

Frugivory at *Juniperus communis* depends more on population characteristics than on individual attributes

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Summary

1 We investigated the spatio-temporal variation in the interactions between the juniper *Juniperus communis* and its vertebrate frugivores (avian dispersers of *Turdus* spp. and predatory rodents *Apodemus sylvaticus*) in the Mediterranean mountains of south-east Spain.

2 Frugivore activity was evaluated at six sites and for 3 years, in relation to both plant reproductive traits (plant size, cone crop and cone size) and characteristics of the immediate environment (distance to the nearest female, abundance of perches, fruiting environment and habitat).

3 Plant characteristics and levels of frugivory varied strongly among the six populations. Cone production, cone size and frugivory also differed significantly among years for the same population. Avian frugivory was only occasionally affected by density of cones per plant, abundance of perches or abundance of other fruiting species, or by habitat. Rodent predation was positively related only to the density of cones per plant and then only in two sites.

4 Levels of both avian frugivory and rodent predation significantly increased in populations with higher cone production.

5 Both groups of vertebrate frugivores responded to the spatio-temporal variation in cone abundance at a regional scale, discriminating more between juniper populations than between individual plants within a population. The outcome of interactions with frugivores at the individual plant level thus proved more dependent on the whole-population characteristics than on individual attributes.

Key-words: common juniper, Mediterranean mountains, plant–animal interactions, seed dispersal, seed predation

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Introduction

Spatial and temporal variation in the interactions between a plant species and its frugivores may be a major influence on the process of seed dispersal, and thus have demographic and evolutionary effects (Jordano 1992, 1994; Thompson 1994; Herrera 1995). Patterns of interaction are known to vary at several spatial (among individual plants, among patches or habitats within a given site and among populations within a region) and temporal scales (between season and years, e.g.

Herrera 1984a, 1998; Willson & Whelan 1993; Jordano 1994).

Such interactions have been shown to be affected by different plant attributes (see Jordano 1992 for a review), for example traits such as fruit size (Jordano 1987; Sallabanks 1993) and individual crop size (Davidar & Morton 1986; Jordano 1987; Laska & Stiles 1994). In addition, frugivore activity around a given plant can also be affected by environmental characteristics, such as vegetation type or habitat structure (Herrera 1984a; Levey 1988; Alcántara *et al.* 1997) and the abundance and proximity of conspecifics (Moore & Willson 1982; Denslow 1987; Sargent 1990), as well as the presence of other plant species fruiting at the same time (Herrera 1984b; Englund 1993).

However, no study has questioned whether the well-documented relationships between plant attributes

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and frugivory are the source of variability in the observed interactions. In other words, to what extent does the spatio-temporal variation in plant–frugivore interactions mirror differences between plants, sites and years in plant attributes that affect frugivory? To answer this question, plant attributes and outcomes of the interactions must be studied simultaneously in a range of populations and years in the same region. The integration of data from plants within a given population and populations within a region will determine the most relevant scale for the interactions between plants and frugivores.

Common juniper (*Juniperus communis* L.) is a fleshy-fruited plant dominant in the Mediterranean mountains of south-east Spain, where it interacts with a small assemblage of avian dispersers (*Turdus* spp.) and one rodent predator (*Apodemus sylvaticus* L.). This relatively simple system allows the investigation of the consequences of the spatio-temporal variability of frugivory, without the complexities that often complicate the detection of general patterns (Sallabanks 1993; Rey 1995). We examined:

- The magnitude of interactions between juniper and both classes of vertebrate frugivores, and their variation over six populations and 3 years.
- The degree to which such variation was related to either plant reproductive traits or the surrounding environment.
- The spatial scale where the patterns of plant–frugivore interactions emerge.

The plant–frugivore system

Juniperus communis (Cupressaceae) is widely distributed in central and northern Europe but further south its populations become restricted to scattered mountain areas around the Mediterranean Basin. In the Mediterranean mountains of south-east Spain *J. communis* inhabits altitudes from 1500 to 2500 m a.s.l., along with *J. sabina* L., *Berberis hispanica* Boiss. & Reuter, *Prunus rambourii* Boiss., *Genista versicolor* Boiss. and *Hormathophylla spinosa* (L.) Küpfer (Molero *et al.* 1992). It is a dioecious plant, with females bearing yearly fleshy cones (galbulae) which contain 1–4 seeds per cone (see García 1998a for a comprehensive description of cone development).

In the Mediterranean mountains seeds are dispersed by migrant thrushes, almost exclusively by the Ring-ouzel (*Turdus torquatus* L.), which overwinters in these areas, and the Mistle thrush (*Turdus viscivorus* L.), which visits juniper shrublands in the autumn (Jordano 1993; García *et al.* 1999a). During their stay both species feed almost exclusively on ripe juniper cones, collected either from branches or on the ground (Zamora 1990; García 1998b).

The generalist vertebrate woodmouse (*Apodemus sylvaticus* L.) also feeds on juniper cones in the region, consuming both pulp and seeds from cones. It is therefore a pre- and post-dispersal seed predator (García *et al.* 2000).

Methods

STUDY SITES

Six populations in south-east Spain were studied: Campos de Otero (2300 m a.s.l., Sierra Nevada, Granada), Dornajo (2000 m a.s.l., Sierra Nevada), Trevenque (1800 m a.s.l., Sierra Nevada), Maitena (2100 m a.s.l., Sierra Nevada), Collado Cabañas (1800 m a.s.l., Sierra de Cazorla, Jaén) and Boleta (2000 m a.s.l., Sierra de Baza, Granada, see García *et al.* 1999b for an extensive site description).

PLANT CHARACTERISTICS

A minimum of 20 female plants were randomly sampled in early autumn (late September–early October) for each population, with Campos de Otero, Dornajo and Boleta being repeatedly sampled for 3 years (1994, 1995, 1996), whereas the other sites were sampled only in 1995. A first group of parameters that might affect interactions with vertebrate frugivores involved plant traits (i.e. intrinsic characteristics). *Plant size* was measured as the basal area covered by the prostrate shrub and assuming ellipsoidal shape, *cone density per plant* was calculated as the mean number of ripe cones in a 0.04-m² quadrat placed on the plant surface ($n = 10$ per plant), and *cone size* was estimated as the ripe cone diameter, averaged from a sample of 30–40 cones collected randomly from each plant.

A second group of variables (extrinsic characteristics) were related to the surrounding environment of individual plants. *Nearest conspecific female distance* (NFD) was measured to the next reproductive plant, *perch abundance* was estimated as the number of potential perches (rocks, shrubs and tree saplings taller than 1 m) within a 25-m-radius, and *fruiting environment* was estimated as the abundance of fleshy fruits of other woody species within the same radius and was expressed as the sum of the values on a three-point scale (1 = 25–50 fruits/m², 2 = 50–100 fruits/m² and 3 = > 100 fruits/m²; see Levey 1988 for a similar procedure) for each plant. In addition, the habitat of each plant in the population of Campos de Otero was assigned as *dry hillside* (typical shrubland) or *wet meadow* (meadows close to mountain streams and abandoned irrigation channels, see García *et al.* 1999b for habitat description).

In autumn 1995, we calculated the percentage cover in each population for *J. communis* and for all other fleshy-fruited species present, by means of 10 linear 50-m transects covering a representative area of the stand (Bullock 1996). Presence/absence and identity of any vegetation cover were recorded at 1-m intervals along each transect and at 1 m either side of these points ($n = 150$ sampling points per transect).

AVIAN FRUGIVORY

In late November of each study year, the interaction

between juniper and avian dispersers (*avian frugivory*) was measured for each plant, by counting the average number of *Turdus* spp. droppings in 20 quadrats, each 0.04 m², arbitrarily located over the plant ($n = 10$) and in its immediate vicinity ($n = 10$). The conspicuous droppings, which were easily identifiable because of their size and content of cone remains and seeds, remained intact for a long period of time. This index provides an indirect estimate of the cumulative cone removal, assuming that consumption is proportional to the time spent by birds on each plant (Gutián 1987; see Herrera 1984b; Santos & Tellería 1994; Santos *et al.* 1999 for similar procedures). It can also be considered as a measure of dispersal success per individual plant, since total cone depletion is rare, and populations with lower disperser activity had more cones remaining on the plants after the dispersal period (personal observation by the authors). This measure of avian frugivory correlated positively and significantly with bird abundance per population and year ($r_s = 0.745$, $P = 0.025$, $n = 10$ populations, García 1998b).

RODENT PREDATION

Most of the plants studied had large accumulations of cone and seed fragments on the ground beneath their crowns, resulting from *A. sylvaticus* activity. In November we determined the interaction between juniper and rodents (*rodent predation*) in the tagged plants by sampling 10 quadrats of 0.04 m², randomly placed beneath plants. We used the proportion of samples containing cone remains with evidence of mouse predation as a direct estimate of the intensity of predation per plant (for similar procedures see Fuentes & Schupp 1998; García *et al.* 2000). This index provides an estimate of pre-dispersal losses, since such remains come from cones collected by rodents rather than seeds extracted from bird faeces. We detected no sign of seed predation attributable to other vertebrates: *A. sylvaticus* teeth marks are easily identifiable and damage attributable to voles (*Microtus* spp.) or greenfinches (*Carduelis chloris*) was never detected.

STATISTICAL ANALYSES

Our sampling design, with plants belonging to several populations monitored for 3 years, enabled us to analyse spatial and temporal variation in both plant traits and interactions with both types of frugivores. We used univariate repeated-measures ANOVAS in which plants were subjects, year was considered as the within-subject factor, and population as the random between-subjects factor. Plants within a population were used as the error term between subjects, and the year–plant interaction used as the error term within subjects (von Enden 1993). This type of analysis requires a balanced design over time (von Enden 1993) and these ANOVAS were therefore performed using only those populations from which we had gathered data every year (Campos

de Otero, Dornajo and Boleta). In order to consider among-population variation, we performed one-way ANOVAS considering 1995 data for all six studied populations, using all plant characteristics and both frugivores.

Relationships were firstly analysed within each population, by means of multiple regression analysis considering plant characteristics as independent variables and each type of frugivory as a separate dependent variable (see Herrera *et al.* 1994 for a similar procedure). In the case of populations from Campos de Otero, Dornajo and Boleta, where sampling was performed on the same plants for 3 years, we used the average values from different years for all variables, for each plant, to avoid pseudoreplication. Habitat was introduced into the models for Campos de Otero as a dummy variable (dry hillside = 1, wet meadow = 0; Zar 1996). Plant characteristics and percentages of plant cover per population were then correlated with the amount of frugivory (Spearman rank test), with each point representing the mean for each site and year for the variables concerned (for similar procedures see Christensen & Whitham 1991; Jordano 1993).

Parametric models were performed using type III sum of squares due to the unbalanced nature of the data. Variables were log transformed when necessary for normality, homoscedasticity and linearity, except for data expressed as frequencies which were arcsine transformed. Significance was fixed at $\alpha < 0.05$, except when analysing more than one related variable, where we used the sequential Bonferroni test to select the significance level to avoid increasing the probability of making a type-I error (Rice 1989).

Results

PLANT CHARACTERISTICS

Both plant traits and extrinsic characteristics varied strongly in space and time (Table 1). For repeatedly sampled sites cone density differed significantly between populations ($F_{2,154} = 82.77$, $P < 0.0001$, repeated measures ANOVA) but not among years ($F_{2,154} = 2.43$, $P = 0.09$), and the differences between populations varied significantly between years (interaction: $F_{4,154} = 37.99$, $P < 0.0001$). Cone size also differed significantly between populations ($F_{2,76} = 46.45$, $P < 0.0001$) but also differed among years ($F_{1,76} = 21.02$, $P < 0.0001$) with a significant interaction term ($F_{2,76} = 10.69$, $P < 0.0001$).

For the six populations studied in 1995, both cone density and cone size again varied significantly among sites (Table 1, $F_{5,168} = 41.67$ and 10.26, respectively, $P < 0.0001$, $P < 0.05$ after Bonferroni adjustment in both cases, one-way ANOVA). Plant size, nearest female distance, perch abundance and fruiting environment also differed significantly among sites ($F_{5,168} > 3.06$, $P < 0.05$ for all variables) as did cover by *J. communis* and by fleshy-fruited plants ($\chi^2 = 858.2$ and 506.8, respectively, $P < 0.0001$, d.f. = 5 in both cases).

Table 1 Characteristics (mean \pm SE) of *Juniperus communis* measured in different populations and years. These characteristics involve both plant traits (plant size, cone density and cone size) and extrinsic characteristics related to the environment surrounding the plant (NFD, nearest female distance; perch abundance, number of perches within a 25 m-radius; and fruiting environment, abundance of fleshy fruits in the same area). The percentage of cover of *J. communis* and of fleshy-fruited plants is also shown

Population	Year	Plant size (m ²)	Cone density (cones 0.04 m ⁻²)	Cone size (mm)	NFD (m)	Perch abundance	Fruiting environment	Cover of <i>J. communis</i>	Cover of fruiting plants
Campos de Otero	1994	–	12.3 \pm 1.4	7.1 \pm 0.1	–	–	–	–	–
	1995	20.3 \pm 3.1	21.1 \pm 1.9	7.0 \pm 0.1	1.6 \pm 0.3	13.6 \pm 1.6	0	30.6	30.6
	1996	–	9.2 \pm 1.1	7.2 \pm 0.2	–	–	–	–	–
Boleta	1994	–	11.3 \pm 2.5	7.2 \pm 0.1	–	–	–	–	–
	1995	9.8 \pm 1.4	30.0 \pm 4.4	7.0 \pm 0.1	1.8 \pm 0.5	18.1 \pm 0.9	3.3 \pm 0.8	18.6	41.3
	1996	–	52.1 \pm 7.1	–	–	–	–	–	–
Dornajo	1994	–	13.2 \pm 2.3	6.8 \pm 0.1	–	–	–	–	–
	1995	12.2 \pm 2.4	2.0 \pm 0.5	6.2 \pm 0.1	6.1 \pm 2.0	37.1 \pm 3.6	0.5 \pm 0.2	4.2	17.5
	1996	–	4.9 \pm 2.2	–	–	–	–	–	–
Trevenque	1995	8.2 \pm 1.4	9.4 \pm 2.5	6.8 \pm 0.1	3.1 \pm 0.8	14.1 \pm 0.6	6.7 \pm 0.6	16.9	50.5
Maitena	1995	9.9 \pm 2.1	2.5 \pm 0.3	7.1 \pm 0.2	1.3 \pm 0.4	19.3 \pm 1.3	0	38.5	39.8
Collado Cabañas	1995	18.9 \pm 2.2	15.1 \pm 2.6	6.5 \pm 0.1	2.8 \pm 0.6	56.4 \pm 3.5	1.0 \pm 0.3	16.4	32.3

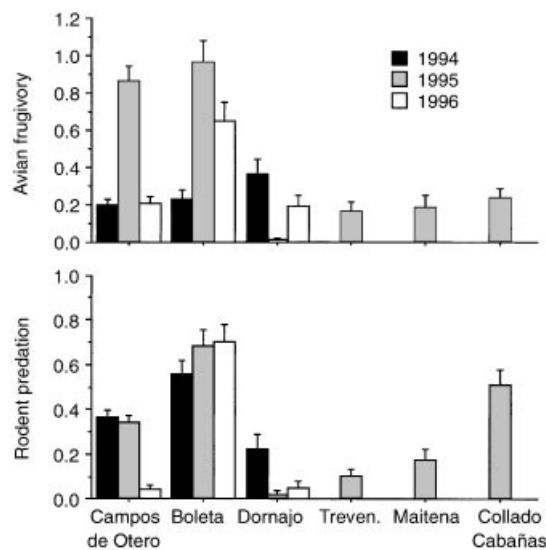


Fig. 1 Interactions between *Juniperus communis* and frugivores (mean \pm SE), for different populations and years. Avian frugivory is measured as average number of bird droppings per 0.04 m² and rodent predation as proportion of samples showing cones with evidence of mouse predation.

INTERACTIONS WITH FRUGIVORES

Frugivory by both avian dispersers and predatory rodents varied greatly between sites and years (Fig. 1). Both population and year were significant factors in the repeated measures ANOVAs for each frugivore, explaining *c.* 75% of variance (Table 2). Significant population \times year terms indicated that between-site differences varied over time (Table 2) and, in the case of rodent predation, that temporal variability was site-dependent (values changed strongly between years in Campos de Otero and Dornajo but were almost constant for the Boleta site, Fig. 1). Considering the six populations in 1995, both avian frugivory and rodent predation varied significantly between sites ($F_{5,168} = 25.21$ and 26.57, respectively, $P < 0.0001$ in both cases, one-way ANOVA).

Table 2 Summary of the repeated measures ANOVAs considering the three populations (Campos de Otero, Boleta, Dornajo) with data for all 3 years (1994–96) and the interaction between *Juniperus communis* and avian frugivores or predatory rodents

	SS	d.f.	F	P
<i>Avian frugivory</i> ($R^2 = 0.729$)				
Population	0.52	2	19.61	< 0.0001
Year	0.22	2	19.04	< 0.0001
Population \times Year	0.69	4	29.27	< 0.0001
Subject (Group)	1.02	77		
Error	0.91	154		
<i>Rodent predation</i> ($R^2 = 0.735$)				
Population	21.41	2	84.83	< 0.0001
Year	1.45	2	7.82	0.0006
Population \times Year	6.81	4	18.44	< 0.0001
Subject (Group)	9.72	77		
Error	14.23	154		

CORRELATIONS BETWEEN PLANT CHARACTERISTICS AND FRUGIVORY

Several significant relationships appeared between plant characteristics and the amount of frugivory (Tables 3 and 4). In the population of Campos de Otero, avian dispersers preferred to visit plants with more nearby perches (Fig. 2) or living in wet meadows (Fig. 3), whereas at Dornajo the only significant correlation was positively with cone density (Fig. 2) and in Collado Cabañas junipers whose neighbours had a higher abundance of fruits were more frequently visited by birds (Fig. 2, Table 3, for all sites). On the other hand, rodent predation levels were only significantly dependent on cone density and then only at Campos de Otero and Dornajo (Fig. 2, Table 4).

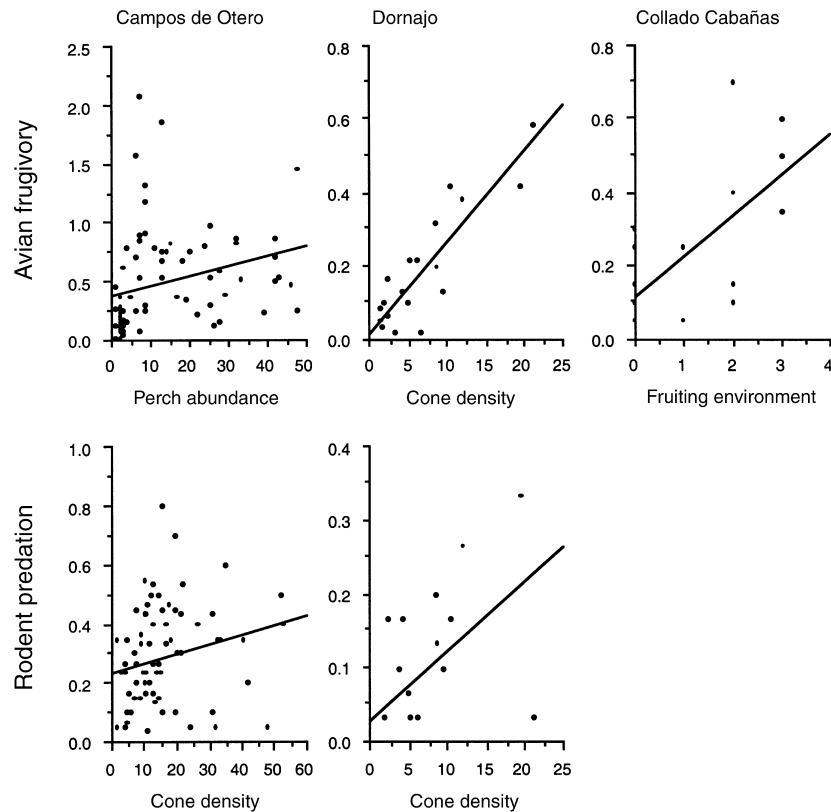
Considering the different populations as sampling units, the only significant correlation was a positive relationship between cone density and both avian frugivory and rodent predation (Fig. 4, Table 5). Neither the remaining plant attributes nor cover values were good predictors of frugivory (Table 5).

Table 3 Multiple regression models considering plant attributes as independent variables and the interaction between *Juniperus communis* and avian frugivores as the dependent variable for each population. Values with a significance level of $P < 0.05$ after sequential Bonferroni adjustment (applied within each model for β -values, and among models for F -values) are shown in bold

Avian frugivory	Campos de Otero $\beta \pm SE$	Boleta $\beta \pm SE$	Dornajo $\beta \pm SE$	Trevenque $\beta \pm SE$	Maitena $\beta \pm SE$	Collado Cabañas $\beta \pm SE$
Plant size	0.18 \pm 0.02	-0.15 \pm 0.05	0.04 \pm 0.05	0.16 \pm 0.06	0.01 \pm 0.08	0.21 \pm 0.07
Cone density	0.15 \pm 0.03	0.39 \pm 0.10	0.81 \pm 0.03	0.12 \pm 0.04	0.44 \pm 0.13	-0.02 \pm 0.05
Cone size	0.06 \pm 0.31	-0.32 \pm 0.64	0.07 \pm 0.36	0.40 \pm 0.39	0.20 \pm 0.54	-0.28 \pm 0.28
NFD	-0.06 \pm 0.03	-0.18 \pm 0.05	-0.11 \pm 0.03	0.17 \pm 0.05	-0.01 \pm 0.07	-0.17 \pm 0.04
Perch abundance	0.39 \pm 0.02	-0.22 \pm 0.22	-0.09 \pm 0.06	-0.39 \pm 0.27	-0.04 \pm 0.02	0.62 \pm 0.07
Fruiting environment	-	-0.27 \pm 0.04	-0.12 \pm 0.06	0.20 \pm 0.13	-	0.96 \pm 0.07
Habitat (dry-wet)	-0.60 \pm 0.01	-	-	-	-	-
R^2	0.58	0.47	0.67	0.29	0.29	0.64
F ratio (n)	15.85 (75)	1.96 (20)	4.12 (19)	0.83 (19)	0.97 (18)	3.52 (19)

Table 4 Multiple regression models considering plant attributes as independent variables and the interaction between *Juniperus communis* and rodent predation as the dependent variable for each population. Values with a significance level of $P < 0.05$ after sequential Bonferroni adjustment (applied within each model for β -values, and among models for F -values) are shown in bold

Rodent predation	Campos de Otero $\beta \pm SE$	Boleta $\beta \pm SE$	Dornajo $\beta \pm SE$	Trevenque $\beta \pm SE$	Maitena $\beta \pm SE$	Collado Cabañas $\beta \pm SE$
Plant size	0.25 \pm 0.06	-0.12 \pm 0.17	0.12 \pm 0.24	-0.27 \pm 0.26	0.42 \pm 0.27	0.41 \pm 0.32
Cone density	0.34 \pm 0.09	-0.07 \pm 0.24	0.68 \pm 0.16	0.33 \pm 0.17	0.21 \pm 0.35	0.61 \pm 0.28
Cone size	0.14 \pm 0.89	-0.05 \pm 1.82	0.01 \pm 1.67	0.29 \pm 1.46	-0.05 \pm 1.66	0.11 \pm 1.46
NFD	-0.04 \pm 0.09	-0.46 \pm 0.17	-0.14 \pm 0.11	0.04 \pm 0.19	-0.03 \pm 0.23	-0.21 \pm 0.22
Fruiting environment	-	0.26 \pm 0.14	0.03 \pm 0.23	-0.14 \pm 0.42	-	0.23 \pm 0.28
Habitat (dry-wet)	0.06 \pm 0.03	-	-	-	-	-
R^2	0.18	0.16	0.40	0.19	0.18	0.49
F ratio (n)	2.98 (75)	0.55 (20)	1.76 (19)	0.62 (19)	0.72 (18)	2.51 (19)

**Fig. 2** Amount of frugivory of *Juniperus communis* by avian frugivores and predatory rodents (units as Fig. 1), in relation to several plant attributes (see Table 1) in different populations. Regression lines represent analyses in Tables 3 and 4 and are shown for all significant effects.

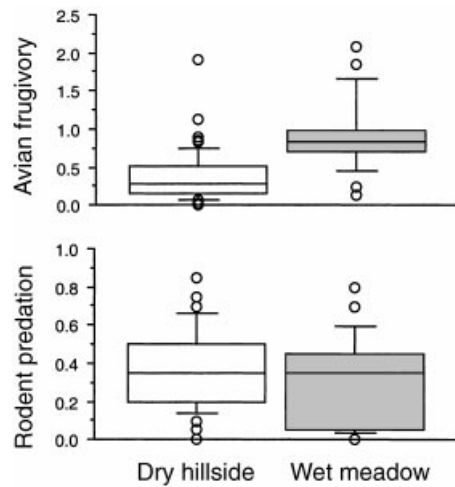


Fig. 3 Box-plots representing the degree of avian frugivory and rodent predation (units as in Fig. 1) as a function of the habitat occupied by plants at Campos de Otero.

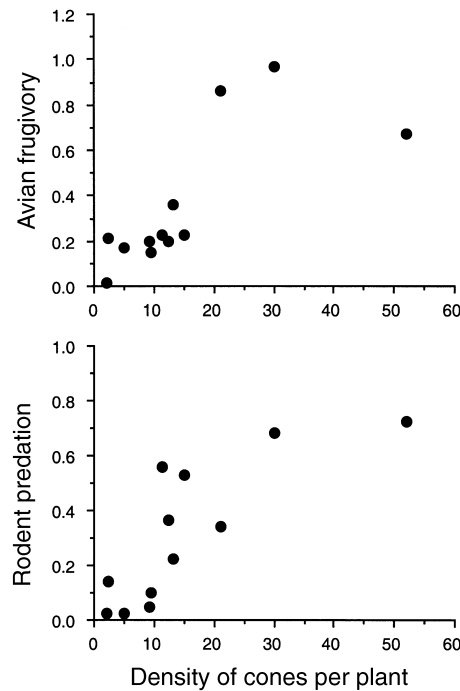


Fig. 4 Relationship between avian frugivory and rodent predation (units as Fig. 1) and cone density (cones/0.04 m²). Each point represents the average values for all the individuals within a particular population and year, for the two variables.

Avian frugivory was positively and significantly correlated with rodent predation at Dornajo ($Rho = 0.658$, $n = 19$, $P = 0.002$, $P < 0.05$ after Bonferroni, $Rho < 0.338$, $P > 0.05$ for all other sites), indicating that, for this site alone, plants more frequently visited by birds were also preferentially attacked by rodents. Avian frugivory and rodent predation were also positively correlated when considering the mean values per population and year for both variables ($Rho = 0.764$, $n = 12$, $P = 0.004$, $P < 0.05$ after Bonferroni).

Table 5 Values and significance level of the Spearman rank correlation coefficients between *Juniperus communis* characteristics (averaged for each population and year), the cover of *J. communis* and fleshy-fruited plants and avian frugivory and rodent predation. The sample size for each correlation is also shown (averaged for each population and year, * $P < 0.05$ after Bonferroni adjustment)

	Avian frugivory		Rodent predation		<i>n</i>
	R_s	<i>P</i>	R_s	<i>P</i>	
Plant size	0.200	0.704	0.143	0.787	6
Cone density	0.846	0.0005*	0.848	0.0005*	12
Cone size	0.273	0.446	0.418	0.229	10
NFD	-0.600	0.208	-0.485	0.329	6
Perch abundance	-0.314	0.544	-	-	6
Fruiting environment	-0.029	0.956	0.116	0.827	6
Cover of <i>J. communis</i>	0.486	0.329	0.314	0.544	6
Cover of fleshy-fruited plants	0.203	0.699	0.348	0.499	6

Discussion

SPATIO-TEMPORAL VARIATION IN JUNIPER CHARACTERISTICS AND THE DEGREE OF FRUGIVORY

J. communis showed great spatial variation in all plant phenotypic traits (plant size, cone production, cone size), both within and between populations. Cone production and cone size also varied considerably between years for some populations. Patterns of interannual change in cone crop differed between sites (Table 1, see also Jordano 1993), indicating that cone production was not synchronous across the region. This strong variation in reproductive traits appears to be typical of several *Juniperus* spp. and may be related to the long cone growth period as well as their masting behaviour, which is probably influenced by climate, resource levels and trade-offs involving previous reproductive events (Jordano 1993; García 1998b; Chambers *et al.* 1999). The extrinsic characteristics of individual plants (i.e. the distance between conspecifics, the abundance of perches and the fruiting environment) also differed between sites. The huge variation in plant characteristics (both intrinsic and extrinsic) thus creates a highly patchy distribution of both the resources for juniper frugivores (cones) and the environmental conditions in which they forage (see also Levey 1988; Herrera *et al.* 1994; Herrera 1998).

Our results also reveal marked spatial and temporal variation in the amount of frugivory on *J. communis* by both avian dispersers and predatory rodents, suggesting a heterogeneous mosaic at population and regional scales. Numerous studies have already suggested that dispersal by birds is highly variable in space and time (e.g. Levey 1988; Willson & Whelan 1993; Herrera 1998; Rey & Alcántara 2000) and seed predation by *A. sylvaticus*

in Mediterranean systems also often differs between plants, habitats, populations and years (Tellería *et al.* 1991; Santos & Tellería 1994; Hulme 1997; Rey & Alcántara 2000). This study is consistent with findings that variability is common in nature, but extends them by simultaneously addressing large-scale variability in both space and time.

FRUGIVORE RESPONSE TO PLANT CHARACTERISTICS WITHIN POPULATIONS

The activity of frugivores within juniper populations was occasionally affected by plant phenotypic traits. Cone density, but not plant or cone size, was significantly related to vertebrate activity, with plants that produced more cones being visited by both more avian frugivores and more rodent predators (Fig. 2). This suggests that plants with large crop sizes strongly attract frugivores because they are more conspicuous and offer higher foraging efficiency (Davidar & Morton 1986; Sallabanks 1993; Laska & Stiles 1994, for avian dispersers; Nilsson & Wästljung 1987, for predatory rodents). Simultaneous attraction of birds and rodents might account for the correlations between their actions, as at Dornajo (Fig. 2). However, the effect of crop size was spatially variable, the correlation appearing at only a few sites (see also Christensen & Whitham 1991; Willson & Whelan 1993; Herrera *et al.* 1994, for avian dispersers; Wästljung 1989, for rodent predation).

Birds may also be affected by the environment of particular juniper shrubs, as at Campos de Otero (Fig. 2), where plants surrounded by more perches were more frequently visited and thereby gained a reproductive advantage. This probably resulted from foraging patterns in Mediterranean mountain areas where thrushes alternate between periods of vigilance from perches and periods of feeding on plants near these perches (Zamora 1990; García *et al.* 1999a; see also Livingston 1972). The presence of other fruiting shrubs (mostly *Crataegus monogyna*, *Rosa* spp. and *J. sabina*) also facilitates dispersal from individual junipers, as shown by increased visitation rates at Collado Cabañas (Fig. 2, see also Herrera 1984b; Englund 1993). Finally, the clear effect of habitat at Campos de Otero (Fig. 3), where plants in wet meadows showed higher levels of avian frugivory than those on dry hillsides, did not depend on the between-habitat variation in cone production (García 1998b) but on the use of the wet meadows as watering sites by the birds (Holthuijzen & Sharik 1985).

CONSEQUENCES OF THE PATTERN OF FRUGIVORY

The frugivore assemblage depicted here might exert an evolutionary selective pressure on *J. communis* traits, as it shows high taxonomic predictability, and both dispersers and predators have a clear demographic effect (García 1998b; García *et al.* 1999a, 2000). However,

this would also depend on the presence of (1) a predictable pattern in space and time in the interaction outcomes and (2) significant correlations between plant traits and frugivory (Jordano 1994; Herrera 1998). These two conditions are not fulfilled by our system, where there is high spatio-temporal variability and few traits are correlated with frugivory. In addition, we found no evidence for a geographical mosaic of selective scenarios (*sensu* Thompson 1994), since there were no significant differences between populations in the way that frugivores affected the relationship between juniper traits and reproductive success.

Despite the scarcity of relationships between juniper characteristics and vertebrate frugivory at the plant level (within populations), a positive correlation between cone production and the activity of both dispersers and predators emerged at the population level, so that increased frugivory would be expected for sites and years with large cone crops (Fig. 4, see also Jordano 1993). The mechanism underlying this coupling is probably related to frugivore behaviour. Flocks of thrushes can move easily between distant populations and search efficiently for sites of higher fruit availability, even across extensive geographical regions (Jordano 1993; Rey 1995; Santos *et al.* 1999). On the other hand, *A. sylvaticus* appears to be attracted to juniper cones when crops are heavy but feeds on other seed resources when juniper is scarce (e.g. Herrera 1984b; Hulme 1997; García 1998b). Although none of the other variables appeared significantly related to frugivore activity at the population level, this might be due to the low number of populations studied.

Avian dispersers as well as predatory rodents appear able to respond to the spatio-temporal variation in cone abundance at a regional scale, discriminating more between juniper populations than between individual plants within a population. Frugivory at the individual plant level therefore is more dependent on whole-population characteristics than on individual attributes (Wästljung 1989; Sargent 1990; Christensen & Whitham 1991). As a result, the most relevant scale of observation in the system composed of *J. communis* and its vertebrate frugivores is the plant population level. It is clearly critical to evaluate an interacting assemblage at different observational scales (plants within populations, and populations within a region) in order to understand fully the ecological and evolutionary consequences of plant–animal interactions.

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