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Plant dispersal syndromes are unreliable, especially for predicting zoochory and long-distance dispersal

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Plant dispersal syndromes are allocated based on diaspore morphology and used to predict the dominant mechanisms of dispersal. Many authors assume that only angiosperms with endozoochory, epizoochory or anemochory syndromes have a long-distance dispersal (LDD) mechanism. Too much faith is often placed in classical syndromes to explain historical dispersal events and to predict future ones. What is usually recorded as the 'endozoochory syndrome' is in reality a 'frugivory syndrome' and this has often diverted attention from endozoochory by non-frugivores (e.g. waterbirds and large herbivores) that disperse a broad range of angiosperms, for which they likely provide the maximum dispersal distances. Neither the endozoochory nor the epizoochory syndromes provide helpful predictions of which plants non-frugivores disperse, or by which mechanism. We combined data from previous studies to show that only 4% of European plant species dispersed by ungulate endozoochory belong to the corresponding syndrome, compared to 36% for ungulate epizoochory and 8% for endozoochory by migratory ducks. In contrast, the proportions of these species that are assigned to an 'unassisted syndrome' are 37, 31 and 28%, respectively. Since allocated syndromes do not adequately account for zoochory, empirical studies often fail to find the expected relationship between syndromes and LDD events such as those underlying the colonization of islands or latitudinal migration rates. We need full incorporation of existing zoochory data into dispersal databases, and more empirical research into the relationship between plant traits and the frequency and effectiveness of different dispersal mechanisms (paying attention to unexpected vectors). Acknowledging the broad role of non-frugivores in facilitating LDD is crucial to improve predictions of the consequences of global change, such as how plant distributions respond to climate change, and how alien plants spread. Networks of dispersal interactions between these vertebrates and plants are a vital but understudied part of the Web of Life.

Keywords: endozoochory, epizoochory, seed dispersal, ungulates, waterbirds, plant traits

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Introduction

Seed dispersal is a key aspect of plant population ecology promoting escape from high mortality around the parent plant, and allowing offspring to reach suitable habitat, including previously unoccupied patches. Dispersal is vital for regional survival, range expansion and plant migration. Research into dispersal of vascular plants has boomed in recent decades, and has been dominated by a scientific paradigm (sensu Kuhn 1996) in which the means of dispersal is predictable from morphological diaspore traits (van der Pijl 1982, Pérez-Harguindeguy et al. 2013, Chen et al. 2020), allowing the definition of 'morphological dispersal syndromes'. We call this the 'dispersal syndrome paradigm' (DSP). This paradigm has been further reinforced by the explosive interest in functional traits, since syndromes can be used as such a trait in an effort to explain or predict patterns in community ecology (Aslan et al. 2019). The DSP has determined how plant dispersal is taught in schools and botanical gardens worldwide.

The number of recognized dispersal syndromes varies between studies. However, the classical syndromes include anemochory or wind dispersal (e.g. presence of wings or plumes), hydrochory or water dispersal (high buoyancy), myrmechory or ant dispersal (presence of an elaiosome) and epizoochory or external dispersal (e.g. presence of hooks or sticky hairs). The endozoochory syndrome is identified by the presence of a fleshy pulp or aril assumed to identify plants that disperse via the inside of animal guts (Vittoz and Engler 2007, Heleno and Vargas 2015), these animals being 'frugivores' (i.e. consumers of fleshy fruits).

Floras are often separated into two groups (Correia et al. 2018, Chen et al. 2020): one considered to have 'long-distance dispersal' (LDD) consisting of those with endozoochory, epizoochory or anemochory syndromes, and the others considered only to have 'short-distance dispersal' (SDD). Among SDD syndromes, there is a puzzling 'non-specialized' (or 'unassisted' or 'non-adapted') syndrome for diaspores with none of the features used to identify other syndromes (van der Pijl 1982, Hughes et al. 1994). This is essentially an 'unknown vector' syndrome, the abundance of which reflects how classical syndromes are inadequate for describing the complex evolutionary and ecological relationship between morphology and dispersal. Heleno and Vargas (2015) allocated the 'unassisted syndrome' to 63% of the native flora of Europe, and over a third of plants have this syndrome in forests in other continents (Willson et al. 1990). Amongst the world's agricultural weeds, 80% have an unassisted syndrome (Benvenuti 2007). Given the selective advantages to dispersal, and its importance as a determinant of 'weediness', it seems untenable that so many species would lack adaptations for dispersal. Indeed, these plants may be regularly dispersed by zoochory, and be adapted for it.

Is the syndrome concept soundly based?

The DSP is based on the adaptationist hypothesis that dispersal depends mainly on morphological adaptations which are 'obvious' to the human eye. This assumes plants and their dispersal vectors occur in a conceptual ecological vacuum, when in reality fruit morphology could be a response to enemies or competitors rather than dispersal vectors (Herrera 1986). The DSP ignores alternative hypotheses to explain the variation in fruit morphology, including neutral, pleiotropic or phylogenetic effects. The syndrome approach is too simplistic given the strong developmental and phylogenetic constraints to how plants may respond to selection from vectors. Differences in fruit or seed traits between unrelated species in a flora largely reflect phylogenetic effects rather than adaptations to specific dispersal mechanisms (Jordano 1995). Even with frugivory, fruit traits can be resistant to changes in selective pressures from contemporary vectors. At best, syndromes are likely to reflect exaptations to contemporary vectors (i.e. traits that evolved for a different purpose, e.g. fleshy fruits appeared long before vertebrates, Herrera 1986).

The DSP also assumes that dispersal mechanisms are highly constrained by morphology, i.e. a given mechanism requires a particular trait. However, zoochory is loosely constrained, as illustrated by the failure of plant traits to explain dispersal by seed-caching (synzoochory, Gómez et al. 2019). Likewise, multiple traits can facilitate ingestion by suitable vectors, followed by survival of gut passage, to enable endozoochory. Many plants are likely to have evolved strategies to ensure endozoochory in the absence of a fleshy-fruit, as supported by the diversity of ways in which seed architecture can resist gut passage (Costea et al. 2019). Furthermore, the DSP focuses primarily on morphology, whilst colour and chemical traits may also be associated with dispersal mechanisms (and not only with frugivory).

A critical failing of allocated syndromes is that they ignore endozoochory by non-frugivorous vertebrates, which are major vectors of a broad range of vascular plants with no fleshy fruit (NFF plants). This mechanism can be considered 'non-classical endozoochory' (Green et al. 2019), and involves a range of animal vectors that ingest and disperse NFF seeds, particularly herbivorous mammals together with a range of omnivorous, herbivorous and granivorous birds (i.e. 'non-frugivorous' birds). Non-frugivorous fishes are also important vectors in aquatic systems (Boedeltje et al. 2019).

Classical, highly cited reviews of the ecology of seed dispersal (Howe and Smallwood 1982) overlook the role of non-classical endozoochory. Recent reviews often recognize that NFF plants can be dispersed by mammalian endozoochory, while failing to acknowledge avian vectors (Ozinga et al. 2004, Cousens et al. 2008). A second major failure of the DSP is the inadequacy of the epizoochory syndrome in predicting which diaspores disperse on mammals and birds (below). Syndromes also fail to account for synzoochory (Gómez et al. 2019), or for dispersal when parrots, bats or other animals drop seeds before they are consumed (Kevan and Gaskell 1986, Blanco et al. 2016). These are fundamental shortcomings of classical syndromes because zoochory via vertebrates is the mechanism with greatest potential for

seed dispersal between habitat patches, and provides longer mean, median and maximum dispersal distances than abiotic mechanisms (Thomson et al. 2011, Tamme et al. 2014, Bullock et al. 2017), as well as highly directed dispersal (Carlo et al. 2013).

Endo- and epizoochory by herbivorous mammals

Large herbivores provide effective dispersal via endo- and epizoochory, releasing diaspores into suitable habitats (Janzen 1984, D'hondt et al. 2012), where they can germinate, be secondarily dispersed or enter the seed-bank (Dai 2000, Heinken et al. 2006, Jaroszewicz 2013). Large herbivores preferentially disperse plants that form persistent seed banks (Albert et al. 2015a, Picard et al. 2016).

Quoting Ridley (1930), Janzen (1984) suggested that large herbivores mainly dispersed small-seeded plants with dry fruits when consuming vegetative plant parts (i.e. 'Foliage is the fruit'). Large ruminant herbivores also consume fleshy fruits but regurgitate the endocarps and seeds within, which are rarely found in faeces (Baltzinger et al. 2019, Delibes et al. 2019). Endozoochory by large wild and domestic herbivores is well studied in Europe, e.g. in dehesas (Malo and Suárez 1995), grasslands (Pakeman et al. 2002) or deciduous forests (Heinken et al. 2002). However, endozoochory of small-seeded herbs also occurs in other biomes including tropical forests (Middleton and Mason 1992, Capece et al. 2013, Baltzinger et al. 2020), and flood plains of Nepal (Dinerstein 1989). Albert et al. (2015a) summarised ungulate studies from temperate, boreal and Mediterranean Europe and stressed plant attributes that favored dispersal. In the landscapes they inhabit, ungulates dispersed 39% of

plant species present by endozoochory. The functional trait space of plants dispersed strongly coincided with that of non-dispersed plants, i.e. potentially any species could be dispersed (Pakeman et al. 2002, Albert et al. 2015a).

Epizoochory by large herbivores has been less studied (Heinken et al. 2002, Couvreur et al. 2005, Schulze et al. 2014). Ungulates dispersed 13% of the plants available by epizoochory (Albert et al. 2015a). However, the unreliability of the epizoochory syndrome was demonstrated by Römermann et al. (2005). They tested the attachment potential of diaspores in sheep wool and cattle hair and showed it is not a binary response, solely dependent on the presence of appendages, but rather a continuum. Furthermore, Tackenberg et al. (2006) found no differences between retention potentials of diaspores without appendages (unassisted syndrome), with hooked, elongated appendages (epizoochory syndrome) or with a 'balloon structure' (e.g. Cyperaceae utricles or Poaceae glumes). Low seed mass was the greatest determinant of high retention. Baltzinger et al. (2019) reviewed evidence for joint endo- and epizoochorous dispersal of many plants by the same vector species, and even individuals (Petersen and Bruun 2019). Mutualistic endozoochorous dispersal can indeed facilitate epizoochorous dispersal (thus extending 'Foliage is the Fruit', Couvreur et al. 2005). Ungulate endo- and epizoochory are both favoured by similar traits, particularly diaspore releasing height, and high nitrogen and light demands (Albert et al. 2015b).

Comparing data gathered in Albert et al. (2015a) for plants dispersed or not by large herbivores with the dispersal syndromes in plant trait databases shows how syndromes fail to predict zoochory (Fig. 1). Plants dispersed by endozoochory include all the major syndromes, but mainly unassisted, epizoochory and anemochory, with only 4% from the endozoochory syndrome (Fig. 1). Furthermore, there
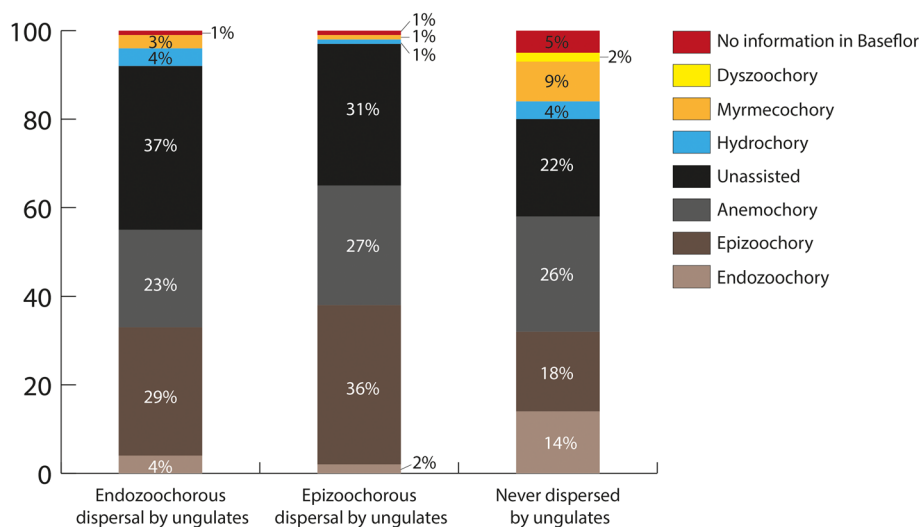

Figure 1. Dispersal syndromes assigned in the Baseflor database (Julve 1998) to 248 plant species dispersed by endozoochory by ungulates in Europe, 83 plants dispersed by fur- and/or hoof- epizoochory and 357 plants never found to be dispersed by ungulates (data from Albert et al. 2015a). Dyszoochory is dispersal by granivores that lose seeds before ingestion. See the Supporting information for other syndrome definitions and results for other trait databases.

is little difference in syndrome frequencies between plants dispersed by endozoochory or by epizoochory (whether by fur or hoof, see Albert et al. 2015a for details). In addition, among plants present in the landscape but not dispersed by ungulates, the epizoochory syndrome is well represented and the endozoochory syndrome is much more frequent than for plants actually dispersed by endozoochory (Fig. 1). The unassisted syndrome was also more frequent for plants dispersed by zoochory than for those not dispersed. These patterns were consistent when applying syndromes from alternative plant trait databases (Supporting information). Similar patterns also occur for plant dispersal by smaller herbivores. For rabbits and hares (lagomorphs), most grassland seeds dispersed by endozoochory belong to unassisted, anemochory and epizoochory syndromes (Supporting information).

Endo- and epizoochory by non-frugivorous birds

Non-frugivorous birds disperse a greater abundance and diversity of NFF plants via endozoochory than via epizoochory, with many plant species dispersed by both modes (Brochet et al. 2010, Costa et al. 2014, Reynolds and Cumming 2016). Importantly, the number of modern studies of seed dispersal by non-frugivorous birds remains small. Most of the work demonstrating that endozoochory by birds is important for NFF plants has been conducted on migratory waterbirds, especially waterfowl (Anatidae) (reviewed by Green et al. 2016). However, there is increasing evidence for a major role of other birds such as corvids, other passerines, parrots, seabirds and galliformes (Costa et al. 2014, Blanco et al. 2016, Orłowski et al. 2016, Green et al. 2019, Martín-Vélez et al. 2021a). The avian digestive system is optimized for calorie uptake per unit time rather than per unit of ingested food, so full digestion of seeds does not generally occur (van Leeuwen et al. 2012). Therefore, NFF plants can develop conditional mutualisms with non-frugivorous birds by providing nutritious seeds, in return for effective dispersal of a proportion of them (Costea et al. 2019).

It is paradoxical that the DSP ignores avian non-classical endozoochory, because repeated studies going back over a century have demonstrated that it is commonplace (Guppy 1906, Heintze 1917 in Green et al. 2019). Alexander von Humboldt seemed aware of its potential ('birds eating the seeds of cereals can easily disseminate them throughout the forests', Humboldt and Bonpland 2009). Ridley (1930) included long lists of alien and native NFF plants in the diet of different birds. De Vlaming and Proctor (1968) and Proctor (1968) showed that shorebirds (Charadriidae) disperse many NFF plants by endozoochory, with maximum gut retention times of $\leq$ 150 h. Such long retention times would allow seeds to be dispersed to oceanic islands and even between continents. Proctor (1968) also recorded retention times for NFF seeds of $\leq$ 25 h for pigeons and passerines.

A particularly broad range of plants are dispersed by European dabbling ducks (92% of which are NFF plants),

representing almost the full spectrum of seed size and light, moisture and nitrogen requirements of the European flora (Soons et al. 2016). Most plant species dispersed by duck endozoochory are terrestrial (Soons et al. 2016, Lovas-Kiss et al. 2018), and have extensive latitudinal ranges covering a large fraction of migratory flyways (Brochet et al. 2009). Although waterbirds often ingest seeds directly from the mother plant, endozoochory also occurs after seeds have been blown or washed into wetlands, or moved within them by hydrochory. Ducks feed extensively on floating seeds or those in sediments (Green et al. 2016, Lovas-Kiss et al. 2018).

Recent studies of geese (Reynolds and Cumming 2016, Green et al. 2018) show them to be important seed vectors, as would be predicted from their grazing behavior and the 'Foliage is the fruit' hypothesis (Janzen 1984). Hattermann et al. (2019) compared those plants dispersed by greylag geese, and those which are not, in Baltic islands. They confirmed endozoochory for 97 vascular plant species (22% of species present). Plants dispersed by geese had smaller seeds, whilst the presence of a fleshy fruit had no influence. Plant species recorded in European dabbling ducks (Soons et al. 2016) illustrate how allocated dispersal syndromes fail to predict endozoochory. Only 7% have a fleshy fruit, with most having an achene (simple dry fruit) (Fig. 2). According to syndromes, few plants dispersed by endozoochory are considered to be animal-dispersed, and most are from unassisted or hydrochory syndromes (Fig. 3).

These results underline the importance of avian vectors for NFF plants widely assumed to have no or little capacity for LDD. They are consistent with recent studies of viable seeds in faeces or pellets of gulls, storks, ducks or shorebirds (Bartel et al. 2018, Lovas-Kiss et al. 2018, 2019, Martín-Vélez et al. 2021a). Waterbirds are major plant vectors in many climatic zones ranging from arctic to subtropical (Green et al. 2008, Reynolds and Cumming 2016, Green et al. 2018, Silva et al. 2021). Germinability of NFF seeds often increases
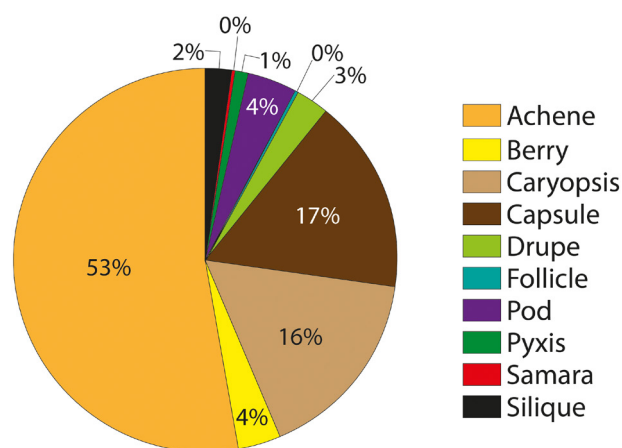

Figure 2. Fruit types assigned in Baseflor (Julve 1998) to 324 plant species with evidence of endozoochory by dabbling ducks (Soons et al. 2016). Only berries, drupes and a small minority of achenes are assigned to the 'endozoochory syndrome' in plant trait databases.
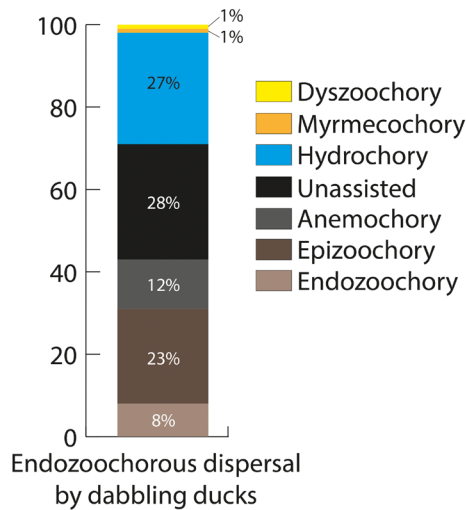
Figure 3. Dispersal syndromes assigned in Baseflor (Julve 1998) to 324 plant species with evidence of endozoochory by dabbling ducks (Soons et al. 2016).

after gut passage, and germination is often accelerated, giving seedlings a head start (Figuerola et al. 2005).

Waterbirds are highly mobile and generally disperse seeds over greater distances than do frugivorous birds (which usually disperse seeds less than 200 m, with maxima of 1.5–14.5 km, Wenny et al. 2016, Bullock et al. 2017). Modelling suggests dabbling ducks regularly disperse seeds over > 300 km on migration (Viana et al. 2016, Kleyheeg et al. 2019). Even during daily movements, half of seeds were dispersed > 3 km (Kleyheeg et al. 2017).

Similarly, birds often disperse seeds externally that do not have characteristics of the 'epizoochory syndrome' (Vazačová and Münzbergová 2014, Hernández-Brito et al. 2021). Eurasian teal illustrate the broad range of syndromes of plants dispersed by epizoochory (Fig. 4). Only 30% of taxa and 36% of diaspores recorded on teal were assigned to the epizoochory syndrome. Furthermore, this syndrome was more dominant amongst seeds dispersed by endozoochory than amongst those dispersed by
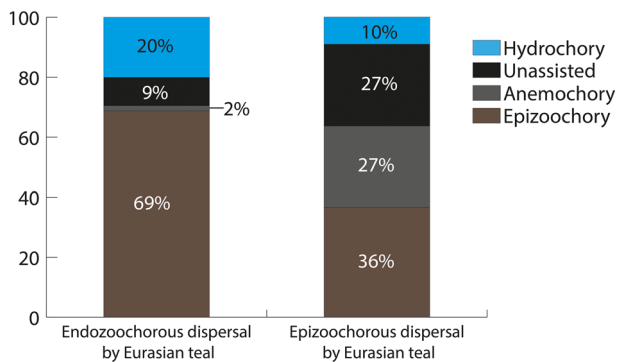

Figure 4. The proportions of intact seeds recovered from Eurasian teal *Anas crecca* by Brochet et al. (2010) from the end of the lower intestine (endozoochory) or from their feathers or skin (epizoochory) assigned to four different syndromes according to Baseflor (Julve 1998).

epizoochory (Fig. 4). The 'epizoochory syndrome' was also dominant amongst seeds dispersed inside shorebirds, storks and gulls (Lovas-Kiss et al. 2019, Martín-Vélez et al. 2021a).

What ungulates and waterbirds have in common as vectors

In both ungulates and waterbirds, the endozoochory and epizoochory syndromes have little, no or even negative predictive power (i.e. plants with an 'endozoochory syndrome' can be less likely to be dispersed by endozoochory than other plants). There is similarity between birds and ungulates in which plants they disperse by endozoochory (Green et al. 2016). Salisbury (1961) found that of 32 species of NFF weeds and aliens germinated from faeces of birds (including pigeons and sparrows), 20 also germinated from livestock dung. At least half of angiosperms dispersed by shorebirds are also dispersed by ungulate endozoochory (Lovas-Kiss et al. 2019). The same NFF seed traits seem to favour survival of gut passage in birds and mammals, especially relatively small, hard and round seeds (Albert et al. 2015b, Costea et al. 2019, Lovas-Kiss et al. 2020), these being traits not used to define classical syndromes.

For waterbirds and ungulates, a short seed shedding period typical outside tropical ecosystems does not mean dispersal is restricted to that period. Some NFF plants retain dead erect stems with seeds attached for an extended period, whereas other seeds remain available to vectors either on the ground, in water or in sediments. These seeds can then be secondarily dispersed by epizoochory when ungulates ruminate and rest, or wallow in mud, or by endozoochory when waterbirds feed in sediments or even on animal prey (Martín-Vélez et al. 2021a). Unsurprisingly, the hydrochory syndrome is better represented amongst plants dispersed by ducks than by ungulates (Fig. 1, 3).

There is an extreme shortage of empirical studies quantifying the importance of zoochory compared to that of other dispersal modes in NFF plants. Available data suggest that, for many plants assigned to abiotic syndromes, zoochory is the main mechanism of dispersal between habitat patches. A major fraction of the populations of different waterbird or ungulate species can disperse the same plant species at the same time (Albert et al. 2015a, Reynolds and Cumming 2016, Farmer et al. 2017, Sebastián-González et al. 2020). Non-classical endozoochory is often a deterministic process, illustrated by the market in North America for providing and sowing plants whose seeds are known to attract migratory waterfowl, so they can be hunted (Baldassarre and Bolen 2006).

When they ignore key vectors, plant trait databases are unreliable

Dispersal syndromes perform better in some contexts (e.g. predicting what plants are dispersed by frugivores) and at some scales than others. They may perform better at predicting dispersal mechanisms in the upper forest canopy (where

frugivory and anemochory dominate) than in the understory (Gottsberger and Silberbauer-Gottsberger 2018, but see Hernández-Brito et al. 2021 for overlooked epizoochory in the canopy). Abiotic syndromes can perform relatively well in environments lacking vertebrate vectors (e.g. due to pollution, Trubina 2020). However, allocated syndromes fail to predict a priori which plants are dispersed by vertebrates, and cannot provide a reliable basis for predicting LDD potential. More than a third of the plant species dispersed by ungulates or waterbirds (Fig. 1, 3) were allocated an SDD syndrome (above). This fraction corresponds to 44% and 57% for flora dispersed by ungulate and waterbird endozoochory respectively, and 35% for ungulate epizoochory.

Plant trait databases, in which dispersal syndromes are allocated based on morphological inspection or laboratory testing (e.g. of buoyancy), have expanded in recent years. Critically, since only fleshy fruits are taken as an indicator of endozoochory, this mode of plant dispersal by non-frugivores is overlooked in such databases (Grime et al. 2007, Thomson et al. 2010, Hintze et al. 2013). Trait databases ignore non-classical zoochory (i.e. when the mechanism of dispersal by animal vectors does not match the syndrome), yet their stated aim is to give priority to the dispersal mechanism with highest maximum dispersal distance (MDD) (Cornelissen et al. 2003, Pérez-Harguindeguy et al. 2013). Once these databases are available, they are readily used for comparative analyses and community models that exclude non-classical zoochory, reinforcing the idea that this does not occur.

Models relying on classical dispersal syndromes to predict the MDD will underestimate it for many taxa. In their metaanalysis, Tamme et al. (2014) overlook endozoochory for many plant taxa. Amongst 576 species considered not to be dispersed by birds, they include 174 from genera identified as duck-dispersed by Soons et al. 2016 (including 58 taxa in common at the species level). For example, Tamme et al. (2014) suggested that *Juncus bufonius* had an MDD (via wind) of only 100 m, yet this species is dispersed by numerous ungulates and waterbirds, including gulls providing an estimated MDD of > 200 km (Albert et al. 2015a, Lovas-Kiss et al. 2019, Martín-Vélez et al. 2021b). As further examples of how databases can mislead, none of 247 Poaceae and 165 Cyperaceae species in an Australian database were considered as dispersed via endozoochory (Thomson et al. 2010), yet avian endozoochory is particularly frequent in these families (Calviño-Cancela et al. 2006, Green et al. 2008). Similarly, Hintze et al. (2013) concluded that, compared to other dispersal modes, endozoochory is particularly unimportant for European Cyperaceae, when the opposite is true (Ridley 1930, Soons et al. 2016). It is therefore vital to improve databases to provide a more reliable resource for modellers.

Underestimation of plant migration in response to global change

To understand the effects of global change on plant migration and connectivity, estimates of dispersal distances must be improved. Dispersal distance is a core attribute of the adaptive capacity of species to climate change (Thurman et al. 2020). Modelling suggests plant migration and colonization rates are highly sensitive to the MDD value and the frequency with which it is attained (Thomson et al. 2011, Bullock 2012). Models must take full account of zoochory by birds and mammals likely to provide the highest MDD values during seasonal or extreme movements, and LDD during daily movements (Pakeman 2001).

Mechanistic models of how plant biodiversity reacts to climate change that rely on dispersal syndromes (Boulangeat et al. 2012) require more realistic information on dispersal mechanisms. Models suggesting most plants have spread rates far too low to keep pace with climate change (Bullock 2012, Corlett and Westcott 2013, Cunze et al. 2013) did not foresee a role for non-frugivorous birds. Bullock (2012) suggested the MDD for zoochory is unlikely to exceed 16 km, a value readily exceeded by an order of magnitude by migratory birds (Viana et al. 2016). Even fish can have a MDD for NFF seeds of 16 km (Mulder et al. 2021). Fifty of 140 plant species modelled by Cunze et al. (2013) are from genera dispersed by ducks (Soons et al. 2016), which can move seeds fast enough to compensate for climate change (Viana 2017). Despite speculation that birds are poor vectors because they migrate towards higher latitudes months after seed production (Pakeman 2001, Cunze et al. 2013), endozoochory is decoupled from seed production and readily occurs during spring migration because seeds are ingested from seed banks (Figuerola et al. 2003, Brochet et al. 2010, but see Lovas-Kiss et al. 2019). Non-frugivorous birds likely reduce the need for the managed translocation of plants foreseen by Corlett and Westcott (2013).

A vital role for animal vectors ignored by dispersal syndromes also underlies the response of plants to historical climate change (Pakeman 2001). Numerous plants dispersed much faster after the last glaciation than can be explained by allocated syndromes (Cain et al. 1998). Cain et al. (1998) cited unrealistically low MDDs for many plant species assigned to anemochory or unassisted syndromes (e.g. 71 species from genera dispersed by European ducks, Soons et al. 2016) that are regularly dispersed by avian or ungulate endozoochory.

Future research is urgently needed into non-classical zoochory

Since morphological syndromes ignore zoochory of plants that lack a fleshy fruit or an obvious means of attachment to animals, there is a deficit of research into zoochory of other plants. A combination of approaches is required to fill this gap. The following list is far from exhaustive (see Gómez et al. 2019 for additional research requirements).

Improved dispersal databases that incorporate empirical data on zoochory

Although more empirical work is required in all climatic regions, important field data on non-classical zoochory have

been generated in recent decades. However, information on those plants dispersed through endozoochory or epizoochory has not been adequately incorporated into databases on native or exotic plant dispersal (Soons et al. 2016). Empirical, easy to update databases are needed that incorporate all current knowledge on zoochory, with incentives and accessibility that ensure newly acquired data are added. Such a database should include the plant dispersed, its vector and associated dispersal mode (e.g. endozoochory), as well as the floristic context (details of local plant inventories). More effective databases are required to improve our capacity to relate dispersal mechanisms to plant distributions and plant traits, as a resource for modelling, and to allow comparison of plants that are and are not dispersed by zoochory within landscapes, or even along migration routes.

Laboratory simulations to quantify dispersal potential

Another way to improve plant trait databases is to incorporate laboratory simulations that quantify zoochory potential for wider sets of plants. Systematic tests for epizoochory potential via fur (Tackenberg et al. 2006) or feathers (Vazačová and Münzbergová 2014) should be conducted with standard protocols, quantifying both attachment and retention potential for seeds. Römermann et al. (2005) showed that retention potential during epizoochory can be predicted from measures of seed mass and morphology (as applied by Rumpf et al. 2018). Measures of seed size, shape and hardness could be combined to provide an index of endozoochory potential (Lovas-Kiss et al. 2020).

Systematic tests of the resistance of seeds to digestion should also be adopted using exposure to an abrasive acid mixture (Vazačová and Münzbergová 2013, Kleyheeg et al. 2018), or a gut simulation environment (Milotić and Hoffmann 2016) as an index of endozoochory potential. Laboratory tests of seed survival and germinability after simulated gut passage could be used to create a ranking index equivalent to those for epizoochory (above), anemochory and hydrochory (Hintze et al. 2013). Research is needed to establish whether laboratory simulations of the digestive process are realistic, and how the gut microbiome influences the germination fate of seeds that survive passage (Fricke et al. 2013, Nelson 2018). Non-mycorrhizal plants (e.g. Cyperaceae) or those carrying mutualistic endophytes within their seeds (e.g. Poaceae), instead of relying on horizontal transmission, may be more likely to establish after LDD via zoochory (Wilson et al. 2009). Palatability tests for seeds using domesticated granivores (e.g. ducks or pigeons) or livestock should also be conducted as an index of potential ingestion rates.

Multi-vector research within landscapes

Ideally, studies of plant dispersal should involve measurements of the seed dispersal effectiveness (Schupp et al. 2017) of different biotic and abiotic vectors within a given landscape. We require tests of the extent to which syndrome dispersal vectors are more effective than non-syndrome vectors, in a manner analogous to tests for pollinator syndromes (Ollerton et al. 2015). However, the answer to this question depends on the scale of the study, as non-syndrome vectors may be more important for dispersal between patches than within. The relative importance of different vectors for a given plant species can vary greatly as a function of dispersal distance (Nathan et al. 2008), and is subject to spatial and temporal variation.

We also need comparisons of which plants are dispersed by vertebrates within a study area (or within their home range) and which are not, looking for traits that predict zoochory (Albert et al. 2015a, Picard et al. 2016, Hattermann et al. 2019). Functional traits such as life forms and seed size can be more useful than classical syndromes. Other useful traits may include diaspore hardness and shape, tegument thickness, seed bank longevity, plant height at which diaspores at released, phenology and Ellenberg indicator values.

Within the framework of such studies, the role of different vectors needs to be compared, including different foraging guilds (e.g. waterbirds, galliformes, pigeons, corvids). So far, the extent of overlap and functional redundancy of different vectors can be assessed for a few waterbird (Reynolds and Cumming 2016, Sebastián-González et al. 2020), passerine (Costa et al. 2014) or ungulate communities (Castley et al. 2001, Picard et al. 2016).

Follow the example of frugivore research

Research into endozoochory by frugivores is more advanced than research into non-classical endozoochory, e.g. through analyses of mutualistic networks between plants and their vectors, movement ecology studies and landscape genetics (Wenny et al. 2016). We must apply similar techniques in studies on non-frugivores. Tracking technology has advanced tremendously in the last two decades, and the movements of many non-frugivorous birds are now well understood, allowing the simulation of seed shadows (Kleyheeg et al. 2017, 2019, Martín-Vélez et al. 2021b). The first waterbird–plant dispersal network analysis was recently completed (Sebastián-González et al. 2020), and more are needed. There are datasets on ungulate zoochory suitable for network analyses (Shiponeni and Milton 2006, Jaroszewicz et al. 2013). The seed dispersal effectiveness and seed shadows of different vectors for the same NFF plants should be compared, as in studies comparing frugivores (Jordano 2017). Frugivore studies can be expanded to include non-classical endozoochory. Small seeds of < 5 mm are often ignored during studies of tropical frugivores, and much could be learned by identifying them (Capece et al. 2013). A conceptual unification of all endozoochory is required, involving frugivores and non-frugivores alike.

There is a need to quantify dispersal kernels for non-classical zoochory, and for diplochory involving non-frugivores. To date, dispersal kernel studies have focused on the mechanism that mirrors the allocated syndrome (Bullock et al. 2017). Reflecting emphasis on frugivory, there is a lack of studies

of kernels realized by vertebrates for plants that are neither trees nor shrubs (only 4 of 168 datasets, Bullock et al. 2017). The suggestion that average dispersal distances are greatest for trees and shrubs (Bullock et al. 2017) could be a consequence of biases in the metadataset, since non-frugivores are more likely to disperse grasses, sedges and rushes.

Frugivores exert important selection pressure on fruit morphology (Galetti et al. 2013), and the selection pressure exerted on plant diaspores by non-classical zoochory should be investigated. Skaien and Arcese (2020) showed a switch to more, smaller, wingless fruits in response to ungulate browsing, a change promoting endozoochory. The DSP focuses on morphology, and ignores colour, chemical and nutrition dimensions of diaspores which could potentially be as important for non-classical endozoochory as they are for frugivory (Jordano 1995). For example, the role of dry fruit coloration as a signal to avian vectors should be investigated, bearing in mind that birds see UV light.

Conclusions

The dispersal syndrome paradigm falls short of providing adequate explanations and predictions for plant dispersal at different scales. Zoochory and dispersal distances have been systematically underestimated for plants lacking a fleshy fruit or appendages. This is particularly crucial for LDD events, of overriding importance in plant biogeography and in plant conservation in the Anthropocene. We question the view that 'the distinction between biotically and abiotically dispersed fruits and seeds is uncontroversial' (Howe 2016). There appears to be no such dichotomy in nature, but rather continuous variation in zoochory potential. Dispersal syndromes overlook LDD mechanisms for a broad array of plants, and should not be relied on as functional traits. They are a failure of reductionism, oversimplifying the complexities of plant dispersal in nature. The classical 'endozoochory syndrome' should be renamed the 'frugivory syndrome', to discourage oversight of endozoochory by non-frugivores.

With hindsight, should this failure of syndromes surprise us? Can we really expect to be able to look at a diaspore and distinguish, for example, if the hairs on a small seed are an adaptation to stick into mud or hair, to catch the wind, as a defense against insect attack, or have some other evolutionary explanation? Dispersal is a form of movement behaviour, and just as syndromes in animals are assigned based on behavioural observations (Comte and Olden 2018), plant dispersal syndromes may be more usefully defined based on field observational data of dispersal movements, not on simple morphological traits.

Major networks of dispersal interactions between non-frugivores and plants are widely ignored (but see Thorsen et al. 2011), yet they are a vital part of the Web of Life. Documenting such poorly understood ecological interactions is crucial to facilitate biodiversity conservation (Jordano 2016). Until the importance of non-classical zoochory is recognized, our understanding of multi-interaction networks (Dáttilo et al.

2016) will be incomplete. Dispersal syndromes are being used to predict which plants are dependent on animal vectors so as to prioritise vertebrate conservation strategies (Albert-Daviaud et al. 2018), but key non-frugivorous vectors will be overlooked. A major research effort is required to extend our knowledge of plant dispersal by non-frugivores, and apply that knowledge in ecological models.

Author contributions

Andy J. Green: Conceptualization (lead); Data curation (lead); Funding acquisition (equal); Investigation (lead); Methodology (lead); Project administration (equal); Writing – original draft (lead); Writing – review and editing (lead). **Christophe Baltzinger**: Conceptualization (supporting); Data curation (supporting); Formal analysis (equal); Funding acquisition (equal); Investigation (supporting); Methodology (supporting); Project administration (equal); Writing – original draft (supporting); Writing – review and editing (supporting). **Ádám Lovas-Kiss**: Conceptualization (supporting); Data curation (supporting); Formal analysis (equal); Funding acquisition (equal); Investigation (supporting); Methodology (supporting); Project administration (equal); Writing – original draft (supporting); Writing – review and editing (supporting).

Data availability statement

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.612jm643n> (Green et al. 2021).

References

Albert, A. et al. 2015a. Seed dispersal by ungulates as an ecological filter: a trait-based meta-analysis. – Oikos 124: 1109–1120.
Albert, A. et al. 2015b. Using basic plant traits to predict ungulate seed dispersal potential. – Ecography 38: 440–449.
Albert-Daviaud, A. et al. 2018. Seed dispersal syndromes in the Madagascan flora: the unusual importance of primates. – Oryx 52: 418–426.

Aslan, C. et al. 2019. Employing plant functional groups to advance seed dispersal ecology and conservation. – AoB Plants 11: plz006.

Baldassarre, G. A. and Bolen, E. G. 2006. Waterfowl ecology and management, 2nd edn. – Krieger Publ. Co.

Baltzinger, C. et al. 2019. Plants on the move: hitch-hiking with ungulates distributes diaspores across landscapes. – Front. Ecol. Evol. 7: 38.

Baltzinger, C. et al. 2020. Ungulates as dispersal vectors of non-native plants. – In: Traveset, A. and Richardson, D. M. (eds), Plant invasions: the role of biotic interactions. CABI, pp. 105–137.

Bartel, R. D. et al. 2018. Endozoochory by mallard in New Zealand: what seeds are dispersed and how far? – PeerJ 6: e4811.

Benvenuti, S. 2007. Weed seed movement and dispersal strategies in the agricultural environment. – Weed Biol. Manage. 7: 141–157.

Blanco, G. et al. 2016. Internal seed dispersal by parrots: an overview of a neglected mutualism. – PeerJ 4: e1688.

Boedeltje, G. et al. 2019. Plant dispersal in a temperate stream by fish species with contrasting feeding habits: the role of plant traits, fish diet, season and propagule availability. – Front. Ecol. Evol. 7: 54.

Boulangeat, I. et al. 2012. Improving plant functional groups for dynamic models of biodiversity: at the crossroads between functional and community ecology. – Global Change Biol. 18: 3464–3475.

Brochet, A.-L. et al. 2009. The role of migratory ducks in the long-distance dispersal of native plants and the spread of exotic plants in Europe. – Ecography 32: 919–928.

Brochet, A.-L. et al. 2010. Plant dispersal by teal (*Anas crecca*) in the Camargue: duck guts are more important than their feet. – Freshwater Biol. 55: 1262–1273.

Bullock, J. M. 2012. Plant dispersal and the velocity of climate change. – In: Clobert, J. et al. (eds), Dispersal ecology and evolution. Oxford Univ. Press, pp. 366–374.

Bullock, J. M. et al. 2017. A synthesis of empirical plant dispersal kernels. – J. Ecol. 105: 6–19.

Cain, M. L. et al. 1998. Seed dispersal and the Holocene migration of woodland herbs. – Ecol. Monogr. 68: 325–347.

Calviño-Cancela, M. et al. 2006. Emus as non-standard seed dispersers and their potential for long-distance dispersal. – Ecography 29: 632–640.

Capece, P. I. et al. 2013. Viability of small seeds found in feces of the Central American tapir on Barro Colorado Island, Panama. – Integr. Zool. 8: 57–62.

Carlo, T. A. et al. 2013. Where do seeds go when they go far? Integrating distance and directionality of avian seed dispersal in heterogeneous landscapes. Ecology 94: 301–307.

Castley, J. G. et al. 2001. The importance of seed dispersal in the Alexandria Coastal Dunefield, South Africa. – J. Coastal Conserv. 7: 57–70.

Chen, S.-C. et al. 2020. Tradeoff between seed dispersal in space and time. – Ecol. Lett. 23: 1635–1642.

Comte, L. and Olden, J. D. 2018. Evidence for dispersal syndromes in freshwater fishes. – Proc. R. Soc. B 285: 20172214.

Corlett, R. T. and Westcott, D. A. 2013. Will plant movements keep up with climate change? – Trends Ecol. Evol. 28: 482–488.

Cornelissen, J. H. C. et al. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. – Aust. J. Bot. 51: 335–380.

Correia, M. et al. 2018. Should I stay or should I go? Mycorrhizal plants are more likely to invest in long-distance seed dispersal than non-mycorrhizal plants. – Ecol. Lett. 21: 683–691.

Costa, J. M. et al. 2014. Endozoochory largely outweighs epizoochory in migrating passerines. – J. Avian Biol. 45: 59–64.

Costea, M. et al. 2019. The effect of gut passage by waterbirds on the seed coat and pericarp of diaspores lacking 'external flesh': evidence for widespread adaptation to endozoochory in angiosperms. – PLoS One 14: e0226551.

Cousens, R. D. et al. 2008. Dispersal in plants: a population perspective. – Oxford Univ. Press.

Couvreur, M. et al. 2005. Complementary of epi- and endozoochory of plant seeds by free ranging donkeys. – Ecography 28: 37–48.

Cunze, S. et al. 2013. Are plant species able to keep pace with the rapidly changing climate? – PLoS One 8: e67909.

D'hondt, B. et al. 2012. A data-driven simulation of endozoochory by ungulates illustrates directed dispersal. – Ecol. Model. 230: 114–122.

Dai, X. 2000. Impact of cattle dung deposition on the distribution pattern of plant species in an alvar limestone grassland. – J. Veg. Sci. 11: 715–724.

Dáttilo, W. et al. 2016. Unravelling Darwin's entangled bank: architecture and robustness of mutualistic networks with multiple interaction types. – Proc. R. Soc. B 283: 20161564.

de Vlaming, V. and Proctor, V. W. 1968. Dispersal of aquatic organisms: viability of seeds recovered from the droppings of captive killdeer and mallard ducks. – Am. J. Bot. 55: 20–26.

Delibes, M. et al. 2019. Spitting seeds from the cud: a review of an endozoochory exclusive to ruminants. – Front. Ecol. Evol. 7: 265.

Dinerstein, E. 1989. The foliage-as-fruit hypothesis and the feeding behavior of south asian ungulates. – Biotropica 21: 214–218.

Farmer, J. A. et al. 2017. Evaluating the potential for weed seed dispersal based on waterfowl consumption and seed viability. – Pest Manage. Sci. 73: 2592–2603.

Figuerola, J. et al. 2003. Passive internal transport of aquatic organisms by waterfowl in Doñana, south-west Spain. – Global Ecol. Biogeogr. 12: 427–436.

Figuerola, J. et al. 2005. Endozoochorous dispersal of aquatic plants: does seed gut passage affect plant performance? – Am. J. Bot. 92: 696–699.

Fricke, E. C. et al. 2013. When condition trumps location: seed consumption by fruit-eating birds removes pathogens and predator attractants. – Ecol. Lett. 16: 1031–1036.

Galetti, M. et al. 2013. Functional extinction of birds drives rapid evolutionary changes in seed size. – Science 340: 1086–1090.

Gómez, J. M. et al. 2019. Synzoochory: the ecological and evolutionary relevance of a dual interaction. – Biol. Rev. 94: 874–902.

Gottsberger, G. and Silberbauer-Gottsberger, I. 2018. How are pollination and seed dispersal modes in Cerrado related to stratification? Trends in a cerrado sensu stricto woodland in southeastern Brazil, and a comparison with Neotropical forests. – Acta Bot. Bras. 32: 434–445.

Green, A. J. et al. 2008. The potential role of waterbirds in dispersing invertebrates and plants in arid Australia. – Freshwater Biol. 53: 380–392.

Green, A. J. et al. 2016. Dispersal of plants by waterbirds. – In: Şekercioğlu, Ç. H. et al. (eds), Why birds matter: avian ecological function and ecosystem services. Univ. of Chicago Press, pp. 147–195.

Green, A. J. et al. 2018. Plant dispersal by Canada geese in Arctic Greenland. – Polar Res. 37: 1508268.

Green, A. J. et al. 2019. Beyond scatter-hoarding and frugivory: European corvids as overlooked vectors for a broad range of plants. – Front. Ecol. Evol. 7: 133.

Green, A. J. et al. 2021. Data from: Plant dispersal syndromes are unreliable, especially for predicting zoochory and long-distance dispersal. – Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.612jm643n>.

Grime, J. P. et al. 2007. Comparative plant ecology: afunctional approach to common British species. – Springer.

Hattermann, D. et al. 2019. Geese are overlooked dispersal vectors for vascular plants in archipelago environments. – J. Veg. Sci. 30: 533–541.

Heinken, T. et al. 2002. Dispersal of vascular plants by four species of wild mammals in a deciduous forest in NE Germany. – Phytocoenologia 32: 627–643.

Heinken, T. et al. 2006. Soil seed banks near rubbing trees indicate dispersal of plant species into forests by wild boar. – Basic Appl. Ecol. 7: 31–44.

Heleno, R. and Vargas, P. 2015. How do islands become green? – Global Ecol. Biogeogr. 24: 518–526.

Hernández-Brito, D. et al. 2021. Epizoochory in parrots as an overlooked yet widespread plant–animal mutualism. – Plants 10: 760.

Herrera, C. M. 1986. Vertebrate-dispersed plants: why they don't behave the way they should. – In: Estrada, A. and Fleming, T. H. (eds), Frugivores and seed dispersal. Springer, pp. 5–18.

Hintze, C. et al. 2013. D3: the dispersal and diaspore database – baseline data and statistics on seed dispersal. – Perspect. Plant Ecol. Evol. Syst. 15: 180–192.

Howe, F. and Smallwood, J. 1982. Ecology of seed dispersal. – Annu. Rev. Ecol. Syst. 13: 201–228.

Howe, H. F. 2016. Making dispersal syndromes and networks useful in tropical conservation and restoration. – Global Ecol. Conserv. 6: 152–178.

Hughes, L. et al. 1994. Predicting dispersal spectra: a minimal set of hypotheses based on plant attributes. – J. Ecol. 82: 933–950.

Humboldt, A. V. and Bonpland, A. 2009. Essay on the geography of plants. – Univ. of Chicago Press.

Janzen, D. H. 1984. Dispersal of small seeds by big herbivores: foliage is the fruit. – Am. Nat. 123: 338–353.

Jaroszewicz, B. 2013. Endozoochory by European bison influences the build-up of the soil seed bank in subcontinental coniferous forest. – Eur. J. For. Res. 132: 445–452.

Jaroszewicz, B. et al. 2013. Endozoochory by the guild of ungulates in Europe's primeval forest. – For. Ecol. Manage. 305: 21–28.

Jordano, P. 1995. Angiosperm fleshy fruits and seed dispersers: a comparative analysis of adaptation and constraints in plant–animal interactions. – Am. Nat. 145: 163–191.

Jordano, P. 2016. Chasing ecological interactions. – PLoS Biol. 14: e1002559.

Jordano, P. 2017. What is long-distance dispersal? And a taxonomy of dispersal events. – J. Ecol. 105: 75–84.

Julve, P. 1998. Baseflor. Index botanique, écologique et chorologique de la flore de France. – <http://perso.wanadoo.fr/philippe.julve/catminat.htm>, accessed 1 July 2020.

Kevan, P. and Gaskell, B. 1986. The awkward seeds of *Gonystylus macrophyllus* (Thymelaeaceae) and their dispersal by the bat *Rousettus celebensis* in Sulawesi, Indonesia. – Biotropica 18: 76–78.

Kleyheeg, E. et al. 2017. Seed dispersal distributions resulting from landscape-dependent daily movement behaviour of a key vector species, *Anas platyrhynchos*. – J. Ecol. 105: 1279–1289.

Kleyheeg, E. et al. 2018. Interactions between seed traits and digestive processes determine the germinability of bird-dispersed seeds. – PLoS One 13: e0195026.

Kleyheeg, E. et al. 2019. A comprehensive model for the quantitative estimation of seed dispersal by migratory mallards. – Front. Ecol. Evol. 7: 40.

Kuhn, T. S. 1996. The structure of scientific revolutions. – Univ. of Chicago Press.

Lovas-Kiss, Á. et al. 2018. Endozoochory of aquatic ferns and angiosperms by mallards in central Europe. – J. Ecol. 106: 1714–1723.

Lovas-Kiss, Á. et al. 2019. Shorebirds as important vectors for plant dispersal in Europe. – Ecography 42: 956–967.

Lovas-Kiss, Á. et al. 2020. Seed mass, hardness and phylogeny explain the potential for endozoochory by granivorous waterbirds. – Ecol. Evol. 10: 1413–1424.

Malo, J. E. and Suárez, F. 1995. Herbivorous mammals as seed dispersers in a Mediterranean dehesa. – Oecologia 104: 246–255.

Martín-Vélez, V. et al. 2021a. Endozoochory of the same community of plants lacking fleshy fruits by storks and gulls. – J. Veg. Sci. 32: e12967.

Martín-Vélez, V. et al. 2021b. Spatial patterns of weed dispersal by wintering gulls within and beyond an agricultural landscape. – J. Ecol. 109: 1947–1958.

Middleton, B. A. and Mason, D. H. 1992. Seed herbivory by nilgai, feral cattle and wild boar in the Keoladea-National-Parl, India. – Biotropica 24: 538–543.

Milotić, T. and Hoffmann, M. 2016. How does gut passage impact endozoochorous seed dispersal success? Evidence from a gut environment simulation experiment. – Basic Appl. Ecol. 17: 165–176.

Mulder, A. J. E. et al. 2021. Tracking temperate fish reveals their relevance for plant seed dispersal. – Funct. Ecol. 35: 1134–1144.

Nathan, R. et al. 2008. Mechanisms of long-distance seed dispersal. – Trends Ecol. Evol. 23: 638–647.

Nelson, E. B. 2018. The seed microbiome: Origins, interactions and impacts. – Plant Soil 422: 7–34.

Ollerton, J. et al. 2015. Using the literature to test pollination syndromes – some methodological cautions. – J. Pollin. Ecol. 16: 119–125.

Orłowski, G. et al. 2016. The effectiveness of endozoochory in three avian seed predators. – J. Ornithol. 157: 61–73.

Ozinga, W. A. et al. 2004. Dispersal potential in plant communities depends on environmental conditions. – J. Ecol. 92: 767–777.

Pakeman, R. J. 2001. Plant migration rates and seed dispersal mechanisms. – J. Biogeogr. 28: 795–800

Pakeman, R. J. et al. 2002. Ecological correlates of endozoochory by herbivores. – Funct. Ecol. 16: 296–304.

Pérez-Harguindeguy, N. et al. 2013. New handbook for standardised measurement of plant functional traits worldwide. – Aust. J. Bot. 61: 167–234.

Petersen, T. K. and Bruun, H. H. 2019. Can plant traits predict seed dispersal probability via red deer guts, fur and hooves? – Ecol. Evol. 9: 9768–9781.

Picard, M. et al. 2016. Functional traits of seeds dispersed through endozoochory by native forest ungulates. – J. Veg. Sci. 27: 987–998.

Proctor, V. W. 1968. Long-distance dispersal of seeds by retention in digestive tract of birds. – Science 160: 321–322.

Reynolds, C. and Cumming, G. S. 2016. Seed dispersal by water-birds in southern Africa: comparing the roles of ectozoochory and endozoochory. – Freshwater Biol. 61: 349–361.

Ridley, H. N. 1930. The dispersal of plants throughout the world. – Reeve L & Company.

Römermann, C. et al. 2005. How to predict attachment potential of seeds to sheep and cattle coat from simple morphological seed traits. – Oikos 110: 219–230.

Rumpf, S. B. et al. 2018. Range dynamics of mountain plants decrease with elevation. – Proc. Natl Acad. Sci. USA 115: 1848–1853.

Salisbury, E. J. 1961. Weeds and aliens. – Collins.

Schulze, K. A. et al. 2014. Epizoochory via the hooves – the European bison (*Bison bonasus* L.) as a dispersal agent of seeds in an open-forest-mosaic. – Tuexenia 34: 131–143.

Schupp, E. W. et al. 2017. A general framework for effectiveness concepts in mutualisms. – Ecol. Lett. 20: 577–590.

Sebastián-González, E. et al. 2020. Waterbird seed-dispersal networks are similarly nested but less modular than those of frugivorous birds, and not driven by functional traits. – Funct. Ecol. 34: 2283–2291.

Shiponeni, N. N. and Milton, S. J. 2006. Seed dispersal in the dung of large herbivores: implications for restoration of renosterveld shrubland old fields. – Biodivers. Conserv. 15: 3161–3175.

Silva, G. G. et al. 2021. Seed dispersal by neotropical waterfowl depends on bird species and seasonality. – Freshwater Biol. 66: 78–88.

Skaien, C. L. and Arcese, P. 2020. Local adaptation in island populations of *Plectritis congesta* that differ in historic exposure to ungulate browsers. – Ecology 101: e03054.

Soons, M. B. et al. 2016. Seed dispersal by dabbling ducks: an overlooked dispersal pathway for a broad spectrum of plant species. – J. Ecol. 104: 443–455.

Tackenberg, O. et al. 2006. What does diaspore morphology tell us about external animal dispersal? Evidence from standardized experiments measuring seed retention on animal-coats. – Basic Appl. Ecol. 7: 45–58.

Tamme, R. et al. 2014. Predicting species' maximum dispersal distances from simple plant traits. – Ecology 95: 505–513.

Thomson, F. J. et al. 2010. Chasing the unknown: predicting seed dispersal mechanisms from plant traits. – Journal of Ecology 98: 1310–1318.

Thomson, F. J. et al. 2011. Seed dispersal distance is more strongly correlated with plant height than with seed mass. – J. Ecol. 99: 1299–1307.

Thorsen, M. J. et al. 2011. Faunal influences on New Zealand seed dispersal characteristics. – Evol. Ecol. 25: 1397–1426.

Thurman, L. L. et al. 2020. Persist in place or shift in space? Evaluating the adaptive capacity of species to climate change. – Front. Ecol. Environ. 18: 520–528.

Trubina, M. R. 2020. Vulnerability to copper smelter emissions in species of the herb–dwarf shrub layer: role of differences in the type of diaspore dispersal. – Russ. J. Ecol 51: 107–117.

van der Pijl, L. 1982. Principles of dispersal in higher plants. – Springer.

van Leeuwen, C. H. A. et al. 2012. Gut travellers: internal dispersal of aquatic organisms by waterfowl. – J. Biogeogr. 39: 2031–2040.

Vazačová, K. and Münzbergová, Z. 2013. Simulation of seed digestion by birds: how does it reflect the real passage through a pigeon's gut? – Folia Geobot. 48: 257–269.

Vazačová, K. and Münzbergová, Z. 2014. The importance of species traits for species distribution on oceanic islands. – PLoS One 9: e101046.

Viana, D. S. 2017. Can aquatic plants keep pace with climate change? – Front. Plant Sci. 8: 1906.

Viana, D. S. et al. 2016. Migratory birds as global dispersal vectors. – Trends Ecol. and Evol. 31: 763–775.

Vittoz, P. and Engler, R. 2007. Seed dispersal distances: a typology based on dispersal modes and plant traits. – Bot. Helvet. 117: 109–124.

Wenny, D. G. et al. 2016. Seed dispersal by fruit-eating birds. – In: Şekercioğlu, Ç. H., et al. (eds.), Why birds matter: avian ecological function and ecosystem services. Univ. of Chicago Press, pp. 107–145.

Willson, M. F. et al. 1990. Seed dispersal spectra: a comparison of temperate plant communities. – J. Veg. Sci. 1: 547–562.

Wilson, J. R. U. et al. 2009. Something in the way you move: dispersal pathways affect invasion success. – Trends Ecol. Evol. 24: 136–144.