



## Seed dispersal between aquatic and agricultural habitats by greylag geese

María J. Navarro-Ramos<sup>a,\*</sup>, Casper H.A. van Leeuwen<sup>b</sup>, Camilla Olsson<sup>c</sup>, Johan Elmberg<sup>c</sup>, Johan Månsson<sup>d</sup>, Víctor Martín-Vélez<sup>a,e</sup>, Ádám Lovas-Kiss<sup>f,g,h</sup>, Andy J. Green<sup>a</sup>

<sup>a</sup> Department of Conservation Biology and Global Change, Estación Biológica de Doñana, CSIC, Américo Vespucio 26, 41092 Sevilla, Spain

<sup>b</sup> Netherlands Institute of Ecology (NIOO-KNAW), Droevendaalsesteeg 10, 6708 PB Wageningen, the Netherlands

<sup>c</sup> Faculty of Natural Sciences, Kristianstad University, SE-291 88 Kristianstad, Sweden

<sup>d</sup> Grimsö Wildlife Research Station, Dept of Ecology, Swedish Univ. of Agricultural Sciences, Uppsala, Sweden

<sup>e</sup> Departamento de Ciencias de la Vida, Universidad de Alcalá, Alcalá de Henares, Madrid, Spain

<sup>f</sup> Wetland Ecology Research Group, Centre for Ecological Research, Institute of Aquatic Ecology, Bem sq. 18/C, 4026 Debrecen, Hungary

<sup>g</sup> Institute of Metagenomics, University of Debrecen, Debrecen, Hungary

<sup>h</sup> ELKH-DE Conservation Biology Research Group, Debrecen, Hungary

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### ABSTRACT

Waterbirds disperse plant seeds within and between aquatic and terrestrial ecosystems in their faeces. However, seed dispersal distances, connectivity among habitat types, and implications for dispersal of weeds remain unquantified in agricultural landscapes. Therefore, we GPS-tagged 31 greylag geese *Anser anser* and collected 300 faecal samples from feeding flocks in seven agricultural habitats (four cereals, hayfields, pasture, and strawberries) across two landscapes in southern Sweden. We identified intact seeds, determined key plant traits, and tested three hypotheses: (1) geese ingest, transport, and egest seeds from a wide range of terrestrial and aquatic plants, including weeds and alien species; (2) the community and trait composition of plant seeds in faeces vary between habitat types; and (3) seed dispersal by geese is a directional dispersal mechanism that connects some habitat types more than others. We recovered 131 seeds from 41 plant species (19 families), including nine agricultural weeds and one alien species. Many seeds were from aquatic plants (45%), dispersed into terrestrial habitats. A connectivity network formed between habitat types (as nodes) and direct flights (as links) revealed that all agricultural habitats were directly connected with each other, although 66% of flights were between aquatic and agricultural habitats. Geese spent most time at lakes (34%), pastures (14%), barley (10%) and wheat (8%) fields, which were also the most interconnected habitats, with high seed species richness and seed abundance in faecal samples. Combining waterfowl movement data with faecal analysis provided support for all three hypotheses. Geese may contribute to previously overlooked agricultural conflicts through weed dispersal. Proximity to aquatic habitats suitable for roosting may increase the use of agricultural habitats, and potentially the seed dispersal into them.

### 1. Introduction

Understanding seed dispersal in agricultural landscapes allows for the prediction of how plant species may adjust spatially to habitat destruction, land use change and climate change, or – alternatively – how alien and weed species will spread (Baguette et al., 2012; van Leeuwen, 2018). Waterbirds act as key vectors of seeds in aquatic and terrestrial ecosystems, allowing plants to reach new habitats through their daily and seasonal movements (Kleyheeg et al., 2017; Green et al., 2016, 2023). However, the importance of waterbirds for seed dispersal has been less studied than the role of many other animal vectors (van

Leeuwen et al., 2020, 2022).

Waterbirds disperse seeds because a fraction of ingested seeds survives gut passage, and is egested elsewhere (i.e. endozoochory, van Leeuwen et al., 2022). Smaller numbers of seeds can also be carried externally (i.e. epizoochory, Green et al., 2023). An increasing number of studies based on faecal analyses has revealed that many plants with a wide range of seed morphologies and other plant traits are regularly dispersed by gulls, herons, ducks, shorebirds, and other waterbirds (Green et al., 2022; Martín-Vélez et al., 2021a, 2021b; Navarro-Ramos et al., 2022; Urgyán et al., 2023). However, faecal sampling alone does not demonstrate where seeds are ingested, and what are the dispersal

\* Corresponding author.

E-mail address: [mjnavarro@ebd.csic.es](mailto:mjnavarro@ebd.csic.es) (M.J. Navarro-Ramos).

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distances or trajectories.

Spatiotemporal aspects of seed dispersal can be studied by combining GPS tracking of waterbirds with faecal samples collected from habitats frequented by waterbirds. However, faecal analysis and GPS tracking of waterbirds has to date been carried out independently, with the exception of a study of gulls wintering in ricefields (Martín-Vélez et al., 2021a, 2021b). The combination of both methods can be used to identify how waterbirds may contribute to connectivity of plant communities in different habitats (Green et al., 2023) and therefore to identify habitats that may be affected by the presence of waterbirds.

The majority of waterbird endozoochory studies have focused on the role of dabbling ducks such as mallards (*Anas platyrhynchos*), which are abundant, widely distributed, and suitable for captive experiments (Green et al., 2016; Uryán et al., 2023). Fewer studies have focused on geese, and we focus on the greylag goose (*Anser anser*), a large, abundant waterfowl widely distributed in Eurasia. The European population is estimated at 950,000 individuals (Wetlands International, 2023). The agricultural impacts of this species through grazing are well investigated (Powolny et al., 2018; Buitendijk et al., 2022; Zhang et al., 2022), but its role in seed dispersal and habitat connectivity is poorly understood. Greylag geese gather in flocks and feed during the day in terrestrial habitats (e.g. grasslands, agricultural fields) near aquatic habitats where they roost at night, safe from terrestrial predators (Avé et al., 2017; Fox et al., 2017). In Sweden, agricultural habitats are frequently used by breeding populations of several goose species (Olsson et al., 2017). Faecal analyses in Swedish Baltic archipelagos have revealed the ability of greylag geese to disperse at least 97 plant species by endozoochory (Hattermann et al., 2019). Compared to dabbling ducks, greylag geese disperse relatively more terrestrial plants and fewer aquatic plants (Almeida et al., 2022).

It is important to evaluate the role of increasing geese populations as vectors of plant dispersal in agricultural habitats, and consider possible implications for spread of weeds. Our main objectives were to quantify seed dispersal by greylag geese in agricultural landscapes, identify key traits of plant species dispersed, and to determine how waterbird-mediated dispersal connects different habitats in such landscapes. Therefore, we collected goose faeces in seven agricultural habitat types within two areas in southern Sweden, and analysed movements of adult geese within these areas. We combined tracking data with the simultaneous collection of faeces in habitats visited by the GPS-tracked individuals. We hypothesised that (1) greylag geese ingest, transport and egest a wide range of terrestrial and aquatic plant seeds, including weeds, native and alien plant species, and seeds with a variety of sizes and morphological dispersal syndromes. Owing to limited research effort to date, we expected to find plant species not previously known to be transported by waterfowl (Anatidae); (2) the community and trait composition of seeds in faeces is unique to each habitat, and related to the level of connectedness of that habitat with other habitat types; and (3) seed dispersal by geese is not a random but a directional dispersal mechanism that connects some habitat types more than others.

## 2. Material and methods

### 2.1. Study species

The greylag goose has expanding populations in northern Europe that often cause agricultural conflicts by reducing yields of grass, cereals and other crops (van Eerden et al., 2005; Buitendijk et al., 2022). The flyway population that includes Sweden has 710,000–780,000 individuals (Wetlands International, 2023). Greylag geese are herbivores feeding mainly in terrestrial habitats, including post-harvest residual crops (van Eerden et al., 2005). They consume up to one third of their body mass daily (~3.3 kg body weight). The proportion of birds wintering at more southern latitudes has declined markedly over the past three decades due to changes in land-use and climate, leading to increases in overall geese numbers and shifts towards northern Europe

(Ramo et al., 2015; Fox and Madsen, 2017; Powolny et al., 2018). In Sweden, the breeding population has also increased, and some of these birds now overwinter in the southernmost parts of the country (Nilsson, 2018; Månsson et al., 2022).

### 2.2. Study areas

This study was carried out in two agricultural landscapes: an area close to the city of Kristianstad in the south (56°01'N, 14°09' E) and an area close to the city of Örebro in south-central Sweden (Kvismaren, 59°10' N, 15°22' E) (Fig. 1). Both study landscapes consist of a similar mosaic of shallow lakes, wetlands, forests, grasslands and agricultural fields, according to the CORINE land use categories (2012, CLC; <https://land.copernicus.eu/>). Both areas are dominated by cereal crops, mainly wheat, barley, rye and oats, but there are also natural grasslands, as well as other crops (Fig. 1). Generally, most crops are harvested from mid-August through October, and some of the cereal crops are re-sown the same autumn in the southernmost parts of the country. The Kristianstad area has a longer growing season and a higher variety of crops, including sugar beet, potatoes, rapeseed, maize and a wide range of vegetables, fruits and other root crops. In both areas, wetlands and lakes are important breeding and roosting sites for geese (Månsson et al., 2022; Nilsson et al., 2022). There are no irrigation canals, drainage ditches or other waterbodies within agricultural habitats.

In both areas, there are three types of grass-dominated fields: 1) pastures, that are grazed by livestock at least part of the year; 2) hayfields, mown several times annually for feed production; and 3) natural, unmanaged grasslands. All three field types are typically composed of a mixture of plant species (e.g. *Trifolium repens*, *Phleum pratense*, *Festuca pratensis*), but grasslands and pastures have a higher species richness than hayfields, which are sown for the sole purpose of feed production.

Geese usually visited fields post-harvest as they preferred to feed on short swards of grasslands (Durant et al., 2004; Fox et al., 2017) and postharvest residuals (Olsson et al., 2017). We collected goose faeces in two grassland types (pastures and hayfields) plus wheat and barley fields. Additional habitats were sampled both in Kristianstad (rye and strawberries) and Örebro (oats). In September 2019, a total of 5300 greylag geese were present in Kristianstad and 6000 in Örebro according to ground counts made by experienced personnel.

### 2.3. Greylag goose movements

Goose movements and connectivity among different habitats were analyzed among the terrestrial habitat types in which it was possible to collect faecal samples, and additionally across lakes, wetlands and islands used for roosting. Movements of 31 greylag geese were monitored between the 1st of June and September 30th 2019 (121 days). In June 2017–2019, individuals greylag geese were captured when foraging in fields and equipped with a solar powered GPS tracking device (Ornitela OT-N35 or OT-N44) that sent a position every 15 min (i.e. modulus of 15) to the Global System for Mobile Communications (GSM) network with an accuracy of  $\leq 10$  m. For further details of the catching procedures and tracking equipment, see Månsson et al. (2022). All catching and handling of geese was performed in 2017–2019 under permit from the Animal Ethics Committee of Central Sweden (# 5.8.18–03584/2017). GPS coordinates were overlaid with cropland maps based on the CORINE Land Cover 2012 and the Swedish Mapping Cadastral and Land Registration Authority.

### 2.4. Faecal sampling

Faecal samples were collected on 28 days between August 6th and September 13th 2019 in fields selected using greylag goose movements. As geese forage and move in flocks (Scheiber et al., 2013), we assumed that GPS-tagged individuals indicate the position of flocks of geese. Based on the position of GPS-tagged individuals, each sampling day

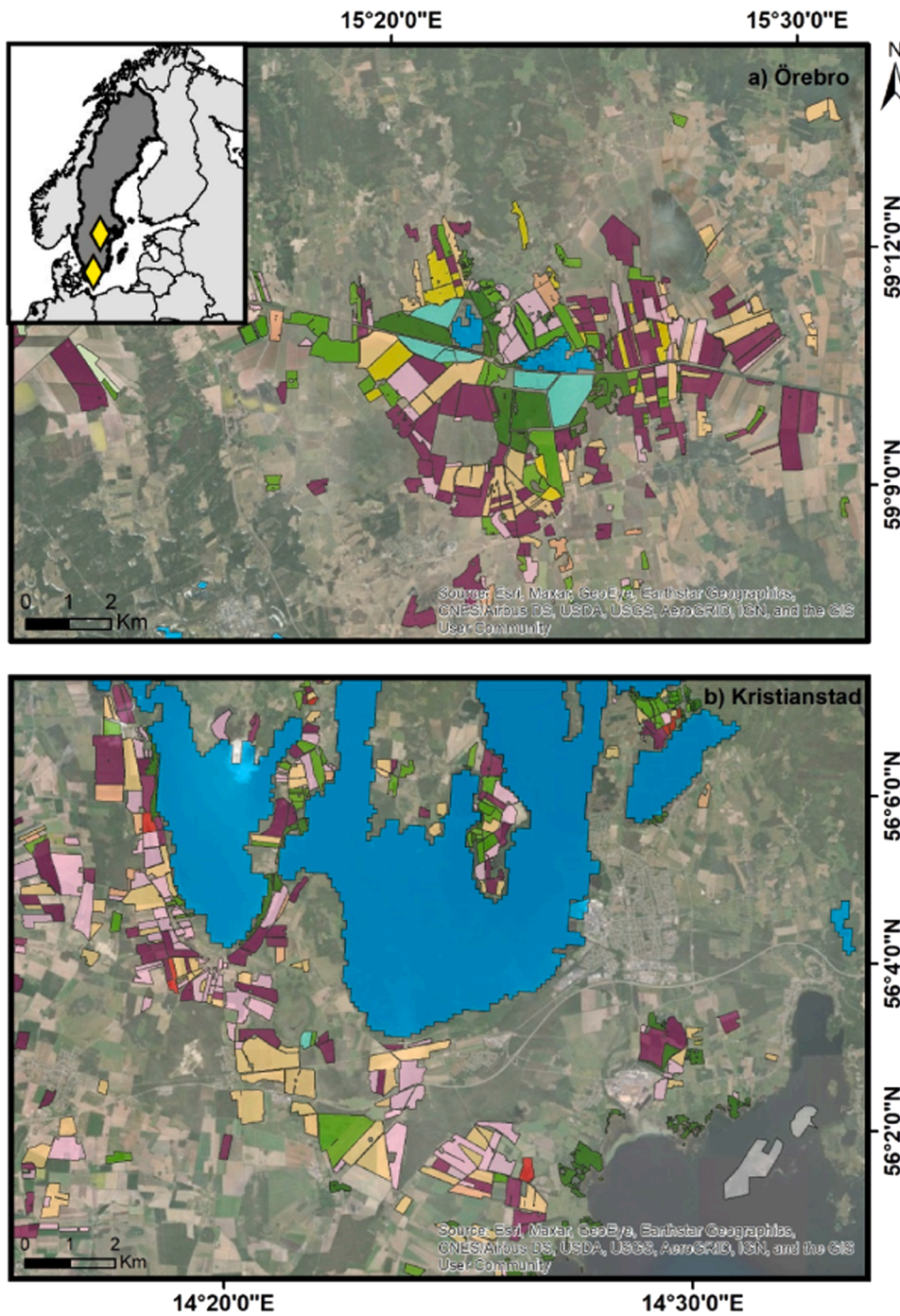


Fig. 1. : Habitat types of the two study locations, showing fields and habitats visited by GPS-tracked geese. (a) Örebro and (b) Kristianstad and around lake Ivö. The background images show other habitats (including other agricultural habitats) that were not visited by our GPS-tracked geese during summer 2019. All polygons coloured according to the legend belong to habitats used by geese. Orthophoto © Swedish Mapping Cadastral and Land Registration Authority, Dnr 2012/892. Insert map shows location of the study areas in Sweden (Örebro northern diamond, Kristianstad southern).



started by selecting the fields for faecal sampling, using exclusively the daily movement data for the 24 h before. Fields were selected where target geese had been present within the past 24 h, and GPS-positioning did not measure instantaneous speeds of > 3 km/h or > 100 m altitudes. This exclusion criterion ensured that fixes in flight were eliminated, allowing us to focus on geese that remained stationary in the selected fields. After identifying fields used by 5–10 target geese, we randomly selected some fields to sample faeces, beginning in early morning. Fresh faeces were collected, with at least 2 m between samples to avoid repeated sampling of the same individual. Each faecal sample was

placed in a plastic bag and refrigerated at 4 °C until seed extraction. We used one GPS-tagged goose to identify each field sampled, although sometimes more than one tagged individual was present in the same field. No field was visited more than once in the same week. In total, 123 faecal samples were collected across six habitats in Kristianstad, and 177 samples across five habitats in Örebro (Table S2).

### 2.5. Seed sample processing

Faecal samples were weighed using a precision balance (Sartorius

MSE225P-100-DA,  $d = 0.01$  mg), then washed with tap water over a 100  $\mu\text{m}$  sieve. Sieve contents were examined for plant seeds in petri-dishes under a stereomicroscope (Stemi 2000-C, Carl-Zeiss). Intact retrieved seeds were photographed with ZEN 2–2.0 software (Carl-Zeiss) and identified to the lowest possible taxonomic level (Bojnanský and Fargašová, 2007; Cappers et al., 2012). When species identification was not possible, genus or family was recorded. All samples were processed within 8 months of collection, with an average delay of 19 weeks.

Mean seed length, Ellenberg F habitat indicator for soil moisture, and morphological dispersal syndromes were obtained as traits for each plant species from the BASEFLOR database (Julve, 1998), LEDA trait-base (Kleyer et al., 2008) or ECOFACT database (Hill et al., 1999). Alien and weed status were determined according to the Euro+Med Plantbase (Euro+Med, 2006+) and the AgroAtlas of Russia (Afonin et al., 2008). Ellenberg F-values indicate the soil moisture preference of each plant species, and range from 1 to 12 (1–2 represents very dry, 3–6 dry to moist, 7–9 moist to wet and 10–12 wet or submerged habitats). We considered aquatic plants to be those with  $F \geq 7$ .

## 2.6. Germination and viability tests

Intact seeds were placed in Petri-dishes with 1% of bacteriological agar in a germination chamber (Binder KBW400) with a 12 h light (22 °C) and 12 h dark (18 °C) cycle. Germination tests were run for three months and checked on almost daily basis for germination. For ungerminated seeds not infected by fungi during germination trials, a Tetrazolium Chloride Test (TZ) was later used to assess viability (following Brochet et al., 2010; Farmer et al., 2017). Prior to the TZ test, seeds were soaked in water for 24 h and a longitudinal cut was made in the seed coat with a scalpel. Seeds were then placed in multidish wells with a 1% tetrazolium solution at 25 °C in the dark. Seeds that turned red or pink within 48 h were considered viable. These viability tests are highly conservative, as they were conducted over one year after samples were collected, and seed viability can decline rapidly after gut passage (Martín-Vélez et al., 2021a).

## 2.7. Movement analysis

Greylag goose movement data were analysed using the following parameters from the GPS devices: individual bird (ID), date, time of day, latitude, longitude, altitude and instantaneous speed. We applied three filters to the raw data related with longitude, latitude, horizontal dilution of precision and data position frequency (see supporting information S1). After filtering, all 31 individuals were retained in the movement database. As well as identifying fields used for faecal sampling (see above), GPS data from June to September ( $94 \pm 13$  days, mean  $\pm$  SD) were used to create a connectivity network to analyse how geese moved among different habitat types.

We distinguished 12 habitat types for the connectivity network, which formed the nodes of a general network for the two study areas combined (details in Table S1). As well as habitats where faeces were collected, five additional habitats were included in the analysis because they were considered hotspots in terms of goose activity, based on the movement data (see supporting information S1). The network was established on direct flights (DF) of geese between nodes, i.e. non-stop flights from one habitat to another when speed  $> 3$  m/s. The nodes represent all the habitat types visited by the tagged geese, and the links represent direct flights in the directions indicated by arrows. The importance of each habitat (i.e. node) was assessed based on calculating two centrality measures: “strength” and “betweenness”. The “strength” measure was an indication of the total number of direct flights (i.e. links) connecting a habitat type/node, and the “betweenness” identified which habitat type/node was used most as the shortest path between two other habitat types/nodes (Brandes, 2001). We used the iGRAPH package in R to build the network and calculate centrality measurements (Csardi and Nepusz, 2006). We also calculated mean distances covered between

habitats by geese.

## 2.8. Statistical analyses

Seed data from faecal samples were analysed using two Generalized Linear Mixed-effects Models (GLMMs). We used negative binomial distributions in the package glmmTMB (Brooks et al., 2017) in R to control for zero-inflated data (only 18% of samples contained seeds). Dependent variables were (1) the number of intact seeds per sample (hereafter “abundance”), and (2) the number of taxa per sample (hereafter “richness”). We also performed separate models for aquatic and terrestrial plant taxa. Habitats present in only one study area were excluded from the analyses to allow models to converge, thus removing three habitats (strawberries, rye, and oats). The remaining four habitat categories (pastures, hayfield, wheat, and barley) were included as levels of a fixed factor. Study area (Kristianstad or Örebro) was included as a random intercept (‘Site’), although the plant distributions in both areas were similar (www.artfakta.se/artbestamning). Variation in sample mass was controlled with a continuous predictor variable. Differences among habitat types were assessed with Tukey’s HSD post hoc tests (Abdi and Williams, 2010). To identify outliers and to assess the distribution of residuals, quantile-quantile plots were compared with fitted values, but no outliers were found.

The number of faecal samples collected differed among the habitat types, potentially biasing comparisons among habitat types in plant species richness. To correct for this sampling error effect, we carried out a rarefaction analysis using the R package “iNEXT” (Sanders, 1968; Hsieh et al., 2016). To identify differences in the plant community composition among the habitats, we used non-metric multidimensional scaling. We applied the metaMDS function in the package “vegan” using a Bray-Curtis distance matrix (Oksanen et al., 2010). Data were transformed using Wisconsin double standardization, and convergence was reached after 20 iterations (stress score  $< 0.1$ ). All statistical analyses were performed in R software version 3.6.3 (R Core Team, 2023).

## 3. Results

### 3.1. Plant species dispersed into different habitats

Faeces were collected within seven habitat types (Table 1, Fig. 1), and intact plant seeds were recovered in faeces from all of these habitats except oat fields. Faecal sample mass was  $8.36 \pm 4.79$  g (mean  $\pm$  SD, range = 1.77–35.04 g,  $n = 300$ ). In total, 131 intact seeds were recovered from 41 plant species and 19 families (Table 1). The mean abundance of seeds per sample was  $0.40 \pm 1.32$  SD and the mean number of plant species was  $0.24 \pm 0.71$  SD. Although we only sampled terrestrial habitats, seed abundance and richness were equally divided between aquatic and terrestrial plants. For aquatic plants, mean seed abundance was  $0.20 \pm 0.88$  and mean richness was  $0.12 \pm 0.49$ . For terrestrial plants, mean abundance was  $0.20 \pm 0.83$  and mean richness was  $0.12 \pm 0.37$ . Overall, 10% of the samples contained a single intact seed and another 8% contained at least two, with a maximum of 11 seeds per sample. Overall, seed viability after gut passage was confirmed for 54% of plant species recorded either by our own germination or tetrazolium tests, or by previous field studies of greylag geese in Sweden (Table 1).

Mean seed length ranged from 0.37 (*Juncus bufonius*) to 7.84 mm (*Bromus secalinus*; Table 1). Morphological dispersal syndromes were identified for 38 species, and included epizoochory ( $n = 10$ ), hydrochory ( $n = 12$ ), barochory ( $n = 8$ ) and anemochory ( $n = 7$ ) syndromes. The strawberry was the only taxon with an endozoochory syndrome (Table 1).

*Conyza canadensis* is an alien species in Sweden and 11 taxa are considered agricultural weeds in Sweden (Table 1). Only 18 species were terrestrial, i.e. Ellenberg  $F \leq 6$ . A total of 23 aquatic taxa were moved into terrestrial habitats, including four *Potamogeton* species (*P. bertholdii*, *P. gramineus*, *P. obtusifolius*, and *P. pectinatus*). Overall,

**Table 1**

Details of intact seeds recovered in greylag goose droppings collected on agricultural lands (n = 300). Information is provided on dispersal syndromes (Julve, 1998), alien/native status, Ellenberg F values (3–6 represent dry to moist, 7–9 moist to wet and 10–12 wet or submerged habitats), seed length, crop type (W=Wheat, B=Barley, R=Rye, H=Hayfield, P = Pasture, S=Strawberries), total number of intact seeds (TI) and the number of samples with each taxon (NS). V identifies cases where viability was confirmed: † = germinated after *Anser anser* gut passage by Jerling et al. (2001); Hattermann et al. (2019); ‡ = seeds germinated in this study; \* = viability confirmed with tetrazolium in this study. Species marked in bold and underlined indicate alien and cultivated, respectively. <sup>a</sup>species considered agricultural weeds (sensu Afonin et al., 2008) and <sup>b</sup>species with herbicide resistance population (sensu Heap, 2009).

Family	Species	Dispersal syndrome	Ellenberg F	Length (mm)	TI	NS	V	Crop type
Poaceae	<i>Agrostis gigantea</i> <sup>a</sup>	Barochory	6	1.75	1	1	*	P
Alismataceae	<i>Alisma plantago-aquatica</i> <sup>a,b</sup>	Hydrochory	10	1.1	2	1	*	R
Poaceae	<i>Alopecurus pratensis</i>	Barochory	5	2.36	3	2	†	P
Caryophyllaceae	<i>Arenaria serpyllifolia</i> <sup>b</sup>	Anemochory	3	0.4	2	1	†*	W
Betulaceae	<i>Betula pendula</i>	Anemochory	5	3.2	9	8	†	W, B, P, S
Poaceae	<i>Bromus secalinus</i> <sup>a,b</sup>	Epizoochory	4	7.84	1	1		W
Cyperaceae	<i>Carex aquatilis</i>	-	10	1.98	3	1		P
Cyperaceae	<i>Carex echinata</i>	Hydrochory	8	1.55	1	1		P
Cyperaceae	<i>Carex elata</i>	Hydrochory	10	2.46	1	1		P
Caryophyllaceae	<i>Cerastium semidecandrum</i>	Anemochory	3	0.45	1	1	†	P
Chenopodiaceae	<i>Chenopodium album</i> <sup>a,b</sup>	Barochory	5	1.29	1	1	‡	P
Asteraceae	<i>Conyza canadensis</i> <sup>a,b</sup>	Anemochory	4	1.19	4	2		P
Cyperaceae	<i>Eleocharis palustris</i>	Epizoochory	10	1.87	1	1		P
Cyperaceae	<i>Eleocharis parvula</i>	Hydrochory	10	0.9	10	3	‡	W, P
Cyperaceae	<i>Eleocharis mammillata</i>	Barochory	10	1.38	1	1	*	P
Onagraceae	<i>Epilobium parviflorum</i>	Anemochory	10	0.82	2	2		P, S
Poaceae	<i>Festuca pratensis</i>	Epizoochory	6	3.65	1	1		H
Rosaceae	<i>Fragaria x ananassa</i> (Strawberry)	Endozoochory	5	1.5	12	2	*	W, S
Poaceae	<i>Helictotrichon pratense</i>	-	4	5.4	1	1		B
Plantaginaceae	<i>Hippuris vulgaris</i>	Hydrochory	10	1.85	1	1	*	B
Juncaceae	<i>Juncus conglomeratus</i>	Epizoochory	7	0.53	11	4	*	P
Juncaceae	<i>Juncus bufonius</i> <sup>a</sup>	Epizoochory	7	0.37	1	1	†	P
Lamiaceae	<i>Lycopus europaeus</i>	Hydrochory	8	1.44	1	1		P
Boraginaceae	<i>Myosotis scorpioides</i>	Barochory	9	1.71	1	1	‡	B
Poaceae	<i>Phleum pratense</i>	Epizoochory	5	1.63	1	1	*	P
Poaceae	<i>Phragmites australis</i> <sup>a</sup>	Anemochory	10	3.29	2	2		P
Plantaginaceae	<i>Plantago major</i> <sup>a</sup>	Barochory	5	1.58	1	1		W
Potamogetonaceae	<i>Potamogeton bertholdii</i>	Hydrochory	12	2.25	3	3	‡*	W, B
Potamogetonaceae	<i>Potamogeton gramineus</i>	Hydrochory	12	2.63	1	1		W
Potamogetonaceae	<i>Potamogeton obtusifolius</i>	Hydrochory	12	3.5	4	2	‡*	W, B
Potamogetonaceae	<i>Potamogeton pectinatus</i>	Hydrochory	12	4.05	5	3	*	W, B
Ranunculaceae	<i>Ranunculus repens</i> <sup>a</sup>	Epizoochory	7	2.53	1	1	*	P
Polygonaceae	<i>Rumex hydrolapathum</i>	Hydrochory	10	3.51	1	1		W
Caryophyllaceae	<i>Sagina nodosa</i>	Barochory	7	0.38	1	1		P
Typhaceae	<i>Sparganium angustifolium</i>	Hydrochory	11	3.13	1	1		W
Caryophyllaceae	<i>Spergularia media</i>	Anemochory	8	1.04	5	2		B, P
Caryophyllaceae	<i>Stellaria media</i> <sup>a,b</sup>	Barochory	5	1.02	18	11	‡‡	W, B, H
Fabaceae	<i>Trifolium repens</i> <sup>a</sup>	Epizoochory	5	1.16	2	2	*	P
Urticaceae	<i>Urtica dioica</i>	Epizoochory	6	1.21	2	1	†	W
Poaceae	<i>Hordeum vulgare</i> (Barley)		4		1	1		B
Poaceae	<i>Triticum aestivum</i> (Wheat)	Epizoochory	5	6.75	2	2		W, S
Juncaceae	<i>Juncus sp.</i>				1	1	*	B
Poaceae	<i>Poa sp.</i>				2	2		B, P
Poaceae	<i>Poaceae</i>				5	4	‡	W, B, R, P
<b>TOTAL</b>					<b>131</b>			

45% of the plant seeds were from aquatic plants, but their proportion was higher in rye and pasture habitats (Fig. 2). Pasture was the habitat with the highest number of plant taxa in faeces, representing 62% of those recorded, even though more samples were collected from barley and wheat (Table S2).

Seed abundance and seed richness did not differ significantly among habitats (Table 2). Similar results were obtained when analysing aquatic and terrestrial plants separately ( $p \geq 0.07$ , Table S4). However, rarefaction analysis for four habitats sampled in both study areas suggested that species richness was much higher in pastures, much lower in hayfields, and intermediate in wheat and barley (Fig. S3). Mean seed abundance and richness were high in the few samples we collected in the strawberry fields (Fig. 2).

Heavier faecal samples contained significantly more seeds and a higher species richness (Table 2). When analysed separately, sample weight had a significant effect for terrestrial plants (abundance:  $Z = 2.6$ ,  $p = 0.01$ ; richness:  $Z = 2.48$ ,  $p = 0.01$ ), but not for aquatic plants (Table S4). Taxonomic composition of the seeds differed among habitats, with only 27% of taxa recorded in at least two habitat types, and

41% of the species only recorded in pasture (Fig. 3).

### 3.2. Habitat connectivity network

There were 12 main habitat types visited by greylag geese: 10 terrestrial (wheat, barley, rye, oats, strawberries, hayfields, pastures, grasslands, islands, and “other crops”) and two aquatic habitats (lakes and wetlands, Fig. 1). A total of 16384 direct flights were performed over 121 days (7381 flights by 13 individual geese in Kristianstad, and 9003 flights by 19 individuals in Örebro (Table S3, Figs. S1, S2). An average goose therefore performed  $5.61 \pm 3.39$  (mean  $\pm$  SD) direct flights per day in late summer between different habitats. There were  $1.77 (\pm 1.45$  SD) flights per day from an aquatic to a terrestrial habitat,  $1.94 (\pm 1.51$  SD) flights from terrestrial to aquatic habitat,  $1.75 (\pm 2.24$  SD) between two terrestrial habitats, and only  $0.15 (\pm 0.52$  SD) between lakes and wetlands. For all flights, 80% were done during daylight hours, whereas 20% were night flights.

All pairs of habitats were interconnected by at least one direct flight, although four (pastures, lakes, wheat and barley) were more strongly

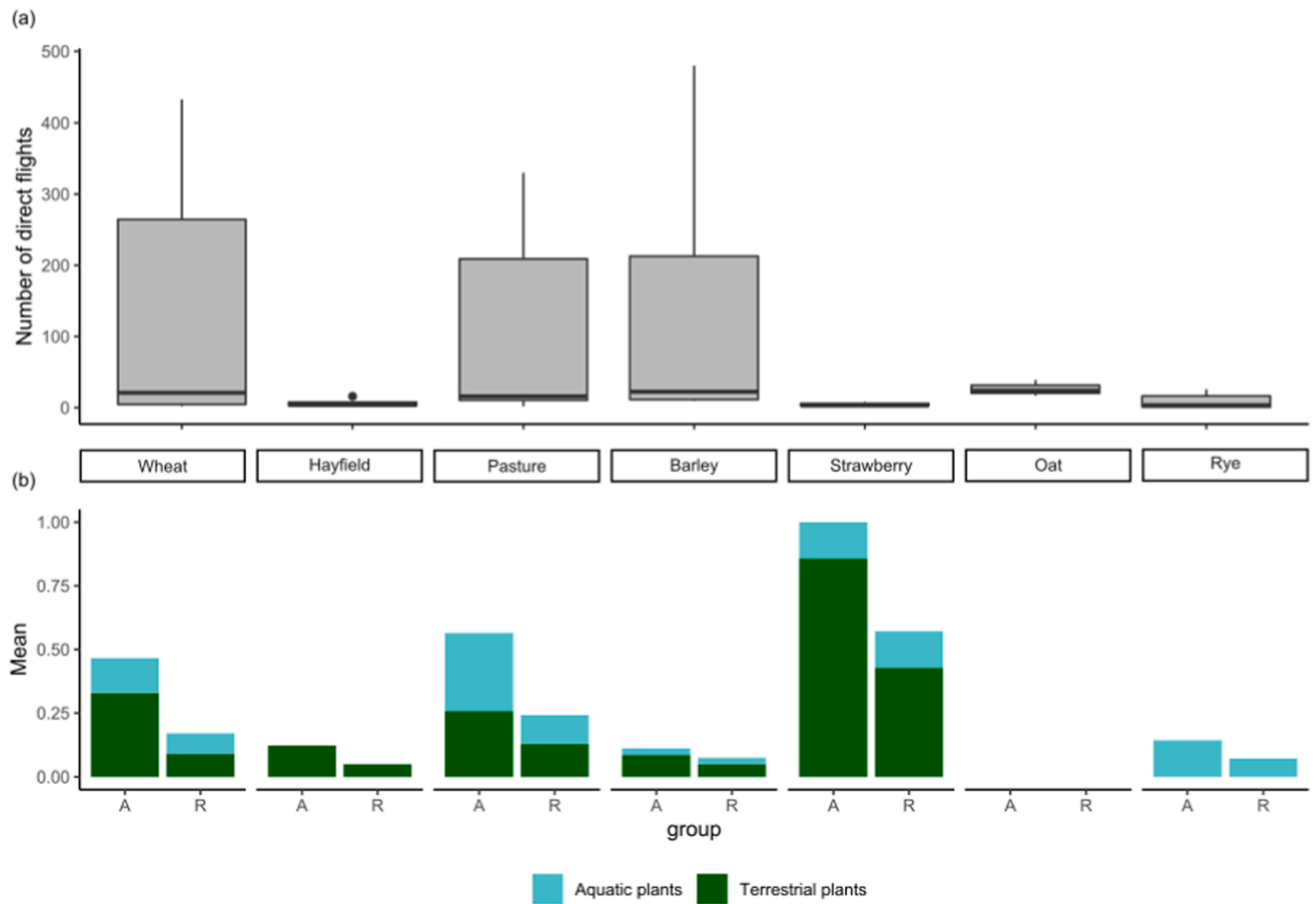


Fig. 2. : (a) Number of direct flights arriving to each habitat for each of 31 tagged geese. The boxes in the plot represent the middle 50% of the data for each habitat type, with the line inside the box representing the median value. The top of the box represents the 75th percentile, and the bottom of the box represents the 25th percentile for the set of geese. Lower and upper whiskers represent maximum and minimum values of the data, excluding outliers that are represented by dots, (b) Mean values of seed abundance (A) and richness (R) of plant species according to Ellenberg F moisture values ( $F \geq 7$  for aquatic plants).

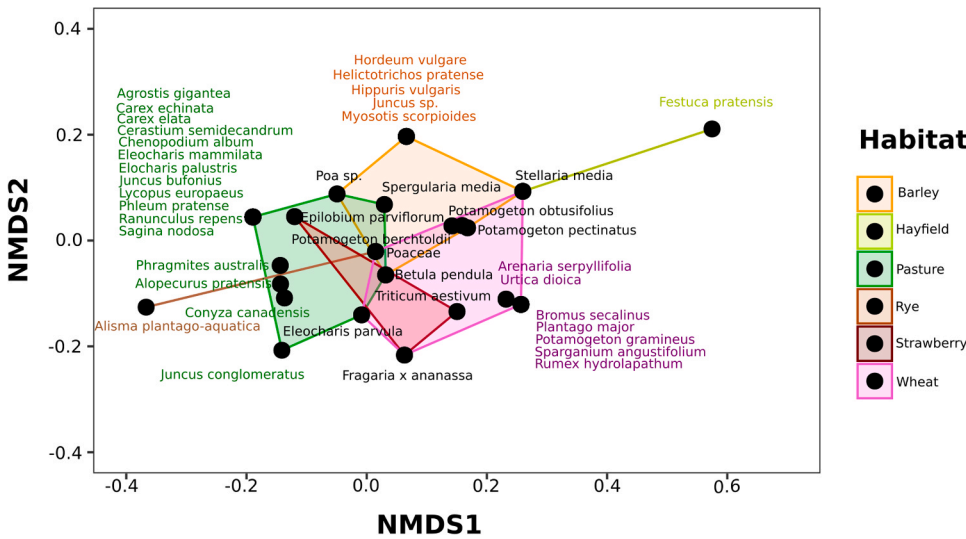
Table 2

Results of generalized linear mixed models (GLMMs) using negative binomial error distribution to test effects of sample mass (weight) and habitat type on seed abundance and seed richness per sample ( $N = 300$ ), giving estimates, standard errors of means, standardised effect sizes (Z- values), and the P-value for each explanatory variable (with significant values in bold). Factor level comparison refers to Tukey’s range tests corrected for multiple comparisons between habitat pairs.

GLM	Response variable	Explanatory variable	Factor level comparison	Estimate	Error	Z-value	P-value
1	Seed abundance	Intercept		-1.55	0.36	-4.31	< 0.001
		Weight (g)		0.07	0.02	3.02	<b>0.003</b>
		Habitat type		1.40	0.76	1.83	0.07
			Hayfield – Barley	-1.35	0.77	-1.77	0.27
			Pasture – Barley	0.46	0.38	1.22	0.59
			Wheat – Barley	0.05	0.38	0.12	0.99
			Pasture – Hayfield	1.82	0.74	2.46	0.06
			Wheat – Hayfield	1.41	0.76	1.83	0.24
			Wheat – Pasture	-0.42	0.37	-1.12	0.66
		2	Seed richness	Intercept		-3.30	0.76
Weight (g)				0.06	0.02	2.73	<b>0.01</b>
Habitat type				1.37	0.76	1.81	0.07
	Hayfield – Barley			-1.37	0.77	-1.79	0.26
	Pasture – Barley			0.48	0.38	1.27	0.56
	Wheat – Barley			0.01	0.38	0.03	1.00
	Pasture – Hayfield			1.85	0.74	2.49	0.06
	Wheat – Hayfield			1.38	0.76	1.81	0.25
	Wheat – Pasture			-0.47	0.37	-1.28	0.56

interconnected and used as sources and/or sinks of most direct flights (Table 3, Fig. 4). Lakes and pastures were involved in the highest number of direct flights (Table S3, “node strength” in Table 3), and they

formed important bridges between other habitats (“node betweenness” in Table 3). Overall, 45% of all flights departed from barley, wheat or pasture, and 34% of flights were towards these habitats (Table 3). Those



**Fig. 3 :** Non-metric multidimensional scaling (NMS2) plot showing the relationship between plant seeds dispersed in greylag goose faeces collected from different habitat types in Sweden (stress value <0.2). NMS1 and NMS2 represent the coordinates obtained from Bray–Curtis matrix distances. Each plant species is assigned these two coordinates, to visualize possible associations or contrasts among plant species in different habitats. Plant species that overlap between habitats are indicated in black, whereas names of species unique to one habitat are given in the colours indicated in the legend.

**Table 3**

Information for the 12 main habitats visited by GPS-tracked greylag geese, in order of time spent there. Includes total surface area (km<sup>2</sup>) per habitat type, mean time spent per tagged goose (represented by percentage) from 1st of June to September 30th of 2019, centrality measures of betweenness (indicating the frequency with which a habitat was used as a node connecting two other nodes), and values of the link weights for each node (i.e. strength, indicating how many direct flights were leaving or arriving to the node, plus the percentage of all direct flights).

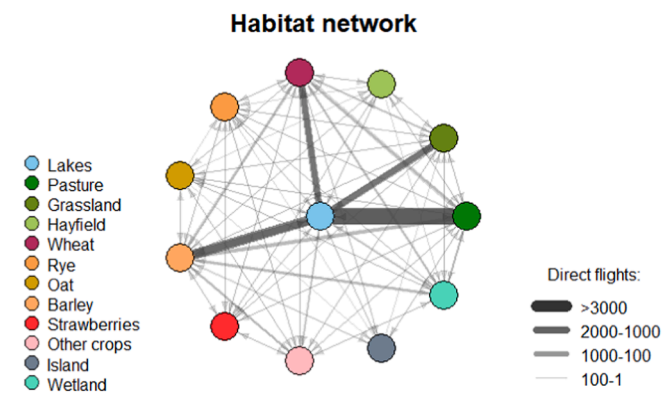
Habitat	Area (km <sup>2</sup> )	Time spent (%)	Node betweenness	Node strength (% DF)
Lakes	2802	34.5	0.96	9062 (28)
Wetland	49	19.5	0.11	2647 (8)
Pasture	15	13.9	0.96	5792 (18)
Barley	24	9.9	0.96	4576 (14)
Grassland	14	8.9	0.96	3325 (10)
Wheat	32	7.4	0.96	4071 (12)
Island	4	0.8	0	107 (<1)
Other crops	13	2.6	0.25	1823 (6)
Strawberries	1	0.5	0.11	226 (1)
Rye	3	1.0	0.96	440 (1)
Oat	3	0.8	0.54	581 (2)
Hayfield	2	0.3	0.25	118 (<1)

habitats with more direct flights generally had faeces that contained a higher diversity, richness and abundance of seeds (Figs. 3, 4). Strawberries were an exception, but there was very little of this habitat available (Table 3), and estimates of seeds in strawberry faeces are likely subjected to high sampling error.

Six individual geese spent more than 24 h continuously in the same habitat type on at least one occasion, and this happened in five different habitats: lakes, wetlands, pasture, natural grasslands, and wheat. Overall, geese spent most time in aquatic habitats (wetlands and lakes, 59% combined) (Table 3). During daylight hours, geese stayed in one habitat type for a mean of 2.21 h (± 1.17, ± SD) before moving to other habitats. They covered linear distances of 6.8 km daily (± 1.54). Only 31% of direct flights were between different agricultural habitat types, whereas 66% connected aquatic and agricultural habitats (Fig. 4, Table S3).

**4. Discussion**

We found greylag geese to be important vectors of seed dispersal in landscapes dominated by agriculture, providing connectivity among different habitat types, both aquatic and terrestrial. Geese dispersed a wide variety of angiosperm taxa with different traits via endozoochory, including weeds and an alien plant species. The combination of tracking individual geese and targeted faecal sampling revealed how different habitats are interconnected, including among terrestrial habitats, among aquatic habitats, and from aquatic to terrestrial habitats. This study revealed how seeds of many aquatic plants are dispersed into agricultural fields, in which they may or may not establish depending on their timing and local conditions.



**Fig. 4 :** Network connectivity between different habitat types. The total number of direct flights between all polygons of a given habitat type is represented by the thickness and darkness of the links. See Table S3 for precise numbers of direct flights.

**4.1. Plant species dispersed by greylag geese, and their traits**

A wide variety of plant species with different seed size, moisture requirements and dispersal syndromes were dispersed across different habitats. Twelve of these plant species (31%) have not previously been reported to be dispersed by any European waterfowl species (see Almeida et al., 2022), providing novel insights into how these plant species can be dispersed.

Geese may ingest the seeds they disperse in different ways. At the time of the study, many of the plants would have been at the seed ripening stage and perhaps seeds were deliberately or accidentally ingested along with foliage during grazing (Janzen, 1984; Jaroszewicz et al., 2023). Geese are often likely to ingest seeds from the parent plant when grazing on land and in the water (Amat, 1995; Green et al., 2016,

2018). However, unlike frugivorous birds (González-Varo et al., 2021), waterbirds do not limit the ingestion of seeds to the period of seed production, but can instead ingest seeds intentionally or otherwise from sediments or soil, or when floating (Alderton et al., 2017; Brochet et al., 2010a; Lovas-Kiss et al., 2018; Urgyán et al., 2023).

With the exception of strawberries, all plant species dispersed by geese lacked a fleshy fruit and were assigned to dispersal syndromes other than the “endozoochory syndrome”, as previously shown for ducks and shorebirds (Green et al., 2022; Urgyán et al., 2023). In most cases, goose endozoochory will allow plants to move much greater distances than those predicted by other dispersal syndromes (Bullock et al., 2017; Green et al., 2022; Lovas-Kiss et al., 2023). Syndromes may still help explain how seeds are ingested by geese. Seeds with a hydrochory syndrome may be ingested when floating in water, as may those with an anemochory syndrome after reaching water by wind. For instance, silver birch seeds *Betula pendula* are often blown onto water where they can be ingested by ducks (Lovas-Kiss et al., 2018), and potentially geese. As yet, there is a near-total lack of research as to how plant traits such as buoyant structures, or hooks and hairs, promote endozoochory by non-frugivorous vectors. On the other hand, seed size is a critical trait for endozoochory (van Leeuwen et al., 2023), and smaller seeds may be ingested when attached to waste grain or other residual crops, as is likely for weed endozoochory in Spanish ricefields (Martín-Vélez et al., 2021a, 2021b).

The diversity and viability of seeds dispersed by geese via endozoochory was likely underestimated in our study because a) our rarefaction analysis suggested that additional plant species may have remained undetected, b) we sampled a tiny fraction of the daily faecal production of geese in agricultural fields (Hahn et al., 2008), and c) long sample storage times led us to underestimate viability. Nevertheless, viability of the dispersed seeds was confirmed by us or in previous studies for 22 (54%) of the species detected.

#### 4.2. Weed dispersal and potential implications for economic impacts

Eleven (27%) of the plant species recorded were weeds, including the widely distributed white goosefoot *Chenopodium album* and the common chickweed *Stellaria media*. These are among the most problematic weeds for Swedish agriculture, with documented herbicide resistance, and are common in our study areas (Afonin et al., 2008; CABI, 2022; Liljander, 2007). Weed seeds were found in all habitat types except strawberry and oat fields. For eight weed species (e.g. *Agrostis gigantea*, *Alisma plantago-aquatica*) we demonstrated their viability, or else their viability after goose gut passage was already demonstrated by previous research (Jerling et al., 2001; Hattermann et al., 2019). The smallest seed we recorded was of *Juncus bufonius*, a weed readily spread from ricefields into other habitats via gull endozoochory, over maximum distances exceeding 100 km (Martín-Vélez et al., 2021a, 2021b; Peralta-Sánchez et al., 2023). Rye brome grass *Bromus secalinus*, a problematic weed in rye, wheat and other crops (CABI, 2022) has particularly large seeds (Table 1). Although larger seeds are more likely to be destroyed during gut passage (van Leeuwen et al., 2023), similarly sized seeds are dispersed by geese in North America (Farmer et al., 2017).

The dispersal of weed species and herbicide resistant varieties, by whatever mechanism, has costly impacts on agricultural crops and their yield (Varah et al., 2020; Vila et al., 2021). The potential role of waterfowl in such dispersal has been largely overlooked. More than 70% of weed species worldwide have been assigned a barochory (i.e. gravity) dispersal syndrome, implying that they have very limited ability to spread, except via human activity (Benvenuti, 2007). Geese may play a previously overlooked role in the spread of weeds and herbicide resistance within and between habitats, possibly resulting in increased costs through yield reduction and the need for more intense herbicide control for individual farmers (Farmer et al., 2017; Chauhan, 2021). Our results suggest geese may possibly have a significant role in spreading weeds, especially since ~10,000 greylag geese are present within our two study

areas during the summer, and their numbers have increased in recent years (Månsson et al., 2022). However, we have not provided evidence that dispersal of weed seeds by geese leads to weed establishment, and this topic is worthy of further research. Furthermore, weeds may also have positive impacts on ecosystem functioning by maintaining populations of macrofauna and microbes that maintain soil quality for crops (Franke et al., 2009).

#### 4.3. Dispersal of plant seeds across habitats and functional connectivity

As shown for dabbling ducks (Urgyán et al., 2023), greylag geese are likely to be important seed vectors during their long-distance migratory flights (Alsos et al., 2015; Ramo et al., 2015). Our study does not study goose migration or cover migratory periods, however it confirms that geese have a high potential to disperse seeds among habitat types within agricultural landscapes. Geese moved daily from roosting areas (usually islands, lakes and wetlands) to feeding sites in agricultural fields (see also Olsson et al., 2017). Considering the seed abundance in faecal samples, a mean dropping rate for greylag goose of  $1.2 \text{ h}^{-1}$  (Hahn et al., 2008), and the numbers of geese, approximately ~100,000 seeds were dispersed daily by geese in our study area. Geese covered mean linear distances of 7 km daily, and likely often dispersed seeds over similar distances. Furthermore, tagged geese occasionally flew non-stop between our two study areas (separated by 300 km), and likely dispersed seeds between them (Lovas-Kiss et al., 2023).

Previous field studies have quantified waterfowl endozoochory through analyses of gut contents or faeces (Green et al., 2016; Soons et al., 2016), but without demonstrating that seeds were actually dispersed between habitats. Within each of our two study areas, geese stayed a mean of 2.2 h before switching habitats, so most seeds may be dispersed into other habitats. Seeds are egested a mean of 7 h or more after ingestion, although median gut retention time is 3 h, and maxima exceed 48 h (García-Álvarez et al. (2015), so a large proportion of seeds ingested may be deposited in other habitats. Dispersal of seeds between habitats is clearly indicated by the abundance of aquatic seeds in faeces from agricultural fields, e.g. hoary willowherb *Epilobium parviflorum* in strawberry fields, water plantain *Alisma plantago-aquatica* in rye, or narrowleaf bur-reed *Sparganium angustifolium* in wheat. Dispersal of aquatic plants into non-irrigated agricultural fields is unlikely to be effective with the possible exception of moist soil plants with Ellenberg F = 7 (van Leeuwen et al., 2022), but effective dispersal is more likely when weed seeds are moved between different crops. A total of 28% of the plant taxa were recorded in at least two agricultural habitat types, further supporting interchange of seeds between them. Strawberry seeds recovered from a wheat field provide further evidence. The exchange of aquatic species between wetlands or lakes is a major ecosystem service that facilitates effective dispersal, ensures gene flow between populations that are otherwise disconnected, and enables the colonization of new habitats (Green et al., 2016, 2023). This process plays a vital role in maintaining biodiversity and enhancing the overall resilience of ecosystems.

The networks we developed based on GPS tagging suggest an important connectivity role of greylag geese in agricultural landscapes, with possible implications for the spread of alien plants and weeds, and for dispersal across the terrestrial-aquatic interface. Although we here show dispersal of plant seeds by geese, our findings also have implications for possible vectoring of microbes and invertebrates (Green et al., 2023), contaminants (Martínez-Haro et al., 2013), nutrients (Dessborn et al., 2016), and microplastics (Coughlan et al., 2021). For all these elements, our movement analysis showed that geese create stronger and more directional connectivity among specific habitat types (e.g. between pasture and barley) than among other habitat types (e.g. between pasture and rye). These strong connectivity patterns, combined with variation in seed availability between habitats, may contribute to differences in plant communities in the studied habitats. Rarefaction analyses supported differences in seed richness in faeces between

agricultural habitats, and community composition of plant seeds in faeces varied among habitats (confirming hypothesis 2). In addition, faeces from the most visited habitats generally presented higher seed abundance and a greater diversity of plant species per unit of faeces, perhaps because these habitats are both the most connected with major sources of seeds (notably lakes and wetlands), and because they provide a diversity of food plants. An important determinant for the number of visits, and therefore the potential impact of geese on agricultural landscapes, was proximity to aquatic roosting habitat. This is in line with a relatively large proportion of small-scale (<1 km) goose movements (Fig. S4) and previous reports in Sweden that showed how geese prefer grasslands, pastures and hayfields that are close to shorelines of lakes and wetlands (Axelsson, 2004; Tennfors, 2013).

## 5. Conclusions and priorities for future research

Waterbirds provide important ecosystem services (Green and Elmberg, 2014) and the present study underlines their role as seed dispersal vectors. Greylag geese act as important connectors within agricultural habitats, potentially spreading weeds. They also connect aquatic and terrestrial ecosystems, which may share weeds such as *J. bufonius* or *R. repens*. Furthermore, nutrients imported into fields from aquatic ecosystems in goose faeces may potentially boost crop growth (Buij et al., 2017). This study suggests that geese may be important drivers of plant communities in agricultural landscapes, and important vectors that exchange plant seeds among aquatic habitats. The combination of GPS tools and faecal sampling identifies important aspects of functional connectivity between different habitats, and reveals how waterbirds disperse native, alien and weed species by local or long-distance movements. Like some other goose species (Buij et al., 2017), greylag geese have shown recent increases in population numbers and altering of migration patterns. For these species, movement studies can be key to reducing crop damage (Månsson et al., 2022), but also to understand seed dispersal. There is ample literature on conflicts caused by increasing goose populations through grazing (Fox et al., 2017), but potential benefits and impacts through seed dispersal have so far been largely ignored. Future studies are needed to compare the flora present in different agricultural habitats, so that seeds coming from elsewhere via geese can be more readily identified. There is also a need to investigate dispersal of plants by geese over longer distances during migrations, not least to understand whether geese can help plants compensate for climate change by moving to cooler latitudes, as shown for dabbling ducks (Viana, 2017; Urgyán et al., 2023; Lovas-Kiss et al., 2023).

Research into weed dispersal and its consequences needs to expand its focus to include geese and other waterbird vectors, as well as human vectors. Our results illustrate how waterbird endozoochory may greatly enhance the dispersal ability of weeds (and herbicide-resistance) across agricultural landscapes. Agricultural strategies for management of weeds and herbicide resistance may need to be improved if a role of geese as effective vectors is confirmed. Future research into the establishment success of weed seeds spread between fields and different crops by geese should be of high priority. In intensively used habitats, the implications of the fungi and other microbes transported in geese faeces (Briscoe et al., 2022) for soil ecology should also be investigated.

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## Declaration of Competing Interest

We wish to confirm that there are no known conflicts of interest associated with this publication.

## Data Availability

Data will be made available on request.

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## Intellectual property

We confirm that we have given due consideration to the protection of intellectual property associated with this work and that there are no impediments to publication, including the timing of publication, with respect to intellectual property. In so doing we confirm that we have followed the regulations of our institutions concerning intellectual property.

## Authorship

All listed authors contributed significantly to the creation of this manuscript. We confirm that the manuscript has been read and approved by all named authors. We confirm that the order of authors listed in the manuscript has been approved by all named authors.

## Contact with the editorial office

The Corresponding Author declared on the title page of the manuscript is:

María J. Navarro-Ramos, Department of Conservation Biology and Global Change, Estación Biológica de Doñana, CSIC, Américo Vespucio 26, 41092 Sevilla, Spain.

Email: mjnavarro@ebd.csic.es.

This author submitted this manuscript using her account in Agriculture, Ecosystems & Environment. We understand that this Corresponding Author is the sole contact for the Editorial process. She is responsible for communicating with the other authors about progress, submissions of revisions and final approval of proofs.

## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2023.108741.

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