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BIRDS IN ECOLOGICAL NETWORKS: INSIGHTS FROM BIRD-PLANT MUTUALISTIC INTERACTIONS

AVES EN REDES ECOLÓGICAS: PERSPECTIVAS DESDE LAS INTERACCIONES MUTUALISTAS AVE-PLANTA

Daniel GARCÍA¹ *

SUMMARY.—Research in ecological networks has developed impressively in recent years. A significant part of this growth has been achieved using networks to represent the complexity of mutualistic interactions between species of birds and plants, such as pollination and seed dispersal. Bird-plant networks are built from matrices whose cells account for the field-sampled magnitudes of interaction (e.g. the number of plant fruits consumed by birds) in bird-plant species pairs. The comparative study of mutualistic networks evidences three general patterns in network structure: they are highly heterogeneous (many species having just a few interactions, but a few species being highly connected), nested (with specialists interacting with subsets of species with which generalists interact) and composed of weak and asymmetric relationships between birds and plants. This type of structure emerges from a set of ecological and evolutionary mechanisms accounting for the probabilistic role of species abundances and the deterministic role of species traits, often constrained by species phylogenies. Although bearing structural generalities, bird-plant networks are variable in space and time at very different scales: from habitat to latitudinal and biogeographical gradients, and from seasonal to inter-annual contrasts. They are also highly sensitive to human impact, being especially affected by habitat loss and fragmentation, defaunation and biological invasions. Further research on bird-plant mutualistic networks should: 1) apply wide conceptual frameworks which integrate the mechanisms of interaction and the responses of species to environmental gradients, 2) enlarge the ecological scale of networks across interaction types and animal groups, and 3) account for the ultimate functional (i.e. demographic) effects of trophic interactions.

Key words: frugivory, interaction diversity, modularity, nestedness, pollination, seed dispersal, specialisation.

RESUMEN.—La investigación en redes ecológicas se ha desarrollado de forma sobresaliente en los años recientes. Una parte significativa de este crecimiento se ha conseguido al usar las redes para representar la complejidad de interacciones mutualistas entre especies de aves y plantas, como en las

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interacciones de polinización y dispersión de semillas. Las redes ave-planta se construyen a partir de matrices cuyas celdas contienen las magnitudes de interacción entre pares de especies ave-planta, muestreadas en el campo (p. ej. número de frutos de las plantas consumidos por las aves). El estudio comparado de las redes mutualistas revela tres patrones estructurales generales: las redes son muy heterogéneas (la mayoría de las especies soportan sólo unas pocas interacciones, mientras que unas pocas especies aparecen muy interconectadas), son anidadas (las especies especialistas interactúan con subgrupos de especies con las cuales interactúan las generalistas), y se componen de relaciones débiles y asimétricas entre aves y plantas. Este tipo de estructura emerge de mecanismos ecológicos y evolutivos que conjugan el efecto probabilístico de las abundancias específicas con el papel determinista de los rasgos de las especies, a menudo condicionados por su filogenia. Aun existiendo generalidades estructurales, las redes ave-planta varían en el espacio y en el tiempo a escalas muy diferentes (desde los contrastes de hábitats a los gradientes latitudinales y biogeográficos; desde los contrastes estacionales a los interanuales). Las redes son además muy sensibles al impacto humano, especialmente en forma de pérdida y fragmentación de hábitat, extirpación de fauna e invasiones biológicas. La investigación futura en las redes mutualistas ave-planta debería: 1) aplicar marcos conceptuales amplios que integran los mecanismos de interacción y las respuestas de las especies a los gradientes ambientales, 2) ampliar la escala ecológica de las redes a través de distintos tipos de interacciones y grupos animales, y 3) tener en cuenta los efectos funcionales finales (i.e. demográficos) de las interacciones tróficas.

Palabras clave: anidamiento, dispersión de semillas, diversidad de interacciones, especialización, frugivorismo, modularidad, polinización.

INTRODUCTION

Ecological networks emerge from the application of network theories to ecological science. This field of research aims to disentangle the structure and the functioning of complex ecological systems, as well as to provide tools for representing and predicting the global response of these systems to environmental changes (Bascompte, 2009; Heleno *et al.*, 2014). In a very general sense, ecological networks are representations of sets of ecological objects with the potential to interact (i.e. to exchange some kind of biological information) among themselves (Bascompte, 2009). Thus, the emphasis is on the number and the composition of the ecological objects in question ("nodes", in network terminology), as well as on the abundance, the magnitude and the distribution of interrelationships between the objects ("links", in network terminology). Nodes may represent genes, individuals, species, habitat patches, or even whole communities, and the diversity of

what is represented by links ranges from the exchange of energy/biomass between species (as defined in trophic interactions) to the movement of individuals between habitat patches (as suggested in metapopulation dynamics). As such, two major ecological domains have particularly benefited from incorporating networks into their conceptual bodies: community ecology, in order to represent food webs and other systems of interspecific interactions (Ings *et al.*, 2009); and landscape ecology, to represent ecological fluxes across landscape mosaics (Urban and Keitt, 2001).

Ornithology has also embraced the increased interest in ecological networks, and the approach has become more and more frequent in bird studies. These studies also demonstrate how widely the different manifestations of networks may be applied to bird ecology, evidencing a variety of types of networks in which birds take part as individuals or species, as either nodes or links. Networks may be classified as one-mode and

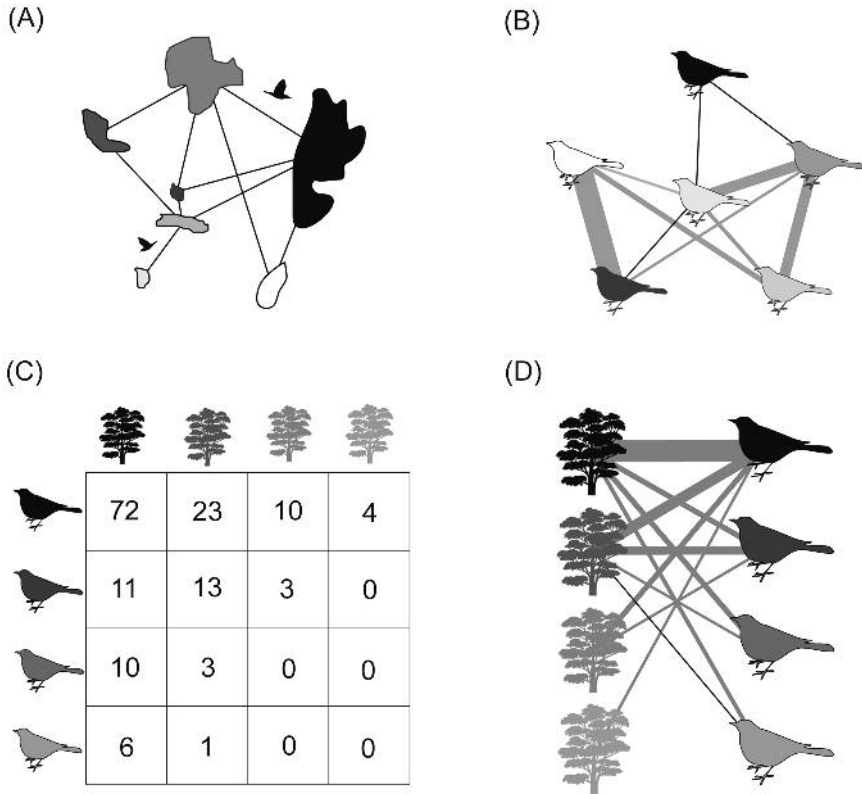


FIG. 1.—Types of networks involving birds: (A) a one-mode, unweighted network of habitat patches (nodes; the different patches each represented by different black-grey-white tones) connected by moving individual birds (links); (B) a one-mode weighted network of birds (nodes; the different bird species each represented by different black-grey-white tones) interrelated by their concurrence (links; the width of the link is proportional to the frequency of concurrence of each pair of species) in multispecific flocks; (C) a two-mode weighted network of trees and birds represented by a matrix of paired interactions such as nesting, pollination or seed dispersal (with plant species as columns and bird species as rows, and numbers in cells representing the frequency of interaction); and (D) the corresponding bipartite graph with species (nodes; the different plant/bird species each represented by different black-grey-white tones) connected by interaction events (links; the width of the link is proportional to the frequency of interaction).

[Tipos de redes con aves: (A) red unimodal no ponderada de rodales de hábitat (nodos; diferentes rodales están representados por distintos tonos de gris) conectados por aves individuales (vínculos) que se desplazan entre ellos; (B) red unimodal ponderada de aves (nodos: diferentes especies de ave representadas por distintos tonos de gris) interrelacionadas por su concurrencia (vínculos; la anchura del vínculo es proporcional a la frecuencia de concurrencia de cada par de especies) en bandos multispecíficos; (C) red bimodal ponderada de árboles y aves, representada por una matriz de interacciones pareadas, tales como anidamiento, polinización o dispersión de semillas (con las especies de árboles como columnas y las de aves como filas, y los números en las celdas representando la frecuencia de interacción); y (D) el correspondiente gráfico bipartito con las especies (nodos; diferentes especies de árboles/aves están representadas por distintos tonos de gris) conectadas por eventos de interacción (vínculos; la anchura del vínculo es proporcional a la frecuencia de interacción).]

two-mode networks (Bascompte and Jordano, 2007). In one-mode networks, nodes belong to a single category and, potentially, any node may be connected to another node by a link. For example, an archipelago of habitat patches connected by the movement of individual birds (fig. 1A, e.g. Saura, Bodin and Fortin, 2014), or an assemblage of interspecific interactions among bird species (fig. 1B; e.g. flocking co-occurrence, Mokross *et al.*, 2013) are both one-mode networks. In two-mode networks, on the other hand, there are two well-defined types of nodes (e.g. nesting birds and the trees where nests are placed, Rodewald *et al.*, 2014) and links occur between but not within node types (that is, nesting interactions are only realised between a bird and a tree). Other notable two-mode networks are those emerging from bird-plant mutualistic interactions, such as pollination (e.g. Maglianesi *et al.*, 2014) and seed dispersal (e.g. Schleuning *et al.*, 2011). Two-mode networks are represented by bipartite graphs (fig. 1C-D).

Focusing on links, networks are considered as weighted when, besides the occurrence of interactions among nodes, they include information on the intensity or weight of these interactions. For example, some pairs of bird species may co-occur in a flocking network in higher proportions than other pairs (fig. 1B), or some bird species may nest in some tree species at a higher frequency than in other trees (fig. 1C-D).

The interaction between plants that provide food to birds –in the form of nectar or the pulp of fleshy fruits– and birds that provide reciprocal positive services to the plants –in the form of pollen transfer or seed dispersal and the concomitant reproductive effect– has attracted the attention of biologists since Darwin's time (Bascompte and Jordano, 2014). Neotropical hummingbirds (Bawa, 1990), Australian honeyeaters (Ford *et al.*, 1979), African sunbirds (Schmid *et al.*, 2015), New Zealand tuis and bellbirds

(Kelly *et al.*, 2010), and even the opportunistic Canarian passerines (Rodríguez-Rodríguez and Valido, 2008) and Galapagos finches (Traveset *et al.*, 2015), are examples of the many nectar-feeding birds contributing to plant pollination in a wide variety of ecosystems across the world. Similarly, frugivorous birds are present in almost all terrestrial biota, and are the dispersers of the seeds of hundreds of plant species, especially in tropical and temperate forests (Jordano, 2000; Herrera, 2002). Mutualistic birds and plants are therefore an important part of the Earth's biodiversity, contributing to pivotal ecological functions and ecosystem services that have consequences on human well-being (Whelan *et al.*, 2008; Schleuning *et al.*, 2015).

Bird-plant mutualistic networks have received much attention in recent years, in the context of the expanding study of plant-animal ecological interactions (Heleno *et al.*, 2014; Gu *et al.*, 2015). It may be argued, then, that the study of plant-bird mutualistic interactions has substantially contributed to the development of the conceptual framework of ecological networks (Bascompte and Jordano, 2007; Ings *et al.*, 2009). In this context, this review summarises recent advances in the knowledge on avian ecological networks, by focusing on the bird-plant mutualistic interactions of pollination and seed dispersal. Firstly, this review provides a methodology-oriented guide through the general structure (i.e. topology) and the emerging patterns of bird-plant networks, with the help of empirical examples of seed dispersal networks from the Iberian Peninsula and the Canary Islands. Secondly, the underlying ecological and evolutionary mechanisms and the spatio-temporal drivers of the structural patterns of networks are presented. Thirdly, the effect of human impact on bird-plant networks is discussed. A final section is devoted to proposing desirable avenues for future research in avian ecological networks.

MEASURING PAIRED INTERACTIONS IN BIRD-PLANT NETWORKS

Bird-plant mutualistic networks are based on data about “who (bird) eats/pollinates/disperses what (plant)”. These data are organised into the cells in a species-species interaction matrix (with birds as rows and plants as columns, or vice versa), containing information about the occurrence (i.e. a binary format) or the intensity (i.e. a continuous format) of each paired interaction (fig. 1C). Although birds are a relatively easy-to-sample group, detecting and measuring bird foraging on specific plants (i.e. the bird’s trophic perspective), and, more importantly, measuring pollination and seed dispersal provided by specific birds (i.e. the plant’s reproductive perspective) can be methodologically challenging. This constraint is far from being trivial, as sample size limitations in interaction matrices may affect the estimation of network topology (Blüthgen *et al.*, 2008; Costa *et al.*, 2015). More importantly, the manner of measuring paired interactions may drastically affect the ecological inferences to be drawn from the network topology, depending on whether the bird’s or the plant’s perspective is finally interpreted.

Direct observation of birds foraging on plants, while avoiding observer interference on bird activity (by using camouflage or even video camera recording), is a typical method for counting the times a flowering/fruitlet plant species is visited by a nectarivorous/frugivorous bird species (e.g. Kelly *et al.*, 2010; Menke *et al.*, 2012; Maglianesi *et al.*, 2014). Complementarily, the number of flowers visited or fruits consumed per visit and per plant are also used to quantify the magnitude of interactions. The advantages of this methodology are that it correctly represents the bird’s trophic perspective, and that it uses detection methods that are not biased towards a particular bird or plant species (standardisation among plant species may

be achieved by assigning equal sampling times to different species). However, as a disadvantage, networks sampled with this methodology actually represent nectarivory/frugivory, rather than pollination/seed dispersal, being thus limited in representing the plant’s reproductive perspective, as different birds may have different qualities as pollinators or seed dispersers. For example, some birds feed on fruits by eating pieces of pulp and discarding the seeds (i.e. pulp eaters; Jordano, 2000) whereas others peck at fruits for seeds ignoring the pulp (i.e. seed predators). Only those birds that discard the intact seeds after feeding on fruits (by removing them after fruit handling, or regurgitating or defecating them after swallowing the fruit) can actually be considered as legitimate dispersers for plants (Jordano, 2000).

Methods based on the direct identification and counting of pollen or seeds transported by individual birds, following capture by mist-netting, are also frequent in network studies. Pollen loads may be collected by gently wiping a bird’s bill or neck with gelatine cubes (e.g. Maglianesi *et al.*, 2015a; Traveset *et al.*, 2015), and seeds can be collected from faecal samples produced after placing mist-netted birds in ringing bags (e.g. Heleno *et al.*, 2013 a, b). Both the occurrence of signs of different plants on/in different birds, as well as quantitative measures of the interaction (number of pollen grains or seeds transported) may be inferred from this sort of sampling. These methods overcome the limitations of using direct observation to represent the plant’s perspective in the mutualistic interaction. However, they may offer a biased picture of the network role of the different bird species, given the differences in mist-netting capturability associated with bird behaviour (Cruz *et al.*, 2013). Moreover, excessive manipulation or bird stress in capture may hamper quantitative estimations of interactions (for example, the number of intact seeds dispersed by

some bird species able to digest small seeds, like *Fringillidae*, could be exaggerated if bagging accelerates gut passage; Heleno *et al.*, 2011).

Recently, an approach based on a DNA-barcoding protocol has been implemented for detecting paired bird-plant interactions from bird-dispersed seeds sampled in the field (González-Varo *et al.*, 2014; see also Marrero *et al.*, 2009). The frugivorous bird species may be identified from its DNA, extracted from the surface of the defecated or regurgitated seed, whereas the plant species is identified from its distinctive morphological seed traits. This method is non-invasive, taxonomically unbiased (at least for legitimate dispersers, in the case of birds) and very precise for representing plant's demographic perspective.

STRUCTURE OF BIRD-PLANT MUTUALISTIC NETWORKS

The first part of this section will be devoted to exploring generalities in the structure of bird-plant mutualistic networks, in terms of how different bird and plant species make different relative contributions to the network, and how the interactions are distributed across species. After this, the form of quantifying and interpreting different aspects of network structure, by means of network metrics, will be explained. Both issues will be illustrated with empirical examples of seed-dispersal networks studied in the Iberian Peninsula and the Canary Islands, from different ecological settings, but sharing species of frugivorous birds and fleshy-fruited plants.

The data set of the temperate secondary forest of the Cantabrian Range (see table 1 for interaction matrix) comes from a global pool of direct observations of fruit consumption by birds during the fall-winter (September-January) of 2012-2013 and

2013-2014, in fourteen 150 × 150 m plots (with eighteen 1-hour observation rounds per plot, totaling 252 observation hours) distributed across sites in the Sierra de Peña Mayor and Bandujo-Puertos de Marabio (Asturias, Spain; 850-1100 m.a.s.l.; for site descriptions see Peredo *et al.*, 2013). Bird abundance was estimated from the cumulative number of birds heard or seen in eighteen sessions of 5-min, 25-m-radius point-count censuses across nine regularly placed points per plot (totalling 189 hours of census). The interaction matrices from Mediterranean upland (Nava de las Correuelas; 1615 m.a.s.l., Jaén, Spain) and lowland (Hato Ratón; 36 m.a.s.l.; Sevilla, Spain) forests are available from Pedro Jordano at https://github.com/pedroj/bipartite_plots. A general description of site characteristics and collection methodology is available in Jordano (1987a; 1995). The interaction matrix from the Canarian thermophilous shrubland (Los Adernos; 220 m.a.s.l., Tenerife, Spain) is available in González-Castro *et al.* (2015), which also contains a description of site characteristics and collection methodology.

GENERAL PATTERNS IN NETWORKS

Studies from different ecological communities, many of them including birds, evidence the existence of generalities in the topology of pollination and seed dispersal networks (e.g. Jordano, 1987b; Bascompte and Jordano, 2007; Bascompte and Jordano, 2014). Three major structural features characterise bird-plant mutualistic networks: high heterogeneity in the distribution of interactions across species, significant nestedness and modularity, and strong asymmetry in interaction strengths between birds and plants.

High heterogeneity in interactions means that mutualistic networks are composed of a core of species that have few interactions, while a small number of species are much

TABLE 1

Seed dispersal interaction matrix in the Cantabrian Range. Cell values are the number of fruits consumed per bird per plant species.

[Matriz de interacciones de dispersión de semillas en la cordillera Cantábrica. Los valores en las celdas representan el número de frutos consumidos por cada especie de ave para cada especie de planta.]

| | <i>Crataegus monogyna</i> | <i>Ilex aquifolium</i> | <i>Rubus fruticosus/ulmifolius</i> | <i>Sambucus nigra</i> | <i>Sorbus aria</i> | <i>Sorbus aucuparia</i> | <i>Taxus baccata</i> |
|------------------------------|---------------------------|------------------------|------------------------------------|-----------------------|--------------------|-------------------------|----------------------|
| <i>Cyanistes caeruleus</i> | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| <i>Erithacus rubecula</i> | 29 | 1 | 15 | 3 | 0 | 1 | 2 |
| <i>Fringilla coelebs</i> | 2 | 0 | 0 | 0 | 1 | 0 | 0 |
| <i>Garrulus glandarius</i> | 0 | 0 | 7 | 0 | 0 | 0 | 1 |
| <i>Lophophanes cristatus</i> | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Parus major</i> | 3 | 0 | 3 | 0 | 0 | 0 | 4 |
| <i>Periparus ater</i> | 4 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Phylloscopus</i> sp. | 0 | 0 | 0 | 2 | 0 | 0 | 0 |
| <i>Poecile palustris</i> | 2 | 0 | 0 | 0 | 0 | 0 | 6 |
| <i>Pyrrhula pyrrhula</i> | 6 | 5 | 151 | 0 | 0 | 53 | 0 |
| <i>Sylvia atricapilla</i> | 4 | 7 | 75 | 77 | 1 | 5 | 7 |
| <i>Turdus iliacus</i> | 241 | 254 | 0 | 0 | 0 | 0 | 5 |
| <i>Turdus merula</i> | 1049 | 467 | 28 | 7 | 13 | 104 | 47 |
| <i>Turdus philomelos</i> | 131 | 40 | 12 | 0 | 8 | 5 | 69 |
| <i>Turdus pilaris</i> | 59 | 0 | 0 | 0 | 0 | 0 | 5 |
| <i>Turdus torquatus</i> | 0 | 0 | 0 | 0 | 8 | 0 | 0 |
| <i>Turdus viscivorus</i> | 15 | 6 | 0 | 0 | 78 | 1 | 25 |

more connected than would be expected by chance. For example, only two of 17 bird species (blackbird *Turdus merula* and red-wing *Turdus iliacus*) accounted for 70% of all interactions with fleshy-fruited plants in the seed dispersal network of the Cantabrian Range, and only two of 16 fleshy-fruited

plants (mastic *Pistacia lentiscus* and wild olive tree *Olea europaea*) accounted for almost 80% of interactions with birds in the Mediterranean lowland forests of Hato Ratón (fig. 2). Heterogeneity can be represented by a bias in the distribution of species degrees (i.e. the number of different species

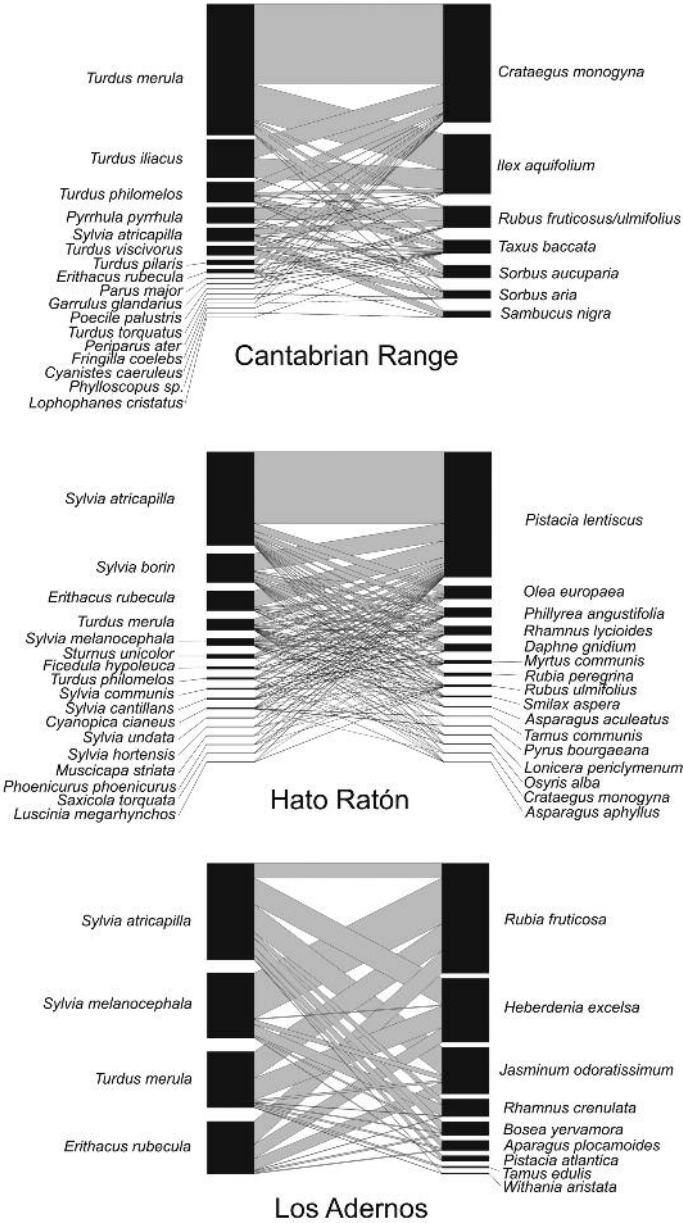


FIG. 2.—Bipartite graphs representing weighted seed dispersal networks at different sites in Spain. Each graph represents the proportion of fruits of different plant species (right column) consumed by different bird species (left column), and the proportion of fruits of each plant species consumed by each bird species (gray links).

[Gráficos bipartitos representando redes ponderadas de dispersión de semillas en diferentes sitios de España. Cada gráfico representa la proporción de frutos carnosos de diferentes especies de plantas (columna derecha) consumidos por diferentes especies de aves (columna izquierda), y la proporción de frutos de cada especie de planta consumida por cada especie de ave (vínculos grises).]

a certain species interacts with) such that only a small proportion of the species of the network interact with many others (fig. 3A). In this sense, degree distributions of many mutualistic networks have been found to adjust well to truncated power-law or exponential functions, highlighting the non-linear decay in the proportion of species accounting for increasing numbers of links (Bascompte and Jordano, 2014; fig. 3A). In weighted networks, where a quantitative weight may be assigned to the interaction of each pair of species, the distribution of interaction weights (i.e. the proportion of interactions accounted for by each pair of species) also evidences that interaction biases, with a few common but many rare interactions, are frequent (fig. 3B). Thus, independently of

the differences in latitude and species composition, bird-plant mutualistic networks display a common and well-defined connectivity distribution (Jordano *et al.*, 2003).

Network nestedness and modularity refers to a non-random pattern in the relative distribution of interactions between species pairs, taking into account the identities of the partners. On the one hand, a network is nested when specialists (i.e. species with small interaction degrees) interact mostly with species that form well-defined subsets of the species with which generalists (i.e. species with large interaction degrees) also interact. In other words, if we rank birds from the most specialised species to the most generalised, we find that the plants interacting with a specialised bird are always

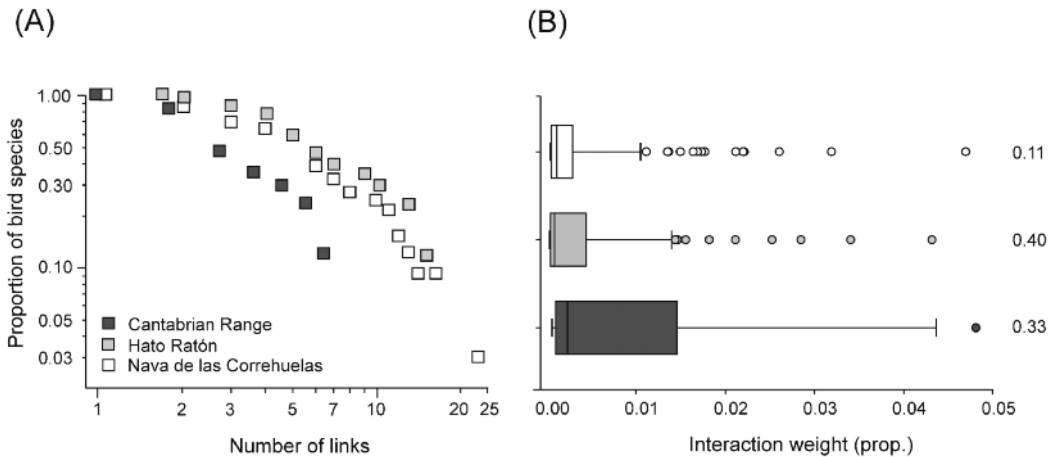


FIG. 3.—Connectivity distributions in seed dispersal networks of different sites in Spain. (A) Distribution of bird species degrees, representing the proportion of birds accounting for different number of links (i.e. number of interacting plant species). (B) Distribution of interaction weights, with box-plots representing the proportion of interactions, from all observed interactions, accounted for by each bird-plant pairing. Maximum values are shown for the different networks.

[Distribuciones de conectividad en redes de dispersión de semillas de distintos sitios de España. (A) Distribución de los valores de grado de distintas especies de ave, representando la proporción de aves que muestran distinto número de vínculos (i.e. número de especies de plantas con las que interactúan). (B) Distribución de los valores del peso de interacción, con diagramas de caja representando la proporción de interacciones correspondiente a cada par de especies ave-planta, con respecto a todas las interacciones observadas. Se muestran los valores máximos para las diferentes redes.]

also one of the partners of a more generalised bird, that is, plants of specialists are successively included within the pools of generalists, as in a 'Russian doll' pattern. Nestedness also implies that the network has a core of generalist birds and plants that interact among themselves, and a tail of specialists interacting mostly with the most generalist

species. For example, in Hato Ratón, birds like the western Orphean warbler *Sylvia hortensis* and spotted flycatcher *Muscicapa striata* have few links in the network, but they are to such plants as mastic, false olive *Phillyrea angustifolia* or Mediterranean buckthorn *Rhamnus lycioides*, which are themselves visited by many different birds, especially by generalists such as the black-cap *Sylvia atricapilla* and European robin *Erithacus rubecula* (fig. 2). Asymmetries in the levels of specialisation between paired species are, therefore, frequent (Vázquez and Aizen, 2004). On the other hand, modularity refers to the existence of modules within networks, aggregated subgroups of species having many interactions among themselves, but very few with other species in other modules (Fortuna *et al.*, 2010; Mello *et al.*, 2011; Schleuning *et al.*, 2014a). This results in the network being represented as a heterogeneous space, combining areas with sparse links among species and distinct areas of tightly linked species. For example, in the Cantabrian Range, the ordination of interactions between birds and plants in a matrix scheme enables modules of bird-plant species with higher frequencies of interactions among them to be represented, like that composed by certain thrushes (*Turdus* spp.) and holly *Ilex aquifolium* and hawthorn *Crataegus monogyna* trees, or the module harbouring other thrushes and tits (*Paridae*) and yew *Taxus baccata* (fig. 4). Significant nestedness and modularity may, thus, occur simultaneously in bird-plant networks (Fortuna *et al.*, 2010). For example, the set of interactions between tits and yew contributes to the modularity in the Cantabrian Range network (fig. 4), but also to its nestedness, as tits emerge as specialists and yew is clearly a generalist tree (fig. 2).

In bird-plant weighted networks, paired interactions may be interpreted in terms of the importance that a given species of bird has for a given species of plant, and vice versa

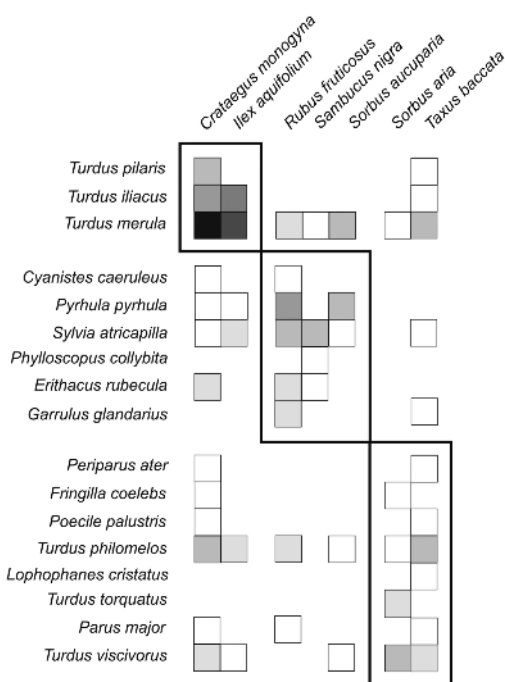


FIG. 4.—Seed dispersal interaction matrix of the Cantabrian Range, featuring modules identified by QuaBiMo (Dormann and Strauss, 2014; see main text for explanation). Small squares indicate realised interactions, and darker tones indicate more observed interactions. Black square frames delineate modules.

[Matriz de interacciones de dispersión de semillas de la cordillera Cantábrica, resaltando los módulos identificados por QuaBiMo (Dormann and Strauss, 2014; véanse explicación en el texto principal). Los cuadrados pequeños indican las interacciones ocurridas, y los tonos oscuros indican mayor frecuencia de interacción. Los marcos cuadrados oscuros delimitan los módulos.]

by means of interaction strengths or dependences (Bascompte and Jordano, 2014). The dependence of a plant on a frugivorous bird, for example, is estimated as the proportion of fruits consumed by that bird species in relation to the total number of fruits of that plant consumed by all birds in the network. Reciprocally, the dependence of the bird on a plant is estimated as the fraction of the total number of fruits consumed by the bird that come from that particular plant. For example, the dependence of hawthorn on blackbird in the Cantabrian Range is 0.67, whereas that of blackbird on hawthorn is 0.61 (fig. 2), evidencing reciprocal dependence. However, the same dependences in Hato Ratón scored 0.28 and 0.004, respectively, as almost a third of all hawthorn seeds were dispersed by blackbirds, but blackbirds mostly feed on other plant species (fig. 2). That is, a given plant may depend strongly

on a given bird, but the bird usually relies significantly less on the plant. However, the opposite case, with a very dependent bird usually linked to a much less dependent plant, is also common. For example, the diet of fieldfare *Turdus pilaris* in the Cantabrian Range was almost exclusively based on hawthorn fruits (dependence = 0.92), but hawthorn scarcely depended on fieldfare for dispersal (dependence = 0.03; table 2; fig. 2). In fact, this sort of strong asymmetry in the dependence values within each paired interaction is the general rule, rather than the exception, in mutualistic networks (Bascompte *et al.*, 2006; Bascompte and Jordano, 2014).

The general patterns of mutualistic networks are thought to have consequences for the dynamic of ecological communities. Losses of bird species in mutualistic networks may cascade into plant secondary

TABLE 2

Values of network metrics for the seed dispersal interaction matrices of different bird-plant assemblages in Spain. All metrics were estimated with the *bipartite* package (Dorman *et al.*, 2009).

[Valores de las métricas de red para las matrices de interacciones de dispersión de semillas de diferentes conjuntos ave-plantas en España. Todas las métricas se estimaron con el programa *bipartite* (Dorman *et al.*, 2009).]

| Metric | Cantabrian Range | Hato Ratón | Los Adernos |
|----------------------------------|------------------|------------|-------------|
| Connectance | 0.470 | 0.444 | 0.777 |
| Interaction diversity | 2.531 | 2.653 | 2.716 |
| Interaction evenness | 0.529 | 0.473 | 0.757 |
| Specialisation degree (H_2') | 0.362 | 0.158 | 0.195 |
| Interaction strength asymmetry | 0.122 | 0.109 | -0.515 |
| Weighted nestedness (NODF) | 46.131 | 55.226 | 47.227 |
| Generality (birds) | 2.744 | 2.990 | 4.102 |
| Redundancy (plants) | 3.020 | 4.261 | 3.134 |
| Modularity (Q) | 0.274 | 0.131 | 0.221 |

extinctions, due to reproductive collapse driven by the removal of pollinators or seed dispersers (Jordano *et al.*, 2003). In this sense, the skewed distribution of interaction degrees would confer networks with high robustness against the random extinction of species (Bascompte and Jordano, 2007; 2014). Although rare species, i.e. those with few interactions, would be expected to be the first to become extinct, the few highly connected species would act as a backbone providing interactions (and hence precluding secondary extinctions) across the whole network (Jordano *et al.*, 2003). Network nestedness, and the associated specialisation asymmetry, would also have a buffering effect against co-extinction (Bascompte *et al.*, 2006; Vázquez and Aizen, 2004). Hence, specialist species would benefit from interacting with generalists, as these latter are more likely to persist in the community in the long-term thanks to their higher abundance and less fluctuating populations. Nestedness is also significant in terms of the maintenance of species diversity, through reducing interspecific competition and hence promoting species coexistence (Bastolla *et al.*, 2009). For example, two plants may compete for seed dispersers, but they may also benefit (facilitate) each other when shared dispersers are disproportionately attracted to those fruiting patches containing both plants (e.g. Martínez *et al.*, 2014). In nested networks, many plant species, both common and rare, typically share generalist abundant dispersers, and thus the potential of facilitation among plants increases. However, in highly compartmentalised networks, sharing seed dispersers may lead more frequently to plant-plant competition as many of these dispersers would be rare and scarce (Bastolla *et al.*, 2009). The number of disperser species shared between plants is usually higher in nested networks than in highly compartmentalised networks, and thus the potential of facilitative interactions between plants increases, promoting coexistence, but also

fostering the incorporation of other plant species into the network (Bastolla *et al.*, 2009). The coexistence of interdependent groups of species in networks also seems to be promoted by asymmetry in interaction dependences (Bascompte *et al.*, 2006). If both bird and plant depend strongly on each other, a decrease in bird abundance will be followed by a similar decrease in the associated plant abundance, which in turn will have a feedback effect on the bird, and so on. This kind of negative loop would, however, be precluded when interactions are uneven, as the plant would probably recover by relying on another bird. Finally, modularity also matters for network stability, especially when confronted by strong disturbances: although extinctions may quickly spread across the highly connected species in the first module impacted by disturbance, the weaker connections between modules may act as a firewall, protecting the rest of the network from disturbance (Olesen *et al.*, 2007; Tylianakis *et al.*, 2010).

MEASURING AND INTERPRETING NETWORK STRUCTURE

Different metrics and indices for quantifying the topology of bird-mutualistic networks have proliferated in recent years (Bascompte and Jordano, 2014). Here, a small sample of different indices for two-mode weighted networks, estimated using the *bipartite* package (version 2.05; Dormann *et al.*, 2009; R statistical software version 3.0.2; R Development Core Team 2008), are applied to the interaction matrices of the Iberian Peninsula and the Canary Islands (table 2). Metrics may refer to characteristics of the global assemblage of interactions (network-level metrics), represent characteristics of separate trophic groups (group-level metrics, birds or plants) or even quantify features of specific species, relative to the rest of the network (species-level metrics).

Some of the most widely used network-level metrics, with their interpretation (Dormann *et al.*, 2009; Blüthgen, 2010), are:

- 1) *Connectance*. This is the proportion of possible links realised, considering all the species in the network. It represents the global density of interactions, the connectivity within the network. For example, the value of connectivity is much higher in Los Adernos than in the Cantabrian Range or Hato Ratón, where many bird and plant species do not actually interact among themselves (table 2; fig. 2).
- 2) *Interaction diversity*. A Shannon Index-based measure of diversity estimated from interaction frequencies, affected both by the number of species and the distribution of interaction weights among species. It is a measure of the complexity of the associations among species in the system.
- 3) *Interaction evenness*. Related to diversity, it better represents how similar the weights of the different paired interactions are. Ranging from 0 to 1, low values indicate strong dominance in the distribution of interactions, with some links being very strong (i.e. high interaction frequencies) and many others weak. As with connectance, it is also a measure of ecological connectivity between birds and plants, but incorporating the information contained in weighted links. For example, Los Adernos network shows a distribution of interactions among species which is much more equitable than that of Cantabrian Range or Hato Ratón where certain links dominate the network (e.g. blackbird-hawthorn in the Cantabrian Range, blackcap-mastic in Hato Ratón).
- 4) *Specialisation (H_2')*. Ranging from 0 to 1, it is a measure of how species are specialised in interaction partnerships or, inversely, that they show a high degree of generalisation in their interactions. Also referred to as complementary specialisation, it represents complementarity-redundancy in the distribution of interactions across species. For example, in Hato Ratón and Los Adernos (where values of specialisation are low; table 2), there are many generalised birds and plants, whereas in the Cantabrian Range (where H_2' is higher), there are more bird species supporting single, or few, interactors (fig. 2).
- 5) *Weighted nestedness (WNODF)*. Nestedness (i.e. the degree to which the interactions of less-connected species are a subset of those of more-connected species) is estimated as a weighted version of the nestedness measure provided by Almeida-Neto *et al.* (2008), with higher values indicating higher nestedness. This measure is based on node overlap (NO, i.e. the proportion of nodes with interactions that coincide when changing from a given column to the adjacent one) and decreasing filling (DF, i.e. the presence of interactions in less-filled columns and rows coincide, respectively, with those found in the more filled columns and rows).
- 6) *Modularity (Q)*. This is a measure of how well the observed links of a network can be grouped into modules in quantitative two-mode networks, calculated by means of the QuaBiMo algorithm (Dormann and Strauss, 2014). It ranges from 0 to 1, with 1 indicating maximal modularity (i.e. all links are within and none between modules). Although modularity values are low in all cases studied here (table 2), the Cantabrian Range network showed higher modularity, corresponding to a stronger segregation of interaction between groups of species,

a pattern probably precluded by the high generalisation of interactions in both birds and plants in networks like Hato Ratón.

- 7) *Interaction strength asymmetry*. It quantifies the average imbalance (difference) between the interaction strengths (dependences) of each pair of species in the network. A positive value indicates a higher specialisation of the consumers than of the resources (birds depend more on specific plants than vice versa), and a negative value, a higher specialisation of plants than of birds. Strong differences in interaction strength asymmetry were found between the Iberian and the Canarian networks (table 2). Birds depended more on plants than vice versa in all Iberian networks, but the opposite pattern was found in Los Adornos network, associated with the high generalisation of all Canarian birds, and to its higher number of plants than of birds (fig. 2).

Among group-level metrics, two which are frequently used are those that represent and compare the degree of generalisation: *generality*, a weighted average number of plant species consumed per bird species, and *redundancy* (*sensu* Albrecht *et al.*, 2013; also called *vulnerability*), a weighted average number of avian seed dispersers per plant. For example, generality values corroborated the stronger generalisation of Canarian frugivorous birds, compared to those in the Iberian networks (table 2). Finally, the *specialisation degree* (d_i'), a species-level analogue to H_2' , is a metric to represent the relative role of individual species in the whole network, indicating not only specialism (i.e. a small species degree) but also selectiveness (i.e. how selective a given species is in its interactions, taking partner availability into account; Blüthgen *et al.*, 2008; Blüthgen, 2010).

MECHANISMS UNDERLYING BIRD-PLANT MUTUALISTIC NETWORKS

This section will be devoted to disentangling the processes that determine the non-random structure of bird-plant mutualistic networks. The goal here is thus to identify the ecological and evolutionary reasons that make two species (bird and plant) interact and the degree to which they do so. Three kinds of species ecological attributes have been identified as sources of variability in the occurrence of bird-plant paired interactions: species abundance, species phenotypic traits and species preferences.

The effects of abundance on bird-plant interaction patterns are conceptualised under a “neutrality hypothesis”, by which interaction frequencies and network patterns would exclusively respond to the random encounters of interacting species, with species’ interaction weights and degrees being directly proportional to their relative abundance (Burns, 2006; 2013; Vázquez *et al.*, 2009a, b; González-Castro *et al.*, 2015). Under a neutral scenario, abundant birds would have links with many different plants and high interaction weights, interacting more with the most abundant plants. Rare birds, on the other hand, would have a higher encounter probability with dominant plants, and a reciprocal rationale could be applied for rare plants, mostly encountered by dominant birds. Thus, abundance differences between interacting species would strongly contribute to the typical patterns of mutualistic networks: heterogeneous degree distribution, high degree of nestedness and asymmetric distribution of dependences (Vázquez, 2005; Vázquez *et al.*, 2007; Bascompte and Jordano, 2014).

As a deterministic alternative to neutrality, the “trait-matching hypothesis” establishes that mutualistic interactions depend on phenotypic coupling among bird and plant traits (Jordano *et al.*, 2003; Vázquez *et al.*, 2009b).

That is, network patterns would depend on how species morphology, physiology and behaviour enable or constrain the occurrence of interactions (e.g. a bird with a narrow gape cannot consume fruits from plant species with large fruit diameter; Burns, 2013). Thus, the concept of “forbidden links” (Jordano *et al.*, 2003; Olesen *et al.*, 2010a; Sankamethawee *et al.*, 2011), by which phenotypic limitations would preclude certain birds and plants interacting even when present in the same habitat, would explain many of the unobserved interactions (“zeros” in the interaction matrix) that contribute greatly to network heterogeneity and nestedness. Among the features underpinning forbidden links are species phenology and physical size and shape.

The flowering and fruiting times of plants impose temporal windows of resource availability of variable span (from a few weeks to several months), to which pollinator and frugivorous birds must adapt. For example, hummingbird plants may differ markedly in the composition of their pollinator assemblage depending on their flowering and nectar production calendars, which are usually non-overlapping (Stiles, 1975; Vizenin-Bugoni *et al.*, 2014). Seed dispersal networks are also frequently controlled by the phenological uncoupling which, in the case of birds, emerges from migration and wintering seasonality. For example, in Hato Ratón (fig. 2; Jordano, 1988; Jordano and Bascompte, 2014), the highly frugivorous garden warbler *Sylvia borin* rarely met winter-fruiting plants (e.g. wild olive tree; Sprenger asparagus *Asparagus aculeatus*) as its migratory passage concentrated in spring and summer. Similarly, in the Cantabrian Range, late-arriving wintering redwings and fieldfares *Turdus pilaris* rarely interacted with, late-summer fruiting whitebeams and rowans (*Sorbus* spp.; figs. 2, 4).

The morphological match between birds and plants (flowers and fruits), in terms of both size and shape, is a generalised driver

of paired interactions across regions and ecosystems (e.g. Jordano *et al.*, 2003; Sankamethawee *et al.*, 2011; González-Castro *et al.*, 2015; Maglianesi *et al.*, 2015a). For example, in tropical hummingbirds, bill length and curvature condition the range of flower species in which nectar consumption is energetically efficient (Maruyama *et al.*, 2014; Maglianesi *et al.*, 2015a, b). Specifically, species with long and curved bills are specialised to relatively rare but rewarding flowers (with long and curved corollas), whereas species with short and uncurved bills, excluded from long flowers, forage on a wider variety of less rewarding plants which, in turn, themselves receive many hummingbird species. The biases in interaction occurrence imposed by bill-flower morphological matching thus lead to strong specialisation and modularity in the pollination networks (Maruyama *et al.*, 2014; Maglianesi *et al.*, 2015a). Concerning seed dispersal networks, the match between bird gape width (which is highly correlated with body size) and fruit diameter (usually correlated with fruit and seed size) would determine the ability of birds to handle and swallow fruits, and hence constrains seed dispersal interactions (Jordano and Bascompte, 2014). For example, in Hato Ratón (fig. 2; Olesen *et al.*, 2010a), small birds, like the Dartford warbler *Sylvia undata* and subalpine warbler *S. cantillans*, restricted their foraging to a few small-fruited plant species, whereas larger birds, like the blackbird, were able to feed on a wide range of fruit sizes belonging to different plant species. As regards plants, large-fruited species (e.g. hawthorn) were dispersed by larger birds, but small-fruited species (e.g. mastic) were visited by birds of all sizes. The resulting pattern is a highly nested network structure (fig. 2).

Phenotypic matching operates by imposing barriers to the occurrence of certain paired interactions between birds and plants.

However, even when birds and plants are present and physically enabled to interact, the frequencies of interaction of paired species may be higher or lower than expected from their abundances, due to positive or negative preferences (Burns, 2013; García *et al.*, 2014). Preferences may be a consequence of species behaviour, ultimately conditioned by phenotypic traits. For example, being big enables birds to consume large fruits thanks to their correlated wide gape, but also it involves having a large gut, which facilitates high consumption rates (number of fruits consumed per visit to plant) and leads to higher than expected interaction weights and degrees (Burns, 2013; García *et al.*, 2014). Other preferences may emerge from the behavioural adaptation of birds to “hidden” plant traits, such as the chemical composition of nectar or fruits. For example, in the Canary Islands, *Sylvia* warblers mostly consume fruits low in sugar and lipids and high in fibre and protein, whereas blackbirds tend to show the opposite pattern (González-Castro *et al.*, 2015). Bird preferences based on fruit composition thus contribute to the network structure beyond the effects of species abundances (González-Castro *et al.*, 2015).

The different mechanisms of network patterns outlined above (abundances, trait-matching, preferences) are not mutually exclusive, and they may operate simultaneously in the same ecological assemblage of birds and plants (e.g. Krishna *et al.*, 2008; Burns, 2006; 2013; Maruyama *et al.*, 2014; Vizentin-Bugoni *et al.*, 2014; González-Castro *et al.*, 2015). The relative importance of each mechanism, usually estimated by means of generalised linear models, may vary greatly, depending on the type of mutualistic interaction and the region of study. For example, forbidden links related to phenological and morphological uncoupling play a greater role than species abundance in structuring the hummingbird pollination networks

in the Atlantic rainforest (Vizentin-Bugoni *et al.*, 2014) and Neotropical savanna (Maruyama *et al.*, 2014) of Brazil. A similar pattern, which also incorporates bird preferences based on fruit composition, has been suggested for the Canarian seed dispersal networks (González-Castro *et al.*, 2015). However, in the Cantabrian Range (figs. 2, 4), bird specific abundance was positively correlated with both species interaction weight (i.e. the quantity of fruits consumed by each bird species; Pearson correlation coefficient: $r = 0.544$, $P = 0.023$, $N = 17$) and species degree (i.e. the number of plant species consumed; $r = 0.543$, $P = 0.024$, $N = 17$; fig. 5). Interestingly, bird species interaction weight (but not species degree) was also positively affected by bird body mass ($r = 0.648$, $P = 0.005$, $N = 17$; fig. 5). Thus large and abundant birds (blackbird and redwing) dispersed many seeds from many plant species. Both abundance and body mass showed independent effects on interaction weights in the Cantabrian Range: some small species (e.g. robin) had higher than expected interaction weight because they were abundant, whereas some large species (e.g. fieldfare) had a significant role despite being scarce. Interestingly, a very similar hierarchy of relative effects of species abundance and body size has also been found for the avian seed dispersal networks of New Zealand forests (García *et al.*, 2014).

When addressing the ecological features that determine the position of species in bird-plant interaction networks, especially phenotypic traits, it is necessary to acknowledge that species are not independent entities, but frequently the result of common evolutionary histories. Species are affected by different degrees of phylogenetic relatedness within each group of interaction partners (birds and plants), and this is frequently expressed in shared values of phenotypic traits. As a consequence, closely related bird species tend to interact with the same set of plant species

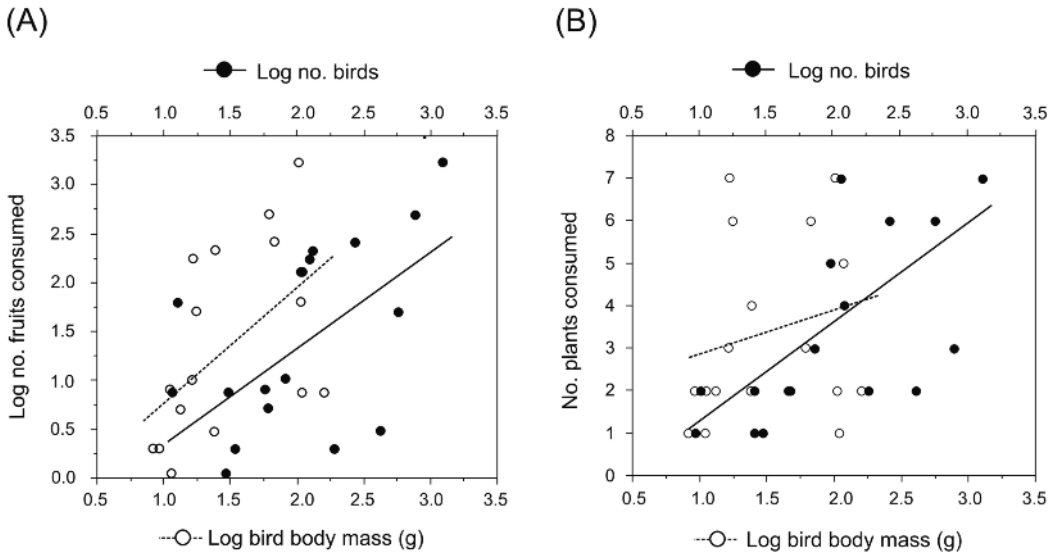


FIG. 5.—Mechanisms of paired interactions in the Cantabrian seed dispersal network. Relationships between (A) bird interaction weight (number of fruits consumed per bird species) and (B) bird degree (number of plant species consumed per bird species), and bird abundance and bird body size (from Dunning, 2008). Lines indicate the best fit linear regressions.

[*Mecanismos de las interacciones pareadas en la red cantábrica de dispersión de semillas. Relaciones entre (A) peso de interacción del ave (número de frutos consumidos por especie de ave) y (B) grado del ave (número de especies de plantas consumidas por especie de ave), y la abundancia del ave y el peso corporal del ave (según Dunning, 2008). Las líneas indican el mejor ajuste de regresión lineal.*]

and vice versa, as there is usually a significant animal phylogenetic signal in both the number of links per species and with whom interactions take place (Rezende *et al.*, 2007; Nogales *et al.*, 2015). This sort of evolutionary determinism in the occurrence of paired interactions may have also consequences in the emergence of network patterns, namely increasing the degree of modularity (Bascompte and Jordano, 2014). For example, one could argue for some kind of phylogenetic effect on the emergence of certain modules in the Cantabrian seed dispersal network, such as that composed of thrushes and trees like hawthorn and holly (figs. 2, 4). However, a recent analysis of avian seed dispersal networks across different regions failed to find a clear relation-

ship between the degree of modularity and avian phylogenetic signal. Thus, although phylogenetic relatedness explains similarities between bird species in their interaction patterns, networks which were more shaped by species phylogeny were not more modular. Other factors, probably related to species abundances rather than phylogenetically conserved traits, could be the main drivers of the modular structure of these networks (Schleuning *et al.*, 2014a).

SPATIO-TEMPORAL VARIABILITY IN BIRD-PLANT MUTUALISTIC NETWORKS

Bird-plant mutualistic networks are aimed at representing communities of interacting

species that co-occur in space and time, but they are usually built from matrices of interactions observed across different local habitats and regions, and even when collected in single ecological locales, across days and seasons. Thus, the synthetic approach provided by global bipartite graphs or topological metrics is frequently blind to the spatial and temporal variability in the richness, the composition and the frequency of paired interaction that inherently occurs in natural communities (Olesen *et al.*, 2010b). Consequently, evaluating the scales and the sources of spatio-temporal variability in network structure is essential for a better understanding of the mechanisms underpinning the occurrence of paired interactions, as well as to forecast the network responses to future environmental change (Burkle and Alarcón, 2011; Bascompte and Jordano, 2014).

Fine-scale spatial variability in structure has been evidenced for tropical avian seed dispersal networks. For example, different degrees of specialisation have been found across forest strata (with canopy networks being less specialised than those at lower strata; Schleuning *et al.*, 2011), and between forest interiors and forest edges (with more specialised and less diverse networks in forest interiors; Menke *et al.*, 2012; Saavedra *et al.*, 2014), these differences being mostly driven by changes in the composition of the bird assemblage (proportion of forest-obligate vs. forest-generalist species). The specialisation degree in tropical seed dispersal networks also varies at larger scales, as evidenced by a study across a mosaic forest landscape in South Africa (Chama *et al.*, 2013) where patches containing bigger fruit densities, but fewer fruiting plant species, harbour more specialised networks, suggesting the importance of resource availability for promoting paired specialised interactions. Spatial variability in seed dispersal network structure has also been found in the temperate woody habitats of central Europe, especially at fine

scales. For example, in the mature forests of Białowieża (Poland), changes in bird assemblage composition underpinned the decreases in redundancy (average number of frugivorous bird species per plant) between forest interiors and edges (Albrecht *et al.*, 2013). However, in the woody hedgerows of central Germany bird-plant networks have been found to show high values of interaction diversity and evenness, with almost no variation across farmlands, orchards and forest edges (Plein *et al.*, 2013). There, the functional redundancy of some birds (e.g. common starling *Sturnus vulgaris* and thrushes) able to move easily and track fruits across the landscape, led to similarly diverse seed dispersal across these habitat types, even with bird species turnover.

Macroecological and biogeographical processes also affect the structure of bird-plant mutualistic networks, as suggested by changes in network structure across altitudinal and latitudinal gradients. Altitudinal changes in network structure and functioning have been evidenced in Neotropical bird-plant assemblages. For example, Costa Rican hummingbirds are less specialised, in terms of the plant species that they use as floral resources, at high than at mid-low altitudes, probably due to a reduction in floral resource availability and increased intraspecific competition, which forces niche expansion in hummingbird species (Maglianesi *et al.*, 2015a). Bird-plant interactions may also be structured along altitudinal gradients, as shown by the positive across-elevation correlation between the functional diversities of frugivorous birds and fleshy-fruited plants, indicating strong phenotypic matching on a macroecological scale (Dehling *et al.*, 2014). Climatic and latitudinal gradients have also been evidenced in bird-plant mutualisms (Kissling and Schleuning, 2015). For example, in the West Indies, rainfall gradients affect the role of hummingbirds in pollination networks, with birds being more impor-

tant than insects at higher rainfall levels, due to their higher energy demand forcing them to feed on flowers even during rain (Martín-González *et al.*, 2009). Specialisation in hummingbird pollination networks also changes with latitude in the Americas, increasing towards the Equator, favoured by higher precipitation, higher plant species richness, and a higher climatic stability during the Quaternary (Dalsgaard *et al.*, 2011). Moreover, historical climatic stability could also lead to more modular and less nested pollination networks across the globe, reflecting the occurrence of subgroups of species that specialise on each other as they have somewhat similar traits, such as hummingbirds and large-sized elongated flowers (Dalsgaard *et al.*, 2013). Conversely, in avian seed dispersal networks, a global study demonstrated that specialisation increases with latitude and decreases with local and regional plant species richness (Schleuning *et al.*, 2012), suggesting that the lower plant richness resources at higher latitudes would force frugivorous birds to specialise on a narrower range of resources. Climate and, especially, assemblage species richness, could also affect nestedness of seed dispersal networks, with assemblages that are more nested occurring in areas with more species and low-rain current climate (Sebastián-González *et al.*, 2015). In this case, a nested structure could be operating as a way for minimising interspecific competition and favouring species coexistence.

Insularity also has large effects on the patterns of mutualistic interactions between birds and plants (Traveset, 1999; Kaiser-Bunbury *et al.*, 2010). Islands are typically small, food-poor habitats where vertebrates often reach high densities, thus being forced to widen their feeding niche and to interact with a greater proportion of species than on the mainland. This process of “interaction release” (Traveset *et al.*, 2015) could force insectivorous and granivorous birds to

forage on other food resources, like flower pollen, nectar and fruits, behaving as “super-generalists” that shape the structure of mutualistic interaction networks. For example, in the Galápagos, native birds exploit a large number of native and exotic plant flower resources, making the bird-plant visitor network highly connected, generalised and nested, even compared with other insular avian pollination networks (Traveset *et al.*, 2015). Island avian seed-dispersal networks also differ from their mainland counterparts. For example, focusing on a common pool of Mediterranean species, González-Castro and collaborators (2012a) showed that Canarian and Balearic networks were smaller and less complex than a mainland network in southern Spain. Bird species on Gran Canaria tend to be more specialised, and to show a higher dependence and interaction symmetry with plants, than on the mainland. However, at a global scale, insular seed dispersal networks, especially those in more isolated islands, are more asymmetric than mainland ones because they comprise fewer species of birds but a similar number of plants, resulting in plants being more dependent on particular frugivores than vice versa (Schleuning *et al.*, 2014b). The higher extinction rates of birds on islands than on the mainland at the same latitude could underpin these differences (Schleuning *et al.*, 2014b).

The structure of interaction networks is also highly variable in time at different scales. The time fluctuations of bird and plant species abundances are expected to cascade into the participation in interactions, with some species occurring only transiently in networks, while others persist for much longer periods (Yang *et al.*, 2013; Bascompte and Jordano, 2014). Individual species may thus achieve high degrees in interaction networks either through interaction concurrence (i.e. many partner species co-occur at the same time) or by sequentially interacting with many successive partners.

For example, in a montane forest of Puerto Rico, most frugivorous bird and fleshy-fruited plant species appear only briefly and participate in few interactions, although a few persistent species have high degrees owing to sequential collection of partners rather than concurrence (Yang *et al.*, 2013). A similar effect of persistence (length of the fruiting phenology) explained plant species degree in a Canarian shrubland seed dispersal network, although bird species degree was mostly related to temporary plant species richness, suggesting an effect of interaction concurrence (González-Castro *et al.*, 2012b). Species concurrence was similarly important in the Hato Ratón network, as suggested by a positive effect of the temporary density of bird species on their degree and interaction strength (the more abundant birds achieving stronger interactions with more concurrent plant species; Carnicer *et al.*, 2009). There, the ability of bird species to switch their diet rapidly between insects in summer and fleshy fruits in autumn, conditioned by bird gape width, also positively affected bird species degree and asymmetry (Carnicer *et al.*, 2009). Despite the evidenced seasonal variability in bird specific roles, some avian seed dispersal networks show an unexpected temporal consistency in their structure motivated by the seasonal turnover of functionally redundant bird species (Plein *et al.*, 2013).

HUMAN IMPACT ON BIRD-PLANT MUTUALISTIC NETWORKS

Human pressure on natural ecosystems has provoked an unprecedented loss of biodiversity worldwide, affecting birds and their ecological functions (Şekercioğlu *et al.*, 2004; Şekercioğlu, 2006). By altering bird and plant abundances and richness, by imposing selective filters on species traits, and even by simply modifying species behaviours and performances, the different drivers of

human-induced global change greatly modify the structure and functioning of mutualistic networks (Tylianankis *et al.*, 2008; 2010; Valiente-Banuet *et al.*, 2015).

Human use of natural resources may affect bird-plant networks through habitat alterations at different scales. Fine-grained habitat degradation, such as logging in mature forests, causes a decline in bird habitat specialists, hence altering the generalisation in interactions with plants (Moran *et al.*, 2004; Albercht *et al.*, 2013). Large-scale habitat destruction has been predicted to disassemble mutualistic networks in a deterministic way, as species extinctions would provoke very fast losses of interactions once a critical value of habitat loss has been reached (Fortuna *et al.*, 2013; Lever *et al.*, 2014). Loss of species and interactions may, however, be decoupled, such that ecological interactions are often lost at a higher rate (Valiente-Banuet *et al.*, 2015). This implies that the loss of interactions may occur well before a species' disappearance, affecting pollination and seed dispersal functioning at a faster rate than bird and plant species extinctions (McConkey *et al.*, 2012; Valiente-Banuet *et al.*, 2015). In most human-impacted landscapes, habitat destruction entails not only habitat loss, but also an increase in patch isolation (i.e. fragmentation). Thus, the combined effects of habitat loss and fragmentation may strongly affect interactions in bird-plant assemblages, especially when bird species have differential responses to habitat loss and isolation depending on, for example, bird body size (with large species being more susceptible to habitat loss due to their typically smaller abundance, whereas small, low-mobility species are more susceptible to isolation effects; Hagen *et al.*, 2012). Thus, extensive habitat losses with small changes in isolation would mostly affect interactions involving large generalist birds and large-flower/fruit specialist plants, decreasing redundancy and nestedness in interaction

networks, whereas when habitat loss is accompanied by fragmentation, a strong decay of interactions (including the many rare links involving small birds) and network impoverishment would be expected (Hagen *et al.*, 2012).

Overexploitation of bird and plant species is having a pervasive effect in disrupting mutualistic interaction networks and provoking functional decays of pollination and seed dispersal services worldwide (Şekercioğlu *et al.*, 2004; Dirzo *et al.*, 2014). Hunting-derived defaunation in tropical forests is causing the loss of large frugivorous birds, with a myriad of effects derived from the associated loss of their seed dispersal service to large-fruited plants, from plant seed evolutionary downsizing (Galetti *et al.*, 2013) to decreases in carbon storage potential (Bello *et al.*, 2015). The selective removal of large, highly endangered birds (e.g. *Cotingidae* and *Ramphastidae*) is expected to change seed dispersal networks in tropical forests dramatically, as these species are the strongest contributors to network organisation (in terms of high connectivity as measured by degree and contribution to modularity and nestedness; Vidal *et al.*, 2013; 2014).

Global climatic warming is altering the natural cycles and phenologies of plants and animals, especially in non-tropical latitudes, increasing the probability of temporal mismatch in many plant-pollinator and plant-seed disperser interactions (Tylianakis *et al.*, 2008). Interaction losses due to increased phenological mismatch have been evidenced for insect-based pollination networks (e.g. Hegland *et al.*, 2009; Burkle *et al.*, 2013). Similar effects are expected for bird-based mutualistic networks, as bird migratory calendars, and plant flowering and fruiting periods, are currently being modified by warming. For example, the redwing has been shown to suffer a decline in the probability of wintering in central and southern Europe

(Rivalan *et al.*, 2007), where this species is a major seed disperser of many woody plants (e.g. Snow and Snow, 1988; Guitián *et al.*, 2000; Martínez *et al.*, 2008). Also, changes in flowering phenology may affect hummingbird populations in the long term, with mismatches relative to nectar availability potentially leading to decreases in bird reproductive success (Hegland *et al.*, 2009).

Besides provoking species declines and extinctions, humans may affect mutualistic networks by introducing new bird and plant species into pre-existing assemblages (Traveset and Richardson, 2014). The effect of interaction introductions has been especially pervasive on islands, due to their typically low original richness and weakly competitive communities (Kaiser-Bunbury *et al.*, 2010). Exotic species frequently become invasive thanks to their generalist niche (Traveset and Richardson, 2014), and take advantage of the usually highly generalised structure of native networks to quickly integrate into them (e.g. Spotswood *et al.*, 2012; Heleno *et al.*, 2013 a, b; García *et al.*, 2014). These alien interactors (e.g. plants in the avian seed dispersal networks of the Galápagos and Azores; Heleno *et al.*, 2013 a, b) frequently promote a rearrangement of links, transferring them from generalist natives to super-generalist invaders, which then become central nodes in the network and increase nestedness. These changes in network structure are assumed to increase network stability and specifically promote the persistence of exotic species, fostering the invasion process with a concomitant, negative effect on native communities (Traveset and Richardson, 2014). However, not all exotic species are thought to have negative impacts through their integration in bird-plant mutualistic networks. For example, in Hawaii, the exotic Japanese white-eye *Zosterops japonicus* has become a frequent flower visitor of many native trees deprived of their native pollinators, contributing therefore to

forest regeneration (Aslan *et al.*, 2104). Similarly, in the New Zealand forests where native frugivorous birds have become rarer (due to predator invasion and habitat loss), the blackbird, song thrush *Turdus philomelos* and common starling introduced by European settlers are now important seed dispersers of fleshy-fruited woody plants (Kelly *et al.*, 2010; García *et al.*, 2014). Interaction networks in which exotic birds have a stronger role as seed dispersers show lower specialisation, higher nestedness and higher redundancy of plants, suggesting that exotic birds probably enhance the stability of the native, community-wide seed dispersal, even in native forests (García *et al.*, 2014).

CONCLUSIONS AND FUTURE DIRECTIONS FOR RESEARCH

This review article suggests that the knowledge of bird-plant ecological networks is now built on solid theoretical and empirical bases. The network approach emerges as a powerful tool for understanding the complexity of avian communities in aspects as diverse as spatial behaviour, habitat use and interspecific interactions. Specifically, the study of bird-plant mutualistic interactions verifies the existence of strong structural generalities in ecological networks, and sheds light on the major ecological and evolutionary mechanisms and the sources of predictable spatio-temporal variability of networks. Despite these findings, at least three issues still require further development, and as such pinpoint major directions for future advance of this research field.

Firstly, a wider conceptual framework could be established for integrating the different ecological and evolutionary mechanisms determining the occurrence and the frequency of paired interactions, and hence the structure of interaction networks, in real-world (i.e. human-impacted) ecosystems

(fig. 6; Schleuning *et al.*, 2015; Bartomeus *et al.*, 2016). Bird and plant species traits and features may be better identified as the mechanisms of paired interactions when divided into three types: filtering traits, matching traits and behaviour. Filtering traits condition the probability of concurrence, but also the relative abundances of bird and plant species in the local communities, as a response to environmental (both natural and anthropogenic) sieves. For example, bird migration phenology is a life-history trait shaped by adaptation to long-term climatic conditions, whereas bird body size is a trait conditioning the response to human-caused overhunting and habitat loss. By restricting concurrence, these traits could thus be conditioning the probability of interaction between species pairs, provoking forbidden links. Once bird and plant species co-occur in local communities, matching (e.g. bird gape width) and behavioural traits (e.g. bird body size shaping feeding preferences) may be conditioning the probability of paired interaction (also causing forbidden links). Traits from all three categories (N.B. a single trait may in fact meet the requirements of each of the types, e.g. bird body size), may be correlated among species through phylogenetic relatedness, which could operate as an evolutionary mechanism on interaction network patterns (fig. 6). Finally, species abundances could have an independent, probabilistic effect on the frequency of interaction between birds and plants, irrespective of their traits (fig. 6). The methodological application of this integrative framework could be based on comparing the predictive ability of models incorporating multiple determinants of interaction probabilities (e.g. Vizentin *et al.*, 2014), controlling for sequential causalities in ecological determinants (e.g. Kaiser-Bunbury *et al.*, 2014), and accounting for the phylogenetic signal in the relationships between traits and paired interactions (e.g. Bascompte and Jordano, 2014).

Secondly, empirical studies should widen their scope to evaluate the role of birds in mutualistic networks at larger ecological scales. This can be achieved by incorporating other animal groups in networks which account for similar interactions with plants (e.g. bats in seed dispersal networks,

Mello *et al.*, 2011; 2014; insects in pollination networks, Dalsgaard *et al.*, 2009). In this way, the functional complementarity and/or redundancy between birds and other animal groups can be highlighted (e.g. Donatti *et al.*, 2011). Also, the building of meta-networks integrating different types

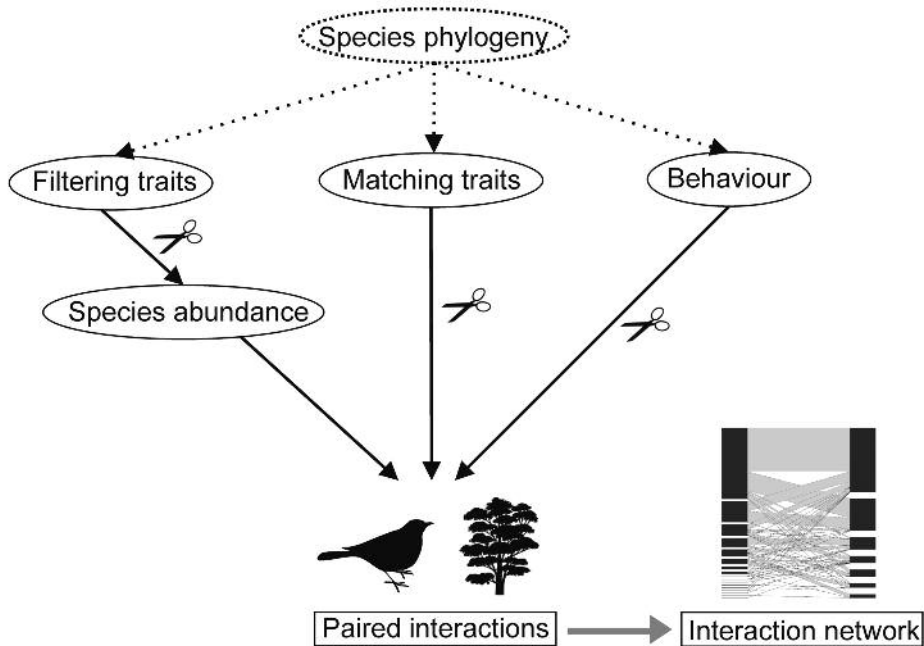


FIG. 6.—Conceptual model for integrating the ecological and evolutionary mechanisms which determine the occurrence and the weight of paired species interactions and the structure of networks. Traits affect bird and plant species occurrence depending on their response to environmental sieves (filtering traits), as well as the occurrence of interaction when species co-occur in the same community, depending on physical constraints (matching traits) and on species preferences (behaviour). Forbidden links occur when traits hamper the occurrence of interactions (indicated by the scissor symbol). Species abundance may have a probabilistic, trait-independent effect on interaction frequency. Traits are ultimately shaped by species phylogenies.

[Modelo conceptual integrador de los mecanismos ecológicos y evolutivos que determinan la aparición y el peso de las interacciones pareadas entre especies y la estructura de las redes. Los rasgos afectan la aparición de las especies de aves y plantas dependiendo de su respuesta a los filtros ambientales (rasgos de filtrado), así como la aparición de las interacciones entre las especies cuando estas concurren en la misma comunidad, dependiendo de sus restricciones físicas (rasgos de encaje) y de las preferencias de las especies (comportamiento). Los vínculos prohibidos surgen cuando los rasgos impiden la aparición de las interacciones (indicado por el símbolo de tijera). La abundancia de las especies puede tener un efecto probabilístico en el peso de las interacciones, independiente del de los rasgos. Los rasgos están finalmente moldeados por la filogenia de las especies.]

of interaction with plants (e.g. pollination, granivory and seed dispersal; Kelly *et al.*, 2010; Pocock *et al.*, 2012; Albrecht *et al.*, 2014) is highly informative about the importance of birds across ecological functions. Finally, an effort must be made to integrate interaction and spatial networks (Hagen *et al.*, 2012). Avian seed dispersal networks are the perfect candidate for such a goal, given that bird-mediated seed movement may be interpreted, by means of spatially explicit approaches, as a process that determines ecological connectivity (e.g. Rodríguez-Pérez *et al.*, 2014).

Thirdly, further steps towards the functionality of ecological networks (i.e. the ecological effects of interaction complexity) are required. This is especially challenging in bird-plant mutualistic networks, where the reciprocal demographic effects of paired interactions are difficult to assess. From the perspective of birds, the result of trophic interactions should be estimated in terms of specific survival and reproduction. As shown for insect pollinators (Vázquez *et al.*, 2012), the tropical hummingbirds may be an adequate group for linking patterns of interactions with plants, bird survival and clutch size (Waser, 1976). However, many avian seed dispersers are only frugivorous during the post-breeding season and in wintering areas, their survival and breeding being more dependent on factors other than frugivory (Jordano, 2000). From the perspective of plants, pollination and seed dispersal networks should account for quantitative components (number of pollen grains deposited on flowers; number seeds deposited far from mother plants), but also for the qualitative components that ultimately determine the demographic fate of fertilised ovules and dispersed seeds (Carlo and Yang, 2011; Schleuning *et al.*, 2015). For example, birds with contrasting spatial behaviours differ in quality as pollinators (by conditioning different rates of xenogamous pollen

crosses; Rodríguez-Rodríguez *et al.*, 2013) and seed dispersers (by determining the microhabitat of seed deposition; Carlo and Yang, 2011). New methodologies, enabling the specific identification of the pollinator from fertilised ovules (e.g. by excluding flowers to allow only one visit per flower per pollinator species; Rodríguez-Rodríguez *et al.*, 2013) and the seed disperser from seeds deposited in specific sites (e.g. by genetic or probabilistic assessment; González-Varo *et al.*, 2014; Donoso *et al.*, 2016), must be applied in order to incorporate ovule and seed fate into pollination and seed dispersal networks.

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