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ORIGINAL PAPER

Seed dispersal by the brown bear in a mixed temperate forest: fruit type matters

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Abstract
The brown bear (*Ursus arctos* L.) is an omnivorous large mammal that has an essential function in many ecosystems as a seed disperser. We studied the brown bear's role as a seed dispersal agent in a mixed temperate forest in northern Anatolia, Turkey. We collected 197 fecal samples from the field during the brown bear's active period for two consecutive years. We extracted seeds of 34 plant taxa from fecal samples. Among these taxa, 29 had intact seeds, whereas seeds of 5 were found to be entirely or mostly physically damaged. Damaged seeds belonged to fruits of acorn, capsule, nut, and drupe-like nut types, while no or few seeds from fleshy fruits such as berry, drupe, pome, and rosehip types had damage. Seeds from pome type fruits of *Malus sylvestris* and *Pyrus elaeagnifolia* had a higher germination percentage in feces than in the control (fresh seeds collected from the field), but that was quite the opposite in berries of *Lonicera caucasica* and *Vaccinium arctostaphylos*. No difference in germination percentage was found between feces and control groups in seeds from rosehips. Our results reveal that seeds of several species found in the study area are dispersed by the brown bear, especially those with fleshy fruits (e.g., Rosaceae members). In this study, we established the role of the brown bear as a seed dispersal agent in northern Anatolian mixed temperate forests. Our study suggests that fruit type is a determinant of the success of endozoochorous seed dispersal by the brown bear.

Keywords Endozoochory · Fecal analysis · Fruit type · Rosaceae · Seed dispersal · *Ursus arctos*

Introduction

Endozoochory is a common mechanism for seed dispersal in plant species in many ecosystems, from tropical to boreal regions (Pakeman et al. 2002). Animals eating seeds or fruits shape the vegetation dynamics in many ecosystems by assisting seed dispersal and, indirectly, the seedling establishment (Herrera 1989; Gill and Beardall 2001; Traveset et al. 2007; Barcelos et al. 2013). Such animal-plant interactions may also have ecological and evolutionary consequences for plant species by driving a selection for some seed traits such as dormancy, seed size and shape, and germination (Manzano et al. 2005; Albert et al. 2015). Besides birds (Herrera and Jordano 1981; Herrera 1995) and large carnivore mammals (Willson 1993; Fedriani and Delibes 2009; Toyran et al. 2009), the grazer and browser large mammals [including ungulates (Gill and Beardall 2001; Anderson et al. 2014), lagomorphs (Bobadilla et al. 2020), and elephants (Campos-Arceiz and Blake 2011)] are the primary seed dispersal agents for many plants using endozoochory as a seed dispersal strategy. These examples can be extended to include various ecosystems and organism groups worldwide.

The brown bear (*Ursus arctos* L.) is an omnivorous large mammal species that has an essential function in ecosystems as a seed disperser (Traveset et al. 2001; Lalleroni et al. 2017; Karimi et al. 2018a). Although the brown bear's diet is more animal-oriented in the northern latitudes of its distributional range, plant materials are of a more prominent place in their diet in the southern parts of the temperate region (Naves et al. 2006; Bojarska and Selva 2012). In addition, the ratio of the ungulate meat in the brown bear diet is inversely related to the mean annual temperature of the region (Niedzialkowska et al. 2019). Accordingly, fruits and seeds constitute the main component of the brown bear's diet in temperate and

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Mediterranean regions (Clevenger et al. 1992; Paralikidis et al. 2010; Ambarlı 2016). The seeds and fruits in brown bear feces have naturally been interpreted as the proof of the plant species in their diet (Paralikidis et al. 2010; Ciucci et al. 2014; Nawaz et al. 2019), but sometimes, it is also assumed that the seeds consumed by the brown bear are successfully dispersed (Lalleroni et al. 2017; Harrer and Levi 2018). However, the successful seed dispersal of endozoochorous plants may depend on several factors and can be complex (Herrera 1989; Willson and Whelan 1990; Bustamante et al. 1992; Traveset et al. 2001; Cosyns et al. 2005; Manzano et al. 2005, Anderson et al. 2014; Ribeiro et al. 2016). Indeed, fruits and seeds of some species consumed by the brown bear might be destroyed during chewing (Seryodkin 2016), while some seeds consumed by the brown bear may survive the gut passage (Traveset et al. 2001; Traveset and Willson 1997; Willson and Gende 2004). Furthermore, the germination of seeds passed through the gut may be enhanced (Traveset and Willson 1997; Steyaert et al. 2019). Therefore, direct evidence of a successful endozoochory mediated by the brown bear can only be obtained by assessing the viability or germination ability of seeds found in fecal samples (Willson and Gende 2004; Samuels and Levey 2005; Karimi et al. 2018a).

Anatolia harbors one of the southernmost populations of brown bears (McLellan et al. 2017), which have an exceptional genetic diversity (Çilingir et al. 2016). The status of the species is “vulnerable” according to the Mediterranean Regional Assessment of the IUCN Red List of Threatened Species (Boitani et al. 2010). There is an ongoing human-bear conflict in Anatolia (Ambarlı and Bilgin 2008; Chynoweth et al. 2016), and the most critical factors that threaten the brown bear in Turkey are habitat loss and degradation (Can and Togan 2004).

The role of endozoochory in seed dispersal has been studied extensively in many ecosystems of the world (Herrera 1989; Willson 1993; Herrera 1995; Traveset et al. 2001; Pakeman et al. 2002; Traveset et al. 2007; Anderson et al. 2014; Lalleroni et al. 2017; Fahimi et al. 2018; Karimi et al. 2018a). However, in biodiversity-rich Anatolian ecosystems, only a few studies have reported the existence of seeds or fruits in the feces of domesticated or wild large mammals (Anderson and Ertug-Yaras 1998; Toyran et al. 2009; Ambarlı 2016), but there is no study with endozoochory as the main focus. Since endozoochory is an essential mechanism for plant establishment and community assembly (Cavallero et al. 2012; Harrer and Levi 2018; Schlägel et al. 2020), there is a need for studies on endozoochory by birds and mammals for a better understanding of plant diversity and distribution in Anatolian ecosystems.

In this study, we examined the brown bear’s potential role as a seed dispersal agent in a mixed temperate forest in northern Anatolia (Turkey). We expected that the brown bear successfully disperses seeds of many plant species found in this ecosystem. We also hypothesized that some seeds consumed by the brown bear would be unsuccessful in completing seed dispersal because the passage through the gut harms them or reduces their germinability. Based on previous observations regarding the importance of fruit traits for seed passage through the gut in various seed-disperser species (Herrera 1989; Otani and Shibata 2000), we expected that the fruit type should be a determinant of the successful seed dispersal by the brown bear. To test these hypotheses, we examined both the damaged and intact seeds in fecal samples of the brown bear, designed an experiment to compare the germination percentages of intact seeds found in feces with those collected from the field, and evaluated the results in relation to the fruit type.

Materials and methods

Study area

The study area was a continuous temperate forest approximately 25,000 ha in size located in the western Black Sea region of northern Anatolia, Turkey (41°24′27″–41°15′40” N, 32°26′58″–32°23′17″ E; 700–1700 m a.s.l.; Fig. 1). The main vegetation consists of mixed forests covered mainly by oriental beech (*Fagus orientalis* Lipsky) and Trojan fir (*Abies nordmanniana* subsp. *equi-trojani* (Asch. & Sint. ex Boiss.) Coode & Cullen) trees. Oriental beech dominates the forest at lower elevations, but with increasing elevation, the forest is dominated by Trojan fir. The climate is warm-summer humid continental according to the Köppen classification system (Peel et al. 2007); the annual total precipitation is 971 mm; and the annual mean temperature is 7.1 °C.

There is no human settlement in the study area, and it is only seasonally occupied by foresters and workers hired by the forestry service of Turkey for logging purposes. A large part of the study area is under protection as a wildlife reserve (Sökü Wildlife Development Area) where hunting is allowed only within a particular game hunting plan including specific quotas when necessary. In addition to a viable brown bear population, the study area harbors many large mammal species, such as gray wolf (*Canis lupus* L.), red deer (*Cervus elaphus* L.), wild boar (*Sus scrofa* L.), and roe deer (*Capreolus capreolus* L.) (Soyumert 2010).

Feces and fresh seed collection and storage

We collected 197 fecal samples belonging to the brown bear during monthly field surveys in the study area from June 2013 to October 2014. No feces were collected between December 2013 and April 2014 because the brown bear individuals were in their inactive period (Soyumert 2010), and the study area was inaccessible due to snowfall. During the field surveys, we searched forest dirt roads and, in some cases, pathways that

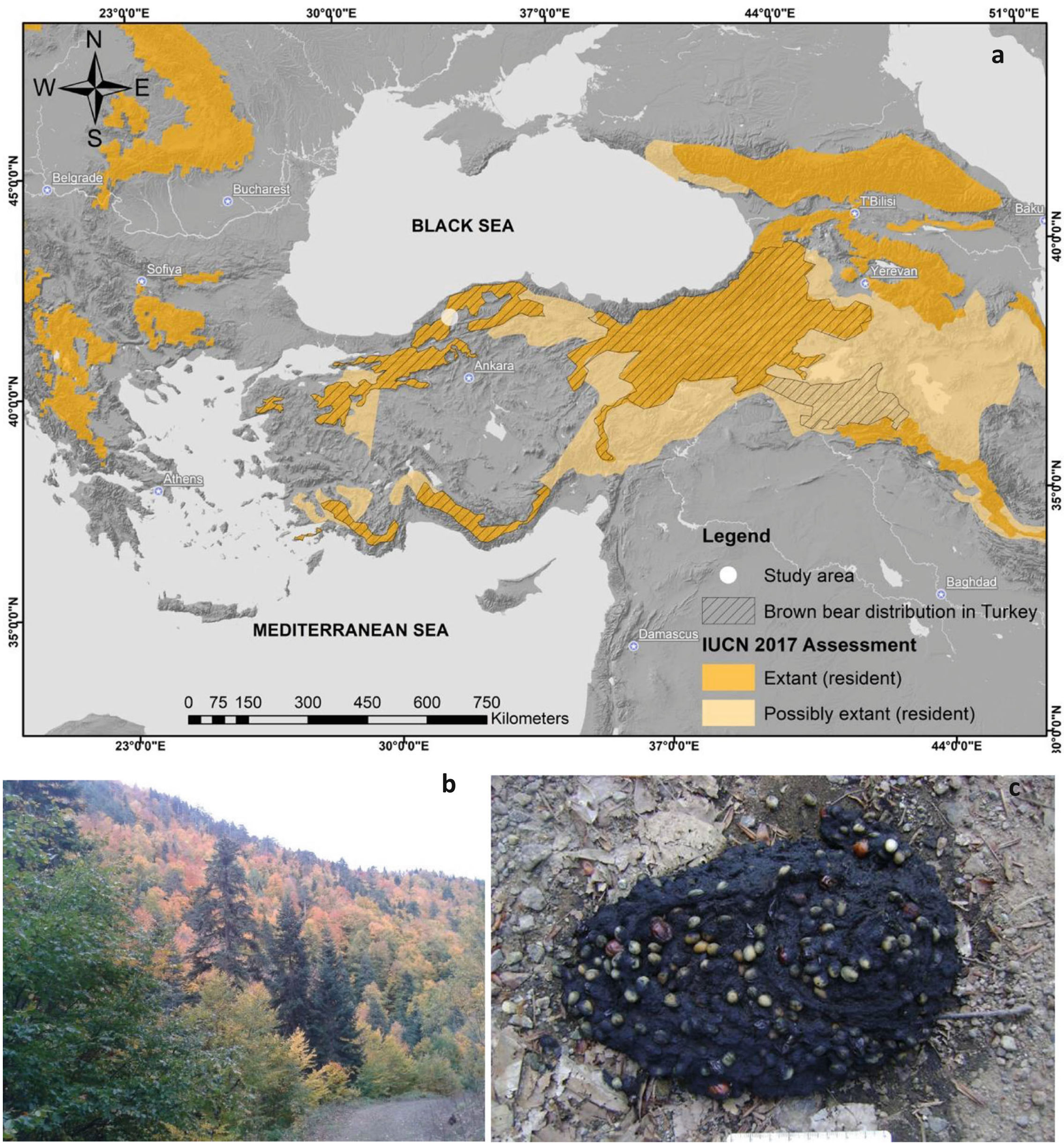

Fig. 1 The location of the study area and the brown bear distribution in and around Turkey (based on McLellan et al. (2017) for general distribution and Ambarlı et al. (2016) for the distribution in Turkey) (**a**), a general view of the vegetation in the study area (**b**), and a fecal sample packed full of *Prunus mahaleb* seeds (**c**)

are potentially used by the brown bear for feces detection. Each monthly survey continued for 4 to 6 days, and approximately 300 km of forest road was covered in each survey. We followed the same route in each monthly survey to collect fresh fecal samples, which were not more than 1-month-old. While collecting fecal samples, we left the bottom part of the sample that comes into contact with the ground to eliminate possible contamination of seeds from the soil. Fresh fruits were also collected from fruit-bearing plants (if any) during each field survey. A proper botanical sample for these plants was also taken to identify plants taxonomically at the herbarium. Fecal samples (in plastic bags) and fresh fruit samples (in paper bags) were placed into a portable fridge (4 °C) until they transferred to the laboratory fridge. In the laboratory, samples were kept in the refrigerator at 4 °C for 3 months until the analysis.

Extraction and identification of seed material in feces

We first removed apparent non-seed/fruit materials such as mushrooms, larvae, plant sprouts, and insects from the fecal samples. The samples were then homogenized in their sample bags with water to facilitate the screening process and leave no material behind. After that, the homogenized samples were washed under running water in superimposed sieves with different mesh sizes. We smoothly mixed the sample during the washing process and avoided any suppression or rubbing to avoid damaging the seeds in the fecal content. The washing process was completed in a maximum of 3 to 5 min to prevent triggering the germination of seeds. Fruits and seeds in the samples were separated and placed on filter papers and left to dry at 20 °C for 24 h. Finally, fruits, fruit parts, and seeds were examined to determine "intact" or "damaged" seeds. Using these observations, the proportion of damaged seeds in fecal samples was assessed in categories (all: 100%; most: 75–99%; few: 1–15%; and none: 0%) for each taxon. All seeds were stored in plastic bags in a closed container in the dark at 20 °C for 2 months until the species identification and germination experiment.

Seeds and fruit parts in the fecal samples were identified using a reference database composed of the fresh plant and seed material collected from the study area. Identification was carried out under the microscope by comparing the anatomical structures of the materials found in the feces with the taxonomically identified fresh plant samples. Plant nomenclature follows Davis (1965–1985) but has been updated by considering recent taxonomic advances (The Plant List 2013). The information on the identified taxa was gathered from various sources: Davis (1965–1985) for the growth form, flowering time, and fruit type; Tavşanoğlu and Pausas (2018) for the dispersal mode; and Baskin and Baskin (2014) for the dormancy type. This information allowed us to explore further functional aspects of seed dispersal by the brown bear.

Germination experiment

A germination experiment was conducted to compare the germination abilities of seeds obtained from fecal samples and fresh seeds collected directly from the plants in the field. In the experiment, fresh seeds collected from the field were considered the control group. The seeds of the 2014 sampling were used in the experiment to prevent possible annual variation in germination or dormancy loss due to a long storage period. We started the experiment at the same time for all species and both experimental groups using the seeds belonging to the August and September 2014 samplings. We included only six species in the experiment due to the insufficient number of seeds of some species collected from the field or obtained from fecal samples. Before the experiment, fresh seeds were removed from fruit parts by hand or using sieves (i.e., were depulped). In this way, we used individual seeds for both groups in the experiment as seeds in fecal samples had already been separated from the fruit parts surrounding them. For each species, the seeds of fecal and control groups with four replicates (25 seeds in each) were sown into Petri dishes containing agar as substrate and stratified at 4 ± 1 °C for 6 months. Afterward, they were incubated at 20 ± 1 °C for 2 months under dark conditions in a temperature-controlled cabinet. Long-term cold stratification is frequently applied to seeds of fruit trees and shrubs in temperate forests of northern Anatolia to break dormancy and ensure germination (Edizer et al. 2009; Güner and Tilki 2009).

The seeds were monitored weekly for germination during the cold stratification period and every 2 or 3 days during the incubation period. Germination checks were done under a stereomicroscope in daylight conditions. At every check, the germinated seeds were recorded and removed from the Petri dishes. At the end of the experiment, the non-germinated seeds in Petri dishes were dissected to check if they had an embryo (the cut test; Baskin and Baskin 2014), and the number of seeds without embryo (i.e., empty seeds) were recorded for each replicate in each treatment and control.

Data analysis

For each monthly survey, the frequency of the occurrence of seeds of each species in the fecal samples was estimated as the number of feces with the seeds of a particular plant species divided by the total number of fecal samples in the given month. To observe the seasonal variation in species whose seeds were consumed, we combined the data of consecutive sampling years and presented it as a percentage. We also performed a correlation analysis to test the relationship between our first observation of seeds of a species in fecal samples and the end of its flowering period to understand the association between the phenology of plant species and the consumption time of fruits by the brown bear.

The germination data analysis was conducted by excluding the number of empty seeds from the initial number of seeds in each Petri dish. Germination percentage was estimated for each Petri dish in the control and feces groups by multiplying the ratio of germinated seeds to seeds sown (excluding the empty ones) by 100. The germination analysis was conducted using the analysis of deviance (a generalized linear model; GLM), assuming a binomial error distribution by considering the number of germinated and non-germinated seeds in Petri dishes. In this analysis, treatment was included as a fixed factor, and analysis was performed separately for each species. In this way, we compared the final germination in the feces group with that in the control group for each species. Using all the germination data (all species and treatments), an additional analysis was performed to test the effect of the fruit type and passage through the brown bear gut on the germination probability of seeds. We used the generalized linear mixed model (GLMM), assuming a binomial error distribution for this analysis with the *glmer* function from the *lme4* package (Bates et al. 2015). In this analysis, the results were obtained by performing likelihood ratio tests based on a comparison of the model with species as the only random factor (null model) with models including both random and fixed factors (gut passage and fruit type). All analyses in the study were performed in the R environment (R Core Team 2019).

Results

We extracted seeds of 34 plant taxa from fecal samples throughout the study. We identified seeds or seed remains of 25 plant taxa at various taxonomic levels and found another 9 unidentified but unique plant species in feces (Tables 1, 2). These taxa had various fruit types, including hard masts such as acorn and nuts, and fleshy fruits such as pome, drupe, and rosehip (Table 1). Among the taxa whose seeds were extracted from fecal samples, 29 had intact or rarely damaged seeds in feces, whereas the seeds of 5 were found to be entirely or mostly damaged after passing through the brown bear gut (Table 2). The seeds that were most frequently consumed by the brown bear belong to several Rosaceae species, which have fleshy fruits (at least 12 taxa, Tables 1, 2). The identified taxa had different growth forms (geophyte, perennial herb, shrub, and tree), but most were long-known endozoochorous species and had physiologically dormant seeds (Table 1).

Most species flowered in May but some also in March–April or June–July (Table 1). There was an approximately 2-month (1.94 ± 0.3, the mean ± SE, $n = 18$) difference and an association ($r = 0.46$, $P = 0.056$) between the last month of the

Table 1 The list of taxonomically identified (at least at the genus level) plant taxa whose seeds were found in the brown bear feces. Total number of seeds extracted from fecal samples (*#seed*) is given for each taxon (> 1: 1–9, > 10: 10–99, > 100: 100–999, > 1000: more than 1000, n/a: not applicable due to damaged seeds). The growth form (*GF*; g: geophyte, p: perennial herb, sh: shrub, str: small tree, tr: tree), flowering time (*Flo*; as months of the year), fruit type (*FT*; ac: acorn, be: berry, cp: capsule, cr: caryopsis, co: cone, dr: drupe, dn: drupe-like nut, nu: nut, po: pome, ro: rosehip), primary seed dispersal strategy (*Disp*; E: endozoochory, G: autochory, S: synzoochory, M: myrmecochory, A: anemochory), and seed dormancy type (*Dorm*; PD: physiological, MD: morphological, MPD: morphophysiological dormancy, and ND: non-dormant) are given for each taxon

Family and taxon name	#seed	GF	Flo	FT	Disp	Dorm
Amaryllidaceae						
Allium L. sp.	n/a	g	–	cp	G	PD
Aquifoliaceae						
Ilex colchica Poj.	> 1	sh	6–7	dr	E	MPD/MD
Betulaceae						
Corylus avellana L.	n/a	sh	2–3	nu	S	PD
Caprifoliaceae						
Lonicera caucasica Pallas	> 1000	sh	5–7	be	E	MPD/MD
Cornaceae						
Cornus mas L.	> 100	str	3–5	dr	E	PD
Ericaceae						
Vaccinium arctostaphylos L.	> 1000	sh	5–7	be	E	PD
Fagaceae						
Castanea sativa Miller	n/a	tr	6–7	nu	S	PD
Quercus infectoria G.Olivier	> 10	str	8	ac	S/E	ND/PD
Juglandaceae						
Juglans regia L.	n/a	tr	5	dn	S/G	PD
Pinaceae						
Abies nordmanniana ssp. *equi-trojani* (Asch. & Sint. ex Boiss.) Coode & Cullen	> 1	tr	–	co	A	PD
Poaceae						
Puccinellia festuciformis (Host) Parl.	> 1	p	5–6	cr	M	PD
Rosaceae						
Crataegus monogyna Jacq.	> 1	str	4–6	dr	E	PD
Malus sylvestris (L.) Mill.	> 1000	tr	4–5	po	E	PD
Prunus mahaleb L.	> 100	str	3–5	dr	E	PD
Prunus spinosa L.	> 100	str	3–4	dr	E	PD
Prunus L. spp.	> 10	str	–	dr	E	PD
Pyrus communis L.	> 1	tr	4–5	po	E	PD
Pyrus elaeagnifolia Pall.	> 1000	tr	4–5	po	E	PD
Pyrus syriaca Boiss.	> 1	tr	4–5	po	E	PD
Pyrus L. spp.	> 100	tr	–	po	E	PD
Rosa canina L.	> 1000	sh	5–7	ro	E	PD
Rosa horrida Fischer	> 1000	sh	5–7	ro	E	PD
Rubus L. spp.	> 1000	sh	–	ro	E	PD

Table 2 Frequency of occurrence (%) of plant taxa whose seeds were found in the brown bear feces in different months. Proportion of damaged seeds in fecal samples (*PDam*) is given for each taxon in four classes (all: 100%, most: 75–99%, few: 1–25%, none: 0%). The combined data for 2013 and 2014 samplings are presented. Taxonomically identified taxa are given in the same order in Table 1

Months									
Taxon	PDam	May	June	July	Aug	Sep	Oct	Nov	Total
Allium sp.	all	0	3.2	0	0	0	0	0	**0.5**
Ilex colchica	none	0	0	0	4.0	1.1	0	0	**1.0**
Corylus avellana	all	0	3.2	0	4.0	1.1	0	0	**1.5**
Lonicera caucasica	none	0	0	0	0	2.2	0	0	**1.0**
Cornus mas	none	0	0	0	4.0	15.2	0	0	**7.6**
Vaccinium arctostaphylos	none	0	0	0	36.0	15.2	0	0	**11.7**
Castanea sativa	all	0	9.7	5.6	8.0	5.4	40.0	33.3	**8.1**
Quercus infectoria	most	0	0	0	8.0	2.2	30.0	33.3	**4.1**
Juglans regia	all	0	3.2	0	0	1.1	0	0	**1.0**
Abies nordmanniana ssp. *equi-trojani*	none	0	0	0	8.0	2.2	0	0	**2.0**
Puccinellia festuciformis	few	0	0	0	4.0	3.3	0	0	**2.0**
Crataegus monogyna	none	0	0	0	0	0	10.0	0	**0.5**
Malus sylvestris	none	0	3.2	0	0	6.5	0	0	**3.6**
Prunus mahaleb	few	0	19.4	5.6	0	5.4	0	0	**6.1**
Prunus spinosa	few	0	6.4	0	0	10.9	10.0	0	**6.6**
Prunus spp.*	few	0	0	0	0	10.9	0	0	**5.1**
Pyrus communis	none	0	0	0	0	1.1	0	0	**0.5**
Pyrus elaeagnifolia	few	0	0	0	24.0	27.2	30.0	0	**17.2**
Pyrus syriaca	none	0	0	0	0	1.1	0	0	**0.5**
Pyrus spp. **	few	0	0	0	8.0	19.6	30.0	100	**13.2**
Rosa canina	none	0	0	0	0	6.5	0	33.3	**3.6**
Rosa horrida	none	0	0	0	0	2.2	0	0	**1.0**
Rubus spp. ***	few	0	3.2	0	68.0	66.3	20.0	0	**41.1**
Unidentified taxa									
Asteraceae sp. 1	none	0	0	0	0	1.1	0	0	**0.5**
Poaceae sp. 1	none	0	0	0	4.0	3.3	0	0	**2.0**
Species 1	none	0	0	0	0	1.1	0	0	**0.5**
Species 2	none	0	0	0	0	1.1	0	0	**0.5**
Species 3	none	0	0	0	0	1.1	0	0	**0.5**
Species 4	none	0	0	0	0	1.1	0	0	**0.5**
Species 5	none	0	0	0	0	1.1	0	0	**0.5**
Species 6	none	0	0	0	0	1.1	0	0	**0.5**
Species 7	none	0	0	0	0	1.1	0	0	**0.5**
Species 8	none	0	0	0	0	6.5	0	0	**3.0**
Species 9	none	0	0	0	0	1.1	0	0	**0.5**
Number of fecal samples		18	31	18	25	92	10	3	**197**

*At least 4 different species; **at least 2 different species; ***2 different species (*R. hirtus* and *R. canescens*)

flowering period of a plant species and the first month when seeds of that species were observed in a fecal sample. We found seeds in feces most frequently in August and September with the highest species richness, but we also recorded seeds of various taxa from June to November (Table 2). *Prunus* seeds were most frequent in June and July fecal samples when the richness of taxa consumed was low, while *Pyrus* and *Rubus* taxa dominated feces in August and September as the diversity of fruit trees and shrubs increased (Table 2). Damaged seeds of *Castanea sativa,* whose flowering period is typically between June and July, were available from June to November with a peak in October (Table 2), suggesting that the brown bear also consumed the previous year's fruits during summer.

The fate of seeds after passage through the brown bear gut varied depending on the fruit type of the plant species. All or most of the seeds in fruits of an acorn, capsule, drupe-like nut, and nut types were physically damaged while from berry, caryopsis, cone, drupe, pome, and rosehip fruits passed through the gut without any or with very little physical damage (Tables 1, 2). Thus, seeds from fleshy fruits were viable after passing through the gut, while those from hard masts were broken into pieces and were unviable.

Seeds of *Malus sylvestris* (European wild apple) (deviance = 13.1, $P = 0.0003$) and *Pyrus elaeagnifolia* (wild pear) (deviance = 5.6, $P = 0.018$) had significantly higher germination percentages in feces than the control (Fig. 2, **Supplementary Data S1**). Conversely, the germination percentage for *Lonicera caucasica* (honeysuckle) (deviance = 175.2, $P < 0.0001$) and *Vaccinium arctostaphylos* (Caucasian whortleberry) (deviance = 12.3, $P = 0.0004$) were significantly lower in feces compared to the control (Fig. 2, **Supplementary Data S1**). In *Rosa canina* (the dog-rose) (deviance = 2.9, $P = 0.090$) and *Rubus* spp. (deviance = 2.9, $P = 0.086$), germination was not different between the groups (Fig. 2, **Supplementary Data S1**). However, we also observed that *Rubus* spp. seeds had already been germinated within a few fecal samples, while the seeds were waiting to be extracted. These results showed that the fruit type also had a significant effect on the germination probability after the passage of seeds through the brown bear gut ($P < 0.01$, Table 3). Among the species that were tested for their germination, indeed, the ones with pome fruits had a higher germination percentage in feces than the control, while those with berries showed an inverse result (Fig. 2, **Supplementary Data S1**). On the other hand, both species with rosehips had low germination values without any significant difference between feces and control groups.

Discussion

Our analysis on fecal samples indicates that the brown bear disperses seeds of several species found in northern Anatolian mixed temperate forests, especially those with fleshy fruits (e.g., Rosaceae members). We also found that the brown bear disperses seeds of many species belonging to other families such as Aquifoliaceae, Ericaceae, and Poaceae. Moreover, the germination of seeds of some wild fruit trees is enhanced after passing through the brown bear gut. More explicitly, among taxa whose seeds were identified in our study, 85% (29 out of 34 taxa) had undamaged (or rarely damaged) seeds in fecal samples. Two-thirds of the taxa tested for germination ability (4 out of 6 taxa) showed a positive or neutral response to passage through the brown bear gut. Accordingly, our study suggests that the brown bear is a significant seed dispersal agent through endozoochory in these mixed temperate forests. This result is consistent with that of studies conducted in other ecosystems in Europe (Clevenger et al. 1992, Paralikidis et al. 2010; Ciucci et al. 2014; Lalleroni et al. 2017) and Asia (Karimi et al. 2018a, b). Moreover, our study sheds light on the role of fruit type in the success of seed dispersal through endozoochory by the brown bear. We found clear differences in the damage level of hard masts and fleshy fruits after passage through the brown bear gut. The germination ability among various fleshy fruit types also differed between fresh seeds collected from the field and those obtained from fecal samples. These differences have never been emphasized in such a clear way, except for a few studies that acknowledged some fruit traits as determinants of the damage or germination level of seeds having passed through the gut of frugivore species (Herrera 1989; Otani and Shibata 2000; Traveset and Verdú 2002).

Our results on the monthly differences in the consumption of seeds belonging to different species are also consistent with previous studies, suggesting that brown bear diet depends on the phenology of fruiting trees and shrubs (Clevenger et al. 1992; Ciucci et al. 2014; Harrer and Levi 2018; Karimi et al. 2018b). However, the brown bear's temporal feeding habits may change briefly as the flowering and fruiting times of the species they consumed are altered by climate change (Bojarska and Selva 2012). Fortunately, the brown bear is an omnivorous species with high plasticity of feeding behavior. It is well-known that when fruits are not available, the brown bear resorts to different food sources such as grasses, ants, or vertebrates, depending on the season (Persson et al. 2001; Paralikidis et al. 2010; Ciucci et al. 2014; Kazancı et al. unpublished data). Studies regarding the effects of plant

Table 3 Summary of the analysis testing the effect of fruit type and passage through the brown bear gut on the germination probability of seeds (generalized linear mixed model, GLMM). Model parameters and *P* values were obtained by performing likelihood ratio tests. *logLik* is log-likelihood, and *df* is the degree of freedom

Model parameters				
Factor	logLik	df	χ^2	*P*
Null	− 185.5			
+ Gut passage	− 175.2	1	19.8	< 0.0001
+ Fruit type	− 180.2	2	10.8	0.004

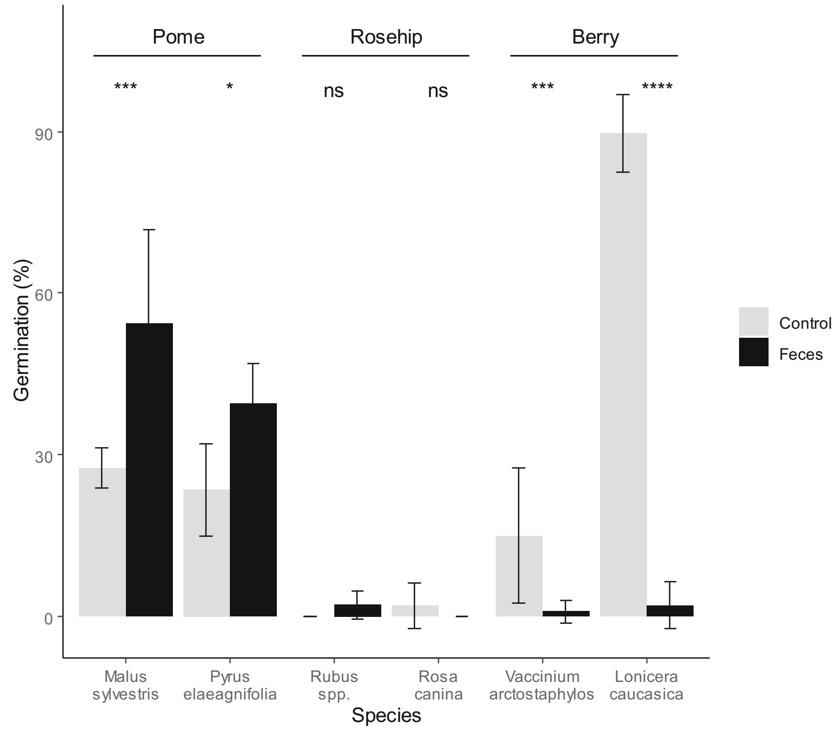

Fig. 2 Mean germination percentages of seeds in fecal samples compared to the corresponding control (fresh seeds collected from the field) for six species included in the germination experiment. Error bars represent the standard deviation of the sample mean. Statistical significance shows the result of the binomial GLM analysis comparing control and feces groups (*ns* non-significant, $*P < 0.05$, $***P < 0.001$, $****P < 0.0001$). Fruit type (pome, rosehip, and berry) of species are also given at the top. *Rubus* spp. includes two species (*R. hirtus* and *R. canescens*). For more details of the analysis, see **Supplementary Data S1**

phenology change on the brown bear's feeding habits would have promising results for the conservation of the brown bear under climate change as they may provide information regarding the possible limits of plasticity in the feeding behavior of the brown bear.

The successful dispersal of seeds through endozoochory depends on the post-dispersal seed survival, which can be characterized by the survival ability of seeds during their passage through the gut of the disperser animal (Cosyns et al. 2005; Anderson et al. 2014), whether the location where animals defecate is a safe place for the development of seedlings (Willson and Whelan 1990; Bustamante et al. 1992), and the ingredients of the feces the seeds are embedded in (Traveset et al. 2001). Like other carnivore mammals, brown bears have shorter digestive systems than many herbivores, but at the same time, they have an omnivorous feeding habit. This gives the seeds consumed by the brown bear a stronger chance to survive passage through the gut as the retention time in the gut is a determinant of seed survival (Cosyns et al. 2005; Soons et al. 2008). In our study, indeed, seeds of many species, especially those from fleshy fruits, passed through the gut without any harm or rarely being harmed. However, seeds of *Corylus avellana*, *Castanea sativa*, *Juglans regia*, and *Quercus infectoria* in fecal samples were damaged and not germinable. Having an inedible hard shell was the common property of the fruits of these species (Smith 2018). Such fruit shells and seeds are likely to be harmed by chewing during consumption by the brown bear (Seryodkin 2016). Most species in *Allium* genera, one of the taxa whose seeds were damaged during passage through the brown bear gut in our study, are known to have seeds without any specialization for dispersal (Sádlo et al. 2018; Tavşanoğlu and Pausas 2018); therefore, these species may not make much investment in seed coating for protection against digestive enzymes (Samuels and Levey 2005). On the other hand, the seeds of *C. avellana*, *C. sativa*, *J. regia*, and *Q. infectoria* are well-known to be dispersed through hoarding by birds and small mammals (Kollmann and Schill 1996; Loacker et al. 2007; Urbisz and Urbisz 2007; Pesendorfer et al. 2016; Smith 2018; Tavşanoğlu and Pausas 2018). However, such plant species are sometimes referred to as endozoochorous (Correia et al. 2018; Tavşanoğlu and Pausas 2018), possibly due to observations on the consumption of their fruits by large mammals such as the brown bear. Our study clearly showed that even if the fruits of these species are consumed by the brown bear, such observations alone do not provide direct evidence for endozoochory mediated by the brown bear. Instead, our results on seed damage suggest that the brown bear behaves as a pre- or post-dispersal (depending on the consumption location, i.e., on the plant or ground) seed predator for these species (e.g., Herrera 1989; Fedriani and Delibes 2009). Consequently, our observation on the presence of damaged and intact seeds in fecal samples suggests that a distinction should be made based on which part of the consumed fruit is used by brown bears for their energy requirements. Thus, the brown bear consumes the fruits covered with a hard shell for their seeds within but the fleshy ones primarily for their pericarp. Consequently, our results suggest that fruit type is a determinant of the success of seed dispersal after passing through the gut in the brown bear. However, empirical evidence regarding the effect of fruit type on the success of endozoochory for different ecosystems and different frugivore animals is needed before general conclusions can be drawn.

The apparent taxonomic clustering of endozoochory by the brown bear as regards the Rosaceae family has frequently been observed in the temperate forests of Europe and Asia (Clevenger et al. 1992; Paralikidis et al. 2010; Ciucci et al. 2014; Lalleroni et al. 2017; Karimi et al. 2020). This pattern observed in the brown bear differs significantly from many other ecosystems, including the Mediterranean and tropical habitats, where frugivore-dispersed plants are more diverse at the family level (Herrera 1995; Campos-Arceiz and Blake 2011). Most Rosaceae members have fleshy fruits, making them attractive for birds and mammals as a food source and allowing long-distance seed dispersal. Such reciprocal interactions have been considered an example of mutualism between animals and plants (Willson 1993). Still, the coevolutionary relationship between plants with fleshy fruits and their seed disperser animals has been questioned (Jordano 1995). This is mainly because of the existence of a phylogenetic signal in the fleshy fruit trait (Jordano 1995; Tavşanoğlu and Pausas unpublished data). However, observations on germination enhancement after passing through the gut (Traveset and Willson 1997; Steyaert et al. 2019) give additional evidence supporting the adaptation hypothesis. In our study, among the taxa in which we tested germination, only Rosaceae members had positive (*Malus sylvestris* and *Pyrus elaeagnifolia*) or neutral (*Rosa canina* and *Rubus* spp.) responses to passage through the gut and germination in two other species (*Lonicera caucasica* and *Vaccinium arctostaphylos*) decreased in comparison to the control. Therefore, we believe that the interaction between many plants of the Rosaceae family and the brown bear could further be identified as a mutualistic one. On the other hand, the fruit type can further explain the germination response of seeds after passage through the brown bear gut as we observed different germination responses even between Rosaceae family members with differing fruit types. The survival and establishment advantages of larger seeds over smaller ones and the trade-off between seed number and size are well-known patterns in plants (Moles and Westoby 2004, 2006). This plant strategy framework predicts that the higher the number of seeds in fruits, the higher the post-dispersal seed mortality rates (Moles and Westoby 2004). Similarly, higher germination percentages in drupe-type fruits in comparison to berries and rosehips might be associated with the extant of investment made to individual seeds in these species, as seeds in drupes are larger in size, with a thicker coating, and the drupe fruits include fewer seeds than other fruit types. Indeed, the survival or germination of seeds that have passed through the gut may depend on the seed size (Otani and Shibata 2000), but observations to the reverse are also present (Herrera 1989; Bruun and Poschlod 2006). We suggest that the observed lower germination for smaller seeds after passage through the brown bear gut compared to that of freshly collected seeds can be a by-product of a risk-reducing strategy for successful long-distance dispersal in these plants (i.e., producing a high number of seeds with low survival in the gut).

There are two possible drawbacks regarding our germination experiment. The first is related to our treatment of fruits collected in the field (i.e., the control groups in the experiment), which we depulped to extract individual seeds before sowing the seeds in Petri dishes. The depulping of fruits may stimulate germination in some species, especially in the case of endozoochory by frugivore species (Travaset and Verdú 2002; Samuels and Levey 2005), including the brown bear (Traveset et al. 2001; Steyaert et al. 2019). The second is the usage of one condition in the germination experiment. Favorable germination conditions vary among species (Baskin and Baskin 2014), and germination results may change under different experimental conditions in the study of endozoochory (e.g., greenhouse vs. natural conditions; Karimi et al. 2020). It should also be noted that our conclusions regarding the germination of species are based on an experiment of only six species. Therefore, one should be cautious while using or interpreting our germination results. A more comprehensive research is needed to elucidate whether the patterns we observed in our germination experiment (i.e., the germination difference among fruit types and the seed size-germination relationship) are common among plant-animal seed dispersal relationships. Trait-based approaches are promising for a better understanding of such relationships in zoochorous seed dispersal systems (Albert et al. 2015).

In conclusion, fruit type is a determinant of the success of endozoochorous seed dispersal by the brown bear. A complete study approach for endozoochory by brown bears, therefore, should include not only a descriptive analysis of fecal samples for seeds but also the identification of the intact and damaged seeds in feces and a test for the germinability of seeds found in feces. In this study, we also established the role of the brown bear as a seed dispersal agent in northern Anatolian mixed temperate forests.

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Authors' contributions A.S., A.E., and Ç.T. designed the study and collected fecal samples in the field; D.D.K. and C.Ü.D. conducted the lab work, including the germination experiment; Ç.T. analyzed data and wrote the first draft of the manuscript; all authors critically contributed to the final version of the manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

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