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Internationally vulnerable Korean water deer (*Hydropotes inermis argyropus*) can act as an ecological filter by endozoochory

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ABSTRACT

Seeds dispersed by endozoochory by large herbivores are disseminated over long distances, which has potential impacts on vegetation dynamics within a region. The Korean water deer (*Hydropotes inermis argyropus*) is a dominant deer species in South Korea, but is considered a vulnerable species internationally. In the present study, we aimed to elucidate the role of Korean water deer in seed dispersal in lowland areas where land-use change is occurring. We assessed seasonal differences in seed dispersal in Korean water deer, and the traits of seeds dispersed in this manner. We identified species dispersed by controlled germination using Korean water deer fecal samples from the Civilian Control Zone adjacent to the Demilitarized Zone between South and North Korea, a mixed lowland habitat of forest and open area. A total of 208 fecal pellet groups were collected throughout the year from April 2017 to March 2018. We found a total of 35 plant species from the deer feces. More seeds and species were dispersed in fall, the main seeding period in South Korea. Dispersed plant species were mainly forbs that were specific to lowland areas and had medium (1–2 mm) seeds with no specific dispersal adaptations. Our results suggest that Korean water deer preferentially disperse particular plant species. They disperse disproportionately more graminoids, species from open areas, shorter than 2 mm, with no special adaptation, and specifically without fleshy/edible fruits, which may result in ecological filtering. We conclude that Korean water deer, as an endozoochorous seed dispersal vector in the lowland of South Korea, can affect plant populations and communities in the region.
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1. Introduction

Seed dispersal over long distances, i.e., over 100 m or more (Cain et al., 2000), is of key importance for ecosystem functioning, because it is related to species diversity, genetic diversity and population dispersal (Bullock et al., 2002; Cain et al., 2000). Therefore, long-distance seed dispersal is crucial in changing environments (Nathan et al., 2008). For plant species, seed dispersal is related to adaptation to global changes, including climate change and land-use change (Travis et al., 2013). Habitat fragmentation affects the dispersal cycle by changing the movement of seeds between habitat patches (Baguette et al.,

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2013). Therefore, elucidating the interactions between seeds and their dispersal vectors is essential for the management and restoration of fragmented habitats (McConkey et al., 2012).

Among mechanisms of long-distance seed dispersal, endozoochory, which is the dispersal of seeds through ingestion and defecation by animals, might explain the current distribution and rapid migration of some plant species (Calviño-Cancela et al., 2006; Myers et al., 2004). According to Janzen (1984), small, tough plant seeds with no special morphological characteristics are unintentionally eaten by herbivores and dispersed endozoochorously. Seeds with these characteristics are likely to survive mastication and exposure to gastric acid in the gut (Pakeman et al., 2002; Picard et al., 2016). Seed production and species abundance in the regional pool of species are reflected in the amount of seeds dispersed by herbivores in the area (Malo and Suarez 1995), as are differences among habitats (Cosyns et al., 2006; Yamashiro and Yamashiro 2006). In endozoochory by the ungulates, seeds from open areas are more likely to be dispersed than seeds from other habitats (Iravani et al., 2011; Myers et al., 2004). By dispersing the species with distinctive traits, endozoochory can function as an indirect ecological filter for dispersed species in a region (Albert et al., 2015).

Large herbivores are considered important endozoochorous seed dispersal vectors in regional plant communities (Baltzinger et al., 2019; Bartuszevige and Endress 2008; Eycott et al., 2007; Heinken and Raudnitschka 2002; Iravani et al., 2011). Deer (Cervidae) are large herbivores that have a long gut retention time and large home ranges, and therefore are potential vectors for long-distance seed dispersal (Iravani et al., 2011; Myers et al., 2004; Zidon et al., 2017).

Water deer (*Hydropotes inermis*) are classified into two subspecies native to Korea (*Hydropotes inermis argyropus*) (Fig. 1) and to the southeastern part of China (*Hydropotes inermis inermis*) (Geist 1998). The water deer is listed as vulnerable by the International Union for Conservation of Nature (IUCN) (Harris and Duckworth 2015). In China, its population continues to decrease despite conservation efforts (Cooke 2019; Kim et al., 2016). However, the Korean water deer is the most dominant wild deer on the Korean peninsula, and in the absence of effective predators, its population density is rising even further (National Institute of Biological Resources, 2018). The distribution of the Korean water deer includes the entire Korean peninsula, from lowland areas to mountainous areas (Cooke 2019; Kim et al., 2011; Kim and Lee 2011). However, due to habitat fragmentation in lowland areas of South Korea, conflicts occur between deer and humans (Kim et al., 2016). For this

Fig. 1. Korean water deer (*Hydropotes inermis argyropus*). Photo credits: Dr. Donguk Han.

reason, people are permitted to hunt Korean water deer in certain areas and seasons (Ministry of Environment 2015). We believe that understanding the potential ecological role of the Korean water deer is necessary to properly conserve and manage this locally dominant but internationally vulnerable species and to further understand its impact on vegetation dynamics at both the population and community levels.

The Korean Demilitarized Zone (DMZ), the border area between South and North Koreas, as a whole is regarded as highly biodiverse and as access to the southern part of the DMZ, Civilian Control Zone (CCZ), is restricted to authorized persons only, it is also recognized for the importance of its natural environment and high biodiversity (Sung et al., 2019). However, land use in the CCZ area has changed over time, especially in the western part, adjacent to Seoul, capital city of South Korea, which is under high development pressure (Park and Nam 2013; Sung et al., 2019).

Therefore, the objectives of the present study were 1) to assess the potential of the Korean water deer as a seed disperser in a lowland area near the DMZ, 2) to understand seasonal changes in the dispersal of species and seeds by water deer, and 3) to elucidate the traits of endozoochorously dispersed seeds by comparison with non-dispersed species.

2. Materials and methods

2.1. Study site

Sampling was conducted in the lowland areas of CCZ in Paju City, Gyeonggi Province, South Korea (37°55′ N, 126°44′ E) (Fig. 2). Recently, the area has experienced forest fragmentation and land-use change due to development and farmland construction (Sung et al., 2019). The CCZ in Paju City features a mixed landscape of arable land, low forested hills, and artificial buildings. The vegetation of the forest is dominated by *Acer ginnala*, *Alnus japonica,* and *Quercus acutissima* (Park and Nam 2013), but as the forested hills are relatively low, wetland and agricultural species are also abundant (Kim and Kang 2019). Annual mean temperature and total precipitation data were obtained from the nearest meteorological observation center, Paju Meteorological Center. The mean annual temperature at the CCZ study site was 10.5 °C and the total annual precipitation was 948 mm in 2017 (Korean Meteorological Administration, 2020).

2.2. Feces sampling and germination test

We carried out field sampling all year round from April 2017 to March 2018. At least ten fresh Korean water deer fecal pellet groups were collected every month, and 208 fecal pellet groups were collected in total (see Appendix A: Table A.1). The collected fecal samples were placed in individual ziplock bags and brought back to the laboratory. We cleaned outer parts of the feces to reduce the possibility of contamination, for example due to seed rain. Then, the feces were air-dried for 4–7 days at room temperature and the dry weight of each pellet group was measured. After weighing, the feces were stored in a cold room for about 90 days for seed vernalization. Then, the feces were gently crushed with running water. Each pellet group was planted in an individual pot in a layer no more than 0.5-cm thick to facilitate seed germination. Pots were kept in a temperature-controlled greenhouse at Seoul National University, Seoul, South Korea. Control pots were also set to check the potential seedlings originated from seed rain or seeds in the compost used as substrate. No seedlings were found from the control pots. All of the pots, including the control pots, were kept moist during the germination periods. We carefully monitored and counted germinated plant seedlings for 12 weeks, after which the pots were left to dry out for three weeks. Watering was then resumed and the pots were monitored for additional germination for a further eight weeks to ensure that all of the seeds had germinated. No additional seedlings germinated from second germination period. Germinated seedlings were identified at the seedling stage and removed to avoid potential competition with other seedlings. When we were not able to identify the emerging seedlings, we replanted them in bigger pots and grew them until flowering and seeding for identification.

2.3. Categorization of species and data analysis

Plant species names were as listed by Korean Plant Names Index (http://www.nature.go.kr/kpni/). Seedlings that died before species-level identification was possible were classified as forb, graminoid, or woody species. Graminoids were identified to the family level where possible. Among 1655 seedlings, 30 seedlings were unidentified to species level, a total of 1625 seedlings were concerned for further analysis. To test the species trait differences between species from the seedlings germinated from the feces and regional flora, regional flora data were listed from Kim and Kang (2019) and Gyeonggi Tourism Organization (2018). The habitat type of each species was determined based on the work of Choung et al. (2012) and Korean Biodiversity Information System (http://www.nature.go.kr). Seed length data were obtained from the Korea National Arboretum (2017), Asano (1995), and the Korea Research Institute of Bioscience and Biotechnology (2009). For seed length data with minimum and maximum value, they were averaged using minimum and maximum seed length. According to seed length, species were grouped into three size categories as follows: small, <1 mm; medium, 1–2 mm; and large, >2 mm. Seeds were further classified into six categories (wind, hooked, fleshy/edible fruit, ballistic, ant, and no special adaptation) according to seed morphology, following the Korea National Arboretum (2017), Asano (1995), Korea Research Institute of Bioscience and Biotechnology (2009), and Kattge et al. (2011).

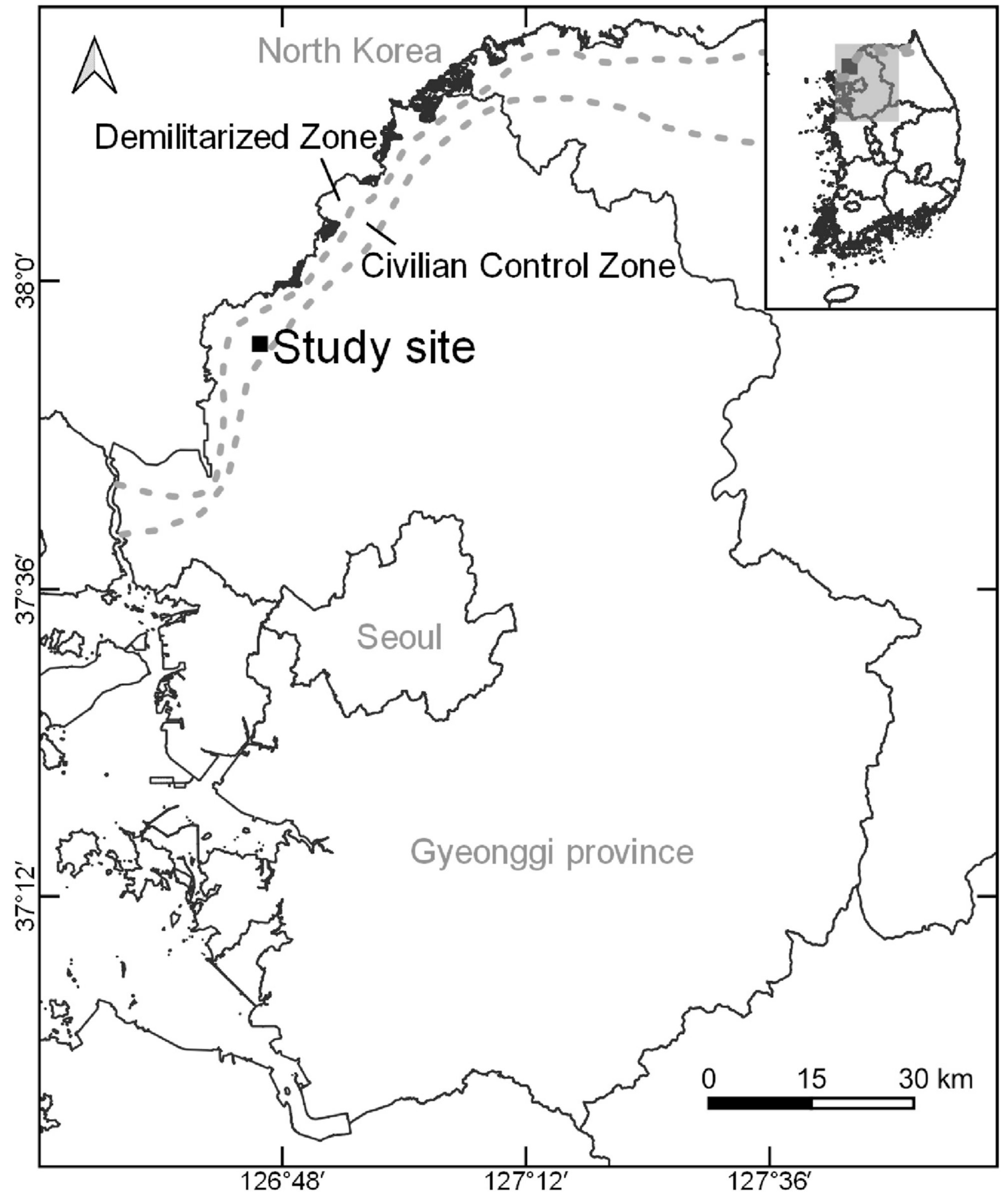

Fig. 2. Map showing where Korean water deer feces were sampled in the Civilian Control Zone, Paju City, Gyeonggi Province, South Korea.

We tested the differences in number of seeds and species among seasons (spring: March–May; summer: June–August; fall: September–November; winter: December–February) using the Kruskal–Wallis test and the significance of differences between seasons by multiple mean comparison with Bonferroni correction. The differences of traits between dispersed species and species from the regional flora were tested with Fisher's exact test. The graphs showing the results were produced using the "ggplot2" package (Wickham 2016) in R version 3.3.2 (R Core Team 2019).

3. Results

3.1. Seeds dispersed endozoochorously by Korean water deer

In the germination test, 1655 seedlings of 18 families, 29 genera, and 35 species germinated in 208 Korean water deer fecal pellet groups. The average weight of fecal pellet group was 6.3 g. Among these fecal pellet groups, 54.8% (114 fecal pellet groups) contained at least one germinable seed. The overall mean germination per pellet group was 8.0 seedlings and the overall mean germination per 100 g of feces was 14.9 seedlings, with a maximum seed density per pellet group of 161 seeds.

For the feces containing at least one germinable seed, mean germination was 14.5 seedlings per pellet group. The most common species that germinated was *Portulaca oleracea*, which had a frequency of 25% in all fecal pellet groups and accounted for 47.6% of all germinated seeds (Table 1). *Chenopodium album* and *Lindernia dubia* were the next most common species, accounting for 13.6% and 10.0% of the total number of seedlings and present at a frequency of 10.6% and 9.6%, respectively.

3.2. Seasonal patterns in seed dispersal

Among the 1655 seedlings that germinated in the 208 Korean water deer fecal pellet groups, 980 seedlings (59.2% of the total number of seedlings) germinated from feces collected in fall. Both the number of seeds and number of species per pellet group were highest in this season. More seeds and species were dispersed in fall compared to winter and summer (Kruskal−Wallis test and multiple pairwise test with Bonferroni correction for post-hoc test $p < 0.05$) (Fig. 3).

3.3. Traits of endozoochorously dispersed seeds and comparison with regional flora

Among the 35 identified species that germinated in the deer feces, most were forb species (22 species; 62.9%) (Fig. 4). Graminoid species accounted for 28.6% of the total number of species, while woody species accounted for 8.6%. The composition of species differed between seed and flora (Fisher's exact test, $p < 0.01$). As well as species from the feces, plant species from flora were mostly forbs (63.7% of species), but graminoid accounted for 11.4% and woody species accounted for 24.9% of species.

Habitat of species were also different between seeds and flora (Fisher's exact test, $p < 0.001$). Species from meadows and shrublands were more likely to be dispersed by Korean water deer, accounting for 62.9% of the total number of species, followed by species from wet meadows (25.7%) and only had 5.7% of species from forest. In flora, species from meadows and shrublands were in high proportion (47.2% of species) similarly, but followed by species from forest habitat (30.9%).

In terms of seed length, the percentage of plant species with medium-sized (1−2 mm) seeds was 51.5%, small-sized (<1 mm) seeds was 36.4%, and that with large (>2 mm) seeds was 12.1%. Most of the species were less than 2 mm in length. However, species from flora were mostly seeds with large (>2 mm) seeds (58.6%), followed by medium (28.4%) and small seeds (13.0%) (Fisher's exact test, $p < 0.0001$).

For diaspore type, species with no particular dispersal adaptations were most common, accounting for 85.7% of plant species. However, seeds with fleshy fruit (8.6% of the total number of species), ballistic and wind-dispersed seeds (2.9% of the total number of species respectively) were also found in the fecal samples. This composition was also different from the species of flora (Fisher's exact test, $p < 0.01$). In flora, the species with no special adaptation were most common (47.7%) and wind-dispersed seeds was accounting for 20.7% and fleshy fruit for 19.1% of the species.

4. Discussion

4.1. Seeds dispersed endozoochorously by Korean water deer

In this study, a total of 35 species germinated from the feces of Korean water deer collected in lowland area. Endozoochory by the ungulates (see Albert et al., 2015; Baltzinger et al., 2019) is well documented in the grasslands (Iravani et al., 2011), wetlands (Flaherty et al., 2018), and forests (Eycott et al., 2007; Myers et al., 2004; Picard et al., 2016) of Europe and North America. However, similar studies on Asian regions are limited (McCullough et al., 2008; Yamashiro and Yamashiro 2006). Here, we investigated Korean water deer endozoochory in lowland area in South Korea. Endozoochorously dispersed species in the present study were mostly forbs, species from meadows and shrublands and seeds with no particular adaptations for dispersal. In line with the "foliage is the fruit" hypothesis (Janzen 1984), the seeds that were endozoochorously dispersed by Korean water deer showed characteristics that enable seeds to survive ingestion. These findings are consistent with those of other studies (Mouissie et al., 2005; Pakeman et al., 2002; Yamashiro and Yamashiro 2006).

The Korean water deer is distributed all throughout the Korean peninsula, including wetland areas and regions close to low mountainous areas. Habitat selectivity is known to result in differences in the plant species that they disperse (Iravani et al., 2011; Yamashiro and Yamashiro 2006). Regarding the feeding preferences of these herbivores, Korean water deer in lowland areas are reported to have different diets to those inhabiting in mountainous areas (Kim et al., 2011). Based on this, we assume that deer in forest and wetland habitats should disperse more plant species associated with these habitats, as reported in other studies (Flaherty et al., 2018; Vellend et al., 2003; Yamashiro and Yamashiro 2006). The composition of plant traits from flora and feces differed significantly. In the present study, we found that species with small and medium-sized seeds ($\leq$2 mm), no specific dispersal adaptation and species from lowland and open areas were preferentially dispersed endozoochorously. As such, the Korean water deer act as an ecological filter of regional flora by dispersing species with distinct traits in particular regions (Albert et al., 2015; Picard et al., 2016).

We observed distinctive seasonal differences in seed dispersal in the present study. More seeds, especially of forb species, were dispersed through endozoochory in fall, the main seeding period in South Korea. Similar patterns have also been reported in other endozoochory studies (Kuiters and Huiskes 2010; Mouissie et al., 2005; Tsuji et al., 2011).

Table 1
Total seedling numbers of plant species that germinated from the feces of Korean water deer in lowland areas of the Civilian Control Zone, South Korea and their habitat, diaspore type, and seed length. "Percentage" denotes the percentage of each species that germinated relative to the total number of seedlings. "Frequency" denotes the percentage of samples in which each species germinated.

Species		Total	Percentage (n = 1655)	Frequency (n = 208)	Habitat	Diaspore type	seed length	seed length categories (S: 1 < mm; M: 1–2 mm; L: >2 mm)
Forb								
Amaranthaceae	*Amaranthus blitum* subsp. *oleraceus*	32	1.9	3.4	meadow and shrubland	No special morphology	1.2[b]	M
Asteraceae	*Centipeda minima*	6	0.4	2.9	meadow and shrubland	No special morphology	1[b]	M
	Erigeron annuus	16	1	3.8	meadow and shrubland	Wind	1[b]	M
Brassicaceae	*Capsella bursa-pastoris*	1	0.1	0.5	meadow and shrubland	No special morphology	0.95[a]	S
	Cardamine flexuosa	3	0.2	1.4	wet meadow	Ballistic	1.01[a]	M
	Rorippa palustris	37	2.2	5.3	wet meadow	No special morphology	0.6[c]	S
Caryophyllaceae	*Cerastium glomeratum*	1	0.1	0.5	meadow and shrubland	No special morphology	0.4[b]	S
	Sagina japonica	2	0.1	1	meadow and shrubland	No special morphology	0.35[a]	S
	Silene firma	5	0.3	1.4	meadow and shrubland	No special morphology	0.88[a]	S
	Stellaria aquatica	90	5.4	6.7	meadow and shrubland	No special morphology	0.86[a]	S
Chenopodiaceae	*Chenopodium album*	225	13.6	10.6	meadow and shrubland	No special morphology	1[b]	M
	Chenopodium ficifolium	4	0.2	1	meadow and shrubland	No special morphology	1[b]	M
Euphorbiaceae	*Acalypha australis*	2	0.1	1	meadow and shrubland	No special morphology	1.71[a]	M
Onagraceae	*Ludwigia prostrata*	31	1.9	4.3	wet meadow	No special morphology	1.56[a]	M
Polygonaceae	*Persicaria hydropiper*	1	0.1	0.5	wet meadow	No special morphology	2.18[a]	L
Portulacaceae	*Portulaca oleracea*	787	47.6	25	meadow and shrubland	No special morphology	0.67[a]	S
Rosaceae	*Potentilla supina*	20	1.2	1.4	meadow and shrubland	No special morphology	0.9[c]	S
Scrophulariaceae	*Lindernia dubia*	165	10	9.6	wet meadow	No special morphology	0.2[b]	S
	Mazus pumilus	2	0.1	1	meadow and shrubland	No special morphology	NA	NA
Solanaceae	*Solanum americanum*	90	5.4	12.5	meadow and shrubland	Fleshy/edible fruit	1.5[b]	M
Urticaceae	*Pilea pumila*	2	0.1	1	meadow and shrubland	No special morphology	1.64[a]	M
	Urtica angustifolia	12	0.7	3.8	forest	No special morphology	1[c]	M
unidentified dicot spp.		7	0.4	2.9				
Graminoid								
Cyperaceae	*Carex neurocarpa*	1	0.1	0.5	meadow and shrubland	No special morphology	1.07[a]	M
	Cyperus difformis	19	1.1	1.9	wet meadow	No special morphology	0.63[a]	S
	Cyperus hakonensis	1	0.1	0.5	wet meadow	No special morphology	0.64[a]	S
	Cyperus iria	10	0.6	2.4	meadow and shrubland	No special morphology	1.34[a]	M
	Cyperus nipponicus	2	0.1	0.5	wet meadow	No special morphology	1.11[a]	M
	Cyperaceae spp.	18	1.1	5.3				
Juncaceae	*Juncus tenuis*	1	0.1	0.5	meadow and shrubland	No special morphology	0.41[a]	S
Poaceae	*Digitaria ciliaris*	15	0.9	5.3	meadow and shrubland	No special morphology	3.21[a]	L
	Eleusine indica	2	0.1	1	meadow and shrubland	No special morphology	1.39[a]	M
	Panicum bisulcatum	13	0.8	1.9	wet meadow	No special morphology	1.77[a]	M
	Panicum dichotomiflorum	1	0.1	0.5	meadow and shrubland	No special morphology	2.2[c]	L

Table 1 (*continued*)

Species		Total	Percentage (n = 1655)	Frequency (n = 208)	Habitat	Diaspore type	seed length	seed length categories (S: 1 < mm; M: 1–2 mm; L: >2 mm)
	Poaceae spp.	5	0.3	2.4				
Woody								
Moraceae	*Morus alba*	1	0.1	0.5	cultivated species	Fleshy/edible fruit	2.2[c]	L
	Morus australis	24	1.5	1.9	forest	Fleshy/edible fruit	1.86[a]	M
Salicaceae	*Populus alba*	1	0.1	0.5	cultivated species	No special morphology	NA	NA

[a] Korea National Arboretum, 2017. Seed Atlas of Korea. Sumeunki Publishing Co. Seoul Korea.
[b] Asano, S. 1995. Seeds/fruits and seedlings of plants in Japan. Zenkoku Noson Kyoiku Kyokai, Japan.
[c] Korea Research Institute of Bioscience and Biotechnology (2009). Seeds of Wild Plants of Korea. CRESEED, Korea.

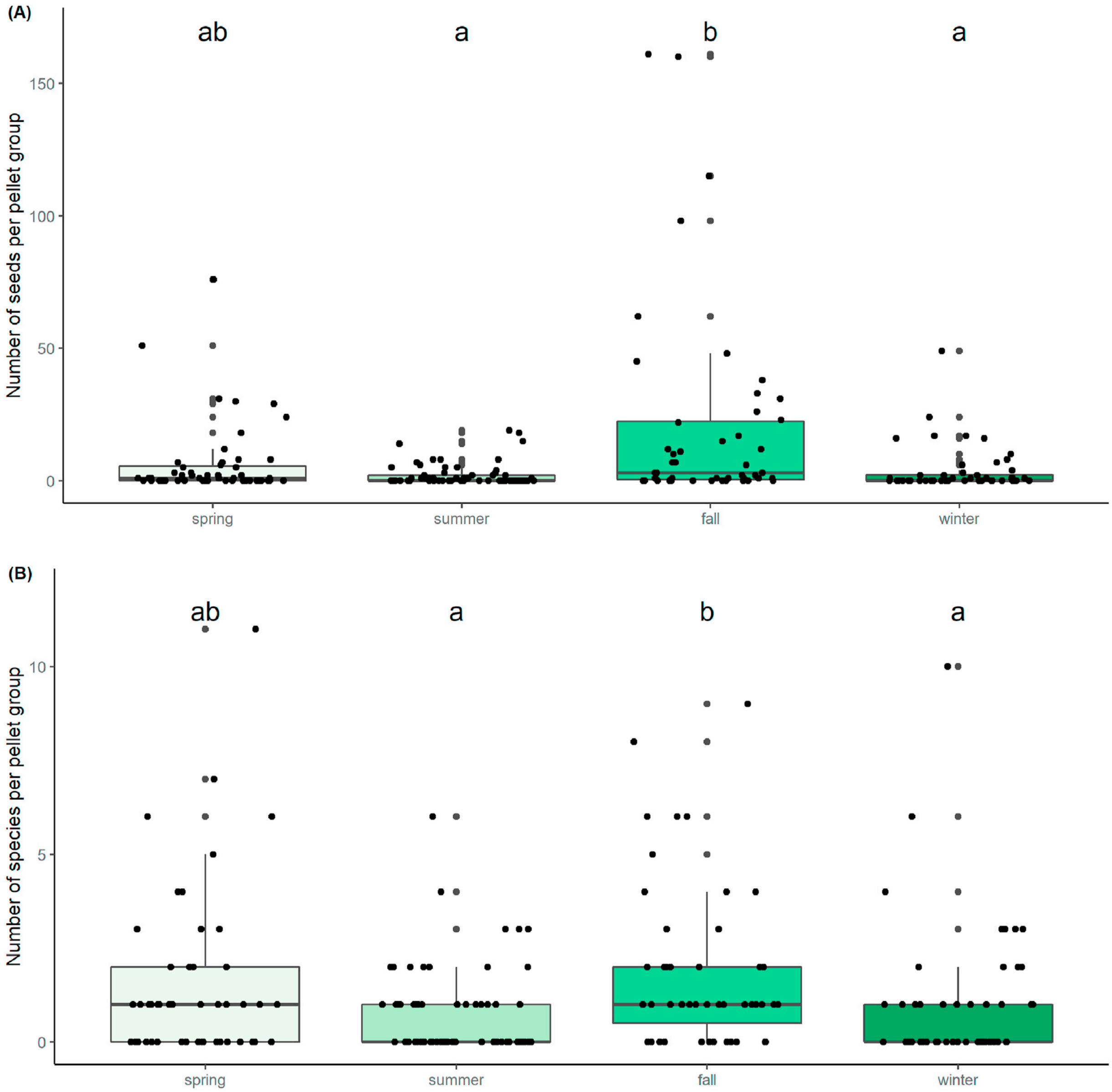

Fig. 3. Number of seeds (A) and species (B) germinated per Korean water deer fecal pellet group according to season (spring: March–May; summer: June–August; fall: September–November; winter: December–February). Statistically significant means are marked with different letters (Kruskal–Wallis test with multiple pairwise test with Bonferroni correction; $p < 0.05$).

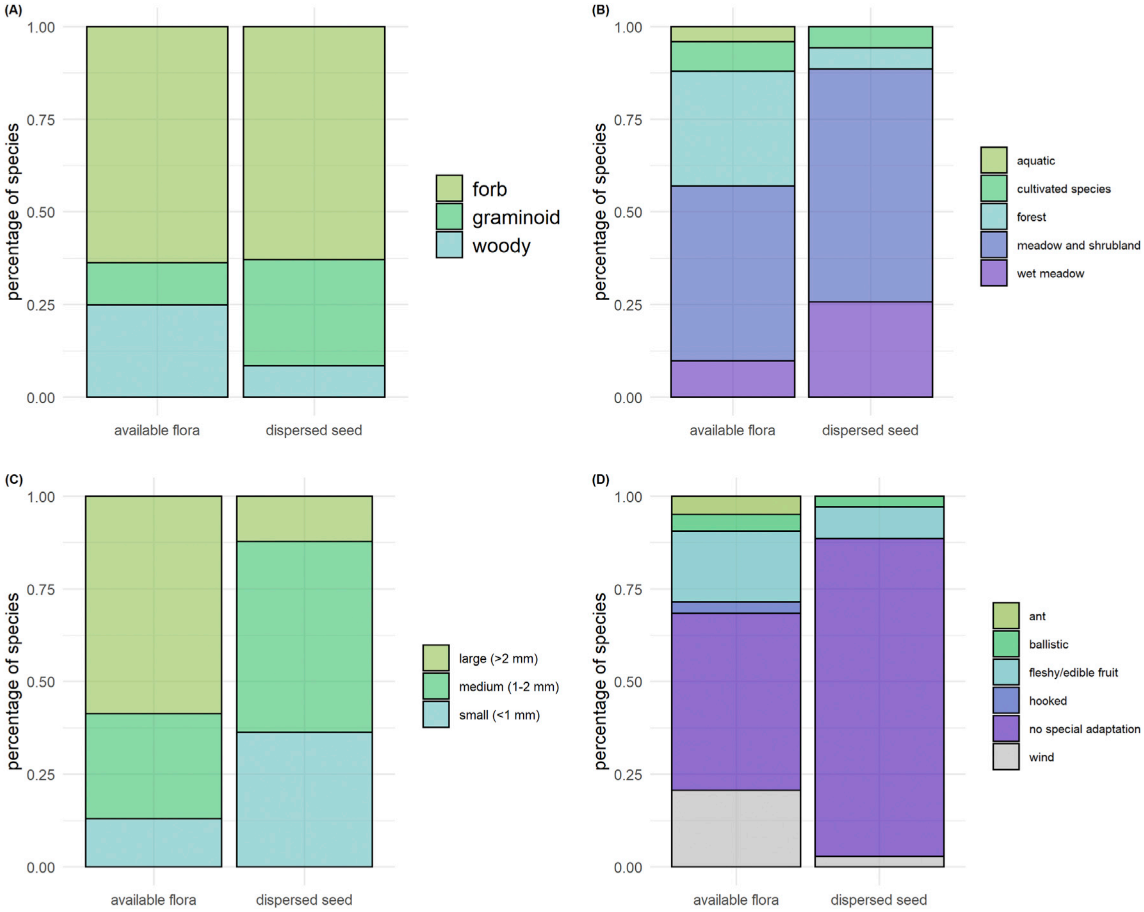

Fig. 4. Proportion of plant traits from the available flora and the seeds germinated from the feces of Korean water deer. (A) Growth form (Fisher's exact test, $p < 0.01$) (B) habitat (Fisher's exact test, $p < 0.001$) (C) seed length (Fisher's exact test, $p < 0.0001$) (D) diaspore type (Fisher's exact test, $p < 0.01$).

According to an analysis of the diet of Korean water deer in lowland areas (Kim et al., 2011), graminoids and woody species constituted only 4.4% and 1.1% of the total diet, respectively, while forb species accounted for 94.5%. This is in agreement with the diet selectivity of this small-sized deer species (concentrate selector), which may explain the high number of forb seeds dispersed in fall in the present study. Picard et al. (2016) concluded that endozoochorous dispersal was rather linked to the diet and feeding behavior of the herbivores. So, habitat feeding preference of deer might be the primary determinant for a plant dispersed by endozoochory. The secondary determinant would be whether the seeds of a given species could survive ingestion. Studies on the relationship between deer diet and endozoochory in different habitats will give us insight into the efficiency of endozoochory and how the dietary preferences of deer affect the dispersal potential of seeds.

Seed dispersal through endozoochory is known to result in a relatively low germination rate in the field (Pakeman and Small 2009). However, although ingestion usually induces lower recovery and germination rates (Cosyns et al., 2006; Milotić and Hoffmann 2016b), endozoochory allows for dispersal over longer distances and the nutrients in feces can help seeds that do germinate to grow better in the longer term (Milotić and Hoffmann 2016a). Additionally, as more seeds and species are dispersed in fall, environmental factors such as temperature and desiccation of the feces will possibly impact post-dispersal events. Thus, further investigations with empirical testing are required to determine the efficiency of endozoochorous seed dispersal and to further understand its costs and benefits.

4.2. Korean water deer as a seed dispersal vector in lowland areas of South Korea

The CCZ, together with the DMZ, is known for its high biodiversity. However, habitat change and forest fragmentation is ongoing in the region (Sung et al., 2019). The CCZ in Paju City is under particularly high development pressure since it is close to Seoul, the capital of South Korea. Under these circumstances, Korean water deer may contribute to the maintenance of connectivity among plant populations by dispersing seeds between habitat patches. Since the Korean water deer prefers open areas (Lee et al., 2017), recent increases in habitat fragmentation are worsening human–wildlife conflicts throughout South Korea, especially in lowland areas (Kim et al., 2016). Deer are considered vermin in South Korea (Ministry of Environment

2015) due to their high density in the region and the damage that they cause to agricultural products. However, internationally, the Korean water deer is considered vulnerable and is on the IUCN Red List of Threatened Species. The natural distribution of Korean water deer population is restricted mainly to the Korean peninsula. So, it is important to recognize the potential role of Korean water deer for conservation and to develop careful plans to manage their populations. From the present research, we conclude that the Korean water deer can act as seed dispersal vector, aiding in the long-distance dispersal of plant species, which is related to the dynamics and diversity of regional plant communities in lowland areas of South Korea.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2020.e01368.

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