1 **Research article**

2 **Endozoochory of aquatic ferns and angiosperms by mallards**

3 **in central Europe**

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14 SHORT TITLE: Fern endozoochory by mallards

15

16 ABSTRACT

17 1. Modern literature on plant dispersal by birds focuses mainly on the importance of frugivory and scatter-

18 hoarding, yet recent studies show that endozoochory by migratory waterbirds is an important mechanism of

19 long-distance dispersal for a broad range of plants. Nevertheless, there is a lack of empirical field studies that

20 identify the plants dispersed by waterbirds in a comprehensive manner. In particular, so far there are no detailed

21 studies of the level of spatial variation in the plant taxa dispersed by a waterbird vector, and no clear

22 demonstration that aquatic ferns can be dispersed by endozoochory. Consequently, we remain ignorant of the

23 networks of dispersal interactions between granivorous waterbirds and plants.

24 2. Five sets of faecal samples (total n = 215) were collected from mallards *Anas platyrhynchos* on autumn

25 migration in the Hevesi-holm and Balaton regions in Hungary, central Europe. Intact diaspores were extracted,

26 identified and their germinability assessed under standard conditions. The plant communities recorded at

27 different sites were compared with PERMANOVA and other multivariate methods.

28 3. Macrospores of the floating watermoss *Salvinia natans* were recorded in 32 samples, and a total of 16

29 macrospores germinated, providing the first field demonstration of endozoochory of ferns by birds. Of 21

angiosperm taxa recorded (of which 8 germinated), 13 were terrestrial species, although the most abundant taxa were aquatic species such as the alkali bulrush *Bolboschoenus maritimus* and the sago pondweed *Potamogeton pectinatus*. Two naturalized alien species, the common fig *Ficus carica* and the hackberry *Celtis occidentalis* were also recorded. Only four of the taxa had an endozoochory syndrome. The plant taxa dispersed varied at two different spatial scales, with minor but significant differences between samples from sites separated by less than 1 km, and major differences between the two regions separated by approximately 220 km.

4. *Synthesis*. This is a unique study of the spatial variation in plants dispersed by endozoochory by a migratory waterfowl species with a high taxonomic resolution, with the first demonstration of avian endozoochory of ferns. We recorded eight taxa not previously reported as dispersed by mallards, showing how more empirical studies are essential so we can understand which plants are dispersed by migratory birds. We found evidence that networks of interactions between granivorous waterbird vectors and dispersed plants vary spatially.

KEYWORDS

Anas plathyrynchos, aquatic plant ecology, aquatic fern, dabbling ducks, endozoochory, granivory, macrospore, *Salvinia natans*, seed dispersal, waterfowl

INTRODUCTION

Research to date on avian dispersal of plants has focused mainly on frugivory or on scatter-hoarding (Forget et al., 2011; Vander Wall & Moore, 2016; Pesendorfer et al., 2016). However, both classic and more recent research has shown that migratory waterfowl can disperse a broad range of other plants by endozoochory (De Vlaming & Proctor, 1968; van Leeuwen, van der Velde, van Groenendael & Klaassen 2012; Green, Soons, Brochet & Kleyheeg 2016). These include angiosperms whose diaspores lack any obvious morphological adaptations for long-distance dispersal (Costea et al., 2016; Soons, Brochet, Kleyheeg & Green 2016). Nevertheless, only a handful of studies have considered which plants are actually dispersed in the field via gut passage by widespread waterfowl species such as mallards *Anas platyrhynchos* (e.g. Charalambidou & Santamaría, 2005; Green, Frisch, Michot, Allain & Barrow 2013; Wilkinson, Lovas-Kiss, Callaghan & Green 2017). Since morphological syndromes do not allow us to predict *a priori* which plants are dispersed (Soons et al., 2016), there is an urgent need for extensive field studies so that we can begin to characterize the networks of dispersal interactions between waterbirds and plants.

Even the broad taxonomic diversity of plants dispersed by waterfowl is currently unclear (Green et al., 2016). It has only recently been demonstrated that waterfowl disperse viable bryophyte fragments by endozoochory (Wilkinson et al., 2017). Despite long-standing speculation about the potential of aquatic ferns to disperse via waterbirds (Ridley, 1930; Reynolds, Miranda & Cumming 2015), this has never been conclusively demonstrated. Laboratory experiments support the potential for epizoochory of *Azolla* over short distances (Coughlan, Kelly & Jansen 2017), and the potential for endozoochory of *Marsilea* (Malone & Proctor, 1965).

Mallards are important plant vectors both during seasonal, migratory movements (Viana, Santamaría, Michot & Figuerola 2013) and during daily movements within a landscape (Kleyheeg, Treep, De Jager, Nolet & Soons 2017). However, no previous studies have considered in detail what spatial differences there are between different waterbodies in the plants that mallards or other waterbirds disperse by endozoochory (i.e. equivalent to studies comparing frugivore-plant dispersal interactions in nearby forest patches; Bascompte & Jordano, 2007). In this study, our aim is to quantify and compare endozoochory of aquatic and terrestrial plants by mallards on autumn migration at different wetlands of Hungary, central Europe. We identify diaspores deposited in faeces with a high taxonomic resolution, assess the germinability of diaspores and analyze the extent of spatial variation in the dispersal of different plant taxa. We also provide the first demonstration of endozoochory of aquatic ferns. We consider how many of the taxa recorded were not previously known to be dispersed by ducks, and the implications of our results for long-distance dispersal processes.

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MATERIAL AND METHODS

Study area and sample processing

Sampling was carried out in two different regions of Hungary, the Hevesi-holm and the riviera of Lake Balaton (Fig. 1). Five sets of faecal samples were collected in the autumn of 2016 with a combined total of 215 samples. In the Balaton region, we collected 90 samples on the 20th (n = 52) and 23th of October (n = 38) from two adjacent sites on the northern shore of Lake Balaton (46.9141º N, 17.89270º E; 46.91736º N, 17.8929º E), and 25 samples on 21th October at the Tihany Inner-Lake (46.90783º N, 17.88707º E). In the Hevesi-holm region, we collected 50 samples on 20th September from Lake Tisza (47.643938 N, 20.660793 E), and 50 samples from the Tisza River (47.60477º N, 20.71102º E) (Fig. 1). All the locations are situated within protected areas, Natura 2000 sites and BirdLife Important Bird Areas.

Lake Balaton is the largest (596 km^2) freshwater lake in central Europe, but has a mean depth of only 3.2 m (Istvánovics et al., 2007). It is c.18,000 years old (Cserny & Nagy-Bodor, 2000), and its trophic state has changed from meso- to eutrophic over the last millennium (Korponai et al., 2011). The northern shore is covered with reed (*Phragmites australis*) and *Typha* beds, with extensive submerged macrophytes. The nearby Tihany Inner-lake (0.2 km^2) is a highly eutrophic volcanic lake covered with reed (*Ph. australis*) and other emergent plants.

Lake Tisza is a reservoir which is usually drained in the late autumn then filled again in the spring with water from the Tisza River. It covers 127 km^2 with average depth varying from 0.7 m and 2.5 m in the shallow bays. Our samples were collected from one of the shallowest bays, which is largely covered by reed (*Ph. australis*) and is rich in submerged and emergent macrophytes (Király, Molnár, Bölöni, Csiky & Vojtkó 2008). The lake is connected to the Tisza River by several channels. The banks of the Tisza River are largely covered by willow-groves and poplar plantations invaded by the false indigo bush (*Amorpha fruticosa*) (Király et al., 2008). During our sampling visits, some mallards were seen feeding within floating mats of the floating watermoss, *Salvinia natans*, at the Lake Tisza and Tisza River sites.

Monospecific flocks of resting mallards likely to be on migration (see discussion) were located on the shoreline of the study sites. Fresh faecal material was then collected early in the morning from the points where birds were resting, immediately after they were flushed by our approach, leaving at least one meter distance between samples to minimize the risk of sampling the same individual repeatedly. The faecal samples were immediately examined, removing any contamination from soil or vegetation from the sample using tweezers, then placed in

105 zip-lock plastic bags. The samples were then kept in the fridge (4°C) until subsequent laboratory investigations,

106 which were completed within 6 months. Faecal samples were weighed on a balance (Ohaus EP213C Explorer®

107 Pro), then washed on a 100 μm sieve using deionized water before inspection under a binocular microscope.

108 Intact diaspores, for which no cracks or missing parts were detectable, were collected and quantified.

109 Angiosperm seeds were photographed and identified based on their shape, size, colour and seed coat pattern

110 following recent literature (Cappers, Bekker & Jans 2012; Bojnanský & Fargašová, 2007). Fern macrospores

111 were identified following Weijdema, Brinkkemper, Peeters and Geel (2011). Dispersal syndromes for each taxon

112 were taken from the plant trait database Baseflore (Julve, 1998),

113 Diaspores were then placed in an Eppendorf® tube filled with deionized water until germination trials.

114 Germinability tests were conducted on Petri-dishes filled with nutrient-free Agar gel for terrestrial plants, and in

115 tissue plates filled with deionized water for aquatic plants (Araceae, Haloragaceae, Potamogetonaceae,

116 Salviniaceae). These were then placed in germination chambers set at 12 h of light at 24 °C, and 12 h of darkness

117 at 18 °C. Germination tests were run for 54 days.

118

119 *Statistical analysis*

120 To compare the number of intact diaspores of a given taxon in the five sets of samples, we used Kruskall-Wallis

121 H test. This test was only performed for those taxa with diaspores recorded in a combined total of at least six

122 faecal samples. Where significant differences were detected, we used Dunn's test (Dinno, 2017) to identify

123 which sites differed significantly.

124 Several additional analyses were conducted using functions implemented in the R package 'vegan'. In order to

125 analyse differences among plant community compositions recorded at the five sites, we used non-parametric

126 permutational ANOVA (i.e., PERMANOVA; Anderson, 2001) using the *adonis* function. The latter analysis was

127 based on a Bray-Curtis dissmiliarity matrix, composed of values between 0 and 1 reflecting the degree of

128 dissimilarity among the five sites. Using these analyses, we inspected the differences in community

129 compositional centroids among sites, but further analyses were performed to inspect differences in group

130 homogeneities, using the function *betadisper* (Anderson, 2006). Using the latter procedure, we calculated the

131 degree of dispersion of each sample from the compositional centroid at each sampling site. This procedure is

132 often referred to as a test for difference in β diversity among the sampling sites. Tukey's HSD tests were used to

133 determine which sites differed in β diversity. Additionally, a posteriori analysis was performed, using the

134 function *simper,* to identify community members that significantly contributed to among-site differences. To

5

135 establish statistical significance, the empirical p value of each variable was calculated using 1000 random

136 permutations. Rarefaction analysis showed that our results were not strongly influenced by the differences in

137 number of samples between sites (Fig. S1).

138 Graphical presentation of the among-sites differences was conducted using principal coordinates analyses,

139 performed using the *cmdscale* function on the above mentioned Bray-Curtis dissimilarity matrix. All statistical

140 analyses were conducted in R statistical software package (version 3.3.2; R Core Team, 2017). Adonis,

141 betadisper and simper functions were implemented in R package vegan (version 2.4-3., Oksanen et al., 2017),

142 while Tukey's HSD and cmdscale were implemented in R package stats (version 3.4.0, R Core Team, 2017).

143 These analyses were run after excluding samples that contained no diaspores.

144

145 RESULTS

146 The mean mass of fresh faecal samples was 3.721 g ± 0.185 (mean ± s.e.). A total of 1327 intact diaspores were

147 found from the 215 samples, belonging to 22 plant species, including 21 angiosperms and an aquatic fern (381

148 macrospores of *Salvinia natans*, Table 1). These taxa represent 15 families (Table 1), with five families of

149 aquatic plants (including 3 submerged, 2 floating and 4 emergent taxa), and 10 families of terrestrial plants (13

150 taxa). Only four of these 22 taxa are recognized as having an "endozoochory syndrome" (Table 2).

151 Almost half the diaspores (47%) were retrieved from the two sets of samples from Lake Balaton, which included

152 484 seeds of common fig (*Ficus carica*, naturalized alien, Uotila 2011b, Table 1). Fig trees are very abundant

153 around Lake Balaton and were present at the sampling sites (Király et al., 2008). The hackberry *Celtis*

154 *occidentalis*, a park tree from North America that is a widespread naturalized alien in Hungary (Uotila, 2011a,

155 Bartha et al., 2015), was represented by one seed. All other plant taxa recorded were native to Hungary. Most

156 plant taxa recorded were rare, with seven taxa represented by only one seed, and another four taxa recorded only

157 in a single sample (Table 1). Overall, 33% of faecal samples contained at least one diaspore (Table 1).

158 Propagules of three plant species were recorded in more than five faecal samples: the alkali bulrush

159 *Bolboschoenus maritimus*, the sago pondweed *Potamogeton pectinatus* and *Salvinia natans* (Table 1). Diaspore

160 numbers of these three taxa differed significantly among the sampling sites (*B. maritimus* χ^2 = 38.33, df = 4, P

161 <0.0001; *P. pectinatus* χ^2 = 10.59, P = 0.032; *S. natans* χ^2 = 47.27, P < 0.0001). For *B. maritimus*, significantly

162 more diaspores were recorded at the Tihany Inner-Lake and at Balaton II than at the other three sampling sites

163 (Table 1). Significantly more *P. pectinatus* seeds were recorded from the Tihany Inner Lake than at the Lake

164   Tisza and at Balaton II sampling sites. We only found *S. natans* macrospores at the two neighbouring sites in the

165   floodplain of the Tisza river, with significantly more diaspores than in the other sites (Table 1.).

166   According to PERMANOVA, the species compositional centroids differed significantly among sampling sites

167   (df = 1, F= 18.381, P < 0.0001, Fig. 2). The *simper* post-hoc test indicated that *Salvinia natans, Bolboschoenus*

168   *maritimus, Ficus carica* and *Cyperus fuscus* were the taxa that made the highest contribution to the among-sites

169   dissimilarities. The β-diversity of the propagules found in the samples differed significantly among the sampling

170   sites, according to the results of betadisper (df = 4, F = 4.31, p = 0.0036). Tukey's HSD test showed significant

171   β-diversity difference (P = 0.0034) between the Balaton II and Lake Tisza sites.

172

173   Out of the 22 species of plants recorded in the faecal samples, diaspores from nine taxa germinated. Overall, 4%

174   of all diaspores germinated. Three taxa had particularly high viability (*Bolboschoenus maritimus* 25%,

175   *Eleocharis palustris* 31% and *Ranunculus sceleratus* 25%, Table 2). Sixteen *Salvinia natans* macrospores

176   germinated (4% of the total, Fig. 3). All taxa with over 20 diaspores detected in the faecal samples contained

177   viable seeds (as shown by the germination tests), with the notable exception of *Ficus carica* represented by over

178   400 seeds in the samples (Table 2).

179

180   DISCUSSION

181   We have demonstrated endozoochory for aquatic ferns and a range of angiosperm taxa by migratory waterfowl

182   in central Europe, and the germinability of all abundant taxa apart from cultivated figs. Although we do not

183   know the distance involved, the diaspores were undoubtedly moved by the mallards between ingestion at feeding

184   sites and egestion at the roost sites sampled (see Kleyheeg et al. 2017 for typical examples of daily movements

185   for mallards not on migration). In terms of the number of faecal samples processed and the diversity and level of

186   identification of intact diaspores recorded, this study represents the most detailed field study of endozoochory by

187   mallards to date (see Green et al., 2016 for review). It is also the first to make a detailed comparison of the

188   spatial variation in plants dispersed. Our results illustrate the importance of mallards as a vector of dispersal for

189   widely distributed (e.g. *Polygonum aviculare*, *Cyperus fuscus*, Bartha et al., 2015) and rare (*Myriophyllum*

190   *verticillatum*, Bartha et al., 2015) plant species, as well as naturalized aliens (*Celtis occidentalis,* Uotila, 2011a).

191   Another naturalized alien *Ficus carica* (Uotila, 2011b) had the highest number of seeds in our study, but none

192   germinated because this cultivar produces their fuits parthenocarpically and these have non-viable seeds in

193   Hungary. *B. maritimus* and *P. pectinatus* were the angiosperms recorded in the highest number of samples.

Seeds of both these subcosmopolitan species have often been recorded in the diet of ducks (Soons et al., 2016) and have been used as models for experimental studies of endozoochory (Santamaría et al., 2003; Espinar, Garcia, Figuerola, Green & Clemente 2004; Brochet, Guillemain, Gauthier-Clerc, Fritz & Green 2010). Modelling based on banding recoveries and feeding experiments suggests that, during migrations, mallards can disperse seeds of these taxa and of *Schoenoplectus lacustris* (which we also recorded) over extraordinary distances with maxima exceeding 400 km (Viana et al., 2013).

We sampled mallards during the autumn migration period when birds move through Hungary towards wintering grounds in the eastern Mediterranean and Black Sea regions (Wetlands International, 2017). Ringing recoveries connect mallards in Hungary with sites over 1600 km away in Russia and France (Faragó, 2009). In the Lake Balaton area, mallard numbers increase during autumn migration from less than 500 individuals in early September to c. 2700 individuals in October, before decreasing again to c.1000 in November (Bankovics, 1997). The entire Hungarian mallard population was estimated to contain around 40,000 individuals in October 2014 (Faragó, Jánoska, Hajas & Kovács 2016), and is part of the Eastern Europe/Black Sea & Eastern Mediterranean flyway population of c.2 million birds (Wetlands International, 2017). Given the number of mallard individuals present in our study area, the plant taxa we recorded are likely to undergo regular long-distance dispersal events along migratory flyways via endozoochory (Viana et al. 2013; Viana, Santamaría & Figuerola 2016).

The proportion of samples containing at least one propagule was similar to that observed in previous studies of waterfowl (van Leeuwen et al., 2012). From our 22 taxa recorded, diaspores of six (27%) were not previously recorded in the diet of European dabbling ducks, and a further two species were not previously reported from mallards (Soons et al., 2016, Table I). This illustrates how much remains to be learned about which plants are dispersed through endozoochory by migratory waterfowl. This is vital knowledge, as these vectors are particularly able to provide the long-distance dispersal required e.g. for redistribution in response to global change (Viana et al., 2016).

In the plant trait database Baseflore (Julve, 1998), most of these 22 species were assigned to dispersal syndromes based on water, wind or self-dispersal (Table 2.). These mechanisms provide much lower maximum dispersal distances than those provided by endozoochory (Bullock et al., 2017). It is notable how mallards disperse trees such as the Silver birch *Betula pendula* or the European hornbeam *Carpinus betulus* that are generally assumed to be wind-dispersed. We have seen mallards searching for and taking birch seeds as they are blown onto the water surface, and also feeding on them when they are concentrated at the shoreline by wave action (Fig. 4). Only four plant species with a fleshy fruit were assigned to an endozoochory syndrome. The majority of taxa we

224   recorded were terrestrial plants, supporting the findings of Soons et al. (2016) in a meta-analysis of the diet of

225   European dabbling ducks. Nevertheless, diaspores of aquatic taxa were generally more abundant, and all three

226   taxa found in six or more samples were aquatic. Most (55%) of the plant taxa we recorded were only recorded in

227   one or two samples. Thus, we would need to study many more samples to record all the plant taxa dispersed by

228   mallards using our study sites, as indicated by rarefaction analyses of mallard gut contents at other European

229   sites (Soons et al., 2016).

230   At the level of individual plant taxa, significant differences in diaspore numbers did not fully coincide with the

231   spatial divide between samplings from the Hevesi-holm and those from the Lake Balaton region further west.

232   We even found significant differences in the frequency of *B. maritimus* between two samplings at Lake Balaton

233   separated by 373 m and by three days. Patchy distribution of seeds in the environment and individual variation in

234   feeding behaviour or movements of ducks (e.g. Green, 1998; Kleyheeg et al., 2017) can translate into important

235   variation in dispersal processes at a fine scale. There was only a clear geographical separation for *S. natans*,

236   which was restricted to the Hevesi-holm (Table 1). *Salvinia natans* is mainly found around the big rivers in

237   Hungary, and is absent from the Lake Balaton area (Bartha et al., 2015). On the other hand, when the whole

238   community of plant diaspores was analysed, there was a clear separation between the eastern and western sample

239   sets (Fig. 2), which is likely to reflect important differences in the plant communities present in the two study

240   regions. However, sampling in the Lake Balaton and Hevesi-holm regions was conducted a month apart, so the

241   spatial differences observed may have been confounded with this temporal change.

242   Our finding of viable macrospores of the pteridophyte *Salvinia natans* is very important, as this represents the

243   first demonstration of avian endozoochory of viable fern diaspores in the wild. Most fern diaspores are dispersed

244   by wind, and a smaller fraction by water (Sharpe, Mehltreter & Walker 2010). A few previous studies have

245   demonstrated endozoochorous dispersal of ferns by other animals, including slugs and insects (Boch et al., 2013;

246   Boch, Berlinger, Prati & Fischer 2016). Fern spores have been shown experimentally to remain viable after

247   passage through the gut of large bats (Sugita, Ootsuki, Fujita, Murakami & Ueda 2013). Dispersal of viable

248   spores by endozoochory has also been demonstrated in the field for mice (Arosa, Ramos, Quintanilla & Brown,

249   2010) and reindeer (Bråthen et al., 2007).

250   We have demonstrated the viability of fern diaspores after avian gut passage for one fern species, but there is

251   evidence to suggest that birds are also vectors for other aquatic and terrestrial ferns. Extinct and extant birds have

252   sometimes been reported to ingest fern sporangia or spores (James & Burney, 1997; Arosa et al., 2009;

253   Mehltreter et al., 2010). Malone and Proctor (1965) did experimental feeding trails with mallards and four other

254   waterbird species using the hairy waterclover *Marsilea vestita*, and recorded passage of intact sporocarps among

255   all bird species. A *Marsilea* sporocarp was recorded from the gizzard of a killdeer (*Charadrius vociferus*)

256   collected in Texas (De Vlaming & Proctor, 1968). It has often been suggested that waterbirds can disperse the

257   alien fern *Azolla filiculoides* (Reynolds & Cumming, 2015), and there is experimental support for epizoochory

258   over distances of a few metres (Coughlan et al., 2017). *Azolla filiculoides* megasporocarps were found in faecal

259   samples of swans and coots in the field, but the viability of the spores was not established (Green, Jenkins, Bell,

260   Morris & Kingsford 2008). Dispersal of ferns as nest material by hummingbirds has also been reported (Osorio-

261   Zuniga, Fonturbel & Rydin 2014).

262   *Salvinia natans* is a widespread Eurasiatic taxon, with the major populations in central and eastern Europe and

263   Asia, extending to Southern Europe and Northern Africa (Allen, 2011). It is an alien species in Cuba and

264   Jamaica (Allen, 2011), and the states of New York and Massachusetts (https://plants.usda.gov/). Ridley (1930)

265   considered *S. natans* to be too large to be dispersed by birds via epizoochory, but speculated that "as the species

266   often occur in isolated pools, it is probable that their spores are somehow transported by birds". Over 80 years

267   later we have confirmed his suspicion.

268   In central Europe, *S. natans* produces male micro- and female macrospores within sporocarps from late August

269   to late September, with the release of sporocarps into the water beginning in late September (Gałka & Szmeja,

270   2013). When not eaten by birds, the sporocarps eventually sink to the bottom of the water column, and during

271   winter the sporocarp walls disintegrate within the sediments. In April, the spores rise up to the water surface and

272   begin to form gametophytes. In late April, the female gametophyte develops archegonia and the male

273   gametophyte develops the antheridia. After fertilisation occurs, the zygote forms and produces the sporophyte

274   (Gałka & Szmeja 2013). When placed for germination, the macrospores we extracted from faeces initially sank

275   to the bottom of our tissue plates, but most floated to the surface after germination. Our laboratory conditions are

276   likely to have accelerated their germination. After surviving gut passage in nature, it is possible that the

277   macrospores delay germination until spring when day length and temperatures increase. When plants germinate

278   sooner because of gut passage, there can be benefits from reduced intraspecific competition, or costs from

279   increased exposure to herbivory (Figuerola & Green, 2004). In our faecal samples, we found only female

280   macrospores, which produced gametophytes with archegonia (Fig. 3). We recorded none of the male

281   microspores that *S. natans* also produces, probably because the microspores are less than 20 μm in diameter

282   (Lawalrée, 1964) and passed through our sieve. It is likely that microspores are also dispersed by mallards when

283 they ingest sporocarps. We found no intact sporocarps in the faeces, and they are likely to have been broken

284 within the gizzard.

285 In conclusion, this study illustrates how much our understanding of plant dispersal can be advanced by focused

286 research on migratory waterfowl as vectors. We can now construct effective spatial models on the dispersal of

287 plants by waterfowl (Viana et al., 2016, Kleyheeg et al., 2017), but we still have very limited information as to

288 which plants are dispersed by which waterbird species. Endozoochory in nature goes well beyond the

289 "endozoochory syndrome", so we cannot simply rely on syndromes if we wish to predict how plants can disperse

290 and these mechanisms relate to plant distributions. Our study provides a unique insight into the networks of

291 dispersal interactions between waterbirds and plants, and the extent of spatial variation that exists in these

292 networks. However, it focuses on the mallard as a particularly abundant and widespread vector, and future work

293 must compare the plants dispersed by other duck and waterbird species in an equally comprehensive manner so

294 that plant-vector networks can be fully characterized, and we can begin to understand the extent of functional

295 redundancy between vectors.

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305

306 AUTHORS' CONTRIBUTIONS

307 ÁLK and AJG conceived the ideas and designed methodology; ÁLK and BV collected the data; ÁLK and OV

308 analysed the data; ÁLK, AMV and AJG led the writing of the manuscript. All authors contributed critically to

309 the drafts and gave final approval for publication.

310

311 DATA ACCESSIBILITY

312 All sample data used in the analyses are available from Dryad – http://dx.doi:10.5061/dryad.5jg1t (Lovas-Kiss
313 et al. 2015)

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TABLES

Table 1. Total number of diaspores (TD), number of samples with diaspores (NS), and maximum number of diaspores in any given sample (Max) for plants recorded in five sets of mallard faecal samples. For three taxa recorded in ≥ 6 samples, no shared superscript letters in the TD column indicate a statistically significant difference between the sites.

Plants		Tisza River (n=50)			Lake Tisza (n=50)			Balaton I. (n=52)			Balaton II. (n=38)			Inner-Lake (n=25)			Total	
Family	Species	TD	NS	Max	TD	NS	Max	TD	NS	Max	TD	NS	Max	TD	NS	Max	TD	NS
Salviniaceae	*Salvinia natans[3]*	253[a]	14	96	128[a]	18	39	-[b]	-	-	-[b]	-	-	-[b]	-	-	381	32
Adoxaceae	*Sambucus nigra*	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1	1
Araceae	*Lemna minor[5]*	-	-	-	15	1	15	-	-	-	-	-	-	-	-	-	15	1
Betulaceae	*Betula pendula*	-	-	-	-	-	-	-	-	-	2	1	2	-	-	-	2	1
	Carpinus betulus[4]	-	-	-	-				-	-	1	1	1		-		1	1
Cannabaceae	*Celtis occidentalis[2,3]*	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1	1
Cyperaceae	*Bolboschoenus maritimus*	-[a]	-	-	1[a]	1	1	-[a]	-	-	45[b]	7	18	15[b]	8	5	61	16
	Cyperus fuscus[3]	-	-	-	-	-	-	-	-	-	20	3	16	166	1	166	186	4
	Eleocharis palustris	-	-	-	13	1	13	-	-	-	-	-	-	-	-	-	13	1
	Schoenoplectus lacustris	-	-	-	1	1	1	-	-	-	53	2	33	-	-	-	54	3
	Schoenoplectus tabernaemontani[3]	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1	1
Fabaceae	*Trifolium pratense*	-	-	-	1	1	1	-	-	-	-	-	-	-	-	-	1	1
Haloragaceae	*Myriophyllum verticillatum[4]*	14	2	13	42	2	37	-	-	-	-	-	-	-	-	-	56	4
Moraceae	*Ficus carica[1]*	-	-	-	-	-	-	117	1	117	367	1	367	-	-	-	484	2

18

Family	Species																	Total	
Plantaginaceae	Plantago major	-	-	-	-	-	-	-	-	-	-	-	-	9	1	9	9	1
Poaceae	Digitaria sanguinalis	-	-	-	-	-	-	1	1	1	-	-	-	-	-	-	1	1
	Echinochloa crus-galli	-	-	-	-	-	-	5	1	5	-	-	-	9	3	7	14	4
Polygonaceae	Polygonum aviculare	-	-	-	-	-	-	3	1	3	-	-	-	2	2	1	5	3
Potamogetonaceae	Potamogeton pectinatus	15[ab]	2	11	-[a]	-	-	1[ab]	1	1	-[a]	-	-	4[b]	3	2	20	6
	Potamogeton pusillus	6	3	2	-	-	-	-	-	-	-	-	-	-	-	-	6	3
Ranunculaceae	Ranunculus sceleratus	-	-	-	1	1	1	-	-	-	13	2	11	-	-	-	14	3
Solanaceae	Solanum dulcamara[4]	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	1	1
	Total	289	22	96	202	20	39	127	3	117	501	14	369	208	12	176	1327	71

476   [1]Ancient cultivated species, [2]Alien taxa, [3]Not reported in *Anas* spp. diet by Soons et al. 2016, [4]Not reported in mallard diet by Soons et al. 2016, [5]Unidentified seeds from the

477   same genus were reported in *Anas* spp. diet by Soons et al. 2016.

478

Table 2. Number of germinated diaspores (NG) and the total number of diaspores (TD) for each plant taxon for all samples combined, together with the propagule length and dispersal syndrome.

Plants				Samples (n=215)	
Family	Species	Dispersal syndrome[*]	Length (mm)[**]	TD	NG
Salviniaceae	*Salvinia natans*	hydrochory	0.6	381	16
Adoxaceae	*Sambucus nigra*	endozoochory	4	1	0
Araceae	*Lemna minor*	hydrochory	0.8	15	0
Betulaceae	*Betula pendula*	anemochory	3.2	2	0
	Carpinus betulus	anemochory	5.77	1	0
Cannabaceae	*Celtis occidentalis*	endozoochory	5.61	1	0
Cyperaceae	*Bolboschoenus maritimus*	anemochory	3.78	61	18
	Cyperus fuscus	barochory	0.9	186	4
	Eleocharis palustris	epizoochory	1.87	13	4
	Schoenoplectus lacustris	hydrochory	3.2	54	4
	Schoenoplectus tabernaemontani	barochory	2.94	1	0
Fabaceae	*Trifolium pratense*	epizoochory	1.9	1	0
Haloragaceae	*Myriophyllum verticillatum*	hydrochory	1.95	56	4
Moraceae	*Ficus carica*	endozoochory	1.66	484	0
Plantaginaceae	*Plantago major*	barochory	1.58	9	0
Poaceae	*Digitaria sanguinalis*	barochory	1.75	1	0
	Echinochloa crus-galli	epizoochory	2.84	14	0
Polygonaceae	*Polygonum aviculare*	barochory	1.9	5	1
Potamogetonaceae	*Potamogeton pectinatus*	hydrochory	4.05	20	3
	Potamogeton pusillus	hydrochory	2.25	6	0
Ranunculaceae	*Ranunculus sceleratus*	hydrochory	0.84	14	3
Solanaceae	*Solanum dulcamara*	endozoochory	2.28	1	0
	Total			1327	57

481 [*] from the BASEFLOR database (Julve 1998), [**]from the LEDA database (Kleyer et al. 2008), the Digital seed atlas (Cappers et al. 2012) or from our own
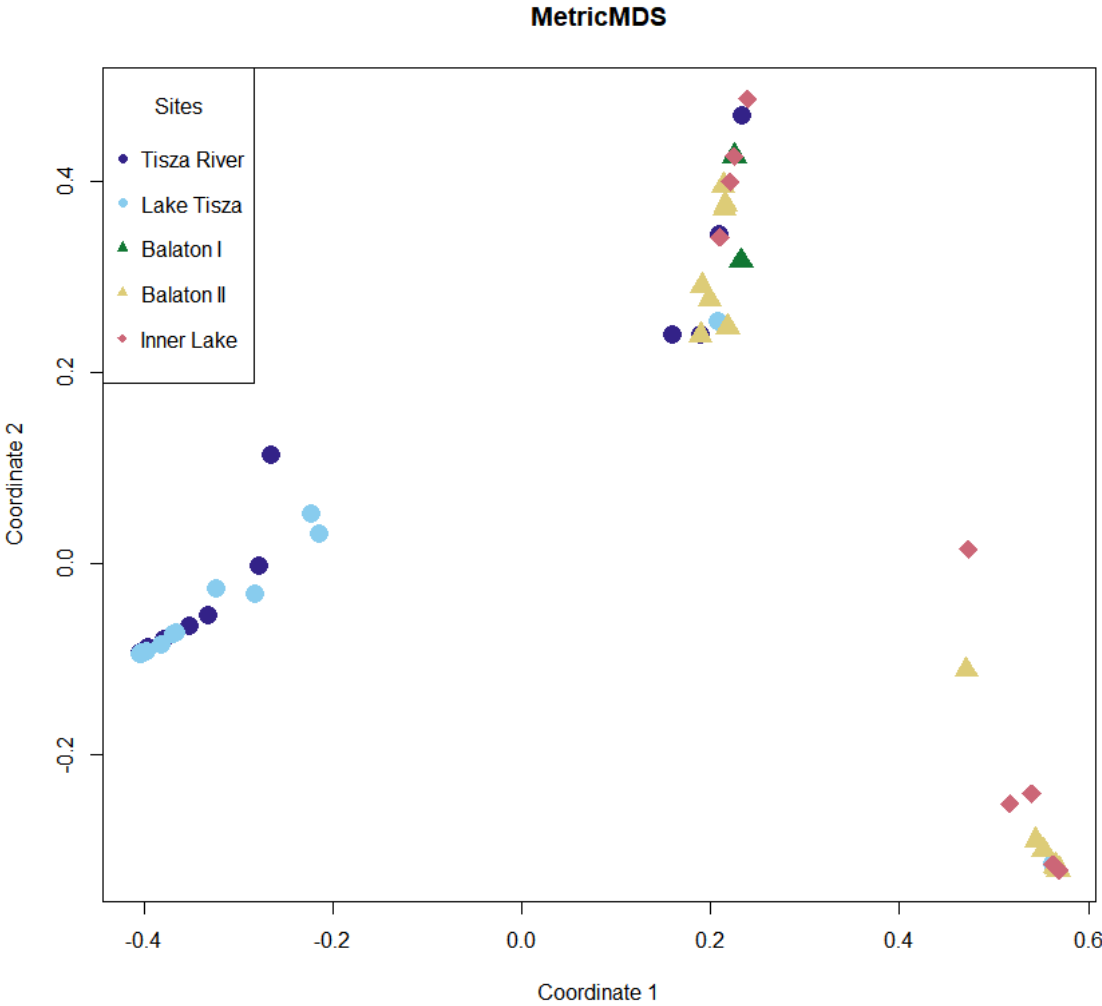
482 measurements.

483

484   **FIGURES**

485   Fig 1. Location of the study areas in Hungary (lower images taken from Google Earth).
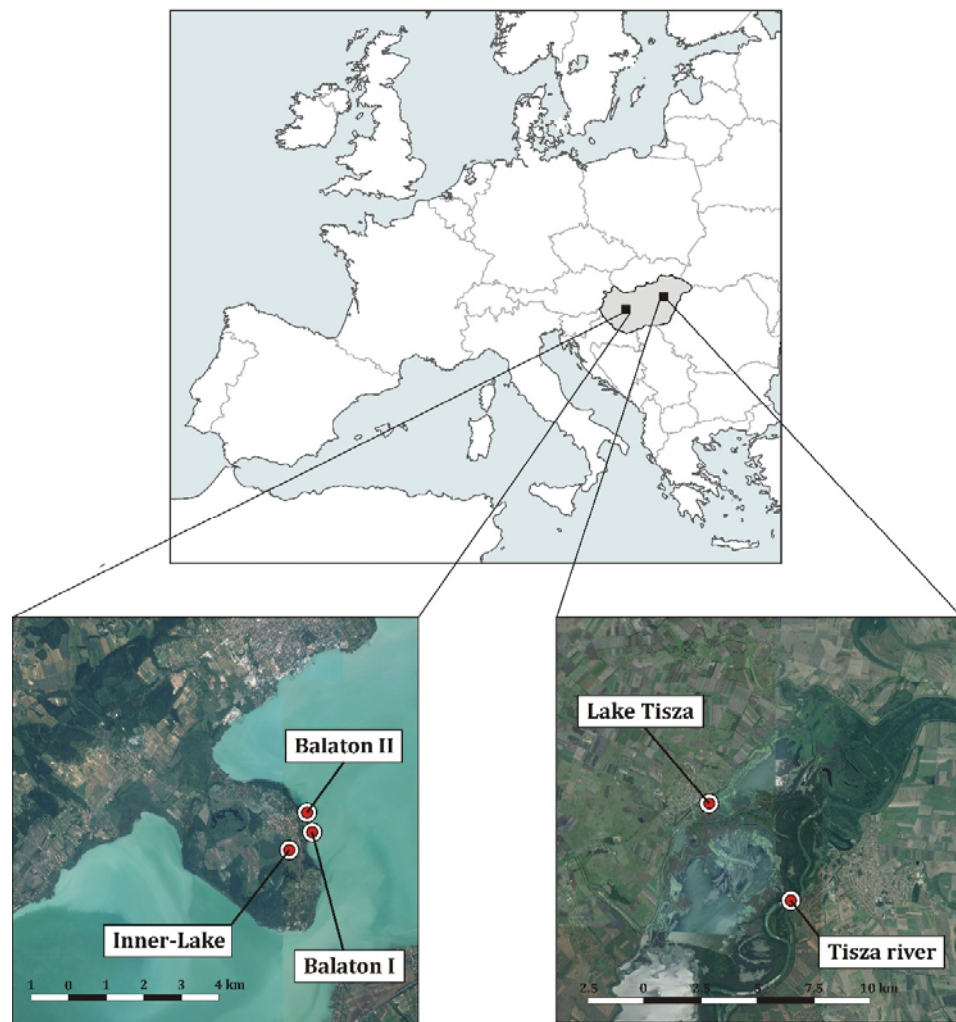

486

487   Fig 2. Ordination based on a Principal Coordinates Analysis of plant communities among the five sample collection sites. The first two PCO axes are shown.

488

489   Fig 3. Photos of *Salvinia natans* female gametophytes extracted from mallard faeces a) before germination and b) after germination, showing the archegonia

490   (dark brown dots). The vertical bars represent one mm. Photographed by Á. Lovas-Kiss.

491

492
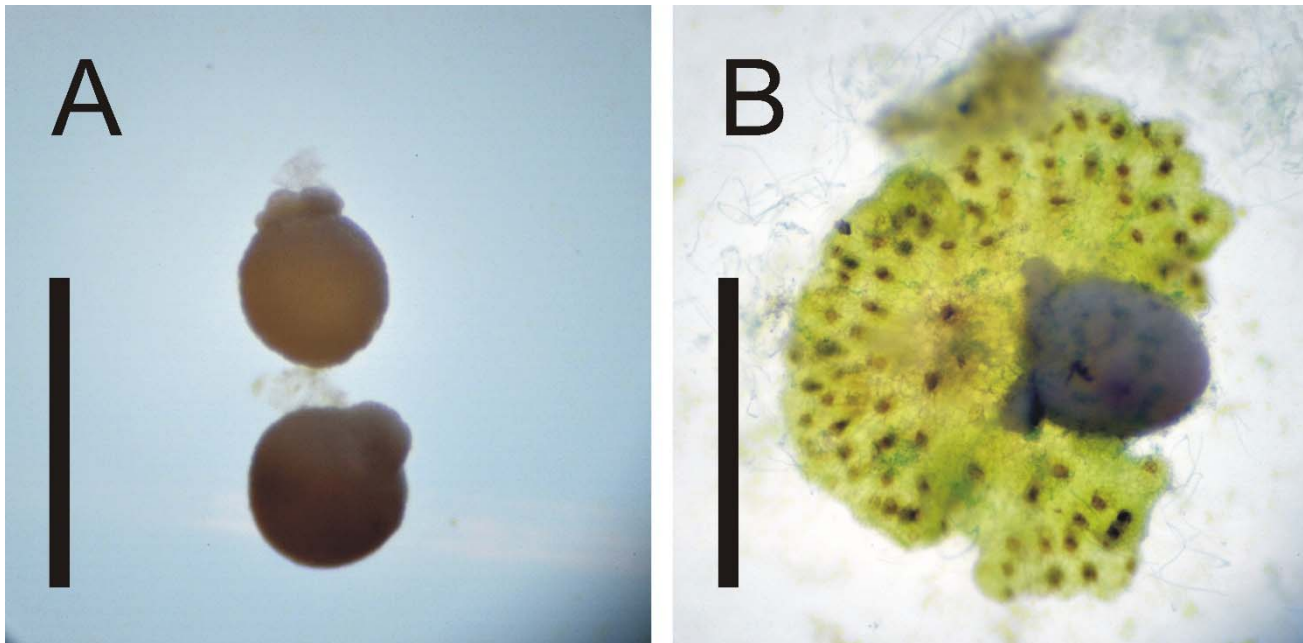
493   Fig 4. Silver birch *Betula pendula* seeds concentrated on a lake shoreline where mallards were feeding. Photographed by A. J. Green.

494