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Geographical ecology and variation of plant-seed disperser interactions: southern Spanish junipers and frugivorous thrushes

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Abstract

Spatial and temporal predictability in the mutual selective pressures of plants and frugivorous birds is a prerequisite for coevolution to occur. I examine the interaction patterns of strongly frugivorous thrushes (*Turdus* spp.) and their major winter food plants (*Juniperus* spp., Cupressaceae) and how they vary in space and time. Spatial congruency, rarely considered in seed dispersal studies, is studied at three spatial scales: 1) the total species range; 2) regional distribution; and 3) local abundance and its variation between seasons. Southern Spanish frugivorous thrushes and junipers show very low congruence in distribution patterns at each of these scales. Most juniper species show geographic distributions that are nested within the geographic ranges of thrush species. Bird species showed greater habitat breadth values than plants and were found in a greater percentage of localities. The local bird abundance was strongly correlated across years and sites with the local availability of juniper cones. Cone production varied markedly between years, but the rankings for different species in different years were statistically concordant at mid-elevation and lowland sites. Both bird abundance and cone production showed greater temporal than spatial variability. Variation of cone productions at both temporal and spatial scales was greater than variability in bird abundance. Species with strong interactions of mutual dependence showed very low values of biogeographic congruence, caused by differences in geographic range and habitat specificity. This obviously limits the possibilities for pairwise, specific coevolution to occur. However, mutual effects of species groups are possible to the extent that the component species are ecologically 'interchangeable' in their selective effects and other constraints on coevolution are not operating. The approach used here to examine the patterns of species interactions at different biogeographic scales might prove useful in comparative studies of plant-animal interactions.

Introduction

Studies documenting the geographical, regional and local variations of species interactions in plant-frugivore systems are uncommon. Mutual selective effects derived from the fruit-frugivore interaction strongly depend upon how the consequences of the interaction observed in a given locality translate and 'scale' at higher biogeographical levels. If evolutionary modification of traits involved in an interaction between mutualists depends on mutual selective pressures derived from the interaction, then the possibilities for coevolution depend to a great extent on the degree of spatial constancy of these selection pressures (Janzen 1980; Schemske & Horvitz

1984; Herrera 1988b; Horvitz & Schemske 1990). 'Spatial' is used here in a biogeographical context to include the geographic range of the interacting species, the different habitats of a given region where the species interact, and their local population sizes.

An extreme example of spatial inconsistency was given by Wheelwright (1988) who showed that at a single Costa Rican locality, emerald toucanets are the chief dispersers of *Ocotea floribunda* and that this fruit is the major food of the bird; this interaction, however, occurs in only a small portion of the ranges of the two species. This situation is probably generalizable to most avian frugivore seed dispersal systems. However, very few studies have explicitly considered spatial variation in bird-fruit interactions beyond the local scale defined as several sites within a local study area (see, e.g., Herrera 1988a; Keeler-Wolf 1988; Willson 1986). To my knowledge, no previous study has examined simultaneously the temporal and spatial variation in the species assemblages of a seed dispersal mutualism considering several years and both regional and local geographical scales.

The interaction pattern for a given pair of species in a particular community depends on the biogeographic 'attributes' (or 'forms of rarity', according to Rabinowitz 1981) of each species and how these interact (Fig. 1). More importantly, these biogeographic attributes determine how the local selective regimes sum up and translate among populations. For example, in a situation of multi-species interactions such as the frequently observed in bird-fruit communities, one can expect a priori a greater coevolutionary potential between species sharing the same combination of biogeographic attributes. Otherwise, a situation of strong asymmetry arises if one species interacts with the other in a small portion of its geographic range, or only in certain highly localized habitats or if the second species is extremely rare. Even in situations of strong asymmetry one interacting species can generate a strong selective pressure on traits of a second species whose geographic range and habitats occupied are included within those of the former.

Frugivorous thrushes (genus *Turdus*, Turdidae) are a prominent group of six species in southern Spanish frugivore communities (Santos *et al.* 1983; Herrera 1984; Jordano 1985; Tellería *et al.* 1988). All of the six species are strongly frugivorous during autumn and winter (Hartley 1954; De Juana & Santos 1981; Herrera 1981; Jordano 1981; Tejero *et al.* 1984; Guitián 1984; Debussche & Isenmann 1985a, 1985b; Obeso 1985; Obeso 1986; Snow & Snow 1988; Zamora 1990). In the highlands (scrublands above 1500 m elevation), the fleshy cones of *Juniperus* species (Cupressaceae) are a staple food of these birds (Obeso 1986; Zamora 1990). Thrushes are numerically dominant members of the frugivorous avifauna in

GEOGRAPHIC RANGE	LARGE		SMALL	
HABITAT SPECIFICITY	Wide	Narrow	Wide	Narrow
LOCAL POPULATION SIZE Large, dominant	*Turdus viscivorus* *Turdus iliacus* *Juniperus communis*	*Juniperus sabina*	*Turdus torquatus* *Juniperus thurifera* *Juniperus phoenicea*	*Juniperus cedrus* *Juniperus brevifolia*
Small, non-dominant	*Turdus merula* *Turdus philomelos* *Juniperus oxycedrus*	*Turdus pilaris*		

Fig. 1. Biogeographic patterns of *Juniperus* and *Turdus* species according to the typology established by Rabinowitz (1981). Each species can be characterized at three different spatial scales (continental, regional, and local) by evaluation of the relative size of its geographic range, the number of habitats occupied, and the average size of its local populations.

everal vegetation types where junipers dominate Santos 1982) and play a central role in the dispersal ecology of *Juniperus* species in Spain as well as elsewhere (Snow & Snow 1988; Holthijzen & Sharik 1985).

The purpose of the paper is (1) to document between-habitat and between-year patterns of interactions between junipers and thrushes and heir variability in several southern Spanish loalities; (2) to assess the degree of congruence between the interaction 'strengths' recorded at ach site and year and the distributions of each pair of species at the regional and continental cales; and (3) to explore some consequences for plant-frugivore coevolution of the non-coincilence between interacting species at different biogeographical scales.

Plant and bird species

unipers are a dominant element of the southern Spanish highland vegetation (Ern 1966), with five pecies reaching the Iberian Peninsula. Only *J. ommunis* has a wide holarctic distribution and he remaining four species (*J. oxycedrus*, *J. phoenicea*, *J. sabina*, and *J. thurifera*) are restricted to he circum-Mediterranean region and certain parts of western Asian mountains (Jalas & Suominen 1985) (see Fig. 2). The six species of he genus *Turdus* (*T. iliacus*, *T. merula*, *T. iscivorus*, *T. philomelos*, *T. pilaris*, and *T. orquatus*) have a wider distribution on a continental scale (Cramp 1988). Their breeding distributions extend throughout the western Palearctic but the wintering areas are concentrated in the western part of the Mediterranean basin, specially n the eastern half of the Iberian Peninsula (Soc. Esp. Ornitología 1985) (Fig. 2).

The female strobili of *Juniperus* species (fleshy cones or 'fruits' or 'berries', hereafter) are functionally analogous to angiosperm fleshy fruits. Fresh mass of *J. oxycedrus* cones averages 0.70 g, 0.36 g of dry 'pulp' and 2.2 seeds/cone. *J. phoenicea* has 0.32 g, 0.15 g, respectively, and 8.5 seeds/cone. *J. communis* has 0.08 g, 0.05 g, respectively, and 1.9 seeds/cone. *J. sabina* has 0.08 g, 0.05 g, respectively, and 1.9 seeds/cone; and *J. thurifera* has 0.28 g, 0.17 g, respectively, and 3.1 seeds/cone. Maximum external cone diameters for these five species are 10.9 mm, 9.1 mm, 5.8 mm, 7.4 mm, and 9.2 mm respectively. Average content of the 'pulp' is 11.5% (dry mass) lipid and 4.4% protein; the fiber content is very high (mean = 44.1%) (Herrera 1987; Obeso 1985; and P. Jordano, unpubl. data).

Both *Juniperus* and *Turdus* are characteristic genera of the southern Spanish highland vegetation and frugivorous avifauna (see below). *J. communis* and *J. sabina* are dominant species in high altitude scrublands (1900–2700 m); *J. phoenicea* dominates mid-elevation vegetation (1200–1500 m) in localized habitats on dry, exposed, rocky outcrops as well as in several coastal sites on sandy soils (e.g., Parque Nacional de Doñana, Huelva; Punta del Sabinal, Almería). *J. oxycedrus* can be found as scattered individuals and is locally dominant in forest gaps and exposed, rocky outcrops at lower elevation (700–1300 m). Finally, *J. thurifera* dominates extensive juniper woodlands in central Spain. Only *J. communis*, *J. sabina*, and *J. phoenicea* – the dominant species in the highlands – are considered in detail here.

With the exception of *T. philomelos*, a lowland species rarely found at high altitude, all *Turdus* species occur in southern Spanish highlands (above 1300 m) during winter, but their abundances vary greatly from year to year (see below). Both *T. merula* and *T. viscivorus* have resident populations that increase in winter with the arrival of migrants. *T. torquatus* is mainly a transient migrant wintering in the Moroccan Atlas mountains with a minority of its population wintering in Spain. Both *T. iliacus* and *T. pilaris* occur regularly in southern Spanish mountains but the latter only in very low numbers; the two species show important between-year changes in their winter densities. A detailed description of migration patterns and geographic and habitat distributions can be found in Santos (1982) and Soc. Esp. Ornitología (1985). A summary of the main patterns of geographic distribution, habitat range, and local abundance is presented in Fig. 1.

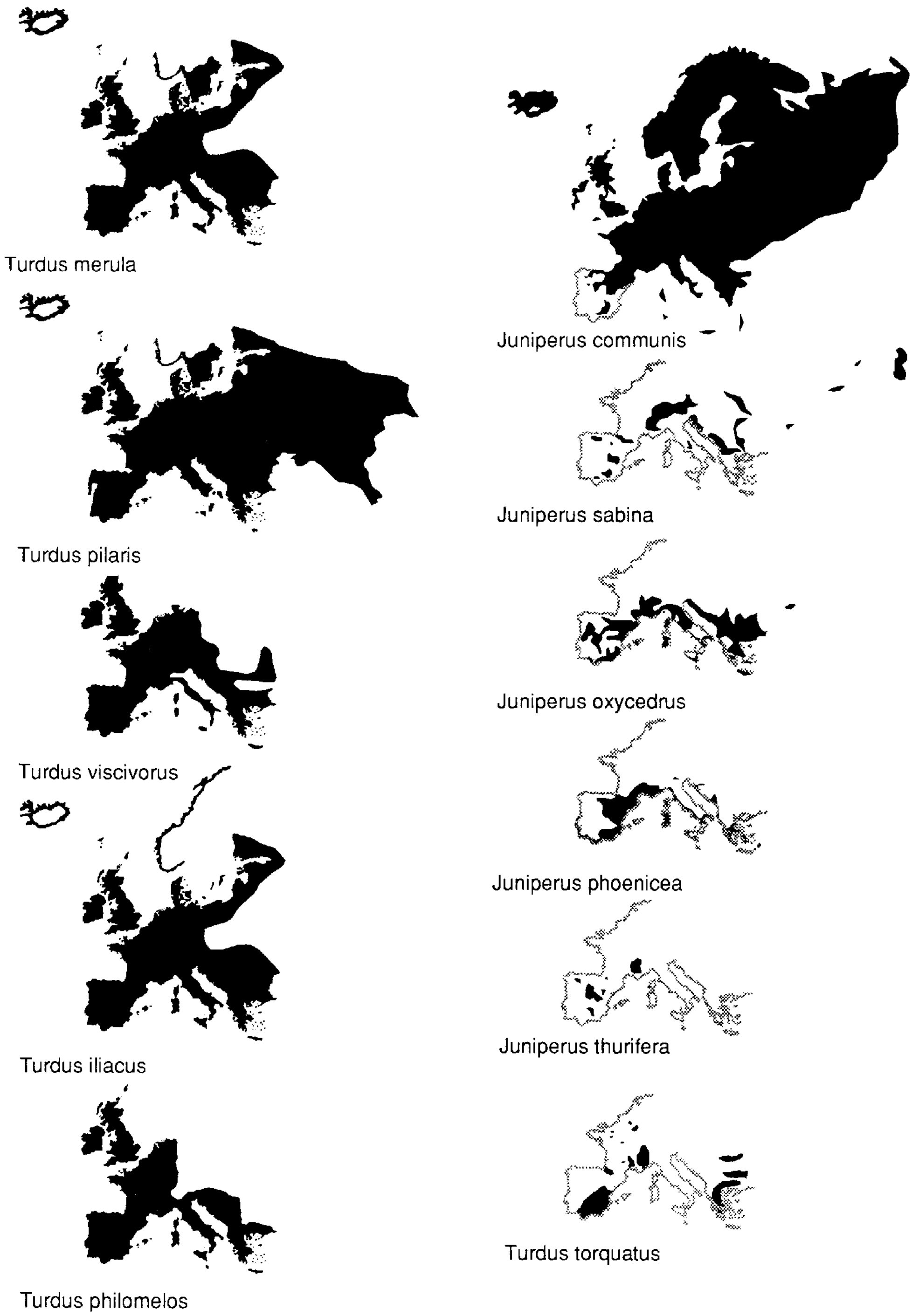

Fig. 2. Digitized outlines of the geographic distribution maps of *Juniperus* spp. and the wintering areas of *Turdus* spp. in the western Palearctic. Source: Jalas & Suominen (1985) and Cramp (1988). Note the extreme asymmetry of certain combinations of plant and bird species that show strong interactions in southern Spanish localities (e.g., *J. communis* and *T. torquatus*; *J. phoenicea* and *T. pilaris*; and *J. phoenicea* and *T. viscivorus*). Dimmed outlines of southwestern Europe have been added to provide a reference for species with restricted ranges.

tudy area and methods

he study was carried out during the autumn and inter (October-March) of 1985–1989 at six lo-ılities in the highlands of Sierra de Cazorla, Jaén rovince (three main sites at 1550–1700 m ele-ation), and Sierra de Baza (2250 m) and Sierra evada (2550–2650 m)(Granada). The vegeta-on at Campos de Otero (Sierra Nevada), a orth-facing slope on siliceous soil, is low scru-land dominated by *J. communis* with *Genista ba-ica* and large areas of open, rocky ground and asture. Santa Bárbara (Sierra de Baza) is struc-ırally very similar to the former site but is on alcareous rock. The vegetation is dominated by *sabina*, *J. communis*, *Berberis vulgaris*, *Daphne leoides*, and *Rosa* spp. surrounded by large atches of open, rocky ground and pasture. The añada de las Sabinas site at Sierra de Cazorla es at the border of pine forest (*Pinus nigra*, subsp. *ılzmannii*) growing on rocky soils, with decidu-us vegetation growing in the deep, cool soils of ıe 'navas' dominated by *Crataegus monogyna*, *runus mahaleb*, *Berberis vulgaris*, *Lonicera ar-orea*, *Daphne laureola*, *Acer monspessulanum*, and *uercus faginea*. On dry and rocky slopes, both *communis* and *J. sabina* dominate the under-ory vegetation of the pine forest, with *J. phoe-icea* being locally dominant in certain ridges and ocky outcrops. The Calarilla, Cañada del ravino and Nava Noguera sites are very similar the preceding one in structural characteristics nd vegetation composition. In the analyses elow, data for the Calarilla site have been pooled ith those of the nearby Cañada de las Sabinas.

Other 13 Southern Spanish localities were also urveyed at varying frequencies to determine local ssemblages of *Turdus* and *Juniperus* species. The ites were: Reserva Biológica de Doñana (Huelva rovince, 20 m elevation); Collado del Calvario Sierra de Cazorla, Jaén; 1400 m); Pinar Negro Sierra de Cazorla, Jaén; 1450 m); Roblehondo Sierra de Cazorla, Jaén; 1300 m); Guadahornil-os (Sierra de Cazorla, Jaén; 1000–1250 m); Dor-ajo (Sierra Nevada, Jaén; 2020 m); Puerto del oyar (Sierra de Grazalema, Cádiz; 1170 m); ierra del Pinar (Cádiz; 1450 m); Torrecilla (Sierra de Ronda, Málaga; 1750 m); Punta del Sabinal (Almería; 14 m); Sierra de Quintana (Jaén; 950 m); Aljabaras (Sierra de Hornachuelos, Córdoba; 750 m) and La Canaleja (Sierra de Baza, Granada; 1100 m). Three highland sites (1400–1500 m) in the Haut Atlas (South Morocco), Agaiouar, near Imigdal, and Tizi-n-At-Imguer were also visited in January-February 1989.

Quantitative information on the local abundances of *Turdus* spp. at each of the main sites were obtained by counts of birds along fixed transects of variable length, usually 1–4 km. At each site, these transects were walked in at least three different months during each study year. All birds seen or heard within a 60 m band at each side of the transect were recorded. Results are given as number of birds/km census to standardize the differences in census effort. Feeding records were tallied (one record = one fruit ingested by a bird) during the census counts and also during observational watches at feeding trees. Additional information on the local abundance of *Turdus* spp. at other Southern Spanish sites was obtained from the literature (Herrera 1984; Jordano 1985; Santos 1982; Suárez & Muoz-Cobo 1984; Obeso 1987).

Counts of mature-sized fleshy fruits present in different permanent quadrats (30 m × 1.5 m; $n = 12–30$ per site) were carried out at each of the six main sites (see Blake *et al.* 1990 for further discussion of the method). Similar but non-permanent transects were used at the other sites to determine the relative cover of each *Juniperus* species and other fleshy-fruited species. Individual *Juniperus* plants at each main site were also marked to determine cone crop sizes, totalling (all sites pooled) 85 *J. phoenicea*, 70 *J. communis*, and 47 *J. sabina*.

Digitized outlines of the geographical ranges of *Juniperus* and *Turdus* species were obtained from Jalas & Suominen (1985) and Cramp (1988). Maps were divided in 5° quadrats ($n = 128$) and the presence-absence of each species was recorded. The percentage of quadrats with presence was used as an index of each species' geographic range. Similarly, the proportion of southern Spanish sites with confirmed presence of each species was used as an index of habitat breadth. Habitat occupancy patterns were derived from the presence-absence data for each species in 19 southern Spanish sites. The average quantitative importance of each species in 9 local assemblages was derived from values of relative cover (plants) or population density (birds) obtained for the study sites as well as from literature sources cited above. Then, for each species, single values were obtained to characterize the relative size of the geographic range (proportion of latitudinal quadrats where present), the proportion of habitats occupied, and the relative local abundance. Similarities between taxa at each of these biogeographical levels were determined using the Sørensen coefficient (presence-absence data for the geographic range and the types of habitats occupied) and the Gower similarity coefficient (for quantitative data on local abundances)(Legendre & Legendre 1979).

Results

Turdus *feeding on* Juniperus *fleshy cones*

Cones of *Juniperus* species made up an important part of the winter fruit diet of *Turdus* spp. (Table 1). Both *T. torquatus* and *T. viscivorus* showed the highest reliance on *Juniperus* with 37.5% and 39.3%, respectively, while *T. iliacus* and *T. pilaris* consumed mainly other fruits (e.g., *Crataegus monogyna* and *Berberis vulgaris*). *T. pilaris* is a very rare species found in very low number only in certain years, with feeding records for *J. phoenicea* at Nava Noguera and for *J. sabina* at Pinar Negro in years of high fruit production. *T. merula* inhabits denser vegetation and feeds chiefly on rosaceous fruits (*C. monogyna*, *Rosa* spp.) and infrequently on juniper berries. Finally, *T. philomelos* and *T. iliacus* are important for *Juniperus* at lower elevations, relying heavily on *J. oxycedrus* and *J. phoenicea*. For example, a mast cone production of *J. phoenicea* occurred at R. B. Doñana during the winter 1986–1987; there, 98.9% of the feeding records for *T. iliacus*, 96.5% for *T. philomelos*, and 91.3% for *T. merula* were for this species. *T. merula* adults were even feeding their young during the 1987 spring with the remaining 'surplus' cones.

At the study sites, *Turdus* species are quantitatively the more important *Juniperus* seed dispersers among frugivorous birds. *Turdus* records made up 97.6% of the feeding observations at these plants. With the possible exceptions of *J. phoenicea* and *J. oxycedrus*, for which carnivorous mammals are also important dispersers (Herrera 1989), *Turdus* species are therefore the most common dispersers of *Juniperus*, especially for *J. communis* and *J. sabina*. *T. torquatus* and *T. viscivorus* are the main dispersers of three species of *Juniperus* in the highlands. Data from Herrera (1984), Obeso (1985) and Santos (1983) indicate that thrush species also disperse most seeds of lowland junipers (*J. oxycedrus*, *J. thurifera*).

Table 1. Feeding records of *Turdus* species on *Juniperus* spp. and other fruits. Data for all southern Spanish highland study sites have been pooled.

Tudus species	*Juniperus* species			Other fruit species	Number of records
	communis	*phoenicea*	*sabina*		
merula	11	10	6	355	382
iliacus	20	2	10	219	251
philomelos	0	0	0	13	13
torquatus	165	189	63	694	1111
pilaris	0	8	0	105	113
viscivorus	43	115	48	318	524
Other birds	0	15	2	528	545
Number of records	239	339	129	2232	2939

For every pair of interacting *Juniperus*/*Turdus* species in Table 1, with the exclusion of *T. philomelos*, I computed the percentage of the bird's feeding records accounted for by the plant species and the percentage of the plant's records made up by the bird species. These values serve as a first quantitative evaluation of the reciprocal dependency between each species pair. Values of plant dependence on bird and bird dependence on plant were strongly correlated across pairs of species ($r_s = 0.854$, $p < 0.01$, $n = 15$), indicating symmetrical interactions. However, as a group, the birds' dependence on junipers was much lower than the plants' dependence on thrushes.

Geographic variation in local Turdus/Juniperus *assemblages: regional and local scales*

Juniper and thrush species differ markedly in their distribution patterns on a continental scale (Fig. 2). As a group, *Turdus* spp. are widely distributed during winter throughout the southwestern Palearctic. Only *T. torquatus* has a relatively localized wintering area in eastern Spain and Morocco. The wintering ranges of all six species overlap over a relatively small area encompassing the southeastern part of the Iberian Peninsula, south France, and northwestern Africa.

This area of highest concentration of wintering thrush species overlaps extensively with the area of maximum diversity of *Juniperus* species, most of which have circum-Mediterranean distributions (Fig. 2). When all possible species pairs are considered, all the ranges of *Juniperus* species are included within the ranges of each *Turdus* spp., with the exception of *T. torquatus*. Thrush species, in contrast, are distributed over vast areas where *J. communis* is the only juniper present. With the exception of *J. communis*, no juniper species is present in more than 17% of the 5° quadrats. This situation contrasts with *Turdus* spp. which, excluding *T. torquatus* (11.7%), occupy more than 36% of the quadrats (Table 2).

To examine the patterns of habitat specificity, I calculated the percentage of the 19 habitats surveyed where each *Turdus* and *Juniperus* species was present, irrespective of their local abundances (Table 2). Plants showed higher habitat specificity than birds, and were present in an average of 44.7% of the habitats surveyed. *Turdus* species, with the exception of the extremely localized *T. pilaris* (10.5%) were present in 63.7% of the sites, and as a group showed greater habitat breadth than *Juniperus* ($U = 1$, $p = 0.016$; Mann-Whitney U-test; Table 2).

Table 2 summarizes the quantitative composition of the local assemblages and its regional variation for the intensively-studied areas (see also Appendix 1 and 2). The total cover of *Juniperus* species reached 62% in the highland scrublands and 52% in the coastal woodland at R. B. Doñana but was only 30% at most sites. *Turdus* species represented, on average, 42% of the censused birds in highland juniper scrub, 48% in coastal sites, and decreased to 8–23% in lowland scrublands, olive groves, and oak woodlands.

The local assemblages of both species groups were usually dominated by one species, particularly at the highland sites. These habitats are dominated either by *J. communis* (62.3% horizontal cover at Campos de Otero) or *J. sabina* (38.6% at Santa Bárbara), with *J. phoenicea* being extremely scarce (Table 2). Common thrushes in these highland sites were *T. torquatus* (70–86% of censused *Turdus*), *T. pilaris* (23%) and *T. viscivorus* (8–16%). Large flocks of *T. torquatus* are characteristic in these sites during large crop years. At Campos de Otero, flocks of 3–62 individuals were recorded during the 1985–1986 winter (mean = 17 individuals, $n = 32$). Flocks of *T. viscivorus* (mean = 9, range = 3–35 individuals, $n = 21$) or *T. iliacus* (mean = 4, range = 3–8, $n = 10$) were less numerous. Local assemblages in the mixed mountain pine forests showed higher equitability, with *T. merula*, *T. viscivorus*, or *T. torquatus* as the dominant species.

Cone production was extremely variable from year to year (see below), but when data for single localities were pooled, only *J. phoenicea* showed statistically significant variation between sites in cone production ($F_{4,11} = 10.84$, $p < 0.001$; data square-root transformed; Appendix 1). The pooled, total production of *Juniperus* ranged from

Table 2. Relative values for size of geographic range, habitat specificity, and local population size of *Juniperus* and *Turdus* species.Values for local population sizes (as %) are given for the main study sites.

	Percent cover				Percent of birds censused					
	JCOM	JSAB	JPHO	JOXY	TMER	TVIS	TILI	TPHI	TTOR	TPIL
Geographic range[1]	66.4	11.7	14.1	17.2	50.8	35.2	50.8	42.9	11.7	62.5
Habitat breadth[2]	63.2	36.8	42.1	36.8	78.9	84.2	94.7	52.6	84.2	10.5
Local population size[3]	12.6	6.1	11.3	0.6	21.1	29.1	7.4	1.4	38.1	2.9
Highland juniper scrubland										
Campos de Otero (Sierra Nevada)	62.3	0.0	0.0	0.0	0.0	8.8	4.9	0.0	86.3	0.0
Sta. Bárbara (Sierra de Baza)	1.6	38.6	0.0	0.0	0.0	15.9	6.8	0.0	77.3	0.0
Pinar Negro (Sierra de Cazorla)	21.3	13.9	0.6	0.0	4.6	13.6	12.7	0.9	45.5	22.7
Mixed mountain forest										
Nava Noguera (Sierra de Cazorla)	8.3	0.0	7.3	0.0	15.2	37.3	8.2	2.1	36.9	0.4
Cañada Travino (Sierra de Cazorla)	8.3	6.2	0.9	0.0	31.2	17.7	11.3	1.6	38.2	0.0
Cañada Sabinas (Sierra de Cazorla)	21.3	13.9	0.6	0.0	15.3	63.5	1.2	0.0	20.0	0.0
Roblehondo (Sierra de Cazorla)*	0.3	0.0	0.4	4.9	49.1	43.9	0.0	7.0	0.0	0.0
Coll.Calvario (Sierra de Cazorla)*	2.1	0.0	0.0	1.3	53.3	32.2	14.2	0.3	0.0	0.0
Coastal juniper woodland										
Reserva Biológica de Doñana	0.0	0.0	51.8	0.01	12.2	2.5	18.4	66.4	0.5	0.0

[1] Percentage of 5° latitude quadrats where the species is present (wintering period for *Turdus* spp.) in the western Palearctic.

[2] Percentage of 19 sites surveyed where each species was recorded.

[3] Local population sizes are given, for each of 9 main study sites in southern Spain, as average % horizontal cover in permanent transects (*Juniperus*) and average % of censused individuals in transect counts (*Turdus*).

* Data from Obeso (1987).

Abbreviations: JCOM – *J. communis*; JSAB – *J. sabina*; JPHO – *J. phoenicea*; TMER – *T. merula*; TILI – *T. iliacus*; TPHI – *T. philomelos*; TTOR – *T. torquatus*; TPIL – *T. pilaris*; TVIS – *T. viscivorus*.

30.5 ± 21.6 cones/m^2 (mean ± s.e.) at Campos de Otero to 2.7 ± 1.9 cones/m^2 at Santa Bárbara ($F_{4,11} = 3.95$, $p = 0.024$). Among *Turdus* species, only the mid-elevation and lowland species (*merula*, *iliacus*, and *philomelos*) showed significant variations in abundance between sites ($F_{4,11} \geq 6.58$, $p < 0.005$), as expected from their greater habitat specificity; the highland species showed no significant variations. Total abundance of *Turdus* did not vary significantly between sites ($F_{4,11} = 1.00$, $p = 0.448$) and ranged from 5.2 ± 1.9 birds/km (Santa Bárbara) to 27.6 ± 21.7 birds/km (Campos de Otero).

Temporal variations in local assemblages

Temporal (between-year) variation in mutualistic assemblages has three main components: different species can be present or absent in a particular year; the rankings of species' abundances can vary between years or remain highly concordant; and, even with low qualitative variation and concordance of the abundance rankings, species can show abundance variations from one year to the next.

A characteristic feature of local *Juniperus* and *Turdus* species assemblages is their extreme between-year variation in cone production and bird abundance. However, presence/absence of particular species is relatively constant. Only *J. phoenicea* and *J. sabina* failed to set fruits in two years at Nava Noguera and Santa Bárbara (Appendix 1), but years of extremely low fruit availability (<0.1 fruits/m^2) are not infrequent and result from a low frequency of reproductive individuals. Among the birds, only *T. pilaris* and *T. iliacus*, two species with irrupting movements, are bsent in certain years (e.g., at Campos de Otero, ava Noguera) and were recorded only in years ith high cone production (Appendix 2). For exmple, *T. iliacus* was observed at Campos de tero only in 1985 and 1986 when crops of *J. ommunis* were large; the following winters, when ery few cones were available (Appendix 1), birds ere seen at lower elevations feeding on *Crataeus monogyna* and *Rosa canina*.

The local thrush abundance in a given year and ite was strongly correlated with both the total vailability of fleshy fruits ($F_{1,15} = 72.0$, $r^2 = 0.847$, < 0.0001) (Fig. 3) and with the total production f *Juniperus* cones ($F_{1,15} = 53.6$, $r^2 = 0.793$, < 0.0001). Between-year peaks in local abunance of *Turdus* matched the local maxima in *uniperus* availability. *T. torquatus* reached 84 irds/km at Campos de Otero during 1985 (Apendix 2), a year with an extraordinary crop of *J. ommunis* (94 cones/m^2; Appendix 1). Similarly, t the Santa Bárbara site, high abundance of *T. rquatus* (6 birds/km) in 1986–1987 matched a ood crop year for *J. sabina* (6.4 cones/m^2). Small ocks of *T. pilaris* at Nava Noguera in 1988 (0.15 irds/km) were feeding mostly on *J. phoenicea*, ith an availability of 4 cones/m^2 that year. This pecies was also recorded at Pinar Negro (Siera de Cazorla) during the 1987–1988 winter when . *sabina* cones were abundant; birds were conuming this species and fruits of *Berberis vulgaris*. bservations at the lowland sites showed similar ends. The 1986–1987 winter, in which *J. phoeicea* had a mast year with 103.5 cones/m^2, was xceptional at R. B. Doñana. *T. philomelos* eached densities of 32.2 birds/km, and two other pecies, *T. torquatus* (0.4 birds/km) and small ocks of *T. pilaris* were also seen.

To determine how consistent between years ere both bird numbers and fruit abundance, I ompared both the abundance rankings of *Turdus* pecies and the availability rankings of *Juniperus* ones at each site, including also the lowland R. . Doñana site (2 years), across study years (see ppendix 1 and 2). Significant values of Kenall's coefficient of concordance for *Turdus* were btained for Nava Noguera, Cañada del Travino nd R. B. Doñana (i.e., the two mixed woodland sites and the lowland site; $W > 0.60$, $p < 0.001$). Non-significant values were obtained for the three highland sites (Campos de Otero, Santa Bárbara, and Calarilla) that showed extreme between-year variations both in the identity of the most abundant species and the abundance of each species. The mixed woodland and lowland sites showed more constancy in the abundance rankings of each species than the highland scrublands, although bird numbers varied extremely. The rankings of juniper cone abundances were compared for the Calarilla and Nava Noguera sites at which two or three species were present. For the former, there was significant between-year constancy in the rankings of juniper species regarding cone availability ($W = 0.933$, $p = 0.05$). At Nava Noguera, annual rankings were inconsistent ($W = 0.758$, $p = 0.435$).

Other fruit crops certainly also have an influence on annual variations in the bird numbers illustrated in Appendix 2. *Crataegus monogyna*, for example, produced a good crop at several Sierra de Cazorla sites (Nava Noguera, Cañada del Travino, Cañada de las Sabinas-N. Correhuelas) in 1987, with > 10 fruits/m^2, and high densities of *T. torquatus* (> 7 birds/km) and *T. iliacus* > 5 birds/km) were recorded there that winter; individuals of all six *Turdus* species were seen feeding simultaneously at the same Crataegus tree.

Annual variations in bird abundance and cone production were greater than between-site variations (Table 3). For all the sites and years pooled, annual variation in both cone production and bird numbers were greater (mean CV = 137.3%) than variation between sites (mean CV = 96.4%) ($F_{1,76} = 11.41$, $p < 0.001$), suggesting that abundance patterns show greater temporal than spatial variability in thee taxa. On the other hand, cone production showed a significantly greater CV (for all years and sites pooled) (mean CV = 132.5%) than *Turdus* abundance (mean CV = 107.9%) ($F_{1,76} = 4.13$, $p < 0.05$). This indicates an overall smaller variation in bird numbers than cone availability.

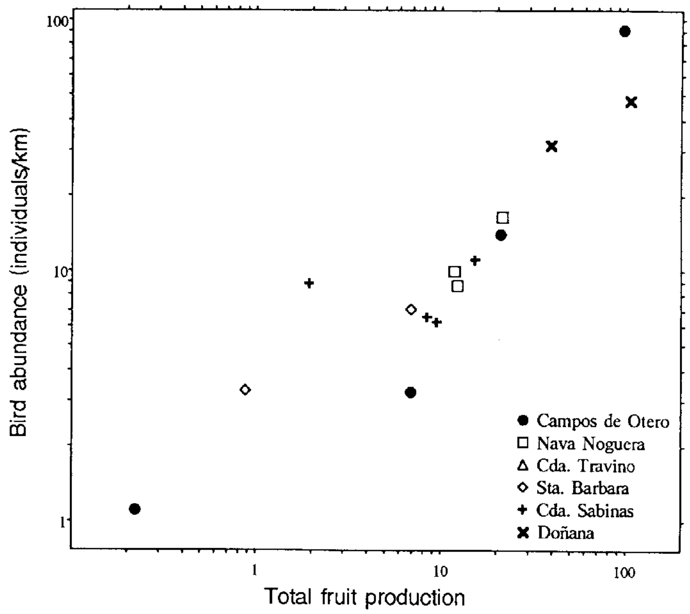

Fig. 3. Relationship between local availability of fleshy fruits (the total production of *Juniperus* cones plus fleshy fruits of angiosperm species) and the total abundance (number of birds/km census) of *Turdus* species. Symbols identify values corresponding to six localities in different study years.

Table 3. Coefficients of variation in the abundance of thrush species (number of birds/km) and the production of juniper cones (number/m^2) in southern Spanish habitats.

Species group	CV (%) Among sites			CV (%) Among years, within sites		
	N*	Mean	Range	N*	Mean	Range
Juniperus species	14	114.31	[65.6–180.4]	15	149.55	[58.3–221.7]
Turdus species	26	86.77	[1.78–181.6]	25	129.92	[58.2–224.1]

* Refers to the number of year-site and site-year combinations for the species in each group.
CV = 100 SD/mean.

Mutual congruency of distribution patterns and interaction strengths

Each species of *Juniperus* and *Turdus* can be characterized by its abundance patterns at three different spatial scales namely, geographic range, habitat use, and local population size (Fig. 1). The congruence patterns between interacting species pairs can be examined by considering their similarities at each of these biogeographic levels (Table 4).

For the species studied, no obvious relationship exists between the size of the geographic range and the degree of habitat specificity (Fig. 4A). *T. pilaris*, with the largest range among *Turdus* (Fig. 2), showed the highest habitat specificity, being found only in highland juniper scrub and mixed mountain forest. *T. torquatus*, in contrast, has a highly restricted wintering range but was recorded in most habitats surveyed (Fig. 4A). The four *Turdus* species with greatest relative importance in the seed dispersal of *Juniperus*, as derived from feeding records (*merula*, *iliacus*, *torquatus*, and *viscivorus*; Table 1), occupy a greater proportion of the habitats surveyed compared with *Juniperus* species. With the exception

Table 4. Similarity values for the geographic ranges, habitat breadth, and relative size of the local populations of *Juniperus* and *Turdus* species pairs. Interaction strength between the two species in each pair was estimated as the number of records for that pair relative to the total number of records for the two species. Dependence of the plant on the bird was estimated as the proportion of fruits consumed by the bird species. Dependence of the bird on that plant species was calculated as the proportion of feeding records on the plant species. A total of 15 pairs of species (excluding *T. philomelos*; see Table 1) were used in the computations.

Species pair	Similarity[1]			Interaction strength	Bird dependence on plant	Plant dependence on bird
	Geographic range	Habitat breadth	Local abundance			
communis-merula	0.361	0.545	0.644	0.0177	2.9	4.6
phoenicea-merula	0.425	0.609	0.868	0.0139	2.6	3.0
sabina-merula	0.389	0.714	0.756	0.0117	1.6	4.7
communis-iliacus	0.425	0.316	0.856	0.0408	8.0	8.4
phoenicea-iliacus	0.364	0.500	0.661	0.0034	0.8	0.6
sabina-iliacus	0.336	0.720	0.475	0.0264	4.0	7.8
communis-torquatus	0.349	0.375	0.728	0.1222	14.9	69.0
phoenicea-torquatus	0.360	0.588	0.707	0.1303	17.0	55.8
sabina-torquatus	0.311	0.545	0.523	0.0508	5.7	48.8
communis-pilaris	0.260	0.222	0.439	0.0000	0.0	0.0
pilaris-phoenicea	0.259	0.632	0.687	0.0117	7.1	2.4
sabina-pilaris	0.208	0.500	0.553	0.0000	0.0	0.0
communis-viscivorus	0.098	0.286	0.740	0.0564	8.2	18.0
phoenicea-viscivorus	0.279	0.636	0.894	0.1333	22.0	33.9
sabina-viscivorus	0.171	0.593	0.669	0.0735	9.2	37.2

[1] Similarities of the geographic ranges and habitats occupied (presence-absence data, see Methods) were calculated with the Sørensen coefficient. Those for local abundances (quantitative data), with the Gower similarity coefficient (Legendre & Legendre 1979).

of *J. communis*, all junipers show reduced, patchy geographic distributions and are restricted to particular habitats. Local population size and geographic range showed no clear association (Fig. 4B), but there was a trend for species with larger population sizes to be habitat generalists and to occupy a greater number of habitats than rare species ($r_s = 0.689$, $p < 0.04$) (Fig. 4C).

No plant-bird species pair emerges from Fig. 4 that would suggest a degree of biogeographic congruence between the two genera. Correlations across species pairs ($n = 15$, see Table 4) between the similarity of geographic range, habitat specificity, and local abundance and the values of interaction strength derived from feeding records were non significant (Table 5). As expected from previous analyses, bird dependence on plants was greater for those species pairs exhibiting similar abundance patterns, suggesting some type of resource tracking, but increasing similarity of geographic ranges or habitat distributions were not correlated with greater mutual dependence.

A situation of close matching between two species at all levels would result in close proximity between their points in each plane depicted in Fig. 4. I computed the inverse euclidean distance between the species in each pair of Table 4 by simultaneously considering the scales of geographic range, habitat use, and local population. This was taken as an estimate of overall biogeographic congruence for each pair, and the resulting correlation coefficient with interaction strength was not significant ($r_s = -0.24$, $p = 0.38$, $n = 15$; Fig. 5). Species pairs with strong mutual dependence such as *J. sabina-T. torquatus*, *J. sabina-T. viscivorus*, and *J. communis-T. torquatus* (Table 1) showed very low values of biogeographic congruency. Thus, *J. sabina* is a geographically restricted species with narrow habitat specificity that interacts strongly with birds species of

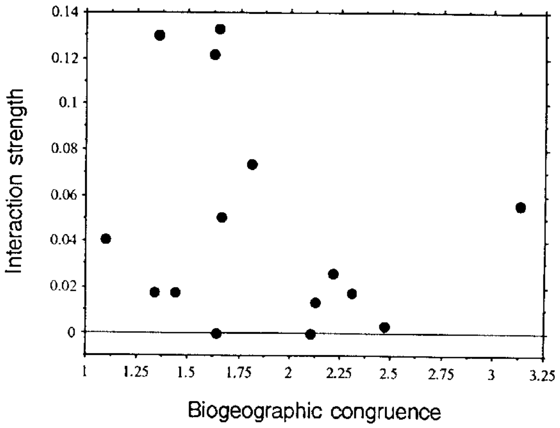

Fig. 5. Plot of biogeographic congruence values between each interacting *Turdus-Juniperus* species pair and their interaction strength in southern Spanish sites (data for the main study sites pooled). Overall biogeographic similarity was estimated as the inverse euclidean distance between the species in each pair when considering size of geographic range, habitat breadth, and local population size. Interaction strength was estimated as the percentage of all feeding records contributed by the records corresponding to each pair of species.

large geographic range and/or wide habitat specificity (*T. viscivorus*, *T. torquatus*). The *J. communis-T. torquatus* pair is also very asymmetric in biogeographic affinities, deriving mainly from differences in geographic ranges (Fig. 2). On the other hand, *J. sabina-T. iliacus* show a high biogeographical similarity but very low interaction strength. Therefore, juniper and thrush species showing strong local interactions in these habitats do not show similar geographic ranges, patterns of habitat use, or relative local popula-

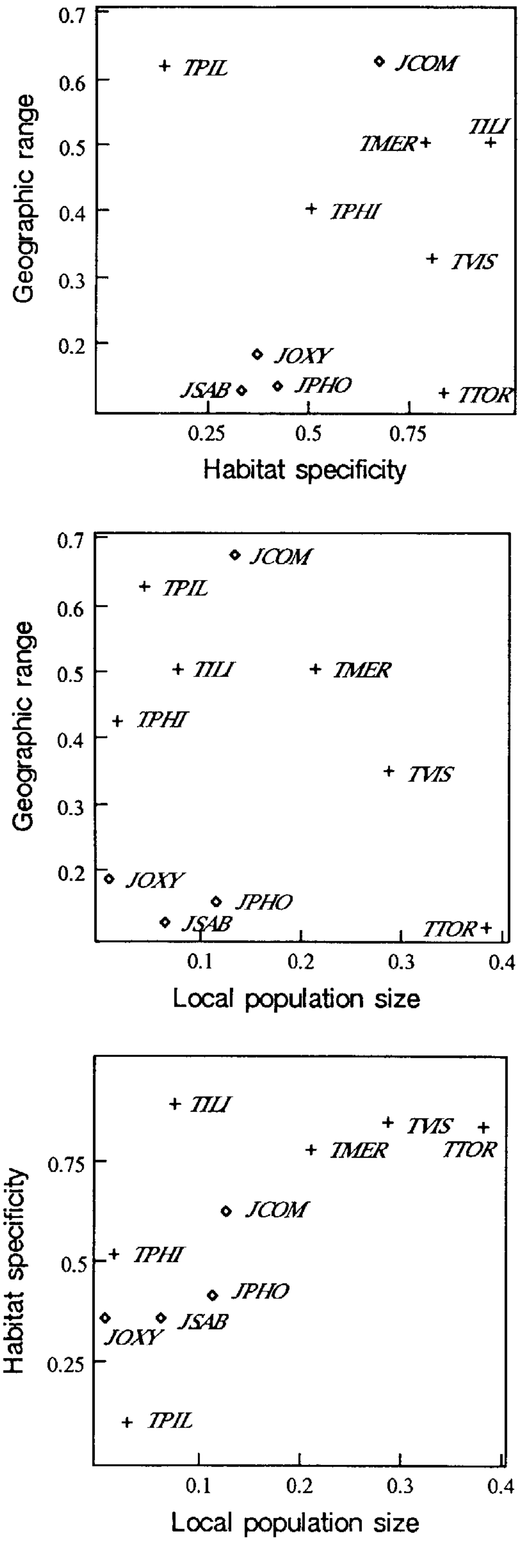

Fig. 4. Patterns of interspecific congruency between the population characteristics of *Juniperus* and *Turdus* species at different biogeographic levels. Importance values at the geographical scale were estimated as the proportion of 5° degrees quadrats where the species is present in the western Palearctic. Values for habitat specificity were calculated as the proportion of southern Spanish localities where the species is present. Figures for the local scale were calculated as the average proportion of total cover (*Juniperus* species) or total thrush abundance (*Turdus* species) in the study localities. The position of each species is indicated by symbols (plus signs, *Turdus* spp.; diamonds, *Juniperus* spp.). Abbreviations for species names as in Table 2.

Table 5. Rank correlations (Kendall's coefficient) between the similarity at different biogeographical levels for each pair of *Juniperus* and *Turdus* species and variables characterizing their interaction pattern at local study sites (see Table 4).

	Similarity between bird and plant in species pair[1]		
	Geographic range	Habitat specificity	Local abundance
Interaction strength	-0.097^{ns}	0.126^{ns}	0.298^{ns}
Plant dependence on bird	0.010^{ns}	0.058^{ns}	0.230^{ns}
Bird dependence on plant	-0.125^{ns}	0.116^{ns}	0.364*

* p = 0.058; ^{ns} non-significant.

[1] See Table 4.

tion sizes. Local interaction patterns of strong interdependency are not mirrored by a high degree of biogeographic congruence between the interacting species. This lack of congruence arises from the marked differences of geographic distribution and habitat breadth among *Juniperus* and *Turdus* species.

Discussion

Comparing congruence of plant and frugivore distributions at different scales

Hypotheses about the coevolutionary implications of local interaction patterns can be addressed only if different spatial scales (i.e. the geographic distribution, the regional patterns of habitat use, and the local population sizes) are considered simultaneously. Variation in the outcome of interactions is the raw material for their evolution (Thompson 1988), and we need to understand how the interaction patterns vary and how their outcomes (in terms of fitness implications for the participants) map onto this variation. Biogeographical levels or spatial scales act as nested filters such that congruence at all levels and scales is a necessary condition for an interaction to have taxa-specific evolutionary implications (Wheelwright 1988; Howe 1984). Otherwise, the selective pressures that emerge from strong localized interactions of mutual dependence, if any, are expected to be 'screened-off' by the variation in mutualistic assemblages between habitats or geographic regions.

This study provided no evidence that plant and frugivore species with more similar distribution patterns at each of the above levels showed greater mutual dependence at a local scale. Several alternative outcomes can be defined and the *Juniperus*/*Turdus* interactions described here illustrate some of them:

1. Close fitting between the geographic range, habitat affinity and local population size, together with strong interdependence. None of the interactions studied here fits this situation, but the case of *T. torquatus* and *J. thurifera* could possibly be an example. In general, I would expect this situation to arise in the interactions between two restricted endemic species or between continental species restricted to insular conditions (e.g., high-elevation habitats, etc.).
2. Close fitting at the regional and local scales but low similarity of geographic ranges. This situation is illustrated by the interaction between, e.g., *J. communis-T. torquatus* and *J. sabina-T. viscivorus*. This type of asymmetry in geographic distribution will be relevant to the evolution of strong interactions when the range of the more restricted species is included within the range of the mutualist. The selection pressures or demographic effects of the widely distributed species will be relevant to the restricted species, given the close habitat association and low variance (e.g., temporal) of the interactions. In contrast, the reciprocal effects of the restricted species are expected to be irrelevant for the widespread species, at

least when considering a large geographic scale. 3. Low congruence in geographic and regional distributions but strong local interdependence. This is a case of association by chance or opportunistic exploitation and is probably very common in plant-frugivore interactions. The interactions between junipers and the two irruptive thrush species (*T. pilaris* and *T. iliacus*) fit in here. Other situations of biogeographic unmatching could be imagined and exemplified, but most *Juniperus*/*Turdus* interactions fit situation 2 because of the general asymmetry of geographic distributions between the two species groups, with most *Juniperus* areas being 'nested' within the winter ranges of *Turdus*. In addition, the four *Turdus* species with greater relative importance in *Juniperus* dispersal occupied a greater range of habitat types than junipers, indicating a higher species turnover among localities for plant assemblages than for the bird assemblages (see also Herrera 1988a). Therefore, when considering simultaneously all three biogeographic levels, no concordance emerged between local interaction strengths and the congruence of abundance patterns. This result provides quantitative support to earlier interpretations of the lack of biogeographic congruence as a serious constraint for the coevolution of mutualisms (Wheelwright 1988; Herrera 1988a; Howe 1984). The analytical procedure outlined here, based on the typology of forms of rarity proposed by Rabinowitz (1981) appears to be a useful tool for comparing interaction patterns in different biogeographic areas and for testing hypotheses about biogeographic factors limiting coevolutionary interactions.

Variations in space and time: their patterns and causes

Results of this study illustrate marked spatial (between habitat types) and temporal (autumn-winter seasons in several years) variations in the abundance and species involved in interaction between *Juniperus* and *Turdus* species. Very few seed dispersal studies have explicitly addressed the question of variation in time and space and its quantification. Instead, they have considered a more restricted spatial or temporal scale than in the present study (Wheelwright 1988; Herrera 1988a; Keeler-Wolf 1988; Willson 1986, Bronstein & Hoffmann 1987; Jordano 1985; Howe 1980; Howe 1981; Levey 1988; Loiselle 1988). These studies have documented strong variations in the interactions and suggested that a spatio-temporal mosaic of sizes and compositions of seed disperser assemblages is the rule in nature.

At the regional level, most spatial variation in local *Juniperus-Turdus* species assemblages is due to differences in habitat selection.Habitat associations, defined by an elevational gradient, exist among the two species groups and the particular species of each genus present in each habitat is highly predictable. Highland habitats show a characteristic composition with *J. communis* or *J. sabina* as the locally dominant juniper species and *T. viscivorus* and *T. torquatus* as the dominant frugivores. Both *T. iliacus* and *T. pilaris* have irruptive movements associated (at particular sites) with the availability of large cone crops, and they can be found both in highland scrublands and in mid-elevation forests. All *Turdus* species enter the mountain forest and mid-elevation oak forest, but *T. merula* and *T. philomelos* are rarely seen in the highland juniper scrubland. Between-habitat differences in the composition of seed disperser assemblages at particular plant species have also been attributed to differential habitat selection patterns among frugivores and how these interact with the particular locations of individual trees (Bronstein & Hoffmann 1987; McDiarmid, *et al.* 1977; Herrera & Jordano 1981).

A clear pattern emerges for *Turdus* as a group to have a greater habitat breadth than *Juniperus* species. This supports earlier findings of Willson (1986) and Herrera (1988a), who found a greater habitat specificity for plants than for frugivorous birds. For example, Willson (1986) reported that the average percentage of habitat types occupied by wintering frugivorous birds in two major eastern North American regions was 58% and 67%; bird-dispersed plants occupied 49% of the habitats in the whole region. Southern Spanish rushes occupy, on average, 64% of the suryed sites ($n = 19$), while *Juniperus* species ocpy 45%. This, together with the fact that the V's for both temporal and spatial variations in *urdus* abundance were much lower than the CV's f *Juniperus* cone abundance, indicates a greater verall predictability of the frugivore assemblage cross habitats and seasons.

Between year variations in juniper cone crop roduction are related to their long ripening and one growth periods (> 1.5 years for the Spanish pecies; Ceballos & Ruiz de la Torre 1979; Obeso, 985; P. Jordano, pers. obs.) and masting behavour (Silvertown 1980; Roques, *et al.* 1984). Cliate, resource levels, and tradeoffs of previous productive events influence the reproductive ehaviour in a given year (Lev-Yadun & Liphshitz 1987). Years with no reproductive individals were frequent in the highland populations, as vealed by the present study, but also in a good rop year cones usually remained during the folwing winter in good condition for consumption nd added to that year's crop. Thus, the greatest ariability observed for the *Juniperus-Turdus* sysm occurred for cone availability among years ithin sites. The temporal variation (among years, ithin sites) of both *Juniperus* and *Turdus* abunances were much higher than the variation mong sites, as estimated by the CV's. These cts, together with coexistence of several *Junipes* species in the same area, result in a highly atchy winter resource distribution for the birds both space and time.

Previous studies of wintering thrushes have ointed out their strong dependence on juniper erries for winter food (Santos, *et al.* 1983; De uana & Santos 1981; Debussche & Isenmann 985a, 1985b; Zamora 1990) and the association f irruptive movements of wintering flocks with e local availability of berries (Tyrväinen 1970; imms 1978). Also, causes external to local food vailability (cold spells, food availability and cliatological conditions outside the wintering reas) have been proposed to explain the extreme ariation and unpredictability of winter bird ovements (see Santos 1982 and Soc.Esp.Ornilogía 1985 for a review). The strong positive relationship between local availability of juniper and other berries and the local abundance of thrushes suggests behavioral 'resource tracking' and strong bird responses to local food conditions. This type of functional response to fruit availability is expected in this particular system since: 1) juniper cone production made up an important percentage of the total fruit production at the highlands and is frequently the only fruit resource available; 2) important differences in cone availability can be found between nearby areas; and 3) frugivorous thrushes, the main seed dispersers, show erratic or nomadic movement patterns resulting in local altitudinal migrations or regional displacements. The positive relationship that exists across juniper-thrush species pairs between the similarity of local abundance patterns and the bird dependence values on the plants supports these conclusions. It is also interesting to point out the absence of a strong asymmetry in the pairwise interactions between plants and birds in this system, in contrast to their generality in plant-disperser interactions (Jordano 1987).

Concluding remarks

In the particular case of the *Juniperus-Turdus* interaction examined here, the strong uncoupling of biogeographic attributes of plants and frugivores implies that taxon-specific coevolved interactions are extremely unlikely. In this scenario, interactions between two species are restricted to a particular subset of their respective populations and show extremely variable outcomes in time and space. This situation might prove to be common in plant-frugivore interactions in nature. There are few studies containing both quantitative descriptions of how the species identity and numbers in local assemblages vary and quantitative descriptions of the outcome of their interactions (e.g., Herrera 1988b; Horvitz & Schemske 1990) but they support the hypothesis of a diffuse selection regime by a variable assemblage of mutualists.

It could be argued that *Turdus* species exert such a diffuse selection regime on plant fruiting traits given the asymmetry and nested interaction with junipers at a large geographical scale and the strong dependence of the plants on *Turdus* spp. for seed dispersal. No information is available, however, on the relative magnitude of bird effects on plant fitness through differential seed removal and influence on seed deposition and early seedling recruitment. Large variation is to be expected among *Turdus* species due to the variability of forging patterns among the main species at the highlands (*T. torquatus*, *T. viscivorus*, and *T. iliacus*). These include territorial defence of fruiting junipers (*T. viscivorus*; Snow & Snow 1988; P. Jordano, pers. obs.), foraging in large flocks in open areas (*T. torquatus*), and foraging at more closed vegetation in small flocks. This variation could have important effects on seed deposition patterns generated by the three species. For example, potential negative consequences of territorial defence include increased rodent seed predation below or nearby juniper patches (Schupp & López-Soria, pers. com.); in contrast, survival of seedlings from seeds dispersed to open areas can be low due to competition with grasses (Johnsen 1962; Fitter & Jennings 1975).

Therefore, a critical evaluation of the diffuse selection hypothesis would need to address at least three main points: 1) variation in space and time of the size, composition and numbers of the species interacting in local areas; 2) evaluation of the outcomes of interactions and mapping their variations (for example, by focusing on key components of these outcomes such as fruit removal, probability of postdispersal seed predation as a result of seed deposition patterns, and effects on early seedling survival); and 3) test the hypothesis that the effects of the interaction outcomes due to different species are not opposed, but rather additive or compensatory.

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Appendix 1. Summary of data on production of fleshy cones ('fruits') by *Juniperus* species in different southern Spanish localities and years. The total production of fleshy fruits (both *Juniperus* and other species included) is also summarized for each site and year.

Site, species, year	Transect surface sampled (m^2)	Number of fruits	Fruits/ m^2	Total fruit production/ m^2
Calarilla-Cda. Sabinas (Sierra de Cazorla)				
J. communis				
1985	3750	365	0.10	1.94
1986	450	2164	4.81	9.32
1987	450	2959	6.58	15.23
1988	450	266	0.59	8.41
1989	450	10	0.02	1.39
J. sabina				
1985	3750	0	0.00	
1986	450	955	2.12	
1987	450	450	1.00	
1988	450	60	0.13	
1989	450	15	0.03	
J. phoenicea				
1985	3750	43	0.01	
1986	450	326	0.72	
1987	450	245	0.54	
1988	450	2268	5.04	
1989	450	30	0.07	
Campos de Otero (Sierra Nevada)				
J. communis				
1985	540	25360	93.93	96.91
1986	540	11345	20.90	20.9
1987	540	1273	6.83	6.89
1988	540	97	0.18	0.22
Nava Noguera (Sierra de Cazorla)				
J. communis				
1985	37500	1270	0.03	–
1986	540	1327	2.55	11.68
1987	540	2090	3.87	21.41
1988	540	165	0.31	12.17
1989	540	765	1.42	30.54
J. phoenicea				
1985	37500	10	0.00	
1986	540	0	0.00	
1987	540	158	0.29	
1988	540	1924	3.56	
1989	540	1068	1.98	
Santa Bárbara (Sierra de Baza)				
J. sabina				
1985	–	–	–	–
1986	900	5777	6.42	6.88
1987	900	417	0.46	0.87
1988	900	1012	1.12	4.09

Appendix 2. Summary of census results (number of birds/km) in different southern Spanish localities and wintering seasons.

Site and Winter	*Turdus merula*	*Turdus philomelos*	*Turdus iliacus*	*Turdus torquatus*	*Turdus pilaris*	*Turdus viscivorus*	*Number of censuses*	*Distance (km)*
Calarilla-Cda. Sabinas (Sierra de Cazorla)								
85–86	0.75	0.00	0.15	2.24	0.00	5.82	9	6.7
86–87	2.00	0.00	0.00	0.50	0.00	3.75	2	4
87–88	3.24	0.00	4.71	0.00	0.00	3.24	10	6.8
88–89	1.32	0.00	0.55	0.11	0.00	4.62	11	9.1
Campos de Otero (Sierra Nevada)								
85–86	0.00	0.00	5.50	83.50	0.00	3.00	2	2
86–87	0.00	0.00	0.42	10.97	0.00	2.64	14	7.2
87–88	0.00	0.00	0.00	0.73	0.00	2.55	8	5.5
88–89	0.00	0.00	0.00	1.11	0.00	0.00	4	2.7
Cda. Travino (Sierra de Cazorla)								
85–86	6.82	0.00	0.45	5.45	0.00	6.82	3	2.2
86–87	8.18	0.00	2.73	1.82	0.00	5.45	2	2.2
87–88	6.49	0.39	5.84	11.43	0.00	5.45	11	7.7
88–89	6.45	0.00	0.97	1.29	0.00	3.23	16	12.4
Nava Noguera (Sierra de Cazorla)								
85–86	3.87	0.97	0.65	4.52	0.00	10.65	5	3.1
86–87	4.00	0.00	0.29	0.86	0.29	4.57	5	3.5
87–88	1.62	0.18	2.43	7.12	0.00	5.14	12	11.1
88–89	2.53	0.00	0.22	2.75	0.15	3.19	32	27.3
Santa Bárbara (Sierra de Baza)								
85–86	–	–	–	–	–	–	–	–
86–87	0.00	0.00	0.48	5.48	0.00	1.13	13	6.2
87–88	0.00	0.00	0.16	0.79	0.00	2.38	9	6.3
88–89	–	–	–	–	–	–	–	–

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