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REVIEW

Dispersal of aquatic and terrestrial organisms by waterbirds: A review of current knowledge and future priorities

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Abstract

1. We review progress in our understanding of the importance of waterbirds as dispersal vectors of other organisms, and identify priorities for further research.
2. Waterbirds are excellent for long-distance dispersal (LDD), whereas other vectors such as fish and mammals disperse similar propagules, but over shorter distances. Empirical studies of internal and external transport by waterbirds have shown that the former mechanism generally is more important. Internal transport is widely recognised for aquatic plants and aquatic invertebrates with resting eggs, but also is important for other organisms (e.g., terrestrial flowering plants not dispersed by frugivores, bryophytes, tardigrades, fish eggs).
3. Waterbird vectors also are important in terrestrial habitats, and provide connectivity across terrestrial–aquatic boundaries. There are important differences in the roles of different waterbird species, especially those using different habitats along the aquatic–terrestrial gradient. Early attempts to predict zoochory based on propagule morphology have been found wanting, and more research is needed into how the traits of vectors and vectored organisms (including life history, dormancy and growth traits) explain dispersal interactions. Experimental studies have focused on the potential of propagules to survive internal or external transport, and research into factors determining the establishment success of propagules after dispersal is lacking.
4. Recent spatially explicit models of seed dispersal by waterbirds should be expanded to include invertebrate dispersal, and to compare multiple bird species in the same landscape. Network approaches have been applied to plant–waterbird dispersal interactions, and these are needed for invertebrates. Genetic studies support effective LDD of plants and invertebrates along waterbird flyways, but there remains a lack of examples at a local scale. Next Generation Sequencing and genomics should be applied to waterbird-mediated dispersal across the landscape. More studies of biogeography, community ecology, or population genetics should integrate waterbird movements at the design stage.

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5. Zoochory research has paid little attention to the dispersal of non-pathogenic microbes (both eukaryotic and prokaryotic). Nevertheless, there is evidence that dispersal via avian guts can be central to the connectivity of aquatic microbial metacommunities. More work on microbial dispersal by waterbirds should explore its implications for biogeochemistry, and the interchange with gut flora of other aquatic organisms. In the Anthropocene, the role of migratory waterbirds in LDD of plants and other organisms is particularly important, for example in compensating for loss of large migratory mammals and fish, allowing native species to adjust their distributions under global warming, and spreading alien species along flyways after their initial introductions by human vectors. Recent technological advances have opened exciting opportunities that should be fully exploited to further our understanding of dispersal by waterbirds.

KEYWORDS
dispersal vectors, endozoochory, epizoochory, global change, seed dispersal

1 | INTRODUCTION

Waterbirds are now recognised as vital vectors of dispersal for all kinds of organisms, and their dispersal capacity constitutes one of the most important ecosystem services provided by these birds (Green & Elmberg, 2014). The importance of waterbirds as vectors for zoochory (dispersal via animals) was initially reviewed two decades ago by Figuerola and Green (2002), who identified many research gaps that have since largely been filled. Here, we review the last two decades of progress on waterbird-mediated dispersal. Four of us completed PhDs on waterbird zoochory during this period, covering three continents, which illustrates the growth of interest in this research field. Our aim is to review the progress that has been made in research on waterbird zoochory, including both dispersal through internal transport (endozoochory) and external transport (ecto-, exo- or epizoochory), without duplicating previous related reviews (Coughlan et al., 2017; Green et al., 2016; Green & Figuerola, 2005; van Leeuwen, van der Velde, van Groenendael, et al., 2012). We also outline priorities for further research in the coming years. Finally, our review is accompanied by a virtual issue of *Freshwater Biology* containing 16 papers on dispersal via waterbirds published since 2002, and cited herein.

The focus of Figuerola and Green (2002) was on aquatic ecosystems, but it has since become clear that waterbirds also disperse many terrestrial plants (Almeida et al., 2022; Kleyheeg et al., 2016; Lovas-Kiss et al., 2019; Soons et al., 2016). Waterbirds play a major role in moving propagules within and between terrestrial and aquatic habitats. We have synthesised the taxonomic range of organisms regularly dispersed by waterbirds (Figure 1). The organisms represented in Figure 1 are dispersed by waterbirds using a range of propagule types, via both epizoochory and endozoochory (Table S1). However, one should keep in mind that zoochory research is subject to important biases in the wider ecological community. Most citations for Figuerola and Green (693, google scholar, 27/6/2022) occurred because authors recognised the contribution that waterbirds potentially could make to connectivity of aquatic organisms, even though they rarely studied the role of these vectors directly. The great majority of the citing studies addressed flowering plants, zooplankton and macroinvertebrates, with scant attention to other plants (such as phytoplankton or bryophytes), fungi and microbes in general (Figure 2). The great number of studies suggesting dispersal by waterbirds without directly studying it suggests that dispersal of organisms by waterbirds is a ubiquitous process that is still greatly under-investigated. Hence the importance of identifying priorities for future research.

2 | THE VARIETY OF ORGANISMS KNOWN TO DISPERSE BY WATERBIRDS CONTINUES TO GROW

The capacity of waterbirds to disperse plants and invertebrates with obvious resistant propagules such as seeds or resting eggs has long been well-established, notably by V.W. Proctor's numerous feeding experiments to demonstrate endozoochory of different organisms (e.g., Proctor, 1959, 1968; see review by Figuerola & Green, 2002). Over the last two decades, evidence of zoochory has been growing and now covers many more taxa that previously were overlooked. Potential dispersal of soft propagules, such as eggs of fish or aquatic insects, had long been the source of speculation, but hard evidence was lacking (Hirsch et al., 2018).

Recently, Silva et al. (2019) provided field and experimental evidence for waterfowl endozoochory of diapaused eggs of killifish (Rivulidae, Cypriniformes), and Lovas-Kiss, Vincze, Kleyheeg, et al. (2020) experimentally demonstrated endozoochory of eggs from carp (Cyprinidae). The latter study showed that a small proportion of soft chorion eggs can survive gut passage. Thus, despite the strong dispersal limitation indicated by the limited range

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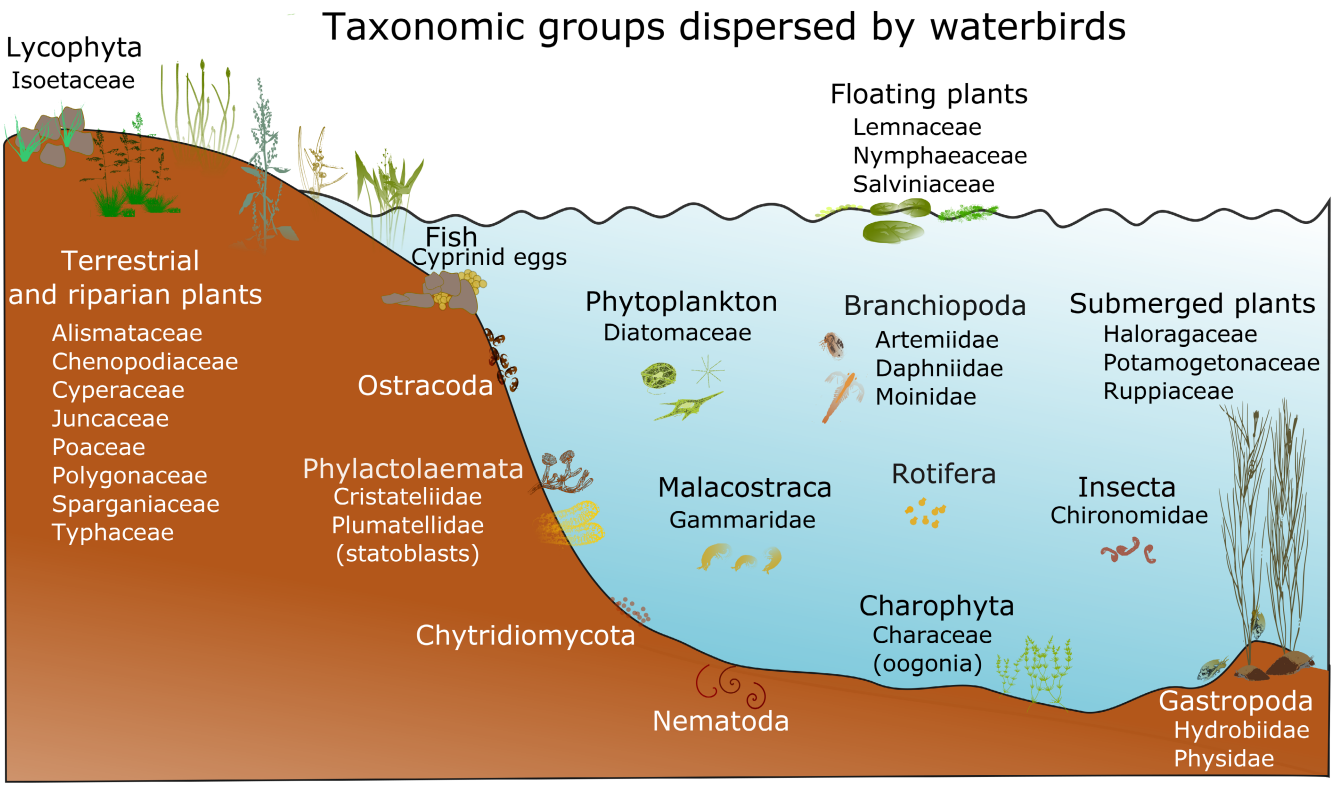

FIGURE 1 Land–water transition zone from terrestrial to littoral to pelagic habitat, illustrating organisms shown to be capable of endo- or ectozoochorous dispersal by waterbirds of the Anatidae and/or Rallidae families. Major taxonomic groups are indicated by the larger font, and key families known to be dispersed in the smaller font. Words in brackets indicate the resting stages dispersed. For each group, representative organisms are drawn in their typical habitat. Blue represents aquatic habitats, brown represents terrestrial habitat and lake sediments. Based largely on the papers in the accompanying virtual issue of *Freshwater Biology*. See Table S1 for more details of these dispersal interactions

of many fish species (Costa, 2014), waterbird zoochory may be a widespread process, potentially contributing to fish invasions, and is worthy of further research, including investigations of epizoochory potential (Coughlan et al., 2017). Small proportions of soft insect eggs can survive digestive processes inside waterbird guts, explaining the widespread distribution of aquatic, flightless beetles (Laux & Kölsch, 2014). Likewise, live chironomid larvae were found in shorebird faeces from the field (Green & Sánchez, 2006). Insect eggs and aquatic snails also may be dispersed by epizoochory, as when corixids lay eggs on bird legs or snails crawl on birds (Carbonell et al., 2021; van Leeuwen & van der Velde, 2012). Alien aquatic snails are now known to be dispersed via endozoochory in regurgitated pellets as well as faeces (Martín-Vélez et al., 2022). Tardigrades are another group with a widespread distribution that may partly be explained by dispersal through bird migration. Mogle et al. (2018) found tardigrades in 70% of crane nests, and in the plumage of 66% of bird carcasses, supporting epizoochory. The presence of tardigrades in shorebird droppings supports endozoochory (Robertson et al., 2020).

Exciting advances also have been made in our understanding of plant zoochory, other than by seeds. There is recent evidence for epizoochory (Lewis et al., 2014) and endozoochory (Wilkinson et al., 2017) of bryophytes, and for endozoochory of entire duckweed plants (*Wolffia*; Silva et al., 2018). Lovas-Kiss, Vizi, et al. (2018) also demonstrated endozoochory of aquatic ferns (*Salvinia natans*) in the field, long after experimental evidence was first provided (for another fern, *Marsilea*; Malone & Proctor, 1965). Viable fragments of the invasive angiosperm *Crassula helmsii* also may disperse by goose endozoochory (Denys et al., 2014), as may fragments of the grass *Puccinellia phryganodes* (Schnaars-Uvino et al., 2018). We expect the zoochory of additional cosmopolitan organisms to be demonstrated in the coming years, especially for relatively obscure taxonomic groups.

3 | HOW DO WATERBIRDS DIFFER FROM OTHER DISPERSAL VECTORS?

3.1 | Comparison with other birds

Most literature on avian zoochory focuses on internal seed dispersal by frugivorous birds, to the extent that it is widely and mistakenly assumed that only plants with fleshy fruits can disperse via endozoochory (Green et al., 2022). Waterbirds have more in common with other herbivorous, omnivorous and granivorous bird groups dispersing plants that lack a fleshy fruit through non-classical

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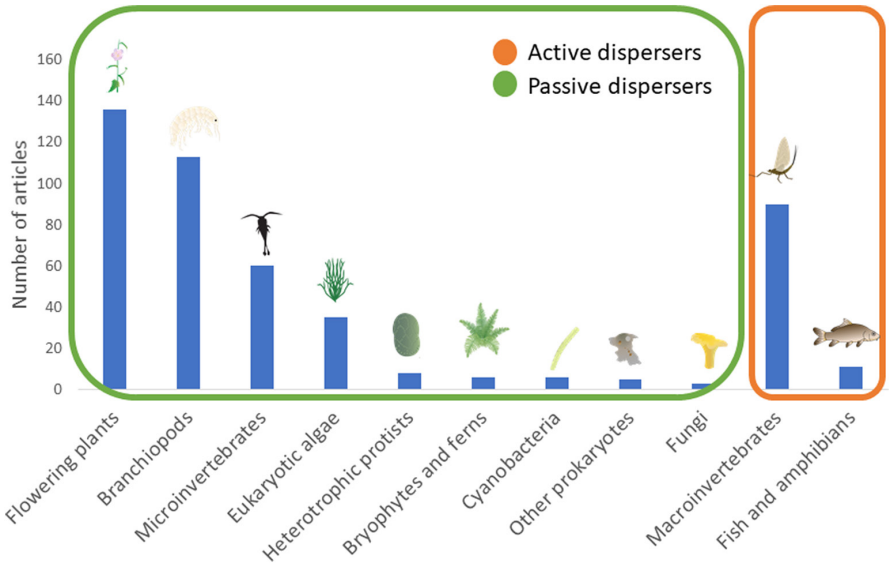

FIGURE 2 Numbers of scientific articles citing the review of Figuerola and Green (2002), according to the taxonomic groups studied in those articles (i.e., those whose dispersal by waterbirds is contemplated). Data extracted from Google scholar on January 18, 2022. Taxonomic groups were identified by reading the titles and abstracts, only proceeding to the main text when the abstract was ambiguous. Some papers covered more than one of the groups illustrated in the figure. For papers not written in English or French, the taxa were identified only where the use of scientific names allowed. Macroinvertebrates and fish are highlighted in orange because they are generally active dispersers, and also can be dispersal vectors for other freshwater organisms (see text)

endozoochory, such as corvids (Green et al., 2019), galliformes (Orlowski et al., 2016) and parrots (Blanco et al., 2016). Birds in these groups provide dispersal mechanisms that complement frugivory, and to some extent overlap with frugivorous birds in the plant species that they disperse.

Predatory waterbirds are similar to predatory seabirds (Maggio et al., 2022) and raptors (Pérez-Méndez & Rodríguez, 2018), in that they disperse propagules inside or attached to their own prey (i.e., secondary dispersal), which can include granivores, herbivores or frugivores. Many plants and invertebrates have now been recorded in excreta of fish-eating cormorants (van Leeuwen et al., 2017) and pelicans (Green et al., 2008), storks and gulls feeding on crayfish (Lovas-Kiss, Sánchez, et al., 2018; Martín-Vélez, Lovas-Kiss, et al., 2021; Martín-Vélez et al.,2022), and also herons that feed on small mammals around wetland edges (Navarro-Ramos et al., 2021). Recent research suggests that such secondary processes are widespread, largely cryptic and unpredictable in nature, and can be strongly influenced by biological invasions involving waterbird prey (Lovas-Kiss, Sánchez, et al., 2018; Navarro-Ramos et al., 2021). All birds also can disperse seeds and other plant diaspores by epizoochory (Hernández-Brito et al., 2021; Johansson et al., 2021), or when constructing nests (Parnikoza et al., 2012). However, the literature for plant dispersal by non-frugivorous birds other than waterbirds is limited, so from here on we compare endozoochory between waterbirds and frugivores (see also van Leeuwen, Villar, et al., 2022).

Waterfowl (Anatidae), shorebirds (waders) and other non-predatory waterbirds are important dispersers by endozoochory for a taxonomically wide range of plants (Kleyheeg et al., 2016; Lovas-Kiss et al., 2019; Soons et al., 2016). Seed dispersal by waterbirds can be as frequent as that of frugivorous birds. For example, Cruz et al. (2013) found intact seeds in 45% of frugivore droppings in an urban ecosystem in Portugal, whereas seeds and other diaspores often are found in the majority of waterbird droppings (e.g., 87% by Green et al., 2008; 65% by Silva et al., 2021). In addition, waterbirds also disperse many aquatic microorganisms and invertebrates, such as ciliates, bryozoans, nematodes, ostracods, rotifers and branchiopods (Green et al., 2008; Lovas-Kiss, Sánchez, et al., 2018; Sánchez et al., 2012; Silva et al., 2022). Here, we highlight four important ways in which the underlying mechanisms by which seeds and other propagules are dispersed by waterbirds can differ from those of frugivores. Firstly, frugivorous birds typically select fruits visually, and preferentially ingest fruits with a high energetic and nutritional content or with specific colours (Sebastián-González, 2017; Wenny et al., 2016). Waterbirds may have lowered selectivity when ingesting propagules, as many waterbirds, such as waterfowl and flamingos, ingest various classes of food items simultaneously via filter feeding. This is especially true for species feeding from sediments, in which seeds are separated from detritus without vision (Gurd, 2008). Secondly, fleshy fruits typically are taken by birds from the mother plant and therefore are only available during a limited period of time (González-Varo et al., 2021). By contrast, waterbird endozoochory is not necessarily coupled with propagule production, because propagules can be ingested from sediments long after they were produced (Brochet et al., 2010; Urgyán et al., 2023). Thirdly, body size plays a more important role for frugivores than for waterbirds, as only species with a large gape can disperse plants with the largest fruits, whereas body size is not correlated with seed size in waterbirds and other non-frugivores (Almeida et al., 2022; Chen & Moles, 2015). Larger waterbirds have a greater surface area available for epizoochory, but there is no evidence that this influences the probability of dispersal events (Coughlan et al., 2017; Raulings et al., 2011).

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Fourthly, the potential dispersal distance of propagules greatly differs. Migratory waterbirds disperse propagules both at shorter distances during daily movements (typically <20 km) and over long distances during migrations, when they connect networks of key sites along flyways (Xu et al., 2022). During migration, endozoochory can provide extreme dispersal distances, regularly exceeding 400 km and sometimes >1,000 km (Kleyheeg et al., 2019; Viana et al., 2013), facilitated by long gut retention times which can reach several days (García-Álvarez et al., 2015). Many frugivores also migrate (e.g., González-Varo et al., 2021), but seed dispersal distances are limited because their gut retention times (a key determinant of seed dispersal kernels) generally are much shorter (Yoshikawa et al., 2019). Consequently, frugivores provide much shorter dispersal distances (rarely >10 km; Wenny et al., 2016).

Among recent developments that facilitate comparisons between plant–frugivore and plant–waterbird interactions are networks between birds and the plants that they disperse. For frugivorous birds such interaction networks have been explored in detail, and important implications for the stability and persistence of interacting communities have been discovered (Rohr et al., 2014; Saavedra et al., 2011; Thébault & Fountaine, 2010), yet network analyses on waterbird-mediated dispersal are in their infancy (van Leeuwen et al., 2017; Sebastián-González et al., 2020; Silva et al., submitted). For both waterbirds and frugivorous birds, seed-dispersal networks seem to be organised following a nested pattern (i.e., animals dispersing few plants interact with a subset of the species dispersed by animals interacting with many plants; Sebastián-González et al., 2020), and this is likely to favour species persistence (Bastolla et al., 2009). Moreover, frugivorous assemblages often show a modular structure (i.e., groups of species interacting more among them than with species in other groups; Donatti et al., 2011). So far, the evidence for modularity in waterbird assemblages is weak (Sebastián-González et al., 2020; Silva et al., submitted). For frugivorous networks, interaction patterns are largely driven by bird and fruit traits, but neutral processes seem more important in waterbird seed-dispersal assemblages, for which interactions may be more driven by local species abundance (Sebastián-González et al., 2017, 2020). Clearly, more studies are needed of the interaction networks between waterbirds and the organisms that they disperse (including plants, invertebrates, and other organisms). To date, such studies have focused on Anatidae and Rallidae, and not included important vectors such as herons, gulls or shorebirds. Different vector groups that use different habitats or are present during different seasons in one landscape could be combined in multilayer networks, as has so far been done only for frugivores (e.g., Timoteo et al., 2018).

3.2 | Comparison with fish and other aquatic vectors

In freshwater systems, fish are major alternative biotic dispersal vectors to birds. Plant dispersal studies have been biased towards frugivorous fish in tropical regions in a similar manner to studies of avian frugivores (Horn et al., 2011). In temperate regions, where fleshy-fruited plants are less abundant, there has been less research into ichthyochory, but omnivorous fish are clearly important vectors of seeds of aquatic plants in a manner comparable to waterbirds (Horn et al., 2011). Seed retention times in cyprinids may reach 15 hr, leading to potential dispersal distances of up to 16 km (Mulder et al., 2021).

Fish only disperse propagules within hydrologically connected habitats, yet they disperse many of the same propagules as omnivorous waterbirds, with which they often compete in littoral habitats. As well as viable seeds and invertebrate propagules, cyprinids disperse vegetative fragments of vascular plants and mosses (Boedeltje et al., 2019), which also are dispersed by waterfowl (Wilkinson et al., 2017). Like waterbirds, fish ingest propagules year-round from the propagule bank, and not only when they are produced (Boedeltje et al., 2019). Fish may be particularly important for dispersal of propagules in sediments found at greater depths than those where waterbirds feed. Waterfowl (including diving ducks) rarely feed at depths exceeding 2 m, although they sometimes feed in sediments at depths of up to 10 m (Green et al., 1999). Thus, fish and waterbirds may be complementary dispersal vectors, and studies are needed to compare their roles within the same ecosystem.

Fish endozoochory has been demonstrated for a variety of invertebrates, including zooplankton, bryozoans and molluscs (Abd-Elfattah et al., 2017; Beladjal et al., 2007; Butkus & Rakauskas, 2020; Gatlin et al., 2013). These include invasive aliens, such as zebra mussels *Dreissena polymorpha* and the mud snail *Potamopyrgus antipodarum*, not known to survive avian gut passage, potentially as a result of lethal temperatures (van Leeuwen, van der Velde, van Lith, et al., 2012). Avian body temperature is typically 40–42°C (Clarke & Rothery, 2008), far exceeding typical temperatures in ectothermic fish. In general, larger fish have longer retention times, favouring long-distance dispersal (LDD; Mulder et al., 2021). By contrast, most evidence suggests that smaller waterbird species have longer retention times (Viana et al., 2013; García-Álvarez et al., 2015, but see Reynolds & Cumming, 2016b).

Other dispersal vectors that share the ability of birds to move over land between waterbodies include turtles, amphibians and crayfish (Lovas-Kiss, Sánchez, et al., 2018; Padgett et al., 2019; Sabagh et al., 2011), which may be especially important vectors for small waterbodies receiving few visits by birds. Aquatic insects also can disperse small propagules, including microbes (Solon & Stewart, 1972), branchiopod eggs (Beladjal & Mertens, 2009) or even fish eggs (Suetsugu & Togashi, 2020).

3.3 | Comparison with aquatic and terrestrial mammals

It has become clear that there is extensive overlap in the range of terrestrial plants dispersed by waterbirds and by herbivorous mammals, as well as in the seed traits that favour endozoochory

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by either group (Green et al., 2022). Since aquatic and terrestrial mammals move through waterbodies or visit them to drink, they also disperse aquatic invertebrate propagules, mainly by epizoochory (Vanschoenwinkel et al., 2008, 2011; Waterkeyn et al., 2010). Indeed, on the one hand, rates of epizoochory are much higher for mammals, since propagules stick more readily to fur than to feathers (Sánchez et al., 2012), and the mechanics of flight have more constraints such that birds spend much of their time preening and cleaning their plumage (Green & El Hamzaoui, 2000). On the other hand, migratory waterbirds are more likely than mammals to disperse propagules over extreme distances, especially between land masses. Given the overlap in the organisms that they disperse, defaunation of large mammals is likely to increase the importance of waterbird vectors. For example, migratory mammoths dispersed a range of plant and invertebrate propagules (Kotov et al., 2019) which may now depend on waterbirds for their dispersal.

4 | UNDERSTUDIED ROLE OF WATERBIRDS AS VECTORS FOR MICROBES

Microbial biogeography has been studied mainly in relation to environmental filtering (e.g., by lake chemistry), yet dispersal has become an increasingly popular topic for microbial research (Custer et al., 2022). Despite early work with microscopic algae, the lack of studies of microbial dispersal by waterbirds was clear in the earlier review of Figuerola and Green (2002), and the relative lack of recent research is evident from the resulting citations (Figure 2). Although many microbes can disperse inter-continentally through dust storms (Custer et al., 2022), such airborne dispersal becomes increasingly unlikely as microbial size increases above a threshold of around 20 μm (Wilkinson et al., 2012). Waterbirds provide a way for microbes to colonise new sites and is likely to become increasingly important as microbial size increases. Birds may be particularly important for dispersing microbes across the equator, for which airborne dispersal is inhibited by atmospheric circulation (Wilkinson et al., 2012). Many species of shorebirds undergo migrations that cross the equator, as well as some Anatidae.

Both epizoochory and endozoochory are important for microbial dispersal by waterbirds, but it is unclear which mechanism is dominant. Manning et al. (2021) investigated the potential of epizoochory by dipping breast feathers from mallards *Anas platyrhynchos* in cultures of diatoms and showed that their survival when stuck to feathers increases with relative air humidity. Tesson et al. (2018) used in vitro gut-simulation to investigate the endozoochory potential of dinoflagellates, confirming that resting cysts survived gut conditions. Many authors consider waterbird zoochory to be the likely explanation of microalgae distributions. For example, Cellamare et al. (2010) suggested that waterbirds dispersed exotic species of microalgae to inland waters of Europe from African lakes and other tropical areas.

Waterbirds disperse a cryptic diversity of microbial eukaryotic parasites, including taxa for which they act as hosts, and many others that parasitize other organisms (Briscoe et al., 2022; Menning et al., 2020), exemplified by myxozoans that parasitize fish and bryozoans (Hartikainen et al., 2016). Faecal eDNA and isolates also suggest that waterbirds disperse a high diversity of pathogenic and non-pathogenic fungi (Briscoe et al., 2022) and prokaryotes (Jarma et al., 2021; Santos et al., 2012). Anatidae can carry the fungus that causes chytridiomycosis, important in amphibian decline, on their feet (Garmyn et al., 2012). Waterbirds have a very diverse gut microbiome that varies between species, and within species according to diet and health status (Boukerb et al., 2021; Cao et al., 2020; Gillingham et al., 2021). They also have a diverse microbiome on their feathers and skin (Giraudeau et al., 2010). Like the nostrils of seabirds (Brito-Echeverria et al., 2009), the feathers of flamingos are rich in haloarchaea, which presumably disperse with flamingos when they undergo long-distance movements (Yim et al., 2015). There is evidence for major exchange between the microbial communities carried in waterbird guts and those present in the lakes they visit (Szabó et al., 2022), suggesting that waterbirds may be vital in maintaining connectivity in microbial lake metacommunities, and that their gut microbiomes might influence lake biogeochemistry, as well as the gut microbiomes of other aquatic organisms (the "meta-gut" concept; Dutton et al., 2021).

There already is an extensive literature on dispersal of pathogens of humans and domestic animals by waterbirds, and here we only give some key examples. *Vibrio cholerae* (the cause of cholera) can be secondarily dispersed by cormorants (Laviad-Shitrit et al., 2017). Ducks can uptake and disperse *Enterococcus* species when in contact with waste waters (Ehn Börjesson et al., 2013). Outbreaks of Avian Influenza have been linked to waterbird movements, and have intensified research into migration patterns (Iverson et al., 2011; Lebarbenchon et al., 2009), improving our understanding of the general role of waterbirds as dispersal vectors. There is ongoing research into the role which waterbirds may play in antimicrobial resistance (AMR), particularly genes and bacteria resistant to antibiotics (see reviews by Dolejska, 2020; Zeballos-Gross et al., 2021). Waterbirds using landfills, wastewater treatment plants and other anthropic habitats (e.g., gulls or storks) carry the most AMR (Jarma et al., 2021), and migrants can disperse AMR into pristine habitats and over spectacular distances (e.g., geese migrating between the Canadian arctic and Ireland; Agnew et al., 2015). Extreme environments, such as high-altitude saline lakes, can be natural reservoirs of AMR in prokaryotes which can then be carried by birds such as flamingos (Fernández-Zenoff et al., 2015).

In the future, there needs to be far more research into microbial dispersal by waterbirds. In particular, there is a need to further clarify which of the microbes detected in barcoding studies of faeces or feathers are viable, and what influence the microbes carried by birds have on pre-established microbial communities, compared to inputs from air or water (Custer et al., 2022; Szabó et al., 2022). The meta-gut concept should be explored, comparing gut microbiomes of waterbirds and co-existing aquatic organisms (Dutton et al., 2021). More studies also are needed to establish how long microbes are able to stay inside waterbirds (i.e., retention time),

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information required to predict how far they can be dispersed (e.g., Ahlstrom et al., 2021; Lebarbenchon et al., 2009). These are important ecological questions which also have major implications for human health.

5 | TO WHAT EXTENT DO TRAITS EXPLAIN PATTERNS IN WATERBIRD ZOOCHORY?

In recent years, several functional approaches have been used to explore variation in seed dispersal by waterbirds. Reynolds and Cumming (2016c) used a literature search to assess possible overlap in the dispersal functions of different waterbird species. They identified five functional groups of dispersers based on the prevalence of plant families in the diets of 16 African waterfowl. In each of three functional groups, multiple waterfowl species dispersed plants from the same family, suggesting a high level of redundancy and resilience in dispersal interactions. However, the other two groups contained single bird species, lacking functional overlap with others. Almeida et al. (2022) also used diet literature in a comparison of the functional traits of plants whose seeds are ingested by different waterfowl guilds in Europe: geese were the most associated with terrestrial plants, diving ducks with submerged plants, and dabbling ducks with shoreline and ruderal plant species.

Other researchers have compared the roles of different waterbird species as plant vectors within particular study areas by quantifying intact seeds in faeces or pellets. Martín-Vélez, Leeuwen, et al. (2021) found that storks and gulls have similar roles in European ricefields, whereas Silva et al. (2021) recorded limited overlap across five South American waterfowl, identifying three functional groups. Overall, these literature-based and empirical results indicate that aggregating waterfowl together under a single category of "seed disperser" overlooks functionally important distinctions between different bird species. Sebastián-González et al. (2020) incorporated traits of both waterbirds and plants in network analyses for four wetland complexes, but found no strong trait effects. More studies of waterbird vectors using trait approaches are clearly needed, not only for dispersal of plants and endozoochory, but also for dispersal of invertebrates and epizoochory. To facilitate such studies, better trait databases are required for dispersed organisms and their vectors.

5.1 | Plant traits

Existing flowering plant databases focus on popular "dispersal syndromes" that are based on specific seed and fruit morphological traits widely assumed to determine dispersal events (e.g., wings for wind, hooks for epizoochory), and these syndromes have been assigned to entire floras. Only plants with a fleshy fruit are assigned to the "endozoochory syndrome". However, most European angiosperms lack these diagnostic traits, and so end up in an "unspecialized" or "unassisted" syndrome (Green et al., 2022). Furthermore, these syndromes fail dismally to predict dispersal events in the case of waterbirds and other non-frugivorous vectors, whether by endozoochory or epizoochory (Green et al., 2022). This implies that research focus should shift from classical syndromes to other traits known to influence the rates of waterbird zoochory, such as seed size, shape, hardness or buoyancy (de Vlaming & Proctor, 1968; Green et al., 2016; Soons et al., 2016; van Leeuwen, Soons, et al., 2022). Plant life forms and habitat requirement (e.g., soil moisture, salinity tolerance) indicators also can partly explain the importance of waterbird vectors (Almeida et al., 2022; Hattermann et al., 2019; Soons et al., 2016).

In general, plants with seeds of a smaller size show higher survival during gut passage, and higher prevalence in field studies of endozoochory, although the latter may partly reflect the inverse relationship between propagule size and propagule abundance across species in nature (Green et al., 2022; Hattermann et al., 2019; van Leeuwen, van der Velde, van Groenendael, et al., 2012). Small seeds pass more quickly from the gizzard into the intestines, not only promoting survival, but also shortening retention time (Kleyheeg, Nolet, et al., 2018; van Leeuwen, Soons, et al., 2022). Hence, plant species with large, hard seeds can have higher seed survival and longer retention times than small, soft-seeded species (García-Álvarez et al., 2015). Plants with small and hard seeds are those that best survive gut passage (de Vlaming & Proctor, 1968; Lovas-Kiss, Vincze, Löki, et al., 2020; Reynolds & Cumming, 2016a). Roundness also can have a positive partial effect on seed survival (Lovas-Kiss, Vincze, Löki, et al., 2020).

No single seed trait is an adequate predictor of fate during gut passage, yet experimental studies to date have focused on only one or two traits, and have usually overlooked the important role of phylogeny (Lovas-Kiss, Vincze, Löki, et al., 2020). In future experiments, larger numbers of plant species and more seed traits should be included, and this may be facilitated via laboratory simulations of gut passage, reducing the need for animal experimentation (Kleyheeg, Claessens, et al., 2018; van Leeuwen, Soons, et al., 2022). However, more work is needed to develop convincing simulations, and clarify how they compare with seed passage through real digestive systems and their microbiomes.

How seed traits interact with gut passage to influence germination patterns is complex, and general patterns remain unclear (Kleyheeg, Claessens, et al., 2018), especially since the results of comparisons with control seeds also are highly dependent on storage and germination conditions, and their own interactions with dormancy strategies of different plant species (see Interaction between zoochory and dormancy section below). However, simulated gut passage increases germinability and germination speed more in aquatic plants than in terrestrial ones (van Leeuwen, Soons, et al., 2022). Some of the seed traits described in this section also may be relevant for epizoochory, although data for waterbirds remain scarce (Coughlan et al., 2017; Green et al., 2016; Raulings et al., 2011; Reynolds & Cumming, 2016b), and should be expanded experimentally.

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5.2 | Invertebrate traits

There have been no systematic attempts to assign dispersal syndromes to invertebrate propagules based on their morphology, and experimental studies testing their ability to disperse via waterbirds are much scarcer than for plants (van Leeuwen, van der Velde, van Groenendael, et al., 2012; van Leeuwen et al., 2020). However, they are sufficient to suggest that propagule size and hardness are key traits. The survival rate after gut passage is higher for hard, resistant structures such as *Artemia* cysts than for softer propagules such as Corixidae eggs (Carbonell et al., 2021; Sánchez et al., 2012). Studies on snails indicate greater survival for smaller operculated species and those with greatest resistance to external stressors such as desiccation (Simonova et al., 2016; van Leeuwen, van der Velde, van Lith, et al., 2012). In general, retention times of invertebrate propagules are shorter than those of plant seeds (Viana et al., 2013), as expected from their smaller size, which facilitates passage through the gizzard. When ingested at later development stages, invertebrates with an ability to protect themselves from the hostile gut environment are more likely to survive gut passage. Ostracods can do so by closing their valves and are repeatedly recorded as alive in waterfowl faeces (Green et al., 2013). More experiments are needed comparing gut passage for a diversity of invertebrates with different traits such as propagule size, structure, shape and hardness.

Attachment experiments also could provide information about epizoochory potential, and how that relates to traits such as hooks or stickiness. *Cristatella* statoblasts and some sponge gemmules have hooks that may promote attachment to feathers (Okamura et al., 2019), yet they may disperse in greater numbers through endozoochory (van Leeuwen et al., 2017). Desiccation resistance influences the frequency and distance of epizoochory events, and has been tested for insect eggs, snails, amphipods and decapods, although propagules hidden underneath feathers are protected from rapid desiccation (Carbonell et al., 2021; Coughlan et al., 2017). The strength of attachment also has been tested, using simulated flights. Attachment strength may be greatly facilitated by properties of sediments, as for snails and mud (van Leeuwen & van der Velde, 2012). Invertebrate behaviour also may play a central role in facilitating dispersal, as when corixids lay eggs on the legs of waterbirds (Carbonell et al., 2021) and when bivalves close around bird feet (Green & Figuerola, 2005).

5.3 | Waterbird traits

Since foraging guilds of waterbirds influence the type of propagule ingested (Almeida et al., 2022), related avian traits also should influence endozoochory. Key traits are likely to include diet, bill length, leg length and feeding strategy. For example, predatory waterbirds will secondarily disperse propagules from their prey (Lovas-Kiss, Sánchez, et al., 2018). Furthermore, predators that dive in the pelagic zone (e.g., cormorants; van Leeuwen et al., 2017) ingest and disperse a different set of propagules to the long-legged predators that stand in the littoral zone or onshore (e.g., herons; Navarro-Ramos et al., 2021). Among ducks, the density of lamellae in the bill influences the feeding process, and species with higher lamellar densities tend to ingest a relatively higher abundance of small propagules (Green et al., 2016; Green & Figuerola, 2005). No studies have yet related waterbird traits to epizoochory.

Specific traits of waterbird species that are known to influence the fate of propagules *after* ingestion include diet and gut morphology (Green et al., 2016; van Leeuwen, van der Velde, van Groenendael, et al., 2012). Some species can regurgitate propagules in pellets (Lovas-Kiss, Sánchez, et al., 2018; Navarro-Ramos et al., 2021) or otherwise (Kleyheeg & van Leeuwen, 2015), allowing larger propagules to disperse even if they cannot survive complete gut passage into faeces. There are complex interactions of propagules with other food ingested simultaneously. Seeds survive better if ingested by ducks on an animal-based diet, whereas invertebrate eggs survive better when mixed with a plant-based diet (Charalambidou et al., 2005). When ingested with a plant-based diet, retention times of propagules or plastic markers were longer (Charalambidou et al., 2005; Kleyheeg, Nolet, et al., 2018). Waterfowl with a more powerful gizzard, and more grit used to crush food, destroy more propagules before they reach the intestines (Figuerola et al., 2002, 2005). Grit size also is important, since smaller propagules can fit into gaps and avoid being crushed between larger particles (van Leeuwen, Soons, et al., 2022).

Variation in gut retention times is influenced less by differences in intestine length than by the period for which propagules are kept in the gizzard (Kleyheeg, Nolet, et al., 2018). This may explain why seeds had a longer retention time when fed to the smaller mallard compared to the greylag goose (García-Álvarez et al., 2015), whereas the opposite occurred when comparing the smaller red-billed teal with the Egyptian goose (Reynolds & Cumming, 2016a) –– seeds probably were retained in the mallard gizzard for relatively longer than in the teal.

6 | INTERACTION BETWEEN ZOOCHORY AND DORMANCY

Dispersal is ubiquitous in ecology as an adaptive response to environmental fluctuations which can make a habitat unsuitable, or to escape competition in stable habitats (Hamilton & May, 1977). However, many plants and aquatic invertebrates have what appears to be an alternative to seed and egg dispersal in space, namely propagule banks in soils and sediments. Here, viable propagules can survive, sometimes for many years, waiting for suitable conditions to germinate or hatch. The standard interpretation is that a persistent propagule bank represents an alternative strategy, in which dormancy is time travel (Alderton et al., 2017). While spatial dispersal allows a propagule to escape its natal site to a potentially more suitable location, a propagule bank allows the propagule to travel in time until suitable conditions arise at the site of origin. In extreme cases, seeds and eggs are known to have survived for hundreds and even thousands of years (Alderton et al., 2017; Frisch et al., 2014). Hence, the ability of many planktonic organisms and small, short-lived

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angiosperms to form persistent propagule banks often is interpreted as an adaptation to disperse through time and not space (Slusarczyk et al., 2019; Thomson et al., 2011).

However, waterbirds show how the reality is more complex. Dormancy gives propagules great potential to disperse through space via migratory birds, allowing them to bide their time until they are ingested by birds (e.g., in wetland sediments until they are ingested by shorebirds, or filtered by ducks). Indeed, many plants dispersed by endozoochory by dabbling ducks are known to have a persistent seed bank (Grime et al., 2007; Soons et al., 2016). For microbes, it is recognised that dormancy can positively covary with LDD (Custer et al., 2022). This raises interesting questions about the selection pressures for developing propagule banks. Furthermore, seed traits favouring persistent seed banks (e.g., hard, impermeable seed coat and round shape; Grime et al., 2007) also favour survival after gut passage. This has major consequences for the ability of plants to undergo LDD in response to climate change, which generally requires dispersal during spring migration (Urgyán et al., 2023). Spring dispersal generally requires seeds to remain viable for several months after their production, and so is more likely for plants that form persistent seed banks or that retain seeds on stems for many months (Urgyán et al., 2023).

Most plants (including most of those dispersed by waterbirds) are considered to have "physiological seed dormancy", whilst many of the others are classified as having "physical dormancy", with the assumption that only the latter require gut passage to induce germination (Penfield, 2017). Despite detailed research into a range of factors (e.g., temperature, light, water, chemical concentrations) that stimulate entry into, and exit from, physiological dormancy, the role of gut passage in such plants has so far received insufficient attention (Soltani et al., 2018). However, recent evidence suggests that dormancy type (physical or physiological) is not a strong predictor of seed survival or degree of damage during avian gut passage, or of the influence of gut passage on germinability (Bravo et al., 2020; Costea et al., 2019). More research is needed to study the interactions between gut passage and other variables driving physiological dormancy, and how that determines germination patterns.

7 | PROPAGULE ESTABLISHMENT AFTER ZOOCHORY

Dispersal is only successful if displacement is followed by propagule growth to maturity, and ultimately the production of offspring (Green et al., 2016). The term "effective dispersal" includes this establishment phase, the success of which is strongly linked to dispersal distance and spatial heterogeneity. Propagule establishment is an important part of the quality component of the Seed Dispersal Effectiveness framework, with which the fitness benefits of zoochory can be compared among different vectors (van Leeuwen, Villar, et al., 2022). Although originally conceived for plants, this framework is applicable to dispersal of invertebrates and other organisms, and can be used to identify knowledge gaps in our current understanding of effective dispersal.

Propagule establishment depends first of all on the capacity of a dispersed propagule to germinate or hatch, and thereafter on external biotic and abiotic conditions in the new habitat that may limit or promote survival to a mature plant or invertebrate. Germination or hatching may occur after a propagule has first spent time in a seed or egg bank, although no research has yet focused on the role of propagule banks *after* zoochory. We are increasingly learning that gut passage is likely to modify the germination or hatching response (see also the Interaction between zoochory and dormancy section). For instance, in a mesocosm experiment, gut passage promoted earlier establishment of *Potamogeton pectinatus* seedlings, although there was no evidence of a fitness advantage over control seeds (Figuerola et al., 2005). Germination and hatching are only possible in suitable conditions, notably with regards to moisture, salinity, nutrient availability, temperature and light. For example, the probability and speed of germination of aquatic plant seeds depend partly on salinity of the water they are found in, and gut passage can itself modify the salinity response (Espinar et al., 2004). Experiments with rotifers suggest that the chance of establishment after endozoochory depends on both the salinity and temperature of the water into which they are introduced (Conde-Porcuna et al., 2018; but see Valls et al., 2017). Similar establishment experiments are needed for more taxa.

If propagules are dispersed from a suitable habitat into another patch with similar abiotic conditions, effective dispersal is more likely. Waterbirds are particularly likely to provide directional dispersal of propagules into suitable habitats, because they regularly move between patches of similar habitat (Kleyheeg et al., 2017; Martín-Vélez, Leeuwen, et al., 2021). Many waterbirds are specialised habitat users (e.g., along water depth or salinity gradients; Almeida et al., 2022; Ramirez et al., 2018).

After arrival and germination or hatching in the new habitat, propagule fitness becomes regulated by the ability to grow and reproduce successfully, and compete with conspecifics and heterospecifics (Hessen et al., 2019; Pannell, 2015). Species with small propagules may arrive in high numbers in or on the same bird, and so be more likely to reproduce readily and to avoid Allee effects, as a consequence of high propagule pressure. Waterbirds typically move in flocks, especially outside the breeding season, so that multiple individuals may introduce propagules at the same time. Clonal or self-fertilising species have an advantage for colonisation (i.e., "Baker's law"; Pannell, 2015; van Leeuwen et al., 2013). These and other traits such as rapid growth may facilitate establishment after zoochory events (Pannell, 2015), helping species to spread after being introduced into a non-native range, or to adapt their distribution in pace with climate change.

8 | GENETIC ANALYSES AS TOOLS TO UNDERSTAND WATERBIRD ZOOCHORY

Genetic analyses have revolutionised our capability to study effective dispersal through waterbird vectors, by detecting colonisation routes and quantifying gene flow. In many genetic studies of aquatic plants and invertebrates, high levels of gene flow are detected which

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support an influence of bird movements. For example, van Leeuwen et al. (2013) demonstrated high rates of genetic interchange for Spanish populations of the alien aquatic snail *Physella acuta*, for which waterbird endozoochory has since been confirmed (Martín-Vélez et al., 2022). Martin et al. (2020) found that the population structure of the gastropod *Planorbella trivolvis* suggested LDD along a migratory flyway. Likewise, variation in mitochondrial clades of brine shrimp *Artemia franciscana* across the Americas is related to shorebird flyways (Muñoz et al., 2013). For cladocerans and the bryozoan *Cristatella mucedo*, Figuerola et al. (2005) found that waterfowl movements explained a significant amount of gene flow across North America.

Repeated studies of bryozoans have provided progressively more evidence of a high zoochory capacity from propagule morphology, field sampling and feeding experiments, combined with genetic analyses supporting effective dispersal (Okamura et al., 2019). The importance of waterbird vectors varies between bryozoan genera in relation to the likelihood of propagule ingestion or attachment. Genetic divergence between populations was smallest for genera that release statoblasts with hooks and positive buoyancy ("floatoblasts"), and greatest for species with "sessoblasts" that remain quiescent in the maternal microhabitat.

Genetic patterns in 25 plant species suggest a key role for migratory geese as vectors in the colonisation of Iceland, Greenland and other North Atlantic Islands, and this is supported by floristic analyses (Alsos et al., 2015). Many of these species are from genera with particularly strong empirical evidence of endozoochory by waterfowl (e.g., *Carex* and *Ranunculus*), and the direction of LDD events after the last glaciation are highly consistent with geese flyways (Alsos et al., 2015). Likewise, genetic patterns for *Ruppia* spp. are consistent with occasional, effective LDD via waterbirds (Martinez-Garrido et al., 2017; Triest & Sierens, 2011), as expected from the high rates of endozoochory detected in the field (Figuerola et al., 2003).

For zooplankton, Hessen et al. (2019) concluded that genetic analyses are most likely to confirm the importance of avian vectors when conducted at a broad spatial scale along flyways. At more limited spatial scales, founder, priority and monopolisation effects for taxa with massive propagule banks can make it hard to detect dispersal through waterbirds, even under high levels of gene flow. Likewise, microsatellite data for *A. franciscana* in natural Canadian lakes suggest that, whilst cysts readily disperse between lakes inside waterbirds, their establishment after dispersal is largely determined by the hydrochemical matching between the lakes of origin and arrival for the dispersed cyst (i.e., environmental filtering; Frisch et al., 2021).

Unfortunately, most studies of population genetics of aquatic organisms only consider waterbirds as an afterthought in an attempt to explain the patterns observed. In the future, there should be better integration of genetic studies of plants and invertebrates with studies of the waterbird vectors themselves. For example, this might involve fitting GPS loggers to birds in the study area, or designing genetic sampling in relation to movement patterns (ideally comparing sampling sites well connected by birds with others that are not). Future studies also should address the possible significance of pollen dispersal by waterbirds for aquatic plants. Waterbirds can carry pollen for long distances (including in the nasal cavity; Tamisier, 1996). Murray et al. (2019) speculated that LDD of pollen on waterbird feathers may contribute to genetic patterns in the river shrub *Duma florulenta*.

9 | UNDERSTANDING WATERBIRD MOVEMENTS AND MODELLING ZOOCHORY

It is vital to be able to predict the spatial distribution of propagules dispersed by waterbirds in order to understand the likely consequences for the spatial structure and population dynamics of the vectored organisms, as well as resulting changes in their distribution (Jeltsch et al., 2008; Russo et al., 2006).

Dispersal kernels (Nathan et al., 2012), demonstrate the scale(s) at which propagules are dispersed, as well as the frequency and extent of LDD events. Mechanistic models predict the spatial patterns of propagule dispersal and typically require data on two interacting subcomponents: (1) the retention time of the propagule in the digestive tract and (2) the displacement of the vector over that time (Côrtes & Uriarte, 2013). Sensitivity analysis for wintering waterbirds suggests that maximum gut retention times have less influence on seed dispersal kernels than the nature of bird movements per se, reinforcing the need to include quality tracking data to obtain valid predictions (Martín-Vélez, Leeuwen, et al., 2021). Some studies of endozoochory have made unrealistic estimates of the scale of dispersal, as they fail to accurately account for waterbird movement, and make simple extrapolations from a retention time curve by assuming propagule ingestion is followed by non-stop flights (e.g., Manning et al., 2021; Raulings et al., 2011). However, ringing recoveries have been used to make general predictions for kernels during seasonal migration, and have shown that migrating ducks can facilitate dispersal on a very large scale, predicting dispersal of over 3.5% of seeds to be over 100 km and up to 1,600 km, although maximum dispersal distances for *Artemia* cysts were about half that of seeds (Viana et al., 2013).

Migratory waterbirds are considered to have "flyways", but, in reality, many species show great variation in movement patterns, with individuals often switching between biogeographical regions once thought to belong to separate flyways (Guillemain et al., 2017). The ongoing boom in tracking technology has revolutionised our understanding of waterbird movements, and allows us to identify predictable pathways by which waterbirds can disperse other organisms at a regional scale. However, migratory movements occur during a small fraction of the annual cycle, and movements during the rest of the year are mainly a succession of daily foraging bouts and returns to roosting areas. This often constrains flight distances to within a few kilometres, although geese sometimes fly over 50 km between feeding and roost sites (Wood et al., 2020). In general, these daily movement patterns still provide extreme dispersal distances exceeding the maxima expected with most abiotic dispersal (which are typically <100 m for seeds; Tamme et al., 2014), and these are still likely to be LDD events.

Even during the breeding season, classical radio-tracking showed that mallards can disperse seeds between isolated waterbodies to maxima exceeding 8 km (Bartel et al., 2018). GPS tracking allows

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inclusion of specific patterns of daily movements into dispersal predictions, and allowed Kleyheeg et al. (2017) to calculate median seed dispersal distances of between 600 m and 3 km for wintering mallards. During spring migration, dispersal distances were extended to medians of up to 413 km (Kleyheeg et al., 2019). A study of wintering gulls found that, even outside migration periods, seeds are dispersed up to 150 km or more, although median distances were around 800 m (Martín-Vélez, Leeuwen, et al., 2021). These studies suggest that aquatic meta-communities can be well-connected by waterbirds. However, spatial models so far have focused on individual bird species even though there are typically multiple species present dispersing similar propagules (Sebastián-González et al., 2020). Different waterbird species dispersing the same plants and invertebrates also can have very different migration patterns (Gaidet et al., 2010). Therefore, models comparing multiple bird species are needed to predict spatial patterns of dispersal and gene flow at broad geographical scales. Furthermore, to date, models have focused on movements of viable propagules, and future work is required to incorporate the probability of establishment after dispersal, and how this varies spatially.

Fortunately, since dispersal by waterbirds is very amenable to mechanistic modelling, focused research can quickly improve our ability to forecast LDD events such as range shifts in response to climate change, or rate of spread of alien species, agricultural weeds or even genetically-modified crops (Martín-Vélez, Leeuwen, et al., 2021; Viana et al., 2016). Modelling supports the capacity of waterbirds to move plants in pace with climate change (Viana, 2017). Recognising the role for waterbird vectors will improve management prescriptions, such as the best designs of nature reserves or migratory passage sites to increase connectivity across landscapes or flyways. However, profound changes in migration patterns are underway, due largely to climate change (Nagy et al., 2021; Pavon-Jordan et al., 2019). This requires new, more complex approaches such as Joint Species Distribution Models (Tikhonov et al., 2020) to enable modelling of simultaneous changes in the distribution of suitable habitat for both the avian vectors and the organisms they disperse.

10 | MORE RESEARCH IS NEEDED OUTSIDE EUROPE

Despite considerable progress in our understanding of waterbird zoochory over the last two decades, there is still much bias in the location of studies, with the focus largely on waterbirds in Europe. For example, 10 of the 16 papers included in the accompanying virtual issue of *Freshwater Biology* are from Europe. Historical research reviewed by Figuerola and Green (2002) was largely conducted in North America, notably by V.W. Proctor and colleagues. This may be partly a result of the huge cultural value that Anatidae and other waterbirds have in these two continents, where birdwatching or hunting provide important economic benefits (Green & Elmberg, 2014). Hunting has facilitated the study of gut contents, helping to establish what propagules are dispersed by waterbirds (Almeida et al., 2022; Soons et al., 2016). Although some waterfowl species are shared between North America and Europe, there are important differences in their migratory behaviour, and maximum dispersal distances for propagules are predicted to be greater in the former (Viana et al., 2013). This underlines the importance of studying intercontinental variation in the future.

Waterbird zoochory in the Southern Hemisphere and Asia is relatively unexplored, which makes this an important focus for future research. In China, India and the rest of Asia, there are still no detailed studies of waterbird zoochory (Corlett, 2017). Many bird species migrating along the East Asian flyway also occur on European flyways, so the dispersal processes for plants and invertebrates in both continents are likely to be related. By contrast, research in temperate regions may be less relevant to tropical and subtropical ecosystems of the Southern Hemisphere. Much of Africa and Australia is arid or semi-arid with unpredictable rainfall, temporary wetlands and dry-downs. In arid and semi-arid regions, waterbirds are nomadic rather than strictly migratory, making movements at different times of the year in relation to water availability, and being relatively flexible in terms of when they breed. There is a need for more studies of waterbird zoochory from African and Australian arid zones (Green et al., 2008; Raulings et al., 2011; Reynolds & Cumming, 2016a, 2016b).

There are even fewer studies of waterbird zoochory in the permanent and temporary wetlands of South America, despite recent pioneering work (Silva et al., 2021, 2022). The role as dispersal vectors of intercontinental migratory waterbirds moving between Nearctic and Neotropical wetlands, with some shorebirds covering up to 30,000 km annually (Niles et al., 2008), are particularly worthy of future attention. Indeed, shorebirds are often cited as likely vectors to explain bipolar and other amphitropical plant distributions in the Americas (Hancock & Prince, 2022).

11 | IMPACTS OF GLOBAL CHANGE ON WATERBIRD ZOOCHORY

In general, global change in the Anthropocene is likely to have increased the importance of LDD events mediated by waterbirds, as the species that they disperse adjust their distributions in line with changes in land-use, climate change and biological invasions. Estimated rates of past plant dispersal in relation to glacial/interglacial cycles suggest that LDD events are critical in facilitating range changes in response to climatic changes (Birks, 2019), and waterbirds are particularly important vectors for those events. As the remaining natural habitats have been increasingly fragmented and isolated by habitat loss, the dependency of many dispersed organisms on waterbirds to maintain connectivity through flights over a terrestrial matrix hostile to other means of dispersal is likely to have increased. Habitat fragmentation and barrier creation in the landscape through human activity are more likely to impair zoochory by fish or mammals than for birds flying between suitable patches (Caplat et al., 2016; Mulder et al., 2021; Saura et al., 2018).

The global distribution of surface waters has changed drastically as natural wetlands have been drained, and many artificial wetlands

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such as ricefields and dams have been created (Albert et al., 2021). For example, small, permanent irrigation impoundments created in arid and semi-arid environments alter waterbird distribution and movements (Okes et al., 2008; Sebastián-González et al., 2010). Dispersal processes mediated by waterbirds in natural wetlands are disrupted, whilst waterbirds can connect nearby natural and artificial wetlands (Almeida et al., 2020). This may facilitate the colonisation of new, artificial wetlands with native species, but also the spread of alien species from artificial into natural habitats (Lovas-Kiss, Sánchez, et al., 2018; Martín-Vélez, Leeuwen, et al., 2021).

In addition, climate change affects waterbird movement patterns, the timing of migrations and waterbird abundance (Lehikoinen et al., 2013; Nagy et al., 2021). Shifting surface water availability and changes in waterbird movement, from both climate change and land-use change, has major implications for the persistence of waterbird populations and their role as dispersal vectors. Indeed, global warming is forecast to have an astounding impact on the ranges of many migratory waterbird species by 2050, especially those breeding in extreme latitudes such as the Arctic, as well as Afrotropical species (Nagy et al., 2021), and this will cause major population declines and threaten many species with extinction. Significant historical and recent declines already have occurred in many waterbird populations (Amano et al., 2020; Lotze et al., 2006), reducing their capacity as dispersal vectors.

Zoochory by waterbirds has been confirmed for a range of alien plants, both aquatic and terrestrial, and alien aquatic invertebrates (Green, 2016). Many alien plants dispersed also are agricultural weeds with important economic impacts (Lovas-Kiss, Sánchez, et al., 2018; Martín-Vélez, Leeuwen, et al., 2021). Alien invertebrates dispersed can have major ecological impacts (e.g., alien brine shrimps eliminating native species; Sánchez et al., 2012), as well as economic impacts (e.g., alien bryozoans causing biofouling of irrigation systems; Wang et al., 2017).

More experimental studies will help to clarify the potential that alien species of concern have to disperse through waterbirds (García-Álvarez et al., 2015; Sánchez et al., 2012). Further field studies can provide important insights into the role of waterbird vectors in the spread of alien plants and agricultural weeds (e.g., Lovas-Kiss et al., 2019; Martín-Vélez, Lovas-Kiss, et al., 2021; Reynolds & Cumming, 2016a). In addition, databases for alien species need to pay more attention to the potential that waterbirds have in promoting their spread, so as to facilitate effective management (Green, 2016).

12 | CONCLUSIONS

Exciting advances have been made over the past 20 years in many aspects of the role of waterbirds as dispersal vectors, and key priorities for more research have been identified. New technologies, particularly through bird tracking and eDNA analysis, have opened excellent opportunities for future work. Disparities in the geographical and taxonomic distribution of research effort need to be addressed. Terrestrial and global change ecologists should pay more attention to the major influence of waterbirds, particularly given their fundamental role in allowing plants to shift their distribution to keep pace with climate change (mainly plant species assigned to classical dispersal syndromes that imply no LDD capacity), thus maintaining ecosystem functionality. We particularly highlight the involvement of waterbirds in the dispersal of organisms within and across terrestrial and aquatic landscapes. The importance of waterbirds as dispersal vectors makes it vital to take measures to increase the resilience of waterbird populations against human impacts (Amano et al., 2020; Breiner et al., 2021).

AUTHOR CONTRIBUTION

Conceptualisation, conducting the research, writing: all authors. Preparation of figures and tables: ESG, CHAVL, DMW.

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CONFLICT OF INTEREST

Andy J. Green is an Editor for *Freshwater Biology* but has been excluded from the assignment of the handling editor, the peer review process and all decision-making for their manuscript. *Freshwater Biology* encourages its Editors to publish in the journal, and their access to Scholar One is limited to separate them completely from the decision-making process for their manuscripts.

DATA AVAILABILITY STATEMENT

No new data were used in this paper.

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