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Songbirds promote connectivity between riparian galleries and adjacent habitats

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Abstract

Riparian galleries are among the most vulnerable habitats in the world and are well known for their importance to the most specialized riparian bird species. In this study, we analyzed songbird composition, songbird diet, trophic ecology and seed dispersal in riparian galleries and adjacent Montado matrices in southern Portugal to address the importance of birds in promoting the connectivity between riparian galleries and adjacent habitats. We used fecal samples to compare diet, and blood samples to compare nitrogen stable isotopes from birds in these two habitats. The seasonal variation in the abundance of arthropods and fruits was evaluated in both habitats and seed movement between both habitats was assessed from fruits marked with fluorescence. Abundance of food resources for birds (arthropods and fruits) declined throughout the season in a similar way for both habitats, and there were strong similarities in the diet and trophic ecology of songbirds in the riparian gallery and adjacent habitat. In both habitats, birds preyed heavily on Hymenoptera and Coleoptera but birds more abundant in the Montado fed more on Araneae and Hymenoptera. Seeds were moved significantly more frequently from the riparian gallery into the adjacent Montado than vice-versa. Our results suggest that birds from the adjacent habitat move frequently to the riparian gallery to forage and disperse seeds into the adjacent habitat as they depart. This study shows that birds play an important role in promoting connectivity between riparian galleries and adjacent habitats.

KEYWORDS

forest matrix, frugivorous birds, habitat complementarity, insectivorous birds, seed dispersal

1 | INTRODUCTION

Riparian galleries are ecosystems with high numbers of species that provide many ecosystem services (Nilsson & Svedmark, 2002; Salinas & Casas, 2007) and often interact with adjacent habitats. Riparian galleries are important for ecosystem functioning and are particularly relevant in dry areas such as savannah-type habitats of the Mediterranean region, forming natural corridors and maintaining high biodiversity on a regional scale (Godinho, Rabaça, & Segurado, 2010; Larsen, Sorace, & Mancini, 2010; Pereira, Godinho, & Rabaça, 2012). Because of water availability throughout the year, and the compositional and structural complexity of vegetation types, riparian galleries provide favorable conditions for mobile animal communities, such as passerine birds, that may use different habitats in different seasons to meet their resource needs (Larsen et al., 2010; Saab, 1999). Birds may have an important functional role in connecting adjacent habitats (Whelan, Wenny, & Marquis, 2008), particularly through seed dispersal (Heleno, Ross, Everard, Memmott, & Ramos, 2011), an important process that connects successive plant generations and influences vegetation dynamics (Nathan & Muller-Landau, 2000) in the riparian gallery and adjacent habitats.

Because bird species can use both riparian galleries and adjacent habitats (Gomes, Rabaça, Godinho, & Ramos, 2017), they are particularly important to the study of inter-dependence (habitat subsidy or complementarity) of riparian galleries and adjacent habitats. Given that vegetation differs in terms of composition and structure between the gallery and the surrounding area, birds may show different food habits between the two habitats. Riparian galleries may be particularly important for bird communities of adjacent habitats by providing shelter during very hot summer periods (Gomes et al., 2017), and a high abundance of insects and fruits throughout the year (Brinson, Swift, Plantico, & Barclay, 1981; Whitaker, Carroll, & Montevecchi, 2000). Fleshy fruits are important food resources for resident and migratory passerines in Mediterranean habitats (e.g., Telleria, Ramírez, & Pérez-Tris, 2005), and are likely to be more abundant within the riparian gallery than in adjacent habitats (Gomes et al., 2017; Leal, Martins, Palmeirim, & Granadeiro, 2011). In temperate and Mediterranean European areas, fleshy-fruited plants commonly produce mature fruit crops in late summer and autumn, or even in winter when flocks of migrant and wintering birds are abundant in those areas (Herrera, 1984; Willson & Traveset, 2000).

The importance of riparian galleries to the most specialized riparian bird species is well known (Bryce, Hughes, & Kaufmann, 2002; Godinho et al., 2010; Pereira et al., 2012), but there are few studies addressing the importance of birds in promoting connectivity between riparian galleries and adjacent habitats. Previous studies clearly showed that seasonal bird abundance is higher for riparian galleries than for adjacent habitats in Mediterranean European areas, but within each season bird species richness is relatively similar between these two habitats (Gomes et al., 2017). Our study addresses the ecological relevance of riparian galleries for both birds and plants, testing the impact of the surrounding landscape on (a) bird activity (measured through diet and trophic ecology) and (b) seed dispersal performance. Specifically, we asked the following questions: (a) does the frequency distribution of bird numbers from riparian gallery-preferring bird species and the adjacent habitat-preferring bird species differ in the interface between these two habitats?; (b) do diet and the trophic niche of birds assessed by nitrogen stable isotopes differ seasonally between riparian gallery-preferring species and the adjacent habitat-preferring species?; (c) is there a seasonal similarity in the abundance of food resources (arthropods and fruits) for birds between these two habitats?; and (d) how relevant is seed dispersal from the riparian gallery into the adjacent habitat, and vice-versa? We present our results in the context of the ecological complementarity between riparian galleries and adjacent habitats.

2 | MATERIALS AND METHODS

2.1 | Study sites

Samples were collected in 2013 and 2014 at two sites in the outskirts of the city of Évora, Alentejo, Portugal. Both sample sites comprised riparian gallery–Montado interfaces: one included a stretch of the River Valverde, located in Herdade da Mitra (a campus of the University of Évora; hereafter Mitra; 38°31′52.8″N; 8°00′47.6″W); the other site was a stretch of the River Degebe close to Canaviais (hereafter Degebe; 38°36′50″N; 7°54′03″W). Cork oak (*Quercus suber*) and holm oak (*Q. ilex*) agroforestry systems, known as Montado, are the dominant element of the landscape (Pereira & Fonseca, 2003). The riparian plant communities were dominated by blackberry (*Rubus ulmifolius*), ash (*Fraxinus angustifolia*) and willow (*Salix* spp.), and the dominant vegetation of our adjacent matrices comprised holm oak and cork oak with a shrub layer of rockrose (*Cistus crispus*, *C. salviifolius*, and *C. ladanifer*) and artichoke (*Cynara* spp.). For sampling purposes, we assumed that the riparian gallery extended up to 40 m from the stream, and the adjacent Montado was between 41 and 150 m from the stream. The annual rainfall in the area varies from 500 to 800 mm (Instituto do Ambiente, 1999). Temperature varies from 9°C in January to 24°C in July, with daily mean temperature records ranging from 7 to 43°C, annual insolation ranging from 2,900 to 3,000 hr/year and altitude varying from 200 to 300 m a.s.l. (Instituto do Ambiente, 1999).

2.2 | Bird trapping

Selected bird species were resident and migratory common songbirds in the interface between riparian galleries and Montado systems in SW Portugal, and were the most frequently captured species in ringing sessions carried out in the area in the 2 years preceding our study.

Additionally, seasonal differences in species richness and bird abundance were clearly demonstrated in a previous study (Gomes et al., 2017). The riparian gallery-preferring bird species were nightingale (*Luscinia megarhynchos*), cetti's warbler (*Cettia cetti*), wren (*Troglodytes troglodytes*), blackcap (*Sylvia atricapilla*) and blackbird (*Turdus merula*), and the Montado-preferring species were robin (*Erithacus rubecula*), sardinian warbler (*Sylvia melanocephala*), chaffinch (*Fringilla coelebs*), great tit (*Parus major*) and blue tit (*Cyanistes caeruleus*) (Godinho et al., 2014; Godinho et al., 2016). Ringing sessions were conducted during four seasons: spring (4 April–29 May 2013 and 27 March–28 May 2014), summer (6 June–18 July 2013 and 4 June–21 July 2014), autumn (4 September–10 October 2013) and winter (23 January–26 February 2014). At the Degebe site birds were mist netted at three locations according to distance from the stream: stream (0–40 m), riparian gallery–Montado interface (41–80 m) and Montado (81–150 m); five 15-m long mist nets (75 m) were placed in each location. At Mitra birds were sampled only at 41–80 m from the stream (riparian gallery–Montado interface): in spring and summer we set 14 mist nets (198 m), in winter we set eight mist nets (87 m) and in autumn we set nine mist nets (108 m). Mist nets were all set up at sunrise and kept open for 5 hr, being checked for captures every 30 min.

2.3 | Fecal sample collection for diet analysis

Birds captured were individually kept in clean cotton holding bags for up to 30 min to defecate, and droppings were preserved in Eppendorf tubes (Eppendorf Ibérica S.L.U., Madrid, Spain) with 70% ethanol until processed in the laboratory. All hard remains in fecal samples (mostly fragmented arthropod parts and seeds) were separated using a binocular microscope. Because of the difficulty in identifying arthropod parts, prey items were identified only to the taxonomic level of order using several reference sources (Barrientos, 2004; Ring, Häuser, Hagedorn, & Wetzel, 2013; Shiel, McAney, Sullivan, & Fairley, 1997).

2.4 | Blood sample collection and stable isotope analysis

The blood was used to give information on the current trophic niche of the birds, a few days to several weeks prior to sample collection (Bearhop, Waldron, Votier, & Furness, 2002). Blood samples were collected only at the Degebe site from birds captured during four seasons: spring (April 2013), summer (July 2013), autumn (October 2013) and winter (January 2014). A blood sample (~75 μL) was taken into heparinized capillary tubes from each bird's brachial vein and kept in a chiller box until it was transported to the laboratory and frozen. The isotopic signature of metabolically active tissues such as blood changes over time according to switches among isotopically distinct diets or movement between isotopically distinct habitats (Bearhop et al., 2002; Inger & Bearhop, 2008). In the laboratory, blood was dried at 55°C for a minimum of 24 hr. Pieces of dried blood were weighed (0.3–0.4 mg) and encapsulated. The samples were analyzed via continuous flow isotope-ratio spectrometry, using a Delta V Plus isotope ratio mass spectrometer (Thermo Electron) (Inger & Bearhop, 2008). The isotope ratio is calculated as.

$\delta X = [(R_{sample}/R_{standard}) - 1] \times 1{,}000$,where X (‰) is ^{15}N and R is $^{15}N/^{14}N$ (Inger & Bearhop, 2008; Kelly, 2000). We measured stable nitrogen isotope ratios (^{15}N:^{14}N, expressed as $\delta^{15}N$). Nitrogen is enriched at each successive trophic level by 2–5‰ (Inger & Bearhop, 2008; Kelly, 2000).

2.5 | Food abundance in the riparian gallery and in the adjacent Montado

2.5.1 | Arthropods

To evaluate seasonal variation in food abundance in the riparian gallery and the adjacent Montado we used the beat sheet method (Boyer & Dumas, 1969; Shepard, Carner, & Turnipseed, 1974) to sample arthropods in the accessible branches of trees and bushes. We used a triangular sheet that was 60 × 60 × 65 cm with a depth of 75 cm, and made a total of 10 beats/sample. We collected 15 samples from the riparian gallery and 15 samples from the adjacent Montado at locations chosen randomly at both study sites. A total of 285 samples were collected in summer and autumn of 2013, winter 2013/2014, spring 2014 and winter 2014/2015. Specimens were identified taxonomically to order (Barrientos, 2004; Ring et al., 2013), dried in an oven at 50°C over 4 days and weighed to obtain dry weight by sample.

2.5.2 | Fruits

Sampling plots were selected in the riparian gallery (up to 40 m from the stream) and in the surrounding Montado (41–150 m from the stream) to evaluate monthly variation in the abundance of fruits in both habitats at the Degebe and Mitra sites. We marked plots of plants with fruits and carried out monthly counts to document fruit-removal from August 2013–April 2014 and August 2014–March 2015 in both areas. Plots were visited monthly until no fruits remained on plants and new plots were established when new fruits appeared. We evaluated seasonal decline in the abundance of the most common fleshy fruit-producing species in the area: blackberry (*R. ulmifolius*), common smilax (*Smilax aspera*), myrtle (*Myrtus communis*), olive (*Olea europaea* var. *sylvestris*), black bryony (*Tamus communis*), mastic (*Pistacia lentiscus*), strawberry tree (*Arbutus unedo*), flax-leaved daphne (*Daphne gnidium*), butcher's-broom (*Ruscus aculeatus*), asparagus (*Asparagus aphyllus*), grapevine (*Vitis* spp.), ivy (*Hedera* spp.), dog-rose (*Rosa canina*) and common hawthorn (*Crataegus monogyna*). For the most abundant plant species we marked 15–20 plots and approximately 10 plots for the less common plant species.

2.6 | Assessing seed dispersal and movement of seeds between the riparian gallery and the adjacent Montado

We used the method proposed by Levey, Bolker, Tewksbury, Sargent, and Haddad (2005) to understand the mechanism of seed movement in the riparian gallery–Montado interface of the Mitra site only. We sprayed a mixture of water and fluorescent powder (fluorescent pigment Holi Powder Color Run, article code 90, manufacturer WeGlow, Sintra, Portugal) of six different colors: yellow, blue, orange, pink, green and red. We marked six different individuals/patches of each plant species, both in the riparian gallery (0–40 m from the stream) and in the adjacent Montado matrix (>40 m from the stream): *S. aspera*, *P. lentiscus*, *M. communis*, *R. ulmifolius*, *O.* var. *sylvestris* and *A. unedo* (Table 1). We did not repeat colors for the same plant species, which allowed us to specifically identify the parent plant of each seed found later in bird feces. In all, an estimated 28,518 seeds were marked with fluorescence, and seed traps were used to assess seed dispersal in relation to distance from the stream, as well as dispersal of marked seeds between habitats.

To assess seed dispersal a total of 81 seed traps were installed at the Mitra site, distributed throughout the riparian gallery (44 seed traps) and the surrounding Montado (37 seed traps). Seed traps were installed on strategic branches of trees and bushes where we observed higher bird activity, and at several distances from the riparian gallery (the maximum average distance between seed traps was 45 m, the minimum distance was 4 m and the maximum distance to the stream was 134 m). Bird droppings were collected from the seed traps once a week. All seeds and fruits were collected from seed traps, checked for fluorescence using a black light flashlight in a room without white light, and identified using a reference collection of seeds from the study area. Each weekly visit to seed traps was also considered as a sampling unit for each plant species, and the abundance of fruits of each species in a 40 m radius around the seed trap was estimated weekly. We also plotted the following data of seed abundance and seed dispersal using three classes of distance to the stream: 0–40 m (44 seed traps), 41–80 m (18 seed traps) and >80 m (19 seed traps).

2.7 | Data analysis

We tested the null hypothesis that the number of birds from the riparian gallery-preferring species and the

TABLE 1 Number of seeds marked ($n = 28{,}518$) and collected ($n = 95$) with fluorescence for each plant species, in the riparian gallery (Gal) and in the adjacent Montado matrix (Mat), and % of seeds moved between habitats (Mat to Gal and Gal to Mat)

	Seeds marked and collected with fluorescence			Seed movement between habitats	
Species	No. of seeds marked in Gal	No. of seeds marked in Mat	Total no. of seeds collected with fluorescence	% of seeds marked in Mat and collected in Gal	% of seeds marked in Gal and collected in Mat
Smilax aspera	2,801	963	67	5	65
Pistacia lentiscus	23,340	0	4	0	0
Olea europaea var. *sylvestris*	242	47	0	0	0
Myrtus communis	446	0	2	0	0
Rubus ulmifolius	404	0	22	2	21
Arbutus unedo	177	98	0	0	0
Total	27,410	1,108	95	7	86

Note: We defined the riparian gallery habitat as up to 40 m from the stream, and Montado matrix as >40 m from the stream.

Montado-preferring species should occur equally at (a) the stream, (b) the riparian gallery–Montado interface and (c) the Montado; this frequency distribution was analyzed with a chi-square contingency table using data from the Degebe site.

We compared the total number of seeds from the riparian gallery that had been moved into the Montado matrix, and vice-versa, using a chi-square test to test the null hypotheses that seeds with fluorescence found in seed traps should be moved equally between the two habitats.

Diet data are presented as percentage of occurrence (% of fecal samples where a particular arthropod order was present) per season (spring, summer, autumn and winter), between April 2013 and July 2014. We performed a principal component analysis (PCA) to describe patterns of diet between birds more recurrent in the riparian gallery and in the adjacent habitat. We used general linear models (GLMs) to test for differences in: (a) stable nitrogen isotope values ($\delta^{15}N$) for each species among seasons, and (b) the abundance of arthropods in relation to habitat type (riparian gallery and adjacent Montado), season (spring, summer, autumn and winter) and their interaction for each study site, after verifying variance homogeneity and normal data distribution. If habitats were similar (inter-dependent) in terms of food abundance for birds, we expected fruit abundance to be closely correlated through time and this was examined with a Spearman correlation coefficient.

A Kruskal–Wallis test was used to assess if the median distance of seeds detected with fluorescence between seed traps and their parent plants differed among plant species. Results are given as means ± *SD* with a significance level at $p < .05$. All statistical analyses were carried out using the program STATISTICA (Version 7, StatSoft, 2004).

3 | RESULTS

3.1 | Frequency distributions of riparian gallery- and Montado-preferring species

For the Degebe study site the number of bird species (and total number of individuals) captured at the stream (0–40 m), riparian gallery–Montado interface (41–80 m) and Montado (81–150 m) were 14 (58), 20 (97) and 17 (70), respectively. The frequency distribution of the total number of individuals for riparian gallery-preferring species ($n = 50$) and Montado-preferring species ($n = 119$) differed significantly between the stream, riparian gallery–Montado interface and Montado ($X^{2}_{2} = 10.0$; $p < .01$, Figure 1). Riparian gallery-preferring species were more abundant at the stream than expected (22:14), and likewise Montado-preferring species were more abundant in the adjacent Montado than expected (43:37). However, at the interface between the two habitats, the abundance of birds was similar to that expected for both riparian gallery-preferring species (18:20) and Montado-preferring species (50:49).

3.2 | Diet

A total of 334 birds were trapped, 169 and 239 at the Degebe and Mitra sites, respectively (6% of individuals were re-trapped on different days and their fecal samples were treated as independent), and 395 fecal samples were collected. A total of 1,018 fragments were recorded and identified, 379 at Degebe and 639 at Mitra. Of all fragments detected, 85% were arthropod remains, 7% fleshy fruit seeds and 9% vegetative plant materials. Analysis of fecal droppings of birds recorded arthropods of 22 families from the following seven orders: Araneae, Hymenoptera, Coleoptera, Hemiptera, Diptera, Lepidoptera and Chilopoda. The orders Araneae, Hymenoptera, Coleoptera and Hemiptera accounted for 73% of birds' arthropod diet, 12% for other arthropod orders and 15% of the arthropod fragments were unidentified. Fecal droppings analysis revealed that birds fed primarily on Hymenoptera (33%), Coleoptera (28%), Hemiptera (11%) and Araneae (5%).

Diet largely overlapped between riparian gallery-preferring species and Montado-preferring species (Tables S1 and S2). However, Montado-preferring species seem to prey more on insects (60% of the samples) than

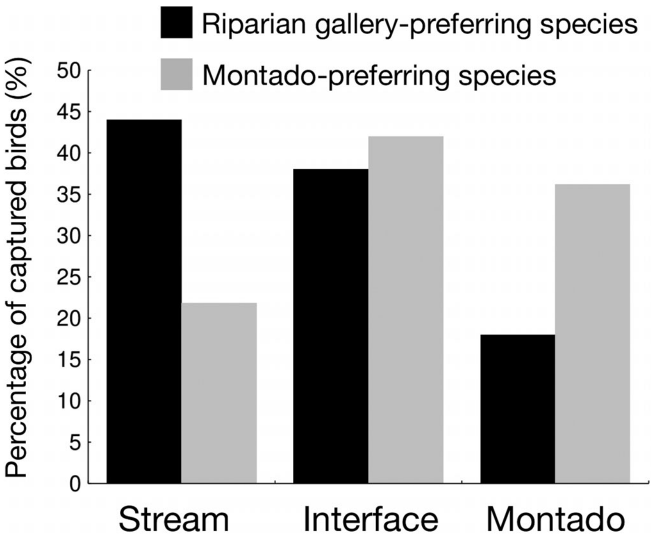

FIGURE 1 Comparison of the frequency distribution of birds captured at Degebe for the riparian gallery-preferring species ($n = 50$ birds) and Montado-preferring species ($n = 119$ birds) along the stream, riparian gallery–Montado interface and Montado

riparian gallery-preferring species (40%), and the opposite occurred for seeds (10% vs 20%). Moreover, Montado-preferring birds fed more on Araneae than riparian gallery-preferring birds (Figure 2). As for fruit consumption, at the Degebe site more *A. aphyllus* and *D. gnidium* were consumed by the Montado-preferring birds, while the riparian gallery-preferring birds consumed more *S. aspera* and *O. europaea* var. *sylvestris*. At the Mitra site a different pattern was observed, with the riparian gallery-preferring birds consuming more *P. lentiscus* and *Hedera* spp., while Montado-preferring birds consumed more *M. communis* and *O. europaea* (Figure 3; Table S2). We did not collect any seeds of *A. unedo*, probably because of seed (with an average size of 1.5 mm) and fruit dimensions, which are unlikely to be entirely consumed, often being only pecked, reducing the probability of seed ingestion.

The PCA of the diet data for the Degebe site extracted three axes with an eigenvalue larger than 1: PC1, PC2 and PC3, with eigenvalues of 2.58, 1.91 and 1.51 respectively, and explaining 37%, 27% and 22% of the variance, respectively. PC1 was positively related to Araneae and negatively related to other arthropod orders, PC2 was positively related to Hemiptera and Hymenoptera and PC3 negatively related to Coleoptera and fruits. For Mitra, the PCA of the diet data extracted two axes with an eigenvalue larger than 1: PC1 and PC2, with eigenvalues of 2.17 and 1.76, respectively, and explaining 31% and 25% of the variance respectively. PC1 was positively related to Coleoptera, other arthropod orders and Araneae. PC2 was positively related to other arthropod orders and fleshy fruits, and negatively related to Araneae. Overall, the PCA for both the Mitra and Degebe study sites also showed a strong overlap in the diet between riparian gallery-preferring species and Montado-preferring species (Figure 4). However, the Montado-preferring species at Degebe were easier to distinguish from the riparian gallery-preferring species along PC1 and PC2, and fed more on Araneae and Hymenoptera, mainly on Formicidae (ants). Conversely, fruits

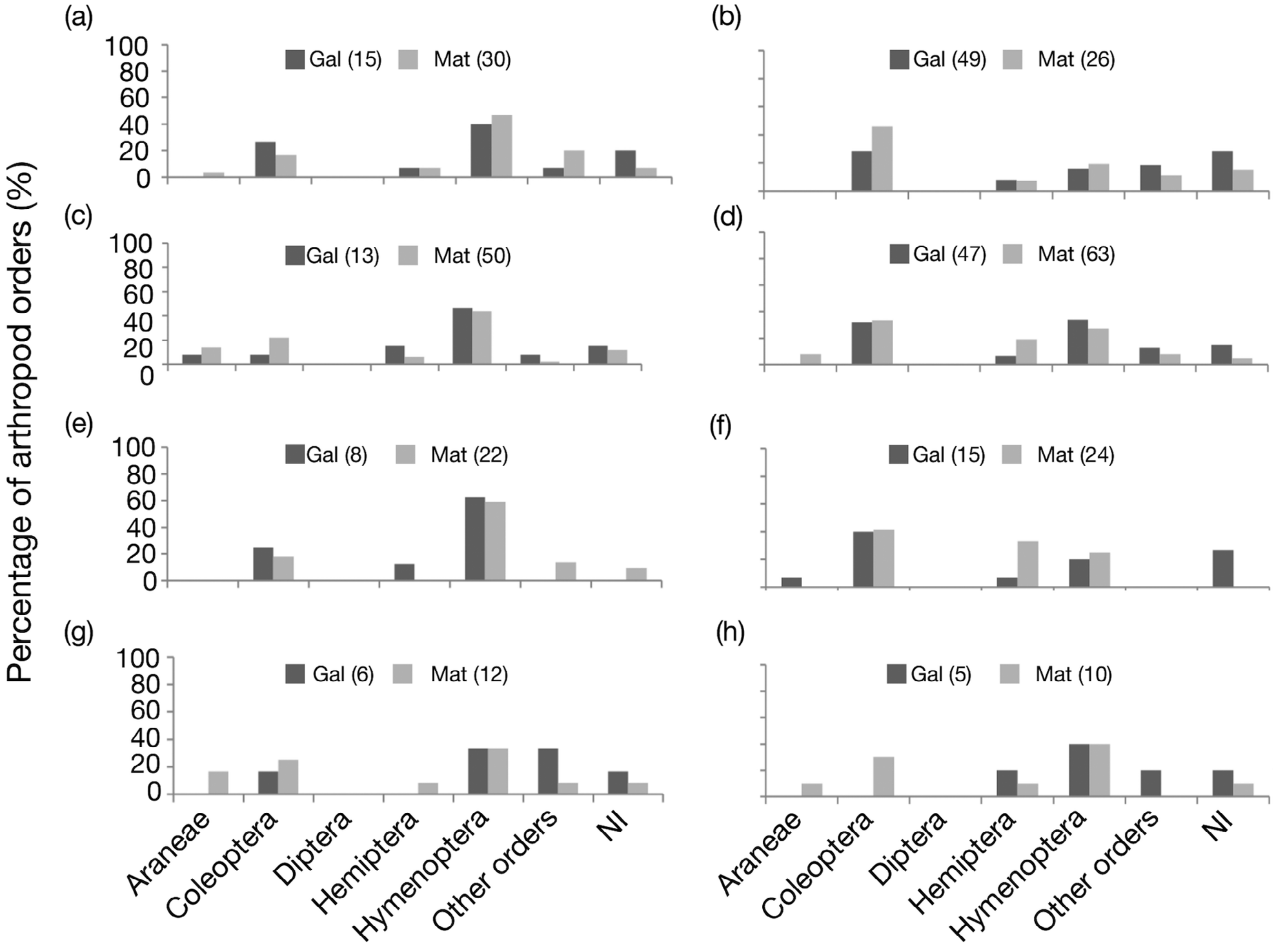

FIGURE 2 Percentage of arthropod orders in fecal samples of all bird species for the riparian gallery (Gal) and Montado matrix (Mat), for (a) spring, (b) summer, (c) autumn and (d) winter at Degebe, and (e) spring, (f) summer, (g) autumn and (h) winter at Mitra. The numbers presented within parentheses are the number of fecal samples for each habitat type. The category NI represents orders that were not identifiable

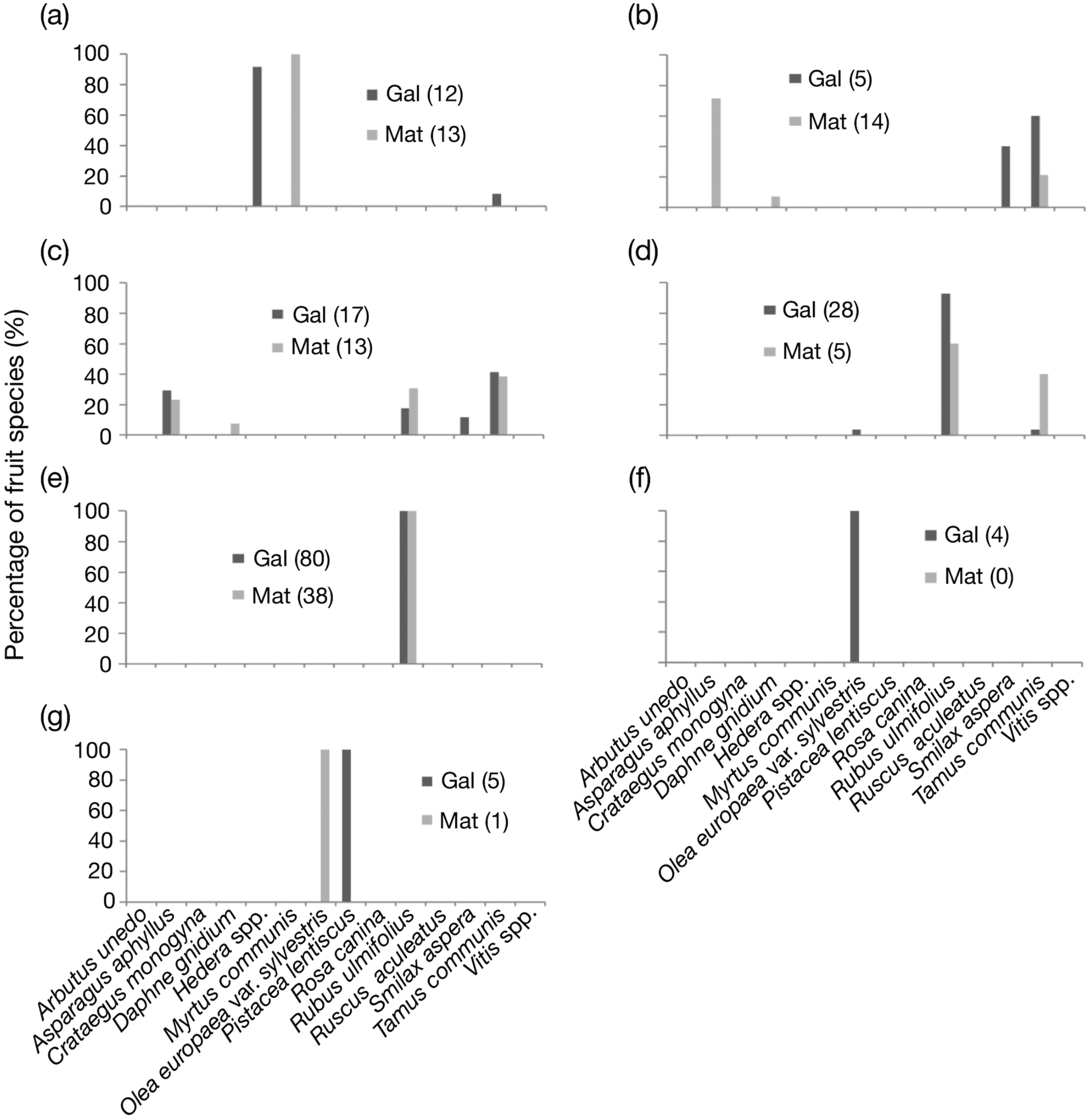

FIGURE 3 Seasonal comparison between fruits in the diet of riparian gallery-preferring bird species (Gal) and Montado-preferring species (Mat), for (a) summer, (b) autumn and (c) winter at Degebe, and (d) spring, (e) summer, (f) autumn and (g) winter at Mitra. No data for spring at Degebe. The numbers presented within parentheses are the number of fecal samples for each habitat

appeared less important in separating these two groups of birds. For Mitra, the Montado-preferring species were also easier to distinguish along PC1 (Figure 4), and fed more on fruits, Araneae and other arthropod orders, and the riparian gallery-preferring bird species fed more on Chilopoda—specifically family Julidae (millipedes)—Lepidoptera (butterflies in larval stage) and other arthropod orders.

3.3 | Stable isotopes

Riparian gallery-preferring species differed from the Montado-preferring species in their δ^{15}N values in relation to habitat ($F_{1,123}$ = 26.97, p < .001) and season ($F_{1,123}$ = 5.77, p = .001), but there was no interaction between these two variables ($F_{3,123}$ = 1.90, p = .134; Figure 5). Riparian gallery-preferring species fed consistently at a higher trophic level than Montado-preferring species, particularly in spring, summer and autumn (Figure 5). Montado-preferring species fed at lower trophic levels in spring and winter, and there was a gradual decrease in their trophic level from summer to winter (Figure 5). In the GLMs performed on the δ^{15}N values for each individual species (Table S3) there were significant difference among seasons for blackcap ($F_{3,19}$ = 7.2, p = .002), Sardinian warbler ($F_{2,12}$ = 5.0, p = .026), blue tit ($F_{3,22}$ = 5.3, p = .007) and great tit ($F_{1,16}$ = 39.3, p < .001), but no significant difference for robin ($F_{1,17}$ = 0.5, p = .476).

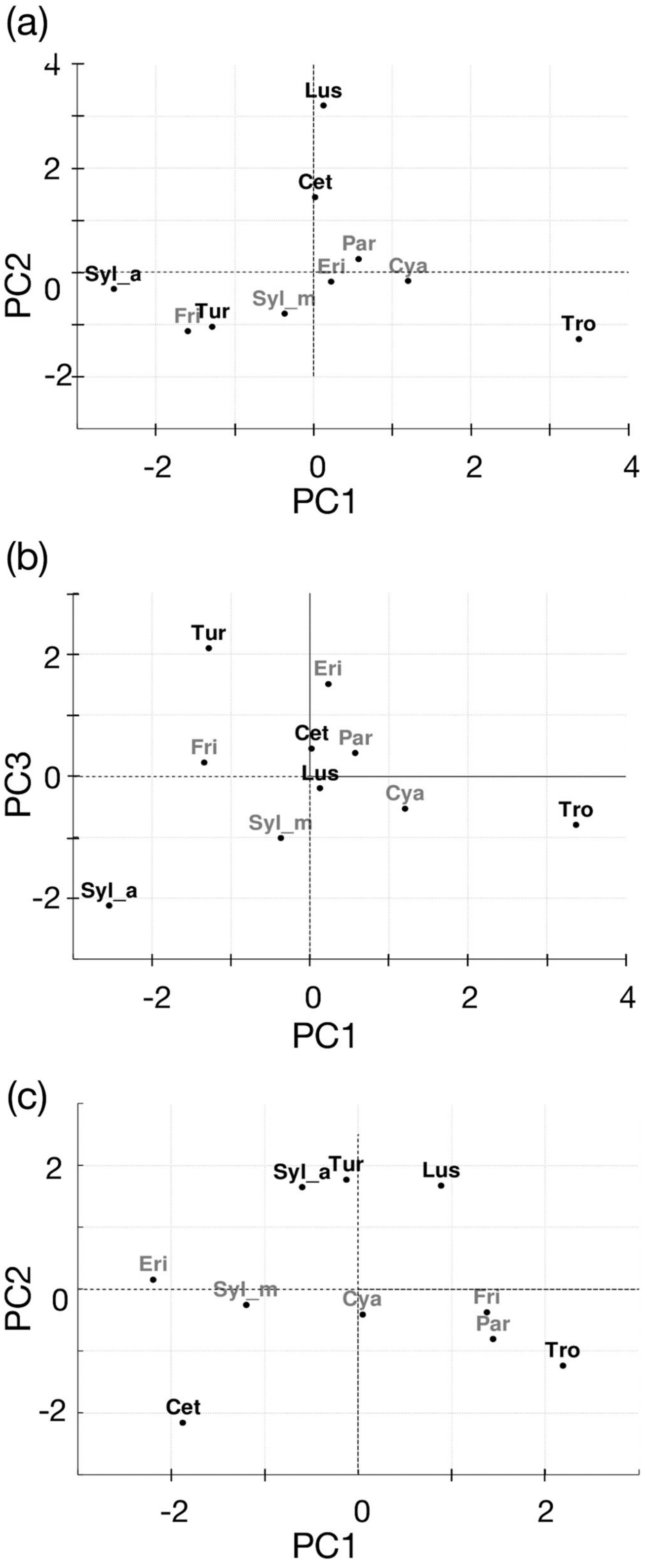

FIGURE 4 Principal component analysis of bird diet composition, assessed from fecal samples for (a) PC1 versus PC2 from Degebe, (b) PC1 versus PC3 from Degebe, and (c) PC1 versus PC2 from Mitra. Riparian gallery-preferring species are shown in black and Montado-preferring species are shown in grey. Bird species abbreviations: Lus, *Luscinia megarhynchos* (nightingale); Cet, *Cettia cetti* (cetti's warbler); Tro, *Troglodytes troglodytes* (wren); Syl_a, *Sylvia atricapilla* (blackcap); Tur, *Turdus merula* (blackbird); Eri, *Erithacus rubecula* (robin); Syl_m, *Sylvia melanocephala* (sardinian warbler); Fri, *Fringilla coelebs* (chaffinch); Par, *Parus major* (great tit); and Cya, *Cyanistes caeruleus* (blue tit)

3.4 | Food abundance

Seasonal variation in arthropod abundance was similar for both habitats in the two study areas (Figure 6). For both areas, there was only a significant effect of season on insect biomass (Degebe: $F_{3,127}$ = 26.61, Mitra: $F_{3,142}$ = 8.79, both p < .001), with an overall higher insect biomass during autumn (Figure 6). Marked plots of fleshy fruit species in September showed a steep decline in fruit abundance until December, with a significant correlation in the rate of decline between both habitats for both Degebe (r_s = 0.96, n = 7, p < .001) and Mitra (r_s = 0.98, n = 8, p < .001, Figure 7). After January there were virtually no fruits left in the Montado, but approximately 10%–20% were still available in the riparian gallery (Figure 7).

3.5 | Seed dispersal between the riparian gallery and the adjacent Montado

Parent plants that produced fruits were more abundant closer to the stream, and as distance to the stream increased, both the abundance and the dispersal of seeds declined rapidly (Figure 8). We collected 95 seeds with fluorescence in seed traps; it was clear that, of all the seeds that were moved by birds between the two habitats (n = 87), significantly more seeds were transported from the riparian gallery into the adjacent Montado (87%) than vice-versa (5%, X^2_1 = 40.2; p < .001, with Yates correction, Table 1); 6% of the seeds marked in the riparian

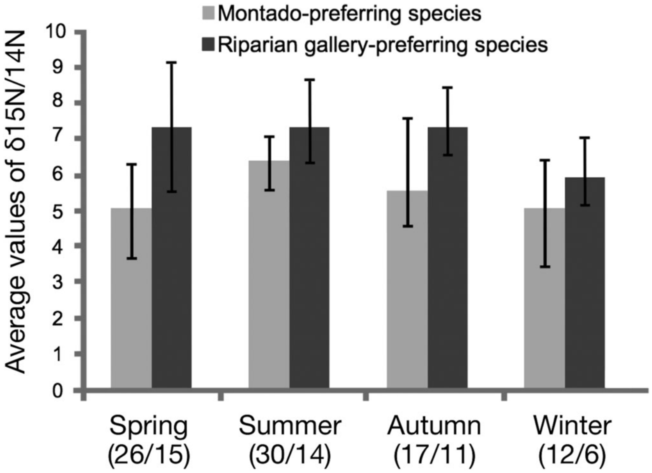

FIGURE 5 Seasonal variation in trophic level for Montado-preferring bird species and riparian gallery-preferring species, assessed from the δ^{15}N levels in whole blood. Values are shown as the mean ± *SD* for each season. Spring (March–June); Summer (June–September); Autumn (September–December); Winter (December–March). The numbers within parentheses refer to the sample size for each season and habitat

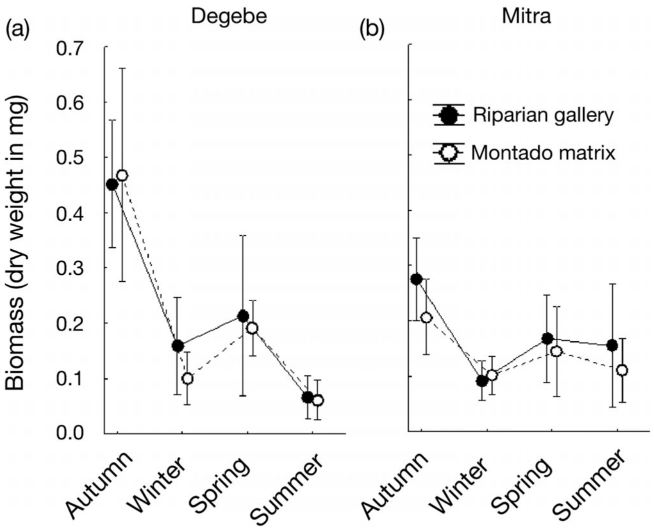

FIGURE 6 Seasonal variation in arthropod biomass (mean ± *SE*) between the riparian gallery and Montado matrix for Degebe and Mitra sites. Spring (March–June); Summer (June–September); Autumn (September–December); Winter (December–March)

gallery were collected in the same habitat, which was the case for *P. lentiscus* ($n = 4$) and *M. communis* ($n = 2$). The distance of dispersal from parent plants differed significantly between species (Kruskal–Wallis test: H [3, $n = 95$] = 45.68, $p < .001$). For *S. aspera* (33.6 ± 48.6 m, $n = 67$) the seeds were dispersed at shorter distances, while for *P. lentiscus* (84.3 ± 50.6 m, $n = 4$) seed dispersal covered greater distances, and even greater distances were covered for *M. communis* (146.0 ± 206.4 m, $n = 2$) and *R. ulmifolius* (373.8 ± 119.5 m, $n = 22$). We did not collect any seeds of *O. europaea* var. *sylvestris* or *A. unedo*.

4 | DISCUSSION

Our results show that songbirds play an important role in promoting connectivity between riparian galleries and adjacent habitats. Abundance of food resources for birds (arthropods and fruits) declined throughout the season in a similar way for both habitats, and there were important similarities, but also some consistent differences, in the diet and trophic ecology of common birds in the riparian gallery and in the adjacent Montado. It was clear that birds show a strong overlap at the interface between the riparian gallery and adjacent habitat, and that seeds were moved significantly more frequently from the riparian gallery into the adjacent habitat than vice-versa. Our study area includes two species of insectivorous birds that are relatively reliant on riparian areas, the nightingale (a migrant present in the area from spring to summer) and cetti's warbler, a resident species (Godinho et al., 2014, 2016; Gomes et al., 2017). The other riparian gallery-preferring species, particularly the blackbird and the blackcap, although more abundant in the riparian gallery, also occur in the adjacent Montado and feed on both arthropods and fruits (Godinho et al., 2014, 2016; Gomes et al., 2017), and move relatively more frequently between these two habitats. Taken altogether, our results suggest that birds from the adjacent habitat move frequently to the riparian gallery to forage, and, as they depart, disperse seeds into the adjacent habitat.

Overall, the diet of songbirds was relatively similar between the riparian gallery and the adjacent Montado. However, the spatial and seasonal changes in the abundance of arthropods and fruits at our study sites may be important in explaining the main differences in diet of birds between these two habitat types. Montado-preferring species seemed to feed more on Araneae than riparian gallery-preferring species. This may be largely explained by the fact that Montado-preferring species include relatively smaller bird species (i.e., blue tit and sardinian warbler) dwelling in shrubs and tree foliage, where they take small spiders (Ceia, Machado, & Ramos, 2016; Navalpotro, Pagani–Núñez, Hernández–Gómez, & Senar, 2016). Both riparian gallery-preferring species and Montado-preferring species gradually decreased their trophic level from summer to winter, which may be explained by an increase in fruit consumption by partially frugivorous species such as robins and Sardinian warblers. In winter, these two species are

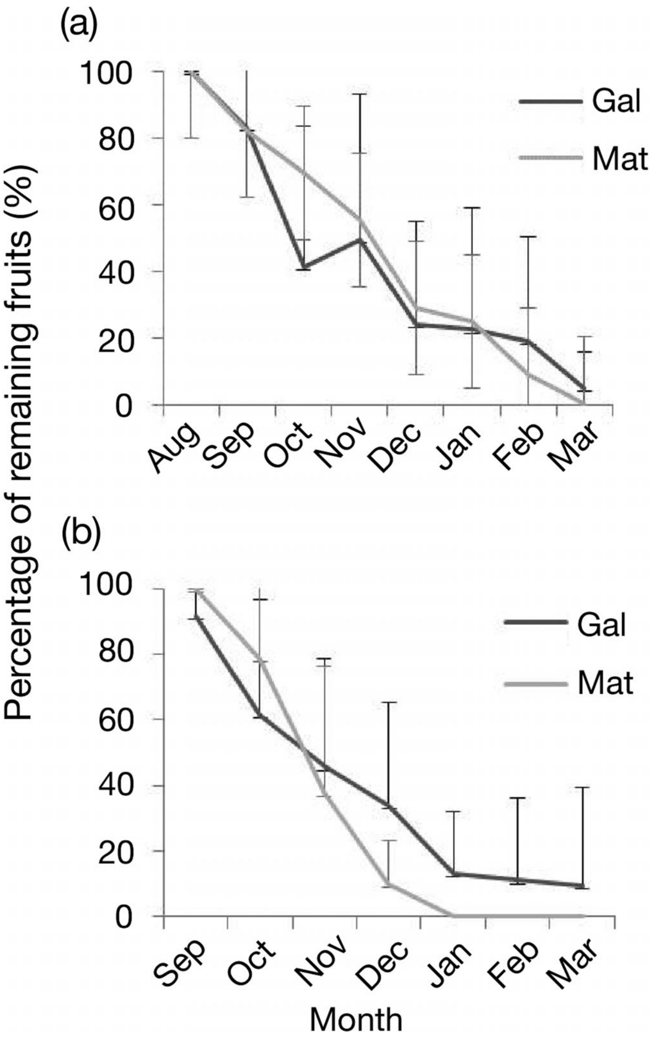

FIGURE 7 Percentage of fruits remaining (mean ± *SD*) for (a) Degebe and (b) Mitra sites per month for berry-producing species: Gal, riparian gallery and Mat, Montado matrix

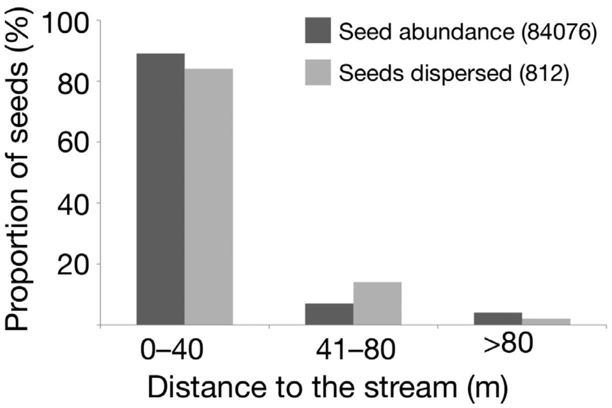

FIGURE 8 Comparison between the total proportion of seeds available (dark column) and dispersed (light column) detected in bird droppings collected in seed traps, per class of distance to the stream, at Mitra. The numbers presented within parentheses for seed abundance and seed dispersed refer to the total number of seeds

relatively more abundant in the riparian gallery than in the other seasons (Gomes et al., 2017), suggesting their importance in connecting these two habitats. Altogether, the riparian gallery-preferring species were mostly insectivorous in spring and summer and, to a large extent, switched to fruits in autumn and winter, when the abundance of arthropods decreased. During the autumn and winter migration, both resident and migratory birds in Mediterranean areas benefit from a higher abundance of fruit resources provided by riparian galleries and adjacent habitats (Herrera, 1984; Jordano, 1987; Leal et al., 2011).

The seasonal variation in food resources was very similar between the riparian gallery and the Montado matrix, but fruits in the Montado disappeared at a faster rate than those in the riparian gallery. Apart from animal consumption, the sparser vegetation and higher wind speeds in the Montado may result in both insects and fruits being lost or blown away at a higher rate in the Montado than in the sheltered riparian gallery during the first autumn storms (e.g., Whitaker et al., 2000). This corresponds with the higher abundance of fruits in the riparian gallery for frugivorous birds in autumn and winter (Kollmann & Schneider, 1999, this study), and our data suggest that Montado-preferring species moved to the riparian gallery to exploit such resources. However, it must be noted that birds' perception of fruit availability is influenced by many variables, such as plant morphology that affects birds' access to fruits, and fruit nutritional value. For instance, the fact that *S. aspera* was abundant in bird feces and in seed traps may be, at least in part, related to the fruit´s pericarp quantity and quality, which in turn is related to the benefit obtained by birds when consuming this fruit (Herrera, 1981).

Our results suggest that seed dispersal is influenced by local seed abundance, and that most bird species overlap in the riparian gallery–Montado interface to exploit fruit and insect food resources. Carlo and Morales (2008) found that the rate of fruit removal by birds increased in areas with higher abundance of fruiting plants, and that seed dispersal distance decreased away from parent plants. The dispersal of several plant species was not proportional to its abundance in each class of distance to the stream, meaning that seeds of some plant species were transported further than others. Our data set of seeds with fluorescence showed that seeds could be dispersed mostly to a distance of approximately 150 m from parent plants, which was also observed by Carlo, García, Martínez, Gleditsch, and Morales (2013). Nevertheless, *R. ulmifolius*, the second-most detected species with fluorescence, was dispersed up to a distance of approximately 375 m from the parent plant. This might be explained by two reasons: (a) *R. ulmifolius* was the species with the second-highest number of seeds per fruit (37 seeds per fruit), which likely increases the probability of collecting a larger number of seeds with fluorescence (Moermond & Denslow, 1985), and (b) most bird species feed on *R. ulmifolius*, including granivorous and insectivorous species (Costa et al., 2014) that are more common in the Montado, which may explain why this species was dispersed at greater distances from the stream. Therefore, our data and those of previous studies suggest that higher fruit abundance in riparian galleries mainly influences the immediate surroundings, but further studies are needed to evaluate the role of songbirds in long distance dispersal. Because seed abundance in the riparian gallery appears to determine the seed dispersal of different plant species, it may be appropriate to manipulate the abundance of plant species to favor the dispersal of a given species of conservation concern.

In summary, riparian galleries are a fundamental structure for birds living in the interface between riparian galleries and adjacent matrices, by providing a high abundance of food resources and shelter for longer time periods. This is particularly important for bird species that are more common in the adjacent habitat, as they may move opportunistically to the riparian gallery to forage and will disperse seeds in the adjacent matrix as they leave. In our study, birds as dispersers of large amounts of seeds in the riparian gallery–Montado interface were a key factor promoting the complementarity between these Mediterranean habitats, and contributed to the improvement of landscape connectivity. Such connectivity among habitats deserves further study, detailing bird movements between adjacent habitats, and their importance for conservation.

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