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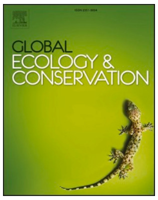

A global review on the role of small rodents and lagomorphs (clade Glires) in seed dispersal and plant establishment

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ABSTRACT

Zoochory is an ecologically and evolutionarily important seed dispersal type. The decline and extinction of seed-dispersing large herbivores severely threatens dispersal-driven ecosystem processes in many regions. Hence the relative importance of small rodents and lagomorphs (Glires, Mammalia) as dispersal vectors might increase due to their ubiquity, diversity and abundance. Here we provide a review of rodent- and lagomorph-mediated seed dispersal based on approximately 600 papers found in an extensive literature search. We highlight that small rodents and lagomorphs disperse seeds via various mechanisms. The seldom documented epi- and endozoochory are probably universal in these groups. Due to their small home range, short fur and small body size, these mechanisms generally operate at small scales and mainly for small seeds. Taxon-specific feeding, nesting and behavioural characteristics provide a wide spectrum of other seed dispersal types, such as synzoochory (food caching). The studied taxa generally support seed dispersal within a particular habitat patch, contributing to the persistence of local populations, but in rare cases, long-distance dispersal events might occur. Besides seed dispersal, rodents and lagomorphs can also support plant establishment and provide safe sites for seeds where they can survive stochastic events. Studies reviewed here show a strong bias both in scope and geographical distribution: synzoochorous dispersal of woody plants is known in detail, and most studies were conducted in the same few countries and habitat types. In contrast, other mechanisms such as endozoochory, epizoochory and habitat types like grasslands and anthropogenic habitats have rarely been studied. We show examples on ecosystem services and disservices related to rodent- and lagomorph-mediated seed dispersal as well as the importance of these processes in habitat conservation and restoration.

1. Introduction

Dispersal is one of the key ecological processes that determine the distribution, abundance and population structure of organisms. The ability of species to move between and colonise new habitats can help to ensure their regional persistence and to reduce the risk of local extinctions (van der Pijl, 1969; Hanski, 1999). In the case of mobile species such as most animal taxa, dispersal is generally

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possible by the movement of individuals (Auffret et al., 2015). As full-grown individuals of most vascular plant species have limited mobility (e.g. clonal spreading), their spatial movement is generally realised by the dispersal of reproductive units, most often seeds (Nathan, 2006). Effective seed dispersal allows plants to maintain population stability even at large spatial scales, to sustain functional connections among meta-populations and to colonise new habitats (Hanski, 1999; Auffret et al., 2015). With contemporary increases in habitat loss and fragmentation, dispersal has become an even more relevant process, as it can influence the species composition and functioning of ecosystems on regional and global levels (Fletcher et al., 2018; Deák et al., 2018). Plant species with long-distance dispersal potential are expected to be less sensitive to fragmentation than short-distance dispersers as they might be able to move between fragmented habitat patches and establish functional connections among meta-populations (Auffret et al., 2015).

The effectiveness of dispersal is influenced by the evolutionary adaptations of the plant species and the available dispersal vectors. Anemochory and zoochory are considered the two most widespread effective long-distance plant dispersal types in terrestrial ecosystems. Anemochory, i.e. dispersal by wind, is a unidirectional means of dispersal. Distance and direction of the dispersal are highly influenced by meteorological conditions, and seeds have a high risk of being dispersed into an unsuitable environment (Nathan, 2006). Zoochory is a more directed means of dispersal, especially when the interacting species specialise in the same habitat, e.g. grassland specialist plant species and grazing livestock (van der Pijl, 1969; Deák et al., 2018). Mammals and birds play an active role globally in dispersing seeds over both short and long distances in terrestrial habitats (Willson, 1993; Manzano and Malo, 2006; Sekercioglu, 2012). Previous studies on zoochory in terrestrial ecosystems have focused primarily on the role of large herbivores and birds (e.g. Poschlod and WallisDeWries, 2002, Traveset et al., 2007). However, the global decline and extinction of seed-dispersing large herbivores severely threatens the dispersal-driven ecosystem processes in many regions (Cardillo et al., 2005; Corlett, 2007; Farwig and Berens, 2012; Ripple et al., 2015). Also, the body mass distribution of mammal assemblages was significantly reduced by now (from 95th-percentile of ∼ 14 kg to ∼ 4 kg) due to hunting pressure and habitat loss (Bogoni et al., 2020). These imply that the relative importance of other dispersal vectors, such as small rodents and lagomorphs, will increase (Burney and Flannery, 2005; Wotton and Kelly, 2011).

Whereas large herbivores have disappeared from many landscapes, small mammals (up to around 5 kg body mass) including representatives of the orders Rodentia and Lagomorpha (Glires, Mammalia), still occur in both semi-natural habitats and agricultural landscapes (Burgin, 2020). In addition, this group is generally more tolerant to habitat fragmentation and less prone to extinction than large-bodied herbivores (Cardillo et al., 2005; Ripple et al., 2015). They are distributed on all continents with high species richness (e.g. 42% of all mammal species are rodents, Burgin et al., 2018) and with high population densities (Burgin, 2020). Members of the clade Glires are often considered keystone species affecting many processes in ecosystems, e.g. by creating establishment gaps for plant species by plant biomass removal and soil perturbation and because they are important prey items (Milton et al., 1997; Alves et al., 2008; Ferguson-Lees and Christie, 2001; Jansen et al., 2012; Wu et al., 2015). Many of these species, especially small rodents, are also known as seed consumers and dispersers; however, their role in seed dispersal has been underestimated in the past (but see Reynolds and Glendening, 1949, Brewer and Rejmánek, 1999), and their function in dispersal processes was only poorly known (Dickman, 1999). Vander Wall et al. (2005a) already suggested that seed removal by rodents is not only seed predation leading to the destruction of the seeds. Now it is acknowledged that rodents have an important role in seed dispersal processes in both novel and natural ecosystems (Pires et al., 2014, van Leeuwen et al., 2020). In addition, small rodents and lagomorphs depend largely on plant material and they may play an important role in understudied means of seed dispersal, such as dispersing seeds from herbs. Also, they can disperse seeds by unusual subtypes of endozoochory (van Leeuwen et al., 2020).

Our aim was to provide a global synthesis of the role of the clade Glires in seed dispersal and plant establishment. We reviewed published studies focusing on the interactions between rodents or lagomorphs and seeds and on the activities of them such as feeding, transporting food and nest material, caching, pilfering and burrowing that might influence seed dispersal and plant establishment patterns. We followed the entire dispersal process step by step, from seed encounter to the transport of seeds to new localities to the activities and environmental factors influencing seedling establishment. We focused on the following questions: (1) What are the main types of seed dispersal mediated by small rodents and lagomorphs? (2) Which environmental factors affect the interactions? (3) How do small rodents and lagomorphs influence germination and seedling establishment? We also aimed to highlight the knowledge gaps about the seed dispersal by small rodents and lagomorphs and suggest new research directions.

2. Methods

2.1. Inclusion criteria

We included in our review small mammals from the clade Glires. These small mammals share many common behavioural and functional adaptations, such as feeding habits and morphological characteristics of skull and teeth (Fostowicz-Frelik, 2017). These makes them capable for gnawing or chewing, but e.g. many rodent species morphologically exhibit intermediate phenotypes suitable for both, so are characterized by generalist nature and feed at least partly on seeds or plant material (except some obligate carnivorous species) (Maestri et al., 2016; Fostowicz-Frelik, 2017). Teeth, jaws and jaw muscles of rodents and lagomorphs are adapted to deal with tough plant materials, like hard-coated seeds and woody plants (Corlett, 2017; Smith, 2018). Morphology of teeth largely determines the chance of crushing seeds in the mouth, thus seed dispersal may have different outcomes than that by other groups with different adaptations or body size (Malo and Suárez, 1995; Corlett, 2017).

2.2. Literature search

We performed a literature search in the ISI Web of Science Core Collection on January 25th, 2021. The terms for the clade Glires, seed dispersal and particular seed dispersal types characteristic of the clade were each combined within parentheses using the Boolean operator 'OR'. The three bracketed expressions were then combined using the Boolean operator 'AND'. We used the asterisk (*) as a 'wildcard' to include different word endings, e.g. scatter-hoard* for [scatter-hoard OR scatter-hoarded OR scatter-hoarding]. Quotation marks ("") around two words were used to restrict the search to instances where the resulting exact phrase occurs.

We searched for: ((TS=(("rodent*" OR "mammal*") AND ("seed dispersal" OR "dispersal vector*" OR "dispers*") AND ("scatter-hoard*" OR "larder-hoard*" OR "nest material" OR "caching" OR "cache" OR "burrow*" OR "feed*")))) and ((TS=(("lagomorph*" OR "rabbit" OR "pika" OR "hare") AND ("seed dispers*" OR "epizoochor*" OR "endozoochor*" OR "burrow*")))).

The literature search resulted in 1468 articles. Studies were evaluated for inclusion at three successive levels. We considered every paper that studied small rodents or lagomorphs with regard to seed predation, removal or hoarding, endozoochory, epizoochory, or activities associated with moving nest material or burrowing. First, we evaluated the papers by their title to exclude articles not relevant to our review. Next, we evaluated the relevance of the remaining studies based on their abstracts. Finally, the matching studies were evaluated as full texts. When reading the full-text papers, we also looked for relevant cited papers, which may include useful data for this review. To fill the gaps caused by the constrained time period covered in Web of Science, we repeated the search in Google Scholar to complement our literature search and find articles published before 1975. As a result, 583 research articles were evaluated for this review. We also considered previous reviews and books on this topic. The list of studies included in this review is given in Appendix S1.

3. Results and discussion

3.1. Types of rodent- and lagomorph-mediated seed dispersal

Similarly to primates, large carnivores and birds, small rodents and lagomorphs can also disperse seeds with endo- and epizoochory. There are other special dispersal types (synzoochory, caliochory) that are typical for the clade Glires, and also present in certain bird species (see the examples below at the subsections). The number and proportion of the articles sorted by activity, habitat type, the most studied animal taxa, continent and experimental setup can be found in Table 1.

Table 1
Number and proportion of articles sorted by activity, habitat type, the most studied animal taxa, continent and experimental setup.

		No. studies	% of total studies
All research articles		583	100
Activity	epizoochory	5	0.86
	endozoochory	51	8.75
	synzoochory (seed removal & synzoochory; chance for seed dispersal)	402	68.95
	seed encounter/predation/recovery, seedling herbivory (no dispersal)	81	13.89
	microhabitat creation (burrowing & herbivory)	50	8.58
Habitat type	wooded habitats	441	75.64
	open habitats	91	15.61
	laboratory experiments	27	4.63
	mixed	24	4.12
Most studied animal taxa	*Sciurus* spp.	79	13.55
	Tamias spp.	112	19.21
	Dipodomys spp.	50	8.58
	Peromyscus spp.	61	10.46
	Apodemus spp.	136	23.33
	Rattus spp.	45	7.72
	Niviventer spp.	57	9.78
	Dasyprocta spp.	43	7.38
	Oryctolagus sp.	36	6.17
Continent	Africa	25	4.29
	Asia	183	31.39
	Australia	13	2.23
	Europe	96	16.47
	North-America	164	28.13
	Central- and South-America	102	17.50
Experimental setup in case of seed removal/predation & synzoochory	Multiple plant species – multiple animal species	115	19.73
	Multiple plant species – single animal species	71	12.18
	Single plant species – multiple animal species	143	24.53
	Single plant species – single animal species	93	15.95

3.1.1. Endozoochory

Endozoochory is the dispersal of propagules that remain viable after ingestion by an animal. Seeds of many plant species can germinate from animal excrement (Traveset et al., 2007). This mechanism is a well-known phenomenon and has been extensively studied in the case of birds (Herrera, 2002; Vander Wall et al., 2005b; Lovas-Kiss et al., 2019), large herbivores (Pakeman et al., 2002; Metera et al., 2010; D'hondt and Hoffmann, 2011) and primates (Chen et al., 2017). It is also known for small rodents and lagomorphs, but is less widely studied. Large herbivores can disperse larger seeds, in larger cohorts for longer distances than herbivores with smaller body size (Ripple et al., 2015). Van Leeuwen et al. (2020) emphasize that endozoochory literature is dominated by studies on plants with a fleshy fruit but that many non-fleshy fruits may also be dispersed by endozoochory.

Small seeds with a hard seed coat have the potential to pass through the digestive system intact and can thus be dispersed by small rodents or lagomorphs (Pakeman et al., 2002; Cousens et al., 2010). Theoretically, any small rodent or lagomorph species (including approximately 2050 rodent and 91 lagomorph species, (Burgin, 2020)) feeding on plant material containing seeds are potential endozoochorous vectors. However, most studies examined endozoochorous seed dispersal by only a few species, most often brown or house rats (*Rattus norvegicus* and *R. rattus*) and European rabbit (*Oryctolagus cuniculus*) (Appendix S1.). These species are abundant and widely distributed across the globe and in certain cases can even be highly invasive (Shiels, 2011; Riofrío-Lazo and Páez-Rosas, 2015; Duron et al., 2017; Bobadilla et al., 2020). While frequently serving as seed predators, seeds can pass intact through their gut so they can also disperse small-seeded plant species. For example, rats can disperse seeds by endozoochory up to a seed length of 1.5 mm (Shiels, 2011), while rabbits ingest seeds as large as 5 mm (Mancilla-Leytón et al., 2013; Perea et al., 2013).

Intact and viable seeds can be found in the faecal samples of many species such as the cloud forest grass mouse (*Akodon torques*), the Peruvian vesper mouse (*Calomys sorellus*), the forest small rice rat (*Microryzomys minutus*), the Andean pygmy rice rat (*Oligoryzomys andinus*), some oldfield mouse species (*Thomasomys kalinowskii, T. oreas, T. aureus*) (Sahley et al., 2016) and the European rabbit (*Oryctolagus cuniculus*) (Castro et al., 2008). However, even intact seeds in the faeces of common and bank voles (*Microtus arvalis*, *Myodes glareolus*) barely germinated, although this study was notable for small sample size ($n = 5$ intact seeds; Fischer and Türke, 2016). Consumed seeds get different treatments in animal's gut that determines the chance for seed dispersal and germination (Cosyns et al., 2005; Mancilla-Leytón et al., 2013; Campos et al., 2020). As it is demonstrated for various taxa, there are connections between basal metabolic rate (BMR) and retention time. That is, species with low BMR generally have higher retention time. Seeds that spend longer time interval in the gut are more exposed to physical and chemical impacts which may highly influence the level of scarification and so the viability and germination capacity of ingested seeds (Peinetti et al., 1993; Cosyns et al., 2005; Varela and Bucher, 2006; Van Leeuwen et al., 2016; Campos et al., 2020). Small rodents and lagomorphs – compared to large herbivores – show remarkably high variation in BMR, from extremely high (golden hamster *Mesocricetus auratus*) to relatively low rate (some desert rodents like Tristram's jird *Meriones tristrami*) (Careau et al., 2009; Clarke et al., 2010). This suggests that small rodent and lagomorph species with different BMR may differently affect germination rate of identical plant species. As we did not find any study which described the effect of BMR of small rodent and lagomorph species on the ratio of viable seeds in their faeces and the number of germinated seeds, we suggest considering this aspect when studying the topic in the future.

Endozoochorous seed dispersal by the clade Glires is mostly ignored in scientific researches, only a few experimental articles are available (number of studies=51, Table 1., Appendix S1.). These studies cover on a very few small rodent and lagomorph species (>30 species). Half of these studies focus only on a single species (European rabbit — *Ornitholagus cuniculus*), while several species are included in only one experimental study (Appendix S1.). Despite the low number of studies evidence show that small rodents and lagomorphs can play an important role in endozoochorous dispersal of small seeds. Sahley et al. (2015, 2016) and Riofrío-Lazo and Páez-Rosas (2015) also emphasise the importance of small rodents as potential endozoochorous seed dispersers and call for future seed dispersal studies focusing on this topic. It would be important to carry out further studies using proper sample sizes, i.e. sufficient number of animals and seeds (e.g. see Fischer and Türke, 2016) and considering the most important influencing factors (e.g. seed traits and BMR, see also Campos et al., 2020). Characteristics of the faeces (nutrient and moisture content and possibly adverse compounds) and the number and density of seeds in the faeces might also be an important factor influencing seed survival and germination of the dispersed seeds (Traveset et al., 2007); however, until now studies focusing on this issue are completely lacking.

3.1.2. Epizoochory

Epizoochory, i.e. dispersal by attachment to the external parts of animals (such as fur, hooves, bill) is widely recognised as an ancient and effective long-distance seed dispersal mechanism (Manzano and Malo, 2006; Nathan, 2006). To promote dispersal, plants have evolved many devices for efficient adhesion to fur (van der Pijl, 1969; Poschlod and WallisDeVries, 2002). Adhesive propagules do not possess nutritional or energetic attractants; animals usually pick them up unintentionally and by chance. However, there are numerous factors affecting the success of such adhesion, including rainfall, vegetation structure and fur type (Sorensen, 1986; Couvreur et al., 2004, Will and Tackenberg, 2008; Cousens et al., 2010).

There is an overwhelming number of studies describing epizoochory by vertebrates, especially by large herbivores (Couvreur et al., 2004; Schulze et al., 2014), but other groups, e.g. carnivores (Hovstad et al., 2009) and birds (Costa et al., 2014) are also frequently mentioned. Small rodents and lagomorphs barely got attention (number of studies=5, Table 1., Appendix S1.). However, many low-growing herbaceous plant species with adhesive fruits are present in the ground layer, which is often inhabited by a large number of small mammals (Sorensen, 1986). Therefore, epizoochory by small rodents and lagomorphs is likely a more universal and widespread dispersal type than previously documented. For instance, hares (*Lepus capensis*) and rabbits (*Sylvilagus floridanus*) may be efficient epizoochorous seed dispersers, as they are prevalent in their habitats and due to their small size can reach all microsites near the ground surface (Agnew and Flux, 1970; Couvreur et al., 2008, see also Appendix S1.).

According to the only study we found on epizoochory by small rodents, yellow-necked field mice (*Apodemus flavicollis*) were found to be effective epizoochorous seed dispersers. Small seeds were in general more efficiently dispersed by the species than large ones, but large seeds with adhesive appendices (e.g. *Agrimonia eupatoria*) also remained in their fur for a considerable period. The maximum potential dispersal distance was 26 m, and the retention time reached almost ten minutes (Kiviniemi and Telenius, 1998). Based on this, small rodents and lagomorphs generally disperse seeds at the local scale, within a radius of a few tens of metres, which ensures that the dispersed seeds remain in the same habitat type where they were collected; thus, the new place is likely to be suitable for the establishment of the transported plant species. This suggests that given their generally small home range, small rodents and lagomorphs with short fur and small body size may be efficient epizoochorous seed dispersers on a small scale and mainly for small seeds. However, future studies are needed to investigate this mechanism for additional species and in more detail.

3.1.3. Synzoochory

Synzoochory is the dispersal of seeds by seed-caching animals. Many plant species are dependent upon synzoochory (Vander Wall et al., 2005c; Borchert et al., 2003). It is a key mechanism of dispersal for many trees and shrubs (Zwolak et al., 2016; Longland and Dimitri, 2018). In special cases, synzoochory is the only way of recruitment (Beck and Vander Wall, 2010). It occurs when animals gather food to prepare stores to survive harsh periods and a part of the stored seeds somehow escape being eaten (Vander Wall, 1990). It is also a characteristic of several bird species, best known examples are crows and woodpeckers (Gómez et al., 2019).

Food hoarding is typical in the orders Rodentia and Lagomorpha (Appendix S1.). There are two main types of food hoarding: 'scatter-hoarding' and 'larder-hoarding'. Scatter-hoarders usually prepare shallow holes for hiding one or more seeds in each and burying them under a few millimetres or centimetres of soil or simply under leaf litter (Vander Wall, 1990). Scatter-hoarded seeds are transported to an environment which can be suitable for germination, but the seeds are at a risk of theft (Perea et al., 2016). Larder-hoarding animals collect seeds in large caches located farther from the source, usually in cavities, such as deep underground burrows (approx. >10 cm) or tree hollows. As the unsuitable environment of cavities usually prevents the successful germination and establishment of the seeds, larder-hoarding is less likely lead to successful seed dispersal in itself (Benvenuti et al., 2001; Vander Wall et al., 2005b).

An uncommon type of food-hoarding is when stores reach enormous sizes, and placed aboveground. The mound-building mouse (*Mus spicilegus*), prepares mounds of soil in autumn to store seeds. These mounds can contain more than ten kilograms of seeds covered by a shallow soil layer, and within the mounds, propagules of 84 plant species have been found so far (Sokolov et al., 1998). The stored plant material not exclusively serves as food, but has an important insulating role, which increases the chance of seeds to survive until the next spring (Szenczi et al., 2012). There is only indirect data available on the seed dispersal potential (i.e. seed content of the mounds) of hoarding; however, hoarding can be a relevant process in many ecosystems considering the wide distribution of small rodents and lagomorphs practicing it (Coroiu et al., 2016). Another species, pikas (*Ochotona* spp.) build large caches of vegetation (called 'haypiles') from summer to late September in mountains in rock, adjacent to vegetated areas (Broadbooks, 1965). The piles can reach even the weight of 6000 g. Their content is highly depending on the availability and relative abundance of plant species. Piles are characterised by containing a single species in abundance over all others and species from at least 20 plant genera are used, including grasses, herbs, shrubs and trees (Millar and Zwickel, 1972). As by time the degrading haypiles form patches of nutrient-rich substrates, pikas can locally enhance nutrient availability to plants (Millar and Zwickel, 1972; Aho et al., 1998). By the hay transfer pikas may contribute to seed dispersal, as moving considerable amount of plant material during the seed ripening period. As they collect whole plants and large particles, it is highly possible that the hay contains seeds. The increased nutrient availability may help the germination and establishment of the transferred seeds. This kind of transfer of soil and plant material by mice and pikas could be an effective measure of seed dispersal, and could also provide optimal microsite for the seedlings. In lack of evidence of the seed dispersing role of these activities, further research is needed.

The above examples show the still unexplored nature of food-hoarding activities. Though synzoochory is the most frequently studied dispersal type mediated by small rodents and lagomorphs (number of synzoochory studies=402, Table 1., Appendix S1.), many studies focus only on the seed removal and caching phases without mentioning the final seed fate (number of studies=81, Table 1., Appendix S1.), including seed-to-seedling transition, and quantitative evaluation of the animal's role (Aliyu et al., 2014; Morán-López et al., 2015). Handling of seeds and behavioural decisions can vary enormously as food hoarding consists of many discrete steps depending upon numerous interacting factors such as motivation, food value, cost of ingesting plant secondary metabolites, handling time, cost of missed opportunities, metabolic costs, perishability, pilferage risk and predation risk (Lichti et al., 2017). The seed dispersal effectiveness of a scatter-hoarder and thus the final seed fate is determined by the interaction of these variables (Schupp et al., 2010). Through these, the interactions between seeds and small rodents or lagomorphs are not exclusively positive (seed dispersal) or negative (seed predation), but located at some point along a mutualism–antagonism continuum, which makes food-hoarding animals conditional mutualists (Theimer, 2005; Gómez et al., 2019). Zwolak and Crone (2012) propose that the overall outcome of the interactions tends weakly towards mutualism, but it is largely context-dependent. Zhang et al. (2021) also emphasize the context-dependent outcome of the interactions. They highlight that in most cases the signs of the interactions are not fixed, so the interactions are not monotonic, but can change depending on spatio-temporal scale. One should consider that density-dependent transition from mutualism to antagonism and vice versa is a more general phenomenon than was previously thought, although it can be difficult to detect. It is important to take this into account when planning an experiment. Performing manipulative experiments and using the proper seed-tracking method, which enables us to follow the process until the final stage (either predation or seedling establishment) with the evaluation of costs and benefits, we could get a much more complete picture about the seed dispersal effectiveness of this group which is crucial to get a better insight into mutualistic-antagonistic relationships in seed dispersal systems by small rodents (see also Forget and Wenny, 2005; Yi et al., 2008; Hirsch et al., 2012; Zwolak and Crone, 2012; Rosin and Poulsen, 2017; Elwood et al., 2018; Zhang et al., 2021).

3.1.4. Caliochory

Caliochory means that an animal is dispersing seeds by gathering and transporting nest material (Camacho et al., 2019). Many rodent species use plant material for building their nests (Hansell, 1993; Farkas et al., 2018) and for insulation (Szenczi et al., 2012). They often harvest and transfer the whole plant or pieces of it and use it for nest building or padding the nest chamber to moderate thermal variation. Paddings generally consist of large fibrous particles (Blom et al., 1996; Farkas et al., 2018). Taking whole plants decreases the risk of seed damage during the harvest and enhances the probability of transferring intact seeds. As burrows are mostly placed deep under the ground, they are usually not suitable for seed germination (Benvenuti et al., 2001). However, the nest building process has a potential role in seed dispersal during the building stage and by taking seeds back to the surface from the burrow by epizoochory (Kiviniemi and Telenius, 1998; Laughlin, 2003). While caliochory has been confirmed by several studies on birds (e.g. Dean et al., 1990; Camacho et al., 2019), there is no direct evidence on small rodents and lagomorphs for the seed dispersal potential of the nest building processes; therefore, further studies are needed.

3.2. Influence of environmental factors and biotic interactions

Abiotic and biotic factors (e.g. fire regimes, climate and inter- and intraspecific interactions) can have a strong effect on seed and fruit physical, chemical, and phenological traits, determine the relationship in which plants co-evolve with their dispersers and influence animals' decisions (Hollander and Vander Wall 2009; Beck and Vander Wall 2010; Rusch et al., 2014). The effects of seed characteristics on the decisions of small rodents are further modified by various environmental factors. Here we discuss those factors that were not explained in detail by Lichti et al. (2017), who synthesised the literature on scatter-hoarding rodents and identified several processes and variables that make the process context-dependent and with these aimed to develop a comprehensive mechanistic seed-fate model.

3.2.1. Soil properties

Small rodents have a good spatial memory and use visual cues for seed recovery; however, in contrast to seed-storing birds, they also use their keen sense of smell to retrieve buried seeds, which increases their effectiveness. However, olfaction performs poor under dry conditions compared to cases when the soil moisture is high (Geluso, 2005; Downs and Vander Wall, 2009; Vander Wall and Jenkins, 2011; Hollander et al., 2012). Olfaction is also less effective in burnt areas when ash is present (Briggs and Vander Wall, 2004). Since naive foragers and pilferers, such as young animals, seem to use mainly olfactory cues for seed detection (unless they actually observe a cache being made by others), changes of the soil properties occasionally render them incapable of recovering others' caches so that the rate of pilfering becomes negligible (Ribeiro and Vieira, 2016, Briggs and Vander Wall, 2004). Rodents bury food shallower in soils where digging is energetically costly. If possible, they avoid such substrates and use alternative sites (Vander Wall, 1993), maybe because shallower caches are at a higher risk of exploitation, especially when combined with high soil moisture (Geluso, 2005). Thus, changes in soil properties, most importantly in soil moisture, have a considerable effect on the seed dispersal process. It affects seed recovery rate from caches, and by that the number of seeds which have a chance to germinate.

3.2.2. Habitat structure and predation risk

Seed removal is often influenced by the availability and spatial distribution of safe microhabitats like shrubs or dense patches of tall-growing grasses and forbs, which offer shelter from predators during seed handling (Hulme, 1994; Sun and Zhang, 2013; Miguel et al., 2017). For example, finer seed selection was observed for the long-tailed field mouse (*Apodemus sylvaticus*) under shelter. In a safe microhabitat, field mouse selected seeds by species rather than size; thus, the selection of seeds was risk-sensitive (Perea et al., 2011a). Also, more seeds were dispersed to shelters, where larger caches were made, but seeds had higher predation rates in safe microhabitats (Perea et al., 2011b; Rusch et al., 2014; Ribeiro and Vieira, 2016). In contrast, in open habitats or in vegetation gaps, seed removal may be negligible or happen more hastily without finer selection due to the high risk of the seed disperser to become prey (Seiwa et al., 2002; Gallego et al., 2017; Morán-López et al., 2018). Predation risk on seed dispersers influences risk of cache pilfering. Pilfering by conspecifics forces small rodents to take avoidance actions result in altered seed dispersal patterns (Lichti et al., 2020). As the increased predation risk in gaps decreases the risk of pilfering, more nutritious seeds may more likely be cached in gaps, which promotes natural regeneration because the emerging seedlings have less competition (Seiwa et al., 2002; Muñoz and Bonal, 2011; Perea et al., 2011b, but see Wang and Corlett, 2017). Ungulates also compete with small rodents for seeds; hence, the presence of large herbivores may alter the caching patterns and stimulate seed hoarding, caching and retrieval, which also increase the pilfering risk (Muñoz and Bonal, 2007). With an increased presence and pilfering risk by conspecifics, the spatial distribution of cached seeds became sparser (Puerta-Piñero et al., 2010), and small rodents avoided shrubs (safe sites) as caching sites (Muñoz and Bonal, 2007). In sites characterised by the presence of ungulates the short-term recovery rate was almost fifteen-fold; resulting that very low percent (1.4%) of cached seeds remained unretrieved. In the absence of ungulates, this value reached 19.9% (Muñoz and Bonal, 2007). During foraging mice may also focused on food acquisition at the expense of vigilant behaviours (Gallego et al., 2017). Lichti et al. (2020) demonstrated that pilfering-avoiding mechanism by small rodents may be a driver of the evolution of seed traits. As the animals usually hide valuable (bigger or more nutritious) seeds into gaps, plants with high light requirements invest more into seeds that are valuable for their dispersers, thus these seeds are generally cached in less sheltered sites. However, it should be considered, that caching in opened sites is not always profitable for light demanding plants. In drier habitats, such as in the Spanish dehesa, even if cache pilferage is much lower in opened sites than in forest, seedling emergence is very low and seedling mortality is very high, mostly due to desiccation (Smit et al., 2009). Thus, even the light demanding plant species may have a higher establishment success rate in shaded microsites.

According to these results, microhabitat structure, that in this case express the distribution of safe sites and gaps, is an important factor affecting small rodent densities and related dispersal patterns. Intra- and interspecific interactions can influence seed handling behaviour as small rodents should compete for seed sources with conspecifics or other seed consumers. Pilfering-avoiding mechanisms may affect the seed dispersing potential of small rodents and can have either positive or negative effects on plant establishment. These factors determine fundamentally the quantity and quality of seed dispersal by small rodents, while some plant species try to take advantage on these to increase their establishment success. However, it should be considered that cache survival is not always the ultimate measure of seed dispersal success, as habitat conditions may hinder seed germination or establishment. It should be also considered, that many previous studies derived conclusions using experiments focusing on single animal species, when such correlations are not revealed (Table 1., Appendix S1.).

3.2.3. *Other biotic interactions*

Sympatric plant species can facilitate or hinder the removal and establishment of seeds of other species by making one of the seeds more attractive than others. For example, in the presence of oriental white oak (*Quercus aliena*, producing medium-size acorns), the acorns of Chinese cork oak (*Q. variabilis*, producing large acorns) were more likely to be scatter-hoarded by Pallas's squirrels (*Callosciurus erythraeus*), while the removal of acorns of Chinese oak (*Q. serrata* var. *brevipetiolata*, producing small acorns) decreased relative to foraging in the absence of *Q. aliena*. As a result, the oak with medium-sized acorns indirectly promoted seedling establishment of the one with large acorns, but hindered seed-seedling transitions in the oak with small acorns (Yi and Wang, 2015). Furthermore, Xiao et al. (2013) found that seeds with no or short dormancy period can support the survival of seeds with long dormancy period as dormant seeds are less attractive for immediate consumption but are preferred for long-term storing. In another case, the co-occurrence of two heterospecific acorns, Chinese chinquapin (*Castanea henryi*) and Chinese cork oak, which are equally attractive to small rodents, resulted in enhanced dispersal services for both species (Xiao and Zhang, 2016). The result of these interactions caused by the co-occurrence of heterospecific acorns may alter masting patterns: synchronous masting of various tree species can increase dispersal effectiveness, which in the long term may influence the evolution of synchrony or asynchrony among sympatric tree species (Lichti et al., 2014; Yang et al., 2020). Indirect interactions, such as the co-occurrence of several palatable plant species can influence an animal's behaviour and result in context-dependent seed dispersal. This means that there may be remarkable differences in the seed dispersal effectiveness of small rodents in certain habitats with variable proportion of the seeds of palatable plant species. However, in case of these interactions a high proportion of previous studies also derived conclusions using experiments focusing only on a single plant species (Table 1., Appendix S1.).

3.3. *Threat factors*

Many ecosystems are facing a rapid destruction and transformation globally, which is the greatest threat to biodiversity, amplified by the effects of climate change (Segan et al., 2016). Human activities threaten semi-natural habitats and seed disperser assemblages and may thus result in altered seed dispersal patterns.

3.3.1. *Habitat loss and degradation*

Above we highlighted the importance of habitat structure for the seed dispersal by small rodents. After deforestation, animals become more exposed to predators in the remaining fragmented forest patches, which can result in reduced movements and thus in a decline of dispersal services (Morán-López et al., 2015, 2018). The fragmentation of habitats can alter the interactions between seeds and small rodents significantly as plants and animals vary in their response to fragmentation and fragment size (Theimer, 2005; Lai et al., 2014; Zhang et al., 2016). The two extremes are when heavy seed predation inhibits successful seedling establishment in forest fragments (Yang and Yi, 2011) or when seed removal collapses (Galetti et al., 2006). Another possible outcome is that the original seed removal rate is apparently maintained, but the removal does not lead to effective seed dispersal due to different seed-handling behaviour by another animal species (Goheen and Swihart, 2003). The most "probable" scenario is that in smaller fragments the number of removed seeds is the same or larger, but seed predation is also intense, and hence the percentage of cached seeds is much lower. These changes are further accompanied by a significant decrease in dispersal distance within the fragment to lower the unaffordable predation risk (Jorge and Howe, 2009; Yang and Yi, 2011; Aliyu et al., 2014; Morán-López et al., 2015). Also, in fragmented landscapes small rodents become more selective feeders to ensure the collection of most valuable food in the given time (Morán-López et al., 2018). Moreover, as animals' individual personality affects seed handling, any habitat transformation that shifts the distribution of personalities within a population may further affect the dispersal of seeds (Brehm et al., 2019). Seeds were seldom moved across roads by Chinese white-bellied rats (*Niviventer confucianus*) and remained in the fragmented stand so that long-distance dispersal was hindered (Niu et al., 2018). Likewise, Chen et al. (2019) found that hoarded seeds accumulated near roads, and the age of most adult plants along these roads matched road ages, indicating that roads functioned as impenetrable barriers for hoarding. Thus, roads not only decreased seed dispersal distances, but also caused a shift from scatter-hoarding to larder-hoarding, diminishing rodent-mediated seed dispersal services and disrupting recruitment dynamics, which are essential mechanisms for promoting diversity in forest ecosystems. Some plant species show adaptive responses to fragmentation, which also affect the interactions. The alteration to costly (either more or bigger) fruits could be an adaptive strategy for mitigating the negative effects of increased seed removal by rodents in fragmented habitats (Andreazzi et al., 2012; Morán-López et al., 2018). Habitat loss alters seed dispersal patterns and can have a wide variety of outcomes. Studying seed dispersal in altered habitats applying a behavioural perspective and involving multiple animal and plant species would be essential to be able to plan proper interventions to maintain this important service by small rodents.

Management practices and related disturbances can highly affect small rodent populations and their seed dispersal services, too.

Selective logging or thinning of forests decreases the abundance and diversity of small rodents, but strongly increases the seed predation rate. The increasing predation rate reduces the chance for successful dispersal events and also the dispersal distance by up to half (Gutiérrez-Granados, 2011; Zhang et al., 2016; Yu et al., 2017). Five years after low-intensity logging (150 stems/ha), the seed dispersal distance (4.44 ± 0.36 m) almost reached the distance measured in unlogged forest stands (5.75 ± 0.41 m) (Yu et al., 2017). In isolated habitat patches the small home range of small rodents might be beneficial for dispersed habitat specialist plant species as animals will probably disperse propagules within the particular suitable habitat patch and not to the hostile matrix (Nathan, 2006; Deák et al., 2018). Grassland management, such as grazing can enhance and maintain habitat heterogeneity by selective biomass removal and trampling (Poschlod and WallisDeVries, 2002), which is essential for small rodent and lagomorph species. Accordingly, Zhang et al. (2009) and Miguel et al. (2017) found that seed dispersal services were improved by grazing. Seed removal and caching by scatter-hoarding rodent assemblages increased and concentrated on grazed sites compared to ungrazed sites. Although mowing is also a frequently applied form of management, we found no studies about its effect on seed dispersal by small rodents and lagomorphs.

3.3.2. *Defaunation*

Although small rodents and lagomorphs are generally more tolerant to habitat loss and less prone to extinction than large-bodied herbivores (Cardillo et al., 2005; Ripple et al., 2015), this group also experiences defaunation at different levels (Galetti et al., 2006; Corlett, 2007; Bogoni et al., 2020). Hunting, trapping and poisoning for various reasons negatively affect their populations (Corlett, 2007; Bogoni et al., 2020). The parallel loss of their natural predators and large mammals may be able to counterbalance this process in some cases as predation risk and competitive pressure decreases (Galetti et al., 2015; Tomiya and Miller, 2021). Despite the importance of the topic, we have little evidence on how these human-induced effects influence the abundance and distribution of small rodents and lagomorphs and thus their seed dispersal service in different habitats (but see Galetti et al., 2015; Rosin and Poulsen, 2016; Zeng et al., 2019).

3.3.3. *Alien species*

The presence of seeds of alien plant species may alter the removal, dispersal and recruitment rate of native seeds, similarly, when native seeds co-occur (Sommers and Chesson, 2016, see also Section 3.2.3). The more attractive seeds of introduced and cultivated plant species can alter animals' preference and divide their attention and energy investment, which may result in a decreased dispersal rate of native plants and may support the colonization of non-native plants (Blythe et al., 2015; Bieberich, 2016; Merceron et al., 2017; Zhang et al., 2017).

In contrast, Bogdziewicz et al. (2019) found that in case of the co-occurrence of the native sessile oak (*Q. petraea*) and the alien red oak, field mice (*Apodemus* sp.) preferentially caches the acorns of the native species. In this case small rodents hindered rather than facilitated the spread of red oak in European forest ecosystems. The contradicting results may be explained by the differences in the studied seed-dispersing animal taxa as seed preference and handling can vary greatly among species (Lichti et al., 2017). There is a considerable variation in the herbivores' ability to cope with secondary metabolites present in acorns (Onodera et al., 2017) and the effects of other seed characteristics (such as seed size; Shimada et al., 2015) which can both influence the seed-herbivore interactions. Moreover, the ratio of native and alien oak species could also affect the caching rate of acorns. If red oak becomes dominant, its encroachment may further accelerate as its animal-mediated suppression ceases because of the low proportion of native oak species in the landscape (Bogdziewicz et al., 2019).

The spread of alien small rodent and lagomorph species could also considerably change seed removal rate, seed availability as well as seed and seedling survival (Rumeu et al., 2011; Riofrío-Lazo and Páez-Rosas, 2015; Shiels and Drake, 2015). Rats for example, which become increasingly abundant globally, may disperse seeds of native species by endozoochory. They may, however, be less efficient in seed dispersal than native frugivores that are specialist dispersers of certain plants. Duron et al. (2017) found that rats destroyed more seeds by chewing and did not scarify seeds, which resulted in lower rates of germination and elongated germination time for the surviving seeds, similar to unscarified seeds with unremoved calyx (see also Section 3.1.1). Also, introduced European rabbits can disrupt natural seed dispersal systems in island ecosystems, as they damage high percentage of consumed seeds of the native plants (Rumeu et al., 2011).

A special case is when alien plants and animals interact in a mutualistic relationship, as in the French Mediterranean islands, where alien ice plant species (*Carpobrotus* spp.) and rats co-occur. Rats are one of the primary seed dispersers of ice plants, and the ratio of germinated seeds and speed of germination is improved by gut passage since the hard seed coat is partially digested (Stebbins, 1971). As a reward, ice plants provide a water- and nutrient-rich food source for the rats during the dry season (Bourgeois et al., 2005). A similar relationship was observed in Argentina between two invasive species, European rabbits (*Oryctolagus cuniculus*) and rose species (*Rosa rubiginosa* and *R. canina*). Passage of rose seeds through the digestive tract of rabbits did not diminish their viability. While rose seeds served as food for rabbits, rabbits enhanced the dispersal of rose seeds, which can accelerate the invasion process of both taxa (Bobadilla et al., 2020).

As it is demonstrated by several studies, small rodents and lagomorphs can play a role in dispersing seeds of non-native species, as in some cases these plants offer easily available and more nutritious food source than native plants. However, we own little evidence about this dispersal service regarding the number and abundance of non-native animal and plant species present in almost every ecosystem. It would be particularly important to investigate this issue in relation to spread of non-native species in protected habitats.

3.4. *Role of small rodents and lagomorphs in seed dispersal and seedling establishment from an ecological and evolutionary perspective*

Seed dispersal by small rodents and lagomorphs is mostly associated with their feeding habits and daily movements. When evaluating their role in seed dispersal, one must consider some important characteristics that differ from large herbivores and affecting the process fundamentally (Table 2).

Considering the special characteristics of small rodents and lagomorphs it can be assumed that these animals occasionally provide additive dispersal services to large mammals and birds that determines final seed fate (Table 2., Hämäläinen et al., 2017). This means that large herbivores and birds rather have an important role in transporting seeds between distant habitats and thus contribute to the maintenance of metapopulation dynamics, while small rodents and lagomorphs disperse seeds within the habitat in short distances (Schupp et al., 2010) and provide secondary seed dispersal services on the local scale (removing of pre-dispersed seeds e.g. seeds that were discarded, defecated, regurgitated or primarily dispersed by other means) (Johnson et al., 2003, Vander Wall et al., 2005b, Enders and Vander Wall 2012, Srbek-Araujo et al., 2017, Freire Filho et al., 2021). Studies suggest that this process may help seeds to escape microsites that are not suitable for germination and establishment (Vander Wall et al., 2005b; Enders and Vander Wall 2012; Hämäläinen et al., 2017). All these characteristics and the special dispersal mechanisms emphasize the important and irreplaceable role of small rodents and lagomorphs in seed dispersal and plant establishment.

3.4.1. *Effects of small rodents and lagomorphs on seedling establishment*

Small rodents and lagomorphs enhance post-dispersal seedling establishment in several ways (number of studies=50, Table 1., Appendix S1.). Studies have shown that burrowing rodents and lagomorphs affect soil structure and microtopography and by this also the species composition of the vegetation (Gálvez et al., 2008; Davidson et al., 2012; Wu et al., 2015). Burrowing generally promotes seedling establishment via creating establishment gaps by clearing litter and breaking up crusts (Davidson and Lightfoot, 2008; Milton et al., 1997, but see Gurney et al., 2015). Digging can modify the physical structure and reduce the compaction of soil. It also brings nutrient-rich soil to the surface and thus provides optimal conditions for germination (Andersen and MacMahon, 1985; Walker et al., 2015). Furthermore, burrowing activities can bring deeply buried seeds back to the soil surface, enabling them to germinate (Valkó et al., 2021). Lovegrove and Jarvis (1986) found that bulb parts may fall off while mole-rats (*Spalax ehrenbergi*) feeding on them in the burrow. These fell-off parts are then dispersed throughout the burrow system as animals move the soil.

Caching and soil disturbance can provide safe sites for seeds to survive stochastic events and drive the post-disturbance demography of many plant species. In fire-prone ecosystems with periodic fire events, seeds are regularly exposed to intensive heat pulses, which are detrimental for some of the native plant species (Scott et al., 2010). For these less fire-tolerant species, caches of small rodents that are at a sufficient depth provide safe sites where seeds can survive even severe fire events (Rusch et al., 2014, Moore and Vander Wall, 2015). Caches are often placed at a depth that allows seeds to avoid the heat shock of a fire and to germinate post-fire (Moore and Vander Wall, 2015). Andersen and MacMahon (1985) found that after a volcanic eruption, the diversity and cover of plants were higher on small rodent mounds than on other surfaces. The environmental transformation caused by stochastic events converts seed caching from a dispersal mechanism to a key mechanism for the survival of certain plant species. It might stimulate life history evolution in the plant, thus the development of seed traits like dormancy, possession of persistent soil seed bank and obligate seeding life history, that are supported by this mutualism (Parker, 2015).

3.4.2. *Plant adaptations influencing small rodent-mediated seed dispersal*

The existing knowledge describing the mutual phenological and physiological adaptations of small rodents and seeds suggests a range of relationships from entirely incidental to loosely co-evolved, mutualistic relationships. The specialised seed preferences (e.g. nutrient content), abilities (e.g. olfactory system) and needs (e.g. satiation) of small rodents actively influence the evolution of the affected plant species. In order to increase the chance of successful seed dispersal they became able to manipulate the behaviour of their dispersers. There are several ways to enhance hoarding behaviour and survival of cached seeds, such as (1) production of attractive seeds, (2) production of 'odourless' seeds, (3) masting and (4) imposed handling costs, like thick seed coat or presence of secondary chemicals (Vander Wall, 2010).

3.4.2.1. Production of attractive seeds. Differences in seed dispersing assemblages may result in regional divergences, like in the case of Japanese walnut (*Juglans ailanthifolia*). Japanese squirrels (*Sciurus lis*) preferred larger nuts and hoarded them more frequently and at

Table 2
The unique aspect of seed dispersal by small rodents and lagomorphs: internal and external factors that fundamentally affect the quality and quantity of seed dispersal in the case of small rodents or lagomorphs and large herbivores as comparison.

Characteristics of seed dispersers	Small rodents and lagomorphs	Large herbivores	Attribute of seed dispersal affected	Reference
Population dynamics	highly fluctuating	rather stable	removal rate	Schupp et al. (2010)
Body weight	less than 5 kg	from 10 kg to 1000 kg	maximum size of dispersed seed	Shiels (2011); Mancilla-Leytón et al. (2013); Owen-Smith (2013)
Home range	small (from a few hundred to a few ten thousand m^2)	large (up to 12 km^2)	dispersal distance (frequent events)	Bowman et al. (2002); Rühe and Hohmann (2004); Couvreur et al. (2008); Santini et al. (2013); Merceron et al. (2017)
Long-distance migration	rather not typical (except e.g. lemmings (*Lemmus* sp.) and rare events such as diplozoochory)	rather typical	long-distance dispersal	Hansson (1999); Wilcove and Wikelski (2008); Jansen et al. (2012); Santini et al. (2013); Hämäläinen et al. (2017)
Making caches	widespread in many taxa	not typical	removal rate	Feer and Forget (2002)

greater distances, while large Japanese field mice (*Apodemus speciosus*) preferred smaller nuts, which they hoarded more frequently and transported farther. As a result, Japanese walnut trees were found to produce larger nuts where squirrels occurred and smaller ones where mice were more abundant (Tamura and Hayashi, 2008). Chen and Chen (2011) found that in regions with many nutcrackers (*Nucifraga caryocatactes*), pines were characterised by smaller cones, smaller seeds and thinner seed coats, whereas in regions without nutcrackers, pines had larger cones with larger seeds, which could enhance caching activities by scatter-hoarding rodents. Some North American *Ephedra* species are dispersed by rodents and have large, conspicuous seeds, which are attractive for scatter-hoarders. This seed type does not occur in *Ephedra* species from other continents, perhaps because of a less diverse assemblage of scatter-hoarding rodents than in North America (Hollander and Vander Wall 2009).

3.4.2.2. Production of odourless seeds. Some plant species evolved to have seeds with a reduced olfactory detectability (Vander Wall, 2010). In a field experiment, rodents located higher percent of seeds of the less desirable plant species (cheatgrass — *Bromus tectorum*), as it had stronger olfactory signal than the preferred one (Indian ricegrass — *Achnatherum hymenoides*). Along with this, it was observed that Indian ricegrass is highly dependent on rodents, as most seedlings emerged from caches (Longland and Dimitri, 2018), probably because many seeds remained cached while uncached seeds became predated. Rodents may hoard seeds with weaker or stronger odour at different rates, while hoarding rate may also modified by the animals' olfactory ability. Yi et al. (2016) found that when seed odour intensity was modified and the animals' olfaction ability was known, seeds with weaker odour were preferentially cached, probably to minimise the probability of the cache being recovered by other small rodents. Also, rodents with weaker olfactory ability hoarded more seeds than the ones with keen sense of smell. Although olfaction and seed odour signals apparently play an important role in the interactions between small rodents and seeds, proportionally very few studies considered this factor during field experiments.

3.4.2.3. Masting. Masting can increase dispersal effectiveness of plant species by satiating animals feeding on their fruits or seeds. Forget (1990) demonstrated that there may be a loose mutualistic relationship between wacapou tree (*Vouacapoua americana*), red acouchy (*Myoprocta exilis*) and red-rumped agouti (*Dasyprocta leporine*). Masting of wacapou tree starts at the same time when the scatter-hoarding of seeds. Small rodents cache high percent of seeds that would be otherwise predated, infected by insects or may lose the ability to germinate. Even if rodents recover soon a high percent of the cached seeds, many seeds became forgotten or abandoned in caches and have a chance to germinate. Yi et al. (2011) and Zwolak et al. (2016) got similar results, that masting does not satiate rodents during seed removal but in mast years in proportion more seeds remain cached and cached seeds have higher chance to germinate than non-cached ones.

3.4.2.4. Imposed handling costs. Chemical compounds may play a significant role in reducing general predation levels; however, they have no precise control over the behaviour of their mutualistic partner. Some rodents apply avoidance mechanisms, like spitting the seeds which cause toxic reactions (Dearing et al., 2005; Samuni-Blank et al., 2012), while others evolved tolerance mechanisms such as enhanced detoxification e.g. secreting tannin-binding salivary proteins in their guts (e.g. proline-rich proteins) to remove tannins. Proline-rich proteins are effective precipitants of tannins, but this response varies among species. Synthesis induced by ingesting tannins has exclusively been confirmed in rodents. Proteins are secreted by rats, mice, hamsters, root voles and Japanese wood mice, which are all omnivores or frugivores, but not by grazers like meadow voles (Shimada, 2006; Lichti et al., 2017). The golden spiny mouse (*Acomys russatus*), a toxin-adapted species, exhibits an almost fivefold increase in microbial β-glucosidase when fed with activated toxins, while for other species of *Acomys* (*A. cahirinus*, *A. minous*) slight decreases were detected (Kohl et al., 2016). Tannins do not affect the digestive system of grey squirrels and have therefore no influence on their food preference, but they seem to serve as a cue for caching, preventing the animals from caching perishable seeds (Hadj-Chikh et al., 1996). The metabolism of mole-rats has adapted to cope with chemical compounds of geophytes that are generally toxic to other mammals, which gives mole-rats a competitive advantage (Lovegrove and Jarvis, 1986). However, Onodera et al. (2017) point out that toxin tolerance can be very different even among closely related species and that many studies overlooked this ability. They highlight the need to evaluate the secondary metabolite content of seeds and the tolerance of rodents to understand how seed producing patterns are related to rodent population dynamics.

3.4.3. Ecosystem services and disservices

Small rodents can provide regulating ecosystem services in agricultural fields by consuming weed seeds, which outweighs the disservice of weed recruitment by endozoochory (Fischer and Türke, 2016). They may be promising passive restoration agents (de Almeida et al., 2018) as in some cases seed-caching rodents can facilitate the dispersal and establishment of target species in restored sites and during natural regeneration (Xiao et al., 2004; Yoshihara et al., 2009; Longland and Ostoja, 2013; Suárez-Esteban et al., 2013). Suárez-Esteban et al. (2013) found that dispersers of desirable native plant species, like the European rabbit prefer roadside verges for foraging. Hence rabbits can support roadside restoration and potentially save financial resources.

Although, the opposite pattern has also been demonstrated. Post-dispersal seed predation or the predation of sown target species by small rodents and lagomorphs may strongly influence vegetation recovery. It may result in seed limitation and decreased seedling emergence that lowers the number of established plants, thus impedes natural regeneration or restoration efforts (Hulme, 1994; Bricker et al., 2010; Maron et al., 2012; Pearson et al., 2019, see also Appendix S1.). Feeding on emerging seedlings and young plants has similarly negative result on vegetation development (Holl et al., 2000; Watts, 2010). Seed predation level may vary greatly between plant species; it can be species-specific and sensitive to disturbance and to microhabitat characteristics (Holl and Lulow, 1997). Even when hoarded, seeds sometimes experience partial predation, which helps to elongate dormancy, thus long-term storing.

Non-dormant propagules often suffer seed pruning or embryo excision to prevent or slow down early germination (Cao et al., 2011a; Xiao et al., 2013). Perea et al. (2018) found, that the probability of embryo excision is positively correlated with seed size, but the extent of damage (i.e. amount of the consumed part per seed) was almost constant across all sizes. Thus, larger seeds with longer embryos showed a higher capacity to regenerate from embryo excision. To simulate partial predation, more than 50% of the cotyledon was removed artificially from acorns of oak species *Quercus* spp., which then germinated successfully and produced seedlings (Bartlow et al., 2018). Seeds of other species, like Pyrenean oak (*Quercus pyrenaica*), dipark (*Lithocarpus gracilis*), white seraya (*Parashorea malaanoan*) and lucumillo (*Myrcianthes coquimbensis*) also developed seedlings even after 87% of their storage tissue was removed (Loayaza et al., 2014, Wells and Bagchi, 2005, Perea et al., 2011c). Yang and Yi (2012) demonstrated that lightly damaged seeds are not only able to germinate, but germinate more rapidly and exhibit stronger growth of roots and shoots, that is able to compensate the negative effects.

Hoffmann et al. (1995) and Maron et al. (2012) found that seed foraging by rodents was positively related to seed size, but seed densities did not influence encounter rate. While Hulme (1994) found that single seeds were encountered less than half as frequently than seeds in groups. This suggests that applying 'decoy' seeds, i.e. inexpensive seeds that are preferentially consumed by small rodents instead of the seeds of target species, can apparently be an efficient technique to reach restoration goals (Longland and Bateman, 1998). Also using seed-coating with secondary defence compounds, for example capsaicin (the active ingredient in chili pepper *Capsicum* spp.) may also be a good solution (Pearson et al., 2019; Taylor et al., 2020).

It is important to emphasise that seed predation is always context-dependent. Comparing previous results is important to evaluate possible scenarios in a given situation and to choose the most proper restoration strategy. Also, not every seed predation event result in the death of the seed but may decrease seedling viability and increase variability in the dormancy period, thus result in asynchronyzed germination, that might influence regeneration of the habitat. Performing further experiments in different contexts is still needed.

3.5. Major knowledge gaps

Based on our review, we identified the following major knowledge gaps, which should be addressed in future studies.

3.5.1. Global spatial patterns of seed dispersal mediated by small rodents and lagomorphs

Out of the more than 2100 species of the clade Glires living on Earth, seed dispersal potential was studied only in the case of approximately 250 species. The most studied genera include *Apodemus*, *Dasyprocta*, *Dipodomys*, *Niviventer*, *Oryctolagus*, *Peromyscus*, *Sciurus* and *Tamias* (Table 1., Appendix S1.). Therefore, we are still far from being able to draw general conclusions about the seed dispersal potential of small rodents and lagomorphs. As most of the species are covered by fur and feed at least partly on plant material that contains seeds, we can assume that most of them can act as epi- or endozoochorous dispersal vectors. However, these dispersal syndromes have been studied for very few small rodent or lagomorph species so far (endozoochory: >30 species, epizoochory: 4 species; Table 1, Appendix S1.). To determine the importance of dispersal by epi- and endozoochory, focused case studies are needed on the above-mentioned well-studied taxa and on the taxa not studied so far, with a special emphasis on globally important and widespread genera.

Our results and those of Gómez et al. (2019) highlight that there are also huge geographical gaps in our knowledge about seed dispersal mediated by small rodents and lagomorphs, including the most often studied synzoochory. This knowledge gap is rather due to the lack of studies than to the rarity of these dispersal syndromes in particular regions. Available studies show an aggregated pattern concentrating in forested environments. The distribution of studies by country is also strongly biased, with China, the USA and Spain in the frontline. To evaluate the global relevance of this group in seed dispersal, studies are needed from regions that have not been covered so far (see Table 1). Information is especially needed from the Afro-tropical region and many parts of the Palearctic realm, which are both considered as small rodent and lagomorph biodiversity hotspots (Amori and Gippoliti, 2001), but from where there are only a few studies available (Table 1., Appendix S1.).

3.5.2. Mutualistic and antagonistic associations between small rodents or lagomorphs and plants

There are several studies that aimed to determine the sign and strength of the synzoochorous interactions between small rodents and plant species (Zwolak and Crone, 2012; Bogdziewicz et al., 2019, 2020; Sawaya et al., 2018; Zhang et al., 2021, see also Section 3.2.3). It would be also necessary to identify traits that define endo- and epizoochorous dispersal syndromes involving small rodents and lagomorphs and evaluate the relations between the interacting partners. Hence, relative frequencies of mutualistic, antagonistic and neutral outcomes of events and cases when transition from one to another occurs can be assessed. This could further deepen our knowledge on the seed dispersal effectiveness of small rodents and lagomorphs by epi- and endozoochory.

To test the interactions between plants and dispersers from the evolutionary viewpoint in the future, long-term, large-scale and multi-species experiments would be needed in relation to all types of seed dispersal mechanisms. Studies on the co-evolution between the plant and the animal partner would offer new exciting horizons for our understanding of mutual plant and animal adaptations supporting the dispersal of plant species by small rodents and lagomorphs.

3.5.3. Role of small rodents and lagomorphs in seed dispersal in open terrestrial habitats

There is a strong bias towards studies on woody habitats while open habitats such as grasslands and several types of novel ecosystems have been less studied so far (Table 1., Appendix S1.) despite they harbour a large number of small rodent and lagomorph species that occur in great abundances (Gibb et al., 2020). The importance of epizoochory by large herbivores and livestock is well studied in open habitats like grasslands (Will and Tackenberg, 2008). Evolutionary adaptations of plants that support zoochory by large herbivores might also favour dispersal by smaller animals. As in grasslands the ground-layer harbours dense vegetation with many adhesive seeds, epizoochory by small rodents and lagomorphs might be an important seed dispersal process (Agnew and Flux, 1970; Sorensen, 1986; Willson et al., 1990; Laughlin, 2003); however, there is barely any evidence of it. Additionally, many rodent species that are recognised as effective synzoochorous dispersers and frequently studied in woody habitats, such as field mice (*Apodemus* spp.), mice (*Mus* spp.) and voles (*Microtus* spp.) (Lichti et al., 2017), are also present in vast numbers in non-woody habitats (Aulagnier et al., 2018). Nevertheless, researches investigating seed dispersal by synzoochory in open landscapes are rare and often focus on seed removal and predation without revealing the final seed fate (e.g. Janzen, 1982, Murillo et al., 2007, Laborde and Thompson, 2009).

3.5.4. *Seed dispersal types specific to small rodents and lagomorphs*

Besides universal dispersal types such as epi- and endozoochory, there are alternative ways in which small rodents and lagomorphs can disperse seeds. Several rodent species, especially species in tribe Marmotini move a considerable amount of plant material during nest building or food hoarding. However, only little is known on the seed content of the plant material used for making nests, and it is also unknown whether any fraction of the hoarded seeds has a chance to germinate and establish. In studies focusing on caliochory, a new and potentially important seed dispersal mechanism could be tested. Burrow-dwelling rodents and lagomorphs are present in many ecosystems, where they are important ecosystem engineers, so their activities influence great areas especially in arid environments (Gálvez et al., 2008; Davidson et al., 2012; Zhao et al., 2020). The vegetation near burrows is often characterised by a unique plant species composition different from that of the surrounding drylands (Valkó et al., 2021). It would be important to study the role of seed dispersal mediated by small rodents and lagomorphs in the succession of burrow vegetation. It would also be important to consider diplozoochory, i.e. secondary dispersal by far-ranging predators feeding on small rodents or lagomorphs. As rare events occasionally have significant role in seed dispersal (Fridriksson, 1987; Nathan et al., 2002), this process may also provide complementary dispersal services by increasing dispersal distances and facilitating the colonisation of new suitable habitats even in fragmented landscapes (Schupp et al., 2010; Hämäläinen et al., 2017).

3.5.5. *Conservation and restoration importance of small rodents and lagomorphs as seed dispersers*

The global decline of the seed-dispersing large herbivores threatens the dispersal-driven ecosystem processes worldwide (Farwig and Berens, 2012; Ripple et al., 2015), and implies that the relative importance of other dispersal vectors might increase (Burney and Flannery, 2005; Wotton and Kelly, 2011). A severe decline of large herbivores occurred recently in the Palaearctic steppes where due to poaching the populations of wild grazers have decreased remarkably, whereas the area grazed by livestock has been retreated to the vicinity of settlements, leaving vast steppe areas without any large herbivores (Kamp et al., 2016). In South America, the accelerated changes in land use, habitat loss and hunting increasingly threaten the functional diversity of large herbivores, and related seed dispersal systems, which may lead to a compositional change in savanna vegetation (Periago et al., 2015; Bogoni et al., 2020). In such ecosystems it is increasingly important to understand the role of small rodents and lagomorphs as substitute dispersal vectors since due to their plasticity, high species richness and population densities they might have the potential to counterbalance the decline of large herbivores (see also Cao et al., 2011b; Jansen et al., 2012; Valkó et al., 2021). It would be important to reveal the quality and consequences of this replacement in defaunated habitats, with a special attention on changed context (no competition with large herbivores) and the effect of anthropogenic disturbance (e.g. fragmentation). Finally, the role of small rodents and lagomorphs as passive restoration agents in the recovery of degraded areas has occasionally been mentioned (Longland and Ostoja, 2013; Suárez-Esteban et al., 2013; de Almeida et al., 2018), but is still poorly known and questionable in some cases, maybe due to the improper experimental setup. Further large-scale and long-term studies are necessary to answer the question whether these animals can facilitate the dispersal, establishment, and persistence of target species in habitat restoration projects. The forthcoming UN Decade on Ecosystem Restoration would be the perfect time for such investigations.

4. Conclusions

Our review emphasises that small rodents and lagomorphs have an essential role in seed dispersal and plant establishment processes worldwide due to their ubiquity, abundance and species richness (Burgin, 2020). Members of the clade Glires occur wherever seeds are present and most of the seeds deposited on the surface will likely be encountered and eaten, dispersed, or ignored by these animals. Therefore, these taxa play a crucial role in defining final seed fate as primary and secondary seed dispersers and seed predators. We pointed out that seed dispersal mediated by small rodents and lagomorphs includes various mechanisms and operates at multiple spatial scales involving mostly short (epizoochory) and intermediate (endozoochory, synzoochory) distances, however, a few reports are also available on extremely rare, long-distance dispersal events (diplozoochory). There are dispersal types that are especially typical to these taxa among mammals (e.g. synzoochory, caliochory). The dispersal process involves many discrete steps, and influenced by factors like seed characteristics, abiotic environmental conditions, biotic interactions and the interacting animals' characteristics and personality, therefore it is highly context-dependent. Human-induced changes such as the spread of alien species, defaunation, inappropriate land use, habitat loss and degradation also considerably affect dispersal processes. It would be important to include small rodents and lagomorphs in context-dependent multi-species experiments, applying sufficient sample sizes. Seed dispersal studies should also put much larger emphasis on small rodents and lagomorphs in the future, considering their effect by secondary seed dispersal and predation, especially when studying other seed dispersing groups, such as large mammals and birds.

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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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Declarations

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2021.e01982.

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