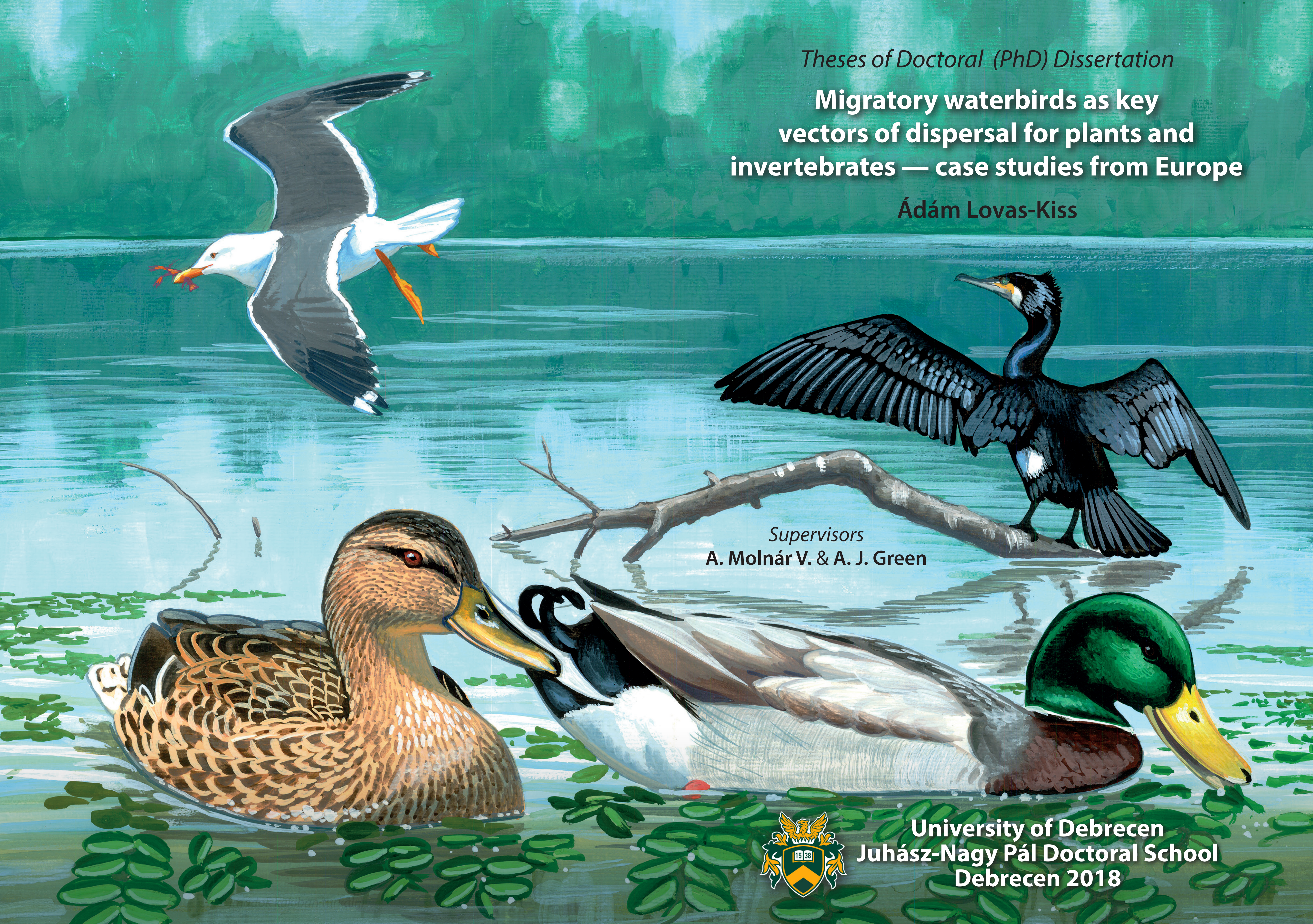

Theses of Doctoral (PhD) Dissertation

Migratory waterbirds as key vectors of dispersal for plants and invertebrates — case studies from Europe

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A doktori értekezés betétlapja

Migratory waterbirds as key vectors of dispersal for plants and invertebrates – case studies from Europe

Vándorló vízimadarak mint növények és gerinctelen állatok kulcsfontosságú terjesztő vektorai – esettanulmányok Európából

Értekezés a doktori (Ph.D.) fokozat megszerzése érdekében
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1. Introduction and literature overview

1.1. On the dispersal

One of the most important part of an organism life cycle is the dispersal phase. Dispersal means that the organism moves in a voluntary or involuntary manner from its natal/reproduction site to a new location where it reproduces itself sexually or asexually (TESSON *et al*., 2005). This movement helps to avoid local competition and to occupy a new territory or home range after passing across barriers like mountains, rivers and even continents. Dispersal or movement for animals are often obvious, and are referred to as active dispersal (TESSON *et al*., 2005). Those organisms which can't relocate themselves by active movement only disperse when they are in a mobile life history stage (e.g. egg, larva, diaspore) in the form of passive dispersal TESSON *et al*., 2005). The mechanism of passive dispersal implies that the diaspores, eggs and other propagules are moved by a vector, which can be abiotic (wind, water etc.) or biotic (animals, humans). In recent years, with natural habitats continuously shrinking and being fragmented worldwide due to human land usage and climate change, the ability to disperse is the only possibility to leave unfavourable conditions or to keep the gene flow between populations to avoid inbreeding or even to colonize new areas.

There are three main hypotheses on the advantages of dispersal for plants (HOWE & SMALLWOOD, 1982). The first one is the escape hypothesis, where the aim is to avoid the seed and seedling mortality (which can be caused by predation, pathogen attack and seedling competition) around the mother plant. The second hypothesis is the colonization hypothesis, where dispersal allows a parent to produce offspring capable of taking advantage of habitats with low competition as they become avaible. This hypothesis presumes that habitats changes over time. The third hypothesis is the directed dispersal hypothesis. This hypothesis suggests that the dispersal is the only way to reach special suitable habitats which the plant requires.

The propagules are the passive dispersal unit, which are seeds, spores or vegetative parts in the case of plants, or can be resting eggs in the case of invertebrates. Dispersal can be a highly effective selective driving force, resulting in several morphological adaptations for several vectors. These vectors can be classified into abiotic and biotic groups. The abiotic group has several vectors, including water or wind. The first one is the so called hydrochory, where the seeds are adapted to float on the water surface with buoyant diaspores. There is a sub-group in this kind of dispersal, which is thalassochory, where the vector is ocean currents. Anemochory is when the propagules are blown away from the mother plant by wind. The wind lifts the seeds with their morphologically adapted attachment, such like a pappus or wings. These dispersal methods are usually the least direct. In contrast, the biotic vectors, i.e. animals or humans, are often referred as direct dispersal agents.

Animal mediated seed dispersal (zoochory), is one of the most important forms of dispersal, and can appear in wide range of animals. Seed dispersal is one of the most important ecosystem services provided by birds and other vertebrates (ŞEKERCIOĞLU, 2006; GREEN & ELMBERG 2014)]. Zoochory can occur in different forms, including epizoochoory, where the propagules are transported on the outside of the animals. Diaspores can be attached to the fur of mammals and to the feathers or beaks of the birds, either with sticky mud or owing to their adapted morphology. The second type is endozoochory. During this mechanism, the propagules are consumed by the vector and later egested, while retaining their viability. The third form is scatter hoarding, when animals collect and hide large diaspores (i.e. food resources) in their home ranges or territories, meanwhile dispersing the diaspores. Endozoochory can be considered to have two forms, these being primary endozoochory when only one vector is transporting the propagules, and secondary endozoochory when there are two vectors. The latter has been recorded in the case of predators, when the first vector consumed the propagules and later this organism was hunted down and ingested by a second animal, and the diaspores are later defecated by the second vector (e.g. kestrels predating on lizards; NOGALES *et al.*, 2007).

In the following text, I will focus on the bird mediated dispersal, because birds are the subject of this thesis. Ornithochory can appear in the above mention forms of zoochory, but there is also an additional method, the caliochory (WARREN *et al.*, 2017), where the birds are dispersing the diaspores as nest-material. One of the biggest advantages of birds as vectors is the long-distance migrations of many species, allowing long-distance dispersal (LDD) of plants. LDD can lead to species expansion, colonization of islands and one important form of this is through the endozoochory by migratory birds (VIANA *et al.* 2016a). For example, this was demonstrated for the case off Eleonora's falcon, *Falco eleonorae* catching migrant birds, which were brought back to their nest site in the Canary Islands by the predator for later consumption. VIANA and his colleagues (2016b) collected these predated birds' digestive system and analysed their contents. They found 45 intact seeds, including viable *Rubus* seeds giving an example for another type of secondary dispersal.

Endozoochory has another specialized form, which is the so called frugivory. Those plants which have adapted to frugivory lure the bird vectors with fleshy, coloured fruits (VAN DER PIJL, 1982). These plants can receive several benefits provided by the transport agents. They can remove the pulp from the seeds while handling, ingesting the fruit and causing germination acceleration, because of the removal of germination inhibitors (SAMUELS & LEVEY, 2005; ROBERTSON *et al.*, 2006). This can also increase the germination success (TRAVESET *et al.*, 2007). Passing through, the digestive system of the birds can even remove the fungal pathogens and the chemical cues of the seed predators (FRICKE *et al.*, 2013, WENNY *et al.*, 2016). Some level of avian frugivory was reported in almost 4000 bird taxa and in the dispersal of almost 69 000 plant species from 240 families (WENNY *et al.*, 2016). Frugivory is the most intensively researched form of the bird mediated endozoochory. Since 1986, the articles published on frugivory are booming, reaching almost 100 papers per year at 2010 (FORGET *et al.*, 2011) and frequently referred to as the principal ecosystem service by birds (ŞEKERCIOĞLU, 2006). In comparison, the studies on the granivorous waterbirds are underrepresented since the 19th century with a peak of five publications per year in recent time (VAN LEEUWEN *et al.*, 2012).

1. 2. Plant dispersal by waterbirds

Endozoochory can be more important than epizoochory in the case of birds (BROCHET *et al.* 2010b; COSTA *et al.*, 2014), especially in waterbirds (REYNOLDS & CUMMINGS, 2016). The high mobility (regular movement between wetlands) of the waterbirds, their long-distance migrations and high number of individuals makes them good candidates for acting as vector in seed dispersal (CLAUSEN *et al.*, 2002). Studying waterbirds as vector goes back to the 1800s. One of the first scientists to do so was CHARLES DARWIN (1859). His work on seed dispersal showed the importance of thalassochory (dispersal by sea or ocean currents), but he also stated:

"*The wide distribution of fresh-water plants and of the lower animals, (...), apparently depends in main part on the wide dispersal of their seeds and* *eggs by animals, more especially by fresh-water birds, which have great powers of flight, and naturally travel from one piece of water to another.*"

His works on waterbirds were focused on epizoochorous dispersal and secondary endozoochorous dispersal. DARWIN in the sixth edition of his most famous book wrote about how he found a viable toad-rush (*Juncus bufonius*) seed in mud which was attached to a woodcock (*Scolopax rusticola*) leg. Several experiments were conducted by him on secondary dispersal using waterbirds like pelicans, gannets and maribu storks. These were the first scientific attempts to show the possibility of secondary seed dispersal. He replaced the intestines of dead fish with seeds (wheat, millet, canary seed etc., WEB1) and later fed these to the birds. Many hours after the feeding they regurgitated or defecated the seeds in a viable state. ANTON KERNER (1895) found twenty-one species of plants in the washed mud from several bird species (including snipe). HENRY B. GUPPY (1894) argued that waterbirds can be important vectors for plants to reach remote islands. He obtained shot wild ducks from the market and dissected their digestive tract and found more than 800 seeds from 10 species of plants, and he also showed their viability. HENRY N. RIDLEY (1930) was the first to show that several waterbirds (*Anatidae*, *Laridae* etc.) families are capable of seed dispersal and emphasised their importance with data collected about diet, and reviewing all the evidence provided by other scientists.

In the second half of the 20th century VERNON W. PROCTOR did prominent work and landmark studies on endozoochorous seed dispersal by waterbirds. PROCTOR (1968) did several trials with different bird families where he showed the importance of shorebirds (e.g. killdeer, *Charadrius vociferus*) as LDD vectors. He was a pioneer who introduced the mallard (*Anas plathyrhynchos*) as a model animal to show that algae (desmids, 1959) and their propagules (oogonia from *Charophyceae*, 1962), and even crustacean eggs can survive ingestion and gut passage of the birds (PROCTOR *et al*., 1967). LDD events caused by migratory waterbirds are likely to be frequent, as shown by modelling studies (VIANA et al., 2013). However, mallards have been shown to be important for dispersing propagules not only during their migrations, but also their daily movements (KLEYHEEG *et al*., 2017). A wide range of waterbirds (GREEN *et al*., 2002, GREEN, 2016; RIDLEY, 1930) are capable of dispersing plant propagules. To assess the waterbird mediated dispersal by endozoochory, there are several methods:

1.3. Experiments as a method to study seed dispersal by waterbirds

CHARALAMBIDOU & SANTAMARÍA (2002) presented a review of 26 papers. They showed that most of these papers worked with mallards (*A. plathyrhynchos*). This shortage of diversity of vectors can be important, because of the big variability in the differentiation of digestive tract among waterbirds. The importance of the variance of the morphology of the hindgut and foregut is not negligible in these experiments, because it can affect the retention time (RT) of the propagules (CHARALAMBIDOU & SANTAMARÍA, 2002). The RT can be a determining factor, not only for seeds and other propagules to reach longer distances, but longer RT can lead to a stronger mechanical scarification, which in turn can lead to lower seed survival, but also to a greater germination rate in some plant species (BROCHET *et al.*, 2010c). The passage through the digestive tract can change the germination rate of *Schoenoplectus litoralis* in saline environments (ESPINAR *et al.*, 2004), causing decreased germination in higher salinities and increased germination at the lower salinities, compared to the controls. The diaspore traits can also be a determining factor for dispersal. Experiment by SOONS et al. (2008) showed that smaller sized seeds can have a faster passage through the mallard gut, hence a larger proportion of them can remain intact and viable compared to large seeds. Lately published articles showed how these experiments can underestimate the viability of the seeds, owing to the fact that the vectors were resting. Active birds can have a shorter retention time, which can give the seeds a higher survival rate (KLEYHEEG *et al.*, 2015). Not only defecation can serve as a mechanism in the case of waterbird endozoochory, but also regurgitation. This may appear in natural conditions, when the birds suddenly find a patch with a high abundance of available food and gorge themselves, and in particular it can be a suitable dispersal mechanism for bigger seeds (KLEYHEEG & VAN LEEUWEN, 2015). Regurgitation can also be a suitable process for LDD, as experiments by PROCTOR (1964) showed that the killdeer (*Ch. vociferus*) can regurgitate some viable seeds after long periods of up to 340 hours.

1.4. Value of diet studies in the understanding of seed dispersal

A recent big review on dabbling ducks *Anas* spp. collected 71 articles identifying seeds of more than 400 species of plants, which are part of their diet (SOONS *et al.*, 2016). To examine the potential for waterbird-mediated seed dispersal scientist often use field shot animals. These studies collect the hunted bird's digestive tract and quantify the propagules from the different parts of the alimentary canal. For the great majority of the plant species whose seeds are found in the upper gut (e.g. in the gizzard or oesophagus), some of those seeds survive the gut passage process (BROCHET *et al*., 2009), so diet studies can be a good proxy for endozoochory potential. Some studies focus on the end of the intestine, to confirm that the seeds observed have survived gut passage intact. E.g. in the Camargue BROCHET *et al*., (2010b) found 21 plant species with a total of 902 propagules from the rectum of shot teals (*Anas crecca*). Twenty percent of the birds contained diaspores, and 16 of the species were germinated. Mallard individuals were also collected in the Netherlands where systematic analysis showed that the foregut contained more plant propagules than the hindgut (73% vs 33 %, KLEYHEEG *et al*., 2016). This study presented overall 4,548 ingested seeds from 66 species, and of these only 249 diaspores from 30 taxa were in the hindgut. This is partly because seeds spend more time in the foregut than in the intestines. Such studies underline the need for more field collection studies, to see which species can survive gut passage and achieve waterbird-mediated dispersal. Collecting bird excreta in the field is a non-destructive method that guarantees that the propagules recorded have already withstood the gut passage process.

1.5. Field collection of excreta: a non-destructive method with no need for animal experimentation

This method of data collection has not been used very often to gain data on propagule dispersal by non-frugivorous birds, despite this being the method with the lowest impact on birds, and providing the most accurate data on dispersal under field condition. Only a few studies have relied on the field collection of fresh excreta. MUELLER & VAN DER VALK (2002) carried out a field collection of faeces by capturing birds. From six taxa of waterfowl they obtained 80 samples from which 53 contained seeds from seven common wetland plant genera. An extensive study was carried out in Doñana in Spain on 11 migratory waterfowl species, with more than 380 collected faecal samples (FIGUEROLA *et al*., 2003). Seasonal variation of the dispersed propagules was observed, and these belonged to 7 plant genera and invertebrate eggs. Shorebirds also showed seasonal variation in the dispersed propagules in the Odiel marshes, Spain demonstrated by faecal and pellet samples collected from three species (SÁNCHEZ *et al*., 2005, 2006). Even a small amount of field samples of faeces can provide valuable information. Overall twenty-two faeces were gathered from killdeer, mallard and green-winged teal (*A. carolinensis*) in Oklahoma, USA, which contained ten plant species and six invertebrate taxa (GREEN *et al*., 2013). One of the first studies carried out in Australia, on three waterfowl taxa and the Australian pelican (*Pelecanus conspicillatus*) showed that piscivorous birds can egest enormous numbers of intact propagules and more than the other three bird species, based on field collected samples (GREEN *et al*., 2008). A South African study collected over 300 samples from six waterbird species containing over 1,300 diaspores, from which 10% were viable (REYNOLDS & CUMMINGS, 2016).

1.6. Freshwater invertebrate dispersal by waterbirds

Freshwater invertebrates can occur in distant habitats lacking hydrological connections habitats and can have wide distributions. Most of these species are do not have a mechanism for active dispersal, but some taxa have the ability to reach new habitat patches with their active dispersal via aerial forms that fly, i.e. adult insects (BILTON *et al*., 2001). Zooplankton and other invertebrates which are unable to disperse themselves are dependent on vectors like wind or rain (CÁCERES & SOLUK, 2002; COHEN & SHURIN, 2003; HAVEL & SHURIN, 2004), waterflow between connected waterbodies (MICHELS *et al*., 2001), ballast water (BAILEY *et al*., 2003) and other human mediated shipping forms (HAVEL & SHURIN, 2004). DARWIN (1859) was the first one who noticed that waterfowl can have a potential role in dispersing aquatic invertebrates passively. One of the first experiments was carried out by him placing a duck foot in an aquarium full of recently hatched snails. The hatchlings immediately climbed to the leg and remained alive for 12-20 hours in damp air. A recent review (VAN LEEUWEN *et al*., 2012) identified 39 macroinvertebrate species which are carried by *Anatidae* and *Rallidae* species. Field studies have demonstrated that invertebrate diapause eggs can be dispersed in both ways, epi- and endozoochorously (BROCHET *et al*., 2010a; REYNOLDS & CUMMINGS, 2015). Despite the lack of studies, the available articles show a broad diversity in the dispersed invertebrates (Table 1).

Focusing on the bryozoans, as a group of particular interest, some experimental studies were carried out. BROWN (1933) showed that statoblasts (diapause eggs of the bryozoans) of *Fredericella sultana*, *Pectinatella magnifica*, *Plumatella repens* and *P. emarginata* can survive the gut passage through a mallard. Pintails (*Anas acuta*) and shovelers (*Anas clypeata*) can retain viable statoblasts of *Cristatella mucedo* over four and eight hours respectively, potentially providing a 250-600 km dispersal distance for this bryozoan species (CHARALAMBIDOU *et al*., 2003a).

Field collection of killdeer (*Charadrius vociferus*) faeces showed three species (*Plumatella fungosa*, *P. reticulata*, *P. vaihiriae*) of the colonial plumatellid bryozoans, and in addition they found ostracod individuals from the *Crustaceae* family (GREEN *et al.*, 2013). PROCTOR's experiment (1964), where he fed field-collected macrophytes and eggs to domesticated mallards and wild waterbirds proved that eggs of several Crustacean (like *Artemia franciscana*, *Triops longicaudatus*, *Cyzicus mexicanus*, *Alona guttata*, *Cyprinotus dentatus* etc.) can be dispersed by waterfowl. A feeding study by MELLORS (1975) found that the 27 % of the ephippia of the *Daphnia pulex* fed to Black-crowned night heron (*Nycticorax nycticorax*) survives the digestive system showing the potential for secondary dispersal. The cladoceran *Bythotrephes longimanus* recently expanded from north to south and this may can be explained by the massive autumn waterfowl migration, when the species produces diapause eggs. The propagules of this species are able to survive the digestion of waterbirds (CHARALAMBIDOU *et al.*, 2003b). Even Protozoan, Rotifer and Nematode species can be dispersed by waterbirds (FRISCH *et al.*, 2007; GREEN *et al.*, 2008). A seperate study demonstrated that the larvae of *Chironomus salinarius* are able to be dispersed by Black-tailed godwits (*Limosa limosa*) (GREEN & SÁNCHEZ, 2005). Genetic data analyzed for a bryozoan and two cladocera species reveal that waterfowl movements gives a better explanation to genetic population structure than the geographical distances (FIGUEROLA *et al.*, 2005).

Table 1. Examples of the types of aquatic invertebrates that have been shown to be dispersed by waterbirds. (ND = No data on further identification)

Phylum / Class / Order	Reference
Ciliophora / ND / ND	GREEN *et al.*, 2008
Rotifera / Monogononta / Plioma	GREEN *et al.*, 2008
Bryozoa / Phylactolaemata / Plumatellida	GREEN *et al.*, 2008; BROCHET *et al.*, 2010a
Nematoda / ND / ND	GREEN *et al.*, 2008
Arthropoda / Branchiopoda / Anostraca	PROCTOR, 1964; GREEN *et al.*, 2005
Arthropoda / Branchiopoda / Cladocera	GREEN *et al.*, 2008; CHARALAMBIDOU *et al.*, 2003b
Arthropoda / Branchiopoda / Notostraca	PROCTOR, 1964
Arthropoda / Branchiopoda / Spinicaudata	PROCTOR, 1964
Arthropoda / Hexanauplia / Harpacticoida	FRISCH *et al.*, 2007
Arthropoda / Ostracoda / Podocopida	BROCHET *et al.*, 2010a
Arthropoda / Insecta / Diptera	FRISCH *et al.*, 2007

1.7. Waterbirds as distributors of alien species

Several studies showed that waterbirds can be good vector for native species (BROCHET *et al*., 2009; SOONS *et al*., 2016). Most of the above-mentioned studies were focusing on native taxa. More than 40 native species of plants were shown in the diet of dabbling ducks by BROCHET *et al*., (2009). Native invertebrates also benefit from waterbird vectors (GREEN *et al*., 2005). However, alien species are now frequent in natural ecosystems, and the spreading of the alien species is one of the biggest threats to biodiversity in Europe (BRUNDU *et al*., 2001). When waterbirds disperse native species, they are likely to disperse similar alien species found in the same environments.

Our knowledge on exotic species dispersal by waterbirds are still low owing to a shortage of studies, however the zoochorous dispersal of alien taxa are widely demonstrated by other animals (VAN LEEUWEN, 2018). Recent reviews (REYNOLDS *et al*., 2015, GREEN, 2016) identified 78 alien plants and eight alien aquatic invertebrates, which can be dispersed by waterbirds. One experiment was made by GARCÍA-ÁLVAREZ and his colleagues (2016) which showed that the alien primrose (*Ludwigia grandiflora*) can be dispersed by mallards and greylag geese (*Anser anser*) over longer distances. Moreover, redshanks (*Tringa totanus*), dunlins (*Calidris alpina*) and black-tailed godwits (Limosa limosa) in Spain and Portugal can transport the introduced *Artemia franciscana* as well as small numbers of the native *A. parthenogenetica* (GREEN *et al*., 2005), which can lead to huge problems, because the native species can disappear after the introduced one arrives (AMAT *el al*., 2005). An Australian study found the highly invasive waterfern (*Azolla filiculoides*) megasporocarps in black swan (*Cygnus atratus*) and coot (*Fulica atra*) faeces but failed to germinate them (GREEN *et al*., 2008). When migratory teal individuals were shot in Camargue, France, 14 alien species of plants were found in their digestive system (BROCHET *et al*., 2009). The above-mentioned examples show that waterbirds can a high potential to distribute alien plant and aquatic invertebrate species, but there is still lack of information, which often leads to the overlooking of zoochory by waterbirds as a major pathway of alien species.

1.8. Endozoochory of aquatic ferns and angiosperms by mallards in central Europe.*

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 *et al.*, 2012; GREEN *et al.*, 2016). These include angiosperms whose diaspores lack any obvious morphological adaptations for long-distance dispersal (COSTEA *et al.*, 2016; SOONS *et al.*, 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 *et al.*, 2013; WILKINSON *et al.*, 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 *et al.*, 2015), this has never been conclusively demonstrated. Laboratory experiments support the potential for epizoochory of Azolla over short distances (COUGHLAN *et al.*, 2017a), and the potential for endozoochory of Marsilea (MALONE & PROCTOR, 1965).

Mallards are important plant vectors both during seasonal, migratory movements (VIANA *et al.*, 2013) and during daily movements within a landscape (KLEYHEEG *et al.*, 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).

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* Based on: Lovas-Kiss Á., Vizi B., Vincze O., Molnár V. A., Green, A. J. (2018a): Endozoochory of aquatic ferns and angiosperms by mallards in central Europe. – *Journal of Ecology* doi: 10.1111/1365-2745.12913

1.8.1. Aims

In the first study, our aim was to quantify and compare endozoochory of aquatic and terrestrial plants by mallards on autumn migration at different wetlands of Hungary, central Europe. We identified diaspores deposited in faeces with a high taxonomic resolution, assessed the germinability of diaspores and analyzed the extent of spatial variation in the dispersal of different plant taxa. We also provided the first demonstration of endozoochory of aquatic ferns. We considered 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.

1.9. Great Cormorants reveal overlooked secondary dispersal of plants and invertebrates by piscivorous waterbirds**

Dispersal is crucial for the persistence of species inhabiting aquatic habitats because these are often discontinuous in space and time (HOWE & SMALLWOOD, 1982). Many aquatic species disperse as seeds or diapausing stages by vectors such as water, wind, fish, waterbirds or mammals (BILTON *et al.*, 2001). Successive transportation by multiple vectors (secondary dispersal) can extend dispersal routes, increasing connectivity for plants and invertebrates (HÄMÄLÄINEN *et al.*, 2017). Although waterbirds and fish are both major vectors (HORN *et al.*, 2011; VAN LEEUWEN *et al.*, 2012), the possibility of secondary dispersal by their interactions has been little explored (GREEN, 2016).

After daytime fishing, piscivorous birds such as cormorants, mergansers, pelicans and herons commonly roost close to water at night and regurgitate indigestible prey remains as pellets. The potential of this bird-fish interaction for secondary dispersal previously led DARWIN (1859) and MELLORS (1975) to experimentally feed fish containing seeds or invertebrates to piscivorous birds, later retrieving viable propagules in excreta. There are anecdotal observations of endozoochory by piscivorous birds in the field, i.e. one Australian pelican *Pelecanus conspicillatus* dropping contained seeds and invertebrate eggs, and two great cormorant *Phalacrocorax carbo* stomachs contained Carex seeds

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** Based on: van Leeuwen, C. H., **Lovas-Kiss, Á.,** Ovegård, M. & Green, A. J. (2017): Great cormorants reveal overlooked secondary dispersal of plants and invertebrates by piscivorous waterbirds. –*Biology Letters* **13**(10): 20170406.

(GREEN *et al.*, 2008; STERBERTZ, 1992). This supports potential dispersal by piscivorous birds, but quantitative evidence is lacking (GREEN, 2016).

1.9.1. Aims

The aim of the second study was to quantify the importance of secondary dispersal of plants and invertebrates by piscivorous birds. Specifically, we considered (1) the taxonomic and ecological diversity of propagules egested by piscivores, (2) the relationship between ingested fish species and propagules retrieved, (3) the frequency and generality of this dispersal mechanism across localities. We studied these questions in seven colonies of great cormorants.

1.10. Crayfish invasion facilitates dispersal of plants and invertebrates by gulls·***

Many plants and invertebrates are able to disperse with vertebrate vectors, although current knowledge of these interactions remains limited (TESSON *et al.*, 2015). Propagules (mostly seeds or resting eggs) can be dispersed internally (in vector digestive system, i.e. “endozoochory”) or externally (attached to vector body, i.e. "epizoochory" or "ectozoochory"). Endozoochory by frugivores is particularly well studied, and illustrates how dispersal interactions are major determinants of the composition and gene flow in biological communities, and a vital part of the architecture of biodiversity, or “interactome” (GARCÍA *et al.*, 2017). Increasingly, it is becoming clear that waterbirds are key vectors of plants lacking a fleshy fruit, as well as of a range of invertebrate groups (COUGHLAN *et al.*, 2017b; SOONS *et al.*, 2016; GREEN, 2016; VALLS *et al.*, 2017). This often happens because waterbirds feed directly on seeds or invertebrates but only digest a fraction of them, and this can be considered as “primary dispersal”.

Such dispersal is vital for metacommunity dynamics, and for maintaining connectivity between populations in isolated catchments and in fragmented landscapes (TESSON *et al.* 2015; GREEN *et al.*, 2016). Migratory waterbirds are also vectors for the long-distance dispersal (LDD) that allows species to achieve widespread distributions, and to respond to global change (NATHAN *et al.*, 2008; GREEN *et al.*, 2016). DARWIN

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(1872) showed experimentally that "secondary dispersal" may also be important, in which birds predate on organisms such as fish which have previously ingested seeds or other propagules. Secondary plant dispersal by birds of prey and carnivorous mammals has been demonstrated (NOGALES *et al.*, 2002; HÄMÄLÄINEN *et al.*, 2017), yet such secondary dispersal processes by waterbirds have hardly been investigated (GREEN *et al.*, 2016). Recently, however, cormorants have been shown to disperse a variety of propagules previously ingested by fish (VAN LEEUWEN *et al.*, 2017a). Secondary dispersal can provide several benefits to dispersed taxa, since the secondary vector may have higher mobility and greater capacity for LDD. In addition, propagules that may not survive gut passage in one organism may still be dispersed if a predator ingests this organism, and the propagules within, before gut passage has been completed (HÄMÄLÄINEN *et al.*, 2017). Studies of secondary dispersal by waterbirds are therefore required to assess its importance in the maintenance of biodiversity, and its role in the interactome in aquatic ecosystems (REYNOLDS *et al.*, 2017; VAN LEEUWEN *et al.*, 2017a).

Fig. 1. Two crayfish *P. clarkii* at the edge of a ricefield in the study area. The upper specimen is coated in mud, whereas the lower specimen is cleaner owing to the effect of the water in its burrow. Credit A. J. Green.

The red swamp crayfish (*Procambarus clarkii*) is increasingly widespread as an alien species, and is considered to be amongst the world's worst aquatic invaders owing to major impacts on aquatic ecosystems and ecosystem services (GEIGER *et al.*, 2005; MCLAUGHLAN *et al.*, 2014). In Europe, it was first introduced into Doñana, SW Spain from Louisiana, USA in 1973. Although the influence of this invasion on dispersal interactions has yet to be fully examined, crayfish have been shown to act as vectors of dispersal for the eggs or juveniles of aquatic invertebrates that can adhere to their external surfaces, or survive ingestion and gut passage (MOORE & FAUST, 1972; PÉREZ-BOTE *et al*., 2005). In Europe, for example, the exotic ostracod *Ankylocythere sinuosa* (RIOJA, 1942) and the branchiobelid *Xironogiton victoriensis* (GELDER & HALL, 1990) have been found to co-occur with the widely distributed *P. clarkii*, including those populations located across the Iberian Peninsula (DIÉGUEZ-URIBEONDO *et al*., 1997; GELDER, 1999; AGUILAR-ALBEROLA *et al*., 2012).

Procambarus clarkii is often abundant in habitats used by large numbers of migratory waterbirds, such as European ricefields (PERNOLLET *et al*., 2015). The Doñana wetlands in Spain are one of the most important wintering sites for waterbirds in the western palearctic (RENDÓN *et al*., 2008), and support many bird species that can predate on *P. clarkii* (including grey heron *Ardea cinerea*, white stork *Ciconia ciconia*, little egret *Egretta garzetta*, glossy ibis *Plegadis falcinellus*, and lesser-black backed gull *Larus fuscus*; TABLADO *et al*., 2010). Doñana includes up to 37,000 ha of ricefields (GREEN *et al*., 2017), where bird numbers peak at the time of rice harvest, with many of the same birds switching to natural wetlands in Doñana and other parts of Andalusia during the rest of the wintering period (RENDÓN *et al*., 2008, BOUTEN *et al*., 2013). Gulls (*Laridae*) are opportunistic and omnivorous birds that often feed on alien crayfish (CHRISTEL *et al*., 2012, MORTIMER *et al*., 2012, GYIMESI *et al*., 2016). Equally, gulls also consume grains and other seeds, and can be important vectors for dispersal of native and alien plants (GREEN, 2016; GREEN *et al*., 2016). However, there have been no previous reports of secondary dispersal by gulls. *Larus fuscus* is a migratory species with an increasing population wintering in southern Spain but breeding in northern Europe (BOUTEN *et al*., 2013), and up to 15,000 are present in the Doñana ricefields at harvest time (RENDÓN *et al*., 2008). Gulls can be observed feeding in muddy fields that have been drained for harvesting. When caught, crayfish are covered in mud (Fig. 1) owing to absence of standing water, and are swallowed quickly to avoid kleptoparasitism, i.e. before they can be stolen by other birds (ORO & MARTÍNEZ-VILALTA, 1994).

1.10.1. Aims

In this study, we evaluate the potential for secondary dispersal of propagules by gulls that are feeding on crayfish in the ricefields of the Doñana area. Our aims were to investigate what kinds of seeds and invertebrates are transported by *P. clarkii* and *L. fuscus*, and determine whether organisms dispersed by gulls are ingested together with crayfish prey (i.e. carried within or upon crayfish). We compared propagules dispersed by gulls in pellets and faeces, because the latter are likely to be retained in the gut for longer, with more chance of undergoing LDD (NOGALES *et al.*, 2001). We also investigated whether taxa dispersed included alien species or agricultural weeds, whose dispersal by migratory birds may constitute an ecosystem disservice (GREEN *et al.*, 2016, FARMER *et al.*, 2017).

2. MATERIALS AND METHODS

2.1. Endozoochory of aquatic ferns and angiosperms by mallards in central Europe

2.1.1. 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. 2). 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. 2). 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 *et al*., 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.

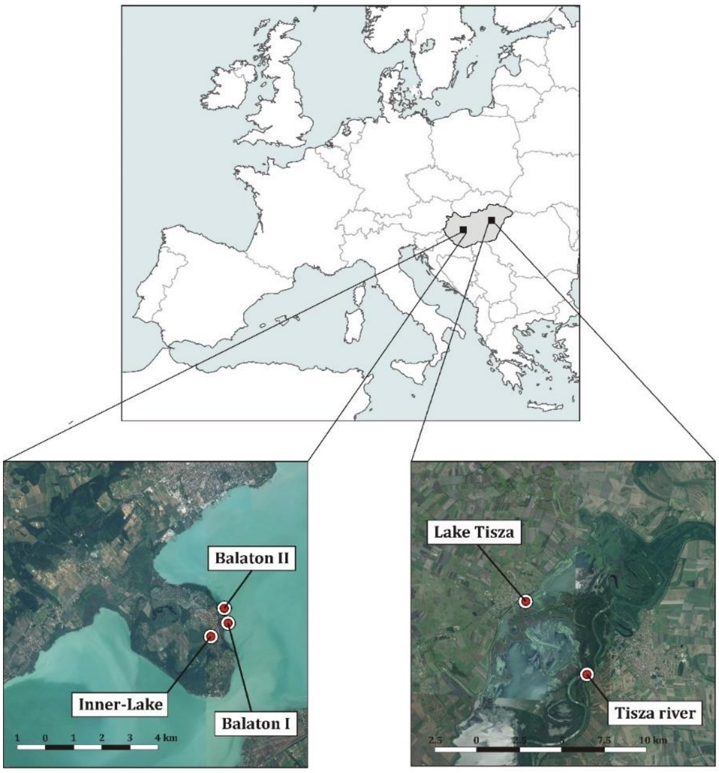

Fig. 2. Location of the study areas in Hungary (lower images taken from Google Earth).

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 zip-lock plastic bags.

The samples were then kept in the fridge (4°C) until subsequent laboratory investigations, which were completed within 6 months. Faecal samples were weighed on a balance (Ohaus EP213C Explorer® Pro), then washed on a 100 µm sieve using deionized water before inspection under a binocular microscope. Intact diaspores, for which no cracks or missing parts were detectable, were collected and quantified. Angiosperm seeds were photographed and identified based on their shape, size, colour and seed coat pattern following recent literature (CAPPERS *et al*., 2012; BOJNANSKÝ & FARGAŠOVÁ, 2007). Fern macrospores were identified following WEIJDEMA *et al*. (2011). Dispersal syndromes for each taxon were taken from the plant trait database Baseflore (JULVE, 1998).

Diaspores were then placed in an Eppendorf® tube filled with deionized water until germination trials. Germinability tests were conducted on Petri-dishes filled with nutrient-free Agar gel for terrestrial plants, and in tissue plates filled with deionized water for aquatic plants (*Araceae*, *Haloragaceae*, *Potamogetonaceae*, *Salviniaceae*). These were then placed in germination chambers set at 12 h of light at 24 °C, and 12 h of darkness at 18 °C. Germination tests were run for 54 days.

2.1.2. Statistical analysis

To compare the number of intact diaspores of a given taxon in the five sets of samples, we used Kruskall-Wallis H test. This test was only performed for those taxa with diaspores recorded in a combined total of at least six faecal samples. Where significant differences were detected, we used Dunn's test (DINNO, 2017) to identify which sites differed significantly.

Several additional analyses were conducted using functions implemented in the R package 'vegan'. In order to analyse differences among plant community compositions recorded at the five sites, we used non-parametric permutational ANOVA (i.e., PERMANOVA; ANDERSON, 2001) using the adonis function. The latter analysis was based on a Bray-Curtis dissmiliarity matrix, composed of values between 0 and 1 reflecting the degree of dissimilarity among the five sites. Using these analyses, we inspected the differences in community compositional centroids among sites, but further analyses were performed to inspect differences in group homogeneities, using the function betadisper (ANDERSON, 2006). Using the latter procedure, we calculated the degree of dispersion of each sample from the compositional centroid at each sampling site. This procedure is often referred to as a test for difference in β diversity among the sampling sites. Tukey's HSD tests were used to determine which sites differed in β diversity. Additionally, a posteriori analysis was performed, using the function simper, to identify community members that significantly contributed to among-site differences. To establish statistical significance, the empirical p value of each variable was calculated using 1000 random permutations. Rarefaction analysis showed that our results were not strongly influenced by the differences in number of samples between sites (LOVAS-KISS *et al*., 2018a; Fig. S1).

Graphical presentation of the among-sites differences was conducted using principal coordinates analyses, performed using the cmdscale function on the above mentioned Bray-Curtis dissimilarity matrix. All statistical analyses were conducted in R statistical software package (version 3.3.2; R CORE TEAM, 2017). Adonis, betadisper and simper functions were implemented in R package vegan (version 2.4-3., OKSANEN et al., 2017), while Tukey's HSD and cmdscale were implemented in R package stats (version 3.4.0, R CORE TEAM, 2017). These analyses were run after excluding samples that contained no diaspores.

2.2. Great Cormorants reveal overlooked secondary dispersal of plants and invertebrates by piscivorous waterbirds

2.2.1. Study species

The great cormorant is a widespread colonial waterbird with an expanding population of 120000 individuals in Northwestern Europe and a global population of several million (WETLANDS INTERNATIONAL, 2017). Great cormorants are piscivorous and forage during daytime in coastal areas, estuaries, lakes and rivers (MAGATH *et al.*, 2016). Important freshwater prey species include *Cyprinidae* (e.g. common roach *Rutilus rutilis*, common carp *Cyprinus carpio*) and *Percidae* (e.g. European perch *Perca fluviatilis*) (e.g. BOSTRÖM *et al.*, 2012). Indigestible prey remains are regurgitated daily in one pellet of 5 to 10 g dry mass (BOSTRÖM *et al.*, 2012).

2.2.2. Field sampling and examination

Pellets were collected below roosting trees or on shores at seven locations in Denmark, Sweden and The Netherlands (Fig. 3, VAN LEEUWEN *et al.*, 2017a; Table S1). Pellets were individually stored in zip bags at -20°C (n=61), at 7°C (n=31) or were lost in the post for several weeks (n=20). Pellets were weighed and examined in the laboratory for plant diaspores (hereafter “seeds”), intact invertebrates (including diapausing stages), and fish remains. To exclude propagules that potentially attached to the exterior of pellets after egestion, we only included propagules completely covered in mucus (Fig. 3).

Fish remains and propagules were identified and examined for damage under a microscope (VAN LEEUWEN *et al.*, 2017a; Table S2). Fish length was estimated using species-specific regressions for sagittal otolith width (LEOPOLD *et al.*, 2001). For plant taxa, Ellenberg habitat indicator values for moisture (‘Feuchtigkeit’; F) (ELLENBERG *et al.*, 1992, HILL *et al.*, 1999) and dispersal syndromes (JULVE, P. 1998) were identified.

We attempted to hatch or germinate propagules from 51 unfrozen pellets. Individual seeds were placed on 1% agar with a 14h light (22±2ºC) to dark (18±2ºC) schedule, and monitored daily during two months. Invertebrate propagules were placed at 25°C in Tissue-Culture-plates with 1 ml deionized water in the shade (total darkness for sponge gemmules).

2.2.3. Statistical analysis

Non-random co-occurrence patterns among particular fish species and propagules were analysed in a network analysis in R (R CORE TEAM, 2017). For every pairwise combination of species in the pellets we calculated Spearman rank correlations (ρ) to analyse possible associations of their presences. All pairwise combinations formed a co-occurrence matrix for all pellet contents, which we visualized for correlations with $\rho>0.3$ and $p<0.05$ as edges (connections) between nodes (species) using the plot.network function in package statnet (HANDCOCK *et al.*, 2016). Node size is proportional to the number of pellets containing that species, and edge width is proportional toρ. The R code including more details is available in the electronic supplementary material.

Fig. 3. Regurgitated pellet from a great cormorant in Sweden. Credit M. Ovegård.

2.3. Crayfish invasion facilitates dispersal of plants and invertebrates by gulls

2.3.1. Sample collection

A large area of rice is harvested from late September to late December in ricefields of Sevilla province within the Guadalquivir delta. On three separate days in November-December 2014 and 2015, we collected 13 adults of *Procambarus clarkii* that were crawling out at the edge of ricefields that were being harvested, as well as gull faeces and pellets from different locations (Figs. 1, 4, 5; Lovas-Kiss *et al.*, 2018b; Table S1).

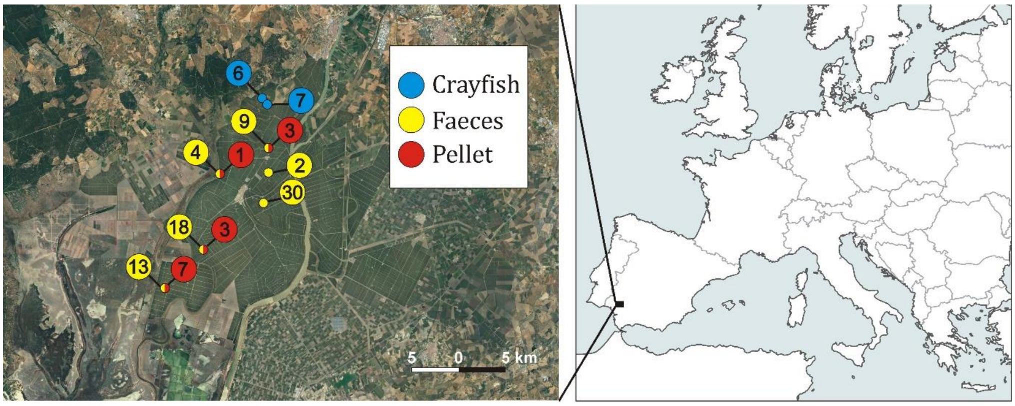

Fig. 4. Location of the study area and of sampling points in the ricefields on the west side of the River Guadalquivir. Numbers refer to sample sizes. The town of Isla Mayor lies in the middle of the points. Based on an image from Google Earth.

We put crayfish immediately into individual plastic jars (12 cm high, 9 cm diameter) filled with deionized water for 10 minutes to wash off propagules attached to the outside of the animals. Crayfish were then placed in a cool box on ice in the field and frozen on arrival to the laboratory.

Fig. 5. Fresh pellet regurgitated by a *Larus fuscus* in the study area, full of pieces of *P. clarkii* exoskeleton. Credit A. J. Green.

Fresh samples of *L. fuscus* excreta (with a characteristic shiny appearance before air drying begins) were collected from large, monospecific flocks that were flushed while resting on the dykes separating individual fields. Samples were taken from points separated by >1 m and were likely to be from distinct individuals. Excreta were carefully inspected, removing any soil or gravel from the sample with tweezers or a knife before placement in a plastic zip-bag and storage at 4°C for up to 3 weeks until processing. Prior to processing, once removed from the fridge, each sample was again checked under the microscope to remove any seeds or eggs on the outside that potentially had stuck on from soil or via wind).

2.3.2. Sample processing

Within 2 days, the contents of the plastic jars where crayfish had been washed were sieved through a 100 µm sieve and inspected in petri dishes under a stereomicroscope, to search for plant diaspores (angiosperm seeds and charophyte oogonia) and invertebrates or their eggs. Gull samples were weighed then processed in a similar way, washing them on the sieve with deionized water. The mass of freshly collected *L. fuscus* faecal samples (n = 76) was 1.8 g ± 0.30 (mean ± s.e., range 0.21-6.67 g) and the mass of regurgitated pellets (n = 14) was 6.9 g ± 1.34 (range 3.82

– 12.79g). The frozen crayfish were defrosted and dissected, inspecting the contents of the whole digestive system under the stereomicroscope coupled with a digital camera.

Intact propagules were collected and counted. Propagules were photographed and measured via Axiovision software, then stored within a fridge (4°C) in Eppendorf® tubes filled with deionized water. For seed identification we inspected shape, size and seed coat pattern and compared these traits with available literature (CAPPERS *et al.*, 2012; BOJNANSKÝ & FARGAŠOVÁ, 2007; TALAVERA & CASTROVIEJO, 1999; BENEDÍ & ORELL, 1992). For seeds whose identification was problematic, we compared them with token specimens held within the University of Seville Herbarium. Intact diaspores were later placed in petri dishes with moistened filter paper in germination chambers set at 12 h of light at 24 °C and 12h of darkness at 18 °C. Germination tests were run for 3 months, checking every day for new germinants, which we counted and removed from the petri-dishes.

Live invertebrates and eggs found in the samples obtained from washed crayfish were placed directly into 90% ethanol for later identification. Bryozoans were identified in Sevilla after WOOD & OKAMURA (2005). Any remaining invertebrates and their eggs were sent to Valencia, where identifications were made following ALONSO (1996), DUSSART (1967), EINSLE (1993), HART & HART (1974), MEISCH (2000) and KARANOVIC (2012). Invertebrate eggs extracted from the excreta of gulls were then introduced in a 50 ml polypropylene aquarium with 40 ml of commercial mineral water (Cortes™) with the aim of stimulating hatching. Aquaria were placed in a culture chamber for one month at a constant temperature of 20ºC and a 12 h light: 12 h dark photoperiod.

2.3.3. Statistical analysis

Total numbers of propagules were compared between sample types (i.e. crayfish, faeces or pellets) using generalized linear models (GLMs), with a negative binomial error distribution using the glm.nb function in the MASS package (VENABLES & RIPLEY, 2002) for the R stats package (version 3.3.2; R CORE TEAM 2016). Sample type and sample year were fitted as categorical variables, and sample mass (log transformed) was included as a continous variable when comparing pellets with faeces (mass data were not available for mud washed from crayfish). At the level of individual propagule taxa, we were unable to develop satisfactory GLMs due to the dominance of zero values in the data, and problems of model convergence and overdispersion. Because pellets were expected to contain larger items than faeces, we used a non-parametric Mann-Whitney test to compare the number of rice grains (including zero values) between pellet and faecal samples using R stats package. Rice grains were much larger than other propagules recorded (Table 5). The germinability of diaspores recovered from gull excreta and from crayfish was compared for the most abundant taxon (toadrush *Juncus bufonius*) with a Fisher exact test.

The structure of the communities of plant and animal propagules present in different sample groups (faeces, pellets or washed crayfish) and years were compared with Permanova (i.e., permutational MANOVA; ANDERSON, 2001) using the adonis function of vegan in R. Only samples for which at least one propagule was recorded were used for Permanova, and data were Hellinger-transformed (LEGENDRE & LEGENDRE, 2012). One sample (which contained only one species *Streptocephalus torvicornis*, not found in any other sample) was excluded from further analyses in Permanova and other multivariate tests (see below). When differences between groups (i.e. sample types) were observed in Permanova, we checked which taxa contributed most to those differences using SIMPER (similarity percentage; CLARKE, 1993, also implemented in vegan). Groups of samples were also analysed to test for multivariate homogeneity of group dispersions (ANDERSON, 2006), with the function betadisper in vegan. This test is a multivariate analogue to Levene's test, and is related to a comparison of the beta-diversity observed for each group of samples. Non-metric multidimensional scaling (NMDS) was used to obtain an ordination of the community composition for the same sets of samples used in Permanova. NMDS was carried out using the metaNMDS function in vegan, and the Bray-Curtis distance was applied to calculate the distance matrix.

3. RESULTS

3. 1. Endozoochory of aquatic ferns and angiosperms by mallards in central Europe

The mean mass of fresh faecal samples was 3.721 g ± 0.185 (mean ± s.e.). A total of 1327 intact diaspores were found from the 215 samples, belonging to 22 plant species, including 21 angiosperms and an aquatic fern (381 macrospores of *Salvinia natans*, Table 2). These taxa represent 15 families (Table 2), with five families of aquatic plants (including 3 submerged, 2 floating and 4 emergent taxa), and 10 families of terrestrial plants (13 taxa). Only four of these 22 taxa are recognized as having an "endozoochory syndrome" (Table 3).

Almost half the diaspores (47%) were retrieved from the two sets of samples from Lake Balaton, which included 484 seeds of common fig (*Ficus carica*, naturalized alien, UOTILA, 2011b, Table 2). Fig trees are very abundant around Lake Balaton and were present at the sampling sites (KIRÁLY *et al.*, 2008). The hackberry *Celtis occidentalis*, a park tree from North America that is a widespread naturalized alien in Hungary (UOTILA, 2011a, BARTHA *et al.*, 2015), was represented by one seed. All other plant taxa recorded were native to Hungary. Most plant taxa recorded were rare, with seven taxa represented by only one seed, and another four taxa recorded only in a single sample (Table 2). Overall, 33% of faecal samples contained at least one diaspore (Table 2).

Propagules of three plant species were recorded in more than five faecal samples: the alkali bulrush *Bolboschoenus maritimus*, the sago pondweed *Potamogeton pectinatus* and *Salvinia natans* (Table 2). Diaspore numbers of these three taxa differed significantly among the sampling sites (*B. maritimus* $\chi2 = 38.33$, df = 4, $P <0.0001$; *P. pectinatus* χ $2 = 10.59$, $P = 0.032$; *S. natans* χ $2 = 47.27$, $P < 0.0001$). For *B. maritimus*, significantly more diaspores were recorded at the Tihany Inner-Lake and at Balaton II than at the other three sampling sites (Table 2). Significantly more *P. pectinatus* seeds were recorded from the Tihany Inner Lake than at the Lake Tisza and at Balaton II sampling sites. We only found *S. natans* macrospores at the two neighbouring sites in the floodplain of the Tisza river, with significantly more diaspores than in the other sites (Table 2).

Table 2. 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
Betulaceae / 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
Cyperaceae / Cyperus fuscus[3]	-	-	-	-	-	-	-	-	-	20	3	16	166	1	166	186	4
Cyperaceae / Eleocharis palustris	-	-	-	13	1	13	-	-	-	-	-	-	-	-	-	13	1
Cyperaceae / Schoenoplectus lacustris	-	-	-	1	1	1	-	-	-	53	2	33	-	-	-	54	3
Cyperaceae / 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

Table 2. Continue

Plantaginaceae / Plantago major	-	-	-	-	-	-	-	-	-	-	-	-	9	1	9	9	1
Poaceae / Digitaria sanguinalis	-	-	-	-	-	-	1	1	1	-	-	-	-	-	-	1	1
Poaceae / 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
Potamogetonaceae / 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
	289	22	96	202	20	39	127	3	117	501	14	369	208	12	176	1327	71

[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 same genus were reported in *Anas* spp. diet by SOONS *et al.*, 2016.

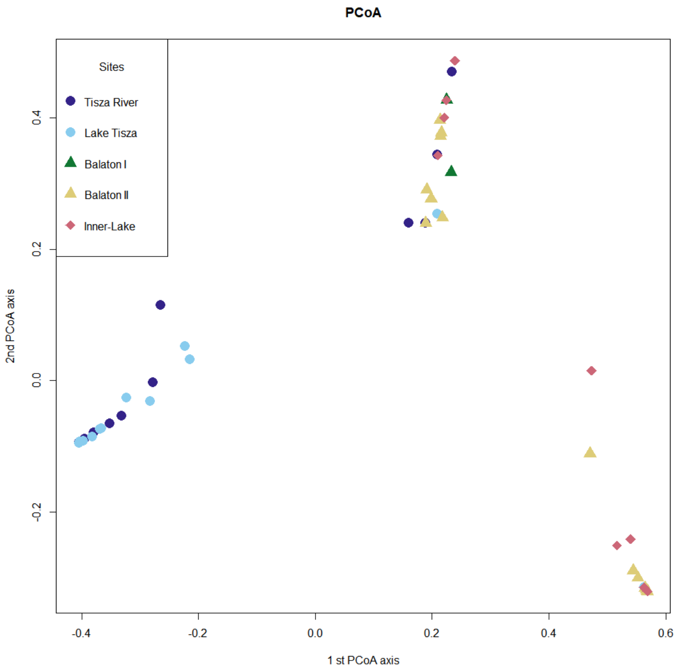

Fig. 6. Ordination based on a Principal Coordinates Analysis of plant communities among the five sample collection sites. The first two PCO axes are shown.

Table 3. 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

* 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 measurements.

According to PERMANOVA, the species compositional centroids differed significantly among sampling sites (df = 1, F= 18.381, P < 0.0001,

Fig. 6). The simper post-hoc test indicated that *Salvinia natans*, *Bolboschoenus maritimus*, *Ficus carica* and *Cyperus fuscus* were the taxa that made the highest contribution to the among-sites dissimilarities. The β-diversity of the propagules found in the samples differed significantly among the sampling sites, according to the results of betadisper (df = 4, F = 4.31, p = 0.0036). Tukey's HSD test showed significant β-diversity difference (P = 0.0034) between the Balaton II and Lake Tisza sites.

Out of the 22 species of plants recorded in the faecal samples, diaspores from nine taxa germinated. Overall, 4% of all diaspores germinated. Three taxa had particularly high viability (*Bolboschoenus maritimus* 25%, *Eleocharis palustris* 31% and *Ranunculus sceleratus* 25%, Table 3). Sixteen *Salvinia natans* macrospores germinated (4% of the total, Fig. 7). All taxa with over 20 diaspores detected in the faecal samples contained viable seeds (as shown by the germination tests), with the notable exception of *Ficus carica* represented by over 400 seeds in the samples (Table 3).

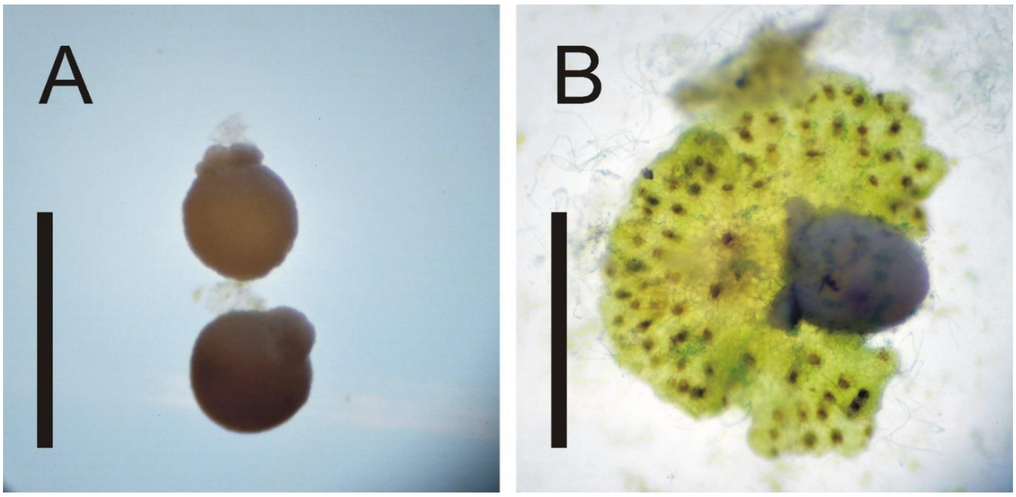

Fig. 7. Photos of *Salvinia natans* female gametophytes extracted from mallard faeces a) before germination and b) after germination, showing the archegonia (dark brown dots). The vertical bars represent one mm. Credit Á. Lovas-Kiss.

3.2. Great Cormorants reveal overlooked secondary dispersal of plants and invertebrates by piscivorous waterbirds

Forty-eight of 112 pellets (43%) contained at least one intact plant or invertebrate propagule (van Leeuwen *et al.*, 2017b). Broken propagules were found in a further eight pellets. Thirty-seven pellets (33%) contained ≥ one intact seed, and 22 pellets (20%) ≥ one intact invertebrate propagule. Seeds were found at six of seven locations, and invertebrate propagules at two locations (Table 4). Mean±SD pellet dry mass was 7.65±6.96 g (range 1.59–49.23 g, n=83).

Seventy-three intact diaspores were recovered from 16 families of angiosperms plus *Charophyceae*. Among intact seeds, we identified 21 taxa to species-level and three to family level (Table 4). Three plant families (*Adoxaceae*, *Fabaceae*, *Polygonaceae*) and the *Potamogeton*-genus were represented only by broken seeds. *Actinidia deliciosa* (Kiwi fruit) is alien to Europe, although common in gardens. Five of the 21 species are characteristic of wet or submerged habitats, five of moist to wet habitats and ten of dry to moist habitats. Dispersal syndromes varied, with only two species assigned to endozoochory compared to five for hydrochory and eight for barochory (unassisted, Table 4). Three of 54 unfrozen seeds (5.6%) germinated: one *Chenopodium glaucum*, one *Schoenoplectus tabernaemontanii* and one *Atriplex patula*.

We found 256 intact invertebrate propagules, including 186 gemmules of the sponge *Ephydatia fluviatilis* from one pellet. Seven different invertebrate taxa were found (from four families), a lower diversity than of plants (X2=74.9, df=1, P<0.001). One *Plumatella casmiana* statoblast was found in a Dutch pellet (probably alien for Europe, T. Wood pers. comm. 2017), and one *Plumatella repens* statoblast hatched.

Fish remains were found in 104 pellets, with a mean±SD of 1.5±1.2 fish taxa (range 0-4) and 10.9±12.8 individuals per pellet (range 0-51), of a mean length of 7.7±3.7 cm (range 3.2-41.3). Common taxa were European perch (*Perca fluviatilis*), Eurasian ruffe (*Gymnocephalus cernuus*) and common roach (*Rutilus rutilus*) (van Leeuwen *et al.*, 2017a; Table S3). Fish lengths varied between species and locations (van Leeuwen *et al.*, 2017a; Table S4).

Table 4. Intact plant seeds and invertebrates from cormorant pellets. Ellenberg F classes 4–6 as representing dry-to-moist, 7–9 moist-to-wet and 10–12 wet-or-submerged habitats [HILL *et al*., 1999]. Species are sorted by the number of recovered propagules, while indicating the number of pellets, viable propagules that germinated or hatched (per number tested). Sampling locations (Ringkøbing Fjord (RK), Roxen Lake (RL), Havsstensfjord Vadholmen (HV), Björningarna (B), North Mittholmarna (NM), South Mittholmarna (SM), Fortmond (F)). Assigned dispersal syndromes [JULVE, 1998]. Species indicated in bold are not known to be dispersed by European dabbling ducks [SOONS *et al*., 2016]. *Actinidia deliciosa* is alien to Europe, and therefore has no Ellenberg F-value.

Species / Family	**Ellenberg F**	**Dispersal syndrome**	**Number of intact propagules**	**Number of pellets**	**Number of germinated or hatched / tested**	**Sampling locations**
Unknown / Charophyceae			15	5	0/15	RK, F
Urtica dioica / Urticaceae	6	epizoochory	11	6	0/9	RL, F
***Schoenoplectus tabernaemontani* /** Cyperaceae	10	barochory	8	6	1/7	RK, RL
Betula pendula / Betulaceae	5	anemochory	5	5	-	RL, HV, B
Suaeda maritima / Amaranthaceae	8	hydrochory	5	5	0/4	B, F
Atriplex patula / Amaranthaceae	5	epizoochory	3	3	1/3	RK
***Limosella aquatica* /** Scrophulariaceae	8	barochory	3	2	0/3	F
Zannichellia palustris / Potamogetonaceae	12	hydrochory	3	1	0/3	F
Chenopodium glaucum / Amaranthaceae	6	barochory	4	3	1/4	RK
Potentilla anserina / Rosaceae	5	barochory	2	1	0/2	F
***Actinidia deliciosa* /** Actinidiaceae	ND	endozoochory	1	1	0/1	F
Alopecurus pratensis / Poaceae	5	barochory	1	1	-	RL
Carex nigra / Cyperaceae	8	hydrocory	1	1	0/1	F
***Cochlearia officinalis* /** Brassicaceae	6	barochory	1	1	-	SM
Eleocharis uniglumis / Cyperaceae	9	epizoochory	1	1	0/1	RK
Plantago major / Plantaginaceae	5	barochory	1	1	0/1	F

Table 4. Continue

Rubus fruticosus / Rosaceae	6	endozoochory	1	1	0/1	F
Ruppia cirrhosa / Ruppiaceae	12	hydrochory	1	1	-	NM, SM
***Sagina apetala* /** Caryophyllaceae	4	anemochory	1	1	-	B
***Salix triandra* /** Salicaceae	8	anemochory	1	1	0/1	F
Veronica beccabunga / Plantaginaceae	10	barochory	1	1	0/1	F
Zostera marina / Zosteraceae	12	hydrochory	1	1	-	B
unknown / Apiaceae			1	1	0/1	RK
unknown / Poaceae			1	1	-	RL
Ephydatia fluviatilis / Spongillidae			186	1	0/186	F
Daphnia pulex agg. (Group) / Daphniidae			24	7	0/23	RL, F
Cristatella mucedo / Cristatellidae			19	14	0/11	RL, F
Plumatella repens / Plumatellidae			12	6	1/11	RL,F
Plumatella fungosa / Plumatellidae			10	4	0/10	F
Plumatella emarginata / Plumatellidae			3	3	0/3	F
Plumatella casmiana / Plumatellidae			1	1	0/1	F

Fish, plant and invertebrate contents of pellets were partly interrelated (VAN LEEUWEN *et al*., 2017a; Table S5). Pellets with more fish held a higher diversity of invertebrates, and pellets with more invertebrate taxa held significantly more plant taxa. Fish species associated with multiple propagule species were Zander (*Sander lucioperca*) and bullhead (*Myoxocephalus scorpius*); five additional fish species were associated directly with one propagule species (Fig. 8, VAN LEEUWEN *et al*., 2017a; Table S6).

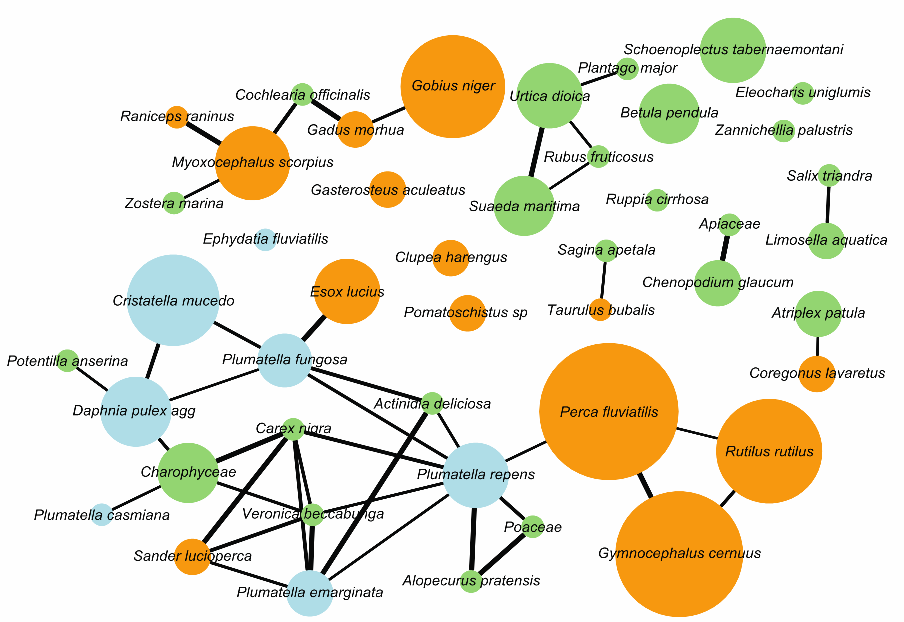

Fig. 8. Network visualization of pellet contents depicting fish (orange), plant (green) and invertebrate (blue) species in nodes whose size depicts their abundance on a log-scale. Connecting lines depict correlations among species; line width scales to ρ. Unconnected species have no significant associations.

3.3. Crayfish invasion facilitates dispersal of plants and invertebrates by gulls

The contents of pellets indicated the birds were feeding mainly on alien crayfish (*Procambarus clarkii*) and rice grains (*Oryza sativa*). Of 14 pellets examined, 13 were dominated by pieces of crayfish exoskeleton (Fig. 5).

In total 175 plant diaspores from 11 taxa (Table 5) were attached externally to crayfish (mean ± s.e. = 13.46 ± 5.89 per crayfish; median = 6.0) and were washed off together with the mud coating the exoskeleton (Fig. 1). Diaspores were dominated by *Juncaceae*, 56 % being *Juncus bufonius* and 14 % *J. subnodulosus*. Overall, 19 % of the diaspores germinated, representing seven taxa (Table 6). Upon dissection of the 13 crayfish, only broken seeds (2 fragments of *Juncus bufonius*, one each of *Cyperus difformis*, *Juncus* sp., and *Polypogon* sp.) were recovered from the stomach contents, and no diaspores were recorded in the intestines.

In total, 122 diaspores (mean ± s.e. = 1.61 ± 0.34 per sample; median = 1) were found in faecal samples and 49 (mean± s.e. = 3.50 ± 2.19; median = 0.5) in pellets (Table 5). These belonged to 11 plant taxa, but 63% of the diaspores were of *Juncus bufonius*. Pellets contained significantly more rice grains per sample than faeces (Mann-Whitney test, N = 76, 14, W = 602, pP = 0.013). However, in a GLM of the total number of diaspores per sample, there was a positive partial effect of sample mass (N = 90, z = 2.872, P = 0.004), but no significant difference between pellets and faeces (z = -0.861, P = 0.39) or between years (z = 0.301, P = 0.76). When this GLM was repeated after removing rice grains, the partial effect of sample mass was retained and there were significantly more other diaspores in faeces than in pellets (z = 4.136, P < 0.001).

Germination was recorded for six plant taxa with 23% germinability overall for diaspores from faeces and no germination for pellets (Table 6). Few *J. bufonius* seeds were recovered from pellets (Table 5), and although none germinated, the difference in germinability with those from faeces (18%) was not significant (Fisher Exact Test, P = 0.60).

Table 5. Details of intact plant diaspores found in gull excreta and on the outside of crayfish, including the number of samples in which each taxon was recorded, the total number of diaspores for each taxon, and the maximum number of diaspores recorded in a single sample. (NS = Number of samples containing the species, ND = number of diaspores in the samples, Max = maximum number of diaspores in any given sample)

Plants	Seed	Gull Faeces (n=76)			Gull Pellets (n=14)			Crayfish (n=13)		
Family / Species	Length (mm)	NS	ND	Max	NS	ND	Max	NS	ND	Max
Amaranthaceae / *Amaranthus retroflexus*†, ‡	1.09	1	2	2	1	2	2	1	1	1
Asteraceae / *Senecio vulgaris*‡	2.42	1	1	1	-	-	-	3	5	3
Asteraceae / *Unidentified*	0.78	-	-	-	-	-	-	2	2	1
Charophyceae / *Unidentified*	0.56	10	17	7	-	-	-	5	14	8
Cyperaceae / *Cyperus difformis*‡	0.62	1	1	1	-	-	-	5	9	3
Euphorbiaceae / *Chamaesyce humifusa*†	1.04	8	9	2	-	-	-	-	-	-
Juncaceae / *Juncus subnodulosus*	0.36	5	7	3	-	-	-	7	25	13
Juncaceae / *Juncus bufonius*‡	0.43	30	77	12	3	3	1	9	97	62
Poaceae / *Oryza sativa*	8.35	1	2	2	2	43	29	1	1	1
Poaceae / *Polypogon monspeliensis*‡	0.78	2	2	1	-	-	-	1	1	1
Polygonaceae / *Rumex dentatus*	2.4	1	1	1	-	-	-	-	-	-
Portulacaceae / *Portulaca oleracea*‡	0.68	-	-	-	-	-	-	3	3	1
Ranunculaceae / *Ranunculus sceleratus*‡	1.06	3	3	1	1	1	1	10	17	3
Total		42	122	33	7	49	33	13	175	97

† species alien to Spain, ‡species considered agricultural weeds according to Heap (2009) and Agroatlas (2005), http://agroatlas.ru.

Table 6. Germinations of plant diaspores found in gull faeces and on the outside of crayfish. No germination was recorded for diaspores from pellets.

Plant	Gull Faeces (n=76)		Crayfish (n=13)	
Family / Taxa	N Diaspores	N Germinated	N Diaspores	N Germinated
Amaranthaceae / *A. retroflexus*†, ‡	2	2	1	1
Asteraceae / *Senecio vulgaris*‡	1	-	5	4
Asteraceae / Unidentified	-	-	2	-
Charophyceae / Unidentified	17	2	14	1
Cyperaceae / *Cyperus difformis*‡	1	-	9	3
Euphorbiaceae / *Chamaesyce humifusa*†	9	5	-	-
Juncaceae / *Juncus subnodulosus*	7	-	25	2
Juncaceae / *Juncus bufonius*‡	77	17	97	23
Poaceae / *Oryza sativa*	2	-	1	-
Poaceae / *Polypogon monspeliensis*‡	2	-	1	-
Polygonaceae / *Rumex dentatus*	1	1	-	-
Portulacaceae / *P. oleracea*‡	-	-	3	-
Ranunculaceae / *R. sceleratus*‡	3	1	17	1
Total	122	28	175	35

† species alien to Spain, ‡species considered agricultural weeds according to Heap (2009) and Agroatlas (2005), http://agroatlas.ru.

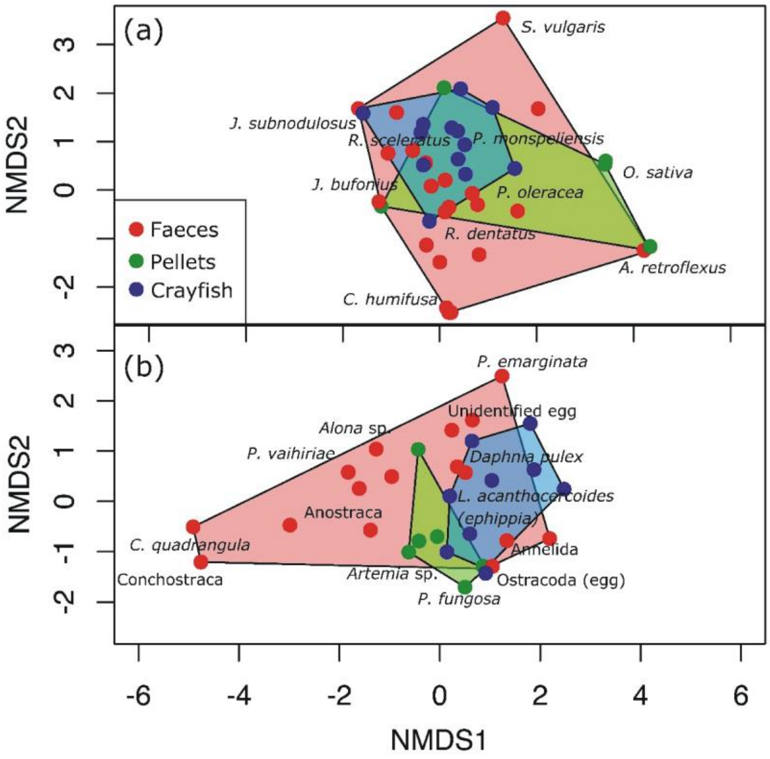

Fig. 9. Non-metric multidimensional scaling (NMDS) plot showing the relation between propagules from mud washed off crayfish, and from the pellets and faeces of *Larus fuscus*, a) for plant propagules, b) for invertebrate propagules.

There was a similarity in the observed species composition between the plant diaspores found on the outside of crayfish, and those found in gull excreta, especially in faeces (Table 5, Fig. 9a). Of 13 taxa recorded, nine were found in both crayfish and gull faeces, and *J. bufonius* was dominant in both. In a GLM comparing the total number of diaspores between sample types (including rice, without controlling for sample mass), there were significantly more diaspores in crayfish samples than both groups of gull excreta ($N = 103$, $z = 4.654$, $P < 0.001$) and more in pellets than faeces ($z = 2.123$, $P = 0.034$), whilst the year had no effect ($z = -1.140$, $P = 0.17$). When this analysis was repeated without rice grains, there remained significantly more diaspores on the crayfish than in excreta ($P < 0.001$), and there were now fewer diaspores in pellets than in faeces ($P = 0.03$). There was no difference in the germinability of *J.*

bufonius seeds recovered from gull faeces (18%) and from outside crayfish (22%, Fisher exact test, P = 0.58).

Table 7. Details of adult or juvenile living invertebrates recovered from the mud attached to the crayfish, including the number of samples in which each taxon was recorded, the total number of propagules for each taxon, and the maximum number of propagules recorded in a single sample. No living adults or juveniles were found in gull faeces or pellets.

	Invertebrate taxa	N samples with taxon	N taxon	Max per sample
Cladocera	*Macrothrix hirsuticornis*	4	4	1
	Alona affinis	1	1	1
	Leydigia acanthocercoides	2	7	6
	Tretocephala ambigua	1	1	1
Copepoda	*Eucyclops* sp. juveniles	3	12	10
	Eucyclops cf. *serrulatus*	12	97	40
	Onychocamptus mohammed	8	48	14
Ostracoda	*Ilyocypris* sp. juveniles	4	11	6
	Ilyocypris gibba	2	3	2
	Cyprididae juvenile	1	1	1
	Hemicypris reticulata†	1	2	2
	Ankylocythere sinuosa†	5	19	12
Nematoda	Unidentified	3	5	3
Total		13	213	100

† species alien to Spain

We found significant differences in the community composition of plant propagules between sample types (faeces, pellets or washed crayfish, N = 42, 7, 13 respectively, P = 0.001), and between sampling years (P = 0.015) when analysed with a Permanova, and these differences were not related to differences in multivariate dispersion, as there was a similar average distance to the median in both years (betadisper, P = 0.2) and the three types of samples (P = 0.6). The observed difference between years was due to changes in abundance for some species. In 2015 there were significantly more *R. sceleratus* and *J. subnodulosus* seeds than in 2014 (SIMPER, P < 0.001). Also, there were significantly more *J. bufonius* and *A. retroflexus* in faeces than in pellets, more *O. sativa* seeds in pellets (SIMPER, P < 0.05), and more *R. sceleratus* on crayfish than in gull excreta (SIMPER, P < 0.001).

Table 8. Details of intact invertebrate eggs recovered from gull excreta and from mud attached to crayfish, including the number of samples in which each taxon was recorded, the total number of propagules for each taxon, and the maximum number of propagules recorded in a single sample. (NS = Number of samples containing the species, NP = number of propagules in the samples, Max = maximum number of diaspores in any given sample)

		Gull Faeces (n=76)			Gull Pellet (n=14)			Crayfish (n=13)		
	Invertebrate taxa	NS	NP	Max	NS	NP	Max	NS	NP	Max
Anostraca	*Artemia* cf.‡	5	9	4	4	11	5	3	4	2
	Streptocephalus cf. *torvicornis*	1	1	1	-	-	-	-	-	-
	Unid. Anostracan egg	4	6	2	-	-	-	-	-	-
Cladocera	*Alona* sp.	8	8	1	1	1	1	1	1	1
	Daphnia (*Daphnia*) "*pulex* group"	-	-	-	-	-	-	3	6	3
	Leydigia acanthocercoides (ephippia)	-	-	-	-	-	-	5	11	7
	Moina sp.	7	8	2	1	2	2	2	3	2
	Ceriodaphnia cf. *quadrangula*	3	4	2	-	-	-	-	-	-
Conchostraca	*Triops* sp.	1	2	2	-	-	-	-	-	-
Ostracoda	Ostracoda	11	33	8	5	17	8	5	21	12
Bryozoa	*Plumatella emarginata*	-	-	-	2	2	1	2	4	3
	Plumatella fungosa	2	2	1	-	-	-	-	-	-
	Plumatella vaihiriae†	1	1	1	-	-	-	-	-	-
Annelida	Unidentified	7	22	8	-	-	-	-	-	-
Non. Det.	Unidentified eggs	-	-	-	-	-	-	2	4	2
Total		32	96	32	7	33	17	9	54	32

† species alien to Spain; ‡Morphologically these appear to be *Artemia*, but from the habitat this seems unlikely (due to low salinity), suggesting they are an unidentified Anostracan.

In total 213 living adult or juvenile invertebrates (mean ± s.e. = 16.23 ± 3.14 per crayfish; median = 18) from at least ten taxa were recorded in mud samples washed from crayfish (Table 7). The most abundant invertebrates were the *Copepoda*, but the most diverse groups were the *Cladocera* (four species) and *Ostracoda* (at least three species). A total of 54 invertebrate propagules were also recovered from external surfaces of crayfish (mean ± s.e.= 4.15 ± 2.07 per crayfish; median = 2), representing at least eight taxa (Table 8). The most abundant propagules were anostracan eggs, cladoceran ephippia and ostracod eggs, with smaller numbers of bryozoan statoblasts (Table 8). No invertebrate eggs were recovered in the digestive system of the crayfish.

In total, 96 invertebrate propagules were recovered from gull faeces (mean ± s.e. = 1.26 ± 0.31 per sample; median =0) and 33 (mean = 2.36 ± 0.83 per sample; median = 1) from pellets, representing 12 crustacean, bryozoan and annelid taxa, five of which were also recorded on crayfish (Table 8). The most abundant propagules were from *Anostraca*, *Annelida*, *Cladocera* and *Ostracoda*. Statoblasts of three *Plumatella* species (Bryozoa) were recorded, including *P. vaihiriae*, which is an alien species spreading across Europe (TATICCHI *et al*., 2008). In a GLM of the total number of invertebrate propagules per excreta sample, there was no significant partial effect of sample mass (N = 90, z = 1.210, P = 0.23), nor a difference between pellets and faeces (z = -0.624, P = 0.53), but there were significantly more propagules in 2015 (z = 2.50, P = 0.013).

Unlike crayfish samples, live adult or juvenile invertebrates were not recorded from gull excreta (Table 8). Indeed, we found differences in community composition between crayfish samples, pellets and faeces (N = 9, 7, 31 respectively, Permanova, P = 0.001), owing mainly to the abundance of adult or juvenile Eucyclops and Onychocamptus copepods on crayfish (SIMPER, P < 0.001), and the greater abundance of Artemia type eggs (SIMPER, P < 0.01) and ostracod eggs (P < 0.05) in pellets (Table 8, Fig. 9b). These differences in community composition were also related to significantly wider multivariate dispersion (betadisper, P = 0.002) in faeces (average distance to median = 0.61) compared to pellets (average distance = 0.43) and crayfish (average distance = 0.47), as the former contained a wider array of taxa (Table 8, Fig. 9b).

4. DISCUSSION

4.1. Endozoochory of aquatic ferns and angiosperms by mallards in central Europe

We have demonstrated endozoochory for aquatic ferns and a range of angiosperm taxa by migratory waterfowl in central Europe, and the germinability of all abundant taxa apart from cultivated figs. Although we do not know the distance involved, the diaspores were undoubtedly moved by the mallards between ingestion at feeding sites and egestion at the roost sites sampled (see KLEYHEEG *et al.*, 2017 for typical examples of daily movements for mallards not on migration). In terms of the number of faecal samples processed and the diversity and level of identification of intact diaspores recorded, this study represents the most detailed field study of endozoochory by mallards to date (see GREEN *et al.*, 2016 for review). It is also the first to make a detailed comparison of the spatial variation in plants dispersed. Our results illustrate the importance of mallards as a vector of dispersal for widely distributed (e.g. *Polygonum aviculare*, *Cyperus fuscus*, BARTHA *et al.*, 2015) and rare (*Myriophyllum verticillatum*, BARTHA *et al.*, 2015) plant species, as well as naturalized aliens (*Celtis occidentalis*, UOTILA, 2011a). Another naturalized alien *Ficus carica* (UOTILA, 2011b) had the highest number of seeds in our study, but none germinated because this cultivar produces their fuits parthenocarpically and these have non-viable seeds in 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 *et al.*, 2004; BROCHET *et al.*, 2010c). 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 *et al.*, 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 *et al.*, 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 2). 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 3). 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. 10).

Only four plant species with a fleshy fruit were assigned to an endozoochory syndrome. The majority of taxa we recorded were terrestrial plants, supporting the findings of SOONS *et al.* (2016) in a meta-analysis of the diet of European dabbling ducks. Nevertheless, diaspores of aquatic taxa were generally more abundant, and all three taxa found in six or more samples were aquatic. Most (55%) of the plant taxa we recorded were only recorded in one or two samples. Thus, we would need to study many more samples to record all the plant taxa dispersed by mallards using our study sites, as indicated by rarefaction analyses of mallard gut contents at other European sites (SOONS *et al.*, 2016).

Fig. 10. Silver birch (*Betula pendula*) seeds concentrated on a lake shoreline where mallards were feeding. Credit A. J. Green.

At the level of individual plant taxa, significant differences in diaspore numbers did not fully coincide with the spatial divide between samplings from the Hevesi-holm and those from the Lake Balaton region further west. We even found significant differences in the frequency of *B. maritimus* between two samplings at Lake Balaton separated by 373 m and by three days. Patchy distribution of seeds in the environment and individual variation in feeding behaviour or movements of ducks (e.g. GREEN, 1998; KLEYHEEG *et al.*, 2017) can translate into important variation in dispersal processes at a fine scale. There was only a clear geographical separation for *S. natans*, which was restricted to the Hevesi-holm (Table 2). *Salvinia natans* is mainly found around the big rivers in Hungary, and is absent from the Lake Balaton area (BARTHA *et al.*, 2015). On the other hand, when the whole community of plant diaspores was analysed, there was a clear separation between the eastern and western sample sets (Fig. 6), which is likely to reflect important differences in the plant communities present in the two study regions. However, sampling in the Lake Balaton and Hevesi-holm regions was conducted a month apart, so the spatial differences observed may have been confounded with this temporal change.

Our finding of viable macrospores of the pteridophyte *Salvinia natans* is very important, as this represents the first demonstration of avian endozoochory of viable fern diaspores in the wild. Most fern diaspores are dispersed by wind, and a smaller fraction by water (SHARPE *et al.*, 2010). A few previous studies have demonstrated endozoochorous dispersal of ferns by other animals, including slugs and insects (BOCH *et al.*, 2013; BOCH *et al.*, 2016). Fern spores have been shown experimentally to remain viable after passage through the gut of large bats (SUGITA *et al.*, 2013). Dispersal of viable spores by endozoochory has also been demonstrated in the field for mice (AROSA *et al.*, 2010) and reindeer (BRÅTHEN *et al.*, 2007).

We have demonstrated the viability of fern diaspores after avian gut passage for one fern species, but there is evidence to suggest that birds are also vectors for other aquatic and terrestrial ferns. Extinct and extant birds have sometimes been reported to ingest fern sporangia or spores (JAMES & BURNEY, 1997; AROSA *et al.*, 2009; MEHLTRETER *et al.*, 2010). MALONE and PROCTOR (1965) did experimental feeding trails with mallards and four other waterbird species using the hairy waterclover *Marsilea vestita*, and recorded passage of intact sporocarps among all bird species. A *Marsilea* sporocarp was recorded from the gizzard of a killdeer (*Charadrius vociferus*) collected in Texas (DE VLAMING & PROCTOR, 1968). It has often been suggested that waterbirds can disperse the alien fern Azolla filiculoides (REYNOLDS & CUMMING, 2015), and there is experimental support for epizoochory over distances of a few metres (COUGHLAN *et al.*, 2017a). *Azolla filiculoides* megasporocarps were found in faecal samples of swans and coots in the field, but the viability of the spores was not established (GREEN *et al.*, 2008). Dispersal of ferns as nest material by hummingbirds has also been reported (OSORIO-ZUNIGA *et al.*, 2014).

Salvinia natans is a widespread Eurasiatic taxon, with the major populations in central and eastern Europe and Asia, extending to Southern Europe and Northern Africa (ALLEN, 2011). It is an alien species in Cuba and Jamaica (ALLEN, 2011), and the states of New York and Massachusetts (https://plants.usda.gov/). RIDLEY (1930) considered *S. natans* to be too large to be dispersed by birds via epizoochory, but speculated that "as the species often occur in isolated pools, it is probable that their spores are somehow transported by birds". Over 80 years later we have confirmed his suspicion.

In central Europe, *S. natans* produces male micro- and female macrospores within sporocarps from late August to late September, with the release of sporocarps into the water beginning in late September (GAŁKA & SZMEJA, 2013). When not eaten by birds, the sporocarps eventually sink to the bottom of the water column, and during winter the sporocarp walls disintegrate within the sediments. In April, the spores rise up to the water surface and begin to form gametophytes. In late April, the female gametophyte develops archegonia and the male gametophyte develops the antheridia. After fertilisation occurs, the zygote forms and produces the sporophyte (GAŁKA & SZMEJA 2013). When placed for germination, the macrospores we extracted from faeces initially sank to the bottom of our tissue plates, but most floated to the surface after germination. Our laboratory conditions are likely to have accelerated their germination. After surviving gut passage in nature, it is possible that the macrospores delay germination until spring when day length and temperatures increase. When plants germinate sooner because of gut passage, there can be benefits from reduced intraspecific competition, or costs from increased exposure to herbivory (FIGUEROLA & GREEN, 2004). In our faecal samples, we found only female macrospores, which produced gametophytes with archegonia (Fig. 7). We recorded none of the male microspores that *S. natans* also produces, probably because the microspores are less than 20 µm in diameter (LAWALRÉE, 1964) and passed through our sieve. It is likely that microspores are also dispersed by mallards when they ingest sporocarps. We found no intact sporocarps in the faeces, and they are likely to have been broken within the gizzard.

In conclusion, this study illustrates how much our understanding of plant dispersal can be advanced by focused research on migratory waterfowl as vectors. We can now construct effective spatial models on the dispersal of plants by waterfowl (VIANA *et al*., 2016, KLEYHEEG *et al*., 2017), but we still have very limited information as to which plants are dispersed by which waterbird species. Endozoochory in nature goes well beyond the “endozoochory syndrome”, so we cannot simply rely on syndromes if we wish to predict how plants can disperse and these mechanisms relate to plant distributions. Our study provides a unique insight into the networks of dispersal interactions between waterbirds and plants, and the extent of spatial variation that exists in these networks. However, it focuses on the mallard as a particularly abundant and widespread vector, and future work must compare the plants dispersed by other duck and waterbird species in an equally comprehensive manner so that plant-vector networks can be fully characterized, and we can begin to understand the extent of functional redundancy between vectors.

4.2. Great Cormorants reveal overlooked secondary dispersal of plants and invertebrates by piscivorous waterbirds

This is the first quantitative field study of dispersal of plants and invertebrates by piscivorous birds. Great cormorants regurgitate pellets containing intact propagules previously ingested by fish prey. Pellets contained seeds of terrestrial, freshwater and marine plant species, indicating potential secondary dispersal for species with a range of habitat requirements. Terrestrial seeds are often blown or washed into the water and ingested (like aquatic seeds) by fish, followed by avian secondary dispersal. We confirmed the viability of seeds of three plant species and one bryozoan statoblast, and many of the other taxa we recorded are already known to survive passage through the guts of waterfowl (VAN LEEUWEN *et al*., 2012). Our first exploration of species interactions (Fig. 8) suggests secondary dispersal may connect aquatic and terrestrial environments, e.g. associations of Atlantic cod *Gadus morhua* with *Brassicaceae* and longspined bullhead *Taurulus bubalis* with *Caryophyllaceae*.

Among prerequisites for effective secondary dispersal are that (1) birds reach a new suitable location before egestion, and (2) propagules can establish in a suitable microhabitat. Both aspects depend on bird behaviour. Many cormorants roost in trees partially overhanging the water and partially above land, providing opportunities for both aquatic and terrestrial plants to reach suitable microhabitats. Cormorants may also provide germinating plants with nutrient-rich guano (KOLB *et al*., 2010). Great cormorants often travel up to 45 km between roosting and foraging locations, with occasional movements >200 km (WRIGHT, 2003). Tags inserted in fish have been retrieved >39 km from tagging locations (WRIGHT, 2003), and >10 km in one of our study locations (Lake Roxen). Dispersal over several tens of kilometres is therefore possible throughout the annual cycle, and perhaps much further during migrations.

Our results raise key questions for future research, including (1) possible overlap of secondary dispersal with primary dispersal by other vectors, e.g. ducks. We found six plants in cormorant pellets not recorded from the diet of European dabbling ducks (Table 4), and reported bird-mediated dispersal of freshwater sponges for the first time. Detailed comparisons between primary and secondary dispersal by different avian vectors are needed. (2) The importance of secondary dispersal relative to other vectors, and how its importance varies with colony size, over seasons and between individual birds. This study found considerable spatial and temporal variability in pellet content, which deserves more detailed investigations. (3) Germinability of unfrozen seeds was low compared with studies on omnivorous waterbirds; possibly because passing two digestive systems severely impacts viability. Future research should extract propagules quickly from piscivore excreta, and study effects of double gut passage on viability. (4) We found secondary dispersal of alien species (Table 4), but further exploration is needed. (5) Associations among particular fish species, among propagule species and between fish and propagule species require more detailed inspections to unravel specific secondary dispersal pathways.

We conclude that piscivorous birds may be major dispersal vectors that require more scientific attention. Since most plants dispersed lack a fleshy fruit, they are assumed to rely on mechanisms with less potential for long-distance dispersal than endozoochory (Table 4). Secondary dispersal by piscivorous birds may play an important role in maintaining connectivity in meta-populations and between river catchments, and in the movement of plants and invertebrates in response to climate change.

4.3. Crayfish invasion facilitates dispersal of plants and invertebrates by gulls

We have shown *L. fuscus* may facilitate secondary-dispersal of plants and invertebrates, including agricultural weeds and exotic invertebrates (Tables 5, 7). Apart from the much larger rice grains ingested as food items, the propagules we detected are small and inconspicuous and likely to be overlooked in conventional studies of avian diet. With the exception of adult and juvenile invertebrates, the propagules recorded in gull excreta and on crayfish are from similar taxa and often in similar proportions. Where differences were observed in community composition (e.g. Fig. 9b), this is likely to be explained by the greater sampling effort for gull excreta, which detected propagules from a greater number of invertebrate taxa. Our results suggest most of the propagules dispersed by gulls are ingested inadvertently when feeding on crayfish. This constitutes secondary dispersal, since the crayfish themselves were dispersing these propagules within mud adhering to their exoskeleton while moving within the ricefields. The daily movements of the gulls between fields (BOUTEN *et al.*, 2013) are likely to greatly facilitate the spread of propagules across the 37,000 ha of ricefields in the Doñana area. Most of the propagules recorded in gull excreta will readily survive in the moist or dry fields until conditions become suitable for growth. For aquatic species, this will be after the reflooding and sowing of fields with rice in May. Many of the plants are more terrestrial, e.g. *A. retroflexus* or *S. vulgaris*, and can complete their life cycle before May.

On extreme occasions, *P. clarkii* have been known to disperse up to 4 km on land in one day, but they usually move <10 m per day (*ANAS*TACIO *et al*., 2015). Over time, short distance dispersal (SDD) may lead to range extension through multiple SDD events (COUGHLAN *et al*., 2017c). Nevertheless, secondary dispersal by gulls will greatly increase the overall dispersal distance for most taxa whose propagules become attached to crayfish. Many of the taxa identified in gull excreta have not previously been recognized to have a capacity for avian zoochory. *Larus fuscus* has an increasing population of around 600,000 birds in western Europe and west Africa (WETLANDS INTERNATIONAL, 2017). Therefore, given their regular movements within and beyond southern Spain (BOUTEN *et al*., 2013, SHAMOUN-BARANES *et al*., 2017), *L. fuscus* may facilitate LDD of plants and invertebrates, enabling their rapid spread over broad areas. Tracking of individual gulls shows they move between Doñana ricefields and other Andalusian wetlands including Doñana fish ponds and natural closed-basin lakes such as Fuente de Piedra in Malaga (see BOUTEN *et al*. 2013).

Most of the plants we recorded are agricultural weeds, and many of them are aliens (Table 5). Earlier studies have shown gulls to be vectors of other alien plants and weeds (GREEN, 2016), although such dispersal has not previously been linked to predation on other seed vectors such as crayfish. In the plant trait database Baseflore (JULVE, 1998), only 4 of the 11 plant taxa found in gull excreta are considered to have zoochory dispersal syndromes (i.e. to be animal-dispersed), and none of them are assigned to the endozoochory syndrome because they all lack a fleshy fruit. The most abundant plant we recorded, *Juncus bufonius*, is assigned to the epizoochory syndrome, and DARWIN (1872) germinated a seed removed from mud attached to the leg of a woodcock *Scolopax rusticola*. In particular, *J. bufonius* can be a highly abundant weed in agricultural fields sown with different crops across Europe (DEVLAEMINCK *et al*., 2005), and when dispersed by birds it is often likely to be moved to suitable habitat.

Given the large number of *L. fuscus* present, and the high proportion of plant taxa recorded in small numbers (Table 5), it is likely that many other plant species are dispersed by gulls in Doñana ricefields (e.g. other ricefield weeds found in Spain, KRAEHMER *et al*., 2016). On the other hand, *L. fuscus* is unlikely to be the only avian vector for the plant species we recorded. Other waterbirds feeding on crayfish in ricefields (TABLADO *et al*., 2010) are likely to disperse these plant species, and a recent review of dabbling duck diet recorded four of the 11 species (SOONS *et al*., 2016). Moreover, the migration routes of *L. fuscus* and other waterbirds feeding on crayfish in Spain (e.g. white stork *Ciconia ciconia*) extend into Africa (SHAMOUN-BARANES *et al*., 2017; ROTICS *et al*., 2017). Accordingly, there is a potential for LDD of plants and invertebrates between continents.

European ricefields are affected by many weed species, some of which are alien species (VASCONCELOS *et al*., 1999). All seven of the agricultural weeds we recorded (Table 5) are already known to have herbicide resistant populations (HEAP, 2009). Herbicide resistant weeds reduce crop production and increase herbicide costs (POWLES & YU, 2010), and LDD of herbicide-resistant genotypes via waterbirds is likely to exacerbate these problems (FARMER *et al*., 2017). Furthermore, two of the plants recorded are alien to Europe (Table 5), and others are important aliens in other continents (BENEDÍ & ORELL, 1992; PYŠEK *et al*., 2009). Migratory ducks have previously been found to act as primary dispersal vectors for alien plants and weed species in ricefields in France and the USA (POWERS *et al*., 1978; BROCHET *et al*., 2010b).

We found that the largest seeds (rice grains) are more likely to be egested in pellets, as consistent with size selective treatment of food items in other waterbirds producing pellets (SÁNCHEZ *et al*., 2005). We germinated seeds recovered from gull excreta for all species (except rice) for which more than seven seeds were recovered (Table 6). This suggests that, as for *Anatidae* (GREEN *et al*., 2016), small seeds from any plant taxon are likely to survive passage through the alimentary canal of gulls. Moreover, a study examining endozoochory by yellow-legged gull *L. michahellis* suggests that seeds egested in faeces are retained in the gut for longer (median 14 h for glass beads) than those in pellets (median 5 h; NOGALES *et al*., 2001). Faeces are also produced at any time of the day in a range of habitats, whereas pellets are more likely to be produced at roost sites.

To our knowledge, this is the first study to report evidence of endozoochory of invertebrates by any gull species. Our observations of various microcrustacean groups and bryozoans in both dispersal vectors show that crayfish and gulls can increase propagule pressure of aquatic invertebrates at local scales, and also facilitate LDD. Our failure to hatch invertebrate propagules may be due to our protocol which involved storing eggs in water in one lab for several months before posting to a second lab for identification and hatching. When fresh waterbird excreta are placed rapidly for hatching, many invertebrate taxa hatch (FRISCH *et al*., 2007; BROCHET *et al*., 2010a; VALLS *et al*., 2017).

We recorded a variety of ostracods, cladocerans and copepods as adults or juveniles on the external surface of *P. clarkii*, which is likely to be an important dispersal vector at a local scale (RAMALHO & ANASTÁCIO, 2015), and to enable the survival of microcrustaceans moved to water (e.g. to drainage canals) on crayfish when they would otherwise die when the ricefields are dried out. Ostracods recorded included the entocytherid *Ankylocythere sinuosa*, an alien of American origin which is commensal on *P. clarkii* in Europe (AGUILAR-ALBEROLA *et al.*, 2012), and the cypridid *Hemicypris reticulata* (KLIE, 1930), which has not previously been recorded in Europe. This latter species has been found in various biogeographical regions (including the Neotropical, Oriental and Paleotropical), usually in ricefields (SAVATENALINTON & MARTENS, 2008; MARTENS *et al.*, 2013). It has been recorded in North Africa, which shares migratory waterbirds with our study area (RENDÓN *et al.*, 2008). It is possible that *H. reticulata* is native to southern Spain but has been overlooked until now; however its wide distribution and the common occurrence of exotic ostracods in ricefields (VALLS *et al.*, 2014) suggest this is most probably a new alien which is potentially invasive in Europe. The abundance of ostracod eggs in gull excreta, plus previous evidence that ostracod eggs can survive gut passage by waterbirds (BROCHET *et al.*, 2010a; ROGERS, 2014; VALLS *et al.*, 2017), suggest that these ostracods are secondarily dispersed by *L. fuscus*. This is less clear in the case of the *A. sinuosa*, which is not known to produce diapausing eggs (MESTRE *et al.*, 2013). However, adult ostracods can also survive gut passage through waterbirds (GREEN *et al.*, 2013; ROGERS, 2014).

We recorded adults or ephippia of eight cladoceran taxa, including six species previously reported from the Doñana area (FAHD *et al.*, 2009) and which have an extensive geographical distribution. We also recorded anostracan eggs, which are known to be readily dispersed through the avian gut (ROGERS, 2014), and may also survive passage through the gut of crayfish (MOORE & FAUST, 1972). We found eggs of tadpole shrimps *Triops* in gull faeces, which is consistent with previous records of their dispersal on the outside of *P. clarkii* (PÉREZ-BOTE *et al.*, 2005), and with genetic evidence suggesting a major role for avian vectors for *Triops* (KORN *et al.*, 2010). In the case of copepods, we only recorded the presence of living animals on crayfish. However, we may have overlooked their small eggs in gull excreta. Equally, encysted adults may also be transported through the avian gut (FRISCH *et al.*, 2007). Both genera recorded (*Eucyclops* and *Onychocamptus*) are littoral/benthic and commonly associated with periphyton (DUSSART, 1967), which grows on the carapace of crayfish. This is the first time the harpacticoid *Onychocamptus mohammed* has been reported in the Doñaña region, but it has been previously reported from wetlands in Spain, Morocco and France (AGUESSE & MARAZANOF, 1965; ALFONSO & MIRACLE, 1990; DAKKI, 1997; MARTINOY *et al.*, 2006).

Plumatellid bryozoans are frequently recorded in waterbird excreta (BROCHET *et al.*, 2010a; GREEN *et al.*, 2013), but to our knowledge this is the first confirmation that birds are vectors for alien bryozoans such as *P. vaihiriae*, although this is considered likely for other aliens such as *Pectinatella magnifica* (BALOUNOVÁ et al., 2013). The ability of bryozoans to disperse by birds may increase the economic costs they impose through biofouling of pipes and pumps (MANT *et al.*, 2013). It is likely that the *Plumatella* statoblasts we recorded became stuck onto *P. clarkii* via mud. Although *P. repens* colonies have been reported growing directly on other alien crayfish in Europe (DURIS *et al.*, 2006), this has not been observed with *P. clarkii*.

Procambarus clarkii is now the world's most cosmopolitan freshwater crayfish, and its introduction has led to dramatic negative impacts on aquatic ecosystems, the plant and animal communities they contain, and the ecosystem services they provide (MCLAUGHLAN *et al.*, 2014; SOUTY-GROSSET *et al.*, 2016). We have shown that *P. clarkii* invasion also leads to novel dispersal pathways for plants and invertebrates through interactions with its predators. This represents an additional impact of this alien species on ecosystem services, which has not previously been recognized (MCLAUGHLAN *et al.*, 2014). Given that so many of the species dispersed by *L. fuscus* are agricultural weeds or alien invertebrates, this dispersal facilitation is often likely to represent an ecosystem disservice rather than a service. Furthermore, because gulls and other birds move regularly between ricefields and other wetlands, they are likely to disperse alien species into natural habitats, promoting the invasion of the latter by novel species. Novel habitats such as ricefields can thus have unexpected impacts on natural ecosystems as a consequence of such dispersal interactions. Other biological invasions have been shown to lead to novel dispersal interactions involving alien vectors and/or alien propagules, but our study reveals one of few known cases of secondary dispersal in which the primary vector is alien (HÄMÄLÄINEN *et al.*, 2017). To our knowledge, it also constitutes the first demonstration of secondary dispersal that involves epizoochory in the primary phase and endozoochory in the second.

This work illustrates how biological invasions can reshape dispersal interactions in an unforeseen way, creating new pathways with the potential to increase rates of SDD and LDD and the spread of both alien and native organisms, including herbicide resistant weeds. Further empirical research is vital to identify the taxa dispersed by migratory waterbirds such as gulls in both natural and artificial wetlands, since they cannot simply be predicted, e.g. from seed morphology. Once such dispersal interactions are identified, movement ecology approaches will allow us to quantify their implications for metacommunities, the connectivity between artificial and natural ecosystems, and the geographical range of vectored organisms.

SUMMARY – NEW SCIENTIFIC RESULTS

This dissertation focuses on the importance of migratory waterbirds as vectors of plant and invertebrate dispersal. This work contains three case studies from Europe that include primary and secondary dispersal. Each case demonstrates the lack of previous empirical field studies and how these systems are under-studied in various ways, demonstrating the importance of the further investigations.

- The first study (*Endozoochory of aquatic ferns and angiosperms by mallards in central Europe*) provides the first evidence of avian endozoochorous dispersal of ferns, which was previously assumed to occur, but never proven.
- Our work showed that dispersal events caused by migratory waterbirds vary spatially.
- Thirteen of them were terrestrial species and two were aliens to Hungary. We recorded eight plant taxa which were never previously reported as ingested by mallards.

- The second case study (*Great Cormorants reveal overlooked secondary dispersal of plants and invertebrates by piscivorous waterbirds*) presents one of the first field studies on propagule dispersal by a piscivorous waterbird, which was suggested to occur by Darwin.
- One-third of the samples contained at least one diaspore, covering terrestrial, marine and freshwater species. Twenty-one plant species were found overall in the samples, but only two of them had an "endozoochory dispersal syndrome".
- Seven invertebrate taxa were found, with invertebrate propagules in one-fifth of the pellets.

- In the third study (*Crayfish invasion facilitates dispersal of plants and invertebrates by gulls*) we investigated the dispersal of plants and invertebrates by a migratory waterbird feeding on the highly invasive red swamp crayfish *Procambarus clarkii* in European ricefields.
- We recorded more than eleven plant species and eight invertebrate taxa on the exoskeleton of the crayfish. Regurgitated pellets of the gull were mainly constituted by pieces of crayfish exoskeleton.
- Twelve plant species and twelve aquatic invertebrate taxa were recorded in the gull excreta. Diaspores of six plant species were

shown to be viable. We found strong similarity between the taxa whose propagules were recovered from the gull samples and from crayfish.

- Additionally, we recorded the presence of new alien species, like the *Plumatella vaihiriae* (Bryozoa) and *Hemicypris reticulata* (Ostracoda).

ÖSSZEFOGLALÁS – ÚJ TUDOMÁNYOS EREDMÉNYEK

Jelen értekezés a vándorló vízimadarak növények és gerinctelen állatok terjesztésében játszott szerepére hívja fel a figyelmet. A dolgozat három esettanulmányt tartalmaz Európából, amelyek az elsődleges és másodlagos terjesztést is bemutatják. A munka bemutatja, hogy eddig milyen kis számú terepi vizsgálatot végeztek a témában, illetve, hogy ezek a rendszerek minden tekintetben alulkutatottak; így demonstrálva a további vizsgálatok szükségességét.

- Az első tanulmány (*Endozoochory of aquatic ferns and angiosperms by mallards in central Europe*) során elsőként szolgáltattunk bizonyítékot arra a régi, de mindeddig nem igazolt feltételezésre, hogy a madarak képesek endozoochór módon harasztokat terjeszteni.
- Munkánk emellett bemutatta, hogy a vízimadarak által közvetített terjedési események térben eltérő mintázatot mutatnak.
- Összesen 22 növényfaj propagulumait mutattunk ki. Közülük tizenhárom volt szárazföldi faj és kettő behurcolt (idegenhonos). A mintákban megtalált propagulumok 9 faj esetében bizonyultak életképesnek. Továbbá nyolc olyan növényfajt találtunk, amelyek korábban nem volt kimutatva tőkés récék étrendjéből.

- A második tanulmány (*Great Cormorants reveal overlooked secondary dispersal of plants and invertebrates by piscivorous waterbirds*) egyike a korábban már Darwin által is feltételezett másodlagos propagulum-terjesztés első terepi vizsgálatainak.
- A minták egyharmada tartalmazott legalább egy diaspórát, amelyek tengeri és édesvízi fajokhoz tartoztak. Összesen huszonegy növényfajt tartalmaztak a minták, de ezek közül csak kettő rendelkezett „endozoochor terjedési szindrómával”.
- A minták ötöde tartalmazott gerinctelen petét, amelyek hét fajhoz tartoztak.

- A harmadik tanulmány (*Crayfish invasion facilitates dispersal of plants and invertebrates by gulls*) a kiemelkedően inváziós kaliforniai vörösrákot (*Procambarus clarkii)* fogyasztó vándorló vízimadarak által terjesztett növényeket és gerinctelen állatokat vizsgáltuk Európai rizsföldeken.
- A kaliforniai vörösrák példányainak kültakaróján tizenegy növény és nyolc gerinctelen állatfajt azonosítottunk. A sirály köpetei túlnyomórészt a rák vázát tartalmazták.

- Tizenkét növény és tizenkét vízigerinctelen fajt mutattunk ki a sirály köpet és ürülék mintáiból. Hat növény taxon diaspóráit találtuk életképesnek. Jelentős hasonlóságot találtunk a sirály ürülékmintáiban és a rákokról gyűjtött fajok összetételében.
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List of publications

List of core publications published in international journals

	IF(2016)	**SJR**
van Leeuwen, C. H., **Lovas-Kiss, Á.,** Ovegård, M. & Green, A. J. (2017): Great cormorants reveal overlooked secondary dispersal of plants and invertebrates by piscivorous waterbirds. –*Biology Letters* **13**(10): 20170406.	3.089	Q1
Lovas-Kiss Á., Vizi B., Vincze O., Molnár V. A., Green, A. J. (2018): Endozoochory of aquatic ferns and angiosperms by mallards in central Europe. – *Journal of Ecology* doi: 10.1111/1365-2745.12913	5.813	Q1
Lovas-Kiss Á., Sánchez M.I., Molnár V. A., Valls L., Armengol X., Mesquita-Joanes F. & Green A.J. (2018): Crayfish invasion facilitates dispersal of plants and invertebrates by gulls. – *Freshwater Biology* **63:** 392-404.	3.225	Q1

List of international publications related to the dissertation

	IF	**SJR**
Lovas-Kiss Á., Sonkoly J., Vincze O., Green A. J., Takács A., & Molnár V. A. (2015): Strong potential for endozoochory by waterfowl in a rare, ephemeral wetland plant species, *Astragalus contortuplicatus* (Fabaceae). – *Acta Societatis Botanicorum Poloniae* **84**(3): 321–326.	1.213	Q3
Wilkinson D. M., **Lovas-Kiss Á.,** Callaghan D. A., & Green A. J. (2017): Endozoochory of large bryophyte fragments by waterbirds. – *Cryptogamie, Bryologie* **38**(2): 223–228.	1.062*	Q1
Takács A., Molnár V. A., Horváth O., Sramkó G., Popiela A., Mesterházy A., **Lovas-Kiss Á.**, Green A. J., Löki V., Nagy T., Lukács, B. A. (2017): The rare aquatic angiosperm *Elatine gussonei* (Elatinaceae) is more widely distributed than previously thought.– *Aquatic Botany* **141**: 47–50.	1.714*	Q1

Bartel, R. D., Sheppard, J. L., **Lovas-Kiss, Á.**, Green, A. J. (2018). Endozoochory by mallards in New Zealand: what seeds are dispersed and how far? – *PeerJ* 6:e4811, doi:10.7717/peerj.4811	2.177*	Q1
Takács A., Molnár V. A., Lukács B. A, Nagy T., **Lovas-Kiss Á.**, Green A.J., Popiela A., Somlyay L. (2018). Resurrection and typification of Elatine campylosperma (Elatinaceae), a long-forgotten waterwort species. – *PeerJ* 6:e4913, doi: 10.7717/peerj.4913	2.177*	Q1

* IF (2016)

Popular scientific articles related to the dissertation (in Hungarian)

Lovas-Kiss Á., Fekete R. & Molnár V. A. (2014): A madarak növényi potyautasai. – *Madártávlat* 21(4): 24–25.

Lovas-Kiss Á., Vizi B. & Molnár V. A. (2018): Növényi potyautasok – Amikor a rucaöröm szárnyra kap. – *Élet és Tudomány* 73(5): 134–136.

List of other publications

List of international publications

	IF*	**SJR**
Löki V., Tökölyi J., Süveges K., **Lovas-Kiss Á.**, Hürkan K., Sramkó G. & Molnár V. A. (2015): The orchid flora of Turkish graveyards: a comprehensive field survey. – *Willdenowia* **45**(2): 231–243.	0.5	Q3
Molnár V., A., Sonkoly, J., **Lovas-Kiss, Á.**, Fekete, R., Takács, A., Somlyay, L. & Török, P. (2015): Seed of the threatened annual legume, *Astragalus contortuplicatus*, can survive over 130 years of dry storage. – *Preslia* **87**: 319–328.	2.711	Q1
Molnár V. A., Löki V., Máté A., Molnár A. Takács A., Nagy T., **Lovas-Kiss Á.**, Sramkó G. & Tökölyi J. (2017*c*): The occurrence of *Spiraea crenata* and other rare steppe plants in Pannonian graveyards. – *Biologia* **72**(5): 500–509.	0.759*	Q3
Molnár V. A., Mészáros A., Csathó A. I., Balogh G., Takács A., Löki V., **Lovas-Kiss Á.**, Tökölyi J. & Bauer N. (2018): Distribution and seed production of the rare, dry grassland specialist *Sternbergia colchiciflora* (Amaryllidaceae) in Pannonian cemeteries. – *Tuexenia* **38** (accepted for publication)	1.325*	Q3

List of articles published in Hungarian peer reviewed journals

SJR

Ljubka T., **Lovas-Kiss Á.**, Takács A. & Molnár V. (2014): *Epipactis albensis* (Orchidaceae) in Ukraine : New data on occurrence and ecology – *Acta Botanica Hungarica* **56** (3-4): 399–408. Q2

Takács A., Nagy T., Fekete R., **Lovas-Kiss Á.**, Ljubka T., Löki V., Lisztes-Szabó Zs. & Molnár V. A. (2014): A Debreceni Egyetem Herbáriuma (DE) I.: A „Soó Rezső Herbárium". – *Kitaibelia* **19**(1): 142–155.

Takács A., Nagy T., Sramkó G., **Lovas-Kiss Á.**, Süveges, K., Lukács B. A., Fekete R., Löki V., Malatinszky Á., E. Vojtkó A., Koscsó J., Pfliegler W. P., Nótári K. & Molnár V. A. (2016): Pótlások a Magyarország edényes növényfajainak elterjedési atlaszához I. *Kitaibelia* **21**(1): 101–115.

Lovas-Kiss Á., Löki V. & Molnár V. A. (2017): A csipkés gyöngyvessző (*Spiraea crenata* L.) újabb temetői előfordulása. – *Kitaibelia* **22**(2): 409–410.

Popular scientific article (in Hungarian)

Molnár V. A., **Lovas-Kiss Á.** & Süveges K. (2014): Orchideák – kultúrtájban. Madársisakok, nőszőfüvek és nyárültetvények. – *Élet és Tudomány* **69**(40): 1254–1256.