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Conservation of seed-dispersing migrant birds in Mediterranean habitats: Shedding light on patterns to preserve processes

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Abstract

Migratory frugivorous birds disperse the seeds of many plant species, forming mutualistic associations that render frugivores a priority for conservation in many habitats worldwide. We analysed the distribution of seed-dispersing frugivorous passerines in southern Spain, which is an important area for the conservation of European birds during winter. Frugivorous birds showed similar regional abundance and richness during four winters, although fruit availability changed among years. However, the spatial distribution of frugivorous birds in the area changed among years. These changes were principally determined by annual variation in the distribution of fruits in the area, revealing a clear ability of birds to track the distribution of fruits. The unpredictable distribution of fruits each year suggests that regional fruit crops, rather than selected habitat patches, need to be protected for the long-term conservation of frugivorous bird populations in wintering grounds. Remarkably, the distribution of frugivores was independent of forest development or general cover of shrubs, which helps to reconcile the protection of fruiting shrubs with forest cleaning, an usual management to prevent devastating summer fires that is destroying fleshy-fruited plant communities in many areas of southern Spain. Thus, leaving a part of the fruiting shrubs untouched when cleaning forest undergrowth will allow the settlement of frugivorous birds. Interestingly, both abundance and richness of frugivores decreased with elevation, probably as a consequence of impaired climatic conditions at high altitude, revealing the importance of lowland shrublands as wintering grounds for frugivorous birds. These habitats deserve special conservation efforts, as they are seriously threatened by the ongoing encroachment of agricultural and urban areas along the Mediterranean coasts.

Keywords: Bird–fruit abundance correlations; Conservation of frugivorous birds; Mediterranean forests and shrublands; Spatio-temporal distribution; Wintering habitats

1. Introduction

The long-term preservation of a large variety of habitats worldwide depends on mutualistic interactions between different organisms. For example, many animals play a direct role in the reproduction of many plants, by securing either pollination or seed dispersal (Herrera and Pellmyr, 2002). Specialization has made some plants and animals completely dependent on each other for long-term persistence, and cases of co-extinction are unfortunately well known (Stork and Lyal, 1993). Although animal–plant mutualisms are normally less specialized, they may be easily disrupted by population declines of one or another component of the interaction, for example due to habitat alteration (Alcántara et al., 1997; Santos et al., 1999; Ortiz-Pulido et al., 2000). Thus, many animal-dispersed plant populations require the regular visit of large numbers of frugivorous animals to secure recruitment. Such a mutualistic interaction has been the focus of extensive research (Herrera, 1995, 2002), and a general

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conclusion may be drawn from these studies: frugivorous animals need to be protected if we are to preserve the structure and diversity of plant communities in a context of global habitat alteration (Cordeiro and Howe, 2001; Tabarelli and Peres, 2002; McCarty et al., 2002; Moegenburg and Levey, 2003; Nyhagen et al., 2005).

Migratory frugivorous birds are of particular conservation concern, as they play a prominent ecological role by dispersing the seeds of many plants in different habitats and regions connected by migration routes (Jordano, 1992; Debussche and Isenmann, 1994; Honnay et al., 2002; Márquez et al., 2004). Besides, the protection of migrant birds needs to be approached at different scales. Many temperate migrant birds have wide distributions during the breeding season, but assemble during winter in restricted geographic areas, so that local population regulation in winter may have larger-scale effects on breeding population dynamics (Webster et al., 2002). For example, the temperate Mediterranean environments in southern Europe and northern Africa are important wintering grounds for many species of European birds, to the point that a vast proportion of their populations depend on these confined habitats during autumn and winter (Newton and Dale, 1996; Tellería et al., 1999). In warm Mediterranean areas, autumn rains eliminate the pervasive effects of summer drought, favouring the ripening of many fleshy-fruited plants (Mooney and Kummerow, 1981; Herrera, 1985; Jordano, 1992; Fuentes, 1992). Oil-rich fleshy fruits constitute an ideal resource for birds to secure body reserves, and therefore survival, during the winter months (Herrera, 1984, 1985; Blem, 1990). Not surprisingly, frugivorous birds are the most diverse and abundant components of wintering bird communities in Mediterranean forested habitats, where they play a critical role as seed-dispersers of many plants (Herrera, 1984, 1985).

Obviously, understanding the mechanisms underlying winter population regulation of migratory frugivorous birds is a priority for conservation. Winter population limitation is of particular concern, not only because bird populations have a restricted distribution during this period, but also because it is in winter when they are likely to face the strongest limitations for survival (Baillie and Peach, 1992; Sherry and Holmes, 1996; Goss-Custard et al., 1994; Rappole et al., 2003; Newton, 2004). However, although both the distribution and the demography of wintering birds have been extensively studied, little effort has been devoted to analyse the ecological factors underlying such patterns (Johnson and Sherry, 2001), and still less is known of how such bird-habitat associations vary in space and time (Fretwell, 1980; Greenberg, 1986; Sherry and Holmes, 1996). In summary, if we are to protect frugivorous birds, it is urgent to unravel which factors determine the carrying capacity of their wintering areas, and how these factors change in space and time.

Different factors may affect the regional distribution of frugivorous passerines in Mediterranean wintering grounds. Fruit abundance is a good predictor of bird abundance in this region (Rey, 1995; Tellería and Pérez-Tris, 2003), but the bird–fruit abundance correlation cannot be universal if fruit resources are not limiting, birds are unable to track variation in food availability across

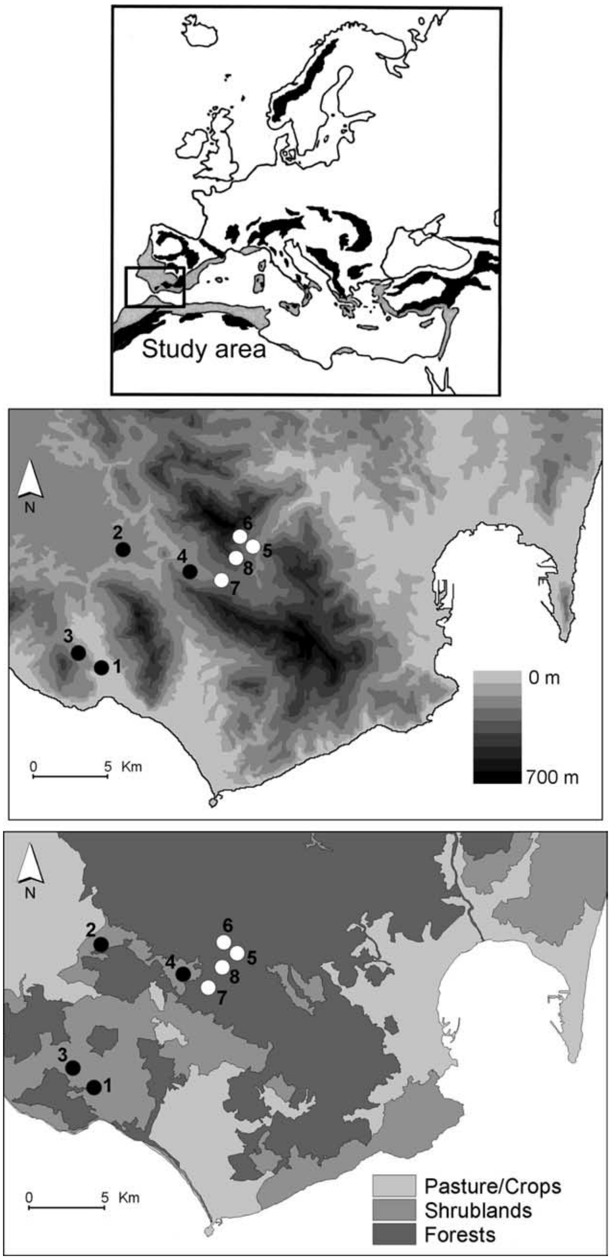

Fig. 1. Distribution of warm Mediterranean lowlands (grey areas in the top map) and mountains (in black) in the western Palaearctic, according to Aschmann (1971). The location of the study area is also shown. The other two pictures show the distribution of our study sites in the Campo de Gibraltar area (southern Spain), in relation to elevation (middle graph) and vegetation structure (bottom graph). Forest sites are indicated by open circles, and shrubland sites by dots (1: Río Valle; 2: Tornos; 3: Betis; 4: Almodóvar; 5: San Carlos; 6: Pista; 7: Ojén; 8: Alcornocal).

habitats, or they rely on alternative food resources (Jordano, 1992). For example, climate may disrupt fruit–bird abundance relationships, as meteorological disturbances (low temperatures, frosts, snowfalls, etc.) will override the role of fruit abundance as a determinant of bird abundance (Herrera, 1988, 1998). Although climatic disturbances are largely unpredictable in general, they have an increasing impact at high altitudes, where birds face further difficulties to maintain energy balance (Huertas and Díaz, 2001; Carrascal et al., 2002). On the other hand, most Mediterranean frugivorous birds are typical of forests or shrubby environments, and their distribution could be influenced by such habitat preferences (Hutto, 1985).

We studied the relationships among fruit availability (abundance and richness of fruits), elevation and habitat structure and the regional abundance and species richness of seed-dispersing frugivorous passerines in the Campo de Gibraltar area (southern Spain), which is located in the core of the western Mediterranean wintering grounds of these species (Fig. 1). Abundance and species richness of frugivores are two components of seed-dispersal potential, as a high abundance of frugivores will increase the number of seeds dispersed per year, and a large variety of frugivores will increase the range of fruit sizes and types that can be dispersed (Jordano, 1992; Herrera, 1995). To avoid drawing our conclusions from uninformative "snapshots" (Herrera, 1998), we analysed the spatio-temporal distribution of abundance and richness of frugivores in eight different localities during four winters, which allowed us to assess the importance of the region as a wintering ground for this bird guild.

2. Methods

2.1. Study area

We studied an area of about 200 km^2 on the northern side of the Strait of Gibraltar (36°01′N, 5°36′W; Fig. 1) during January of 1999, 2000, 2002 and 2003. The area is crossed by low-elevation mountain ranges, with a maximum altitude at 786 m (Tajo de la Corza peak). These mountains are mainly covered by cork-oak forests (*Quercus suber*), mixed with Algerian oaks (*Quercus canariensis*). The surrounding lowlands are covered by shrublands, grasslands and croplands that extend westwards to the Atlantic Ocean and eastwards to the Mediterranean Sea (Fig. 1). Both forests and shrublands have abundant fruit-producing shrubs dominated by lentiscs (*Pistacia lentiscus*) and wild olives (*Olea europaea sylvestris*). In winter, the region is occupied by a large number and variety of wintering birds that, in some cases, meet resident conspecifics (Tellería et al., 2001; Pérez-Tris and Tellería, 2002; Tellería and Pérez-Tris, 2004). We studied eight sites in an altitudinal gradient ranging from sea level to 265-m elevation since higher sites were occupied by sharp slopes and cliffs (Figs. 1 and 2). Half of the study sites were located in forests, and the other half were distributed in shrublands at the hill slopes and valleys (Fig. 1).

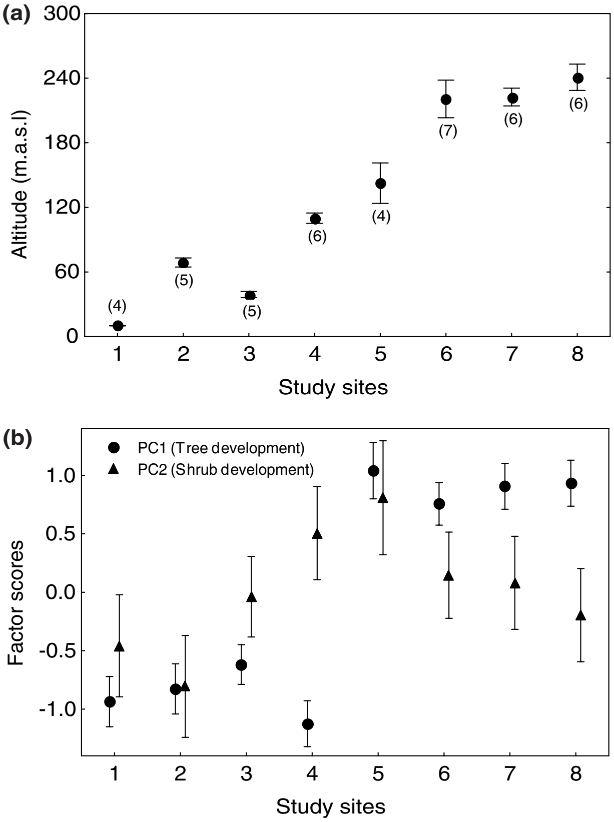

Fig. 2. Variation (mean ± SE) in altitude (a) and habitat structure (b; PC1: tree development, PC2: shrub development; see Table 1) among study sites. The number of transects per site is shown in brackets. Site labels are as in Fig. 1.

2.2. Bird counts, habitat features and analyses

We counted birds along 43 line transects, 500-m long and 50-m wide (25 m at either side of the progression line, meaning a 2.5-ha census area). The same transects were used during the four study years. We defined the guild of seed-dispersing frugivorous passerines according to previous studies on food habits of birds wintering in Southern Spain (Herrera, 1984, 1985, 1998; Jordano, 1985). We did not consider fruit or seed predators, such as tits and several finch species, which depend on different food resources (annual plants, insects, etc.) and do not contribute to seed dispersal. During bird counts, we measured fruit abundance by counting the number and species of plants holding ripe fleshy fruits in a 10-m wide belt, 5 m at either side of transects. As we moved across homogeneous habitat patches, we accepted that this sampling of fruit availability was a proper evaluation of fruit crops of the study sites. We used this index of fruit abundance after exploring inter-site variation of fruit crops in January 2000 (authors' unpublished data). To evaluate fruit abundance, we used two different approaches: (a) we multiplied abundance of fruits per plant by the number of plants holding fruits in each study site (fruit crop); and (b) we classified the fruit loads of counted plants according to a logarithmic scale in high (score 100), medium (10) and low (1) to get a semi-quantitative index of fruit abundance. As between-site variation in fruit crop was strongly correlated to the number of plants holding fruits (Spearman's Rank Order Correlation, fruit crop, $r = 0.93$, $p < 0.05$, $n = 8$; semi-quantitative index, $r = 0.76$, $p < 0.05$, $n = 8$), we used the number of fruiting plants as a proper and easy way of evaluating fruit abundance in the study area.

We also measured cover of shrubs (vegetation below 2-m height), cover of trees, density of trees (number of trunks with <10, 10–30 and >30-cm diameter at breast height) and number of tree and shrub species. We evaluated visually these habitat variables in three 25-m radius circular plots evenly distributed along the 500-m long line transects (Larsen and Bock, 1986). We also measured the mean elevation of each transect.

To reduce the number of parameters in our models, we conducted a Principal Component Analysis (PCA) of vegetation variables, which extracted two components of habitat structure (Table 1). The first component (PC1) was related to increasing forest development, as it weighed tree cover and abundance of large trees with high positive loads. The second component (PC2) was positively correlated to shrub cover and number of woody plant species, therefore indicating increasing cover and diversity of shrubs (Table 1). These two components of habitat structure showed different patterns of variation among sites (Fig. 2).

We used repeated-measures ANOVA to analyse variation in abundance and richness of birds among years and study sites. Given that the same transects were repeated each winter, we used year as a repeated-measures factor in these analyses. Then, we analysed the role of fruit availability, altitude and habitat structure as determinants of the regional distribution of frugivores each year. These variables were included as covariates in a mixed general linear model with year and study site as random factors, using Satterthwaite's (1946) method of denominator synthesis to obtain appropriate error terms for each effect. Given that this method uses fractions of sources of variation in synthesizing error terms for significance testing, the degrees of freedom for the denominator mean squares were sometimes fractional rather than integer values. All analyses were done with the Visual GLM module in the program Statistica 6.1 (StatSoft, 2002).

Table 1
Results of a Principal Component Analysis of the variables describing the habitat structure of the study sites

	PC1	PC2
Tree cover	0.938	0.118
Number of trunks below 10 cm dbh	0.550	−0.062
Number of trunks 10–30 cm dbh	0.853	−0.030
Number of trunks over 30 cm dbh	0.841	0.073
Shrub cover	−0.084	0.876
Woody plant species	0.109	0.836
Eigenvalue	2.64	1.49
Explained variance (%)	43.97	24.83

3. Results

3.1. Variation in the abundance of fruiting plants

Fruiting plants were dominated by lentiscs (*Pistacia lentiscus*) and wild olives (*Olea europea sylvestris*) during the four study winters. These shrubs accounted for 84% of fruiting plants (mean ± SE of four winters; lentiscs: 52.9% ± 0.05, olives: 31.1% ± 0.04, $n = 47$ transects). Together with some scattered *Smilax aspera* plants, lentiscs and wild olives were the only fleshy-fruited plants in shrub-dominated landscapes (these habitats are also covered by other shrub species, principally of the genera *Erica*, *Genista*, *Calluna*, *Calicotome* and *Cistus*). However, lentiscs and wild olives were accompanied by other fleshy-fruited plants in forest sites, principally *Myrtus communis*, *Phillyrea latifolia*, *Hedera helix* and *Arbutus unedo*.

The abundance of fruiting shrubs changed between years and sites, and it showed strong annual variation within study sites (repeated-measures ANOVA: year $F_{3,105} = 13.21$, $P < 0.0001$, site $F_{7,35} = 7.19$, $P < 0.0001$, interaction $F_{21,105} = 3.11$, $P < 0.0001$; Fig. 3). However, richness of fruiting shrubs per transect changed between winters but not between sites (repeated-measures ANOVA: year $F_{3,105} = 5.23$, $P = 0.002$, site $F_{7,35} = 1.60$, $P = 0.16$, interaction $F_{21,105} = 1.62$, $P = 0.058$; Fig. 3). Controlling for these effects in a mixed general linear model, shrub development (cover and variety of shrubs, see Table 1) was the best predictor of the distribution of fleshy-fruited shrubs in the study area, as both abundance and richness of fruiting plants were strongly correlated to the PC2 of habitat structure (Table 2). In addition, the richness of fruiting plants per transect, but not their abundance, decreased at high altitude in the study area (Table 2).

3.2. Variation in bird abundance and richness

The guild of seed-dispersing frugivorous birds was composed of seven species: European robin (*Erithacus rubecula*), blackbird (*Turdus merula*), song thrush (*T. philomelos*), redwing (*T. iliacus*), mistle thrush (*T. viscivorus*), blackcap (*Sylvia atricapilla*) and Sardinian warbler (*S. melanocephala*). These species accounted for 60.5% ± 0.03 (mean ± SE) of the total density of bird communities wintering in the study area (Fig. 4,

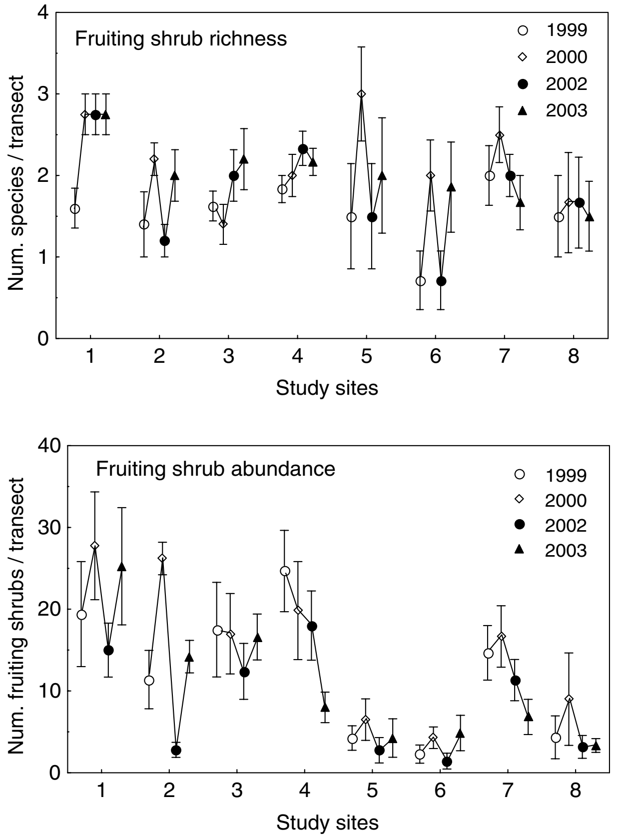

Fig. 3. Spatio-temporal variation (mean ± SE) in richness and abundance of fruiting shrubs in the study area. Site labels are as in Fig. 1.

Appendix A). This ratio was higher in shrublands (69.3% ± 0.03, $n = 24$) than in forests (51.4% ± 0.04, $n = 23$), principally because forest bird communities had a higher representation of insectivores and fruit-predators (tits, finches, etc.).

Repeated measures ANOVA of the average abundance of each species revealed that, after controlling for the effect of site, four species (robin, blackbird, redwing and Sardinian warbler) showed significant annual changes in abundance ($P < 0.05$ in all cases), while the remaining species (blackcap, song thrush; mistle thrush was only recorded in 2003) maintained fairly constant numbers during the study period (all $P > 0.25$). Overall, we did not find significant annual variation in abundance of frugivorous birds, which however showed dramatic changes among study sites, as well as between years within sites as shown by a significant interaction (repeated measures ANOVA; year $F_{3,105} = 2.59$, $P = 0.057$; site $F_{7,35} = 7.72$, $P < 0.0001$; interaction $F_{21,105} = 3.44$, $P < 0.0001$; Fig. 4). The same result was found for frugivorous species richness, although the interaction between year and site was not significant in this case (repeated measures ANOVA: year $F_{3,105} = 1.51$, $P =$

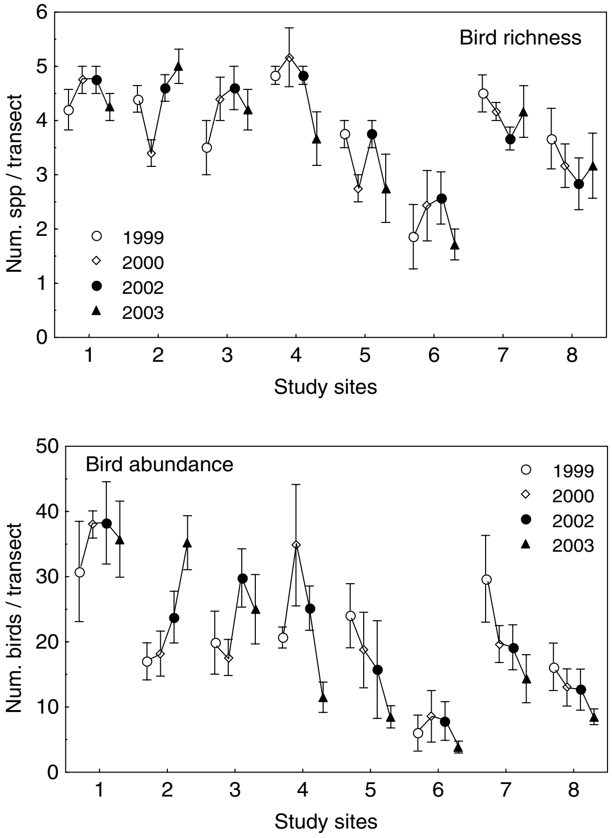

Fig. 4. Spatio-temporal variation (mean ± SE) in richness and abundance of seed-dispersing frugivorous birds in the study area. Site labels are as in Fig. 1.

Table 2
Results of mixed general linear models analysing shrub richness and abundance in function of elevation and habitat structure (principal components, see Table 1), controlling for variation among years and sites (random effects)

	Richness of fruiting shrubs				Abundance of fruiting shrubs			
	d.f.	Beta	F	P	d.f.	Beta	F	P
Elevation	1141.0	−0.563	5.09	0.026	1141.0	0.041	0.04	0.848
Tree cover (PC1)	1141.0	0.072	0.19	0.661	1141.0	0.071	0.26	0.610
Shrub cover (PC2)	1141.0	0.229	7.79	0.006	1141.0	0.234	11.25	0.001
Year (random)	322.1		3.84	0.024	321.9		4.35	0.015
Site (random)	732.4		2.12	0.070	730.0		4.00	0.003
Year × site (random)	21141.0		1.16	0.296	21141.0		1.44	0.109

Beta parameters are shown for comparison of the effect sizes of each variable.

Table 3
Results of mixed general linear models analysing species richness and abundance of frugivorous birds in function of elevation, habitat structure (principal components, see Table 1), and fruit availability (abundance and richness), controlling for variation among years and sites (random effects)

	Bird richness				Bird abundance			
	d.f.	Beta	*F*	*P*	d.f.	Beta	*F*	*P*
Elevation	1138.0	−0.699	7.83	0.006	1139.0	−0.780	16.81	0.0001
Tree cover (PC1)	1138.0	0.016	0.01	0.922	1139.0	−0.112	0.83	0.363
Shrub cover (PC2)	1138.0	−0.204	5.80	0.017	1139.0	−0.104	2.62	0.108
Fruit abundance	1138.0	−0.044	0.18	0.670	1139.0	0.466	34.80	<0.0001
Fruit richness	1138.0	0.089	1.02	0.313	1139.0	0.108	2.58	0.110
Year (random)	323.3		2.74	0.066	322.1		1.89	0.160
Site (random)	730.0		2.71	0.026	725.3		1.58	0.185
Year × site (random)	21138.0		1.60	0.058	21139.0		3.23	<0.0001

Beta parameters are shown for comparison of the effect sizes of each variable.

0.21; site $F_{7,35} = 10.90$, $P < 0.0001$; interaction $F_{21,105} = 1.63$, $P = 0.057$; Fig. 4). Controlling for these effects in a mixed general linear model, both abundance and species richness of frugivorous birds were positively correlated with fruit abundance, and negatively correlated with elevation (Table 3). Abundance of frugivorous birds was not affected by habitat structure, as defined by PC1 and PC2 of vegetation variables, but species richness was negatively correlated to shrub development (Table 3).

4. Discussion

The number of birds arriving to wintering areas each year may depend on different, largely disconnected factors, such as annual breeding success or unpredictable meteorological events (such as cold waves; Newton, 2004). This stochasticity will render local-scale approaches unable to reveal functional relationships between the inter-year abundance of wintering birds and potential components of habitat quality, such as food abundance or vegetation structure (Burns, 2004; García and Ortiz-Pulido, 2004). In addition, the distribution of birds may be affected by unpredictable variation in such components of habitat quality. In particular, fruit production is largely unpredictable both in space and time (Levey and Stiles, 1992; this study), so that a reliable examination of the determinants of the distribution of birds needs to be carried out in several habitats during several years (Herrera, 1998). Our results showed that, during four winters, the distribution of frugivorous birds was fairly dependent on some habitat characteristics that are susceptible of management, thus providing a suitable basis for the design of conservation plans for these birds in Mediterranean environments.

4.1. The unpredictable distribution of fruiting resources

Both abundance and richness of fruiting plant species showed strong variation from winter to winter, and the annual distribution of fruits greatly changed among study sites. Spatio-temporal unpredictability is a common feature of the distribution of fruit crops in the Mediterranean region (Jordano, 1985; Herrera, 1998). Fruit availability depends on local processes affecting shrub reproduction, including plant flowering success, efficiency of pollination and effects of precipitation on the fruiting process, which take place several months before fruits are available (Herrera, 1998). Interestingly, we did not find any effect of tree cover or altitude on fruit abundance, although these habitat characteristics are potentially related to micro and meso-climatic environmental factors that might affect both flowering and fruiting processes (moisture, wind impact, frosts, etc.). However, we found a reduced species richness of the fruiting plant community at high altitude in our study area, probably mediated by both the preference of certain plant species for moist ravines in forests and the inability of other species to grow exposed to wind and frosts at high elevations in the area. Both abundance and richness of fruiting shrubs were positively correlated with shrub development (i.e., increased cover and variety of shrubs), but they were independent of forest development (tree cover). In fact, fruit producing plants – particularly lentiscs – make the bulk of the shrub undergrowth in many sectors of the study area.

4.2. Temporal stability of the community of frugivores

Although the regional availability of fruits changed among years during the study period, the community of avian frugivores wintering in the area showed a fairly constant structure. Thus, neither abundance nor richness of frugivorous birds changed during four study years. Although annual variation in bird abundance was close to statistical significance ($P = 0.057$), such an effect was negligible compared to between-site differences within years.

There are several possible reasons why the abundance and richness of frugivorous birds hardly changed among years. Firstly, climatic conditions showed little variation during the study period. For example, Europe remained free of strong cold waves during the four study winters, and hence massive southwards movements of birds were not observed in southern Europe (for examples of these movements, see Bernis, 1966–1971; Santos, 1982). On the other hand, some of these species have local resident populations in the forests in the study area, which would prevent a large increase in bird abundance in these habitats even in years with high fruit abundance, due to social interactions (Tellería et al., 2001; Pérez-Tris and Tellería, 2002; Tellería and Pérez-Tris, 2004). In addition to these and other proximate determinants, the annual constancy of the community of wintering frugivorous birds was probably influenced by evolutionary constraints on migratory patterns of these species. Migration distances and directions are genetically programmed in warblers, robins and thrushes (Berthold, 1996), so that their migratory patterns are maintained by long-term selection regimes favouring individual behaviours that take birds to suitable wintering grounds (e.g., Berthold et al., 1992). In relation to this, migratory frugivorous birds are strongly constrained in their choice of wintering grounds, which are mainly restricted to fruit-rich sectors in the Mediterranean area. As a consequence, the bulk of their populations will move every autumn to these areas, completely blind with respect to the carrying capacity to be realized in their final destination (in relation to food abundance, for example). In these circumstances, a given wintering area will likely receive a similar amount of birds each year that will redistribute according the carrying capacity of habitat patches. This process, which could explain the observed annual differences in the spatial distribution of birds, has important implications for the demography of migratory frugivorous birds given that a synchronic reduction of the regional carrying capacity of all the habitat patches will have a negative impact on wintering populations with a wide range of European origins (Bibby, 2003).

4.3. Spatial unpredictability of bird distribution

One of the most important results in our study was the observation that, despite both regional abundance of wintering birds and species richness remained largely invariable during the study period, they showed strong differences among sites. Most importantly, spatial differences followed different patterns each year, making it difficult to predict annual abundance or richness of frugivorous birds in a given sector of the study area. This spatio-temporal variation in the distribution of birds was primarily influenced by the strong variation in fruit availability among sites and years. Therefore, our results support the idea that frugivorous birds are able to track local differences in fruit abundance (Levey and Stiles, 1992; Johnson and Sherry, 2001; Moegenburg and Levey, 2003 ; Tellería and Pérez-Tris, 2003), in agreement with previous studies that have found a close relationship between fruit abundance and bird abundance in other lowland regions of southern Spain (Rey, 1995).

Interestingly, the abundance of frugivorous birds was not influenced by vegetation cover, measured as forest development and cover and variety of shrubs, despite of the fact that fruit resources were more abundant in areas with abundant undergrowth. This suggests that frugivorous birds actively select habitat patches with abundant fruiting plants, which are not necessarily the shrubbiest sites. In fact, controlling for fruit abundance, we found a negative association between shrub development and richness of frugivorous birds. This effect could be due to habitat preferences of particular species (for example, song thrushes are frequent in open habitats in this area). Nevertheless, our results support the idea that a large cover of shrubs is not necessary for the establishment of an abundant and diverse community of frugivorous birds, as long as the abundance of fruits remains relatively high.

Not surprisingly, we found a negative effect of altitude on the abundance and richness of frugivorous birds (Table 3). Although the range of altitudes in our study area is somehow restricted (Fig. 2), the highest study sites were frequently affected by stronger winds and frosts, which are less frequent at lower altitude (pers. obs.). Climate hardness strongly affects the distribution of small passerines in temperate mountains (Root, 1988; Huertas and Díaz, 2001), as a consequence of an impaired ability of birds to secure and maintain body reserves (Blem, 1990). In addition, we found a negative correlation between altitude and fruit richness. Although we did not find a clear association between fruit richness and abundance or richness of frugivores, a lower diversity of fruits could further accentuate the negative energetic consequences of living at high elevation, as a restricted choice of fruits is likely to impair nutrient balance in birds' diet (Herrera, 1985). These results suggest that the lowland sectors located between the Mediterranean coast and the nearby mountains (Fig. 1) maintain the highest long-term carrying capacity for wintering populations of frugivorous birds. Besides, such a preference of birds for warm lowland sectors could explain the frequent decoupling of bird and fruit abundance in mountains and plateaux of southern Spain (Jordano, 1995; Herrera, 1998).

4.4. Conclusions applied to conservation

The shrublands and forests of the Campo de Gibraltar area are occupied by large numbers of frugivorous birds every year, which demonstrates the importance of this region as a major wintering ground for these species. Our results show that this community follows largely variable patterns of regional distribution, primarily determined by annual variation in fruit availability. Birds tracked the availability of fruits across the region, being hardly influenced by other habitat features, such as forest development or overall cover of shrubs. However, fruit production was not the only determinant of the distribution of frugivores, which was negatively affected by elevation as well. Altogether, these results can be used to put forward general guidelines for the conservation of frugivorous birds in Mediterranean forests and shrublands.

For centuries, Mediterranean habitats have been subjected to intense management. In particular, Mediterranean forests are often cleared of undergrowth to reduce fuel loads and prevent summer fires, as well as to favour selected tree species (usually oaks for logging or cork production) and herbaceous plant communities (such as pastures for cattle). Traditional management activities have greatly contributed to maintain the landscape and species diversity typical of the Mediterranean (Blondel and Aronson, 1999). But modern practices, in particular the use of machinery in an excessive and unselective forest cleaning, can wipe out fruit resources for birds and other wild animals, thus disrupting the basis for the seed-dispersal process. Particularly in areas where forests are most threatened by devastating summer fires, such as the warmer Mediterranean sectors, unselective shrub removal is a common practice that has been considered as one of the main threats for biodiversity (Ojeda et al., 2000; Andrés and Ojeda, 2002; Alejano and Martínez, 2003; C.M. Herrera, pers. com.). According to our results, large-scale removal of fruiting shrubs could greatly reduce the carrying capacity of these habitats for frugivorous birds, thus causing a stronger population limitation during winter, which might translate into population declines all across the European breeding range of these birds (Bibby, 2003).

However, our results suggest a way to reconcile forests cleaning with the conservation of migratory frugivorous birds. Frugivorous birds select sectors with a high abundance of fruiting shrubs, which do not necessarily need to have a high cover of other shrubs. Therefore, a selective clearing, skipping a certain amount of fruiting shrubs, would contribute to maintain populations of both fruiting plants and frugivorous birds. Most importantly, given the spatio-temporal unpredictability of fruit production and its effect on bird distribution, selective forest cleaning should help to buffer the negative impact of fruiting failure on bird populations, as a larger number of fruit-producing habitat patches will assure that at least some of them will have a suitable crop each year, which birds will be able to track as shown by our results. As a consequence, selectively cleared forest patches will attract an abundant and rich community of frugivorous birds, which will contribute to maintain a diverse plant community, both locally and in nearby forest sectors within the range of seed dispersal (McCarty et al., 2002). Habitat management decisions are often based on immediate conservation needs, such as the prevention of fires or the protection of endemic plant species (the most evident conservation priorities in the Campo de Gibraltar area; Ojeda et al., 2000). However, the complexity of interactions between different components of natural communities make patent that, if we are to protect biodiversity in the long run, we need to design conservation plans that incorporate processes acting over broader spatial and temporal scales, such as seed dispersal by migrant birds (Price et al., 1999).

Another important result in our study was the negative effect of altitude on the distribution of many frugivorous bird species. According to this result, fruit-rich forests and shrublands located in lowlands or coastal Mediterranean areas are of particular conservation concern for protecting these species. Unfortunately, these lowlands have been under strong human pressure for centuries (Blondel and Aronson, 1999). This has rendered Mediterranean forests and shrublands confined to higher areas surrounding productive valleys or coastal sectors, where a few vestiges of the original vegetation remain today interspersed with croplands, urban areas and infrastructures (Castro et al., 1997; Ruiz de la Torre, 2002). In addition, today we witness new modes of urban encroachment and agriculture intensification, promoting irrigated areas and greenhouse cultivations, which take advantage of the favourable climate of these areas (in particular for tourism and winter production of vegetables). Such activities are affecting the last vegetation remnants in the narrow coastal belt ranging from France to Portugal, a problem that seems to be expanding – or will likely spread in the future – to other European countries along the Mediterranean. Therefore, within the framework of ongoing efforts for the conservation of migratory birds and their habitats (European Union's Bird directive 79/409/ECC and Habitat directive 92/43/ECC), it is urgent to consider the protection of vegetation remains in Mediterranean lowlands as an important wintering resource for European frugivorous birds.

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Appendix A

Inter-winter distribution of fleshy-fruited plant abundance (mean number of plants and species per transect ± SE, $n = 43$) and bird abundance (mean number of individuals or species per transect ± SE, $n = 43$)

Winter (January)	1999	2000	2002	2003
Fruiting shrubs				
Number of plants	12.53 ± 1.81	15.26 ± 1.89	8.19 ± 1.26	9.65 ± 1.35
Number of species	1.51 ± 0.13	2.14 ± 0.15	1.72 ± 0.15	1.98 ± 1.47
Fruiting plant species				
Pistacia lentiscus	9.09 ± 1.67	10.60 ± 1.82	5.58 ± 1.05	6.40 ± 1.24
Olea europaea	3.32 ± 0.74	4.28 ± 0.75	2.28 ± 0.38	2.12 ± 0.44
Bird community (all species)				
Number of birds	32.04 ± 2.60	28.19 ± 2.45	32.30 ± 2.31	30.35 ± 3.90
Number of species	8.70 ± 0.44	7.51 ± 0.43	8.26 ± 0.32	7.77 ± 0.39
Seed-dispersing bird community				
Number of birds	20.09 ± 1.88	20.51 ± 2.17	20.84 ± 1.96	16.86 ± 2.06
Number of species	3.77 ± 0.20	3.74 ± 0.21	3.86 ± 0.18	3.53 ± 0.21
Seed-dispersing bird species				
Sylvia atricapilla	8.00 ± 1.14	8.23 ± 1.03	9.58 ± 1.15	8.19 ± 1.36
Sylvia melanocephala	2.17 ± 0.37	1.40 ± 0.27	2.53 ± 0.44	1.91 ± 0.41
Erithacus rubecula	6.32 ± 0.46	5.47 ± 0.48	4.86 ± 0.48	4.12 ± 0.38
Turdus philomelos	2.02 ± 0.32	2.49 ± 0.73	2.56 ± 0.49	1.49 ± 0.31
Turdus iliacus	0.04 ± 0.03	1.14 ± 0.66	0	0
Turdus merula	1.34 ± 0.20	1.53 ± 0.25	1.30 ± 0.21	0.79 ± 0.15
Turdus viscivorus	0	0	0	0.05 ± 0.04

Results for the main individual species of fleshy-fruited plants and seed disperser birds are also shown. See text for details on the counting methods.

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