



RESEARCH ARTICLE

Functional Ecology



Waterbird seed-dispersal networks are similarly nested but less modular than those of frugivorous birds, and not driven by functional traits

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Abstract

1. Frugivory is widely recognized as vital for the dispersal of many plants. Moreover, plant species and their frugivorous dispersers form seed-dispersal assemblages whose structure has important implications for the persistence and stability of the community. However, dispersal interactions between plants and non-frugivorous animal groups such as waterbirds remain largely understudied.
2. We aimed to characterize the structure of waterbird seed-dispersal networks, assess if this structure is similar to that of networks formed between frugivorous birds and fleshy-fruited plants, and identify bird or plant functional traits important for the maintenance of network structure.
3. We used network analyses and data from four community-level studies on waterbird gut contents, including 12 bird and 88 plant species. We compared the network structure of waterbirds to those from previous studies of frugivorous birds. We also related the contribution of each species to the network structure with functional traits (e.g. size, habitat requirements, diet).
4. Waterbird seed-dispersal networks are similarly nested (i.e. specialists interact with a subset of those species that interact with generalists) but less modular (i.e. fewer semi-independent groups of highly interacting species) than those of frugivores. Dabbling ducks, diving ducks and rallids did not separate into modules. The contribution of bird or plant species to network structure was not related to any functional trait.
5. Seed-dispersal networks of waterbirds share some organizational patterns with those of frugivores, but the underlying processes are not related to functional traits. This is probably related to fundamental differences between waterbirds and frugivores in how seeds are ingested. Differences in the functional role of waterbirds for seed dispersal are likely driven by other processes such as differences in population size, movement, ecology or gut processing of seeds.

KEYWORDS

diet, endozoochory, functional traits, modularity, nestedness, wetlands

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1 | INTRODUCTION

Mutualisms between frugivores (i.e. animals eating fleshy fruits) and fruiting plants are crucial for plant dispersal and ecosystem functioning, and therefore are well-researched (Bascompte & Jordano, 2007; Wenny, Sekercioglu, Cordeiro, Rogers, & Kelly, 2016). Frugivores and fruit-producing plants usually participate in nested seed-dispersal networks (i.e. specialists interact with a subset of species that interact with generalists) and, sometimes, these are modular (i.e. with semi-independent groups of highly interacting species, Sebastián-González, Dalsgaard, Sandel, & Guimarães, 2015). The extent of nestedness and modularity influences the stability and persistence of the animal and plant communities involved (Rohr, Saavedra, & Bascompte, 2014; Thébault & Fountain, 2010).

Importantly, in seed-dispersal assemblages, not all animal and plant species play the same role. Some animal species disperse plants at high rates while others do it opportunistically. Also, some plant species are dispersed by many animal vectors while others are only dispersed by few (Jordano, García, Godoy, & García-Castaño, 2007; Mello et al., 2011). The most important frugivorous vectors are often large animals that can swallow seeds with different sizes (Donoso, Schleuning, García, & Fründ, 2017; but see Ruggera, Blendinger, Gómez, & Marshak, 2016), or generalist species that forage on a wide variety of fruit species to cover all their nutritional requirements (Sebastián-González, 2017). Also, small seeds in fruits with nutritious energetic pulp are dispersed in larger numbers because they are ingested by more animal species (Blendinger et al., 2015; Sebastián-González, 2017).

However, only 8% of the angiosperm flora of continental Europe have fleshy fruits (Heleno & Vargas, 2015). Most angiosperms have dry indehiscent fruits or small seeds released from dehiscent fruits (Julve, 1998). Many plant taxa are dispersed by vertebrate vectors such as ungulates or waterbirds, in which plants obtain benefits from seeds that survive gut passage and are effectively dispersed, and animals obtain food from foliage and from the fraction of seeds digested during gut passage (Albert et al., 2015; Costea et al., 2019). Migratory waterbirds are particularly important for long-distance dispersal, and hence for maintaining ecosystem biodiversity and functioning, genetic flow or mixing between plant populations (Kleyheeg, Treep, de Jager, Nolet, & Soons, 2017). Over 400 European species of angiosperms lacking a fleshy fruit are dispersed via gut passage ('endozoochory') by dabbling ducks alone (Soons, Brochet, Kleyheeg, & Green, 2016). Such dispersal interactions are a feature of all waterbirds (Green, Brochet, Kleyheeg, & Soons, 2016), and recent studies have underlined the importance of shorebirds, gulls and geese as plant vectors (Hattermann, Bernhardt-Römermann, Otte, & Eckstein, 2019; Lovas-Kiss et al., 2018, 2019). However, almost nothing is currently known about how waterbird-seed dispersal assemblages are organized.

Experimental studies with dabbling ducks and shorebirds suggest that longer maximum retention times during gut passage of relatively

small and hard seeds confer a higher seed survival and increase long-distance dispersal (Green et al., 2016; Lovas-Kiss et al., 2020; Soons, van der Vlugt, van Lith, Heil, & Klaassen, 2008). However, there is an absence of community-level analyses of how animal and seed traits determine the structure of waterbird-plant assemblages, and of which traits drive dispersal interactions. Network analyses are a useful tool to compare the structure of different assemblages and are widely used in frugivore assemblages, but have never before been applied to plant dispersal by waterbirds.

In this study, we use network analyses of four detailed community level studies on waterbird diet, including 12 waterbird and 88 plant species to: (a) characterize the structure of waterbird seed-dispersal networks, (b) assess if this structure is similar to that of networks formed between frugivorous birds and fleshy-fruited plants and (c) identify the functional traits of waterbird species and dispersed plants that play important roles in the maintenance of network structure. We tested for a relationship between body size or bill size and seed size. As ducks ingest food items that get retained on the lamellae, which serve as a filter (Gurd, 2008), we expected that duck species with higher density of lamellae in their bills would disperse a broader range of seed sizes (i.e. a higher diversity of plant species), especially including (but not restricted to) those falling in the smaller end of the seed size range (Brochet et al., 2012). Finally, given differences in bill morphology and microhabitat use between rallids, diving ducks and dabbling ducks (Cramp & Simmons, 1977), we expected dispersal networks of waterbirds to be modular, as are some of those for avian frugivores.

2 | MATERIALS AND METHODS

2.1 | Dataset for waterbird-plant interactions

We used data from four published studies that evaluated the gut contents of waterbirds (sensu Wetlands International, 2020) at the community level in different wetlands of international importance in England, France and Spain (details in Table 1; Figure 1; Appendices S1 and S2). These four studies are the only ones we were aware of in Europe that identify the seeds ingested to a high level of accuracy, and also include ≥ 4 waterbird species from the same site (see Soons et al., 2016 for other studies which did not meet our criteria). The data were collected exclusively from the non-breeding period and from birds shot by hunters or under scientific permits. All four studies included dabbling ducks (seven species), two of them included diving ducks (three species) and two included rallids (two species). The species studied were selected because they were the most abundant waterbirds at each study site. We only included species whose diet was determined for at least five individuals.

Diet was determined from the content of the digestive tract, and seeds were identified to the genus or species level in most cases. Presence of seeds in the upper digestive tract is a suitable proxy for

TABLE 1 Description of the four study sites, with location, number of waterbird and plant species (and of plants with fleshy fruits), which waterbird guilds are present in the dataset (DB dabbling ducks, DV diving ducks, RL rallids), from which part of the gut the seeds were extracted, and the reference for the study. OPG: oesophagus + proventriculus + gizzard

	Ebro Delta	Champagne	Camargue	Ouse Washes
Location	NE Spain	N France	S France	E England
Study period	October–March	August–February	October–March	September–January
No. waterbird species	4	9	5	9
No. birds sampled	176	151	216	873
No. plant species	35	46	33	41
Fleshy-fruited	1	1	1	2
Guilds	DB	DB, DV, RL	DB	DB, DV, RL
Diet extracted from	Gizzard	OPG	Oesophagus	OPG
Main reference	Soons et al. (2016)	Mouronval, Guillemain, Canny, and Poirier (2007)	Pirot (1981)	Thomas (1982)

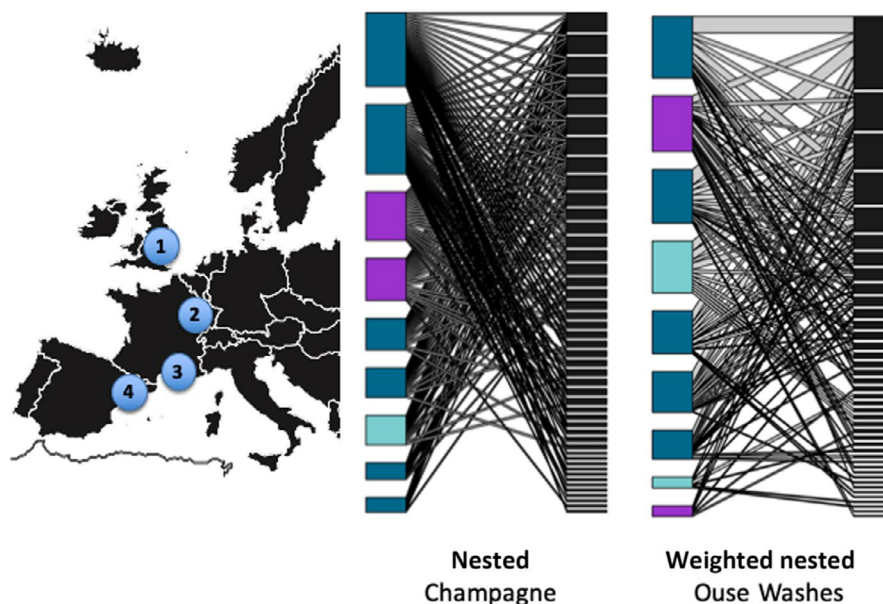


FIGURE 1 Locations of the four study sites and the network structure for a nested (Champagne) and a weighted nested (Ouse Washes) assemblage. Each coloured rectangle represents one waterbird species and each black rectangle a plant species. Dabbling ducks are represented in dark blue, diving ducks in purple and rallids in light blue. For unweighted networks, the size of the rectangles is proportional to species degree (i.e. number of links that a given species established, or number of partners with which a given species interacted); for weighted networks, they are proportional to the number of interactions recorded for a given species. The waterbird is linked to the plant if it ingested its seeds. In the weighted network, the width of the line represents how many times the interaction was observed (i.e. the number of seeds found in the gut of the waterbird). Sites: (1) Ouse Washes, (2) Champagne, (3) Camargue and (4) Ebro Delta. See Figure S1 for networks from the remaining sites

seed dispersal, because experimental and field studies show that a proportion of ingested seeds (often exceeding 30%) from all taxa survive digestion via rapid gut passage or regurgitation (Brochet, Guillemain, Gauthier-Clerc, Fritz, & Green, 2010; Lovas-Kiss et al., 2020; Soons et al., 2008). The probability of effective dispersal increases with the number of seeds in a bird's digestive tract, so that the number of seeds ingested provides a *quantitative* proxy for seed dispersal (Schupp, Jordano, & Gómez, 2010).

When present in the dataset, we eliminated crops (wheat *Triticum aestivum*, barley *Hordeum vulgare*, rice *Oryza sativa*, oats *Avena sativa*, rye *Secale cereal*, maize *Zea mays*, sunflower *Helianthus annuus*,

Sorghum bicolor and grape *Vitis vinifera*) because they are often used by hunters to attract birds and may not have been eaten naturally, and because they are generally not viable after gut passage (Bartel, Sheppard, Lovas-Kiss, & Green, 2018; Lovas-Kiss et al., 2018). Plants with fleshy fruits were rare in the datasets (Table 1).

2.2 | Network structure

We constructed one network matrix for each community, where each column represented a plant species and each row a waterbird

species. Each cell in the matrix a_{ij} was filled with the number of seeds of the plant j that were dispersed by the waterbird i . We chose to use 'number of seeds in the digestive tract' as the interaction weight because this is the metric that makes more sense in our system. Frugivorous birds feed on fruit, so the number of seeds may vary depending on the seeds per fruit. Waterbirds, by contrast, feed on seeds themselves, from both on and off (e.g. on water surfaces, in sediments) the plant. With this matrix, we calculated two network metrics: weighted nestedness and weighted modularity. Then, we transformed this matrix into a binary one where all cells with $a_{ij} > 0$ were assigned a value of 1, and all other cells were assigned a 0. With this binary matrix we calculated nestedness, and modularity.

For each study site, we calculated nestedness using the metric NODF, and weighted nestedness using WNODF. A seed-dispersal assemblage is highly nested when the birds that disperse the most plant species include both those dispersed by many other birds and those dispersed by few birds, whereas birds dispersing the fewest plant species only disperse those dispersed by many other birds. Both WNODF and NODF range from 0 to 100, where large numbers indicate highly nested assemblages. Since nestedness values are affected by differences in the number of interactions across species, we compared the observed nestedness value for each matrix with the nestedness values of 1,000 matrices constructed following null models. We chose two models widely used in seed dispersal interaction studies to allow comparisons with other studies. In the null model for NODF the probability of a cell a_{ij} to show a presence is $\left(\frac{P_i}{C} + \frac{P_j}{R}\right) / 2$, in which P_i is the number of presences in the row i , P_j is the number of presences in the column j , C is the number of columns and R is the number of rows. In the null model for WNODF, the species-specific probabilities are proportional to the relative weight (i.e. number of seeds) of each species.

We also estimated the modularity of each qualitative network using the metric M (Newman & Girvan, 2004). A seed-dispersal assemblage is considered modular if there are groups of waterbird species that preferentially disperse particular groups of seed species, but not the seeds of other groups. We computed M using the simulating annealing algorithm. We also calculated the weighted modularity metric Q using the algorithm QuanBiMo (Dormann & Strauss, 2013). Both M and Q vary from 0 to 1, with large values characterizing highly modular networks. Null models for modularity fix the probability that any two species interact, based on that observed in real networks. In all null models for nestedness and modularity, the number of animal and plant species (and therefore network size) is kept constant, but the marginal totals (i.e. sum of all cells in each column or row) change, so that the connectance of the matrix (i.e. proportion of realized interactions) is also different in each randomized matrix. These null models aim to disentangle whether the network metrics are driven by species-specific frequency distributions, independently of species traits, or whether species traits may constrain the interaction.

Because some level of nestedness and modularity is expected even in randomly organized assemblages, we also evaluated whether the observed modularity and nestedness were statistically significant, that is, if the observed values fell outside the 95% confidence intervals

calculated from randomized matrices. Finally, we standardized the modularity and nestedness values as z-scores, to allow comparisons among matrices as a z-metric = $(\text{metric} - \text{mean}(\text{metric}_{\text{null}})) / SD_{\text{null}}$, where $\text{mean}(\text{metric}_{\text{null}})$ is the mean of all the metric values of null model matrices and SD_{null} is its standard deviation. We calculated all the network metrics using the BIPARTITE package (Dormann, Freund, Blüthgen, & Gruber, 2009) in R version 3.5.2 (R Development Core Team, 2018).

We chose to include both weighted and unweighted metrics because they represent different aspects of our system. Nestedness measures whether specialist plant species tend to rely on generalist bird species, and vice versa, whereas weighted nestedness identifies interactions in which, in addition to the specialization pattern being nested, the interaction frequency (or weight) of the most generalist species is larger than that of the specialist species. For example, a fruit can be consumed by many bird species (e.g. because it is small and has some essential nutrients) but not in large numbers (e.g. because it is not abundant). A matrix with many species like this may be nested but not weighted nested. For modularity, the most important connectors (i.e. species with important network roles) interact with many species from their module in unweighted networks, but these species also need to have a large interaction frequency in weighted networks to be key connectors. Thus, the most important species may change depending on the metric used.

2.3 | Species-level network metrics

Additionally, we calculated some network metrics at the species level to identify those species that have a particularly important role in maintaining network structure. As the networks showed a more nested than modular structure (see Section 3), we focused on nestedness. For each species and network, we calculated the contribution to nestedness. In a perfectly nested network, when the degree (i.e. number of species with which a given species interacts) of the species i is lower than the degree of species j , the set of species interacting with i are a subset of the set of species interacting with j . Any species following this pattern will make a high contribution to nestedness, while species that deviate from the pattern will make a low contribution. Species that make a high contribution to nestedness interact with most of the partners with which the other species in the network interact, and are responsible for maintaining the structure of the assemblage. Species with a low contribution to nestedness may also have an important role because they interact with those partners with which no one else interacts. The contribution to weighted nestedness depends on similar reasoning, but accounts for the number of seeds found in the duck gut. We calculated the contribution to nestedness using ANINHADO software (Guimarães & Guimarães, 2006) and the weighted contribution with the BIPARTITE package.

2.4 | Waterbird and seed traits

We used five waterbird traits that can be related to diet and thus to their role as seed dispersers: (a) Lamellae density, calculated as

the number of lamellae in the upper mandible per cm, for dabbling ducks and Pochard *Aythya ferina* (Mateo, Guitart, & Green, 2000; Pöysä, 1983). Rallids do not have lamellae, and comparable measures for other diving ducks were not available; (b) Body mass, in g (Dunning, 1993); (c) Bill length, in cm. We also calculated two variables that describe (d) the percentage of food items (i.e. invertebrates, fish, other vertebrates, scavenging, seeds and other plant parts) in the diet and (e) the proportional use of different microhabitats to obtain food (i.e. below the water surface, around the water surface, on the ground and in the understory). Data for (c)–(e) were obtained from Wilman et al. (2014). All duck species in this study have a filtering foraging method (Cramp & Simmons, 1977). They swallow seeds intact that are filtered in the lamellae, discarding small items (which may include some small seeds), water and sediments (Gurd, 2008). Rallids also swallow seeds intact. Thus, handling method was not included as a variable.

We used eight plant traits, including Ellenberg indicator values for (a) habitat soil fertility (N), (b) moisture (F) and (c) light (L; Ellenberg et al., 1991; adapted by Hill, Mountford, Roy, & Bunce, 1999). We also used (d) seed length, in mm; (e) seed mass, in g; (f) seed roundness, calculated as seed height/seed length; (g) Raunkiaer life form (Ellenberg & Mueller-Dombois, 1967) and (h) Dispersal syndrome (Heleno & Vargas, 2015). Data for (d) and (e) were from the LEDA traitbase (Kleyer et al., 2008), data for (g) and (h) from the Baseflor database (Julve, 1998). Dispersal syndromes are not reliable indicators of dispersal mechanisms since they only assign endozoochory for fleshy-fruited plants (Costea et al., 2019). However, since they assign the plant species studied to water, wind and other vectors, birds feeding in different ways may be expected to ingest seeds from different syndromes.

2.5 | Statistical analyses

Because the trait data for waterbird diet and foraging strata were provided by several variables, we performed principal component analyses (PCA) to summarize them (Table S1 in Appendix S4). The first two axes of the PCA accounted for 62.9% of the variability for diet, and 88.0% for foraging strata, so we used these as summary variables.

We first used ANOVAs to test if there were differences in the contribution to nestedness and to weighted nestedness for waterbird or plant species among the four study sites. When significant, study site was included as a covariate in further models (see below, and Table S2). The weighted contribution to nestedness was log-transformed in all models to meet normality criteria.

We then performed generalized linear mixed models with the contribution to nestedness and its weighted version metrics as response variables, waterbird and seed traits as predictors, study site as a covariate (when significant in ANOVAs) and species as a random factor to account for repeated measurements for the same species in different study sites. We ran univariate (i.e. one predictor) models. We also explored multivariate (i.e. several predictor) models (results not shown), and none of them improved model fit in terms of AIC. All predictor variables were standardized to the same scale (i.e. they were transformed

to have a mean of 0 and standard deviation of 1). We used a normal distribution for all models, and we performed all analyses with the `lme4` package (Bates, Maechler, Bolker, & Walker, 2015).

No error distribution fitted our response variable for the contribution to nestedness in the plant species dataset, so we also tested the effect of each variable using a randomization approach. We first ran a GLM with a Gaussian distribution to obtain the coefficients of the model. Then, we re-calculated the model including the contribution to network structure as response variable and each of the species traits as explanatory variables, but randomizing the contribution to networks. We repeated the analyses 1,000 times and checked if the coefficients of the predictor variable in our model were within the range of values of coefficients from models with randomized variables. All analyses were done in R version 3.5.2 (R Development Core Team, 2018).

2.6 | Comparing waterbird and frugivore dispersal networks

We compared the network structure of the waterbird seed-dispersal networks in terms of nestedness, weighted nestedness, modularity, weighted modularity and the z-score of their metrics to that of 22 frugivore seed-dispersal networks (16 of them weighted, see Appendix S3 for details) from Sebastián-González et al. (2015), using Mann–Whitney *U*-tests. All the frugivore networks used included only bird species.

3 | RESULTS

Of 12 waterbird species, three were present in a single study site (one species in Ouse Washes and two in Champagne), while Mallard *Anas platyrhynchos* and Eurasian teal *A. crecca* were present in all four sites (Tables S3 and S4). The only plant species recorded in all sites was *Potamogeton pectinatus*, while 58 of the 88 plant species were recorded in a single site. Seeds were mostly achenes, and only three seed species were from fleshy fruits (Appendix S2).

3.1 | Assemblage structure

The structure of the waterbird seed-dispersal networks was nested in all four assemblages (Table 2; Figure 2). The weighted nestedness metric was also significant in three out of four, while no site showed a modular or weighted modular structure.

As many as 78% of waterbird and 60% of plant species had a large contribution to nestedness (>60; Appendices S1 and S2). The bird species with the largest contribution was the Mallard in the Champagne. The values for the contribution to weighted nestedness were high overall, and the European wigeon (*Mareca penelope*, Ebro Delta) had the largest contribution. Plants showed a similar pattern, with mostly high values of contribution to nestedness, which were especially large for *Carex riparia*, but low for *C. nigra* and *Rubus fruticosus* (all three from the Ouse Washes). The

	NODF	p-Value	WNODF	p-Value	M	p-Value	Q	p-Value
Ebro Delta	71.2	<0.01	47.5	<0.01	0.30	0.27	0.23	0.62
Champagne	71.1	<0.01	47.7	<0.01	0.25	0.15	0.24	1
Camargue	71.8	<0.01	52.3	0.03	0.23	0.06	0.18	0.7
Ouse Washes	42.0	<0.01	24.3	0.17	0.32	0.32	0.29	1

TABLE 2 Summary of network metrics and their significance for four study sites. Significant values are marked in bold

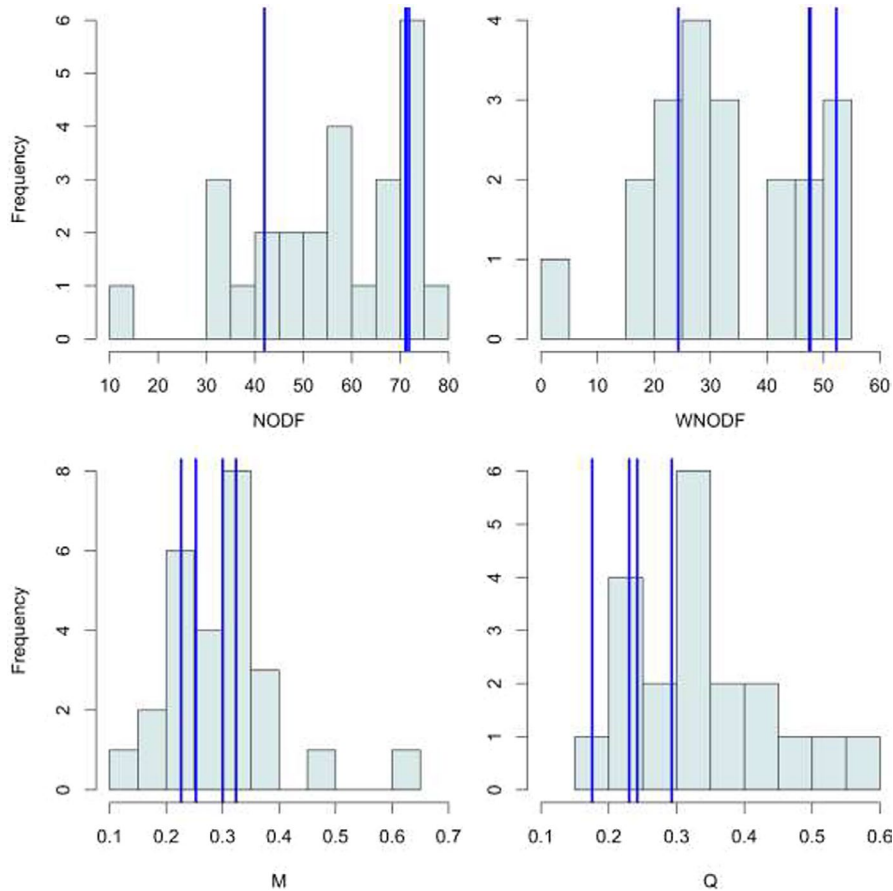


FIGURE 2 Distribution of NODF, WNODF, M and Q values for avian frugivore networks (taken from Sebastián-González et al., 2015). Blue lines represent observed values for the four waterbird seed-dispersal networks

values of the contribution to weighted nestedness for plants were all low (<0.27).

None of the waterbird or seed traits were related to their role in the network structure (Tables S5–S7), neither for contribution to nestedness nor for weighted nestedness. The contribution to nestedness of a given bird or plant species varied greatly among sites (Table S2; Figure S2). For example, the contribution of *Polygonum amphibium* was twice as high in the Champagne as in the Ouse Washes (Appendix S2).

3.2 | Comparing waterbird and avian frugivore dispersal networks

When comparing the waterbird seed-dispersal network structure with that of frugivore networks, we found that the nestedness values were similar (Figure 2; Figure S3; Table S8). However, frugivore networks had significantly larger values of weighted and standardized modularity (i.e. using z-scores, Figure 2; Figure S2; Table S8).

4 | DISCUSSION

Seed-dispersal networks formed between omnivorous waterbirds (ducks and rallids) and angiosperms showed a nested structure, in an analogous manner to the dispersal networks of avian frugivores (e.g. Bascompte & Jordano, 2007). This non-random pattern may confer higher stability and persistence to waterbird dispersal networks, as with frugivore networks (Rohr et al., 2014; Thébaud & Fountain, 2010). However, we found evidence of important differences between waterbird and frugivore networks. The structure of avian frugivore seed-dispersal networks is related to bird traits such as body size or the importance of frugivory in the diet, and plant traits such as fruit energetic content (Sebastián-González, 2017). None of the functional traits we analysed, and that have proven to be important for the nestedness of frugivore-seed dispersal networks, had a significant effect in waterbird networks. This suggests that predicting how global change will influence waterbird–plant dispersal networks will be more difficult than has been proposed for frugivore–plant networks (Schleuning et al., 2020).

Also, the non-significance of bird traits in the explanation of nestedness contrasts with earlier studies that found duck species with high lamellar density to ingest smaller seeds (Brochet et al., 2012; Green et al., 2016). However, seed size selection does not depend solely on lamellar density, but also on the flexible distance between maxillary and mandibular lamellae, allowing ducks to ingest seeds that would not be predicted by lamellar density (Gurd, 2008). Also, waterbird species in our study range from 305 to 962 g, and the largest seed diameter is 6.2 mm. Therefore, even the largest seed can be easily swallowed by any of these waterbirds (Burns, 2013). We also found no influence of seed size on network structure. However, seed size is linked to the *effectiveness* of seed dispersal, since small and hard seeds survive gut passage in larger numbers (Lovas-Kiss et al., 2020; Soons et al., 2008). Morphological dispersal syndromes also played no role in the assemblage structure, although this is not surprising since they ignore endozoochory of non-fleshy fruited plants (i.e. 'endozoochory' is assigned only to plants with a fleshy fruit), such that the syndrome cannot match the dispersal mechanism in these networks (Lovas-Kiss et al., 2019).

Despite the lack of relationships between the species role in the networks and their traits, the assemblages were nested, suggesting that other processes are behind that structural pattern. For example, as the abundance of seeds of different plant species in wetlands varies greatly across space, the most abundant species may be consumed in large quantities while rare species may be ingested less consistently. Such interspecific differences in abundance can drive the interaction asymmetry that is characteristic of nested communities (Vázquez et al., 2007). Species phenology may also affect interaction patterns in dispersal networks (Encinas-Viso, Revilla, & Etienne, 2012), but this is more likely for frugivores that take fruits directly from the plant. We can expect more decoupling between seed production and ingestion in waterbird networks, since seeds can be ingested months or even years after production, when taken from the seed-bank in sediments (Brochet et al., 2010; Figuerola, Green, & Santamaría, 2003; Green et al., 2016).

The lack of modularity in the results suggests that dabbling ducks, diving ducks and rallids are functionally redundant seed dispersers to some extent, as different waterbird species may disperse the same seeds. This agrees with previous findings that the diet of coexisting duck species overlaps, and that each species shows considerable plasticity (Cramp & Simmons, 1977; Figuerola et al., 2003). Ducks often take a mix of seeds from different plants in the same mouthful. Once a mixture of seeds is taken into the bill, separation of seed types is restricted, likely due to energy and time costs (Gurd, 2008). However, the effective dispersal of these seeds also depends on waterbird gut traits, habitat selection, seasonality and movement patterns, which are variable within and among species (Cramp & Simmons, 1977; Wetlands International, 2020). For example, the species studied include long-distance migrants such as Pintail *A. acuta* and Garganey *A. querquedula*, as well as sedentary species such as Moorhens *Gallinula chloropus*. Ducks also undergo longer daily movements between feeding and roosting sites than rallids (Guillemain et al., 2010). Thus, there seems to be considerable functional redundancy in the quantitative component of the

seed dispersal effectiveness, but the qualitative component of different waterbird species would potentially show a great variation, mainly due to variability in their movement patterns.

None of our waterbird seed-dispersal networks showed a modular structure. Modularity in seed-dispersal networks is more common when animal dispersers have large morphological or ecological differences (e.g. Donatti et al., 2011). Our dataset includes three of six waterbird guilds identified by Ramírez, Rodríguez, Seoane, Figuerola, and Bustamante (2018). The study of other assemblages at different wetlands that include other groups known to disperse seeds, such as shorebirds, gulls or herons (Green et al., 2016), may increase the modularity of the networks. However, we believe that we have captured the main structure of the networks in our study sites outside the breeding period, when ducks and rallids were highly dominant. Each assemblage includes the commonest waterbird species at that study site, all of which are known to be generalist seed eaters (Cramp & Simmons, 1977). Thus, we would not expect large changes in the network structure by including rarer waterbird species. Even waterbirds as different morphologically as gulls and storks can disperse the same set of plant species (Martín-Vélez, Lovas-Kiss, Sánchez, & Green, submitted).

Despite using the most complete datasets available for waterbird seed-dispersal networks, our study has limitations. None of the studies we used includes the complete seed-dispersal network (i.e. all waterbird species present in the wetland and all plants dispersed). In wetlands, this is not practical because sampling gut contents is impossible for some species, and many plants are likely to be dispersed in low numbers. Soons et al. (2016) found that new plant species would still be recorded in duck species even after sampling 400 individuals. Further studies may achieve large sample sizes via non-destructive sampling. Data from foraging observations are not suitable for sampling seed dispersal interactions in waterbirds, as it is hard to specify what seeds individuals are ingesting, especially when feeding below the water surface or when seen from a distance. However, excreta have proved valuable for quantifying seed dispersal by some waterbird species in different locations (Hattermann et al., 2019; Lovas-Kiss et al., 2019), and future studies may acquire similar data at community level. Also, it would be interesting to include birds that are secondary seed dispersers due to predation of fish or crayfish (Lovas-Kiss et al., 2018). Sample size is known to affect the structure of mutualistic networks (Costa, da Silva, Ramos, & Heleno, 2016; Rivera-Hutinel, Bustamante, Marín, & Medel, 2012), and thus may also affect some of our results. However, we used the most detailed information available on both seed ingestion and traits, so our study represents an important first step towards disentangling the structure of waterbird seed-dispersal networks.

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AUTHORS' CONTRIBUTIONS

E.S.-G. and A.J.G. conceived the ideas and designed methodology; E.S.-G., Á.L.-K., M.B.S., B.v.d.B. and A.J.G. collected the data; E.S.-G. analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

All data used in this study can be found in Figshare <https://doi.org/10.6084/m9.figshare.12707969> (Sebastián-González, Lovas-Kiss, Soons, van den Broek, & Green, 2020) and in the Supplementary Material of this article.

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SUPPORTING INFORMATION

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

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