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Traits for transport: Alien wetland plants gain an advantage during endozoochorous seed dispersal by waterfowl

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Abstract

1. The expansion of alien plant species is of global concern, yet our understanding of their dispersal mechanisms is limited. Here we address the potential of alien plant seeds to disperse via ingestion, transport and egestion in waterfowl (endozoochory). Based on their general rapid expansions, we expected alien plant species to have several advantages for endozoochory compared to native plant species. We hypothesised that seeds of alien species would have higher passage rate, longer gut retention times, higher germinability after gut passage and shorter time-to-germination after egestion by waterfowl.
2. In order to test our hypotheses, we compared the endozoochorous dispersal ability of six pairs of congeneric alien and native wetland plant species in a feeding experiment with mallards (*Anas platyrhynchos*). We focused on differences in seed survival, gut retention time, germinability and time-to-germination. In the analyses we corrected for seed shape and volume as these seed traits are known to have important effects.
3. With gut passage, alien species had higher passage rates and germinated slower, whereas native species had shorter retention times and greater germinability. Controlling for seed traits did not alter these conclusions, but seed traits affected all aspects of the endozoochory process. This suggests that alien species may have particular traits correlated with a higher endozoochory potential. Among control seeds, alien seeds germinated faster and their germinability was higher than natives. Seed traits explained differences in germinability and time-to-germination in control seeds.
4. Seeds of alien plant species have traits that correlate with successful endozoochory. This may provide alien species with a competitive advantage over native plant species by ensuring higher endozoochory rates in new environments, potentially enabling their rapid expansions. Our study underlines the important role of seed traits in the endozoochory potential of alien and native plant species, notably through their influence on retention time and germination.

Ádám Lovas-Kiss and María J. Navarro-Ramos contributed equally.

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KEYWORDS

Anas platyrhynchos, endozoochory, plant–animal interactions, propagule pressure, seed dispersal, seed traits

1 | INTRODUCTION

Plant invasions contribute to the current biodiversity crisis via their effects on ecosystems and ecosystem services (Vilà et al., 2011; Vilà & Hulme, 2017). After initial introductions by human vectors, in order to become invasive alien, plant species must overcome geographical, environmental, reproductive and dispersal barriers (Blackburn et al., 2011; Richardson et al., 2000). A major scientific challenge is to understand what factors determine their further spread via natural vectors in the new environment. Therefore, previous work has sought to identify possible traits or trait syndromes associated with the competitive success of invasive alien species (Crawley et al., 1996; Pyšek & Richardson, 2008). Comparative studies have tried to explain the dispersal ability of native and alien species by focusing on variation in traits such as seed mass or seed size (van Kleunen et al., 2015). However, it remains difficult to estimate how these traits may affect long-distance dispersal (LDD) events (Nathan et al., 2008).

Range expansion of alien species can occur slowly and steadily via local dispersal mechanisms (e.g., wind, water), but also can occur in a stepwise manner by long-distance dispersal (LDD) mechanisms such as zoochory (Higgins & Richardson, 1999; Nathan et al., 2008). While invasive alien plants are generally believed to have better dispersal capacities than native plants, more systematic comparisons among native and alien species are required to understand how they use different dispersal mechanisms at different spatial scales (Flores-Moreno et al., 2013). Dispersal of diaspores by animals via gut passage (endozoochory) is particularly important for LDD (Bullock et al., 2017), yet has been understudied for plants lacking a fleshy fruit (i.e., non-classical endozoochory, see Green et al., 2019; Green et al., 2022).

Migratory waterbirds play a key role in the spread of alien plant species (Green, 2016; Green et al., 2023). However, their role in LDD of alien plants via endozoochory has often been overlooked because of the shortcomings of the dispersal syndrome paradigm (Green et al., 2022). Therefore, there are major knowledge gaps in our understanding of alien species LDD, and our knowledge is biased towards endozoochory by frugivorous vertebrates (van Leeuwen, 2018). Less attention has been paid to alien plants without fleshy fruits, and to non-frugivorous vertebrates (Green et al., 2022).

Wetlands can harbour many highly invasive plant species (Zedler & Kercher, 2004), which can be transported by a diversity of waterbirds including gulls (Lovas-Kiss et al., 2018; Martín-Vélez, van Leeuwen et al., 2021), cormorants (van Leeuwen et al., 2017), herons (Navarro-Ramos et al., 2021), geese (Hattermann et al., 2019), shorebirds (Lovas-Kiss et al., 2019) and especially dabbling ducks (Soons et al., 2016; Uryán et al., 2023; van Leeuwen et al., 2012). Passage through the avian gut has diverse effects on the physical

and physiological attributes of seeds, and seed survival during passage is influenced by traits such as shape, size, thickness of seed coat, and seed hardness (Costea et al., 2019; Lovas-Kiss et al., 2020; Traveset et al., 2007; van Leeuwen et al., 2023). These traits also influence gut retention time, which in turn can determine dispersal distance (Martín-Vélez, van Leeuwen et al., 2021). Despite the potential importance of endozoochory in plant invasions, there is a lack of experimental studies comparing the survival and germination of alien and native plants during endozoochory. For example, García-Álvarez et al. (2015) compared the dispersal ability of two alien and two native plant species in a feeding experiment using mallards (*Anas platyrhynchos*) and greylag geese (*Anser anser*), and no consistent differences were found between alien and native species. However, they did not incorporate seed traits into their analysis, and traits can help explain the variation between plant species in endozoochory rates, including components of ingestion, seed survival, retention times and germination capacity (Green et al., 2023; van Leeuwen et al., 2023).

Here, we compare the potential for endozoochory by waterfowl between closely related alien and native wetland plant species. Our aim was to investigate experimentally whether the endozoochory potential differed consistently across six genera of alien and native plant species. Based on their generally rapid expansions, we assumed better dispersal ability of alien species, possibly via selection for traits favouring spread. We hypothesised (H1) that alien plant species would have higher seed survival (i.e., passage rates), longer gut retention times, higher germinability and a shorter time-to-germination than native species; and (H2) that seed traits would partly explain these patterns.

2 | MATERIALS AND METHODS

2.1 | Plant species and seed traits

In order to investigate the dispersal differences between alien and native congeneric species, we conducted a feeding experiment. Twelve wetland plant species (six native, six aliens) were used for the experiments (Figure 1). The alien species were *Bidens frondosa*, *Cyperus difformis*, *Juncus tenuis*, *Lindernia dubia*, *Najas gracillima* and *Typha laxmanii*. All of these species also are considered invasive throughout their introduced ranges (see details of invasiveness in Appendix S1). We paired these with native European congeners *Bidens tripartita*, *Cyperus fuscus*, *Juncus compressus*, *Lindernia procumbens*, *Najas minor* and *Typha angustifolia*. These species cover six plant families. Trait differences between species are illustrated in Appendix S2. Except *Lindernia*, seeds from all of these genera are known to occur naturally in mallard diet (Soons et al., 2016). All seeds

FIGURE 1 Plant species and seeds used in the feeding experiment. Bars, 1 mm.

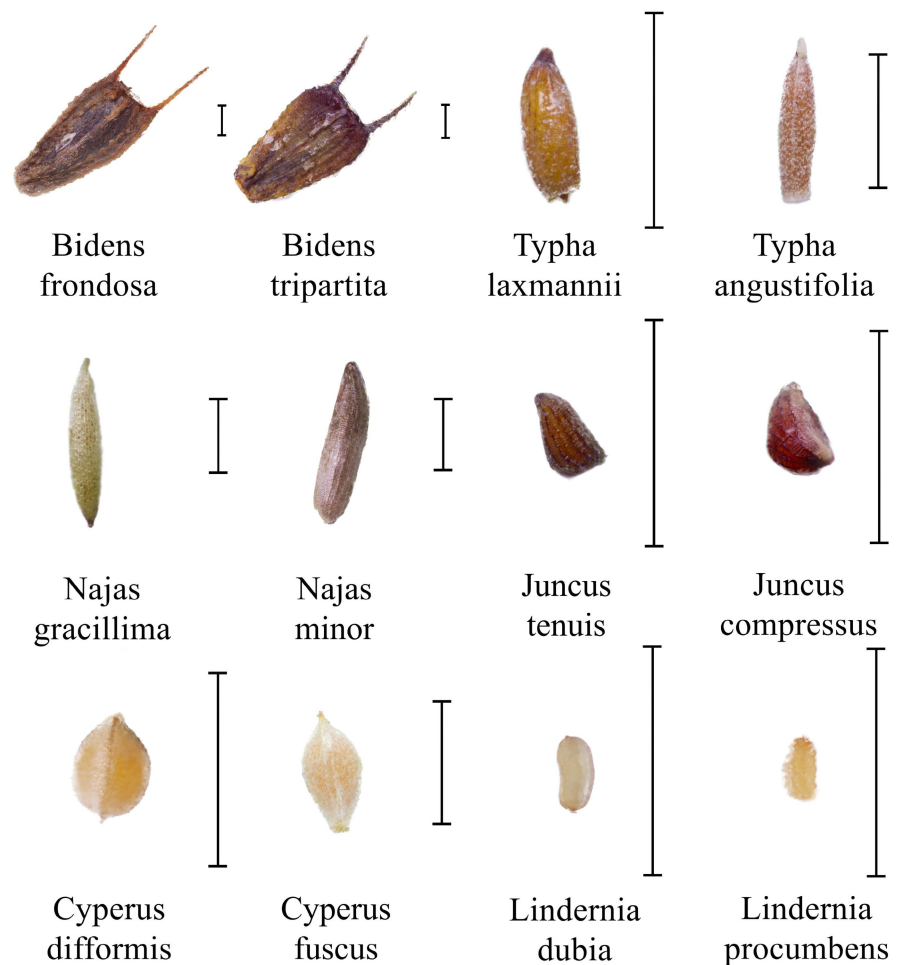


TABLE 1 Average seed traits of plant species included in the experiment.

		Volume (mm ³ ; mean ± SE)	Shape (mean ± SE)	Length (mm; mean ± SE)	Width (mm; mean ± SE)	Height (mm; mean ± SE)
<i>Bidens frondosa</i>	Alien	3.297 ± 0.307	0.109 ± 0.004	5.168 ± 0.352	1.859 ± 0.101	0.657 ± 0.029
<i>Bidens tripartita</i>	Native	4.352 ± 0.282 ^a	0.135 ± 0.005 ^a	4.207 ± 0.157 ^a	2.429 ± 0.075 ^a	0.817 ± 0.045 ^a
<i>Cyperus difformis</i>	Alien	0.024 ± 0.001	0.045 ± 0.002	0.531 ± 0.007	0.333 ± 0.006	0.266 ± 0.008
<i>Cyperus fuscus</i>	Native	0.044 ± 0.003 ^a	0.085 ± 0.004 ^a	0.812 ± 0.008 ^a	0.410 ± 0.007 ^a	0.252 ± 0.017 ^a
<i>Lindernia dubia</i>	Alien	0.003 ± 0.001	0.049 ± 0.004	0.312 ± 0.005	0.156 ± 0.007	0.138 ± 0.006
<i>Lindernia procumbens</i>	Native	0.005 ± 0.001 ^a	0.063 ± 0.005	0.324 ± 0.006	0.185 ± 0.007 ^a	0.164 ± 0.007 ^a
<i>Najas gracillima</i>	Alien	0.184 ± 0.007	0.134 ± 0.001	1.898 ± 0.026	0.437 ± 0.005	0.421 ± 0.008
<i>Najas minor</i>	Native	0.270 ± 0.012 ^a	0.133 ± 0.000	2.178 ± 0.036 ^a	0.501 ± 0.009 ^a	0.471 ± 0.008 ^a
<i>Juncus tenuis</i>	Alien	0.012 ± 0.001	0.036 ± 0.002	0.401 ± 0.003	0.248 ± 0.007	0.232 ± 0.006
<i>Juncus compressus</i>	Native	0.012 ± 0.001	0.046 ± 0.003 ^a	0.437 ± 0.011 ^a	0.246 ± 0.005	0.227 ± 0.004
<i>Typha laxmannii</i>	Alien	0.018 ± 0.001	0.128 ± 0.003	0.696 ± 0.016	0.228 ± 0.006	0.215 ± 0.004
<i>Typha angustifolia</i>	Native	0.033 ± 0.001 ^a	0.103 ± 0.003 ^a	1.041 ± 0.021 ^a	0.274 ± 0.005 ^a	0.223 ± 0.007

Note: Seed shape index can vary from 0 (perfect sphere) to 0.2 (slim disk or a thin needle).

^aSignificant differences between native and alien species within the genus (Student's *t*-test).

used here were collected in Hungarian wetlands during the summer before the experiments. The seeds were stored in the dark at 4°C for several months until experiments began. All species are considered to have physiological dormancy (Baskin & Baskin, 2014).

We measured three key seed traits for each species: seed width, height and length, and used these to calculate two additional traits used in subsequent analyses: seed volume and seed shape (Table 1). For each species, the width, height and length of 10 seeds were

measured with TCCAPTURE (version 5.1) software using a microscope (Lovas-Kiss et al., 2020). Seed shape was calculated following Bekker et al. (1998). Seed volume was calculated as the volume of an ellipsoid: $(4/3)\pi \times (\text{seed width}/2) \times (\text{height}/2) \times (\text{length}/2)$ (Chen & Moles, 2015). Differences in seed traits between native and alien species were investigated with Wilcoxon-paired tests.

2.2 | Experimental set-up

We used eight mallard individuals obtained from a local captive breeder, which had been fed freshly picked plants and mixed grains throughout their lives. All birds were born in captivity and were adults (c. 1.5 years, mean body mass $1.05 \text{ kg} \pm 0.19 \text{ SD}$). Before the experiment, they were housed communally in outdoor facilities and fed with mixed grains (corn, wheat and oat) and green plants (e.g., *Stellaria media*, *Taraxacum officinale*). Grit was freely available to the birds outside the experimental trials. The experiment had ethical approval from the scientific council of the Babeş-Bolyai University of Cluj Napoca (reference no. 14689/31.08.2018).

The experimental procedure was as follows. Each mallard was force-fed using a plastic cone to ensure that all seeds entered the oesophagus. This method eliminates seed handling by the birds in the bill, but this is unlikely to bias our results as waterfowl have soft bills that do not damage seeds (Gurd, 2007). We conducted three feeding trials on 1, 3 and 5 April 2019. We allowed 1 day (i.e., 24 hr) breaks between trials because during a longer break, the digestive tract of the birds might change, thus influencing the outcome of the experiment (Kleyheeg, Nolet et al., 2018). In each trial, 500 seeds of each of two plant species (counted under a stereomicroscope) were fed to each mallard individual (i.e., 1,000 seeds per mallard per trial). We randomised which plant species pair was fed to each mallard during each trial in order to minimise the effects of individual differences (Pollux, 2017), but never fed both species from the same genus together. This way, we ensured that no duck was fed with the same combination of species over the three trials, but also avoided the difficulty of separating similar looking congeneric seeds from the faeces. During 48 hr before the force-feeding, the mallards were kept individually in cages with mesh floors ($60 \times 40 \times 50 \text{ cm}$) equipped with bowls filled with water and mixed and minced grains (corn, wheat and oat), for the animals to feed and drink ad libitum. Plastic sheets and trays were placed underneath to recover faecal samples.

Faecal samples were collected in plastic bags from the trays at 1, 2, 4, 6, 8, 12 and 24 hr after seed ingestion; similar collection intervals were used in previous experiments (Kleyheeg, Claessens, & Soons, 2018; Lovas-Kiss et al., 2020). After collection, samples were placed in the fridge at 4°C until the separation of the seeds within 1–46 days. Samples were washed through a $100\text{-}\mu\text{m}$ sieve using deionised water, and seeds were separated under a stereomicroscope. Owing to its potential effect on seed viability, separation time (i.e., number of days passed between sample collection and processing) was recorded (Barnea et al., 1991). In order to minimise the effect of separation time, we aimed to keep differences within species pairs

to a minimum (Table 2). Intact seeds were immediately placed to germinate in covered Petri-dishes filled with moistened filter paper. For each plant species, 100 undigested seeds also were placed as controls in Petri-dishes under the same germination conditions at the same time as the last separated seeds. Petri dishes were kept at room temperature ($20\text{--}25^\circ\text{C}$) under a 16 hr:8 hr, light:dark photoperiod, illuminated with special horticultural lamps (Sylvania GRO-LUX F18W/GRO-T8). Each Petri-dish was monitored daily for 2 months and germinated seeds were removed to avoid repeated counting. Data were collected for each individual seed, resulting in a database of 24,000 entries for fed seeds and 1200 for control seeds.

2.3 | Statistical analyses

In order to test how seed passage (i.e. the proportion of seeds recovered after gut passage), germinability (i.e. the proportion of seeds that germinated), retention time (i.e., hours passed between seed ingestion and egestion) and time-to-germination (i.e., number of days until germination, log-transformed) differed between alien and native species, we constructed (Generalized) linear mixed models ([G]LMMs) with Poisson, Gaussian and Binomial error distributions. Because our study aimed to explicitly explore the role of origin (alien or native), we avoided model selection and we retained origin as a fixed explanatory variable in all models, whereas passage rate, retention time, germination rate and days until germination were used as dependent variables in the appropriate models (Table 3). For each dependent variable, we constructed two models: firstly, we constructed a model exploring the dependent variable in function of origin in a single fixed predictor model. Secondly, in order to test how seed traits explained potentially detected differences between alien and native species, we added seed traits as covariates to the previous model (Table 3). Models of germinability and time-to-germination also included separation time (i.e., days passed between faecal collection and seed separation) as a covariate owing to its potentially negatively effect on seed viability (Guttal et al., 2011; Martín-Vélez, Lovas-Kiss, et al., 2021).

For control seeds, models exploring germinability and time-to-germination also were run using identical model structures, but excluding separation time. Since separation time was non-existent for control seeds, but this variable is a key predictor of viability of passed seeds, we arbitrarily set separation time to the minimum value of any passed seeds (i.e., 1 day). Note that this model also excludes individual duck ID and experimental ID as potential confounding factors.

In all models, seed traits were log-transformed (using natural logarithm) to ensure model residual normality. Statistical significance of fixed terms in GLMMs was accepted if $|t| > 2.00$ (Crawley, 2007). All statistical analyses and graphical presentations were performed in the R statistical and programming environment, version 4.0.4 (R Core Team, 2021). All LMMs were run using R package *lme4* and functions “lmer” (for models with Gaussian error distributions) or “glmer” (for models with binomial/Poisson error distributions; Bates et al., 2015).

TABLE 2 Descriptive statistics of the experimental results for the number of passed seeds, number of seeds germinated, and time-to-germination according to native and alien congeneric species pairs.

Species pair	Seeds fed	Seeds passed	Passed seeds germinated	Control germinated seeds	Time to passed seeds germination (mean days ± SE)	Time to control seeds germination (mean days ± SE)	Retention time (mean hr ± SE)	Separation time (mean days ± SE)
<i>Bidens frondosa</i>	2000	19 (1%)	1 (2.9%)	0	2 ± NA	NA	1.2 ± 3.829	19.56 ± 2.795
<i>Bidens tripartita</i>	2000	16 (0.8%)	1 (9%)	2 (2%)	9 ± 2.449	37.52 ± 0.366	3.4 ± 0.871	19.607 ± 2.739
<i>Cyperus difformis</i>	2000	739 (37%)	281 (38%)	98 (98%)	13.078 ± 0.502	12.66 ± 0.533	8.5 ± 1.538	23.458 ± 3.170
<i>Cyperus fuscus</i>	2000	838 (42%)	303 (36%)	97 (97%)	4.815 ± 0.1799	11.59 ± 0.531	6.882 ± 1.311	20.444 ± 2.772
<i>Juncus tenuis</i>	2000	963 (48%)	152 (16%)	91 (91%)	35.117 ± 0.630	33.87 ± 1.128	6.882 ± 1.311	20.444 ± 2.772
<i>Juncus compressus</i>	2000	741 (37%)	165 (22%)	1 (1%)	32.203 ± 0.541	23.44 ± 0.446	8.166 ± 1.580	23.458 ± 3.170
<i>Lindernia dubia</i>	2000	604 (30%)	162 (27%)	63 (63%)	6.686 ± 0.435	21.61 ± 1.294	3.272 ± 0.540	10.037 ± 1.268
<i>Lindernia procumbens</i>	2000	590 (30%)	97 (16%)	14 (14%)	7.969 ± 0.552	6.33 ± 0.965	7.857 ± 1.459	10.8 ± 1.205
<i>Najas gracillima</i>	2000	750 (37%)	42 (6%)	11 (11%)	14.872 ± 1.720	34.09 ± 0.849	6.466 ± 1.469	10.8 ± 1.205
<i>Najas minor</i>	2000	579 (29%)	156 (27%)	10 (10%)	14.004 ± 1.042	34.32 ± 0.848	6.25 ± 1.874	10.037 ± 1.268
<i>Typha laxmanii</i>	2000	922 (46%)	328 (36%)	66 (66%)	7.205 ± 0.229	20.15 ± 1.320	5.888 ± 1.325	19.607 ± 2.739
<i>Typha angustifolia</i>	2000	736 (37%)	308 (42%)	63 (63%)	8.731 ± 0.455	20.83 ± 1.316	7.333 ± 1.797	19.56 ± 2.795
Total of	12,000	3997 (32%)	966 (24%)	329 (55%)	13.160 ± 0.352	24.476 ± 0.512	7.165 ± 0.834	18.621 ± 1.162
Total of	12,000	3500 (29%)	1030 (29%)	187 (31%)	12.787 ± 0.435	25.540 ± 0.373	6.645 ± 0.741	18.621 ± 1.162

Note: Separation time is the days passed between faecal collection and seed separation.

TABLE 3 List of dependent and explanatory variables, fixed predictors included in (Generalized) linear mixed models ([G]LMM) built to investigate the effect of origin (alien/native) on seed passage/survival, retention time (hr), seed germination rate and time-to-germination (days) for passed seeds and control seeds, respectively.

	Model name	Dependent variable	Explanatory variable	Predictors
Passage (<i>Binomial</i>) passed seeds only	Model for passed seeds without traits	Seed passage	Origin	Species pair + Experiment ID + Duck ID
	Model for passed seeds with traits	Seed passage	Origin	Species pair + Experiment ID + Duck ID + Seed volume + Seed shape
Retention time (<i>Poisson</i>) passed seeds only	Model for passed seeds without traits	Time to passage	Origin	Species pair + Experiment ID + Duck ID
	Model for passed seeds with traits	Time to passage	Origin	Species pair + Experiment ID + Duck ID + Seed volume + Seed shape
Germinability (<i>Binomial</i>)	Model for passed seeds without traits	Germinability	Origin	Species pair + Experiment ID + Duck ID + Separation day
	Model for passed seeds with traits	Germinability	Origin	Species pair + Experiment ID + Duck ID + Seed volume + Seed shape
Model for control seeds without traits	Model for control seeds without traits	Germinability	Origin	Species pair
	Model for control seeds with traits	Germinability	Origin	Species pair + Seed volume + Seed shape
Time-to-germination (<i>Gaussian</i>)	Model for passed seeds without traits	Number of days until germination	Origin	Species pair + Experiment ID + Duck ID + Separation day
	Model for passed seeds with traits	Number of days until germination	Origin	Species pair + Experiment ID + Duck ID + Separation day + Seed volume + Seed shape
Model for control seeds without traits	Model for control seeds without traits	Number of days until germination	Origin	Species pair
	Model for control seeds with traits	Number of days until germination	Origin	Species pair + Seed volume + Seed shape

3 | RESULTS

3.1 | Seed passage and retention time

Native taxa had significantly higher seed volume (Wilcoxon test, $Z=9.5$, $p<0.001$) and were more elongated (Wilcoxon test, $Z=9.5$, $p<0.001$). Seed passage (i.e., survival) was significantly lower for native species (Tables 2 and 4; Figure 2). For all species combined, 32% of the alien seeds passed the digestive tract of mallards intact, compared to 29% of native seeds, indicating a slightly higher probability of alien

plant seeds to survive (Table 4). However, effects were genera-specific as natives had higher passage rates in *Bidens* and *Najas* (Table 2).

Models that also included seed traits showed that neither seed volume nor seed shape influenced passage rate (Table 4). Consequently, the effect of seed origin remained significant after including seed traits in the model, indicating higher seed passage in alien compared to native plants (Table 4).

Mean retention time never exceeded 12hr (Table 2) and no seed from previous feeding trials was ever recorded in samples collected during subsequent trials (as would be expected if there were extreme retention

TABLE 4 Result of models exploring variation in passage rate, retention time, germinability and germination time.

	Estimates	SE	Z	Pr (> z)
Passage rate				
Intercept	-1.172/-0.205	0.659/0.882	-1.776/-0.233	0.075/0.702
Origin	-0.202/-0.320	0.031/0.070	-6.565/-4.548	<0.001/<0.001
Seed shape	0.225	0.155	1.455	0.146
Seed volume	0.103	0.111	0.934	0.350
Retention time				
Intercept	1.270/4.461	0.146/1.148	8.675/3.824	<0.001/<0.001
Origin	0.093/-0.457	0.012/0.028	7.435/-15.850	<0.001/<0.001
Seed shape	-0.025	0.047	-0.550	0.582
Seed volume	1.367	0.060	22.566	<0.001
Germinability of control seeds				
Intercept	0.371/6.220	1.199/2.145	0.309/2.634	0.757/0.008
Origin	-0.681/0.082	0.180/0.334	3.787/0.248	<0.001/0.804
Seed shape	4.170	0.821	5.077	<0.001
Seed volume	-2.017	0.609	-3.311	<0.001
Germinability of passed seeds				
Intercept	-0.698/-5.288	0.535/1.101	-1.302/-4.802	0.193/<0.001
Origin	0.571/1.356	0.059/0.139	9.530/9.747	<0.001/<0.001
Separation time	-0.918/-1.227	0.081/0.098	-11.335/-12.527	<0.001/<0.001
Seed shape	-1.081	0.328	-3.286	0.001
Seed volume	-0.568	0.209	-2.706	0.006
	Estimates	SE		t-value
Time-to-germination of control seeds				
Intercept	3.094/0.724	0.184/0.534		16.754/1.374
Origin	0.066/0.162	0.030/0.071		2.154/2.271
Seed shape	-1.211	0.162		-7.450
Seed volume	0.475	0.104		4.530
Time-to-germination of passed seeds				
Intercept	2.397/0.272	0.284/0.382		8.419/0.712
Origin	-0.395/-0.062	0.025/0.045		-15.687/-1.376
Separation time	-0.027/-0.072	0.031/0.028		-0.899/-2.564
Seed shape	-0.851	0.088		-9.625
Seed volume	0.030	0.074		0.413

Note: Some cells provide two values: effect of the particular predictor in the base model (without seed traits)/in the multivariate model (including seed traits). Positive slopes of origin indicate higher values in the dependent variable for native species. Higher values of seed shape indicate more elongated shape. In the case of models with Gaussian error distribution (i.e., time-to-germination) $|t| > 2.00$ indicates statistically significant effects. Significant effects also are marked in bold.

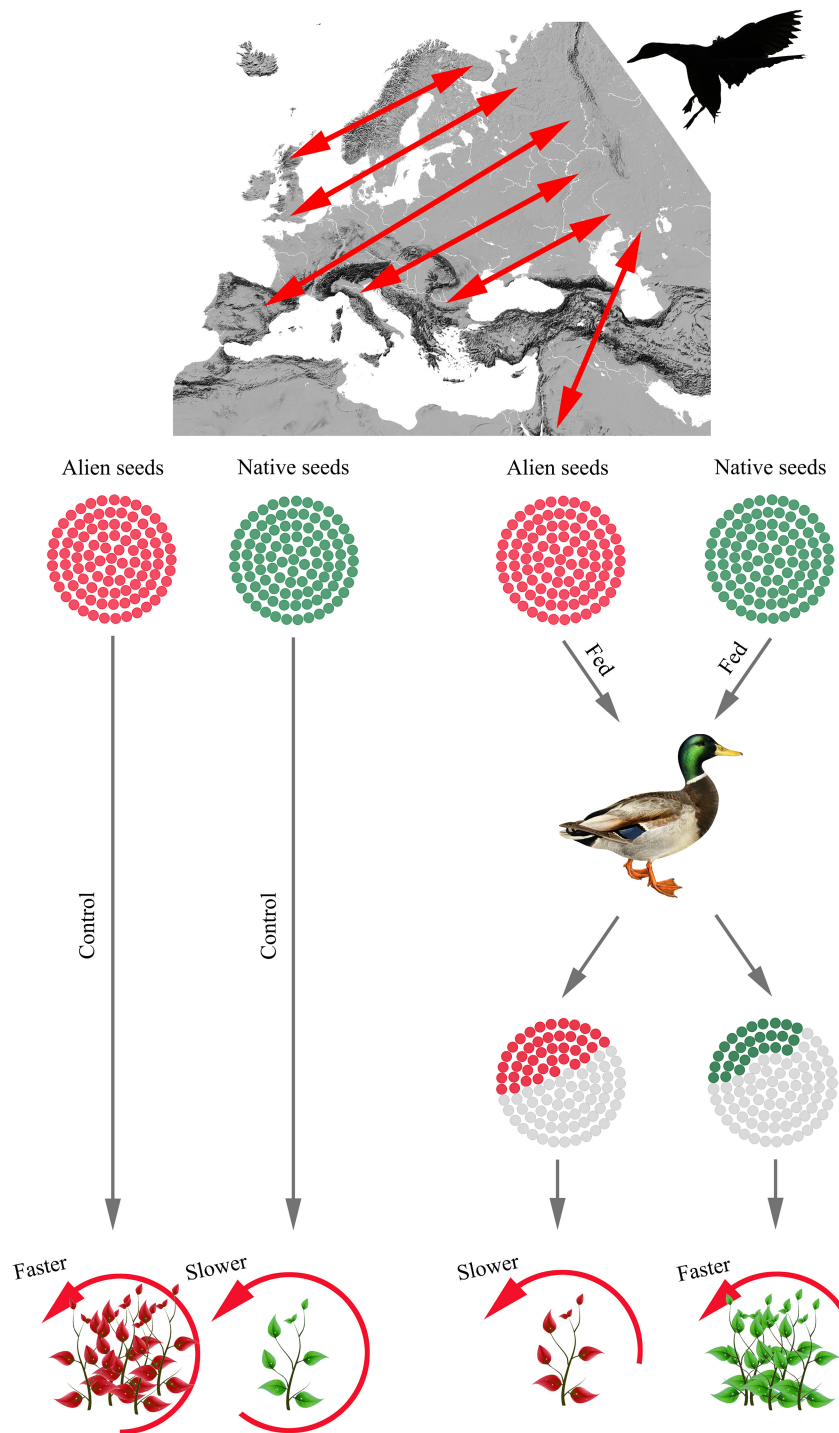


FIGURE 2 Schematic representation of the experiment and results. The map depicting movements of Mallard in Europe is based on published information and ring recoveries (following the map of Delany et al., 2006). Dotted clusters (top) illustrate alien (red) and native (green) seeds used in the experiment in control (left two clusters) and seeds fed to mallards (right two clusters). The graph shows seed survival during gut passage (bottom dotted clusters), germinability (leafy plants) and germination time (red arrows). Grey dots mark seeds lost during digestion; the number of leafy plants represents the differences in germinability. Alien seeds germinated faster than native seeds in both treatments. Length of the red arrows indicates the time elapsed to germination compared among treatments.

times exceeding 48hr). Native taxa had longer retention times (Table 4). After correcting for seed traits, the trend changed, indicating that native seeds had shorter retentions for a given volume than aliens. This model also indicated longer retention times for larger seeds (Table 4).

3.2 | Seed germinability

Mean separation time varied from 10.0 (*Lindernia dubia*) to 23.4 (*Juncus compressus* and *Cyperus difformis*) days. For genera, it

varied from 0.047 (*Bidens* and *Typha*) to 3.0 days (*Juncus* and *Cyperus*; Table 2). Control seeds of native species had significantly lower germinability than seeds of alien plants (Tables 2 and 4). By contrast, after gut passage, intact seeds of native plants had significantly higher germinability than seeds of alien plants (29% vs. 24% relative to passed seeds; and 8.5% vs. 8% relative to initial number ingested). Longer separation time significantly reduced germinability (Tables 2 and 4). After correcting for effects of seed traits, seed origin no longer explained differences in germinability of control seeds. For control seeds, germinability of smaller, elongated seeds was higher,

whereas germinability of seeds after gut passage was higher for smaller, rounder seeds (Tables 2 and 4). Hence, gut passage disproportionately reduced the germinability of more elongated seeds.

After gut passage, germinability remained significantly higher for native species when traits were included in the model, and separation time retained a significant negative effect (Table 4). Passed seeds germinated significantly more often than control seeds, regardless of whether seed traits were included in the model or not (Appendix S3).

3.3 | Time-to-germination

Among controls, native seeds needed significantly more days to germinate than alien ones, a result that remained consistent after including seed traits in the model (Tables 2 and 4, Appendix S4). Seed shape had a significant negative effect on germination time, indicating that elongated seeds germinate faster. Moreover, seed volume also had a significant positive effect on germination time, indicating that smaller seeds germinate faster.

For passed seeds, alien species needed significantly more time to germinate than natives (Tables 2 and 4; Appendix S4), suggesting that the observed difference is explained by differences in seed shape between alien and native species. Longer separation time decreased the time-to-germination, but this effect was identical between native and alien species (Table 4). Seed shape had a similar influence as for control seeds, with elongated seeds germinating faster after gut passage. When passed and control seeds were analysed together, passed seeds germinated later than control seeds, regardless of whether seed traits were included in the model or not (Appendix S3). However, upon conducting a separate analysis on each species of passed and control seeds, we found that four native species and three alien species germinated earlier after gut passage than in controls (Table 2).

4 | DISCUSSION

This experimental study showed that waterfowl can play an important role in dispersal of both native and alien plant species. Seeds of all native and alien plant taxa were retained for up to 24 hr in the digestive system of birds, and germinated after gut passage. However, we found strong effects of seed traits (shape, volume and other suggested traits) on all aspects of the endozoochory process. This suggests that alien species may have particular traits correlated with a higher endozoochory potential. Our experimental approach can be useful to identify which traits facilitate long-distance dispersal of alien species.

4.1 | Effect of passage rate

Seeds of alien plant species had a higher overall passage rate (i.e., survival) than native species. This might be explained by the smaller

and less elongated seeds of alien species, as seed size is a known determinant of gut passage (Lovas-Kiss et al., 2020). Greater passage rates suggests a higher propagule pressure for alien wetland plant species (Lockwood et al., 2005), which is a significant predictor of invasiveness because it increases the chances of establishing self-sustaining populations in new environments (Colautti et al., 2006; Lockwood et al., 2009). Previous studies have shown that plants with smaller and rounder seeds tend to have a higher survival rate in the digestive tracts of waterfowl than larger or more elongated seeds (Lovas-Kiss et al., 2020; Soons et al., 2008). However, even after statistically controlling for the effect of these traits, species origin (i.e., native or alien) remained significant. This suggests there may be additional seed traits that contribute to endozoochory dispersal potential and possible differences between alien and native species (e.g., seed hardness; Lovas-Kiss et al., 2020, van Leeuwen et al., 2023).

4.2 | Effect of gut passage on germinability

High germinability reflects seed vigour and viability (Jiménez-Alfaro et al., 2016), and positively affects species establishment, spread and impact (Colautti et al., 2006). Alien species often have a higher germinability than native species, and can germinate under broader environmental conditions (Gioria & Pyšek, 2017). In our experiment, passed seeds showed significantly higher germinability than control seeds, regardless of whether we controlled for traits or not (see Appendix S3). Likewise, we detected higher germinability of alien species compared to natives, but only among control seeds (Tables 2 and 4). These differences disappeared when we controlled for differences in seed traits, with smaller, more elongated control seeds having a higher germinability than larger, rounder seeds (as recorded in previous studies; Bu et al., 2016; Vera, 1997). These effects of indigenous status and seed shape were reversed for seeds that survived gut passage, after which native species had a higher germinability. Perhaps the native seeds were less able to resist gut acids, leading to greater breaking of physiological seed dormancy (Bravo et al., 2020).

Previous studies found similar contradictory effects on germinability. For example, Soons et al. (2008) found that smaller seeds had higher germinability whereas Kleyheeg, Claessens, and Soons (2018) found the opposite, although they did not control for seed shape. Gioria and Pyšek (2017) argued that germinability under one set of controlled conditions is not a reliable predictor of invasiveness, because germination patterns are strongly dependent on environmental conditions, so that alien species can only be expected to have a competitive advantage from high germination under certain conditions. For example, changing the salinity can radically change the germination response of wetland plants, and interact with the effects of gut passage by waterfowl (Espinar et al., 2004). In addition, the fact that the inclusion of seed traits had major effects in our models of germinability underlines the crucial role of seed traits, and suggests that the remaining partial effects of origin may ultimately

be explicable based on additional traits (e.g., hardness and water permeability of the seed coat). Therefore, further studies with a larger set of species and a more diverse set of seed traits are needed to clarify these issues (van Leeuwen et al., 2023).

Seed dormancy plays a key role in the germination of the seeds, and can occur in several forms. According to Baskin and Baskin (2014), physiological and physical dormancy are the most common forms, of which physiological dormancy is the most common in aquatic non-salt tolerant (non-halophyte) plant species such as those used in our experiments. For example, *Bidens frondosa* needs approximately 270 days to break its dormancy after a cold stratification, so this may explain its low germinability (see Table 2). Only physical dormancy was thought to require gut passage by animals in order to break and accelerate germination (Penfield, 2017). By contrast, it was believed that gut passage would only decrease the germinability of certain seeds with physiological dormancy (Soltani et al., 2018). However, our results bring the paradigm of dormancy strategies into question, since gut passage increased germinability in five of our 12 study species (Table 2). Theoretically, all of the tested seeds had physiological dormancy, but they still seemed to be affected by the physical and chemical effects during gut passage, similar to previous findings by García-Álvarez et al. (2015) and Bravo et al. (2020). Despite detailed research into a range of factors (e.g., temperature, light, water, chemical concentrations) that stimulate entry into and exit from physiological dormancy (Baskin & Baskin, 2014), the role of gut passage has not yet been fully clarified, and has so far received little attention. Further research is needed to study the interactions between gut passage and other variables driving dormancy and germination in alien plants with physiological dormancy. In our experiment, we found that longer separation time can hinder germination. The longer the seeds were stored in faecal material, the higher the likelihood of fungus infection, which in turn can lead to decreased germination rate. To address this issue, we ensured an equal separation time between the alien and native species (Table 2).

4.3 | Time-to-germination and retention time

The time a seed requires to germinate has a crucial effect on its colonisation potential and success. Species with fast germination can gain a competitive advantage and speed up recruitment for the next generation (Jiménez-Alfaro et al., 2016).

Contrary to our first hypothesis (H1), we found that passed seeds germinate later than control seeds, and only control seeds of alien species showed significantly faster germination compared to native species, in line with previous studies (Gioria & Pyšek, 2017; Pyšek & Richardson, 2008). Germination time is often decreased by gut passage, but also often varies according to retention time (Brochet et al., 2010; García-Álvarez et al., 2015), which in turn is related to seed traits that can differ between alien and native species. Native seeds stayed longer in the digestive tract and germinated faster than alien seeds, probably as a consequence of their bigger size/larger

volume (see Appendix S4; Brochet et al., 2010). We also found that time-to-germination decreased with increasing separation time of the seeds across all taxa involved in the current study. Nonetheless, potential differences in separation time between species pairs were controlled for by the design of our experiment, and are therefore not expected to bias our results. Future works should explore germination dynamics, especially under natural condition, where seeds are not removed from the faecal matter, which might positively or negatively influence germinability of passed seeds.

Overall, seed traits did not influence the effect of gut passage on germination time. We found that elongated seeds persistently needed less time for germination, both for controls and after gut passed. This result is consistent with previous studies showing that elongated seeds tend to germinate faster, compensating for other ecological effects in which such seeds are less likely to reach the seed bank and are exposed to higher predation pressure (Bu et al., 2016; Grime et al., 1981; Thompson, 1987; Thompson et al., 1993). The effect of earlier germination on the fitness of wetland plants needs more investigation, because it may have costs from increased herbivory, as well as benefits from more rapid growth (Figuerola et al., 2005; Figuerola & Green, 2004).

Similar to previous studies (Brochet et al., 2010; Lovas-Kiss et al., 2015; Soons et al., 2008), most seeds were recovered within 8 hr of ingestion. Considering that mallards typically move several kilometres per day and even longer during migrations (Bartel et al., 2018; Kleyheeg et al., 2019; Urgyán et al., 2023), long-distance dispersal might be common and important for all studied plant species. Mallards also make shorter daily movements between wetlands (Bartel et al., 2018; Kleyheeg et al., 2017), which might assist alien species to become fully established after their introduction to an area (Rouget et al., 2016). Thus, the large populations of mallards can facilitate effective dispersal for alien plant species at both local and wider scales (see also Urgyán et al., 2023).

4.4 | Consequences for plant invasions

Dietary studies from Europe showed that ducks can disperse hundreds of plant species, including many aliens (Almeida et al., 2022), and field data show that this extends to many other waterbirds. We showed that endozoochory has the potential to give alien plants an advantage for LDD by increasing their propagule pressure compared to native species. However, internal dispersal may delay germination of alien species compared to natives. Nonetheless, this delay also can offer a competitive edge to non-native species, particularly if they exhibit a fast growth rate and higher trait plasticity (Ruprecht et al., 2014; Szabó et al., 2019). Seed traits are important in determining endozoochory potential, notably through their influence on retention time and germination. This information, supplemented with knowledge on additional traits such as growth rate, will allow better predictions about range expansions of alien species.

AUTHOR CONTRIBUTIONS

Conceptualisation: BAL. Developing methods: ÁL-K and CvL. Conducting the research: BAL, ÁL-K, MJN, FP-K, VL & RU. Data analyses: OV. Data interpretation: OV, ÁL-K & BAL Writing: all authors.

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CONFLICT OF INTEREST STATEMENT

Andy J. Green is an Associate editor in Freshwater Biology but was not involved in any journal processes with regard to this manuscript. The authors declare that there is no other conflict of interest.

DATA AVAILABILITY STATEMENT

Data used in the analyses are available at: <https://doi.org/10.6084/m9.figshare.23901999>.

ETHICAL STATEMENT

The experiment had ethical approval from the scientific council of the Babeş-Bolyai University of Cluj Napoca (reference no. 14689/31.08.2018).

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REFERENCES

Almeida, B. A., Lukács, B. A., Lovas-Kiss, Á., Reynolds, C., & Green, A. J. (2022). Functional traits drive dispersal interactions between

- European waterfowl and seeds. *Frontiers in Plant Science*, 12, 795288. <https://doi.org/10.3389/fpls.2021.795288>
- Barnea, A., Yom-Tov, Y., & Friedman, J. (1991). Does ingestion by birds affect seed germination? *Functional Ecology*, 5, 394. <https://doi.org/10.2307/2389811>
- Bartel, R. D., Sheppard, J. L., Lovas-Kiss, Á., & Green, A. J. (2018). Endozoochory by mallard in New Zealand: What seeds are dispersed and how far? *PeerJ*, 6, e4811.
- Baskin, C., & Baskin, J. (2014). *Seeds* (2nd ed.). Elsevier.
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Bekker, R. M., Bakker, J. P., Grandin, U., Kalamees, R., Milberg, P., Poschlod, P., Thompson, K., & Willems, J. H. (1998). Seed size, shape and vertical distribution in the soil: Indicators of seed longevity. *Functional Ecology*, 5, 834–842. <https://doi.org/10.1046/j.1365-2435.1998.00252.x>
- Blackburn, T. M., Pyšek, P., Bacher, S., Carlton, J. T., Duncan, R. P., Jarošík, V., Wilson, J. R., & Richardson, D. M. (2011). A proposed unified framework for biological invasions. *Trends in Ecology and Evolution*, 26, 333–339. <https://doi.org/10.1016/j.tree.2011.03.023>
- Bravo, C., Chamorro, D., Hiraldo, F., Speziale, K., Lambertucci, S. A., Telle, J. L., & Blanco, G. (2020). Physiological dormancy broken by endozoochory: Austral parakeets (*Enicognathus ferrugineus*) as legitimate dispersers of calafate (*Berberis microphylla*) in the Patagonian Andes. *Journal of Plant Ecology*, 13, 538–544. <https://doi.org/10.1093/jpe/rtaa041>
- Brochet, A. L., Guillemain, M., Gauthier-Clerc, M., Fritz, H., & Green, A. J. (2010). Endozoochory of Mediterranean aquatic plant seeds by teal after a period of desiccation: Determinants of seed survival and influence of retention time on germinability and viability. *Aquatic Botany*, 93, 99–106. <https://doi.org/10.1016/j.aquabot.2010.04.001>
- Bu, H.-Y., Wang, X.-J., Zhou, X.-H., Qi, W., Liu, K., Ge, W.-J., Xu, D.-H., & Zhang, S.-T. (2016). The ecological and evolutionary significance of seed shape and volume for the germination of 383 species on the eastern Qinghai-Tibet plateau. *Folia Geobotanica*, 51, 333–341. <https://doi.org/10.1007/s12224-016-9271-y>
- Bullock, J. M., Mallada González, L., Tamme, R., Götzenberger, L., White, S. M., Pärtel, M., & Hooftman, D. A. P. (2017). A synthesis of empirical plant dispersal kernels. *Journal of Ecology*, 105, 6–19. <https://doi.org/10.1111/1365-2745.12666>
- Chen, S. C., & Moles, A. T. (2015). A mammoth mouthful? A test of the idea that larger animals ingest larger seeds. *Global Ecology and Biogeography*, 24, 1269–1280.
- Colautti, R. I., Grigorovich, I. A., & MacIsaac, H. J. (2006). Propagule pressure: A null model for biological invasions. *Biological Invasions*, 8, 1023–1037. <https://doi.org/10.1007/s10530-005-3735-y>
- Costea, M., El Miari, H., Laczkó, L., Fekete, R., Molnár, V. A., Lovas-Kiss, Á., & Green, A. J. (2019). The effect of gut passage by waterbirds on the seed coat and pericarp of diaspores lacking external flesh: Evidence for widespread adaptation to endozoochory in angiosperms. *PLoS One*, 14, e0226551. <https://doi.org/10.1371/journal.pone.0226551>
- Crawley, M. (2007). *The R book*. John Wiley & Sons, Ltd.
- Crawley, M. J., Harvey, P. H., & Purvis, A. (1996). Comparative ecology of the native and alien floras of the British Isles. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 351, 1251–1259. <https://doi.org/10.1098/rstb.1996.0108>
- Delany, S., Veen, J., & Jacquie, C. (Eds.). (2006). Mallard movements. In *Urgent preliminary assessment of ornithological data relevant to the spread of Avian Influenza in Europe. Report to the European Commission* (pp. 141–142). Wetland International and EURING. https://www.researchgate.net/publication/270215703_Urgent_preliminary_assessment_of_ornithological_data_relevant_to_the_spread_of_Avian_Influenza_in_Europe

- Espinar, J. L., García, L. V., Figuerola, J., Green, A. J., & Clemente, L. (2004). Helophyte germination in a Mediterranean salt marsh: Gut-passage by ducks changes seed response to salinity. *Journal of Vegetation Science*, 15, 315–322. <https://doi.org/10.1111/j.1654-1103.2004.tb02267.x>
- Figuerola, J., & Green, A. J. (2004). Effects of seed ingestion and herbivory by waterfowl on seedling establishment: A field experiment with wigeon grass *Ruppia maritima* in Doñana, south-West Spain. *Plant Ecology*, 173, 33–38. <https://doi.org/10.1023/B:VEGE.0000026323.56635.4e>
- Figuerola, J., Santamaria, L., Green, A. J., Luque, I., Alvarez, R., & Charalambidou, I. (2005). Endozoochorous dispersal of aquatic plants: Does seed gut passage affect plant performance? *American Journal of Botany*, 92, 696–699. <https://doi.org/10.3732/ajb.92.4.696>
- Flores-Moreno, H., Thomson, F. J., Warton, D. I., & Moles, A. T. (2013). Are introduced species better dispersers than native species? A global comparative study of seed dispersal distance. *PLoS One*, 8, e68541. <https://doi.org/10.1371/journal.pone.0068541>
- García-Álvarez, A., van Leeuwen, C. H. A., Luque, C. J., Hussner, A., Vlez-Martin, A., Pérez-Vázquez, A., Green, A. J., & Castellanos, E. M. (2015). Internal transport of alien and native plants by geese and ducks: An experimental study. *Freshwater Biology*, 60, 1316–1329. <https://doi.org/10.1111/fwb.12567>
- Gioria, M., & Pyšek, P. (2017). Early bird catches the worm: Germination as a critical step in plant invasion. *Biological Invasions*, 19, 1055–1080. <https://doi.org/10.1007/s10530-016-1349-1>
- Green, A. J. (2016). The importance of waterbirds as an overlooked pathway of invasion for alien species. *Diversity and Distributions*, 22, 239–247. <https://doi.org/10.1111/ddi.12392>
- Green, A. J., Baltzinger, C., & Lovas-Kiss, Á. (2022). Plant dispersal syndromes are unreliable, especially for predicting zoochory and long-distance dispersal. *Oikos*, 2022, e08327. <https://doi.org/10.1111/oik.08327>
- Green, A. J., Elmberg, J., & Lovas-Kiss, Á. (2019). Beyond scatter-hoarding and frugivory: European corvids as overlooked vectors for a broad range of plants. *Frontiers in Ecology and Evolution*, 7, 133. <https://doi.org/10.3389/fevo.2019.00133>
- Green, A. J., Lovas-Kiss, Á., Reynolds, C., Sebastián-González, E., Silva, G. G., van Leeuwen, C. H. A., & Wilkinson, D. M. (2023). Dispersal of aquatic and terrestrial organisms by waterbirds: A review of current knowledge and future priorities. *Freshwater Biology*, 68, 173–190. <https://doi.org/10.1111/fwb.14038>
- Grime, J. P., Mason, G., Curtis, A. V., Rodman, J., & Band, S. R. (1981). A comparative study of germination characteristics in a local flora. *Journal of Ecology*, 69, 1017. <https://doi.org/10.2307/2259651>
- Gurd, D. B. (2007). Predicting resource partitioning and community organization of filter-feeding dabbling ducks from functional morphology. *The American Naturalist*, 169, 334–343. <https://doi.org/10.1086/510924>
- Guttal, V., Bartumeus, F., Hartvigsen, G., & Nevai, A. L. (2011). Retention time variability as a mechanism for animal mediated long-distance dispersal. *PLoS One*, 6, e28447. <https://doi.org/10.1371/journal.pone.0028447>
- Hattermann, D., Bernhardt-Römermann, M., Otte, A., & Eckstein, R. L. (2019). Geese are overlooked dispersal vectors for vascular plants in archipelago environments. *Journal of Vegetation Science*, 30, 533–541. <https://doi.org/10.1111/jvs.12742>
- Higgins, S. I., & Richardson, D. M. (1999). Predicting plant migration rates in a changing world: The role of long-distance dispersal. *The American Naturalist*, 153, 464–475. <https://doi.org/10.1086/303193>
- Jiménez-Alfaro, B., Silveira, F. A. O., Fidelis, A., Poschlod, P., & Commander, L. E. (2016). Seed germination traits can contribute better to plant community ecology. *Journal of Vegetation Science*, 27, 637–645. <https://doi.org/10.1111/jvs.12375>
- Kleyheeg, E., Claessens, M., & Soons, M. B. (2018). Interactions between seed traits and digestive processes determine the germinability of bird-dispersed seeds. *PLoS One*, 13, e0195026. <https://doi.org/10.1371/journal.pone.0195026>
- Kleyheeg, E., Fiedler, W., Safi, K., Waldenström, J., Wikelski, M., & Toor, M. L. (2019). A comprehensive model for the quantitative estimation of seed dispersal by migratory mallards. *Frontiers in Ecology and Evolution*, 7, 40. <https://doi.org/10.3389/fevo.2019.00040>
- Kleyheeg, E., Nolet, B. A., Otero-Ojea, S., & Soons, M. B. (2018). A mechanistic assessment of the relationship between gut morphology and endozoochorous seed dispersal by waterfowl. *Ecology and Evolution*, 8, 10857–10867. <https://doi.org/10.1002/ece3.4544>
- Kleyheeg, E., van Dijk, J. G. B., Tsooglou-Gkina, D., Woud, T. Y., Boonstra, D. K., Nolet, B. A., & Soons, M. B. (2017). Movement patterns of a keystone waterbird species are highly predictable from landscape configuration. *Movement Ecology*, 5, 2. <https://doi.org/10.1186/s40462-016-0092-7>
- Lockwood, J. L., Cassey, P., & Blackburn, T. M. (2005). The role of propagule pressure in explaining species invasions. *Trends in Ecology and Evolution*, 20, 223–228. <https://doi.org/10.1016/j.tree.2005.02.004>
- Lockwood, J. L., Cassey, P., & Blackburn, T. M. (2009). The more you introduce the more you get: The role of colonization pressure and propagule pressure in invasion ecology. *Diversity and Distribution*, 15, 904–910. <https://doi.org/10.1111/j.1472-4642.2009.00594.x>
- 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. <https://doi.org/10.1111/fwb.13080>
- Lovas-Kiss, Á., Sánchez, M. I., Wilkinson, D. M., Coughlan, N. E., Alves, J. A., & Green, A. J. (2019). Shorebirds as important vectors for plant dispersal in Europe. *Ecography*, 42, 956–967. <https://doi.org/10.1111/ecog.04065>
- Lovas-Kiss, Á., Sonkoly, J., Vincze, O., Green, A. J., Takács, A., & Molnár, A. V. (2015). Strong potential for endozoochory by waterfowl in a rare, ephemeral wetland plant species, *Astragalus contortuplicatus* (Fabaceae). *Acta Societatis Botanicorum Poloniae*, 84, 321–326. <https://doi.org/10.5586/asbp.2015.030>
- Lovas-Kiss, Á., Vincze, O., Kleyheeg, E., Sramkó, G., Laczkó, L., Fekete, R., Molnár, V. A., & Green, A. J. (2020). Seed mass, hardness, and phylogeny explain the potential for endozoochory by granivorous waterbirds. *Ecology and Evolution*, 10, 1413–1424. <https://doi.org/10.1002/ece3.5997>
- Martín-Vélez, V., Lovas-Kiss, Á., Sánchez, M. I., & Green, A. J. (2021). Endozoochory of the same community of plants lacking fleshy fruits by storks and gulls. *Journal of Vegetation Science*, 32, e12967. <https://doi.org/10.1111/jvs.12967>
- Martín-Vélez, V., van Leeuwen, C. H. A., Sánchez, M. I., Hortas, F., Shamoun-Baranes, J., Thaxter, C. B., Lens, L., Camphuysen, C. J., & Green, A. J. (2021). Spatial patterns of weed dispersal by wintering gulls within and beyond an agricultural landscape. *Journal of Ecology*, 109, 1947–1958. <https://doi.org/10.1111/1365-2745.13619>
- Nathan, R., Schurr, F. M., Spiegel, O., Steinitz, O., Trakhtenbrot, A., & Tsoar, A. (2008). Mechanisms of long-distance seed dispersal. *Trends in Ecology and Evolution*, 23, 638–647. <https://doi.org/10.1016/j.tree.2008.08.003>
- Navarro-Ramos, M. J., Green, A. J., Lovas-Kiss, A., Roman, J., Brides, K., & van Leeuwen, C. H. A. (2021). A predatory waterbird as a vector of plant seeds and aquatic invertebrates. *Freshwater Biology*, 67, 657–671. <https://doi.org/10.1111/fwb.13870>
- Penfield, S. (2017). Seed dormancy and germination. *Current Biology*, 27, PR874–R878. <https://doi.org/10.1016/j.cub.2017.05.050>
- Pollux, B. J. A. (2017). Consistent individual differences in seed disperser quality in a seed-eating fish. *Oecologia*, 183, 81–91. <https://doi.org/10.1007/s00442-016-3749-4>

- Pyšek, P., & Richardson, D. M. (2008). Traits associated with invasiveness in alien plants: Where do we stand? In W. Nentwig (Ed.), *Biological invasions* (pp. 97–125). Springer.
- R Core Team. (2021). R: A language and environment for statistical computing. <https://www.r-project.org/>
- Richardson, D. M., Pyšek, P., Rejmanek, M., Barbour, M. G., Panetta, F. D., & West, C. J. (2000). Naturalization and invasion of alien plants: Concepts and definitions. *Diversity and Distribution*, 6, 93–107. <https://doi.org/10.1046/j.1472-4642.2000.00083.x>
- Rouget, M., Robertson, M. P., Wilson, J. R., Hui, C., Essl, F., Renteria, J. L., & Richardson, D. M. (2016). Invasion debt – quantifying future biological invasions. *Diversity and Distribution*, 22, 445–456. <https://doi.org/10.1111/ddi.12408>
- Ruprecht, E., Fenesi, A., & Nijs, I. (2014). Are plasticity in functional traits and constancy in performance traits linked with invasiveness? An experimental test comparing invasive and naturalized plant species. *Biological Invasions*, 16, 1359–1372. <https://doi.org/10.1007/s10530-013-0574-0>
- Soltani, E., Baskin, C. C., Baskin, J. M., Heshmati, S., & Mirfazeli, M. S. (2018). A meta-analysis of the effects of frugivory (endozoochory) on seed germination: Role of seed size and kind of dormancy. *Plant Ecology*, 219, 1283–1294. <https://doi.org/10.1007/s11258-018-0878-3>
- Soons, M. B., Brochet, A. L., Kleyheeg, E., & Green, A. J. (2016). Seed dispersal by dabbling ducks: An overlooked dispersal pathway for a broad spectrum of plant species. *Journal of Ecology*, 104, 443–455. <https://doi.org/10.1111/1365-2745.12531>
- Soons, M. B., Van Der Vlugt, C., Van Lith, B., Heil, G. W., & Klaasen, M. (2008). Small seed size increases the potential for dispersal of wetland plants by ducks. *Journal of Ecology*, 96, 619–627. <https://doi.org/10.1111/j.1365-2745.2008.01372.x>
- Szabó, S., Peeters, E. T. H. M., Várbiro, G., Borics, G., & Lukács, B. A. (2019). Phenotypic plasticity as a clue for invasion success of the submerged aquatic plant *Elodea nuttallii*. *Plant Biology*, 21, 54–63. [doi:10.1111/plb.12918](https://doi.org/10.1111/plb.12918)
- Thompson, K. (1987). Seeds and seed banks. *New Phytologist*, 106, 23–34. <https://doi.org/10.1111/j.1469-8137.1987.tb04680.x>
- Thompson, K., Band, S. R., & Hodgson, J. G. (1993). Seed size and shape predict persistence in soil. *Functional Ecology*, 7, 236. <https://doi.org/10.2307/2389893>
- Traveset, A., Robertson, A., & Rodríguez-Pérez, J. (2007). A review on the role of endozoochory in seed germination. In A. J. Dennis, E. W. Schupp, R. J. Green, & D. A. Westcott (Eds.), *Seed dispersal: Theory and its application in a changing world* (pp. 78–103). CABI Publishing.
- Urgyán, R., Lukács, B. A., Fekete, R., Molnár, V. A., Nagy, A., Vincze, O., Green, A. J., & Lovas-Kiss, Á. (2023). Plants dispersed by a non-frugivorous migrant change throughout the annual cycle. *Global Ecology and Biogeography*, 32, 70–82. <https://doi.org/10.1111/geb.13608>
- van Kleunen, M., Dawson, W., & Maurel, N. (2015). Characteristics of successful alien plants. *Molecular Ecology*, 24, 1954–1968. <https://doi.org/10.1111/mec.13013>
- van Leeuwen, C. H. A. (2018). Internal and external dispersal of plants by animals: An aquatic perspective on alien interference. *Frontiers in Plant Science*, 9, 153. <https://doi.org/10.3389/fpls.2018.00153>
- van Leeuwen, C. H. A., 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, 20170406. <https://doi.org/10.1098/rsbl.2017.0406>
- van Leeuwen, C. H. A., Soons, M. B., Vandionant, L. G. V. T. I., Green, A. J., & Bakker, E. S. (2023). Seed dispersal by waterbirds: A mechanistic understanding by simulating avian digestion. *Ecography*, 2023, e06470. [doi:10.1111/ecog.06470](https://doi.org/10.1111/ecog.06470)
- van Leeuwen, C. H. A., van der Velde, G., van Groenendael, J. M., & Klaassen, M. (2012). Gut travellers: Internal dispersal of aquatic organisms by waterfowl. *Journal of Biogeography*, 39, 2031–2040. [doi:10.1111/jbi.12004](https://doi.org/10.1111/jbi.12004)
- Vera, M. L. (1997). Effects of altitude and seed size on germination and seedling survival of heathland plants in North Spain. *Plant Ecology*, 133, 101–106. <https://doi.org/10.1023/A:1009729201384>
- Vilà, M., Espinar, J. L., Hejda, M., Hulme, P. E., Jarošík, V., Maron, J. L., Pergl, J., Schaffner, U., Sun, Y., & Pyšek, P. (2011). Ecological impacts of invasive alien plants: A meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters*, 14, 702–708. [doi:10.1111/j.1461-0248.2011.01628.x](https://doi.org/10.1111/j.1461-0248.2011.01628.x)
- Vilà, M., & Hulme, P. E. (Eds.). (2017). *Impact of biological invasions on ecosystem services. Invading nature - springer series in invasion ecology* (Vol. 12, p. 354). Springer International Publishing.
- Zedler, J. B., & Kercher, S. (2004). Causes and consequences of invasive plants in wetlands: Opportunities, opportunists, and outcomes. *Critical Review in Plant Sciences*, 23, 431–452. [doi:10.1080/07352680490514673](https://doi.org/10.1080/07352680490514673)

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