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Seed dispersal by dabbling ducks: an overlooked dispersal pathway for a broad spectrum of plant species

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Summary

1. Dabbling ducks (Anatinae) are omnivorous birds that are widespread, numerous, highly mobile and often migratory, and therefore have great potential for (long distance) dispersal of other organisms, including plants. However, their ability to act as plant dispersal vectors has received little attention compared to frugivores and is often assumed to be relevant only for wetland species.

2. To evaluate the potential for plant dispersal by dabbling ducks, we collated and analysed existing data. We identified all plant species whose seeds have been recorded in the diets of the seven dabbling duck (*Anas*) species in the Western Palaearctic, as reported from gut content analyses. We then analysed the habitats and traits of these plant species to identify general patterns, and related these to data on gut passage survival and duck movements.

3. A large number of plant species (>445 species of 189 genera and 57 families) have been recorded in the diet of dabbling ducks. These plant species represent a very wide range of habitats, including almost the full range of site fertility, moisture and light conditions, excluding only very dry and deeply shaded habitats. The ducks prefer seeds of intermediate sizes (1–10 mm^3), which have good chances to survive gut passage, but also ingest smaller and larger seeds. Ingested seeds represent a wide range of dispersal syndromes, including fleshy fruits. Many species (62%) were not previously considered animal-dispersed in plant data bases, and 66% were not identified as bird-dispersed. Rarefaction analyses suggest that our analysis still greatly underestimates the total number of plant species ingested.

4. *Synthesis.* Dabbling ducks do not exclusively ingest seeds of wetland plants, which make up only 40% of the ingested species. Rather, they feed opportunistically on a wide cross-section of plant species available across the landscapes they inhabit. Given the millions of ducks, the hundreds to thousands of seeds ingested per individual on a daily basis, and known gut passage survival rates, this results in vast numbers of seeds dispersed by ducks per day. Internal seed dispersal by dabbling ducks appears to be a major dispersal pathway for a far broader spectrum of plant species than previously considered.

Key-words: Anatinae, connectivity, diet, dispersal, endozoochory, movement ecology, plant–animal interactions, plant habitats, seed traits, waterbirds

Considering these facts, I think it would be an inexplicable circumstance if water-birds did not transport the seeds of fresh-water plants to vast distances, and if consequently the range of these plants was not very great. Charles Darwin, The origin of species (1859)

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Introduction

The study of plant dispersal has become a major field of research in recent decades. Dispersal not only drives spatial population dynamics but is also crucial for maintaining population genetic diversity and resilience, colonization of new (and restored) sites, range expansion and migration. As such, it determines regional plant diversity and species survival (Hanski 1998; Nathan & Muller-Landau 2000; Nathan 2001;

Cousens & Dytham 2008). Within the field of plant dispersal research, the study of dispersal of seeds within fleshy fruits by frugivorous animals is a major topic (> 1279 papers, ISI Web of Knowledge, June 2014; e.g. Jordano *et al.* 2007, 2011; Spiegel & Nathan 2007). Seeds from plants lacking a fleshy fruit are widely assumed to disperse by other means, for example by wind or water, which also represent major research topics (> 1221 papers; e.g. Nathan *et al.* 2002; Soons *et al.* 2004; Pazos *et al.* 2013). Such seeds may also be dispersed by large grazing mammals (externally on their fur or internally as 'the foliage is the fruit'; > 198 papers; e.g. Janzen 1984; Will & Tackenberg 2008; Bullock *et al.* 2011). General studies of plant dispersal often rely on these major dispersal categories (dispersal by frugivores, grazing mammals, wind or water). For example, recent papers have indicated how the dispersal and survival of plant species are reduced by ongoing habitat fragmentation, loss of frugivorous bird and grazing mammal populations, and the lowering of water-tables and flooding probabilities (e.g. Soons *et al.* 2005; Ozinga *et al.* 2009; Markl *et al.* 2012).

In the plant dispersal literature, aquatic plants are often considered to be a separate category. Despite their patchy and often isolated habitat, many freshwater plant species are relatively common across broad distribution ranges (Santamaria 2002). This observation led Darwin (1859) to suggest that these plant species are dispersed frequently and over long distances between suitable sites and he proposed waterbirds as vectors of this transport (which he incorrectly assumed to occur exclusively by attachment to the birds' feet and feathers). More than a century later, Proctor and co-workers (e.g. DeVlaming & Proctor 1968) combined field and experimental approaches to demonstrate conclusively that waterbirds disperse a variety of higher plants and Characeae, primarily after ingestion. However, despite an increasing number of field and experimental studies demonstrating the potential for dispersal by waterbirds (e.g. Figuerola & Green 2002; Charalambidou & Santamaria 2005; Van Leeuwen *et al.* 2012), this mode of dispersal receives little or no mention in general reviews of dispersal by animals or in overviews of dispersal syndromes (e.g. Wang & Smith 2002; Ozinga *et al.* 2004; McConkey *et al.* 2012; Hintze *et al.* 2013), and there is an implicit assumption in the literature that waterbirds are relevant as dispersal vectors only in aquatic or wetland ecosystems.

Among seed-dispersing waterbirds, dabbling ducks (Anatinae) are the best-studied. Dabbling ducks are omnivorous birds that feed extensively on plants and seeds (Cramp & Simmons 1977; Hughes & Green 2005). They are widespread, globally numerous (*ca*. 200 million individuals; Wetlands International 2012), highly mobile on a daily basis and often migratory, and therefore have great potential for (long distance) dispersal of plants (Soons *et al.* 2008; Brochet *et al.* 2009; Viana *et al.* 2013; Kleyheeg *et al.* 2015), which is considered one of the vital ecosystem services they provide (Green & Elmberg 2014; Şekercioğlu, Wenny & Whelan 2016). In the Western Palaearctic alone, there are seven species of dabbling ducks, with a total number of breeding individuals estimated between 13.7 and 18.5 million (BirdLife International 2004; Table 1) and even higher numbers in autumn and early winter, when juveniles are added to the population. This means that even low probabilities of dispersal per duck per day amount to an immense dispersal potential for the whole dabbling duck population, and indicates the importance of quantifying this potential.

Dabbling ducks can disperse plant diaspores (seeds, spores or fragments), either externally (*exozoochorous* dispersal) or internally (*endozoochorous* dispersal). External dispersal occurs when diaspores stick to bill, feet or feathers and detach after some period of time and transport. However, given the water-repellent, smooth plumage of dabbling ducks and their frequent preening behaviour, seeds or fragments are not frequently attached to ducks (Brochet *et al.* 2010a). The dominant dispersal mode, internal dispersal, occurs when ducks ingest diaspores and excrete them in a viable state after passage through the digestive tract. In the gizzard, a highly muscular organ containing small hard particles ('grit'), food items are ground to small fragments ready for further digestion in the intestines. Plant fragments generally do not survive this treatment, so that for higher plants, internal transport mainly con-

Table 1. Summary statistics on plant seed dispersal by dabbling ducks. Estimated numbers of duck individuals in Europe from BirdLife International (2004)

Duck species		Estimated breeding population in Europe, number of individuals	Total number of plant species identified in diet studies (including qualitative data*)	Total number of birds sampled in all diet studies	Average number of seeds per bird (range between studies)	Number of birds used for the calculation of average number of seeds per bird
Anas acuta	Northern pintail	640 000–720 000	115 (148)	442	256 (5–645)	200
Anas clypeata	Northern shoveler	340 000–420 000	62 (76)	384	74 (6–138)	209
Anas crecca	Common teal	1 840 000–2 400 000	273 (286)	3014	728 (1–2347)	1600
Anas penelope	Eurasian wigeon	> 3 400 000	86 (109)	507	66 (5–215)	174
Anas platyrhynchos	Mallard	6 600 000–10 200 000	311 (331)	3502	321 (9–882)	1522
Anas querquedula	Garganey	780 000–1 180 000	37 (55)	113	NA	NA
Anas strepera	Gadwall	120 000–192 000	54 (65)	373	320 (43–416)	136
All duck species		13 720 000–18 512 000	413 (445)	8335	462 (1–2347)	3841

*Plant species numbers between brackets include studies with only qualitative evidence, which could not be used to calculate average numbers of species and/or seeds per bird.

cerns seeds and spores. Successful internal seed dispersal by dabbling ducks is common, as indicated by the high percentage of duck droppings containing intact plant seeds in the field (on average *ca*. 50%, range *ca*. 25–70% across duck species; Van Leeuwen *et al.* 2012). Of seeds found in dabbling duck droppings, an average of *ca*. 33% were viable (range *ca*. 10–65% across duck species; Van Leeuwen *et al.* 2012).

Given these numbers of seeds consumed by ducks and their survival rates, it is surprising that dispersal by ducks receives so little attention in dispersal research (*ca*. 43 papers) and that we currently lack a general quantitative framework representing the role of dabbling ducks in plant dispersal. Such a framework would be especially relevant in the face of increased threats to waterbirds throughout the world, due to habitat loss and hunting pressure (Wetlands International 2012), and more recently from culling in relation with the spread of avian influenza (Yong *et al.* 2013). If waterbirds indeed play an important role as vectors for plant dispersal, this should be taken into account in both plant and waterbird management and conservation strategies, from local to continental scales (e.g. Haig, Mehlman & Oring 1998; Amezaga, Santamaria & Green 2002; Verhoeven *et al.* 2008).

As a vital step towards a full understanding of the role of waterbirds in plant dispersal, we present an analysis of which plant seeds are ingested and potentially dispersed by dabbling ducks. We address seed dispersal of vascular plants, which has been quantified much better than the dispersal of spores of non-vascular plants (also likely to be dispersed readily by ducks, but often not detected in gut content samples due to their small size). Our objective was to identify which plant species are ingested and potentially dispersed by dabbling ducks, and to estimate how many plant species are involved. We aim to clarify the general patterns explaining these identities and numbers, by analysing which plant traits and habitat characteristics are related to dispersal frequency and potential. We address these questions by taking advantage of the large volume of data from existing literature, including duck diet studies and experimental studies that assess how plant and duck characteristics determine gut passage survival. We then discuss how widespread and effective seed dispersal by dabbling ducks is likely to be, across bird and plant species, also considering the role of ducks in the dispersal of non-wetland plants. Finally, we examine the consequences of dabbling duck-mediated dispersal for plant ecology and conservation management.

Materials and methods

To create a comprehensive, general overview of plant seeds ingested and potentially dispersed by dabbling ducks, we went through the following steps: (i) we conducted a literature survey on duck diet data, based on gut content analyses, and compiled an overview of all plant species recorded in dabbling duck diets; (ii) we analysed these data at the species level and in combination with plant ecological data from the literature and data bases, to identify functional traits and habitat characteristics of plant species (disproportionally) ingested by dabbling ducks; (iii) we estimated how complete our list of ingested plant species is likely to be, using rarefaction analysis; and (iv) we selected a case study for which sufficient data were available to relate the plant species composition in the duck diet to the regional floristic composition, again using rarefaction analyses. We discuss how likely it is that the seeds ingested by dabbling ducks are effectively dispersed, by comparing the functional traits of the ingested species to traits known to promote gut passage survival, and by comparing the habitat characteristics of ingested species to habitats frequented by ducks. We limited our analysis to the Western Palaearctic, for which a unique combination of detailed duck data and plant habitat and trait data are available. This allowed us to identify general patterns and build a common framework, that is likely to be representative for other continents.

COMPILATION OF LITERATURE DATA ON DABBLING DUCK DIETS

Dabbling ducks are major hunting quarry and their ecology, feeding habits and diet are well studied. However, until now these data remained highly fragmented and were unexploited by plant ecologists. We compiled a complete overview of all plant seed species reported to have been consumed by the seven dabbling duck species in the Western Palaearctic (Table 1), based on analyses of duck gut contents (specifically, from the oesophagus, proventriculus and gizzard, hereafter collectively termed 'foregut', which best represents the total of seeds ingested). Starting with the data set analysed by Dessborn *et al.* (2011), we searched the available literature for any duck diet studies up to December 2012, through ISI Web of Knowledge, ProQuest Biological Sciences, USGS DUCKDATA and by backtracking older studies from references in more recent articles. We also examined original studies referenced in compilations and standard handbooks (e.g. Cramp & Simmons 1977), bringing together 71 different studies in total. When available, we also recorded data on seed numbers (average number of seeds, per plant species, per duck individual) and frequencies (percentage of duck individuals with ingested seeds, per plant species) for each duck species. Plant species names and taxonomy were synchronized using the digital version of the *Flora Europaea* (held in the PANDORA taxonomic data base system at the Royal Botanic Garden Edinburgh, available at: http://rbg-web2.rbge.org.uk/FE/fe.html; accessed January 2013) and updated taxonomically at the family level following The Plant List (version 1.1; available at: http://www.theplantlist.org; accessed June 2014).

ANALYSIS OF PLANT ECOLOGICAL DATA

Data on duck diet composition were supplemented with plant species habitat characteristics from the PLANTATT data base (attributes of British and Irish plants; Hill, Preston & Roy 2004; excerpt 5 December 2006) and plant trait data related to seed dispersal from the LEDA traitbase (life-history traits of the north-west European flora; Kleyer *et al.* 2008; excerpt 13 July 2010). We analysed the plant species' Ellenberg indicator values for habitat soil fertility ('Nitrogen'; N), moisture ('*Feuchtigkeit*'; F) and light (L), as proposed by Ellenberg (Ellenberg *et al.* 1991) and adapted for the British Isles and Ireland (Hill *et al.* 1999), which are representative for Atlantic (north-west) Europe. Ellenberg indicator values quantify the optimal habitat of each plant species along the full range of existing habitat conditions on an ordinal scale (Table S1 in Supporting Information). Functional dispersal traits analysed were seed production (number of seeds per individual plant, ramet, or tussock), seed size (seed volume, in mm^3), seed wind dispersal capacity as approximated by seed terminal velocity (the constant falling rate of a seed in still air, in m s^{-1}) and seed water dispersal capacity as approximated by seed buoyancy (% of seeds still floating after 1 week in water). In addition, we used LEDA to check whether plant species recorded in the duck diets produce fleshy fruits (considered to indicate dispersal by frugivores) and whether they had previously been recorded as endozoochorously dispersed by any animal species, or specifically by birds.

To analyse whether seeds ingested by the seven dabbling duck species form a representative (randomly selected) subset of all plant species, we compared the distributions of Ellenberg values and trait data of the species ingested to those of all species in north-west Europe on which data are available (using the complete PLANTATT and LEDA data bases). More than 88% of all existing duck diet data were reported from north-west Europe, so that this comparison allows us to draw the bigger picture. We performed this comparison using Pearson's chi-square tests. Where test results were significant ($P < 0.05$), standardized residuals were used for significance testing of differences between duck diet and all plant species within individual categories (bins) using z-scores with Bonferroni correction for multiple comparisons (all testing in IBM SPSS Statistics 19).

RELATIONSHIP BETWEEN DIET COMPOSITION AND REGIONAL FLORISTIC COMPOSITION

The diet compilation showed that in studies where more ducks are sampled, more plant species are found. To evaluate the extent of this 'sampling effect' and how complete our list of ingested plant species is likely to be, we carried out rarefaction analyses (Sanders 1968). Rarefaction allows the prediction of species richness for a given number of individual samples, based on the construction of rarefaction curves. Rarefaction curves were produced by repeatedly resampling a pool of $n = 50$ individuals at random (with repetition) and plotting the average cumulative number of seed species represented by 1, 2, …, n individuals as a function of the number of ducks sampled (Gotelli & Colwell 2001). We did this for two studies in regions with large, ecologically important duck populations, where we had access to particularly high-quality diet data at the level of individual ducks: (i) the Camargue in France, a river delta situated at the mouth of the Rhône, consisting of a plain with agricultural land, lakes and marshes (diet data from Brochet *et al.* 2012a; A.-L. Brochet, J.-B. Mouronval, P. Aubry, M. Gauthier-Clerc, A. J. Green, H. Fritz & M. Guillemain, unpublished data; 176 mallards and 371 teal sampled, 60 and 78 seed morphospecies identified in total); and (ii) the Groene Hart area in the Netherlands, a rural area situated in the Dutch lowlands close to the current delta of the rivers Rhine and Meuse, consisting mostly of agriculture and wetlands on peat soils (Kleyheeg 2015: 78 mallards sampled, 63 seed species in total). Rarefaction analyses were performed in R (version 2.15.1; R Development Core Team 2012), using the package 'vegan' (Oksanen *et al.* 2015).

To estimate the proportion of the regional floristic composition ingested by dabbling ducks, we compared the results from the rarefaction analyses to the total number of plant species with seeds available for consumption in the Groene Hart area. We counted the total number of seed-producing plant species in the area from survey data on regional floristic composition (Nationale Databank Flora en Fauna 2014).

Results

SPECIES INGESTED BY DABBLING DUCKS

Our analysis of 71 diet studies, reporting on 152 case studies and a grand total of 8335 duck individuals, identifies *at least* 445 plant species of 189 different genera and 57 different families that were ingested by dabbling ducks in the Western Palaearctic (Tables 1, S2 and S3). The families represented by the most species are the Poaceae (73 species identified) and Cyperaceae (57 species), which both rank among the most species-rich plant families in Europe. An additional 22 plant families were represented by > 5 species in the compilation. These families included not only the Amaranthaceae (34 species) and Polygonaceae (23), but also major plant families not generally considered to be 'waterbird-dispersed' or associated with wetlands: for example, the Rosaceae (20), Asteraceae (18) and Fabaceae (17). The genus represented by the most species is *Carex* (36 species).

Quantitative data were available for 413 of the 445 plant species that were ingested by ducks. These data show that seeds were commonly found intact in dabbling duck foreguts: as many as 462 seeds were reported on average per duck (averaged across all seasons, regions and duck species) (Table 1). This number is highly variable across studies, with the highest average number of seeds per duck reported for a study on *A. crecca* (2347 seeds). Differences between duck species ranged across an order of magnitude, with *A. crecca* harbouring the most seeds (but also most sampled duck individuals), *A. acuta*, *A. platyrhynchos* and *A. strepera* taking highly similar intermediate positions and *A. clypeata* and *A. penelope* containing fewest seeds (Table 1).

CHARACTERISTICS OF SPECIES INGESTED BY DABBLING DUCKS: HABITAT

Ingested seeds represent a wide cross section of the plant kingdom (Table S2). However, more detailed inspection of the characteristics of ingested plant species reveals several general patterns (Figs 1 and 2). Dabbling ducks ingested seeds of plant species from a very wide range of habitats (Fig. 1). The ingested seeds originated from plant species representing the full range of site fertility conditions, from extremely infertile soils (Ellenberg N values 1–2) to extremely nutrient-rich, heavily fertilized soils (values 8–9), with somewhat higher numbers of species from sites of intermediate to rich fertility (Ellenberg N values 4–7; Fig. 1a). The ducks also ingested seeds of species from a very wide range of moisture conditions, from averagely damp to very wet (open water) (Ellenberg F values 3–12), excluding only species from extremely to very dry sites (values 1–2; Fig. 1b). Regarding light conditions, ingested seeds originated from plant species of semi-shade to full-light, open habitats, with a peak at well-lit to open habitats (Ellenberg L values 6–8), excluding deep shade to shade (values 2–4; Fig. 1c). Averaged frequencies of occurrence are remarkably similar across all habitat conditions (blue lines, Fig. 1). The relatively high mean frequency of occurrence at Ellenberg N value 1 is heavily affected by a single study in which a high proportion of ducks had feasted on *Empetrum nigrum* berries, and should be considered in relation to the low numbers of underlying data points.

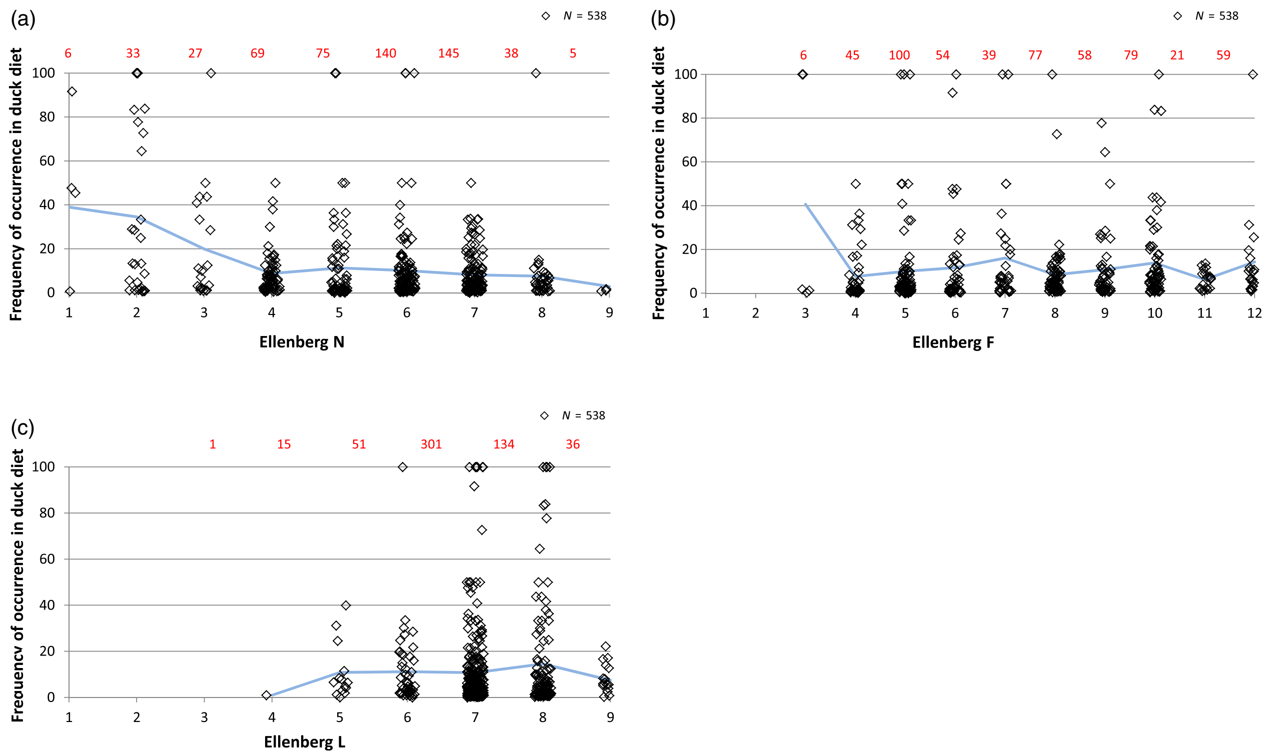

Fig. 1. Analysis of the gut content of dabbling ducks shows that they feed on seeds from plant species growing at a very wide range of site conditions, regarding site fertility (indicated by Ellenberg N values; panel a), moisture (Ellenberg F; b) and light availability (Ellenberg L; c). Each data point represents the frequency of occurrence (% of ducks in the population) of a single plant species ingested by a single duck species, averaged over all studies reporting on that plant species. Ellenberg indicator values were available for 246 out of the 413 identified plant species (60%), resulting in a total of 538 data points for all duck species combined (56% of all identified cases). Data points are jittered around their respective Ellenberg values. Red numbers give the total numbers of data points per Ellenberg value; blue lines connect the averaged frequencies (over all data points) per Ellenberg value. Ellenberg values are defined in Table S1.

Are these plant species a representative selection of all available plant species, or do the ducks preferably ingest plant species from specific habitats? If we compare the relative frequency distributions of Ellenberg values of the species ingested by ducks to those of all plant species for which Ellenberg data are available in the PLANTATT data base (Fig. 3), we see that the ducks appear to select species from specific habitats more than others. The ducks fed disproportionally on plant species from sites of rich (but not extremely rich) fertility (Ellenberg N values 6–8; Fig. 3a), from sites of wet-to-inundated moisture conditions (Ellenberg F values 8–12; Fig. 3b) and from sites that are well-lit, but not fully lit (Ellenberg L value 7; Fig. 3c). Hence, while dabbling ducks ingest a very wide range of plant species in similar frequencies, these species are not a random subset of all available plant species, but over-represent plant species from fertile, wet and open sites. Note, however, that the latter conclusion is based only on the identities of the species ingested by dabbling ducks and not on their associated frequencies of ingestion.

These general patterns of ingested seeds are very similar among the duck species (Figs S1–S3). There are a few subtle differences: *A. querquedula* fed somewhat more on species from low-fertility habitats, and *A. querquedula* and *A. strepera* appeared to prefer wetland and aquatic plant seeds somewhat more than the other ducks. However, the sample sizes for these two duck species are low.

CHARACTERISTICS OF SPECIES INGESTED BY DABBLING DUCKS: TRAITS

Considering the most important dispersal-related plant and seed traits, the following general patterns appear (Fig. 2). Dabbling ducks ingested seeds of plant species across a very wide range of seed production levels, from species that produce only a few seeds to species that produce >100 000 s seeds per individual plant (data not shown). In contrast to that wide range, the ducks predominantly ingested seeds of relatively small to intermediate sizes, particularly those ranging from 1 to 10 mm^3 (Fig. 2a). The ducks sampled a very wide range of species regarding traits associated with other modes of dispersal, but their diet consisted predominantly of species that are poorly dispersed by wind, with seed terminal velocities >1 m s^{-1} (most even >2 m s^{-1}, indicating very poor dispersal by wind) (Fig. 2b), and well-dispersed by water, with long-floating seeds (floating percentages >90%, and many even 100%, after 1 week; Fig. 2c). These patterns are similar for both numbers of species and averaged frequencies of occurrence.

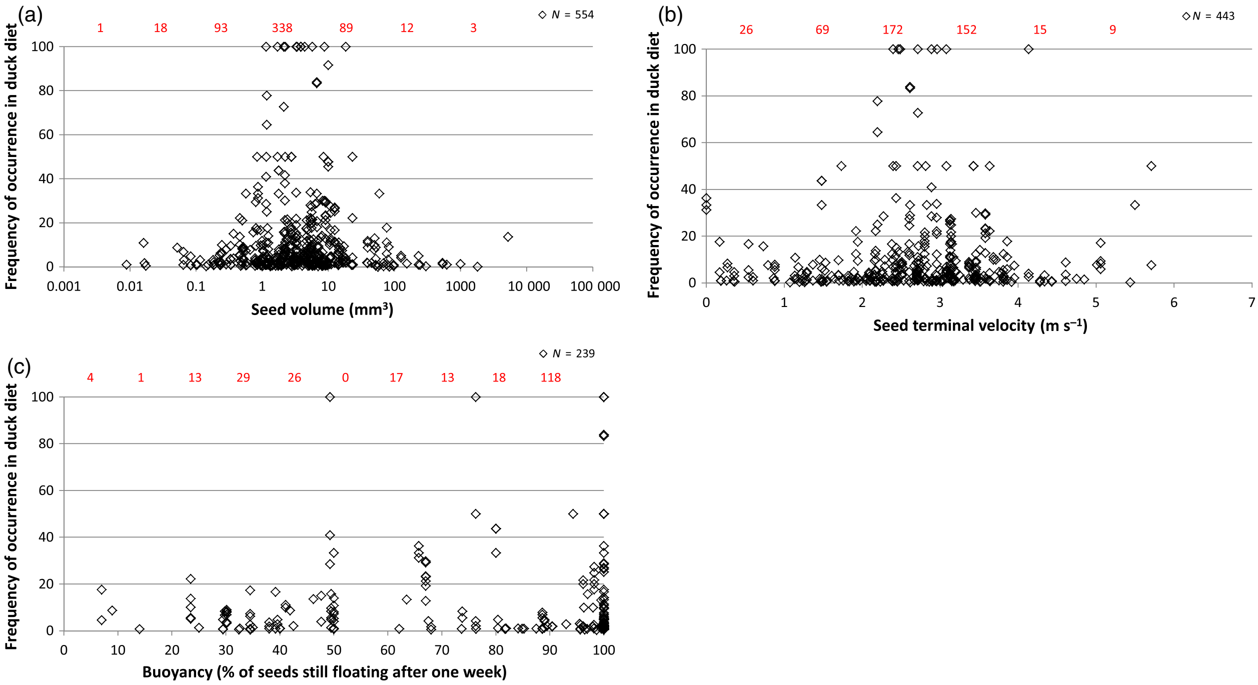

Fig. 2. Analysis of the gut content of dabbling ducks shows that they feed on seeds from plant species with a wide range of dispersal-related traits, including seed size (a) and seed dispersal capacity by wind (b) and water (c). Each data point represents the frequency of occurrence (% of ducks in the population) of a single plant species ingested by a single duck species, averaged over all studies reporting on that plant species. The total number of data points for all duck species combined depends on trait data availability and is indicated in each panel (total number of all identified cases is 961; percentages of total are: (a) 58%, (b) 46% and (c) 25%). Red numbers present the total numbers of data points between two consecutive *x*-axis tick-marks (similar to the bins used in Fig. 4). Note the *x*-axis log scale in panel (a).

Comparison of the plant species identified from the gut content of dabbling ducks to all plant species for which dispersal-related trait data are available in the LEDA data base shows that the ducks more or less proportionally ingest species relative to their seed production (Fig. S4, bottom-right panel; χ^2 (7) = 8.5; NS). In contrast, the ducks fed highly disproportionally on plant species with seeds of intermediate sizes (1–10 mm^3; Fig. 4a). They also disproportionally ingested plant species with relatively high terminal velocities, indicating (very) poor wind dispersal capacity (2–4 m s^{-1}; Fig. 4b) and intermediate seed buoyancies (30–50% still floating after 1 week in water; Fig. 4c, but see Discussion). Again, these general patterns of ingested seeds are very similar among duck species (Figs S4–S7).

The plant species ingested by dabbling ducks include 35 species with fleshy fruits (belonging to the 16 genera *Cotoneaster*, *Crataegus*, *Elaeagnus*, *Empetrum*, *Fragaria*, *Prunus*, *Pyrus*, *Rapistrum*, *Rosa*, *Rubus*, *Sambucus*, *Solanum*, *Sorbus*, *Vaccinium*, *Viburnum* and *Vitis*). Of all the species listed in the duck's diet, 277 species (62%) had not previously been recorded as endozoochorously dispersed by any animal in the LEDA data base. More specifically, 295 species (66%) had not been recorded as dispersed by birds (endozoochorously or exozoochorously). For *Carex*, 33 species (92% of the 36 species listed in the diet) had not been recorded as endozoochorously dispersed, and 32 (89%) had not been recorded as dispersed by birds, in LEDA.

RELATION BETWEEN DIET COMPOSITION AND REGIONAL FLORISTIC COMPOSITION

Rarefaction curves revealed that a large number of individuals would have to be sampled for a reliable determination of the total number of plant species ingested and potentially dispersed by dabbling ducks. The steep slopes on the left of the curves indicate that in studies that sampled low numbers of duck individuals, a large fraction of the seed species diversity went undetected (Fig. 5). This is relevant, as 106 of the 152 case studies (70%) in our compilation sampled <50 individual ducks. Hence, the number of plant species ingested by ducks according to our analysis is likely to severely underestimate the actual total.

In addition, extrapolation of the rarefaction curves for the Groene Hart area indicates that mallards in that area alone may ingest a total of around 100 species (Fig. 5). In systematic grid-based surveys of the flora of the part of the Groene Hart area most likely inhabited by the examined ducks, a total of 1169 plant species have been recorded. This includes 789 rare species, which were recorded for only $<10\%$ of all surveyed 1-km-grid cells (including urban areas and private gardens, where the wild mallards were unlikely to forage). This leaves a total of only 380 species that were recorded for $>10\%$ of all surveyed grid cells. A total of 154 plant species were recorded for $>50\%$ of all surveyed grid cells, and 73 plant species were recorded for all surveyed grid cells,

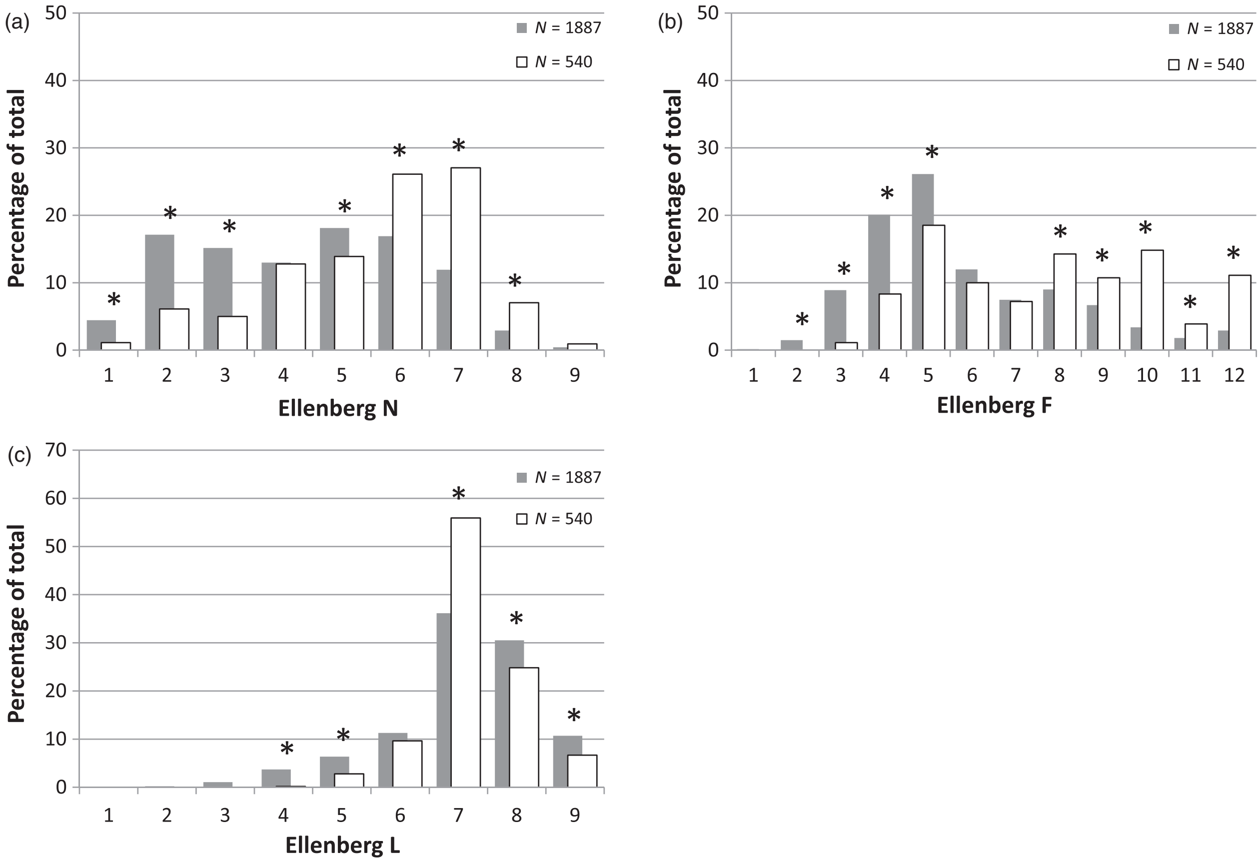

Fig. 3. Analysis of the plant species identified from the gut content of dabbling ducks, in comparison with all plant species for which Ellenberg values are available, shows that the ducks disproportionally ingest plant species from sites of rich fertility (Ellenberg N values 6–8; panel (a); χ^2 (8) = 187.4; $P < 0.001$), wet-to-inundated (open water) moisture conditions (Ellenberg F values 8–12; (b) χ^2 (11) = 266.8; $P < 0.001$) and generally well-lit, but not full-light, light conditions (Ellenberg L value 7; (c) χ^2 (7) = 80.2; $P < 0.001$). Grey bars present the distribution of Ellenberg values over all plant species for which values are available; white bars present the distribution for all plant species identified from gut contents. Asterisks indicate significant differences between duck diet and all plant species ($P < 0.05$). The total number of data points included in the histograms are indicated in each panel. Ellenberg values are defined in Table S1.

suggesting that mallards may ingest a very large proportion of the common plant species occurring in a rural area.

Discussion

WHAT DIET STUDIES TELL US: WHICH SPECIES ARE INGESTED BY DABBLING DUCKS?

Diet studies identify which seed species are ingested, an essential first step for dispersal. Ingestion of plant seeds by dabbling ducks is common, as shown by the high numbers of seeds found in dabbling ducks' foreguts (Table 1). The ducks ingested seeds from a large number of plant species, representing a wide range of genera and families. This range of plant taxa (Table S2) more closely resembles a regular cross section of the plant kingdom than a selection of taxa associated with wetlands, an observation supported by our analyses of the habitats of ingested species. Dabbling ducks disproportionally ingest seeds of plant species from relatively fertile, wet and open sites (indeed, the sites in which they are typically expected to forage; e.g. Legagneux *et al.* 2009; Sauter *et al.* 2012; Bengtsson *et al.* 2014; Kleyheeg 2015). However, they also ingest – in similar frequencies – seeds from a surprisingly wide range of other sites, spanning the entire range of site fertility conditions and excluding only very dry and deeply shaded habitats. If we categorize typical wetland or aquatic species by Ellenberg F values 9–12, these make up only 40% of the species in the dabbling duck diet; the remaining 60% of the species are non-wetland species.

Dabbling ducks also ingest species with a wide range of dispersal-related plant traits. Seed ingestion appeared to be roughly proportional to seed production, underlining the ducks' opportunistic feeding behaviour. Plant species with a wide range of wind and water dispersal capacities were ingested. The ducks were more selective regarding seed size, feeding mostly on seeds of intermediate sizes (1–10 mm^3). This is in line with analyses of duck droppings in the field (Charalambidou & Santamaria 2005) and with the ducks' typical foraging method: the 'dabbling' behaviour for which they are named. This filter-feeding, where ducks create a flow of water containing food particles entering through the anterior opening of the bill and expelled laterally through lamellae,

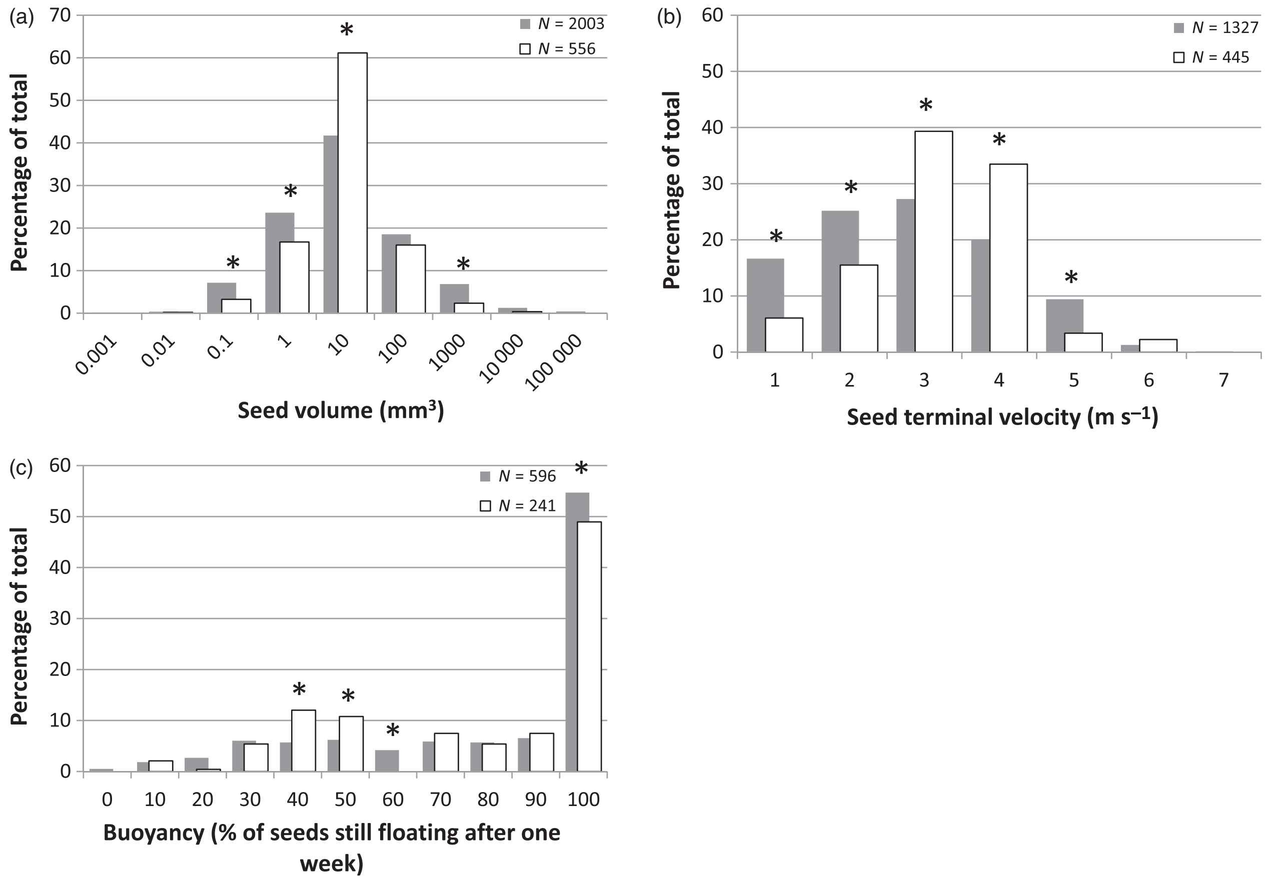

Fig. 4. Analysis of the plant species identified from the gut content of dabbling ducks, in comparison with all plant species for which dispersal-related trait data are available, shows that the ducks disproportionally ingest species of intermediate seed sizes (1–10 mm^3; panel (a) χ^2 (8) = 71.6; $P < 0.001$), relatively high terminal velocities (2–4 m s^{-1}; panel (b) χ^2 (6) = 98.0; $P < 0.001$) and intermediate seed buoyancies (30–50% still floating after 1 week; panel (c) χ^2 (10) = 28.4; $P < 0.01$). *X*-axis values indicate upper limits of bin ranges. Grey bars present the distribution of trait values over all plant species for which these values are available; white bars present the distribution for all plant species identified from gut contents. Asterisks indicate significant differences between duck diet and all plant species ($P < 0.05$). The total number of data points included in the histograms is indicated in each panel. Note the *x*-axis log scale in panel (a).

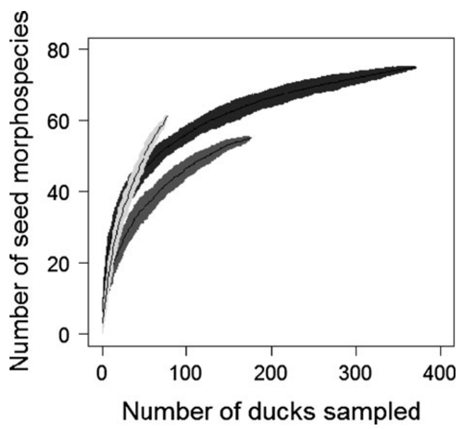

Fig. 5. Estimated numbers of seed species in the duck diet as indicated by rarefaction curves for seed morphospecies in *A. platyrhynchos* (grey) and *A. crecca* (dark grey) in the Camargue, France; and *A. platyrhynchos* in the Groene Hart, the Netherlands (light grey). Rarefaction curves are based on repeatedly resampling 50 random individuals from 176 mallards and 371 teal analysed for the Camargue, and 78 mallards analysed for the Groene Hart.

favours ingestion of medium-sized seeds (Gurd 2006; Brochet *et al.* 2012b). However, the ducks also feed by picking up food items of various sizes on land. They swallow food items whole, including large fleshy items such as grapes and strawberries, but also hard items such as acorns (E. Kleyheeg, pers. obs). Interspecific differences in ingested food item size exist between duck species, most notably for *A. clypeata* with their fine lamellae, which are able to filter out smaller seeds (Green & Figuerola 2005). However, these differences are subtle in relation to the broad patterns (and corresponding bin ranges) analysed here and hence are not significant in our analysis (Fig. S5).

In relation to the selected seed sizes, the ducks mainly ingest seeds with poor ability to disperse by wind (Soons *et al.* 2004; Soons 2006). Thus, dispersal by dabbling ducks is not simply an ‘accidental additional mechanism’ for species already adapted for long-distance dispersal by wind, but is more likely to be a primary mechanism towards long-distance dispersal for many plant species unable to disperse by wind. Considering ability to disperse by water, we observed an over-representation of species with seed buoyancies in the range of 30–50% in the duck diet. However, rather than indicating a real preference, this may reflect our selection of bin ranges and the relatively poor quality of the underlying data, as buoyancy data are rare and notoriously difficult to compare between studies. Dabbling ducks more likely ingest seeds with different dispersal capacities by water more or less proportionally to their abundance, and form a significant secondary dispersal vector for many water-dispersed species.

Overall, the diets of the seven dabbling duck species appeared to be relatively similar. The most important difference relating to their plant dispersal ability is that, on average, fewer seeds are ingested by *A. penelope* and *A. clypeata*. This reflects their ecology, as in comparison with the other dabbling ducks, *A. penelope* is more herbivorous, while *A. clypeata* feeds more on invertebrates (Cramp & Simmons 1977; Dessborn *et al.* 2011). Yet, due to the animal-based diet of *A. clypeata* the ingested seeds are likely to have a high probability of gut passage survival (Kleyheeg 2015). Indeed, droppings of *A. clypeata* have been shown to contain more intact seeds than those of other waterbirds in the field (Figuerola, Green & Santamaria 2003), and this species likely plays an important role in seed dispersal despite the lower numbers ingested.

Our findings provide the strongest support to date of the general view of dabbling ducks as highly opportunistic feeders. Given our results, any ducks' diet probably consists of a wide range of species representative of the landscape it inhabits. Although our analysis included data from 71 studies reporting on 152 case studies, our rarefaction analyses suggest that this may still only be a 'snapshot' of the total number of species ingested by dabbling ducks. More realistically, they may ingest all or a large proportion of the common plant species present in a landscape. Hence, we propose that dabbling ducks are likely to ingest a much higher number of plant species than that reported by our study, spanning a very wide spectrum of habitats.

WHICH SPECIES ARE LIKELY TO BE DISPERSED BY DABBLING DUCKS?

While our diet analyses identify which species are ingested, the next critical step towards assessing the ducks' dispersal potential is to evaluate which species, or more importantly, species with which traits, are likely to survive gut passage. The digestive system of waterbirds, including dabbling ducks, is optimized for calorie uptake per unit time rather than per unit of ingested food, so for most of the time full digestion does not occur (Van Leeuwen *et al.* 2012). Hence, it is inherent to their digestive system that some seeds survive. Feeding experiments with dabbling ducks have shown that intact survival rates vary from 0 to 70% across plant species (Van Leeuwen *et al.* 2012) and germination rates vary from 0 to *ca*. 50% of ingested seeds across plant species (0–32%, Soons *et al.* 2008; 0–5; %, Wongsriphuek, Dugger & Bartuszevige 2008; 1–48%, Brochet *et al.* 2010b). Averaged over all plant and duck species used in feeding trials, *ca*. 7% of the ingested seeds successfully germinated within a few weeks after defecation (Van Leeuwen *et al.* 2012), but the variation around this average is enormous (Soons *et al.* 2008; Brochet *et al.* 2010b; Kleyheeg *et al.* 2015). The above rates underestimate potential survival and germination rates under field conditions, as gut passage survival is much higher (up to 80%) in active ducks than in the resting ducks typically used in feeding trials (Kleyheeg *et al.* 2015). Furthermore, non-germinating seeds may still be viable (Brochet *et al.* 2010b), but dormant, as germination rates are highly sensitive to environmental conditions (e.g. Fraaije *et al.* 2015b).

Survival and germination rates are generally higher for plant species with smaller seeds (Soons *et al.* 2008; Figuerola *et al.* 2010; Van Leeuwen *et al.* 2012). Smaller seeds travel faster through the digestive system (Soons *et al.* 2008) and are retrieved *intact* in higher proportions than larger seeds, both in experiments and in the field (Charalambidou & Santamaria 2005; Van Leeuwen *et al.* 2012). More importantly, smaller seeds are retrieved *viably* in much higher proportions than larger seeds (approximated by a negative logarithmic relationship; Soons *et al.* 2008). Seeds with thicker or harder seed coats also have a higher probability of intact gut passage (Soons *et al.* 2008; Wongsriphuek, Dugger & Bartuszevige 2008; Kleyheeg 2015). However, viability is generally unexplained by seed coat traits, except for species with permeable seed coats (which have particularly low gut passage survival; Kleyheeg *et al.* 2015) and some species with very thick and hard seed coats where gut passage stimulates germination (e.g. *Sparganium* species; Pollux, Santamaria & Ouborg 2005; Soons *et al.* 2008). Unfortunately, data on seed coat hardness and permeability are very limited, so that seed size remains the best – and only available – predictor of gut passage survival for plant species.

If we combine the probability of viable gut passage survival with the data on dabbling duck diets, we obtain a more detailed picture of which plant species are likely to be dispersed. Species with very small seeds (< 0.1 mm^3) are relatively rare and are seldom ingested by dabbling ducks, but have the highest post-gut-passage germination rates (on average $\gg 10\%$, using the relationship identified by Soons *et al.* 2008). Seeds of 0.1–1 mm^3 are much more common, much more frequently found in ducks (on average 7% of individual ducks), and have average germination rates of $> 10\%$. Seeds of 1–10 mm^3 are most common, most frequently ingested by ducks (on average 14% of ducks) and have intermediate average germination rates of $> 5\%$. Species with seeds > 10 mm^3 are again less common, less frequently ingested by ducks (on average 9% of ducks) and have low probabilities of gut passage survival. Yet, for very hard large seeds, endozoochorous dispersal by regurgitation (which can take place up to at least 10 h after ingestion) is an alternative pathway likely to result in dispersal (Kleyheeg & Van Leeuwen 2015). Furthermore, there exists wide variation in duck digestive efficiency, which is caused by large intraspecific variation, but also by major digestive differences following changes in body condition, diet and season (Kleyheeg 2015; Kleyheeg *et al.* 2015). Hence, for *almost all ingested plant species,* there is *some* possibility of successful internal dispersal by dabbling ducks, and average survival rates mentioned above are conservative estimates.

WHICH SPECIES ARE LIKELY TO BE EFFECTIVELY DISPERSED BY DABBLING DUCKS?

Effective dispersal is achieved when viable seeds are dropped at a suitable site – or a site that becomes suitable within the timeframe of seed dormancy. Dabbling ducks defecate seeds across a range of aquatic and terrestrial environments. Newly available high-resolution movement data collected using GPS loggers demonstrate that non-breeding *A. platyrhynchos* individuals spend less than half of their time on open water (Fig. 6; Kleyheeg 2015). The remainder of the time they spend in the shoreline or on land, both during their foraging trips and their resting periods. These data clearly show how likely it is for the most common, widespread and numerous of the dabbling duck species to defecate seeds away from open water.

Such detailed space use data are not yet available for all dabbling duck species. Observational data from southern Sweden suggest that during spring staging, *A. penelope* is by far the most terrestrial of the seven *Anas* species, spending up to *ca.* 50% of their time budget foraging on land (Arzel & Elmberg 2004). *A. crecca* and *platyrhynchos* are largely comparable in being generalist habitat users, foraging on water, in the shoreline and on land; *ca.* 40–60% of their foraging activities were reported on land (Arzel & Elmberg 2004). *A. acuta* and *querquedula* are much less terrestrial, and *A. clypeata* is by far the most aquatic species, spending up to *ca.* 50% of their time budget foraging on the water surface (Arzel & Elmberg 2004). The importance of grassland foraging sites for particularly *A. penelope*, *crecca* and *platyrhynchos* is also established for wintering populations in France (e.g. Duncan *et al.* 1999; Guillemain, Fritz & Duncan 2002; Legagneux *et al.* 2009). During breeding, habitat use may be even more terrestrial (e.g. Pasitschniak-Arts, Clark & Messier 1998). As such, dabbling ducks appear highly suitable for the effective dispersal of plant species of a wide range of habitats.

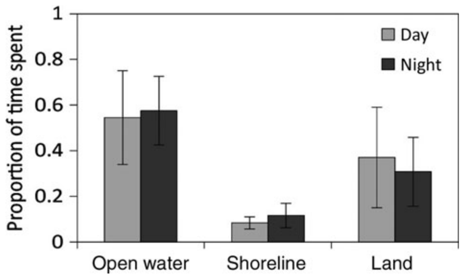

Fig. 6. Habitat use by mallards (*Anas platyrhynchos*) during the foraging period (night) and resting period (day) based on high-resolution GPS tracking data of 112 male mallards in four areas in the Netherlands (modified from Kleyheeg 2015). Percentages of time spent on open water (Ellenberg F values 11–12), in the shoreline (values 9–10) and on land (values 4–8) were calculated from 140 765 GPS positions, which were recorded every 15 min for approximately 2 weeks per individual, over the autumn–winter season of 2012–2013. Error bars represent standard deviations.

AN OVERLOOKED DISPERSAL PATHWAY FOR A BROAD SPECTRUM OF PLANT SPECIES

Summarizing, our analyses demonstrate that dabbling ducks ingest seeds of many plant species, from a wide range of habitats, and with a wide range of dispersal-related traits. Feeding experiments have already established that an ecologically relevant proportion of ingested seeds survives gut passage. Analysis of existing movement data shows that dabbling ducks also frequent a wide range of habitat types (at least across a wet-dry gradient) in the landscapes they inhabit. All combined, this makes dabbling ducks suitable dispersal vectors for the wide range of plant species they ingest. This applies particularly to *A. acuta*, *crecca*, *platyrhynchos* and *strepera* (which ingest the largest quantities of seeds) and to *A. clypeata* (which is likely to have the highest gut passage survival). Insufficient data are available on *A. querquedula* to evaluate its dispersal potential.

However, dabbling ducks receive very little notice in the scientific literature compared to other seed dispersal vectors: Of all papers dealing with seed dispersal (> 6934 papers, ISI WoK, June 2014), only 43 focus on dispersal by waterbirds, and of all species found in our dabbling duck diet compilation, 62% had not previously been identified as endozoochorously dispersed and 66% not as dispersed by birds. Data on dispersal by waterbirds are largely lacking in plant data bases and waterbirds are not mentioned in important overview papers considering animal-mediated plant dispersal (e.g. Wang & Smith 2002; Ozinga *et al.* 2004; McConkey *et al.* 2012; Hintze *et al.* 2013). When mentioned, they are associated to wetland plants only (Gillham 1970). This lack of notice can result in misinterpretation of ecological data. For example, Cyperaceae, which include the most common plant genus reported in our compilation (*Carex*), are ranked as only very poorly endozoochorously dispersed in Hintze *et al.* (2013).

This is all the more remarkable, given the sheer numbers of dabbling ducks and their quantitative potential for dispersing seeds. In Europe alone, > 14 million dabbling duck individuals are available for dispersal. If we multiply this number by the average number of seeds ingested per duck across seasons, geographic regions and years (462 seeds per duck), and assume (for a highly conservative estimate, as median gut retention times are around 2–3 h; Kleyheeg *et al.* 2015) that these numbers represent seeds ingested per day, a total of 6.5×10^9 seeds would be available for dispersal by dabbling ducks per day. Even if their gut passage survival and subsequent germination would be a conservative 7%, this would still amount to *ca.* 0.5×10^9 seeds being viably dispersed by dabbling ducks per day, for Europe. A more realistic estimate would be to assume that, at least during the main seed dispersal season (autumn–winter), the duck population is closer to 19 million individuals, that the average number of seeds ingested per day is around *ca.* 2000 per duck (considering that most diet data are derived from ducks shot in the morning after *ca*. 8–10 h of feeding at night) and that in active birds, gut passage survival rates are almost double those of resting birds (Kleyheeg *et al.* 2015), suggesting a germination rate more like 14%. This would result in *ca*. 5×10^9 seeds being viably dispersed by dabbling ducks per day, for Europe – and Europe's dabbling duck population is only a fraction of the global population.

How could this mechanism be so much overlooked for plant species other than aquatics? Perhaps, because dabbling ducks are intuitively associated particularly (if not only) with wetlands, and not considered of importance for other habitats. Indeed, their diet also reflects this to some extent: *ca*. 40% of ingested species are true 'wetland species'. Also, while dabbling ducks ingest a very wide range of plant species in similar frequencies, these species over-represent plant species from fertile, wet and open sites. However, this association ignores the vast number of 'non-wetland' plant species ingested and potentially dispersed by dabbling ducks. Perhaps, it is overlooked also because plant seeds do not appear to have obvious, easily observable adaptations to promote dispersal by dabbling ducks. Yet, for such opportunistic feeders the only adaptations needed would be to escape the (mostly mechanical) digestive forces. This primarily requires seeds to be small and/or have a hard seed coat – very common and inconspicuous characteristics. Finally, seed dispersal by dabbling ducks may be overlooked because it is generally assumed that dispersal rates must be low because almost all ingested seeds are digested. This, however, is not the case.

IMPLICATIONS

Dabbling ducks fly, and hence can disperse plants over a wide range of distances including long-distance dispersal, as many dabbling duck species are migratory. Given this, it might be that for many of the plant species dispersed by dabbling ducks, the ducks serve as a potentially highly effective, but 'non-standard', long-distance dispersal vector (cf. Higgins, Nathan & Cain 2003; Nathan *et al.* 2008). Yet, considering the above, we propose that dabbling ducks may be a common dispersal vector – and perhaps even a 'standard' dispersal vector – for many more species than previously anticipated. They may form a very important dispersal strategy for wetland plant species, but certainly also an additional dispersal vector for many terrestrial species – particularly those terrestrial species that are not primarily dispersed by wind over long distances. Similarly, there is good evidence that waterbirds are important vectors of numerous terrestrial, alien plants (Green 2016). In our analysis, we limited ourselves to the Western Palaearctic, but there is no reason to assume that the general patterns we identified are not representative for dabbling ducks and plant species on other continents (e.g. Holt-Mueller & Van der Valk 2002; Green *et al.* 2008). As such, we suggest that their role as dispersers should be considered when evaluating the dispersal potential of plant species and that actual dispersal potential of many plant species may be underestimated if dabbling ducks are not taken into account. To facilitate this consideration, data such as those we have reviewed here on duck gut contents should be incorporated into plant dispersal data bases.

In consequence, the role of dabbling ducks as dispersers should also be considered in hunting regulations and population management. Seed dispersal is a limiting factor for plant colonization, vegetation development and restoration success for terrestrial, wetland and aquatic communities alike (e.g. Santamaria 2002; Soons & Ozinga 2005; Brederveld *et al.* 2011; Fraaije *et al.* 2015a). If waterbirds play such an important role as vectors in the dispersal of plant species, this should be taken into account in both plant and waterbird population management and conservation strategies, from local to continental scales (*cf.* Amezaga, Santamaria & Green 2002; Trakhtenbrot *et al.* 2005; Verhoeven *et al.* 2008; McConkey *et al.* 2012).

Conclusions

Considering the above, internal seed dispersal by dabbling ducks appears to be a major dispersal pathway for whole spectrum of plant species. Darwin (1859) was right in his proposition that 'it would be an inexplicable circumstance if water-birds did not transport the seeds of fresh-water plants' – but that is only roughly 40% of the story. The other 60% are non-wetland plants transported by waterbirds, a mechanism that is still generally overlooked and deserving of more attention in future dispersal studies.

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Data accessibility

The diet data presented in this paper are available in Supporting Information Table S2.

References

Amezaga, J.M., Santamaria, L. & Green, A.J. (2002) Biotic wetland connectivity – supporting a new approach for wetland policy. *Acta Oecologica*, **23**, 213–222.

Arzel, C. & Elmberg, J. (2004) Time use, foraging behavior and microhabitat use in a temporary guild of spring-staging dabbling ducks (*Anas* spp.). *Ornis Fennica*, **81**, 157–168.

Bengtsson, D., Avril, A., Gunnarsson, G., Elmberg, J., Soderquist, P., Norevik, G. *et al.* (2014) Movements, home-range size and habitat selection of mallards during autumn migration. *PLoS ONE*, **9**, e100764. doi:10.1371/journal.pone.0100764.

BirdLife International (2004) *Birds in Europe: Population Estimates, Trends and Conservation Status*. BirdLife Conservation Series 12.

Brederveld, R.J., Jaehnig, S.C., Lorenz, A.W., Brunzel, S. & Soons, M.B. (2011) Dispersal as a limiting factor in the colonization of restored mountain streams by plants and macroinvertebrates. *Journal of Applied Ecology*, **48**, 1241–1250.

Brochet, A.L., Guillemain, M., Fritz, H., Gauthier-Clerc, M. & Green, A.J. (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., Guillemain, M., Fritz, H., Gauthier-Clerc, M. & Green, A.J. (2010a) Plant dispersal by teal (*Anas crecca*) in the Camargue: duck guts are more important than their feet. *Freshwater Biology*, **55**, 1262–1273.

Brochet, A.L., Guillemain, M., Gauthier-Clerc, M., Fritz, H. & Green, A.J. (2010b) Endozoochory of Mediterranean aquatic plant seeds by teal after a period of desiccation: determinants of seed survival and influence of retention time on germinability and viability. *Aquatic Botany*, **93**, 99–106.

Brochet, A.L., Mouronval, J.B., Aubry, P., Gauthier-Clerc, M., Green, A.J., Fritz, H. & Guillemain, M. (2012a) Diet and feeding habitats of Camargue dabbling ducks: what has changed since the 1960s? *Waterbirds*, **35**, 555–576.

Brochet, A.L., Dessborn, L., Legagneux, P., Elmberg, J., Gauthier-Clerc, M., Fritz, H. & Guillemain, M. (2012b) Is diet segregation between dabbling ducks due to food partitioning? A review of seasonal patterns in the Western Palaearctic. *Journal of Zoology*, **286**, 171–178.

Bullock, J.M., Galsworthy, S.J., Manzano, P., Poschlod, P., Eichberg, C., Walker, K. & Wichmann, M.C. (2011) Process-based functions for seed retention on animals: a test of improved descriptions of dispersal using multiple data sets. *Oikos*, **120**, 1201–1208.

Charalambidou, I. & Santamaria, L. (2005) Field evidence for the potential of waterbirds as dispersers of aquatic organisms. *Wetlands*, **25**, 252–258.

Cousens, R. & Dytham, C. (2008) *Dispersal in Plants, a Population Perspective*. Oxford University Press, Oxford, UK.

Cramp, S. & Simmons, K.E.L. (eds) (1977) *Handbook of the Birds of Europe, the Middle East and North Africa: The Birds of the Western Palaearctic. Volume I: Ostriches to Ducks*. Oxford University Press, Oxford, UK.

Darwin, C. (1859) *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. John Murray, London, UK.

Dessborn, L., Brochet, A.L., Elmberg, J., Legagneux, P., Gauthier-Clerc, M. & Guillemain, M. (2011) Geographical and temporal patterns in the diet of pintail *Anas acuta*, wigeon *Anas penelope*, mallard *Anas platyrhynchos* and teal *Anas crecca* in the Western Palaearctic. *European Journal of Wildlife Research*, **57**, 1119–1129.

DeVlaming, V.L. & Proctor, V.W. (1968) Dispersal of aquatic organisms –viability of seeds recovered from the droppings of captive killdeer and mallard ducks. *American Journal of Botany*, **55**, 20–26.

Duncan, P., Hewison, A.J.M., Houte, S., Rosoux, R., Tournebize, T., Dubs, F., Burel, F. & Bretagnolle, V. (1999) Long-term changes in agricultural practices and wildfowling in an internationally important wetland, and their effects on the guild of wintering ducks. *Journal of Applied Ecology*, **36**, 11–23.

Ellenberg, H., Weber, H.E., Dull, R., Wirth, V., Werner, W. & Paulissen, D. (1991) Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica*, **18**, 1–248.

Figuerola, J. & Green, A.J. (2002) Dispersal of aquatic organisms by waterbirds: a review of past research and priorities for future studies. *Freshwater Biology*, **47**, 483–494.

Figuerola, J., Green, A.J. & Santamaria, L. (2003) Passive internal transport of aquatic organisms by waterfowl in Donana, south-west Spain. *Global Ecology and Biogeography*, **12**, 427–436.

Figuerola, J., Charalambidou, I., Santamaria, L. & Green, A.J. (2010) Internal dispersal of seeds by waterfowl: effect of seed size on gut passage time and germination patterns. *Naturwissenschaften*, **97**, 555–565.

Fraaije, R.G.A., Ter Braak, C.J.F., Verduyn, B.G., Verhoeven, J.T.A. & Soons, M.B. (2015a) Dispersal *versus* environmental filtering in a dynamic system: drivers of vegetation patterns and diversity along stream riparian gradients. *Journal of Ecology*, **103**, 1634–1646.

Fraaije, R.G.A., Ter Braak, C.J.F., Verduyn, B.G., Breeman, L.B.S., Verhoeven, J.T.A. & Soons, M.B. (2015b) Early plant recruitment stages set the template for the development of vegetation patterns along a hydrological gradient. *Functional Ecology*, **29**, 971–980.

Gillham, M.E. (1970) Seed dispersal by birds. *The Flora of a Changing Britain* (ed. F. Perrings), pp. 90–98. Pendragon Press, Hampton, UK.

Gotelli, N. & Colwell, R. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**, 379–391.

Green, A.J. (2016) The importance of waterbirds as an overlooked pathway of invasion for alien species. *Diversity and Distributions*, **22**, 239–247.

Green, A.J. & Elmberg, J. (2014) Ecosystem services provided by waterbirds. *Biological Reviews*, **89**, 105–122.

Green, A.J. & Figuerola, J. (2005) Recent advances in the study of long-distance dispersal of aquatic invertebrates via birds. *Diversity and Distributions*, **11**, 149–156.

Green, A.J., Jenkins, K.M., Bell, D., Morris, P.J. & Kingsford, R.T. (2008) The potential role of waterbirds in dispersing invertebrates and plants in arid Australia. *Freshwater Biology*, **53**, 380–392.

Guillemain, M., Fritz, H. & Duncan, P. (2002) The importance of protected areas as nocturnal feeding grounds for dabbling ducks wintering in western France. *Biological Conservation*, **103**, 183–198.

Gurd, D.B. (2006) Filter-feeding dabbling ducks (*Anas* spp.) can actively select particles by size. *Zoology*, **109**, 120–126.

Haig, S.M., Mehlman, D.W. & Oring, L.W. (1998) Avian movements and wetland connectivity in landscape conservation. *Conservation Biology*, **12**, 749–758.

Hanski, I. (1998) Metapopulation dynamics. *Nature*, **396**, 41–49.

Higgins, S.I., Nathan, R. & Cain, M.L. (2003) Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal? *Ecology*, **84**, 1945–1956.

Hill, M.O., Preston, C.D. & Roy, D.B. (2004) *PLANTATT – Attributes of British and Irish Plants: Status, Size, Life History, Geography and Habitats*. Centre for Ecology and Hydrology, Huntingdon, UK.

Hill, M.O., Mountford, J.O., Roy, D.B. & Bunce, R.G.H. (1999) *Ellenberg's Indicator Values for British Plants. ECOFACT Volume 2 Technical Annex*. Institute of Terrestrial Ecology, Huntingdon, UK.

Hintze, C., Heydel, F., Hoppe, C., Cunze, S., Konig, A. & Tackenberg, O. (2013) D-3: the dispersal and diaspore database – baseline data and statistics on seed dispersal. *Perspectives in Plant Ecology Evolution and Systematics*, **15**, 180–192.

Holt-Mueller, M.H. & Van der Valk, A.G. (2002) The potential role of ducks in wetland seed dispersal. *Wetlands*, **22**, 170–178.

Hughes, B. & Green, A.J. (2005) Feeding ecology. *Ducks, Geese and Swans*, vol. **1** (ed J. Kear), pp. 27–56. Oxford University Press, Oxford, UK.

Janzen, D.H. (1984) Dispersal of small seeds by big herbivores – foliage is the fruit. *American Naturalist*, **123**, 338–353.

Jordano, P., Garcia, C., Godoy, J.A. & Garcia-Castano, J.L. (2007) Differential contribution of frugivores to complex seed dispersal patterns. *PNAS*, **104**, 3278–3282.

Jordano, P., Forget, P.M., Lambert, J.E., Bohning-Gaese, K., Traveset, A. & Wright, S.J. (2011) Frugivores and seed dispersal: mechanisms and consequences for biodiversity of a key ecological interaction. *Biology Letters*, **7**, 321–323.

Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M. *et al.* (2008) The LEDA traitbase: a database of life-history traits of the Northwest European flora. *Journal of Ecology*, **96**, 1266–1274.

Kleyheeg, E. (2015) Seed dispersal by a generalist duck: ingestion, digestion and transportation by mallards (*Anas platyrhynchos*). PhD thesis, Utrecht University, Utrecht, The Netherlands.

Kleyheeg, E. & Van Leeuwen, C.H.A. (2015) Regurgitation by waterfowl: an overlooked mechanism for long-distance dispersal of wetland plant seeds? *Aquatic Botany*, **127**, 1–5.

Kleyheeg, E., Van Leeuwen, C.H.A., Morison, M.A., Nolet, B.A. & Soons, M.B. (2015) Bird-mediated seed dispersal: reduced digestive efficiency in active birds modulates the dispersal capacity of plant seeds. *Oikos*, **124**, 899–907.

Legagneux, P., Blaize, C., Latraube, F., Gautier, J. & Bretagnolle, V. (2009) Variation in home-range size and movements of wintering dabbling ducks. *Journal of Ornithology*, **150**, 183–193.

Markl, J.S., Schleuning, M., Forget, P.M., Jordano, P., Lambert, J.E., Traveset, A. *et al.* (2012) Meta-analysis of the effects of human disturbance on seed dispersal by animals. *Conservation Biology*, **26**, 1072–1081.

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

Nathan, R. (2001) Dispersal biogeography. *Encyclopedia of Biodiversity*, pp. 127–152. Academic Press.

Nathan, R. & Muller-Landau, H.C. (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution*, **15**, 278–285.

Nathan, R., Katul, G.G., Horn, H.S., Thomas, S.M., Oren, R., Avissar, R. *et al.* (2002) Mechanisms of long-distance dispersal of seeds by wind. *Nature*, **418**, 409–413.

Nathan, R., Schurr, F.M., Spiegel, O., Steinitz, O., Trakhtenbrot, A. & Tsoar, A. (2008) Mechanisms of long-distance seed dispersal. *Trends in Ecology & Evolution*, **23**, 638–647.

Nationale Databank Flora en Fauna (2014) Standaardlevering, available at: www.ndff.nl/het-natuurloket; accessed on 6 August 2014.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R. B., Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. (2015) *Vegan: Community Ecology Package*. R package version 2.3-0, available at: http://CRAN.R-project.org/package=vegan

Ozinga, W.A., Bekker, R.M., Schaminee, J.H.J. & Van Groenendael, J.M. (2004) Dispersal potential in plant communities depends on environmental conditions. *Journal of Ecology*, **92**, 767–777.

Ozinga, W.A., Romermann, C., Bekker, R.M., Prinzing, A., Tamis, W.L.M., Schaminee, J.H.J. *et al.* (2009) Dispersal failure contributes to plant losses in NW Europe. *Ecology Letters*, **12**, 66–74.

Pasitschniak-Arts, M., Clark, R.G. & Messier, F. (1998) Duck nesting success in a fragmented prairie landscape: is edge effect important? *Biological Conservation*, **85**, 55–62.

Pazos, G.E., Greene, D.F., Katul, G., Bertiller, M.B. & Soons, M.B. (2013) Seed dispersal by wind: towards a conceptual framework of seed abscission and its contribution to long-distance dispersal. *Journal of Ecology*, **101**, 889–904.

Pollux, B.J.A., Santamaria, L. & Ouborg, N.J. (2005) Differences in endozoochorous dispersal between aquatic plant species, with reference to plant population persistence in rivers. *Freshwater Biology*, **50**, 232–242.

R Development Core Team (2012) *R: A Language and Environment for Statistical Computing*, R Foundation for Statistical Computing, Vienna, Austria available at: www.R-project.org.

Sanders, H.L. (1968) Marine benthic diversity: a comparative study. *American Naturalist*, **102**, 243–282.

Santamaria, L. (2002) Why are most aquatic plants widely distributed? Dispersal, clonal growth and small-scale heterogeneity in a stressful environment. *Acta Oecologica*, **23**, 137–154.

Sauter, A., Korner, P., Fiedler, W. & Jenni, L. (2012) Individual behavioural variability of an ecological generalist: activity patterns and local movements of Mallards *Anas platyrhynchos* in winter. *Journal of Ornithology*, **153**, 713–726.

Şekercioğlu, Ç.H., Wenny, D.G. & Whelan, C.J. (2016) *Why Birds Matter: Avian Ecosystem Functions and Ecosystem Services*. University of Chicago Press, Chicago, IL, USA.

Soons, M.B. (2006) Wind dispersal in freshwater wetlands: knowledge for conservation and restoration. *Applied Vegetation Science*, **9**, 271–278.

Soons, M.B. & Ozinga, W.A. (2005) How important is long-distance seed dispersal for the regional survival of plant species? *Diversity and Distributions*, **11**, 165–172.

Soons, M.B., Heil, G.W., Nathan, R. & Katul, G.G. (2004) Determinants of long-distance seed dispersal by wind in grasslands. *Ecology*, **85**, 3056–3068.

Soons, M.B., Messelink, J.H., Jongejans, E. & Heil, G.W. (2005) Habitat fragmentation reduces grassland connectivity for both short-distance and long-distance wind-dispersed forbs. *Journal of Ecology*, **93**, 1214–1225.

Soons, M.B., Van der Vlugt, C., Van Lith, B., Heil, G.W. & Klaassen, M. (2008) Small seed size increases the potential for dispersal of wetland plants by ducks. *Journal of Ecology*, **96**, 619–627.

Spiegel, O. & Nathan, R. (2007) Incorporating dispersal distance into the disperser effectiveness framework: frugivorous birds provide complementary dispersal to plants in a patchy environment. *Ecology Letters*, **10**, 718–728.

Trakhtenbrot, A., Nathan, R., Perry, G. & Richardson, D.M. (2005) The importance of long-distance dispersal in biodiversity conservation. *Diversity and Distributions*, **11**, 173–181.

Van Leeuwen, C.H.A., van der Velde, G., Van Groenendael, J.M. & Klaassen, M. (2012) Gut travellers: internal dispersal of aquatic organisms by waterfowl. *Journal of Biogeography*, **39**, 2031–2040.

Verhoeven, J.T.A., Soons, M.B., Janssen, R. & Omtzigt, N. (2008) An Operational Landscape Unit approach for identifying key landscape connections in wetland restoration. *Journal of Applied Ecology*, **45**, 1496–1503.

Viana, D.S., Santamaria, L., Michot, T.C. & Figuerola, J. (2013) Migratory strategies of waterbirds shape the continental-scale dispersal of aquatic organisms. *Ecography*, **36**, 430–438.

Wang, B.C. & Smith, T.B. (2002) Closing the seed dispersal loop. *Trends in Ecology & Evolution*, **17**, 379–386.

Wetlands International (2012) Waterbird Population Estimates 5, available at: www.wpe.wetlands.org.

Will, H. & Tackenberg, O. (2008) A mechanistic simulation model of seed dispersal by animals. *Journal of Ecology*, **96**, 1011–1022.

Wongsriphuek, C., Dugger, B.D. & Bartuszevige, A.M. (2008) Dispersal of wetland plant seeds by mallards: influence of gut passage on recovery, retention, and germination. *Wetlands*, **28**, 290–299.

Yong, D.L., Ng, D., Xiong, G. & Fam, S.D. (2013) Don't cull wild birds yet. *Science*, **340**, 681–682.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Definition of Ellenberg values, from Hill *et al.* (2004).

Table S2. List of all 445 plant species found in dabbling ducks, with data on seed numbers, frequencies of occurrence, sample sizes and metadata per study. With references.

Table S3. List of all papers included in our literature compilation.

Figures S1–S7. Habitat characteristics and dispersal-related traits of plant species identified from gut contents of dabbling ducks, specified per duck species.