Check for
updates

RESEARCH ARTICLE

Journal of Animal Ecology | BRITISH ECOLOGICAL SOCIETY

Frugivore species maintain their structural role in the trophic and spatial networks of seed dispersal interactions

Beatriz Rumeu[1] | **Isabel Donoso**[1,2] | **Javier Rodríguez-Pérez**[1,3] | **Daniel García**[1]

[1]Depto. de Biología de Organismos y Sistemas and Unidad Mixta de Investigación en Biodiversidad, Universidad de Oviedo, Oviedo, Spain

[2]Senckenberg Biodiversity Climate Research Centre (SBiK-F), Frankfurt (Main), Germany

[3]Department of Mathematics and its Applications, Université de Pau et des Pays de l'Adour, Pau, France

Correspondence
Beatriz Rumeu
Email: beatriz.rumeu@uca.es

Present address
Beatriz Rumeu, Departamento de Biología—IVAGRO, Universidad de Cádiz, Campus Río San Pedro, Puerto Real, 11510, Spain

Abstract

1. Trophic relationships have inherent spatial dimensions associated with the sites where species interactions, or their delayed effects, occur. Trophic networks among interacting species may thus be coupled with spatial networks linking species and habitats whereby animals connect patches across the landscape thanks to their high mobility. This trophic and spatial duality is especially inherent in processes like seed dispersal by animals, where frugivores consume fruit species and deposit seeds across habitats.

2. We analysed the frugivore–plant interactions and seed deposition patterns of a diverse assemblage of frugivores in a heterogeneous landscape in order to determine whether the roles of frugivores in network topology are correlated across trophic and spatial networks of seed dispersal.

3. We recorded fruit consumption and seed deposition by birds and mammals during 2 years in the Cantabrian Range (N Spain). We then constructed two networks of trophic (i.e. frugivore–plant) and spatial (i.e. frugivore–seed deposition habitat) interactions and estimated the contributions of each frugivore species to the network structure in terms of nestedness, modularity and complementary specialization. We tested whether the structural role of frugivore species was correlated across the trophic and spatial networks, and evaluated the influence of each frugivore abundance and body mass in that relationship.

4. Both the trophic and the spatial networks were modular and specialized. Trophic modules matched medium-sized birds with fleshy-fruited trees, and small bird and mammals with small-fruit trees and shrubs. Spatial modules associated birds with woody canopies, and mammals with open habitats. Frugivore species maintained their structural role across the trophic and spatial networks of seed dispersal, even after accounting for frugivore abundance and body mass.

5. The modularity found in our system points to complementarity between birds and mammals in the seed dispersal process, a fact that may trigger landscape-scale secondary succession. Our results open up the possibility of predicting the consumption pattern of a diverse frugivore community, and its ecological consequences, from the uneven distribution of fleshy-fruit resources in the landscape.

1 | INTRODUCTION

Trophic interactions involving animals modulate the structure of communities and the functioning of ecosystems (Bascompte & Jordano, 2007; Paine, 1980; Thompson et al., 2012). The complex food webs within which species interact have promoted the use of network theory to better understand ecological communities (e.g. Bascompte & Jordano, 2006; Poisot, Stouffer, & Kéfi, 2016; Proulx, Promislow, & Phillips, 2005). Basically, a trophic network represents interactions as links that reflect energy exchange between consumer and resource species. However, interactions occur within finite spatial extents, and animals move actively across habitats providing ecological functions (e.g. pollination, seed dispersal, nutrient translocation; González-Varo, Carvalho, Arroyo, & Jordano, 2017; Kremen et al., 2007; Polis, Anderson, & Holt, 1997). This means that interspecific interactions can be also envisioned as spatial, species-habitat networks where sites or habitat patches are nodes connected by animal species that move between them while foraging (Hagen et al., 2012; Loeuille, 2010; Thompson et al., 2012). Although the usefulness of networks for addressing the spatial dimension of species interactions has been previously recognized (Carlo, Aukema, & Morales, 2007; Hagen et al., 2012; Tylianakis & Morris, 2017), studies combining the analysis of trophic and of spatial networks are still scarce (but see González-Varo et al., 2017; Hackett et al., 2019; Timóteo, Correia, Rodríguez-Echeverría, Freitas, & Heleno, 2018).

The topological analysis of ecological networks has revealed non-random patterns that ultimately condition community stability and ecosystem functioning (Poisot, Mouquet, & Gravel, 2013; Rohr, Saavedra, & Bascompte, 2014; Thébault & Fontaine, 2010). Among these patterns are nestedness (i.e. when species interacting with specialists are a proper subset of species interacting with generalists), modularity (i.e. when species are organized into tightly linked semi-independent subsets or modules) and heterogeneity in generalism (i.e. when a few species are highly connected while many others are poorly connected; Bascompte & Jordano, 2007; Lewinsohn, Prado, Jordano, Bascompte, & Olesen, 2006; Martín González, Dalsgaard, & Olesen, 2010). Interestingly, different species may contribute differentially to network topology (e.g. Martín González et al., 2010). For instance, in a given trophic network, generalist taxa with broad diets will have a large number of links to prey species, which contributes to increase connectivity within the network (e.g. Dunne, Williams, & Martinez, 2002). Similarly, in spatial networks, a generalist species that moves freely throughout the landscape mosaics would contribute strongly to inter-habitat connectivity (Emer et al., 2018; González-Varo et al., 2017; Timóteo et al., 2018). Thus, the specific contribution of an animal to network structure at the trophic and spatial level will ultimately depend upon the way it moves and copes with landscape heterogeneity

(Hagen et al., 2012; Morales, García, Martínez, Rodriguez-Pérez, & Herrera, 2013; Morales & Vázquez, 2008), which in turn is strongly influenced by species traits. In this sense, body size is a key trait as large-bodied animals tend to have broader diets and larger home range sizes (Woodward et al., 2005). Abundance also strongly influences a species' contribution to networks (Poisot, Stouffer, & Gravel, 2015; Vázquez et al., 2007), affecting both interaction frequencies and habitat occupancy. However, regardless of the influence that species traits and abundance may have on network topology, it remains unclear whether animal species maintain their structural contribution across trophic and spatial networks.

Frugivore–plant interactions shape relevant trophic networks in terrestrial ecosystems (Jordano, 1987). These mutualistic networks have inherent spatial dimensions given that, first, frugivores must cope with spatially aggregated and unevenly distributed fruiting plants (López-Bao & González-Varo, 2011; Timóteo et al., 2018) and second, frugivores generate the spatial template of seed deposition (i.e. seed rain) that drives the regeneration dynamic of plants (Howe, 1989; Nathan & Muller-Landau, 2000; Schupp & Fuentes, 1995). Both spatial dimensions may be approached in heterogeneous landscapes, whose different habitat patches unevenly harbour frugivores that consume different plant species while also depositing seeds (Figure 1a). This scenario would result in distinct modules of interactions at both the trophic (i.e. frugivore–plant) and spatial (i.e. frugivore–seed deposition habitats) networks (Figure 1b). By identifying the specific role that frugivores have in these trophic and spatial networks (Figure 1b), we can evaluate whether a correlation exists in the structural roles of species across networks (Figure 1c). We would expect that animal species highly connected within trophic and spatial modules might act as 'habitat shapers', that is they will strongly influence their habitat composition and structure by recurrently dispersing, within their home ranges, the plants that match their preferences (Herrera, 1985). In contrast, generalist species in both networks would foster connectivity among vegetation patches, improving plant meta-community dynamics and vegetation resilience (Carlo & Morales, 2016; Emer et al., 2018; Timóteo et al., 2018). Finally, in modular networks, frugivore species will be distributed in different units of frequent trophic and spatial interactions. This compartmentalization would reflect the fact that different frugivores feed complementarily on different resources, and deposit seeds on different sites (García, Donoso, & Rodríguez-Pérez, 2018; Mello et al., 2011; Peredo, Martínez, Rodríguez-Pérez, & García, 2013).

Here, we investigate whether the structural roles of frugivore species are correlated across the trophic and spatial networks by characterizing the frugivore–plant interactions and the seed deposition patterns of a diverse assemblage of frugivores. Our study system involved frugivorous birds and mammals, and a highly
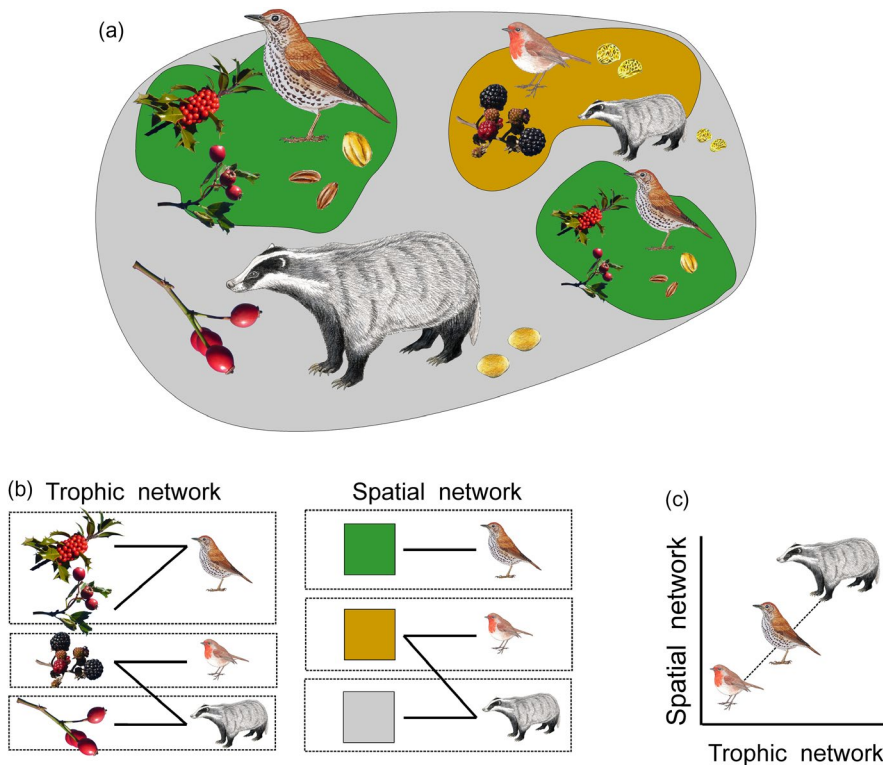
FIGURE 1 (a) Representation of vertebrate frugivore species interacting with fleshy-fruited plant species and depositing their seeds across different habitat patches (different coloured areas) in a given heterogeneous landscape. (b) Trophic (frugivore–plant) and spatial (frugivore–habitat) networks, with unitary links (continuous lines) and modules (discontinuous boxes) identified. (c) The values of the specific contribution to the structure (e.g. modularity) of both trophic and spatial networks may be correlated across frugivore species. Artwork: Daniel García (animals and fruits) and Víctor González (seeds)

heterogeneous landscape in the Cantabrian Range (North Spain). Specifically, we seek to: (a) estimate the specific contribution of frugivores to non-random patterns of nestedness, modularity and complementary specialization, in both the trophic and the spatial network; (b) test whether the role of the frugivore species in the trophic network relates to their contribution to the spatial network of seed deposition; and (c) determine the influence of the abundance and body mass of each frugivore on this potential relationship. We hypothesize that due to the natural association between sites where frugivores spend time foraging and sites where seeds are deposited, the topological role of the different frugivores in the trophic and the spatial network will be linked, which ultimately translates into determinant effects for plant regeneration dynamics.

2 | MATERIALS AND METHODS

2.1 | Study design

This study was conducted in mid-elevation woodland pastures of the Cantabrian Range in northern Spain (see Appendix S1 for more details). The area represents a fragmented landscape containing variable-sized patches of primary and secondary forest, embedded in an extensive open matrix of meadows, heathland and rocky outcrops (Figure S1a). The secondary forest is dominated by fleshy-fruited trees (e.g. hawthorn *Crataegus monogyna*, holly *Ilex aquifolium*) and shrubs (e.g. blackberry *Rubus fruticosus/ulmifolius* and blackthorn *Prunus spinosa*). Fleshy-fruited shrubs also occasionally occur in heathland patches. The main frugivores are birds (passerines; García, 2016) and mammals (carnivores and ungulates; Peredo

et al., 2013). Of the birds, most species (e.g. thrushes, warblers) perform as legitimate seed dispersers (i.e. they swallow entire fruits and deposit intact seeds through regurgitation or defecation), although some are pulp eaters and seed predators. These latter species have a negligible contribution to the seed rain (Simmons et al., 2018), so we used a conservative approach and focused exclusively on observations of legitimate seed dispersers. In the case of mammals, all species considered here as frugivores were found to disperse intact seeds in their faeces (Peredo et al., 2013).

In August 2012, we delimited fourteen 150 m × 150 m plots in two sites in Asturias Province, N Spain (Table S1; see details in García et al., 2018). All plots had similar vegetation types (forest stands embedded in a matrix of pastures and heathland), geomorphology (slope ≤ 25%, limestone substrate, altitude 990–1,250 m a.s.l.) and anthropic management (extensive livestock raising), but were chosen to incorporate a wide range of relative cover of different habitat types (primary and secondary forest, meadows, heathland, rocky outcrops availability; Figure S1a). Sampling was conducted across two consecutive annual fruit production and seed dispersal events, from September to March in both 2012–2013 and 2013–2014.

2.2 | Frugivory and seed dispersal by birds

We monitored the abundance of frugivorous birds by means of point-count censuses, carried out consecutively at nine census points regularly distributed within each plot. To facilitate bird recording from these census points, each plot was subdivided into 36 cells measuring 25 m × 25 m, each census point being in the centre of a set of four adjacent cells (Figure S1b). All plots were sampled

in 4 days (three to four plots per day) and using different access points to the study area. Censuses were performed from 09:00 to 15:00 in consecutive days, as long as the weather conditions were favourable (days of heavy rain and wind were avoided). In each census, all birds heard or seen within the set of four cells over a 5-min period were registered. For each bird encounter, we recorded the fine-scale habitat where the bird was perching by distinguishing between fleshy-fruited tree (e.g. *C. monogyna*), non-fleshy-fruited tree (e.g. hazel *Corylus avellana*), fleshy-fruited shrub (e.g. *R. fruticosus/ulmifolius*), heather (e.g. *Erica tetralix*), pasture (meadow) and rock (limestone rocks and stony outcrops). These fine-scale habitats vary in important features for the post-dispersal fate of seeds, such as moisture, insolation or seed predation. In each plot, bird records were summed across census points and eight (nine in 2013–2014) census rounds were performed per sampling year and plot (1–2 censuses/month from September to February). We estimated the abundance of frugivore species as the proportion of each species' occurrence relative to the total number of plot-based observation events ($N = 238$; 17 rounds × 14 plots).

Fruit consumption by birds was recorded in 17 rounds of 1-hr-per-plot observations from September to February: eight rounds in 2012–2013 and nine in 2013–2014, carried out in slots independent of those of bird censuses. In each round, a given observer visited three to four vantage points (Figure S1b), chosen to ensure that the full extent of the plot was covered (i.e. included the nine bird census points) as well as to be able to focus on all of the different fruiting species present in the plot. Observers recorded every fruit consumption event (i.e. an individual bird consuming fruits) and every feeding bout (i.e. a single bird swallowing a single fruit) detected during the observation round.

Avian seed dispersal was studied by identifying and counting the seeds deposited by frugivores, after regurgitation or defecation, during autumn and winter. This was based on data from seed rain sampling stations distributed in a grid scheme across each entire plot (108 stations per plot; Figure S1b) and using three types of devices for seed collection in the different habitats: hanging plastic pots where there was tree cover (fleshy-fruited tree and non-fleshy-fruited tree), plastic trays under shrub cover (fleshy-fruited shrub) and flag-labelled quadrats on the ground for open areas (heather, pasture and rock). Surfaces of the different seed traps were 0.07, 0.08 and 0.10 m^2 for pots, trays and open quadrats, respectively. All stations were set up in August 2012, just before the monitoring period. Hanging plastic pots and trays were designed with holes to allow the drainage of rainwater, and covered by a wire mesh to protect seeds from predation by small mammals (seed removal by ants is extremely occasional in our systems due to the big size of seeds and the low richness of ants). Seed traps were checked and seeds collected at the end of the seed dispersal season (February–March of 2013 and 2014), except for open quadrats, which were checked in late November and late February of 2012–2013 and 2013–2014. The probability of a seed being deposited in open quadrats is lower than in traps located below bird perches (trees and shrubs), so by checking them twice during the seed dispersal season we assumed that

we applied a sampling effort big enough to detect seed arrival. Seed losses due to predation in these open areas can be considered negligible, as rodents avoid this sort of fine-scale habitat (Garcia, Obeso, & Martinez, 2005; García, Obeso, & Martínez, 2005). Collected samples were oven-dried for 1 week at 60°C for laboratory storage, and then examined under a magnifying glass in order to identify and count all seeds present. Seed species were identified from external morphology by comparison with a seed reference collection from the study area and available literature (Torroba Balmori, Zaldívar García, & Hernández Lázaro, 2013). The density of seeds (seeds/m^2) deposited by birds at each sampling station was estimated according to the area of the different types of seed traps.

2.3 | Seed dispersal by mammals

We monitored the occurrence of mammal scats along two sampling transects in each plot. A main transect (750 m × 1.5 m) was set up to zigzag across the whole extent of each plot (Figure S1c). In order to increase the probability of detecting scats (see López-Bao & González-Varo, 2011), an additional transect of 350–500 × 1.5 m, crossing the plot and following cattle paths, was also established (Figure S1c). Both transects were walked for scat collection in eight (nine in 2013–2014) rounds per sampling year and plot (one to two rounds/month from September to February). Every individual scat (for ungulates this was taken to be all pellet clumps separated from each other by at least 2 m) was collected and identified at the species level (genus in *Martes* spp., *Mustela* spp. and *Canis* spp.) using criteria that combined size, shape and scent. We also recorded the fine-scale habitat where (or under which) the scat was deposited (i.e. fleshy-fruited tree, non-fleshy-fruited tree, fleshy-fruited shrub, heather, pasture or rock). Scats were oven-dried at 60°C for 1 week and then washed in a sieve for seed collection. All undamaged seeds from fleshy-fruited plants were counted and identified at the species level. Based on the presence of scats, we registered the occurrence of the different species of frugivorous mammals across plots. We thus estimated the abundance of mammal species as the proportion of the occurrence of each species relative to the total number of plot-based observation events ($N = 238$; 17 rounds × 14 plots).

2.4 | Trophic and spatial seed dispersal networks

In order to obtain a trophic network representing interactions between frugivores and plants, we built a matrix with the number of seeds from the different fleshy-fruited plant species dispersed by each species of frugivorous vertebrate (birds and mammals) and pooling the information from the fourteen study plots (Table S4; Figure S2). In the case of birds, the number of dispersed seeds was estimated by multiplying the number of fruits consumed (based on cumulative observations of fruit consumption across all plots and years) by the average number of seeds per fruit (García et al., 2018). In the case of mammals, we directly obtained the number of

undamaged seeds dispersed from the scats, also pooling the data across all transects and years. The estimates of the number of seeds dispersed by birds and mammals use different methodologies. Thus, to make them comparable, we first calculated, for both birds and mammals, the number of dispersed seeds per unit area of seed sampling. In the case of birds, seed traps provided a total sampling area of 131.0 m^2, rendering a number of dispersed seeds per area unit of 368.9 seeds/m^2. In the case of mammals, considering a total sampling area of 24,300 m^2 (the summed area of all transects across plots), this number reached 5.2 seeds/m^2. Thus, these values gave a bird:mammal ratio of 70.9:1 for the number of dispersed seeds per m^2. Although the bird relevance in this ratio might seem too high, we assume that the high detectability of mammal scats through the transect method (due to its size and durability in relation to the sampling frequency) largely compensates for a possible underestimation of seed deposition compared to birds (whose droppings were detected by passive traps). Our final matrix of seeds dispersed per frugivore and plant species included a total number of bird-dispersed seeds previously extrapolated from the total number of mammal-dispersed seeds, using the above-mentioned ratio (Figure S2).

We sought to construct a spatial network representing the deposition of seeds by frugivore species in the different fine-scale habitats (i.e. fleshy-fruited tree, non-fleshy-fruited tree, fleshy-fruited shrub, heather, pasture or rock.). Thus, we built a matrix of the number of seeds dispersed per frugivore species and fine-scale habitat (Table S5; Figure S2). For mammals, these numbers emerged directly from the counting of seeds in scats whose deposition habitat had been registered, pooling the data across all transects and years. In the case of birds, as we were unable to identify the frugivore species directly from the seeds dropped in a given habitat, we estimated the deposition habitat from perching behaviour recorded during censuses. Thus, we first built a matrix based on the frequency of perching of different bird species in the different fine-scale habitats, pooling data across all plots and years. Using only perching frequencies may overestimate the contribution to seed deposition of abundant but weakly frugivore species across all habitats. Therefore, we weighted bird perching frequencies using a specific seed dispersal rate, calculated as the proportion of seeds dispersed by each bird species in the trophic interaction matrix. Once bird- and mammal-habitat matrices were obtained, we built a final matrix of seeds dispersed per frugivore and deposition habitat by including a total number of seeds dispersed by birds previously extrapolated from the total number of seeds dispersed by mammals on the basis of the previously mentioned bird:mammal ratio (70.9:1; Figure S2).

2.5 | Data analysis

In order to evaluate the specific contribution of frugivores to the structure of both the trophic and the spatial network, we first looked for global patterns of network modularity (M), nestedness (WNODF) and complementary specialization (H_2'), the latter being a measure of how much the interactions of each node differ from the others

in the network (Blüthgen, Menzel, & Blüthgen, 2006). Network parameters were calculated using the BIPARTITE package version 2.11 (Dormann, Fründ, Blüthgen, & Gruber, 2009) and ran in R 3.5.2. (R Development Core Team, 2015). Modularity was computed using the LPAwb+ algorithm (Beckett, 2016). Due to its stochastic nature, we ran the LPAwb+ algorithm 1,000 times for each modularity calculation. The significance level of the network parameters was tested against 1,000 networks generated by the null model r2dtable (function nullmodel in BIPARTITE) based on the Patefield algorithm (Patefield, 1981), and using z-score tests. This algorithm creates null models (matrices) with marginal totals identical to those of the observed network, although they may contain more links and thus be less sparse than the observed (Dormann et al., 2009). We also tested the significance for nestedness by using three different null models (CRT, conserve row totals; CCT, conserve column totals and RCTA, row column total average), implemented in FALCON (Beckett, Boulton, & Williams, 2014).

The individual role of a species in network modularity can be assessed through the standardized within-module degree (z), which is a measure of the extent to which each species is connected within its module, and the participation coefficient or among-module connectivity (c), which describes how evenly distributed the interactions of a given species are across modules (Guimerà & Amaral, 2005; Olesen, Bascompte, Dupont, & Jordano, 2007). After confirming significant modularity in both the trophic and the spatial network (see Section 3), nonlinear (Spearman) Mantel tests based on binary-Jaccard distance matrices were used to evaluate whether the two networks where correlated in terms of frugivore composition within their modules. We then computed weighted z- and c-scores for each frugivore species through the function czvalues in BIPARTITE.

Since nestedness presented a non-random pattern only for the trophic network (see Section 3), we ruled out any more in-depth analysis to disentangle the specific contribution of frugivores to this pattern. Nevertheless, we found significant values in their degree of complementary specialization (see Section 3). Thus, the specific level of generalization of frugivores regarding plants and deposition habitats was also measured by means of two indices: (a) the normalized degree (ND) of each species, which is the proportion of partners (plants or fine-scale habitats) a given frugivore interacts with out of the total number of possible partners in the network, and (b) its specialization (d'), which quantifies the extent to which a species deviates from a random sampling of its available interaction partners (Blüthgen et al., 2006). These metrics were also calculated using the BIPARTITE package.

In order to test whether the most important frugivores in terms of structuring the frugivore–plant assemblage were also the most important in depicting the spatial organization of the seed rain, we performed Spearman correlations of their z, c, ND and d' values across the trophic and the spatial network. The level of modularity and generalism in mutualistic interactions and habitat use may be strongly influenced by species abundance (e.g. Fort, Vázquez, & Lan, 2016; García, Martínez, Stouffer, & Tylianakis, 2014; Simmons et al., 2019) and body size (e.g. García et al., 2014; Palacio, Valderrama-Ardila, & Kattan, 2016; Wheelwright, 1985). We thus fitted four independent

piecewise structural equation models (SEMs; package PIECEWISESEM, Lefcheck, 2016) to infer the effects of frugivore abundance and body mass (Table S2) on the relationships between z, c, ND and d' across the trophic and the spatial network. Body mass data (as a proxy for body size) were obtained from Wilman et al. (2014). The piecewise *SEM* approach allowed us to deal with complex multivariate relationships among a set of interrelated variables but, in contrast to the classic *SEM* approach, to fit GLMs considering non-Gaussian error distributions in response variables (see Table S6 for model specifications). We specified correlated error structures between z, c, ND and d' of each frugivore species in both networks. The four SEMs were fully saturated models (there were no missing paths), so goodness-of-fit could not be calculated.

3 | RESULTS

We recorded a total of 18 frugivore species (six species of thrushes, four other birds, five carnivores and three ungulates; see Figure 2;

Table S2) dispersing seeds of 11 plant species (Tables S3 and S4) over six fine-scale habitats: fleshy-fruited tree, non-fleshy-fruited tree, fleshy-fruited shrub, heather, pasture and rock (Table S5). The proportion of all possible interactions that were actually observed (i.e. connectance) was 0.44 and 0.57 in the trophic and the spatial network, respectively. On average, each frugivore species interacted with 4.8 plant species and deposited seeds in 3.4 of the six habitats. Only the trophic network was significantly nested (CRT null model; Table 1; Figure S3), so we ruled out any further exploration of the specific role of frugivores to this pattern in both the trophic and spatial networks. However, modularity (M) and complementary specialization (H_2') showed a non-random pattern of interactions in both assemblages (Table 1). The trophic network was compartmented into four modules: three of which were composed only by thrushes (*Turdus* spp), while the remaining module comprised all the mammals and the four bird species that were not thrushes (*Garrulus glandarius*, *Erithacus rubecula*, *Sylvia atricapilla* and *Phylloscopus collybita*; Figure 2a). Notably, *Turdus iliacus* and the holly *Ilex aquifolium* formed a single module. The spatial
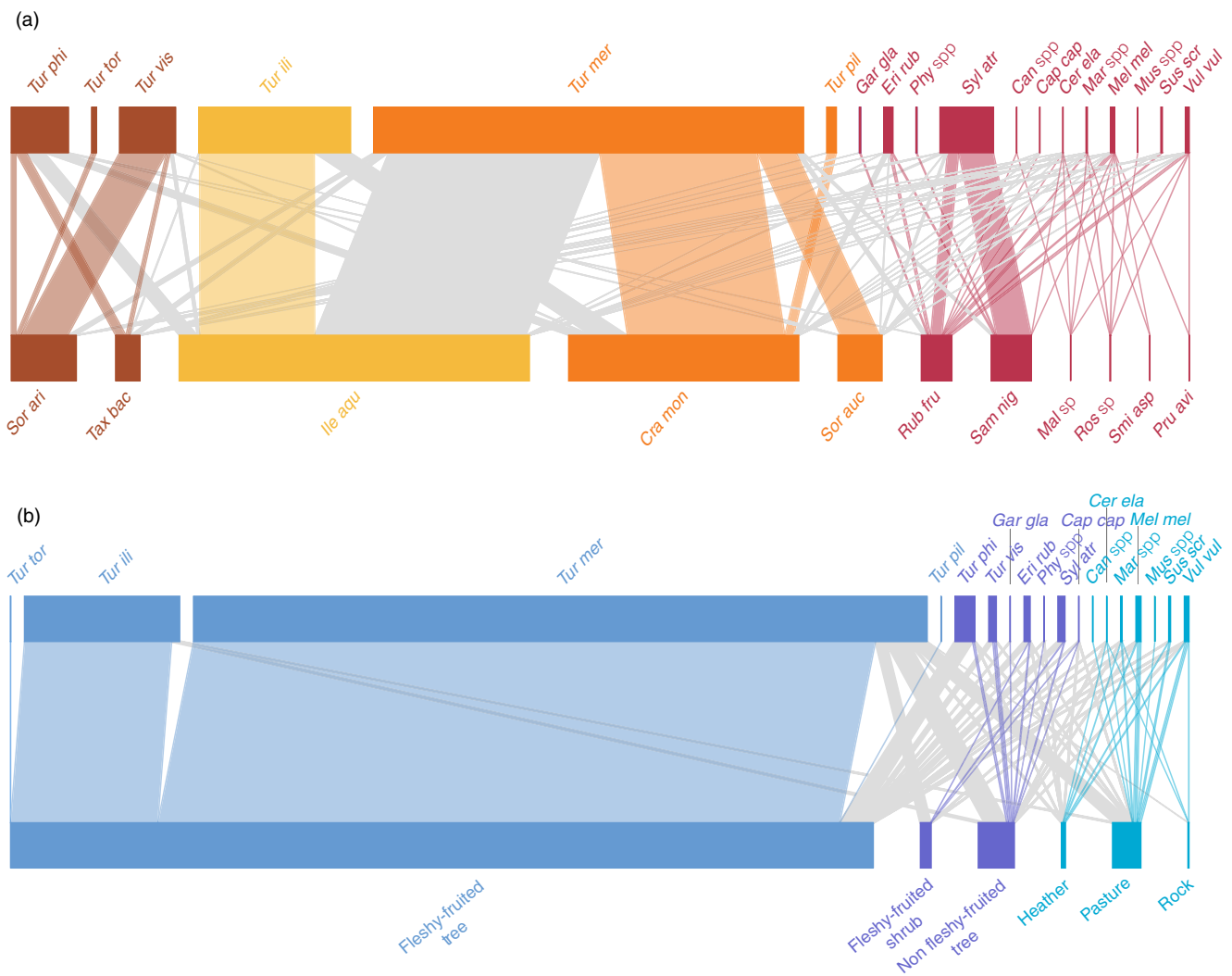

FIGURE 2 Both the trophic (a) and the spatial (b) networks were significantly compartmented in modules (i.e. subsets of partners interacting preferentially which each other). Different colours denote distinct modules, while grey links show the interactions that connect modules. Species codes are based on abbreviated scientific names (see Tables S2 and S3 for codes of frugivores and fleshy-fruited plants, respectively)

TABLE 1 Descriptors of the trophic and spatial networks of seed dispersal interactions. Numbers in bold denote significance (i.e. non-random patterns) based on 1,000 replicate null model runs, and using a z-score test. $|z| > 1.64$ indicate significance at $p = 0.05$. We show the levels of statistical significance for nestedness under the CRT null model, the only one under which the trophic network was nested (see also Figure S3)

Descriptor	Trophic network	Spatial network
Modularity (M)	**0.27** ($z = 13,648.97$)	**0.03** ($z = 2,338.17$)
No. of modules	4	3
Nestedness ($WNODF$)	**37.22** ($p = 0.04$)	49.63 ($p > 0.05$)
Specialization (H_2')	**0.43** ($z = 474,646.80$)	**0.17** ($z = 66,939.10$)

network on the other hand was compartmented into three modules. All mammal species but the European roe deer *Capreolus capreolus* clustered together in one, denoting that seed deposition by mammals occurred predominantly across open habitats (heather, pasture and rock; Figure 2b). By contrast, birds, which were subdivided into two modules, deposited seeds mainly under tree and shrub canopies (Figure 2b). Our Mantel test comparing the rank-order distance of the frugivore composition within modules between the trophic and the spatial network (see Figure 2) indicated that those frugivore species that tend to consume fruits of the same species also tend to deposit seeds in the same habitats ($r = 0.312$, $p < 0.01$).

The species values of the four metrics measuring frugivore contribution to the structure of the trophic network (z, c, ND and d') were
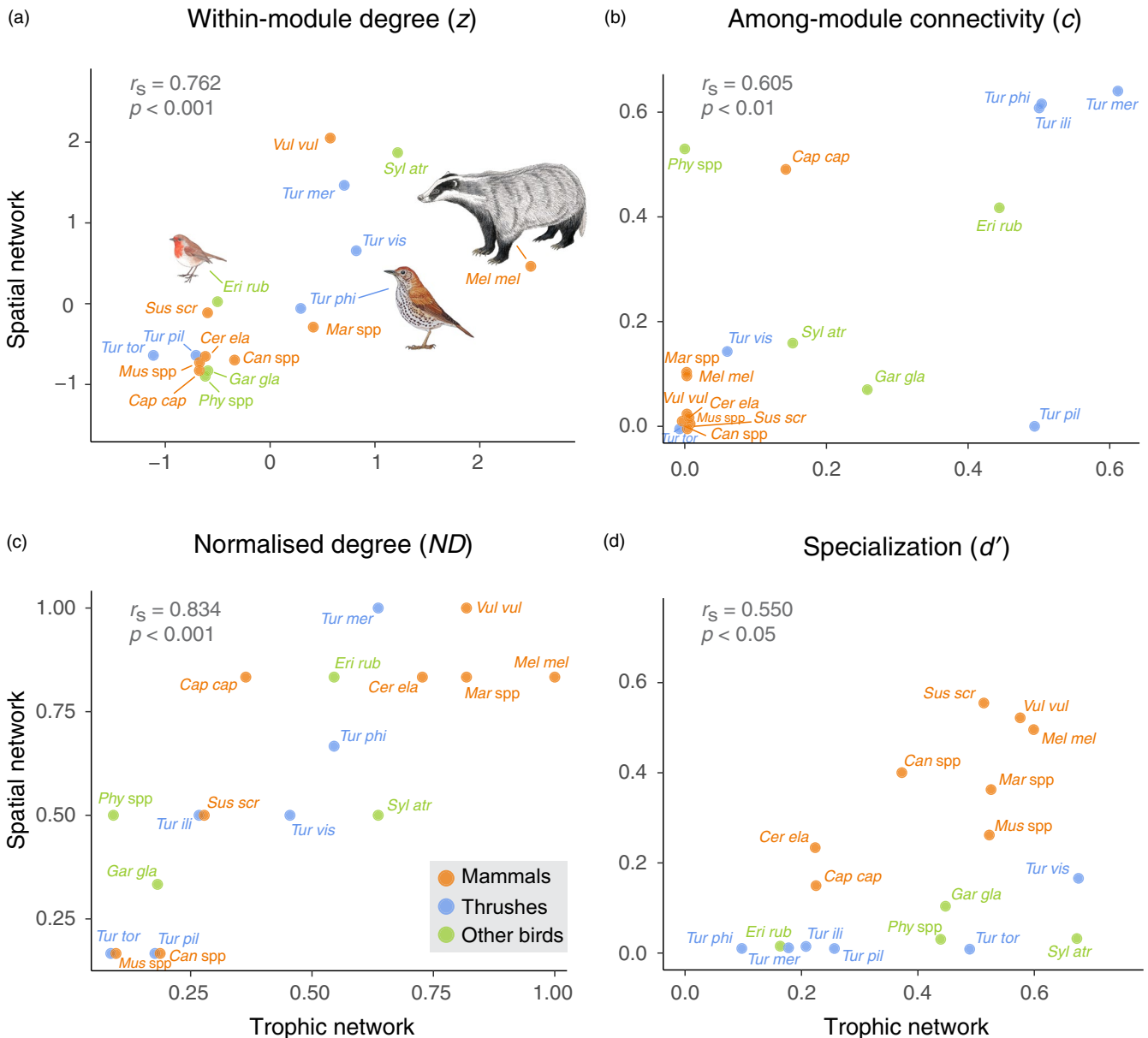
FIGURE 3 Positive relationships between the specific contributions of frugivores to the structure of the trophic and the spatial networks of seed dispersal. (a) Within-module degree (z); (b) among-module connectivity (c); (c) normalized degree (ND); (d) specialization (d'). The colours of the dots indicate different functional groups: orange, mammals; blue, thrushes; green, other birds. Artwork: Daniel García

positively correlated with those of the spatial network ($p < 0.05$ in all cases, Figure 3). This result indicates that more generalist species in terms of fruit consumption deposited seeds in a wider variety of habitats. Birds like *S. atricapilla* and *T. merula* played a relevant role as generalist within their modules (Figure 3a), whereas the most important species for among-module connectivity were thrushes like *T. philomelos*, *T. iliacus* and again *T. merula* (Figure 3b). Mammal species such as *Vulpes vulpes*, *Meles meles* and *Martes* sp. stood out as important generalist species in both networks (see *ND* values, Figure 3c). However, it is notably that these species also showed strong preferences for fleshy-fruited shrubs like *Rubus fruticosus* and open habitats like pastures, which explain their high values of *d'* (Figure 3d).

The piecewise SEMs revealed that, except for the among-module connectivity (*c*), the strong associations of frugivores' contributions to *z*, *ND* and *d'* between trophic and spatial networks clearly remain irrespective of the influence of frugivores' abundance or body mass (Figure 4). This was evidenced by the correlated error structures between the trophic and the spatial metrics, which were statistically significant and positive for *z*, *ND* and *d'* (Figure 4; Table S7). Even so, the influence of frugivores' abundance and body mass on their contribution to both networks was important in some cases. Thus, frugivore abundance was positively correlated with *c* and *ND* (Figure 4b and 4c; Table S7), but it had a negative effect on *d'* (Figure 4d; Table S7) both in the trophic and the spatial network ($p < 0.05$ in both cases). In contrast, body mass had a negative effect on *c* values
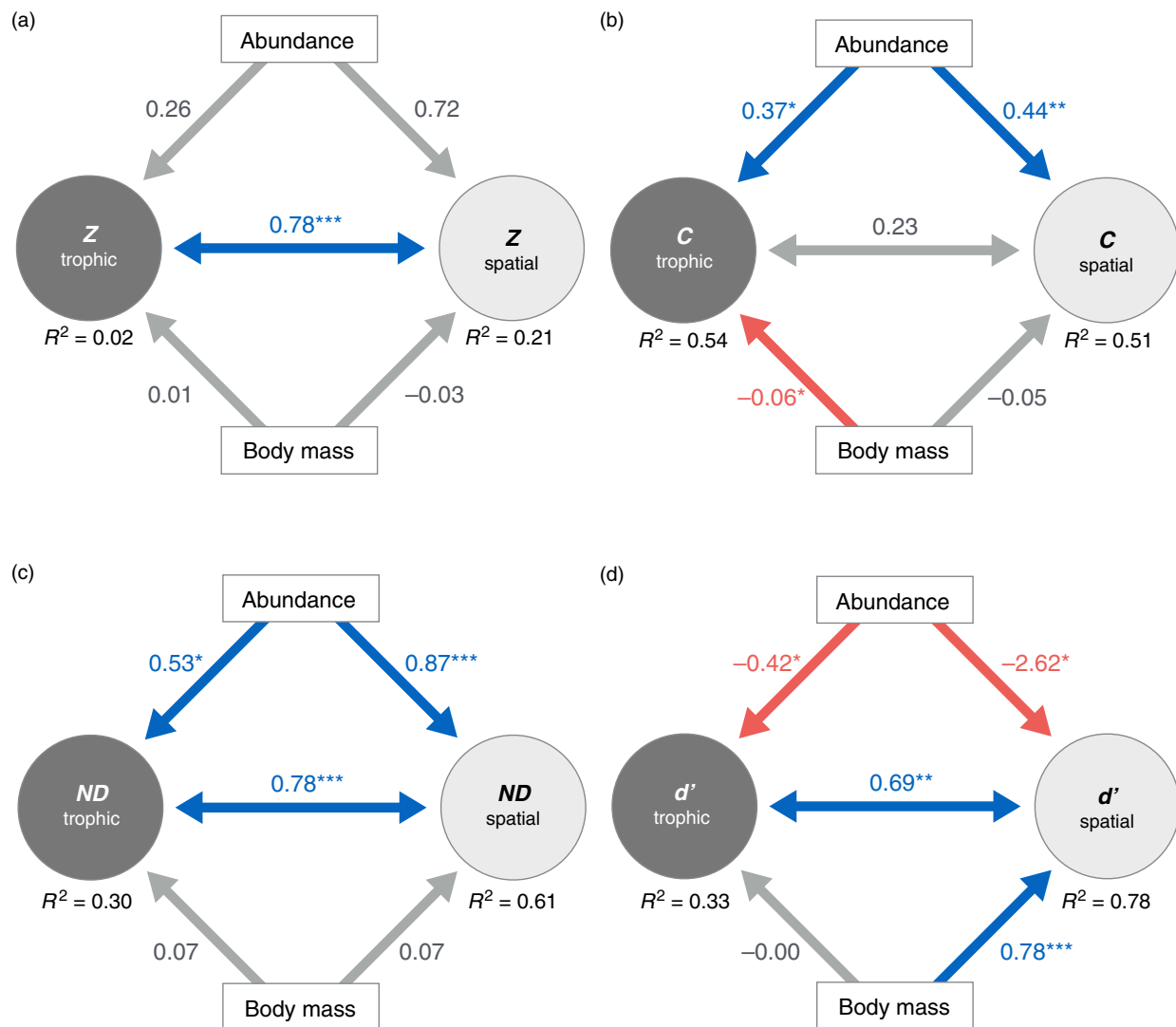
FIGURE 4 Piecewise structural equation models (piecewise SEMs) that include abundance and body mass as predictors of frugivores' contributions to the structure of both the trophic and the spatial networks taking into account: (a) within-module degree (*z*); (b) among-module connectivity (*c*); (c) normalized degree (*ND*) and (d) specialization (*d'*). Dark- and light-grey circles denote metrics for the trophic and spatial network respectively. Single-headed arrows represent directional relationships and double-headed arrows represent correlated errors. Blue arrows represent positive paths ($p < 0.05$), red arrows represent negative paths ($p < 0.05$) and grey arrows represent non-significant paths ($p > 0.05$). Values are the raw regression coefficients assigned to paths. *$p < 0.05$; **$p < 0.01$; and ***$p < 0.001$. R^2 values are given for each predicted variable

of the trophic network ($p < 0.05$; Figure 4b; Table S7), and a strong positive effect on d' values of the spatial assemblage ($p < 0.001$; Figure 4d; Table S7).

4 | DISCUSSION

In spite of the importance that the spatial dimension has in shaping seed dispersal interactions (Carlo et al., 2007; Hagen et al., 2012), to date trophic and spatial networks have been studied separately (e.g. Donatti et al., 2011; García-Cervigón et al., 2018; Timóteo et al., 2018). Here, we introduce for the first time a simultaneous analysis of networks of fruit consumption (trophic network) and seed deposition (spatial network) that emerge from a diverse plant–frugivore assemblage that operates in a heterogeneous landscape. We found that frugivore species maintain their topological role from the network of trophic interactions with the fleshy-fruited plants they consume into the network of habitats where they disperse plant seeds. Furthermore, except for the frugivores' contribution to the connectance of distinct network modules, the positive relationships of the roles played by the different species between trophic and spatial networks were maintained even after controlling for their abundance and body mass. Thus, our findings indicate a link between frugivore diet and the spatial outcomes of seed dispersal, shaped by the uneven activity and preferences of the animal species involved as they move and interact with plant species across patchy landscapes. This would lead to different plant species being more likely deposited into certain microhabitats, because different frugivore species have previously consumed them. In contrast, it explains that when we represent the role of frugivore species in the trophic and spatial networks, these roles match, because global topologies are maintained.

4.1 | Contribution of frugivore species to the structure of trophic and spatial networks

Theory on mutualistic networks predicts a non-random organization of animal–plant interactions (Bascompte & Jordano, 2014). Accordingly, trophic and spatial interactions in the two networks studied were heterogeneous, being nested in the trophic network and highly modular in both cases. In seed dispersal networks, heterogeneity emerges from the co-occurrence of generalist and specialist species (García, 2016). Here, frugivore species maintain this heterogeneity of interactions across both trophic and spatial networks. For instance, species with broad diets (high values of *trophic ND*) such as *M. meles*, *V. vulpes* and *T. merula*, also deposited seeds in a wide variety of habitats (high values of *spatial ND*; Figures 2 and 3c). This trophic and spatial generalism has been also found in insect communities, where the use of different habitats foster the consumption of a wide variety of resources (Hackett et al., 2019). Simultaneously, frugivores such as *T. torquatus* or *T. pilaris* that consumed few plant species only used one kind of habitat for seed deposition (Figures 2

and 3c). On the other hand, network modularity may reflect species segregation in habitat occupancy or foraging behaviour, as well as the phylogenetic clustering of related species (e.g. Donatti et al., 2011; Mello et al., 2011; Nogales et al., 2015). In this sense, we found species such as *S. atricapilla* and *T. merula* with high contributions to trophic and spatial modules (Figure 3a). In contrast, three species of thrushes (*T. merula*, *T. philomelos* and *T. iliacus*) stood out as connectors among modules of both networks (Figure 3b), playing an important role in bridging vegetation patches and fostering the expansion of some plant species towards new areas suitable for establishment.

Species abundance and body size are two major drivers of species performance in ecological networks (Poisot et al., 2015; Vázquez et al., 2007; Woodward et al., 2005). In line with this, we found a positive effect of species' abundance on its role as module connectors (*c*; Figure 4b) and normalized degree (*ND*; Figure 4c) in both the trophic and the spatial network. In addition, species abundance negatively affected the species specialization level (*d'*; Figure 4d), suggesting that the more abundant the frugivore, the more generalized are its trophic interactions, as would be expected in a neutral scenario (Fort et al., 2016). Here, we also stress that abundance might drive habitat generalization in seed deposition, although more research would be needed to uncover the underlying mechanism of this effect. Strikingly, we found a positive influence of body mass on the species specialization level (*d'*) of the spatial network, indicating that the largest frugivores were the most specialized in relation to habitat use. This result might be driven by the preference of mammals for using open sites like pasture and rocks for seed deposition (Jordano, García, Godoy, & García-Castaño, 2007; Martínez, García, & Obeso, 2008; Peredo et al., 2013), despite feeding preferably on fleshy-fruited shrubs. Body mass negatively influenced the among-module connectance of the trophic network (Figure 4b), which may be a consequence of bird species moving and feeding easily on all kind of fleshy-fruited species (trees and shrubs), whereas larger mammals feed preferably on fleshy-fruited shrubs that are more accessible to them. Nevertheless, even when taking into account the influence of abundance and body mass, the correlation of species structural roles between trophic and spatial networks was maintained (Figure 4) with one exception, namely the among-module connectivity, which seems to be strongly influenced by frugivore abundance (Figure 4b). This outcome suggests inherent links between the provisioning and spatial behaviours of the different frugivores. For example, thrushes concentrate their activity on habitat patches rich in fruit resources, resulting in seed deposition being heavily concentrated in these patches (García & Ortiz-Pulido, 2004; Jordano, 1993; Morales et al., 2013). Similarly, the omnivorous diet of carnivores (e.g. badger and fox) fits well with coarse-grain habitat use that promotes deposition on landscape-dominant open areas (López-Bao & González-Varo, 2011). Thus, the interplay between the life-history behavioural traits of species and landscape properties seems to play a crucial role in the conservatism of the structural role of frugivores in trophic and spatial networks.

4.2 | Ecological consequences of frugivore role in trophic and spatial networks

Heterogeneous landscapes harbour habitat mosaics that may be structured in different ways. In the Cantabrian Range, forest patches group fleshy- and non-fleshy-fruited trees, whereas open patches combine heather, pastures and rocks. This habitat mosaic constitutes the template for a seed dispersal process that, as shown here, can be organized into well-defined modules of fruit consumption and seed deposition. The species' role conservatism across trophic and spatial networks (Figure 3) opens up the possibility of predicting the consumption pattern of a frugivore assemblage, and its ecological consequences, from the uneven distribution of fleshy-fruit resources within the landscape. In this sense, the influence of frugivorous birds in plant spatial dynamics has been long recognized (González-Castro, Yang, & Carlo, 2019; Howe, 1989; Nathan & Muller-Landau, 2000; Schupp & Fuentes, 1995), including their role in 'habitat shaping', that is the modification and maintenance of the frugivores' own habitats (Herrera, 1985). In accordance with this, we found bird species, like *T. iliacus*, that predominantly consumed fruits from tree species and preferably deposited seeds in forest patches and, in contrast, mammal species like *M. meles* that mainly dispersed seeds from shrubs in open patches (Figure 2). Species highly connected within modules, like blackcap *S. atricapilla* or red fox *V. vulpes* (Figure 3a), also stand out as habitat shapers, fostering a spatial positive feedback between adult plants and their recruitment by recurrently depositing seeds in sites where parent plants are found and their fruits are preferably consumed (Aukema & Martínez del Rio, 2002; García, Rodríguez-Cabal, & Amico, 2009).

In a modular trophic system, species may be functionally redundant within a module but complementary between modules (Mello et al., 2011; Montoya, Yallop, & Memmott, 2015). As such, our study system points to complementarity between frugivore functional groups: birds (mainly thrushes) mostly consumed tree fruits (e.g. holly *I. aquifolium*, hawthorn *C. monogyna*) and deposited seeds under tree and shrub canopies, whereas mammals mostly dispersed fleshy-fruited shrubs (e.g. bramble *R. fruticosus*, wild rose *Rosa* sp.) in open habitats such as pastures, rocks and heather (Figure 2). This pattern was also supported by the positive correlation of the species composition of modules between the trophic and the spatial network. In other words, species feeding on the same fruit resources also tended to deposit seeds in the same habitats and, at the community-level, are complemented by other frugivore groups. At the landscape scale, this compartmentalization will have consequences for vegetation dynamics, since different disperser guilds can generate an enriched seed rain that increases the probability of finding optimal recruitment sites for different plant species (Morán-López, González-Castro, Morales, & Nogales, 2019). In fact, pioneer shrubs dispersed by mammals and recruited into open or degraded habitats can modify the under-canopy environment (Filazzola & Lortie, 2014) and provide favourable conditions for later establishment of trees dispersed by

birds (e.g. García, Zamora, Hódar, Gómez, & Castro, 2000; Gómez-Aparicio, Valladares, Zamora, & Luis Quero, 2005). Thus, in the present system, despite mammals being quantitatively poor seed dispersers compared to birds (seed deposition of 5.2 vs. 131.0 seeds/m^2), they seem to play a crucial role in triggering the secondary succession of vegetation.

The high abundance of *T. merula*, *T. philomelos* and *T. iliacus* seems to drive the dual role they play as trophic as well as spatial connectors (Figure 4b). We assume that these connector and generalized species act as mobile links (sensu Lundberg & Moberg, 2003), making large contributions to the global cohesion of the community (e.g. Martín González et al., 2010; Palacio et al., 2016). Further studies should explicitly investigate the connections between patches that are forged by these species through measurements of how individual seed dispersers actually cross habitat boundaries (e.g. Gómez, 2003; González-Varo et al., 2017; Vélez, Silva, Pizo, & Galetto, 2015).

5 | CONCLUSIONS

Understanding how species interact and drive ecological processes across space is crucial given the current scenario of worldwide habitat fragmentation. In fact, the movement of frugivores between patches of plant resources may determine the landscape-scale persistence of ecosystem functions (see Loreau, Mouquet, & Gonzalez, 2003). By jointly considering the trophic and the spatial role of frugivores in seed dispersal networks, we reveal the potential of frugivore species to shape vegetation structure and to maintain landscape connectivity. Our results also illustrate how a compartmentalized assemblage of complementary seed dispersers may shape secondary succession. The type of system studied here, with different groups of vertebrate seed dispersers sharing a landscape of contrasted habitat patches in various successional stages is representative of many human-impacted temperate and tropical regions (McConkey et al., 2012). We assumed, therefore, that the spatial dimension of plant–animal interactions evidenced here is generalizable to other terrestrial ecosystems, and encourage further exploration of the interplay between trophic and spatial networks in order to better understand how mobile species provide ecosystem functions within multispecies assemblages and heterogeneous landscapes.

AUTHORS' CONTRIBUTIONS

D.G. and B.R. conceived and designed the study, and wrote the manuscript; D.G., J.R.-P. and I.D. collected field data; B.R. performed the analyses; all the authors revised the manuscript and approved the final version.

DATA AVAILABILITY STATEMENT

The data used in this study are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.5mkkwh739 (Rumeu, Donoso, Rodríguez-Pérez, & García, 2020).

ORCID

Beatriz Rumeu (iD) https://orcid.org/0000-0002-9017-5466
Isabel Donoso (iD) https://orcid.org/0000-0002-0287-9026
Javier Rodríguez-Pérez (iD) https://orcid.org/0000-0002-1292-9090
Daniel García (iD) https://orcid.org/0000-0002-7334-7836

REFERENCES

Aukema, J. E., & Martínez del Rio, C. (2002). Where does a fruit-eating bird deposit mistletoe seeds? Seed deposition patterns and an experiment. *Ecology*, *83*, 3489–3496. https://doi.org/10.1890/0012-9658(2002)083[3489:wdafeb]2.0.co;2

Bascompte, J., & Jordano, P. (2006). The structure of plant-animal mutualistic networks. In M. Pascual & J. Dunne (Eds.), *Ecological networks* (pp. 143–159). Oxford, MS: Oxford University Press.

Bascompte, J., & Jordano, P. (2007). Plant-animal mutualistic networks: The architecture of biodiversity. *Annual Review of Ecology, Evolution and Systematics*, *38*, 567–593. https://doi.org/10.1146/annurev.ecolsys.38.091206.095818

Bascompte, J., & Jordano, P. (2014). *Mutualistic networks*. Princeton, NJ: Princeton University Press.

Beckett, S. J. (2016). Improved community detection in weighted bipartite networks. *Royal Society Open Science*, *3*, 140536. https://doi.org/10.1098/rsos.140536

Beckett, S. J., Boulton, C. A., & Williams, H. T. P. (2014). FALCON: A software package for analysis of nestedness in bipartite networks. *F1000Research*, *3*, 185. https://doi.org/10.12688/f1000research.4831.1

Blüthgen, N., Menzel, F., & Blüthgen, N. (2006). Measuring specialization in species interaction networks. *BMC Ecology*, *6*, 1–12. https://doi.org/10.1186/1472-6785-6-9

Carlo, T., Aukema, J., & Morales, J. (2007). Plant-frugivore interactions as spatially explicit networks: Integrating frugivore foraging with fruiting plant spatial patterns. In I. A. J. Dennis, E. W. Shupp, R. A. Green, & D. A. Westcott (Eds.), *Seed dispersal: Theory and its application in a changing world* (pp. 369–390). Wallingford, UK: CAB International.

Carlo, T. A., & Morales, J. M. (2016). Generalist birds promote tropical forest regeneration and increase plant diversity via rare-biased seed dispersal. *Ecology*, *97*, 1819–1831. https://doi.org/10.1890/15-2147.1

Donatti, C. I., Guimarães, P. R., Galetti, M., Pizo, M. A., Marquitti, F. M. D., & Dirzo, R. (2011). Analysis of a hyper-diverse seed dispersal network: Modularity and underlying mechanisms. *Ecology Letters*, *14*, 773–781. https://doi.org/10.1111/j.1461-0248.2011.01639.x

Dormann, C. F., Fründ, J., Blüthgen, N., & Gruber, B. (2009). Indices, graphs and null models: Analyzing bipartite ecological networks. *The Open Ecology Journal*, *2*, 7–24. https://doi.org/10.2174/1874213000902010007

Dunne, J. A., Williams, R. J., & Martinez, N. D. (2002). Food-web structure and network theory: The role of connectance and size. *Proceedings of the National Academy of Sciences of the United States of America*, *99*, 12917–12922. https://doi.org/10.1073/pnas.192407699

Emer, C., Galetti, M., Pizo, M. A., Guimarães Jr., P. R., Moraes, S., Piratelli, A., & Jordano, P. (2018). Seed-dispersal interactions in fragmented landscapes – A metanetwork approach. *Ecology Letters*, *21*, 484–493. https://doi.org/10.1111/ele.12909

Filazzola, A., & Lortie, C. J. (2014). A systematic review and conceptual framework for the mechanistic pathways of nurse plants. *Global Ecology and Biogeography*, *23*, 1335–1345. https://doi.org/10.1111/geb.12202

Fort, H., Vázquez, D. P., & Lan, B. L. (2016). Abundance and generalisation in mutualistic networks: Solving the chicken-and-egg dilemma. *Ecology Letters*, *19*, 4–11. https://doi.org/10.1111/ele.12535

García, D. (2016). Birds in ecological networks: Insights from bird-plant mutualistic interactions. *Ardeola*, *63*, 151–180. https://doi.org/10.13157/arla.63.1.2016.rp7

García, D., Donoso, I., & Rodríguez-Pérez, J. (2018). Frugivore biodiversity and complementarity in interaction networks enhance landscape-scale seed dispersal function. *Functional Ecology*, *32*, 2742–2752. https://doi.org/10.1111/1365-2435.13213

García, D., Martínez, D., Stouffer, D. B., & Tylianakis, J. M. (2014). Exotic birds increase generalization and compensate for native bird decline in plant–frugivore assemblages. *Journal of Animal Ecology*, *83*, 1441–1450. https://doi.org/10.1111/1365-2656.12237

García, D., Obeso, J. R., & Martínez, I. (2005). Rodent seed predation promotes differential recruitment among bird-dispersed trees in temperate secondary forests. *Oecologia*, *144*, 435–446. https://doi.org/10.1007/s00442-005-0103-7

Garcia, D., Obeso, J. R., & Martinez, I. (2005). Spatial concordance between seed rain and seedling establishment in bird-dispersed trees: Does scale matter? *Journal of Ecology*, *93*, 693–704. https://doi.org/10.1111/j.1365-2745.2005.01004.x

García, D., & Ortiz-Pulido, R. (2004). Patterns of resource tracking by avian frugivores at multiple spatial scales: Two case studies on discordance among scales. *Ecography*, *27*, 187–196. https://doi.org/10.1111/j.0906-7590.2004.03751.x

García, D., Rodríguez-Cabal, M. A., & Amico, G. C. (2009). Seed dispersal by a frugivorous marsupial shapes the spatial scale of a mistletoe population. *Journal of Ecology*, *97*, 217–229. https://doi.org/10.1111/j.1365-2745.2008.01470.x

García, D., Zamora, R., Hódar, J. A., Gómez, J. M., & Castro, J. (2000). Yew (*Taxus baccata* L.) regeneration is facilitated by fleshy-fruited shrubs in Mediterranean environments. *Biological Conservation*, *95*, 31–38. https://doi.org/10.1016/S0006-3207(00)00016-1

García-Cervigón, A. I., Żywiec, M., Delibes, M., Suárez-Esteban, A., Perea, R., & Fedriani, J. M. (2018). Microsites of seed arrival: Spatio–temporal variations in complex seed-disperser networks. *Oikos*, *127*, 1001–1013. https://doi.org/10.1111/oik.04881

Gómez, J. M. (2003). Spatial patterns in long-distance dispersal of *Quercus ilex* acorns by jays in a heterogeneous landscape. *Ecography*, *26*, 573–584. https://doi.org/10.1034/j.1600-0587.2003.03586.x

Gómez-Aparicio, L., Valladares, F., Zamora, R., & Luis Quero, J. (2005). Response of tree seedlings to the abiotic heterogeneity generated by nurse shrubs: An experimental approach at different scales. *Ecography*, *28*, 757–768. https://doi.org/10.1111/j.2005.0906-7590.04337.x

González-Castro, A., Yang, S., & Carlo, T. A. (2019). How does avian seed dispersal shape the structure of early successional tropical forests? *Functional Ecology*, *33*, 229–238. https://doi.org/10.1111/1365-2435.13250

González-Varo, J. P., Carvalho, C. S., Arroyo, J. M., & Jordano, P. (2017). Unravelling seed dispersal through fragmented landscapes: Frugivore species operate unevenly as mobile links. *Molecular Ecology*, *26*, 4309–4321. https://doi.org/10.1111/mec.14181

Guimerà, R., & Amaral, L. A. N. (2005). Functional cartography of complex metabolic networks. *Nature*, *433*, 895–900. https://doi.org/10.1038/nature03288

Hackett, T. D., Sauve, A. M. C., Davies, N., Montoya, D., Tylianakis, J. M., & Memmott, J. (2019). Reshaping our understanding of species' roles in landscape-scale networks. *Ecology Letters*, 22, 1367–1377. https://doi.org/10.1111/ele.13292

Hagen, M., Kissling, W. D., Rasmussen, C., De Aguiar, A. M., Brown, L. E., Carstensen, D. W., … Olesen, J. M. (2012). Biodiversity, species interactions and ecological networks in a fragmented world. *Advances in Ecological Research*, 46, 89–210. https://doi.org/10.1016/B978-0-12-396992-7.00002-2

Herrera, C. M. (1985). Habitat-consumer interactions in frugivorous birds. In M. L. Cody (Ed.), *Habitat selection in birds* (pp. 341–365). New York, NY: Academic Press.

Howe, H. F. (1989). Scatter-and clump-dispersal and seedling demography: Hypothesis and implications. *Oecologia*, 79, 417–426. https://doi.org/10.1007/bf00384323

Jordano, P. (1987). Patterns of mutualistic interactions in pollination and seed dispersal: Connectance, dependence asymmetries, and coevolution. *The American Naturalist*, 129, 657–677. https://doi.org/10.2307/2461728

Jordano, P. (1993). Geographical ecology and variation of plant-seed disperser interactions: Southern Spanish junipers and frugivorous thrushes. *Vegetatio*, 107(108), 85–104. https://doi.org/10.1007/bf00052213

Jordano, P., García, C., Godoy, J. A., & García-Castaño, J. L. (2007). Differential contribution of frugivores to complex seed dispersal patterns. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 3278–3282. https://doi.org/10.1073/pnas.0606793104

Kremen, C., Williams, N. M., Aizen, M. A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., … Ricketts, T. H. (2007). Pollination and other ecosystem services produced by mobile organisms: A conceptual framework for the effects of land-use change. *Ecology Letters*, 10, 299–314. https://doi.org/10.1111/j.1461-0248.2007.01018.x

Lefcheck, J. S. (2016). piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, 7, 573–579. https://doi.org/10.1111/2041-210x.12512

Lewinsohn, T. M., Prado, P. I., Jordano, P., Bascompte, J., & Olesen, J. M. (2006). Structure in plant-animal interaction assemblages. *Oikos*, 113, 174–184. https://doi.org/10.1111/j.0030-1299.2006.14583.x

Loeuille, N. (2010). Consequences of adaptive foraging in diverse communities. *Functional Ecology*, 24, 18–27. https://doi.org/10.1111/j.1365-2435.2009.01617.x

López-Bao, J. V., & González-Varo, J. P. (2011). Frugivory and spatial patterns of seed deposition by carnivorous mammals in anthropogenic landscapes: A multi-scale approach. *PLoS ONE*, 6, e14569. https://doi.org/10.1371/journal.pone.0014569

Loreau, M., Mouquet, N., & Gonzalez, A. (2003). Biodiversity as spatial insurance in heterogeneous landscapes. *Proceedings of the National Academy of Sciences of the United States of America*, 100, 12765–12770. https://doi.org/10.1073/pnas.2235465100

Lundberg, J., & Moberg, F. (2003). Mobile link organisms and ecosystem functioning: Implications for ecosystem resilience and management. *Ecosystems*, 6, 87–98. https://doi.org/10.1007/s10021-002-0150-4

Martín González, A. M., Dalsgaard, B., & Olesen, J. M. (2010). Centrality measures and the importance of generalist species in pollination networks. *Ecological Complexity*, 7, 36–43. https://doi.org/10.1016/j.ecocom.2009.03.008

Martínez, I., García, D., & Obeso, J. R. (2008). Differential seed dispersal patterns generated by a common assemblage of vertebrate frugivores in three fleshy-fruited trees. *Ecoscience*, 15, 189–199. https://doi.org/10.2980/15-2-3096

McConkey, K. R., Prasad, S., Corlett, R. T., Campos-Arceiz, A., Brodie, J. F., Rogers, H., & Santamaria, L. (2012). Seed dispersal in changing landscapes. *Biological Conservation*, 146, 1–13. https://doi.org/10.1016/j.biocon.2011.09.018

Mello, M. A. R., Marquitti, F. M. D., Guimarães Jr., P. R., Kalko, E. K. V., Jordano, P., & de Aguiar, M. A. M. (2011). The modularity of seed dispersal: Differences in structure and robustness between bat– and bird–fruit networks. *Oecologia*, 167, 131–140. https://doi.org/10.1007/s00442-011-1984-2

Montoya, D., Yallop, M. L., & Memmott, J. (2015). Functional group diversity increases with modularity in complex food webs. *Nature Communications*, 6, 7379. https://doi.org/10.1038/ncomms8379

Morales, J. M., García, D., Martínez, D., Rodriguez-Pérez, J., & Herrera, J. M. (2013). Frugivore behavioural details matter for seed dispersal: A multi-species model for Cantabrian thrushes and trees. *PLoS One*, 8, e65216. https://doi.org/10.1371/journal.pone.0065216

Morales, J. M., & Vázquez, D. P. (2008). The effect of space in plant–animal mutualistic networks: Insights from a simulation study. *Oikos*, 117, 1362–1370. https://doi.org/10.1111/j.0030-1299.2008.16737.x

Morán-López, T., González-Castro, A., Morales, J. M., & Nogales, M. (2019). Behavioural complementarity among frugivorous birds and lizards can promote plant diversity in island ecosystems. *Functional Ecology*, 34(1), 182–193. https://doi.org/10.1111/1365-2435.13476

Nathan, R., & Muller-Landau, H. C. (2000). Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution*, 15, 278–285. https://doi.org/10.1016/s0169-5347(00)01874-7

Nogales, M., Heleno, R., Rumeu, B., González-Castro, A., Traveset, A., Vargas, P., & Olesen, J. M. (2015). Seed-dispersal networks on the Canaries and the Galápagos archipelagos: Interaction modules as biogeographical entities. *Global Ecology and Biogeography*, 25, 912–922. https://doi.org/10.1111/geb.12315

Olesen, J. M., Bascompte, J., Dupont, Y. L., & Jordano, P. (2007). The modularity of pollination networks. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 19891–19896. https://doi.org/10.1073/pnas.0706375104

Paine, R. T. (1980). Food webs: Linkage, interaction strength and community infrastructure. *Journal of Animal Ecology*, 49, 667–685. https://doi.org/10.2307/4220

Palacio, R. D., Valderrama-Ardila, C., & Kattan, G. H. (2016). Generalist species have a central role in a highly diverse plant–frugivore network. *Biotropica*, 48, 349–355. https://doi.org/10.1111/btp.12290

Patefield, W. M. (1981). An efficient method of generating random RxC tables with given row and column totals. *Applied Statistics*, 30, 91–97.

Peredo, A., Martínez, D., Rodríguez-Pérez, J., & García, D. (2013). Mammalian seed dispersal in Cantabrian woodland pastures: Network structure and response to forest loss. *Basic and Applied Ecology*, 14, 378–386. https://doi.org/10.1016/j.baae.2013.05.003

Poisot, T., Mouquet, N., & Gravel, D. (2013). Trophic complementarity drives the biodiversity–ecosystem functioning relationship in food webs. *Ecology Letters*, 16, 853–861. https://doi.org/10.1111/ele.12118

Poisot, T., Stouffer, D. B., & Gravel, D. (2015). Beyond species: Why ecological interaction networks vary through space and time. *Oikos*, 124, 243–251. https://doi.org/10.1111/oik.01719

Poisot, T., Stouffer, D. B., & Kéfi, S. (2016). Describe, understand and predict: Why do we need networks in ecology? *Functional Ecology*, 30, 1878–1882. https://doi.org/10.1111/1365-2435.12799

Polis, G. A., Anderson, W. B., & Holt, R. D. (1997). Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics*, 28, 289–316. https://doi.org/10.1146/annurev.ecolsys.28.1.289

Proulx, S. R., Promislow, D. E. L., & Phillips, P. C. (2005). Network thinking in ecology and evolution. *Trends in Ecology & Evolution*, 20, 345–353. https://doi.org/10.1016/j.tree.2005.04.004

R Development Core Team. (2015). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.R-project.org/

Rohr, R. P., Saavedra, S., & Bascompte, J. (2014). On the structural stability of mutualistic systems. *Science*, *345*, 1253497. https://doi.org/10.1126/science.1253497

Rumeu, B., Donoso, I., Rodríguez-Pérez, J., & García, D. (2020). Data from: Frugivore species maintain their structural role in the trophic and spatial networks of seed dispersal interactions. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.5mkkwh739

Schupp, E. W., & Fuentes, M. (1995). Spatial patterns of seed dispersal and the unification of plant population ecology. *Ecoscience*, *2*, 267–275. https://doi.org/10.1080/11956860.1995.11682293

Simmons, B. I., Sutherland, W. J., Dicks, L. V., Albrecht, J., Farwig, N., García, D., … González-Varo, J. P. (2018). Moving from frugivory to seed dispersal: Incorporating the functional outcomes of interactions in plant–frugivore networks. *Journal of Animal Ecology*, *87*, 995–1007. https://doi.org/10.1111/1365-2656.12831

Simmons, B. I., Vizentin-Bugoni, J., Maruyama, P. K., Cotton, P. A., Marín-Gómez, O. H., Lara, C., … Sutherland, W. J. (2019). Abundance drives broad patterns of generalisation in plant–hummingbird pollination networks. *Oikos*, *128*(9), 1287–1295. https://doi.org/10.1111/oik.06104

Thébault, E., & Fontaine, C. (2010). Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science*, *329*, 853–856. https://doi.org/10.1126/science.1188321

Thompson, R. M., Brose, U., Dunne, J. A., Hall, R. O., Hladyz, S., Kitching, R. L., … Tylianakis, J. M. (2012). Food webs: Reconciling the structure and function of biodiversity. *Trends in Ecology & Evolution*, *27*, 689–697. https://doi.org/10.1016/j.tree.2012.08.005

Timóteo, S., Correia, M., Rodríguez-Echeverría, S., Freitas, H., & Heleno, R. (2018). Multilayer networks reveal the spatial structure of seed-dispersal interactions across the Great Rift landscapes. *Nature Communications*, *9*, 140. https://doi.org/10.1038/s41467-017-02658-y

Torroba Balmori, P., Zaldívar García, P., & Hernández Lázaro, Á. (2013). *Semillas de frutos carnosos del norte ibérico: Guía de identificación*. Valladolid, Spain: Ediciones Universidad de Valladolid.

Tylianakis, J. M., & Morris, R. J. (2017). Ecological networks across environmental gradients. *Annual Review of Ecology, Evolution, and Systematics*, *48*, 25–48. https://doi.org/10.1146/annurev-ecolsys-110316-022821

Vázquez, D. P., Melián, C. J., Williams, N. M., Blüthgen, N., Krasnov, B. R., & Poulin, R. (2007). Species abundance and asymmetric interaction strength in ecological networks. *Oikos*, *116*, 1120–1127. https://doi.org/10.1111/j.0030-1299.2007.15828.x

Vélez, M. C. D., Silva, W. R., Pizo, M. A., & Galetto, L. (2015). Movement patterns of frugivorous birds promote functional connectivity among Chaco Serrano woodland fragments in Argentina. *Biotropica*, *4*, 475–483. https://doi.org/10.1111/btp.12233

Wheelwright, N. T. (1985). Fruit-size, gape width, and the diets of fruit-eating birds. *Ecology*, *66*, 808–818. https://doi.org/10.2307/1940542

Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M. M., & Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology*, *95*, 2027. https://doi.org/10.1890/13-1917.1

Woodward, G., Ebenman, B., Emmerson, M., Montoya, J. M., Olesen, J. M., Valido, A., & Warren, P. H. (2005). Body size in ecological networks. *Trends in Ecology & Evolution*, *20*, 402–409. https://doi.org/10.1016/j.tree.2005.04.005

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Frugivore species maintain their structural role in the trophic and spatial networks of seed dispersal interactions

Beatriz Rumeu, Isabel Donoso, Javier Rodríguez-Pérez, Daniel García

Electronic Supplementary Material

Appendix S1. Study system and sampling methodologies

Figure S1. Representation of the study system and sampling design. A) A landscape view of the Bandujo-Puertos de Marabio site, showing habitat heterogeneity with forest patches, remnant trees, pastures, heathland and rocky outcrops. B) View of study plot indicating vantage points for monitoring fruit consumption by birds (yellow stars), point-counts for monitoring bird abundance and perching behavior (red dots), and seed deposition sampling stations with different types of seed traps (blue and purple squares, yellow dots). C) Transects for mammal scat sampling related to one study plot (main and additional transect represented by the white and yellow lines, respectively) and detail of a mammal scat on a rocky habitat.

(A)

(B) Bird frugivory and seed deposition

Fruit consumption
© L. Ojembarrena

Abundance
Perching behavior

Seed deposition

(C) Mammal scat sampling

Main transect

Additional transect

© J.P. González-Varo
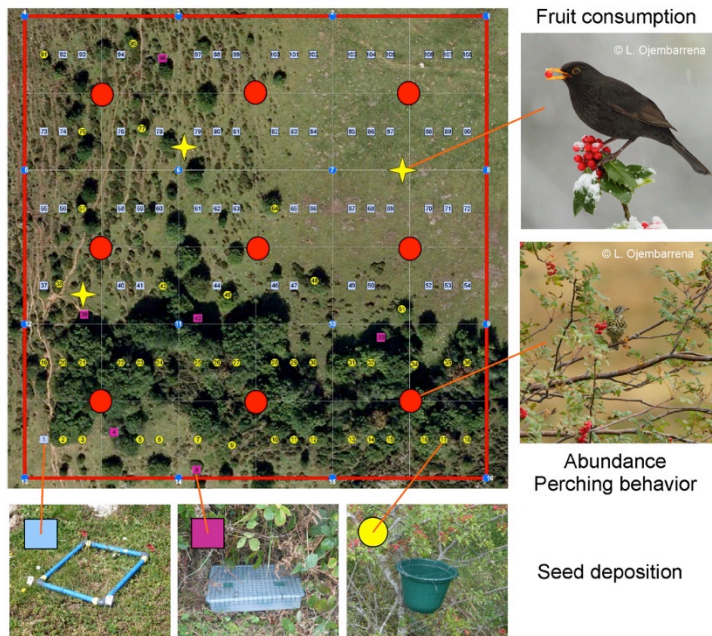
Table S1: Geographical description of the fourteen 2.25-ha study plots in the Cantabrian Range (Asturias, Spain).
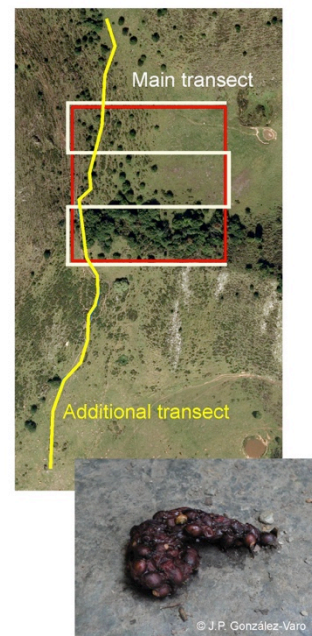
Plot code	Site	Elevation (m) asl	Geographic coordinates (N-W)		Forest cover (%)
P1	Sierra de Peña Mayor	1034	43° 17' 18.1"	05° 29' 56.0"	19.98
P2	Sierra de Peña Mayor	1001	43° 17' 50.4"	05° 30' 12.2"	31.31
P3	Sierra de Peña Mayor	1067	43° 18' 09.5"	05° 30' 32.6"	8.87
P4	Sierra de Peña Mayor	1092	43° 18' 38.7"	05° 30' 44.7"	68.74
G1	Sierra de Peña Mayor	993	43° 17' 15.3"	05° 30' 28.0"	11.12
G2	Sierra de Peña Mayor	1078	43° 17' 29.8"	05° 30' 32.8"	18.88
G3	Sierra de Peña Mayor	1093	43° 17' 47.4"	05° 30' 46.4"	39.28
B1	Bandujo-Puertos de Marabio	1124	43° 14' 37.2"	06° 05' 03.7"	3.11
B2	Bandujo-Puertos de Marabio	1145	43° 14' 35.2"	06° 05' 41.4"	26.66
B3	Bandujo-Puertos de Marabio	1183	43° 14' 18.6"	06° 05' 38.9"	47.32
B4	Bandujo-Puertos de Marabio	1253	43° 14' 09.7"	06° 06' 21.3"	20.88
M1	Bandujo-Puertos de Marabio	1020	43° 13' 09.5"	06° 07' 19.0"	33.54
M2	Bandujo-Puertos de Marabio	1020	43° 13' 01.1"	06° 07' 37.1"	11.36
M3	Bandujo-Puertos de Marabio	1012	43° 12' 20.2"	06° 07' 25.7"	54.93

Table S2 Frugivore species sorted by functional type (thrushes, other birds and mammals), family, abbreviation codes and traits included in the piecewise SEMs (relative abundance and body mass; see Table S6 in Appendix S4). Abundance of frugivores was estimated as the proportion of occurrences of each species relative to the total number of plot-based observation events (N = 238; 17 rounds x 14 plots). Body mass data were obtained from Elton Traits (Wilman et al., 2014).

Frugivore species	Family	Code	Abundance	Body mass (g)
Thrushes				
Turdus iliacus	Turdidae	*Tur ili*	0.36	61.2
Turdus merula	Turdidae	*Tur mer*	0.90	102.7
Turdus philomelos	Turdidae	*Tur phi*	0.32	67.7
Turdus pilaris	Turdidae	*Tur pil*	0.02	106.0
Turdus torquatus	Turdidae	*Tur tor*	0.08	109.0
Turdus viscivorus	Turdidae	*Tur vis*	0.02	117.4
Other birds				
Erithacus rubecula	Muscicapidae	*Eri rub*	0.79	17.7
Garrulus glandarius	Corvidae	*Gar gla*	0.08	159.5
Phylloscopus collybita/ibericus	Phylloscopidae	*Phy* spp	0.07	8.3
Sylvia atricapilla	Sylviidae	*Syl atr*	0.21	16.7
Mammals				
Canis lupus/familiaris	Canidae	*Can* spp	0.01	32183.3
Capreolus capreolus	Cervidae	*Cap cap*	0.33	22500.0
Cervus elaphus	Cervidae	*Cer ela*	0.32	165015.9
Martes martes/foina	Mustelidae	*Mar* spp	0.18	1420.4
Meles meles	Mustelidae	*Mel mel*	0.15	13000.0
Mustela nivalis/erminea	Mustelidae	*Mus* spp	0.01	111.6
Sus scrofa	Suidae	*Sus scr*	0.13	96118.1
Vulpes vulpes	Canidae	*Vul vul*	0.36	5476.2

Reference

Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M.M., & Jetz, W. (2014) EltonTraits 1.0: Species‐level foraging attributes of the world's birds and mammals. *Ecology, 95*, 2027-2027

Table S3 Fleshy-fruited species included in the study, family and abbreviation codes.

Feshy-fruited species	Family	Code
Crataegus monogyna	Rosaceae	*Cra mon*
Ilex aquifolium	Aquifoliaceae	*Ile aqu*
Malus sp.	Rosaceae	*Mal* sp
Prunus avium	Rosaceae	*Pru avi*
Rosa sp.	Rosaceae	*Ros* sp
Rubus fruticosus	Rosaceae	*Rub fru*
Sambucus nigra	Adoxaceae	*Sam nig*
Smilax aspera	Smilacaceae	*Smi asp*
Sorbus aria	Rosaceae	*Sor ari*
Sorbus aucuparia	Rosaceae	*Sor* auc
Taxus baccata	Taxaceae	*Tax bac*

Appendix S2. Seed dispersal matrices

In order to obtain the trophic and spatial networks we built trophic and spatial matrices following a three-step approach (Fig. S2). First, we estimated *raw matrices* for birds and mammals separately, based on field data obtained from different methodologies, and representing the number of dispersed seeds by different frugivore species (trophic network; Fig. S2A) and in different fine-scale habitats (spatial network; Fig. S2B). In the case of the raw spatial matrix of birds, cell values represented observations of different birds perching on different fine-scale habitats. Second, we transformed raw matrices into *proportional matrices*, in which each cell represented the proportion of seeds relative to the total number of seeds of the raw matrix. In the case of the proportional spatial matrix of birds, we corrected it by a seed dispersal rate, by multiplying the values of each bird species by the proportion of seeds dispersed by the bird species in the trophic interaction matrix. This product matrix was transformed again into proportional, by dividing the value of each cell by the total sum of cell values in the product matrix (for simplicity, this step was omitted from Fig. S2). Third, for both the trophic and the spatial case, we merged bird and mammal proportional matrices in a single *final matrix*, after multiplying the proportional matrices by a total number of seeds according to a ratio 70.9:1 for, respectively, birds and mammals (and with a 10^N coefficient enabling the transformation of any proportional value into an integer value).

Figure S2 Procedure followed to construct our seed dispersal matrices: (A) trophic interaction matrix, and (B) spatial matrix of seed deposition fine-scale habitats (H). Interactions were weighted by using a bird:mammal ratio based on the seed rain (seeds/m^2) generated by both birds and mammals (see green box).
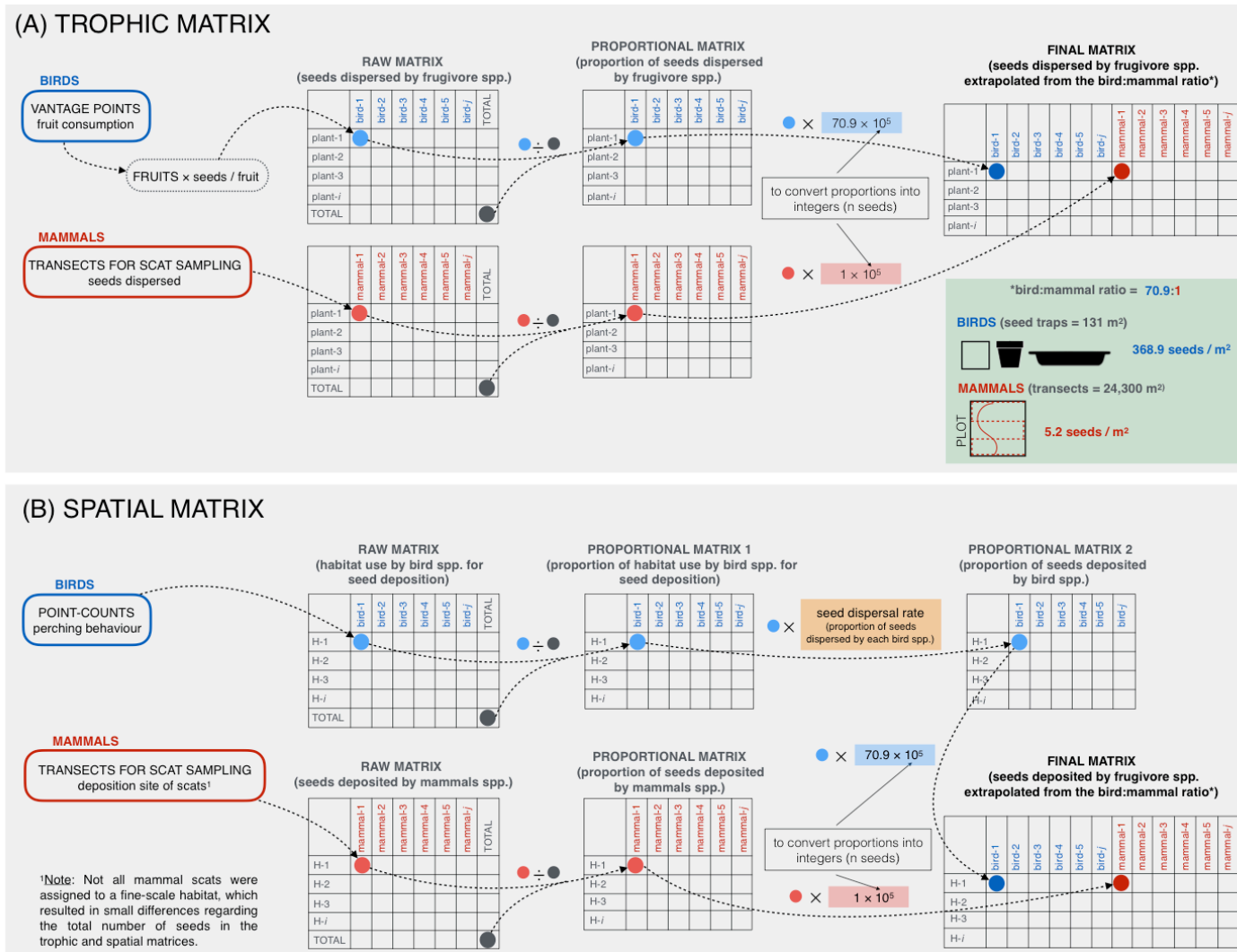
Table S4 Trophic interaction matrix, with plant species as rows and frugivores as columns. Matrix cells show the estimated number of seeds dispersed as a result of each interaction.

	Erithacus rubecula	*Garrulus glandarius*	*Phylloscopus spp*	*Sylvia atricapilla*	*Turdus iliacus*	*Turdus merula*	*Turdus philomelos*	*Turdus pilaris*	*Turdus torquatus*	*Turdus viscivorus*	*Canis spp*	*Capreolus capreolus*	*Cervus elaphus*	*Martes spp*	*Meles meles*	*Mustela spp*	*Sus scrofa*	*Vulpes vulpes*	TOTAL
Crataegus monogyna	39994	0	0	5516	332365	1441169	184801	81367	0	20687	0	2	136	23	116	0	14	319	2106509
Ilex aquifolium	4137	0	0	28961	1050881	1932132	165493	0	0	24824	0	6	6	12	2	0	2	2	3206458
Rubus fruticosus	20687	9654	0	103433	0	38615	16549	0	0	0	1066	101	444	8713	35029	0	13154	32108	279553
Sambucus nigra	12412	0	8275	318574	0	28961	0	0	0	0	0	0	1	0	2	0	0	0	368225
Sorbus aria	0	0	0	5516	0	71714	44131	0	44131	430282	0	0	2	34	7	0	0	98	595915
Sorbus aucuparia	4137	0	0	17928	0	358568	17928	0	0	4137	0	11	2	118	122	0	0	361	403312
Taxus baccata	2758	1379	0	9654	6896	64818	95159	6896	0	34478	0	0	0	148	660	0	0	32	222878
Malus sp.	0	0	0	0	0	0	0	0	0	0	11	0	1	2	7	0	0	24	45
Rosa sp.	0	0	0	0	0	0	0	0	0	0	0	0	4	2579	2415	12	0	1635	6645
Smilax aspera	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	3
Prunus avium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	458	0	0	1	459
TOTAL	84125	11033	8275	489582	1390142	3935977	524061	88263	44131	514408	1077	120	596	11630	38820	12	13170	34580	7190002

Table S5 Spatial matrix of seed deposition, with habitats as rows and frugivores as columns. Matrix cells show the estimated number of seeds dispersed per frugivore species in each fine-scale habitat.

	Erithacus rubecula	*Garrulus glandarius*	*Phylloscopus spp*	*Sylvia atricapilla*	*Turdus iliacus*	*Turdus merula*	*Turdus philomelos*	*Turdus pilaris*	*Turdus torquatus*	*Turdus viscivorus*	*Canis spp*	*Capreolus capreolus*	*Cervus elaphus*	*Martes spp*	*Meles meles*	*Mustela spp*	*Sus scrofa*	*Vulpes vulpes*	TOTAL
Fleshy – fruited shrub	922	0	0	4175	0	76716	0	0	0	0	0	13	0	0	178	0	0	78	82082
Fleshy – fruited tree	39148	121	202	44134	1122755	5202291	132788	1075	269	31332	0	23	128	1074	2346	0	12	2061	6579759
Non-fleshy-fruited tree	5739	134	60	5368	49110	167816	13406	0	0	25692	0	57	20	1841	3868	0	0	1830	274941
Heather	102	0	10	0	0	9589	1277	0	0	0	0	12	163	2249	5750	0	4073	6987	30212
Pasture	410	0	0	0	11854	134253	3830	0	0	627	1128	24	281	5970	25993	13	9715	21569	215667
Rock	0	0	0	0	0	4795	0	0	0	0	0	0	32	123	0	0	0	2388	7338
TOTAL	46321	255	272	53677	1183719	5595460	151301	1075	269	57651	1128	129	624	11257	38135	13	13800	34913	7189999

Appendix S3. Nestedness significance

Figure S3 Significance test for Nestedness under the CRT (Conserve Row Totals) null model implemented in *FALCON* (Beckett, Boulton, & Williams, 2014). (A) Trophic network; (B) Spatial network. Only the trophic network was significantly nested under this null model.
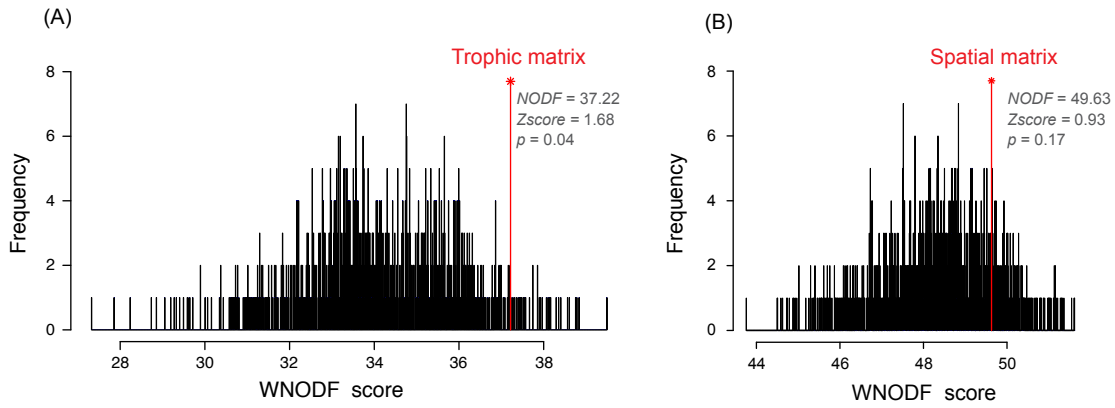
Reference

Beckett, S.J., Boulton, C.A., & Williams, H.T.P. (2014) FALCON: a software package for analysis of nestedness in bipartite networks. *F1000Research, 3*, 185. doi: 10.12688/f1000research.4831.1

Appendix S4. Piecewise structural equation modeling

Table S6 Piecewise SEM model specifications including distributions for response variables and R-squared values. Model types include generalized linear models (GLM) and linear models (LM). In the four piecewise SEMs (Fig. 4), we specified correlated error structures between the topological metrics (z, c, ND and d') of both the trophic and the spatial network.

Response variable	Model	Distribution	Predictors	R^2
z – trophic	GLM	Gamma (link = log)	Abundance + Log(body mass)	0.02
z – spatial	GLM	Gamma (link = log)	Abundance + Log(body mass)	0.21
c – trophic	GLM	Gamma (link = log)	Abundance + Log(body mass)	0.54
c – spatial	GLM	Gamma (link = log)	Abundance + Log(body mass)	0.51
ND – trophic	LM	Gaussian	Abundance + Log(body mass)	0.30
ND – spatial	LM	Gaussian	Abundance + Log(body mass)	0.61
d' – trophic	LM	Gaussian	Abundance + Log(body mass)	0.33
d' – spatial	GLM	Gamma (link = log)	Abundance + Log(body mass)	0.78

Table S7 Piecewise SEM coefficients from each pathway (arrows) and correlated error structures (~~) associated to the four models shown in Fig. 4. Values in bold-italics are statistically significant ($p < 0.05$).

Piecewise SEM model	Path	Estimate	SE	*df*	*p* value
within-module degree (*z*)	$Abundance \rightarrow z_{trophic}$	0.256	0.456	14	0.607
	$Abundance \rightarrow z_{spatial}$	0.722	0.451	14	0.132
	$Body\ mass \rightarrow z_{trophic}$	0.014	0.090	14	0.876
	$Body\ mass \rightarrow z_{spatial}$	-0.029	0.084	14	0.734
	$z_{trophic}$ ~~ $z_{spatial}$	0.781	NA	17	***<0.001***
among-module connectivity (*c*)	$Abundance \rightarrow c_{trophic}$	0.373	0.134	15	***0.014***
	$Abundance \rightarrow c_{spatial}$	0.439	0.149	15	***0.010***
	$Body\ mass \rightarrow c_{trophic}$	-0.059	0.025	15	***0.031***
	$Body\ mass \rightarrow c_{spatial}$	-0.054	0.027	15	0.068
	$c_{trophic}$ ~~ $c_{spatial}$	0.023	NA	18	0.190
normalised degree (*ND*)	$Abundance \rightarrow ND_{trophic}$	0.529	0.25	15	***0.050***
	$Abundance \rightarrow ND_{spatial}$	0.869	0.187	15	***<0.001***
	$Body\ mass \rightarrow ND_{trophic}$	0.074	0.046	15	0.125
	$Body\ mass \rightarrow ND_{spatial}$	0.073	0.034	15	0.052
	$ND_{trophic}$ ~~ $ND_{spatial}$	0.776	NA	18	***<0.001***
Specialization (*d'*)	$Abundance \rightarrow d'_{trophic}$	-0.425	0.157	15	***0.016***
	$Abundance \rightarrow d'_{spatial}$	-2.623	0.826	15	***0.021***
	$Body\ mass \rightarrow d'_{trophic}$	-0.004	0.029	15	0.894
	$Body\ mass \rightarrow d'_{spatial}$	0.777	0.152	15	***<0.001***
	$d'_{trophic}$ ~~ $d'_{spatial}$	0.690	NA	18	***0.001***