–0.49]	0.12 ± 0.05 [−0.09–0.34]
	ø	1.52 ± 0.19 [0.77–2.26]	1.65 ± 0.11 [1.44–1.92]			
	θ	3.07 ± 5.32 [−18.20–24.34]				
	c					0.01 ± 0.01 [−0.01–0.03]
	F	97.3*****	91.21****	37.26****	15.04***	424.15*****
	R^2	0.99	0.89	0.77	0.56	0.99
	SCB*	16.48	21.18	26.78	35.66	22.35
Afforestation	a	†	4.69 ± 5.49 [−17.26–26.64]	6.92 ± 5.47 [−14.96–20.11]	8.36 ± 4.42 [1.04–17.91]	−0.10 ± 0.07 [−0.32–0.03]
	b			0.02 ± 0.10 [0.28–0.20]	0.0004 ± 0.01 [0.01–26.03]	0.02 ± 0.01 [0.01–0.05]
	ø		0.33 ± 0.58 [−2.64–1.99]			
	c					0.04 ± 0.01 [0.02–0.09]
	F		3.838^{ns}	1.00^{ns}	0.08^{ns}	48.53****
	R^2		0.20	0.001	0.09	0.90
	SCB		56.74	57.32	57.42	22.35
Open pinewood	a	†	5.61 ± 8.50 [−28.38–39.61]	8.16 ± 8.41 [−25.49–41.80]	9.57 ± 6.50 [−16.42–35.56]	−0.20 ± 0.14 [−1.71–0.01]
	b			0.0003 ± 0.14 [−0.56–0.55]	0.002 ± 0.01 [−0.04 + 0.04]	0.04 ± 0.02 [0.01–0.28]
	ø		0.23 ± 0.77 [−3.3–2.83]			
	c					0.03 ± 0.01 [0.01–0.15]
	F		0.786^{ns}	0.09^{ns}	0.05^{ns}	33.4***
	R^2		0.02	0.09	0.09	0.75
	SCB		56.75	57.32	57.42	38.15

† Model failed to converge after 100 iterations.
* SCB refers to the Schwarz Bayesian Criterion.

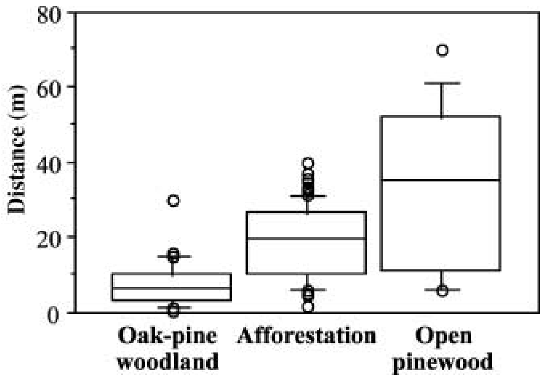

Fig. 2. Box-plots of the distance of the caches found in each patch type considered in this study to the nearest reproductive oak.

Pattern of acorn dissemination at landscape and microhabitat scales

This study has shown that European jays disperse acorns in heterogeneous landscapes nonrandomly. Birds completely avoided the shrubland-grasslands for caching acorns whereas the proportion of acorns moved within- or among-oak stands was also lower than expected based on the surface covered by this type of habitat. In contrast, jays dispersed most of the acorns to pine stands, whether afforestation or open pinewoods. This tendency to move acorns outside oak stands has been observed for European jays in other places (Patterson et al. 1991, Kollmann and Schill 1996, Rolando 1998) as well as for other jay species (Johnson et al. 1997), and it is presumably a strategy to decrease the risk of intraspecific kleptobiosis and secondary predation (Bossema 1979, Vander Wall 2001, Emery and Clayton 2001). Buried holm-oak acorns in Mediterranean woodlands are consumed mainly by two mammals species, the wild boar *Sus scrofa* and the woodmouse *Apodemus sylvaticus* (Focardi et al. 2000, Gómez et al. 2001a, Gómez 2003). In the study site, these two mammals look for acorns during the dispersal period (October–November) mainly in the oak stands and, consequently, postdispersal predation is significantly higher in oak woodlands than in pinewood patches (Gómez 2003). By caching acorns in afforestation, jays are surely decreasing the probability of lossing acorns to predators.

Spatial patterns of habitat use by jays is also heterogeneous within each patch type, with jays having also a strong preference for caching acorns in some microhabitats. Thus, in oak-pine woodlands jays cached acorns mainly under pines (60% of the caches), under tall shrubs and under spiny shrubs. This pattern also appeared in the open pinewoods, where jays also cached acorns mainly under pines. Finally, in the afforestations, where virtually the entire area is covered by pines, jays showed distinct preference, by caching acorns closer to the pine trunks than expected by chance. Consequently, > 95% of the acorns moved by jays were buried under pines in the study area. This spatial arrangement of caches has been previously reported for European jays and for other North-American jays (Bossema 1979, Vander Wall 1990), and three main reasons have been proposed to explain it. First, birds use these microhabitats as reference points, since most corvids use visual landmarks to rediscover their caches (Vander Wall 1990). Second, birds could try to avoid open sites to decrease their own risk of being preyed upon by hawks and mammalian carnivores, as has been observed in other places (e.g. Rolando 1998). Third, the most probable cause of caching acorns under pines is because it decreases the probability of postdispersal predation by some mammals like wild boars and rodents that use these microhabitats less intensely when searching for acorns (Gómez 2003). In this respect, to cach under spiny scrubs or shrubs could also decrease the probability of predation by boars since they are deterred by the spiny barrier of the plants.

Long-distance dispersal of acorns in heterogeneous landscapes

The average distance of holm-oak acorn dispersal was high in the study site, over 250 m, with some dispersals occurring up to 1 km from source oak trees. In addition, it is very probable that the long-distance dispersal reported in this study be underestimated since only the bill-transported acorns contributed to reliable distance estimates, and it is possible the existence of carryover among different locations of the acorns transported in the esophagous. Long-distance events have been reported for some plant species, many of them dispersed by jays, which can move acorns and nuts over several kilometers (Chettleburgh 1952, 1955, Swanberg 1969, Vander Wall and Balda 1977, Johnson and Adkisson 1985, Vander Wall 1990, 2001, Lanner 1996, Johnson et al. 1997). However, only a few studies have systematically measured the frequency of long-distance dispersal events, and there still is not a clear picture of the importance of long-distance dispersals for plant population dynamics (Higgins and Richardson 1999, Cain et al. 2000). This scarcity of reports of long-distance dispersal events can be partially due to the usual methodology used to quantify dispersal. The ability to follow seed dispersers from the focal trees to the places of seed deposition as in this study allows the exact determination of the seed shadow patterns (Overton 1994, Wenny 2000, Levey and Sargent 2000). In contrast, using seed traps or seedling distribution pattern rather than observing true movements of sedes makes it difficult to infer the exact source tree, and thus the true distance of dispersal can be understimated (Bossuyt et al. 1999, Jordano and Schupp 2000, Nathan and Muller-Landau

Table 3. Characteristics of the caches found in each microhabitat of each patch type. It is shown the distance in meters of caches to nearest adult oak, the burial depth in cm, from the acorns to the top of the ground and the percentage of caches made in mineral soil. The distance covered by jays when caching acorns in each microhabitat is also shown, estimated from the point where the jays collected the acorns to the cache destination per microhabitat.

Microhabitat	Jays flights		Oak-pine woodland				Afforestation				Open pinewood			
	n	Distance (m)	n	Distance (m)	Depth (cm)	% caches n soil	n	Distance (m)	Depth (cm)	% caches in soil	n	Distance (m)	Depth (cm)	% caches in soil
Holm-oak	2	35.0 ± 15.0	15		2.0 ± 0.3	35.7	0				0			
Pine	32	38.4 ± 04.6	32	8.7 ± 0.9	1.7 ± 0.2	75.0	92	19.0 ± 1.0	1.4 ± 0.1	32.6	2	9.5 ± 3.5	2.0 ± 1.0	100.0
Tall shrubs	7	21.5 ± 01.9	5	7.1 ± 1.6	1.6 ± 0.2	80.0	0				4	54.2 ± 5.4	1.7 ± 0.5	100.0
Low shrubs	1	20.0	1	8.2	1.0	0.0	0				0			
Spiny scrubs	5	10.4 ± 03.7	2	11.5 ± 4.9	2.5 ± 0.5	100.0	0				2	18.0 ± 7.0	1.5 ± 0.5	100.0
Non-spiny scrubs	3	12.3 ± 01.5	5	3.7 ± 0.6	0.7 ± 0.1	80.0	0				1	52.0	1.0	100.0
Open	0		4	9.0 ± 3.8	1.0 ± 0.0	100.0	0				0			
Rock	1	10.00	0				0				1	6.4	1.0	100.0
F-ratio or χ^2		1.34ns		4.4***	1.5ns	15.99*						11.5**	0.2ns	

2000, Nathan et al. 2000, Godoy and Jordano 2001, Jordano and Godoy 2002). My results agree with this idea, since I found that the distances between focal oaks and caches were always greater than the distances between caches and the nearest adult oaks, irrespective of microhabitat (Table 3). By directly observing jay movements I was able to discover many long-distance dispersal events which would be overlooked by other techniques. Unfortunately, such direct observations are not always feasible.

The dispersal kernel produced by jays in the study site showed a shape differing from those quantified for many other plants, both wind- and endozoochorously-dispersed species. Most plants show a seed dispersal curve in which the dispersal probability is highest close to the focal tree, decreasing gradually with distance from this point source (Willson 1993, Greene and Johnson 1996, Clark 1998, Clark et al. 1999b, Cain et al. 2000), and this general pattern occurs even after considering long-distance dispersal events (Clark 1998, Clark et al. 1999b, Bullock and Clarke 2000). In contrast, I have found that the dispersal curve produced by jays had two peaks, one local within the same oak patch (1–20 m) and another produced by long-distance dispersals to pine patches (ca 200 m), which suggests that jays move holm-oak acorns in the study site according to a stratified process (Shigesada et al. 1995, Higgins and Richardson 1999, Clark et al. 1999a, b, Cain et al. 2000). I think that this situation is site-dependent, only occurring in those heterogeneous landscapes like the one study here that have two relevant spatial scales, among stand and among microhabitats within stand. Furthermore, the second peak of dispersed acorns was much higher than the first. That is, contrary to most other cases reported, the long-dispersal events (considering those higher than 100 m from the source, Cain et al. 2000), rather than being scarce, were the most frequent. Consequently, the highest probability of finding a jay-dispersed acorn is far from rather than close to the maternal plant, and this is apparently driven largely by the distance to an afforestation patch. In fact, the average minimum distance between oak patches and afforestation patches was ca 160 m, very close to the distance to the maximum probability of acorn dispersal (Fig. 1). Furthermore, the jays produced a small but important amount of extreme dispersal events (sensu Clark et al. 2001), those being > 800 m from the focal tree. The directed dispersal displayed by jays, which shows a strong preference for pine stands for caching acorns (see also Vander Wall 1990, 2001, Lanner 1996, Johnson et al. 1997, and references therein), and the landscape-level heterogeneity of the study site are the two main reasons that synergistically produce the dispersal curve observed in this study. Nevertheless, this type of dispersal curve should be more frequent than previously reported, especially in heterogenous landscapes and for plant species having several modes of dispersal, as has been suggested by Clark et al. (1998); see also Shigesada et al. 1995, Clark et al. 1999b). For example, Fragoso (1997) have shown that the neotropical palm *Maximiliana maripa* is dispersed by organisms moving at two different spatial scales, with rodents and other small mammals producing movements at a scale of meters and tapirs inducing movements at a scale of kilometers. It may in fact not be uncommon for tree species to be dispersed locally by one set of dispersers and over long distances by another set (Clark et al. 1998); the former are seen in published dispersal kernels, the later are generally missed.

Implications for oak population dynamics in heterogeneous landscapes

Acorns of holm oaks are dispersed by only two organisms in the study site, jays and woodmice. Jays, however are presumably much more important as dispersers than are mice, which act mainly as seed predators (see also Bossema 1979, Lanner 1996, Wenny 2001). First, due to their restricted home ranges rodents relocate and consume most of the acorns (up to 99%) buried in their territories (Miyaki and Kikuzawa 1988, Wada 1993, Herrera 1995, Iida 1996, Kollmann and Schill 1996, Santos and Tellería 1997, Wang et al. 1999). Moreover, many rodents are larder-hoarders, and usually hoard the acorns in huge and deep piles located within their own nests, from which successful establishment of seedlings is unlikely (Vander Wall 1990). In fact, unpublished observations carried on the same study site suggests that woodmice consumed > 95% of the dispersed acorns (Gómez unpubl.). In contrast, jays are scatter-hoarders, storing acorns individually and separated by > 1 m, in some cases up to 15 m. Jays also appear to retrieve a smaller proportion of the caches (DeGange et al. 1989, Lanner 1996). In addition, jays buried acorns at 1–3 cm depth, most time in mineral soil, which can enhance the probability of seedling emergence and survival through summer drought (Vander Wall 1990, Kollmann and Schill 1996). Furthermore, jays move acorns over much longer distances than rodents (Sork 1984, Iida 1996, Kollmann and Schill 1996, Hoshizaki et al. 1999), and thus can decrease the potential mortality caused by density-dependent factors near conspecifics (Wenny 2001). Nevertheless, a potential indirect positive effect of rodents is that by their pilfering of jay caches near oaks, they are forcing jays to cache in afforestations. Cache site selection by jays is to a large extent influence by rodents.

The main consequence of the non-random pattern of jay movement reported in this study is a concomitant heterogeneous spatial pattern of seed shadow, a common phenomenom in most animal-dispersal plants (Jordano and Schupp 2000, Jordano and Godoy 2002, Schupp et al. 2002) and that affect the recruitment dynamic of the oaks (Houle 1995, Schupp 1995, Jordano and Herrera 1995, Schupp and Fuentes 1995, Schupp et al. 2002). Most studies analyzing disperser effects on spatial pattern of plant recruitment dynamics have traditionally centered on a local scale, quantifying the between-microhabitat differences in recruitment probabilities (Rey and Alcántara 2000, García 2002 and references therein). At this local scale, jays presumably play an important role determining holm-oak recruitment, since seedling and saplings are usually located in the study site under pines, under shrubs and under scrubs (Gómez et al. 2001a), the microhabitats most used by jays to hide acorns. Nevertheless, in the case study here, non-random seed rain not only occurs at the most frequently studied small-spatial scale, that is, among distinct microhabitat types, but also at a larger spatial scale, among different patch types. Thus, this study has also reported a net movement of acorns from oak stands to pine stands. Gómez et al. (2001b) have showed that, according to this pattern of acorn movement, holm-oak seedlings and saplings are extremely abundants under the canopy of pines in most afforestation patches of the study site, whereas pine seedlings are virtually nonexistent (see Espelta 1996, Mosandl and Kleinert 1998, Retana et al. 1999, Lookingbill and Zavala 2000 for similar results). It seems that jays can also influence the recruitment patterns of oaks at the landscape scale. These birds probably play a key role in providing a bank of seedlings that, since close overstory constrains holm-oaks sapling growth (Retana et al. 1999), are "awaiting for a gap" in the afforestation canopy to grow to adulthood. This would allow the successful colonization of pinewoods by oaks and the presumably jay-mediated successional trend from pines to oaks that is widely observed in many western Mediterranean montane areas (e.g. Espelta 1996, Retana et al. 1999, Lookingbill and Zavala 2000).

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