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Patterns of resource tracking by avian frugivores at multiple spatial scales: two case studies on discordance among scales

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Scaling is relevant for the analysis of plant-frugivore interaction, since the ecological and evolutionary outcomes of seed dispersal depend on the spatial and temporal scale at which frugivory patterns emerge. We analyse the relationship between fruit abundance and frugivore activity at local and landscape spatial scales in two different systems composed, respectively, by the bird-dispersed woody plants *Juniperus communis* and *Bursera fagaroides*, and their frugivore assemblages. We use a hierarchical approach of nested patchiness of fruit-resource, where patches are defined by individual plants within site, at the local scale, and by sites within region, at the landscape scale. The structure of patches is also described in terms of contrast (differences in fruit availability among patches) and aggregation (spatial distribution of patches). For *J. communis*, frugivore activity was positively related to fruit availability at the landscape scale, this pattern seldom emerging at the local scale; conversely, *B. fagaroides* showed a general trend of positive local pattern that disappeared at the landscape scale. These particular trends might be partially explained by differences in contrast and aggregation. The strong contrast among plants within site together with a high aggregation among sites would promote the *B. fagaroides* pattern to be only local, whereas in *J. communis*, low aggregation among sites within region would favour a sharp landscape-scale pattern. Both systems showed discordant patterns of fruit-resource tracking among consecutive spatial scales, but the sense of discordance differed among systems. These results, and the available multi-scale frugivory data, suggest that discordance among successive scales allows to link directly frugivory patterns to resource-tracking mechanisms acting at particular scales, resulting, thus, more informative than concordance observational data, in which landscape patterns might result from accumulated effect of local mechanisms. In this context, we propose new methodological approaches for a better understanding of the hierarchical behavioural mechanisms underpinning the multi-scale resource tracking by frugivores.

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Frugivory by vertebrates is a main ecological interaction in many temperate and tropical environments (Willson et al. 1989, Fleming 1991, Herrera 1995, Jordano 2000). By means of seed dispersal, frugivores may affect both population biology and evolutionary trends of plants (Howe and Smallwood 1982, Fleming 1991, Willson and Traveset 2000, Herrera 2002). These outcomes are highly dependent of the spatial and temporal scales at which frugivory performs (Herrera 1985a, b, 1998, Jordano 1995, Kollmann 2000, Thompson 2002). For example, frugivores acting at small spatial scale, and selecting among different fruits within the same infructescence or individual plant, might affect sib-competition as well as paternity patterns within the plant population (Bertin

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1988, Lee 1988). At a wider spatial scale, such as the site or locality scale, selective dispersal among individual plants filters qualitative and quantitatively the seed output, affecting plant population dynamics (Herrera et al. 1994, Willson and Traveset 2000, Jordano and Godoy 2002). Moreover, the local effect on single-species population dynamics might be also interpreted in terms of plant community sorting, when dispersal affects differentially the species sharing the same habitat (Herrera 1985a, Kollmann 2000, Muller-Landau et al. 2002, Schupp et al. 2002). At the higher scale of landscape, frugivores may modify regional diversity patterns by means of a differential demographic effect at different sites (Kollmann 2000, Ortiz-Pulido et al. 2000, Terborgh et al. 2002). From an evolutionary perspective, dispersal can be considered as an important component of fitness, and thereby differences in dispersal rate among co-occurring plants might result in significant phenotypic selection on several fruit traits (Thompson 1994, 2002, Jordano and Godoy 2000, 2002, Herrera 2002). However, the variation in the fruit-frugivore patterns among sites or geographical regions might screen-off the local selective pressures or, alternatively, could be the context for local adaptation or even geographical mosaics of coevolution (Jordano 1993, Thompson 1994, 2002). In addition, selective pressures by frugivores might be diluted at the long term due to temporal inconsistencies in plant-frugivore patterns (Herrera 1998, Levey and Benkman 1999).

The aforementioned effects of frugivory are conditioned by the frugivore response to the variable levels of fruit availability at different spatial and temporal scales. Fruits occur as a sessile, strongly heterogeneous, resource, their abundance varying among branches within plant (e.g. Gill 1986, Thébaud and Debussche 1992, Obeso and Grubb 1993), among individual plants within site (e.g. Jordano 1987, Sallabanks 1992, Alcántara et al. 1997), among sites and even among geographical regions (e.g. Herrera 1985a, Levey and Stiles 1992, Jordano 1993, Ortiz-Pulido and Rico-Gray 2000, García et al. 2001), as well as at different scales of the temporal spectrum (e.g. Herrera 1985a, 1998, Levey 1988, Loiselle and Blake 1991). Moreover, fruit-resource heterogeneity is usually scale-dependent, the levels of variability changing among successive scales. To cope with this scale-dependent heterogeneity, frugivores might show different life-history and behavioural mechanisms allowing an effective fruit-resource tracking (Fleming 1992). Among their foraging decisions, frugivores might choose larger or more profitable fruits within the individual plant (e.g. Jordano 1987, Sallabanks 1992, 1993), plants with bigger crop sizes within a site (e.g. Davidar and Morton 1986, Laska and Stiles 1994, Ortiz-Pulido and Rico-Gray 2000), and sites, habitats or even regions, depending on their fruit availability (e.g. Herrera 1985a, Loiselle and Blake 1991, Levey and Stiles 1992, Jordano 1993, García et al. 2001). Despite these findings, little is known about the multi-scale patterns of fruit-frugivore interactions, that is how fruit-tracking patterns move up-down across successive spatial scales and ecological levels for a given fruit-frugivore system (but see Sallabanks 1993). In other consumer-resource systems, like that of pelagic birds and their fish preys (e.g. Russell et al. 1992, Logerwell et al. 1998, Fauchald et al. 2000; see also Senft et al. 1987, Schaefer and Messier 1995, for mammalian herbivores), the pattern of resource tracking (i.e. the positive relationship among bird and prey abundances) is consistent across successive spatial scales, promoting the occurrence of domains of scale, that is, regions of the scale spectrum over which the pattern does not change (sensu Wiens 1989). However, for the fruit-frugivore system, the scarce available information is somehow contradictory, since the positive relationship among fruit abundance and frugivore activity might be consistent (e.g. Christensen and Whitham 1991, Rey 1995) or inconsistent among spatial scales (e.g. Jordano 1993, Rey 1995). More importantly, the factors determining why sometimes fruit-resource tracking is only expressed at particular scales are poorly understood.

Answering the previous questions requires a framework enabling to represent adequately the patchy nature of fruit resource, the scale-dependent heterogeneity affecting fruit-resource patches, and the effect of patch structure in the occurrence of significant frugivory patterns. This might be achieved by means of a hierarchical model of patch structure (sensu Kotliar and Wiens 1990) where frugivores must cope with fruit-resources clumped in patches hierarchically nested across successive levels: 1) fruits within individual plants covering a few square meters area; 2) individual plants within sites covering areas of several hundred of square meters; 3) sites within regions of at least several ha, representing differentiated plant populations or stands in localities separated by topographic features like hill-tops or valley bottoms; and 4) regions within wide geographical areas of many thousands of square kilometres, separated by geographical features like mountain ranges or basins (Fig. 1). Each level of patchiness might be considered as an observation scale characterised by a combination of grain, the smallest size of a patch represented at the considered scale, i.e. the smallest area at which a frugivore responds to patch structure by differentiating among patches, and extent, the spatial environment considered (e.g. individual plants are the grain in the extent of a given site, Fig. 1; see also Allen and Hoekstra 1991). Frugivores might be classified depending on their particular ability to respond to different levels of hierarchical patchiness, some frugivores determining scale-dependent patterns (e.g. A–D in Fig. 1) whereas others being able to cope with patchiness over a range of successive levels, contiguous or not, determining, thus, the occurrence of consistent patterns

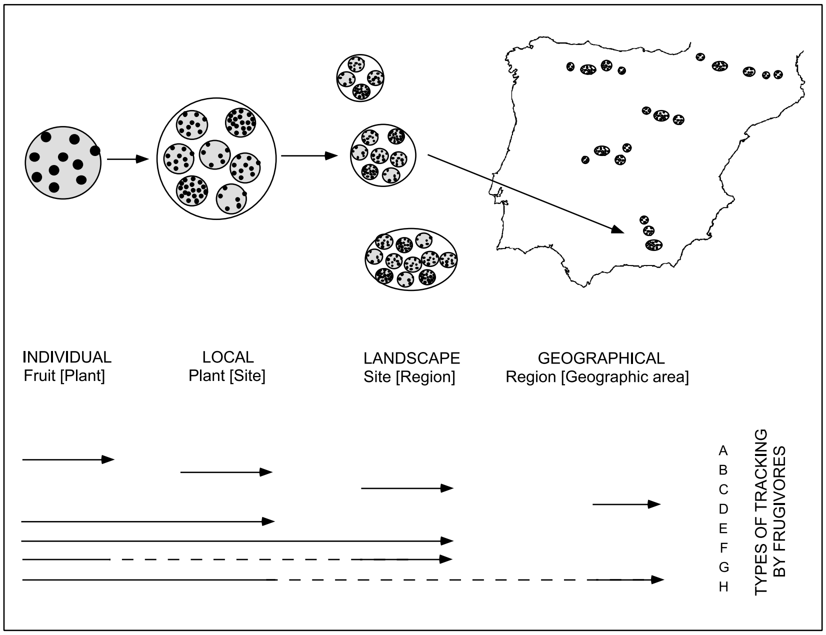

Fig. 1. Representation of a hierarchical system of nested patchiness in fruit-resource abundance. Fruits are clumped within individual plants, plants are nested within sites like mountain slopes or hilltops, sites are nested within regions like mountain ranges, and regions are nested within parts of a wide geographic area like the Iberian peninsula. The case of juniper *Juniperus communis* L. in the Iberian peninsula would match this framework (Jordano 1993, García et al. 2001). Spatial scales are defined by the combination of grain and the extent (e.g. for the local scale, the grain is individual plant and the extent is site). Frugivores might respond to fruit-resource patchiness by different types of tracking, classified as those only expressed at specific scales (A–D) and those expressed at multiple successive scales, contiguous or not (E–H, the dashed line indicates no tracking, the continuous line across successive scale depicting a domain of scale, see also Wiens 1989).

across domains of scales (e.g. E–H in Fig. 1). Finally, frugivore response to patchiness may be affected by the structure of the fruit-resource patch ensemble, mostly determined by two components: contrast and aggregation (Kotliar and Wiens 1990). Contrast refers to the differences among patches in fruit availability, whereas aggregation refers to the spatial distribution or contagion among patches. It is expected that frugivores should be more patch-sensitive in situations of high contrast among patches, where the gradients in fruit abundance are sharp. On the other hand, situations of great aggregation among fruit-resource patches probably would lead to frugivores to be patch-insensitive, considering all patches as a whole.

In this paper, we analyse resource tracking by avian frugivores at multiple spatial scales in two different plant-frugivore systems, in order to understand how the heterogeneous structure of fruit-resource patches might affect the occurrence of concordant frugivory patterns across scales. We discuss our results in relation to the available multi-scale frugivory studies, exploring the current knowledge gaps, evaluating the power of concordant patterns for the inference of scale-specific mechanisms, and suggesting new approaches for a better understanding of fruit-frugivore interaction at multiple scales.

Methods

We analyse the importance of fruit-resource patch structure in multi-scale resource tracking by frugivores in two systems which studied the variation in the frugivore activity by birds in relation to the individual crop size of a given plant species, for a relatively high number of sites in two contrasting biomes (Ortiz-Pulido and Rico-Gray 2000, García et al. 2001). This enabled us to analyse the response of a highly mobile frugivore type in a framework of hierarchical patchiness with adequate sample sizes.

The first system studied frugivory patterns in the common juniper *Juniperus communis* L. (Cupressaceae) inhabiting the Mediterranean high mountains of south-eastern Spain (García et al. 2001). Juniper bears berry-like cones containing 1–3 seeds, which are consumed by a small assemblage of frugivorous thrushes, mainly *Turdus torquatus* L. and *T. viscivorus* L. (Zamora 1990, Jordano 1993, García 2001). The populations of these birds are mainly composed by north European migrants wintering in the region, flocks being able to easily move among distant sites (Santos 1985). We considered seven juniper populations located in large (1–4 ha), almost mono-specific juniper patches with fruiting plant cover ranging from 2 to 20%. They occurred in different mountain slopes and were the main juniper populations over an area of ca 5500 km^2 throughout the Baetic mountain range. Fruit crop size and the frugivore activity were sampled in 20–53 plants per site for 1–3 yr during 1994–1996 (see García et al. 2001, for a comprehensive methods description). Frugivore activity was estimated based on density of bird pellets per plant at the end of the dispersal period (for a similar procedure see Santos and Tellería 1994). Loss of pellets due to rain was considered negligible, precipitation in these Mediterranean localities accumulating mostly in winter, after the sampling was done. Similar assumption was followed in relation to losses due to rodent seed predation, since the depredated seeds are easily identifiable and are eaten by rodents in situ (García 2001, García et al. 2001).

The second study system analysed frugivory patterns in the fragrant bursera *Bursera fagaroides* (H. B. and K.) Engl. (Burseraceae) inhabiting the coastal dunes of central eastern Mexico (Ortiz-Pulido and Rico-Gray 2000). *Bursera fagaroides* bears yearly dehiscent fruits containing one fleshy seed, commonly consumed and dispersed by two bird species, *Dumetella carolinensis* and *Vireo griseus* (Ortiz-Pulido and Rico-Gray 2000). Both bird species stay in the area for brief periods during their migration from north to southern America, showing short flying distances when foraging in fruiting areas (Ortiz-Pulido 2000). We considered four *B. fagaroides* populations located in small patches (0.35 ha) with fruiting plant cover ranging from 2 to 5%, and located in different slopes and orientations in a dune area occupying a total surface of ca 3 ha. For each site, fruit crop size and frugivore activity (accumulated number of bird visits per plant) was evaluated in 9–17 plants, from 1996 to 1999 (see Ortiz-Pulido and Rico-Gray 2000, for a comprehensive description of methods).

For each plant-frugivore system, we analysed the strength and the consistency in the relationship among fruit abundance and frugivore activity at two consecutive spatial scales. We firstly evaluated this relationship at the local scale (grain = individual plant, extent = site) by assessing separately data from each plant population and year, which provided 14 "site × year" cases in *J. communis* and 16 cases in *B. fagaroides*. We assumed that these cases depicted independent situations of frugivore response to the spatial heterogeneity in fruit-resource patchiness, since individual fruit crops and frugivore abundances varied significantly among sites and years (Ortiz-Pulido and Rico-Gray 2000, García et al. 2001; for similar procedures see Christensen and Whitham 1991, Jordano 1993, Rey 1995). The relationship among fruit abundance and frugivore activity was further analysed at the landscape scale, the scaling-up from the local scale being achieved by coarsening the grain simultaneously to widening of the extent. For that, we considered the fruit abundance for every site as the accumulated fruit abundance of all plants within each site. By removing the within-site variability, the possible noise imposed by the heterogeneity at the lower level is eliminated, allowing to clearly relating the emerging patterns to the heterogeneity at the landscape scale. Thus, we obtained frugivore activity (density of bird pellets per plant in *J. communis* and number of bird visits per plant in *B. fagaroides*) and fruit abundance per surface unit (ha^{-1}) for each "site × year" case by multiplying the average values of all plants within site by the respective fruiting plant cover accounting, in this way, for the possible differences among fruit-resource patches (sites) due to the abundance of fruiting plants within site. We used Pearson's product-moment correlations to assess the relationship among fruit abundance and the frugivore activity at both spatial scales.

We accounted for the effect of resource-patch structure in the occurrence and the strength of positive relationships among fruit abundance and frugivore activity, by considering the contrast and the aggregation among fruit-resource patches at different spatial scales, for each study system (Kotliar and Wiens 1990). At the local scale, contrast among fruit-resource patches (individual plants) was measured by means of the Coefficient of Variation (CV) of plant crop size, whereas aggregation was measured as the average nearest neighbour distance between fruiting plants (NND). At the landscape scale, contrast was measured as the CV of the density of fruits per site (fruits ha^{-1}), from all combinations site × year, whereas average distance among sites, obtained from a matrix of distances among all pairs of sites, was used as aggregation measure. We measured the strength of fruit-frugivore relationship by means of the covariance values derived from the above correlations among fruit abundance and frugivore activity. Then, we checked the effect of contrast in the strength of fruit-frugivore relationship by relating covariance to the values of CV of crop size, using Pearson's correlations where each "site × year" case was a sample unit. A similar test was performed respecting to the aggregation effect, but considering a unique value for each site (the average of covariance values per site; $n = 7$, for *J. communis*, and $n = 4$, for *B. fagaroides*) since plant aggregation values were similar among years for each site.

Results

The relationship among fruit abundance and frugivory at the local scale was occasional in the *J. communis* system, with four cases of 14 "site × year" combination showing a positive significant correlation among individual crop size and frugivore activity ($p < 0.05$) but most remaining combinations showing low values of covariance and small correlation coefficients ($p > 0.1$, Table 1). Conversely, in the *B. fagaroides* system, there was a general trend of positive response of frugivorous birds to individual crop size in most sites, with covariance values higher than in *J. communis*, and five from 14 cases showing a correlation coefficient significant at $p < 0.05$ (and four additional cases being marginally significant at $p < 0.1$, Table 1).

In *J. communis*, the strength of the relationship among fruit abundance and frugivore activity at the local scale was unaffected by the contrast in crop size among individual plants (correlation covariance-crop size CV:

Table 1. Values of the Pearson's correlation coefficient (in bold, $p < 0.1$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$) and the covariance among fruit abundance per plant (individual crop size) and frugivore activity per plant for different site × year combinations for the fruit-frugivore systems of *Juniperus communis* (García et al. 2001) and *Bursera fagaroides* (Ortiz-Pulido and Rico-Gray 2000). For each case, the number of sampled plants, the coefficient of variation (CV) of plant crop sizes (contrast), and the average nearest neighbour distance (NND) among fruiting plants (aggregation) are also shown. No correlation value was obtained from East slope 1-1998 and East slope 1-1999 in *B. fagaroides* since frugivore activity was zero for all sampled plants.

Site	r	Covariance	n	CV	NND (m)
Juniperus communis					
Boleta-1994	**0.605** **	0.029	20	1.22	1.82
Boleta-1995	0.279	0.013	20	0.91	–
Boleta-1996	0.293	0.013	20	0.86	–
Collado Cabañas-1995	0.236	0.005	20	0.77	2.82
Dornajo-1994	**0.649** ***	0.031	20	0.91	6.05
Dornajo-1995	0.138	0.001	20	1.66	–
Dornajo-1996	**0.606** ***	0.030	20	1.82	–
Maitena-1995	0.225	0.008	20	0.87	1.26
Campos Otero WM-1994	0.192	0.008	22	0.93	3.25
Campos Otero WM-1995	**0.428** *	0.029	22	1.03	–
Campos Otero DH-1994	**0.204**	0.009	53	1.42	0.95
Campos Otero DH-1995	0.122	0.010	53	1.38	–
Campos Otero DH-1996	0.011	0.0004	40	1.10	–
Trevenque 1995	0.179	0.008	20	1.85	3.16
Bursera fagaroides					
East slope 1-1996	**0.344**	0.024	16	1.20	7.62
East slope 1-1997	0.113	0.015	16	0.84	–
East slope 1-1998	–	0.0	16	1.47	–
East slope 1-1999	–	0.0	16	1.77	–
East slope 2-1996	0.437	0.063	9	1.81	5.77
East slope 2-1997	**0.726** **	0.043	9	1.03	–
East slope 2-1998	**0.895** **	0.183	9	1.99	–
East slope 2-1999	**0.791** **	0.144	9	2.58	–
West slope 1-1996	**0.377**	0.024	17	0.82	0.29
West slope 1-1997	**0.346**	0.043	17	1.08	–
West slope 1-1998	−0.037	−0.006	17	1.13	–
West slope 1-1999	**0.434** *	0.075	17	1.58	–
West slope 2-1996	0.293	0.059	16	1.39	2.19
West slope 2-1997	−0.081	−0.022	16	1.22	–
West slope 2-1998	**0.515** *	0.199	16	1.24	–
West slope 2-1999	**0.350**	0.026	16	1.73	–

$r = 0.013$, $p = 0.97$, $n = 14$). Similarly, the relationship crop size-frugivory was independent to aggregation among plants (Table 1, $r = 0.577$, $p = 0.19$, $n = 7$). In *B. fagaroides* system, frugivory strength was positively related to crop size contrast (correlation covariance-crop size CV: $r = 0.463$, $p < 0.05$, $n = 16$) but was unaffected by plant aggregation (correlation covariance-NND: $r = -0.059$, $p = 0.92$, $n = 4$).

At the landscape scale, the activity of *J. communis* frugivores increased significantly in sites with higher fruit abundance ($r = 0.927$, $p < 0.0001$, $n = 14$, Fig. 2). This was not the case for *B. fagaroides* system, where birds did not respond to the variability among sites in fruit abundance ($r = 0.208$, $p = 0.45$, $n = 16$, Fig. 2). The CV value of fruit abundance at the landscape level was similar in both systems (*J. communis* $CV = 0.867$, *B. fagaroides* $CV = 0.912$), but aggregation among sites was much lower in *J. communis* than in *B. fagaroides* (the average distance among pairs of sites was 31.24 km and 0.11 km, respectively).

Discussion

Our analysis suggests different trends in the multi-scale patterns of the plant-frugivore systems of *J. communis* and *B. fagaroides*. Juniper frugivores were seldom affected by fruit-resource patchiness at the local scale, but clearly responded to fruit abundance at the landscape scale. On the contrary, in many *B. fagaroides* sites, frugivore activity mostly concentrated in those plants with larger crops. However, this general trend disappeared when considering the site as grain, indicating that the relevant scale for fruit-frugivore patterns in *B. fagaroides* is the local one. Thus, both systems showed discordant patterns of resource tracking among consecutive levels of hierarchical patchiness in fruit-resource heterogeneity, the sense of this discordance differing among systems. For *J. communis*, a clear landscape pattern emerged even with scarce patterns at the immediately lower scale (Fig. 3a). Conversely, *B. fagaroides* system could exemplify how a pattern emerging at a local scale dilutes when scaling-up (Fig. 3b).

Effect of contrast and aggregation in the patterns of scaling-up

The contrary scaling-up patterns depicted here might be partially explained by the differences among systems in

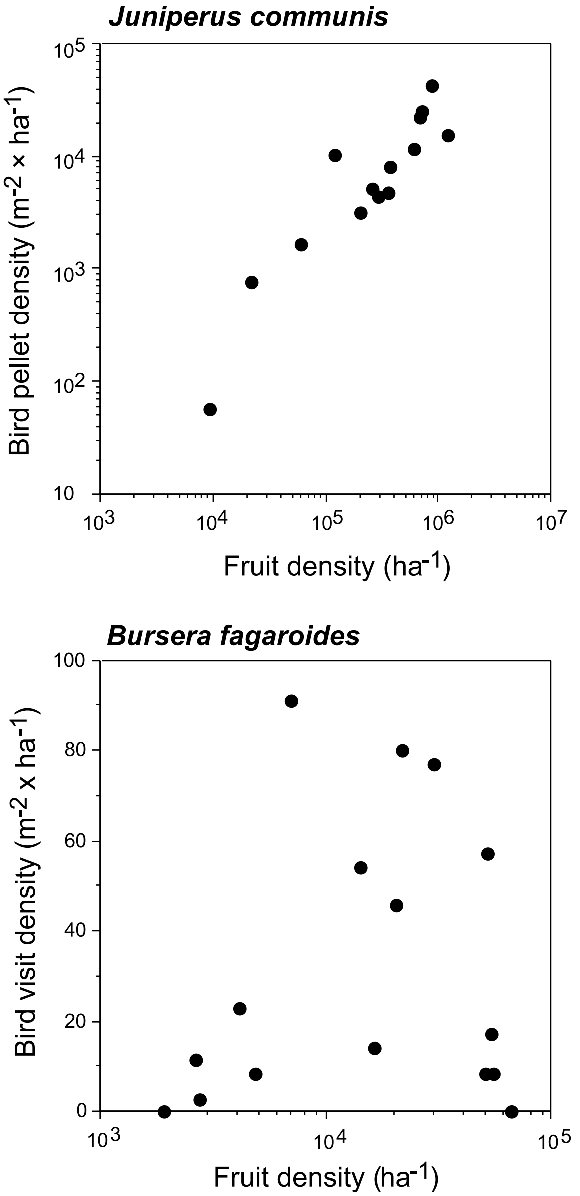

Fig. 2. Values of the activity by frugivorous birds in different sites (combinations "site × year"; cf. Table 1) in relation to fruit abundance, for the plant-frugivore systems of *Juniperus communis* and *Bursera fagaroides*.

the structure of hierarchical patchiness. In the case of *B. fagaroides*, frugivores were clearly affected by contrast in crop size among individual plants, the response of birds to fruit availability being sharper in those sites showing stronger differences among plants in crop size. This was not the case for *J. communis*, where the strength of the relationship among fruit abundance and frugivory at the local scale was unrelated to fruit availability gradients. Contrast and aggregation could also account for the differences in the landscape patterns and, consequently, in the discordance among scales. In fact, in *B. fagaroides*, the value of the coefficient of variation in fruit abundance among sites ($CV = 0.91$) was much lower than those found among plants within-site (mean $CV = 1.43$, see Table 1), suggesting a lower contrast at the landscape scale than that usually perceived by birds at the local scale (Fig. 3b). On the other hand, juniper sites built up an archipelago of largely separated patches in a vegetation matrix without fruits, whereas *B. fagaroides* local patches, despite unconnected in a dune grassland matrix, are relatively close ones from each other. This stronger among-site aggregation, together with the differences in contrast among scales, are probably precluding the occurrence of clear frugivory patterns at the fine-grained landscape scale here considered. Thus, the proper scale for analysing the fruit-frugivory pattern in this *B. fagaroides* system would be probably that considering individual plant as grain and the whole area comprising the four sites as extent.

Discordance vs concordance among scales in fruit-frugivory patterns

The discordance among scales found in our results contrasts with the concordance suggested by other fruit-frugivore systems (e.g. Christensen and Whitham 1991, Rey 1995). For example, *Nucifraga columbiana* tracked positively individual trees with larger crop size within different stands of *Pinus edulis* but also harvested more from pinyon stands with larger crops (Christensen and Whitham 1991). Similarly, *Sylvia atricapilla*, eating fruits of *Olea europaea* var. *europaea*, showed a positive abundance response to the fruit availability at both the local and the landscape scale, mostly concentrating in rich-fruited patches within the sites, as well as in rich-fruited sites within the region. However, the consistency between local and landscape patterns should be interpreted cautiously, since the positive relationship among fruit availability and frugivore activity at the landscape level could result exclusively from the accumulation of the particular positive patterns at the immediately lower scale, that is, at each one of the individual sites (Fig. 3c).

What are the conditions and causes promoting this type of landscape accumulative patterns? Firstly, and differently to described in *B. fagaroides*, these patterns could occur when the gradient of resource heterogeneity (the contrast among patches) is much higher at the landscape than at the local scale (Fig. 3c). Secondly, accumulative patterns are prone to occur when local fruit abundance is measured exclusively by averaging crop size for individual plants, with no consideration of fruiting plant coverage, since differences among sites in plant cover could generate patterns at the landscape scale different from that depicted by merely average crop size. Finally, even when scaling-up is adequately done by simultaneously changing grain and extent (Allen and

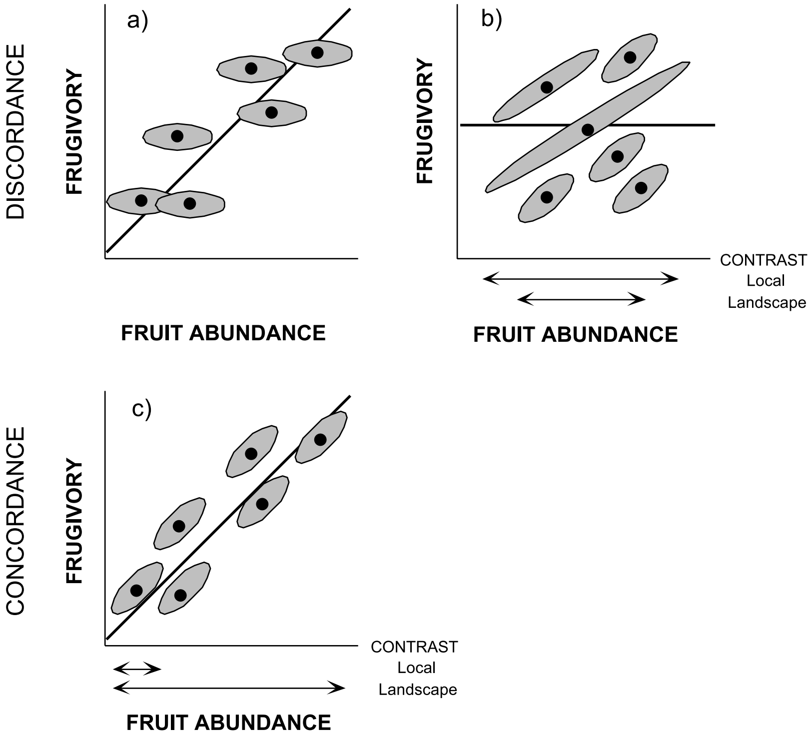

Fig. 3. Representation of the positive relationship among fruit abundance and frugivore activity (resource tracking) at local and landscape spatial scales, showing also the concordance or discordance among scales. Each grey ellipse depicts the data for a group of individual plants within a site, evaluating resource tracking at the local scale. The black point might represent the average or the accumulated within-site value, the line built-up by all black points evaluating resource tracking at the landscape level. The cases a) and b) represent discordance among scales, when, respectively, the pattern emerges at the landscape scale in the absence of site-scale patterns, and when, despite consistent within-site pattern, no landscape pattern emerges. In the case b), the contrast, i.e. the gradient of variation in fruit-resource availability at the local scale is similar or larger than at the landscape scale. The case c) represents concordance among scales resulting from accumulation of particular site patterns, and a situation where the contrast at the local scale is smaller than at the landscape scale.

Hoekstra 1991), bottom-up accumulative patterns might be due to high connectivity in the fruiting landscape. For example, when fruit local patches are linked by isolated, large crop-size plants, frugivores might use these isolated plants as "stepping stones" among local patches (see also Guevara and Laborde 1993, Fischer and Lindenmayer 2002), concentrating progressively in rich-fruited sites merely by searching for rich-fruited individual plants, and not by actively searching for rich-fruited sites.

Our results agree, on the other hand, with that of Jordano (1993) who found spatial coupling among the local fruit production of several juniper species (*J. communis* among them) and the abundance of wintering frugivores (*Turdus* spp.) in southern Spain. This author evidenced that the landscape pattern disappeared when scaling-up, since low congruence in distribution areas among junipers and their dispersers was found at the geographical extent of western Europe (Jordano 1993). Furthermore, by combining Jordano's (1993) findings with our results for the system of *J. communis*, it is possible to evaluate the fruit-resource tracking pattern at three consecutive scales (local, landscape, and geographical). In this system, the discordance among scales is expressed up- and downwards from the landscape, since birds did not couple their ranges with the plant's distribution area, conditioning lack of geographical tracking, nor selected individual plants within sites depending on their crop size, precluding local tracking. Nevertheless, thrushes, thanks to their flocking behaviour and great mobility over relatively large distances, are probably able to use landscape cues and, consequently, track efficiently fruit availability among sites within a region (Fig. 1, frugivore type C). This great mobility might, in fact, account partially for the differences with the *B. fagaroides* system, whose frugivorous birds (*D. carolinensis* and *V. griseus*) scarcely fly over long distances when staying in bursera fruiting areas (Ortiz-Pulido 2000).

Multi-scale resource tracking mechanisms

The mechanisms underpinning the pattern of fruit-resource tracking at different scales could be searched in the frugivore behavioural responses to resource heterogeneity. In the case of pelagic birds, the consistent multi-scale patterns of prey tracking is explained by means of a cascade of levels of behaviour, that is, a foraging pattern where an initial broad exploratory strategy is replaced by a more specific, small scale, searching behaviour (Russell et al. 1992, Fauchald et al. 2000). Similarly, a hierarchical system of decission making has been described for frugivorous birds, at least for the lower levels of resource patchiness: fruits within plants and plants within site (Sallabanks 1993).

However, despite that frugivores are able to track for fruits at the landscape scale (Jordano 1993, Rey 1995, this study) no evidences exist about a clear hierarchical selection including this spatial level. In other words, some frugivores are able to choose actively in which site to land, in which plant to feed, and what fruit to pick, depending on the resource availability (cf. Sallabanks 1992, 1993), but a constancy in the resource abundance as a selection cue across all these successive scales is probably rare. In fact, patch selection might be also affected by scale-dependent factors other than resource abundance (e.g. the availability of perching structures, García et al. 2001), which finally determine the selection of individual plants within site. On the other hand, some frugivorous species might show selection cues at small spatial scales but, due to morphological constraints, be unable to track for fruits at the landscape scale, as it might happen in birds with small body size and low mobility among long-distant local patches.

Concluding remarks

Our empirical results and the current available literature evidence that frugivores are able to cope with spatial heterogeneity of fruit-resource availability at different scales, responding positively to fruit abundance. However, under a framework of hierarchical patchiness, where spatial scales are defined in terms of delimited grain and extent, the positive response patterns are frequently seen as inconsistent across scales, the scale-dependence of the pattern being probably related to the structure of patches within each scale. This discordance among scales in fruit tracking probably translates into scale-dependent differences in seed dispersal and plant recruitment processes, clearly affecting the co-evolutionary potential of plant-seed disperser interaction (Jordano 1993, Kollmann 2000).

The mechanisms determining the occurrence of frugivory patterns at different scales are interpreted as foraging behavioural responses that are themselves scale-dependent and which might occur as hierarchical cascades of successive decisions. However, in cases of concordance of patterns among successive scales, the occurrence of upper scale patterns might be, in fact, explained by the accumulated effect of mechanisms occurring at the immediately lower scale, alternatively to scale-specific mechanisms (see also Wu and Loucks 1995). In this context, the discordance among successive scales allows to clearly link scale-specific patterns to processes occurring at the same scale, being, thus, more informative than concordance for the inference of scale-specific mechanisms.

Our discussion on the limitations to evaluate frugivory patterns and their underpinning mechanisms at multiple spatial scales evidences the need of new methodological approaches in this field. The explicit consideration of contrast, aggregation and connectivity among fruit-resource patches would enhance the power of observational approaches to describe the multi-scale behaviour of frugivores. Complementary approaches could consider the co-variation of fruit abundance and frugivore activity along large spatial or temporal sampling transects, as used in pelagic consumer-resource systems (e.g. Russell et al. 1992, Fauchald et al. 2000), allowing to understanding frugivory patterns from the perspective of spectral dynamics. More importantly, the mechanisms generating the spatial patterns should be explored experimentally, by manipulating nested gradients of fruit-resources at local and landscape scales, in order to detect hierarchical selection processes (see also Sallabanks 1993). Finally, the effects of fruit-resource tracking should be analysed considering not only population approaches, but also community frameworks exploring the relationship among plant and frugivore richness at multiple spatial scales (e.g. Ortiz-Pulido et al. 2000) in order to evaluate seed dispersal consequences on local and regional patterns of diversity.

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