ORIGINAL ARTICLE

Species abundance and migratory status affects large-scale fruit tracking in thrushes (*Turdus* spp.)

José L. Tellería · Luis M. Carrascal · Tomás Santos

Abstract The mutualistic interactions between fruit-producing plants and seed-dispersing birds may be disrupted by the difficulties involved in tracking fruit resources, which are often patchily distributed in space and time. As a consequence, the strength of this interaction will rely on the ability of birds to distribute numbers according to the spatiotemporal patterning of the resource. This paper tests if wintering thrushes (*Turdus*) track inter-winter and inter-site changes of cone abundance in an area that encompasses the main range of the Spanish Juniper *Juniperus thurifera* in the Iberian highlands. We test whether the regional abundance and migratory status of birds affect this fruit-tracking process. Analyses were approached by using the habitat matching rule, a null model applied to explore the effect of spatiotemporal change of resources on bird distribution. All species followed inter-winter food variation over the study area but under-matched the changes. The strength of this bird–plant interaction increased with the regional abundance of individual species. When thrushes were analyzed according to their migratory status, migratory species (*Turdus pilaris, T. iliacus*, and *T. philomelos*) tracked the resource better than sedentary ones (*T. viscivorus* and *T. merula*). This suggests that in a time of rapid environmental change any reduction of vagrant and abundant migratory thrushes could weaken the strength of this bird–plant interaction.

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Zusammenfassung

Artenvielfalt und Zugvogelstatus beeinflussen die großräumige Standortverfolgung von Nahrungsfrüchten bei Drosseln (*Turdus* spp.)

Die gegenseitig vorteilhaften Interaktionen zwischen Frucht tragenden Pflanzen und Samen verbreitenden Vögeln kann gestört werden durch die Schwierigkeit Fruchtressourcen zu finden, da diese häufig unregelmäßig verteilt sind. Daher beruht die Stärke dieser Interaktion auf der Fähigkeit der Vögel sich nach der räumlichen und zeitlichen Verteilung der Ressource zu richten. Diese Studie testet ob überwinternde Drosseln (*Turdus*) Unterschiede in der Zapfenmenge an Spanischen Wacholdern (*Juniperus thurifera*) zwischen Wintern und zwischen den Gebieten der Iberischen Hochlagen verfolgen können. Wir untersuchen, ob der regionale Bestand und der Zugstatus der Vögel einen Einfluss hat auf ihre Fähigkeit Nahrungsfrüchte zu finden. Anhand eines Nullmodels berechneten wir den Effekt der räumlich-zeitlichen Verschiebung der Ressourcenverfügbarkeit auf die Verteilung der Vögel. Alle Arten in unserem Studiengebiet folgten dem Futter zwischen den Wintern, aber konnten mit den Veränderungen nie ganz Schritt halten. Die Interaktion zwischen Vögeln und Pflanzen verstärkte sich mit dem Zugvogelstatus, denn ziehende Vögel (*Turdus pilaris, T. iliacus, T. philomelos*) fanden Ressourcen besser als Standvögel (*T. viscivorus and T. merula*). Das legt nahe, dass in einer Zeit von sich wandelnden Umweltbedingungen ein Bestandseinbruch bei ziehenden Drosseln die Interaktion zwischen Vögeln und Pflanzen stark schwächen würde.

Introduction

Frugivorous birds play a prominent ecological role by dispersing the seeds of numerous plant species (Levey et al. 2002). They also benefit from a rewarding food source that, in the Mediterranean region, is the basis for the carrying capacity of many habitats for wintering birds (Herrera 1984; Tellería et al. 2005; Rey 2011). However, this mutualistic interaction may be disrupted by difficulties in tracking the fruit, which is often patchily distributed in space and time producing a kaleidoscopic succession of crop outputs that may be difficult to follow for birds (Levey 1988). As a consequence, the strength of this bird–plant interaction will rely on the ability of birds to allocate individuals according to the spatiotemporal patterning of the resource. If birds do not track fruit distribution, they will misuse the food and will not disperse the seeds of plant populations according to their actual crops.

It has been postulated that free-moving animals will distribute according to resource availability (Fretwell and Lucas 1969; Pulliam and Caraco 1984; see Kennedy and Gray 1993). However, food tracking will be constrained by some effects, such as habitat preferences (Hutto 1985), difficulty in perceiving resource distribution (Abrahams 1986), the cost associated with accessing the food (Kennedy and Gray 1993) or density-dependent processes regulating the spatial distribution of individuals (Fretwell 1972; Gaston et al. 2000). As a consequence, the strength of this bird–plant interaction will rely on the ability of birds to avoid these constraints and to allocate individuals according to the spatiotemporal patterning of the resource.

This paper examines food tracking by thrushes (*Turdus* spp.) during two consecutive winters in a set of woodlands distributed in an area of 25,000 km^2 encompassing the main range of the Spanish Juniper *Juniperus thurifera* in the Iberian Peninsula (Fig. 1). This tree shows sharp inter-winter and inter-site changes in crop size that seed-dispersing thrushes track in the search of ripe cones, their main food resource in these highlands (Jordano 1993; Tellería et al. 2011). We do not know, however, if thrush numbers match the changes in cone production over this large area, since it is commonly agreed that the perception of food distribution or the costs associated with accessing the resource will sharply increase at large spatial scales, disrupting the fruit-tracking process (Kotliar and Wiens 1990; Ranta et al. 2000; García et al. 2011). To explore this, we will study the following aspects of this juniper–thrush interaction.

First, we will test whether birds distribute among woodlands according to annual changes in ripe-cone availability. A number of approaches have revealed fruit tracking at local scales (e.g. García and Ortiz-Pulido 2004; Shochat et al. 2002; Tellería et al. 2008), but we do not know if this bird–plant interaction is typical at higher spatial scales (Burns
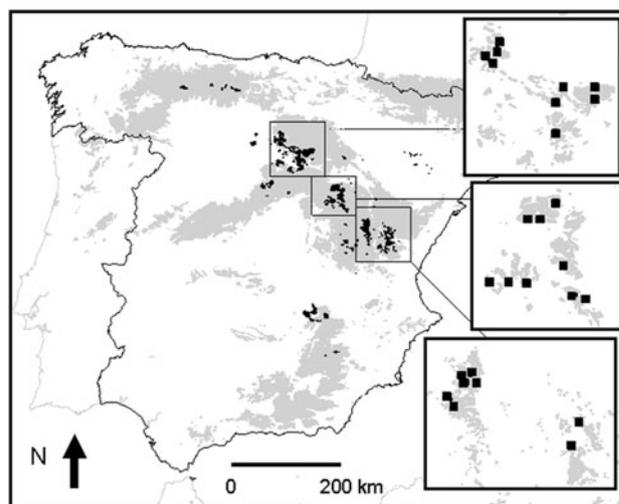

Fig. 1 Distribution of the study woodlands within the range of the Spanish Juniper. *Grey tones* depict areas over 1,000 m above sea level and *black patches* show the actual distribution of the Spanish Juniper woodlands. *Boxes* show the distribution of the study sites (*black squares*) within the expanses of Juniper woodlands (*grey*)

2004; García et al. 2011). The Iberian range of the Spanish Juniper, distributed along a 400-km-long belt (Fig. 1), represents a suitable scenario in which to explore large-scale fruit tracking by birds. Second, we will examine if the migratory status of species affects the pattern. We presume that the wandering behaviour of migratory thrushes across wintering areas (Santos 1982; Cramp 1988) could enhance their skills to track the food over large areas compared to sedentary species (Levey and Stiles 1992; Newton 2004). Finally, we will check whether the regional abundance of thrushes affects the fruit-tracking process. The occupation of a region may be affected by the size of the involved population (Gaston et al. 2000). Thus, food matching will occur if thrush numbers are large enough to allocate individuals in all habitat patches according to the extant availability of resources. We will test this on individual species, but will also explore the fruit-tracking process on the whole assemblage of species occurring in the area. It has been suggested that birds feeding on fruit patches may act as facilitators, enabling the co-occurrence of other individuals and species (Saracco et al. 2004), thus favouring strategies of multi-specific tracking of resources that could improve tracking efficiency (Shochat et al. 2002; Tellería et al. 2008).

Methods

Study area

The study was carried out in 26 woodlands encompassing the main range of the Spanish Juniper in the Iberian

Peninsula (Fig. 1) during two successive winters of contrasting cone and bird abundance (2009–2010 and 2010–2011). This tree forms open woodlands that today extend over 125,000 hectares, mostly between 800–1,200 m.a.s.l., in highlands dominated by hot summers and cold winters, with annual precipitation of 400–500 mm. Winter conditions are severe, with low average temperatures (mean values between 1.8 and 4 °C), a freezing period from mid-October to late May, and relatively frequent snowfalls (average of 10 days per year). Weather during the two study winters (December to 15 February) was characterised by frequent snowfalls (19 % of days) and low average minimum temperatures (−1.2 °C). A large proportion of days showed minimum temperatures below 0 °C (56 % of days; data from Instituto Nacional de Meteorología averaged for Burgos −859 m.a.s.l. and Teruel −915 m.a.s.l. meteorological stations, located at both latitudinal limits of the study region).

Bird and cone abundance

Thrushes were counted along 0.5-km line transects located in the study woodlands in winters 2009–2010 and 2010–2011. The counts were repeated in December, January and February to encompass the main wintering period of the migratory thrushes. From the three counts per winter, we obtained the mean number of thrushes detected per transect as an index of the relative abundance in each locality. Within these data, we arranged the species according to their migratory status: two species (the Mistle Thrush *Turdus viscivorus* and the Blackbird *T. merula*), depicting local movements within the Iberian highlands, were regarded as sedentary, while the four species that migrate from central and northern Europe to winter in Iberia (most of the Song Thrushes *T. philomelos* and Ring Ouzels *T. torquatus,* and all the Redwings *T. iliacus* and Fieldfares *T. pilaris*; Santos 1982; Santos et al. 1983) were considered as migratory. Abundance of ripe cones in both study winters was assessed in 20 Spanish junipers spaced 25 m alongside every line transect used to count birds. In the selected junipers, we counted by eye, after training, the number of ripe cones, which are those selected by thrushes (Tellería et al. 2011). Transects and the trees selected to count cones were marked with numbered labels and recoded with GPS devices so that they could be easily located. We counted cone availability each winter in the last week of November just at the start of the wintering period of thrushes.

Data analyses

We explored cone tracking by thrushes by using the habitat matching rule (Pulliam and Caraco 1984), an ideal free distribution (IFD) model (Fretwell and Lucas 1969). It predicts that, if both resource abundance and population abundance have been measured in two periods, any change in resource abundance between habitat patches will be followed by a concomitant change in population density according to the following algorithm:

$$\log((D_{2i}+1)/(D_{1i}+1)) = a + b\log((R_{2i}+1)/(R_{1i}+1))$$
(1)

where D_{1i} and D_{2i} and R_{1i} and R_{2i} are the abundance of birds and resources, respectively, in the two patches or the two periods of time in the locality i. This model is used to explore whether abundance changes in thrush numbers match ($b = 1$), under-match ($b < 1$) or over-match ($b > 1$) changes in availability of resources (Kennedy and Gray 1993). Although some studies have used the matching rule to specifically test for IFD in fruit–frugivore interactions (Shochat et al. 2002), such a test is outside our scope. Therefore, we will use this method as a null model to explore the effect of spatiotemporal changes in food resources on species distribution, but not to explicitly test IFD (Tellería and Pérez-Tris 2003, 2008; Cassini 2011). Repeated measures ANOVA and simple regression analyses were also used to compare the patterns of fruit and bird abundance between years. Analyses were made with Statistica 7.0®.

Results

Changes in thrush and cone abundance

Cone production showed a sixfold increase during the second winter (repeated measures ANOVA $F_{1,25} = 36.76$, $P < 0.001$) and was followed by a concomitant threefold increase in the regional abundance of thrushes ($F_{1,25} = 11.37$, $P = 0.002$; Table 1). This increase was produced by the arrival of extra-Iberian migratory species (Redwings + Fieldfares + Song Thrushes + Ring Ouzels), which increased the abundance eightfold ($F_{1,25} = 16.91$, $P < 0.001$). Sedentary thrushes (Blackbirds + Mistle Thrushes) also depicted a small, albeit significant ($F_{1,25} = 4.54$, $P = 0.043$), increase in abundance during the winter of high ripe cone availability (Table 1).

The geographical distribution of cone abundance was fairly similar between winters, with the most productive woodlands during the first year showing the highest abundance during the second year. There was, in addition, a synchronic increase in this resource within the range of the Spanish Juniper, with 22 out of 26 woodlands increasing ripe cone production during the second winter (Fig. 2). Thrushes did not show geographical relationships between the distribution of the first and second year,

Table 1 Annual mean scores (±SE) of the study variables in the 26 juniper woodlands

Number per transect	Status	Winter 2009–2010 Mean ± SE	Winter 2010–2011 Mean ± SE	$\log(A_{2i}/A_{1i}) = a + b \log(R_{2i}/R_{1i})$
Blackbird (*Turdus merula*)	Sedentary	0.49 ± 0.14	0.77 ± 0.13	$y = -0.06 + 0.14\,x$, $r = 0.58$, $p = 0.002$
Mistle Thrush (*Turdus viscivorus*)	Sedentary	2.40 ± 0.79	2.66 ± 0.42	$y = -0.09 + 0.22\,x$, $r = 0.48$, $p = 0.014$
Redwing (*Turdus iliacus*)	Migratory	0.59 ± 0.30	2.92 ± 1.52	$y = -0.10 + 0.31\,x$, $r = 0.63$, $p < 0.001$
Fieldfare (*Turdus pilaris*)	Migratory	0.29 ± 0.23	2.94 ± 2.47	$y = -0.23 + 0.34\,x$, $r = 0.68$, $p < 0.001$
Song Thrush (*Turdus philomelos*)	Migratory	0.01 ± 0.01	1.82 ± 0.51	$y = 0.08 + 0.19\,x$, $r = 0.39$, $p = 0.047$
Ring Ouzel (*Turdus torquatus*)	Migratory	–	0.06 ± 0.05	–
Sedentary thrushes		2.88 ± 0.84	3.42 ± 0.46	See Fig. 2
Migratory thrushes		0.90 ± 0.43	7.74 ± 3.93	See Fig. 2
Total thrushes		3.60 ± 1.1	11.20 ± 4.00	See Fig. 2
Ripe fruits per tree		102.5 ± 42.43	611.14 ± 150.27	–

The relationships between bird abundance changes the first (A_{1i}) and second (A_{2i}) winter and changes in cone availability (R_{2i} and R_{1i}) in the study woodland (i) are also shown

although they spread across the woodlands during the year of increased cone availability due to the arrival of great numbers of migratory thrushes (Fig. 2).

Food tracking by thrushes

When we applied the habitat matching rule (Eq. 1), the abundance of all individual species present in the study area during the two study winters followed the spatiotemporal changes of cone abundance among the study woodlands (Table 1). However, thrushes under-matched the changes in fruit abundance ($b < 1$) since spatiotemporal variations in cone availability among woodlands were followed by smaller changes in bird numbers. The whole assemblage of thrushes showed an increased slope (b) with regards to individual species and, when they were arranged according to their migratory status, the assemblage of migratory birds followed the changes better than the sedentary ones (Fig. 2). When we ordered these results according to bird abundance, a trend was evident in which the most abundant species or groups increased the tracking ability (b slopes in Table 1; Figs. 3, 4), suggesting that the spatiotemporal tracking of ripe cone changes was a density-dependent process. In this context, despite small sample size (just 5 species) and considering for the effect of abundance, migratory thrushes tracked the changes in cone abundance better than sedentary species (Fig. 3).

Discussion

Food tracking by thrushes

As in other passerines, wintering thrushes usually move in search for food (Santos 1982; Holthuijzen et al. 1987;

Jordano 1993). This vagrancy can buffer the effect of inter-winter changes in food availability on the regional abundance of birds if they are able to distribute each year over different sets of food patches according to their extant food availability. However, this balanced distribution will vanish if food changes occur synchronically over large areas impeding the alternative use of food patches. This was the scenario depicted by the Spanish Juniper woodlands during the study period in which a synchronic change in the availability of ripe cones over the whole study area was produced (Fig. 2). In such conditions, resource matching will only result if thrushes are able to adjust regional abundances to the annual availability of ripe cones within the range of the Spanish Juniper woodlands and redistribute themselves between woodlands according to the annual changes of the resource.

The manner in which the thrush assemblage adjusted numbers to changes in the annual crop of cones was rather crude. Despite there being a sixfold average increase in cone abundance during the second winter, thrushes showed a threefold increase in regional abundance (Table 1). However, this pattern resulted from two different reactions to food changes: the meagre increase of sedentary species and the sharp reaction of migratory ones. The mild reaction to fruit resources of sedentary thrushes may be explained by the fact that their winter populations are mainly affected by regional demographic processes other than cone crops, such as breeding success or mortality within Iberia. In addition, they are omnivorous species that, despite their strong preferences for juniper fruits in the Iberian highlands, can cope with winter requirements by using a broad set of food resources (e.g. from snails to earthworms). Alternatively, the sharp reaction of migratory thrushes supports their active tracking of this food within the Iberian range. This is interesting because the Spanish Juniper

Fig. 2 Inter-winter patterns in the geographical distribution of cone and thrush abundance (log-transformed) in 26 woodlands within the range of the Spanish Juniper. *Dashed lines* show the hypothetical distribution of a regression line produced by similar scores in the two study winters
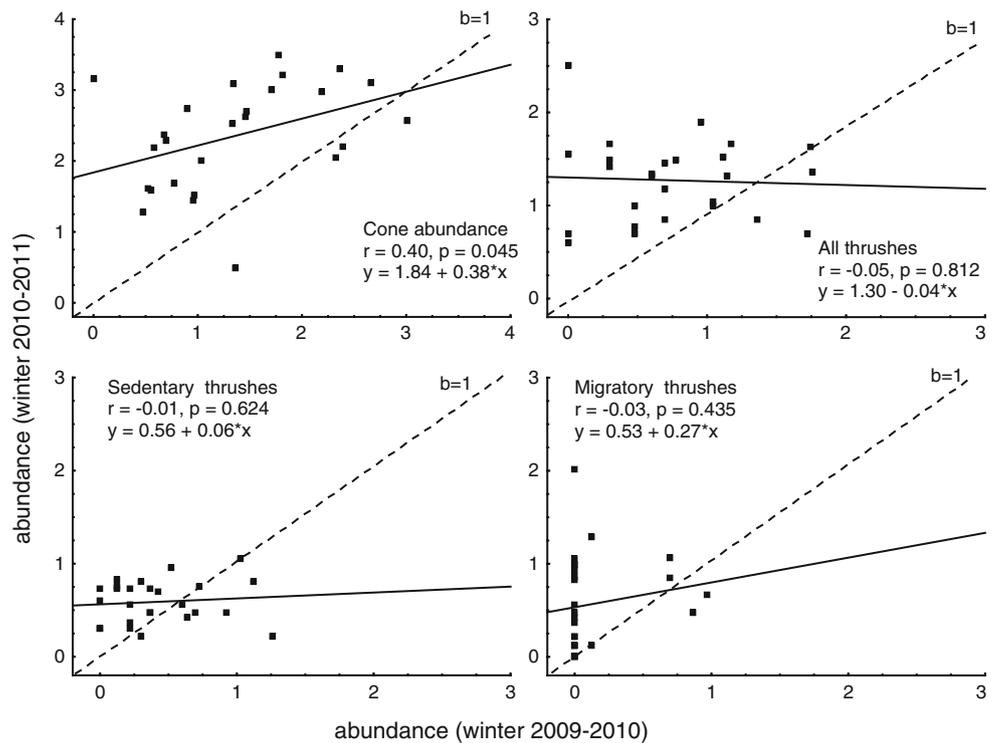
woodlands are just one of the several potential wintering habitats of migratory thrushes in the Iberian Peninsula in which Mediterranean shrublands and forests, olive groves, etc. occur (Santos 1982; Tellería et al. 1999). Since food tracking is interpreted as a behavioural reaction of birds to obtain sufficient food to prevent starvation during winter and to guarantee optimal body conditions for spring migration and breeding (Norris et al. 2004; Newton 2004; Robb et al. 2008), this behaviour suggests that they were under pressure to cope with these requirements by selecting sectors with over-abundant crops. In this context, the active searching for ripe cones in the Spanish Juniper woodlands could be related to their high content of metabolised non-structural carbohydrates (Herrera 1987), one of the most suitable foods to meet energetic requirements of birds during the winter (Herrera 1987; Jordano 1993).

As a rule, the thrushes redistributed among woodlands according to inter-winter changes of cone availability (Fig. 3; Table 1). But the thrushes demonstrated a relative inability to allocate individuals according to the actual variation in cone crops since they under-matched the changes ($b < 1$; Table 1; Fig. 3). Under-matching is typical in wild animals and is often related to the effect of features other than food abundance (habitat preferences, difficulties in perceiving food distribution, etc.; Kennedy and Gray 1993; Ranta et al. 2000) and has been recorded previously in migratory birds in stopover and wintering grounds (Shochat et al. 2002; Tellería et al. 2008). However, despite common under-matching, thrushes displayed

different abilities to track the resource according to their abundance and migratory status.

Effects of abundance and migratory status

Thrush abundance was positively associated with cone tracking ability as depicted by *b* slope in Eq. 1 (Fig. 4). This suggests a density-dependent process in which thrushes increased their ability to track changes in cone abundance when the regional populations were large enough to allocate individuals in all juniper woodlands according to their extant availability of ripe cones (Fretwell 1972; Gaston et al. 2000). This density-dependent process of habitat occupation has been illustrated in other wintering areas where migratory passerines show a sequential, progressive occupation of space according to regional abundance (Tellería et al. 2001, 2008).

Interestingly, the ensemble reaction of species suggested a shared use of cones that reinforces the role of abundance on the tracking ability of thrushes. It has been suggested that the energetic costs of active searching may be reduced by tracking the distribution of other frugivores, and that this type of indirect resource monitoring might allow birds to efficiently locate new patches over broad spatial scales (Saracco et al. 2004). This trend may be improved in fruit–frugivore systems because fruit is often superabundant within the patches and the cost of group foraging may be especially low (Martin 1985). This fact, along with the morphological and biological similarities of thrush species
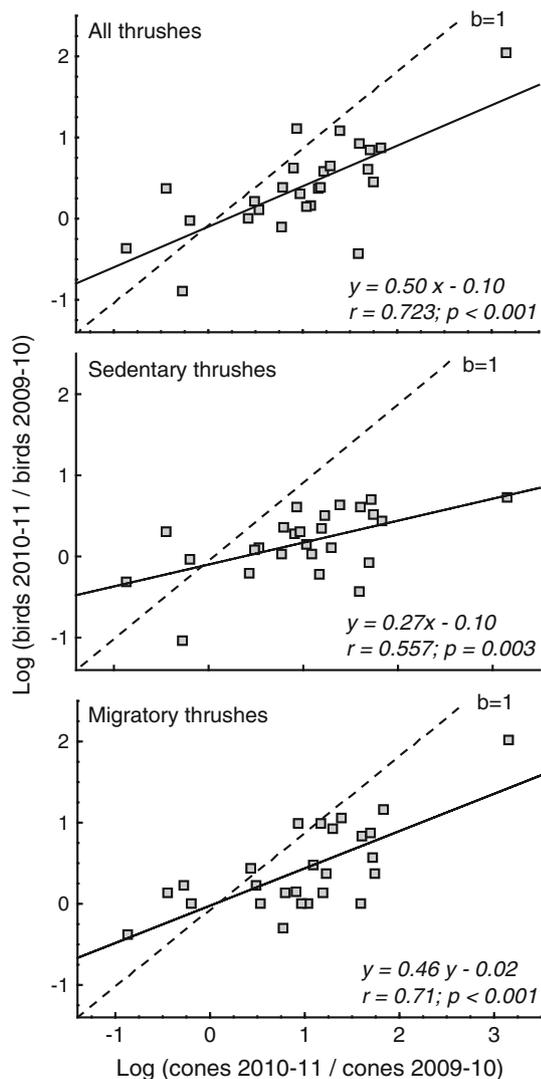
Fig. 3 Relationship between inter-winter cone and thrush abundance changes in the 26 study woodlands
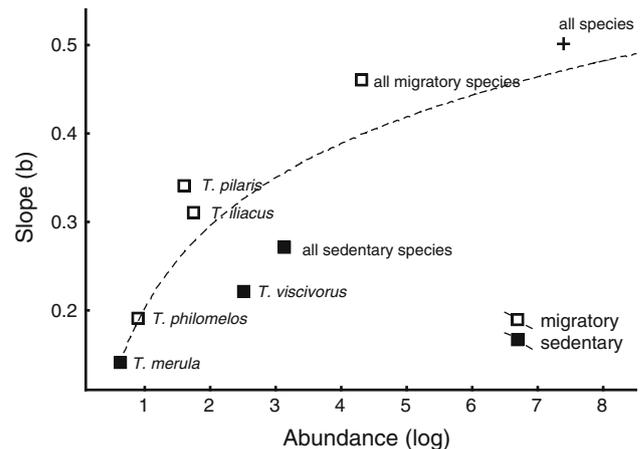

Fig. 4 A schematic view of the effect of abundance (mean of the 2 years) on the ability of thrushes to track ripe cone abundance in the Spanish Juniper woodlands as reflected by the *b* slope provided by the matching rule model (see text). The *left* part shows the patterns depicted by *b* slopes of the individual species, the *central* part shows the patterns resulting from grouping migratory and sedentary thrushes, and the *right* part shows the *b* slope of all thrushes together. One *line* has been adjusted to resume the pattern

involved in the search for ripe cones, suggests the combination of similar individualistic reactions resulting in a similar tracking of the resource. This does not occur in more heterogeneous assemblages where some individual species track the fruit better than the whole assemblage of frugivorous birds (Tellería et al. 2008; Blendinger et al. 2012).

Despite the small sample size (just 5 species), this paper shows that migratory thrushes tracked spatiotemporal changes in cone availability better than sedentary ones (Fig. 4). This agrees with our predictions on the higher skill of wandering birds to track the fruit and supports a main role for migratory thrushes in this bird–plant interaction. In this context, it is interesting to emphasize the following two patterns. Migratory thrushes, despite sharp increases in abundance, were far from matching the extant

spatiotemporal changes of the resource (Figs. 3, 4). And, alternatively, sedentary species, despite meagre inter-winter changes in abundance, were able to track the changes in ripe cone availability. Such a reaction is feasible in Mistle Thrushes, which move in small flocks in the search for food within their winter ranges. However, this appears to be less predictable in territorial Blackbird males, the main component of Blackbird populations wintering in the Iberian highlands (Santos 1982). However, tracking of food resources has also been detected in other territorial passerines to deal with food changes in wintering habitats (Johnson and Sherry 2001; Tellería et al. 2008). Consequently, despite the differences, we can explicitly assert that both the migratory and sedentary thrushes tracked spatiotemporal changes in cone availability.

Concluding remarks

Our results support large-scale tracking by thrushes of spatiotemporal changes in cone crops within the range of the Spanish Juniper woodlands. The ability of thrushes to track changes in cone abundance is a main component of seed delivery within the Spanish Juniper woodlands (Jordano 1993; Santos et al. 1999; Escribano-Avila et al. 2012). Since cone tracking ability appears to be a density-dependent process, this suggests that any reduction of thrush abundance could weaken this bird–plant interaction in juniper woodlands. This is possible in a time of rapid environmental change (Şekercioğlu et al. 2004). In fact,

some abundant thrush species in the Spanish Juniper woodlands during winter, such as the Redwing and the Fieldfare, are decreasing in their North European breeding areas (European Bird Census Council http://www.ebcc. info/). This may also occur in a context of global change in which many European birds are reducing their migratory movements southwards (Visser et al. 2009; Onrubia and Tellería 2012). Given the main role of abundant, migratory thrushes as cone trackers, this may affect seed delivery within the Spanish Juniper woodlands. The potential consequences of these changes require further investigation, but seed dispersion could be resilient to an eventual drop in migratory thrushes throughout the similar functional role developed by sedentary birds. These species, differing from the episodic arrivals of large numbers of migratory birds just in masting years, remain year-round in Spanish Juniper woodlands (Santos et al. 1983). Consequently, they are willing to consume ripe cones from the end of the summer to the spring thus increasing their actual participation in seed delivery (Tellería et al. 2011). In addition, junipers seem to be resilient to the loss of these highly specialized seed dispersers (Jordano 1993), since other vertebrates also feed on ripe cones and disperse the seeds (e.g. mammals; Santos et al. 1999; Escribano-Avila et al. 2012).

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