REVIEW

Taxi drivers: the role of animals in transporting mycorrhizal fungi

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Abstract

Dispersal of mycorrhizal fungi via animals and the importance for the interacting partners' life history as well as for ecosystems is an understudied topic. In this review, we describe the available evidence and the most important knowledge gaps and finally suggest ways to gain the missing information. So far, 33 articles have been published proving a successful transfer of mycorrhizal propagules by animals. The vast majority of research on invertebrates was focused on arbuscular mycorrhizal (AM) fungi, whereas papers on vertebrates (mainly rodents and artiodactyls) equally addressed ectomycorrhizal (ECM) and AM fungi. Effective dispersal has been mostly shown by the successful inoculation of bait plants and less commonly by spore staining or germination tests. Based on the available data and general knowledge on animal lifestyles, collembolans and oribatid mites may be important in transporting ECM fungal propagules by ectozoochory, whereas earthworms, isopods, and millipedes could mainly transfer AM fungal spores in their gut systems. ECM fungal distribution may be affected by mycophagous dipterans and their hymenopteran parasitoids, while slugs, snails, and beetles could transport both mycorrhizal groups. Vertebrates feeding on fruit bodies were shown to disperse mainly ECM fungi, while AM fungi are transported mostly accidentally by herbivores. The important knowledge gaps include insufficient information on dispersal of fungal propagules other than spores, the role of invertebrates in the dispersal of mycorrhizal fungi, the way in which propagules pass through food webs, and the spatial distances reached by different dispersal mechanisms both horizontally and vertically.

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Introduction

Effective dispersal and successful establishment is a key challenge in the life cycle of any organism. Mycorrhizal fungi are ubiquitous symbionts of most terrestrial plant species, and effective dispersal is essential to reach a suitable habitat including a potential mycorrhizal partner. Apart from abiotic dispersal modes (e.g., by wind, water), animals represent vectors of biotic dispersal for many fungi as emphasized already in classical mycological literature (Buller 1922; Ingold 1953). Generally, two ways of spore transport can be distinguished: *endozoochory*–targeted or accidental consumption of propagules followed by their release in feces; and *ectozoochory*– capturing propagules on external parts of animals such as hairs, feathers, or legs (Warner and French 1970). Endozoochory can be associated with ectozoochory when spores adhere to the body surface during consumption of fruit bodies. Surprisingly, our knowledge about the effectiveness of these dispersal routes is scarce and limited only to some fungal and animal groups and, in many cases, without any real experimental evidence of the successful dispersal of infective propagules. Therefore, the aims of this review were to compile and synthesize the existing knowledge on animal dispersal of mycorrhizal fungi and to identify the most important knowledge gaps including interactions between animal vectors and mycorrhizal fungi, mycorrhizal fungal traits aiding animal dispersal, and finally, the ecological significance of these interactions. With this review, we hope to promote new research in this fascinating topic.

Mycorrhizal fungi and their propagules

The fungal partners of the three main mycorrhizal association types significantly differ in their lifestyle and dispersal modes. Arbuscular mycorrhizal (AM) fungi (Glomeromycota, Wijayawardene et al. 2018) reproduce by large nonsexual spores formed in soil, sometimes aggregated in sporocarps. Their propagules can also include mycelium and mycelial structures in the colonized roots. With the exception of some genera forming sporocarps on the soil surface (e.g., Oehl et al. 2011; Redecker et al. 2007), effective long-distance dispersal requires propagules to get aboveground, because movement in the soil is limited. Generally, the specificity of symbiotic relations is rather small in arbuscular mycorrhiza, although the compatibility may vary between specific plant–fungus combinations (Lekberg and Waller 2016) so encountering a compatible host after dispersal may not in general be the biggest problem for AM fungi.

In contrast, the majority of ectomycorrhizal (ECM) fungi (mostly Basidiomycota and Ascomycota) reproduce by meiospores in epi- or hypogeous fruit bodies (Horton 2017). Their challenge is to find their way to new root tips in the soil

in order to complete their life cycle. For ECM fungi, finding a suitable plant host may be an additional challenge, because the specificity of plant–fungal relations at different taxonomic levels is a common phenomenon (Molina and Horton 2015). For ericoid mycorrhizal fungi, the entire spectrum of involved fungi is still unclear (Kjøller et al. 2010), and even for the well-known fungi, e.g., fungi within the *Rhizoscyphus ericae* complex, the range and mode of dispersal has barely been studied. Since ericoid fungi are, in this context, understudied, we focused our review on AM and ECM fungi.

Experimental evidence

Experimental evidence for successful transport of mycorrhizal propagules must include proof of their viability. Therefore, we consider the "bait plant approach" sensu Brundrett et al. (1996) as the best available method. Indeed, from the 33 publications in which successful transport has been proved, 24 used bait plants (see Table 1, more details in Online resource 1–Table S1). Commonly, transported propagules (in feces, etc.) are added to a sterile growth medium where seedlings/plants are allowed to form mycorrhiza. Still this approach is not bulletproof: for example, many ECM species from the genus *Cortinarius*, *Russula*, and *Tricholoma* are known to form mycorrhizas with mature trees, which obviously cannot be maintained under controlled growth conditions. Other constraints that may lead to false negatives are the need for specific triggers to break dormancy (Nara 2008; Halbwachs and Bässler 2015), e.g., the presence of microorganisms like yeasts, low ammonium content, fire, etc. (Fries 1984; Glassman et al. 2016). Although AM fungi are often easier to test using bait plants, evidence of successful transport is equally distributed between both mycorrhizal groups: 11 and 10 papers for AM and ECM fungi, respectively, and 4 papers for both (Table 1). Tests of spore germination that do not lead to the actual formation of mycorrhizas can also constitute proofs of successful propagule transport (Trappe and Maser 1976). Other possibilities include tests for mitochondrial activity based on staining with tetrazolium salts (MTT) (Castillo-Guevara et al. 2011; Ambarish and Sridhar 2014), activity using fluorescein diacetate (FDA) (Mangan and Adler 2002), and the presence of intact nuclei colored by 4′,6-diamidino-2-phenylindole (DAPI) (Lilleskov and Bruns 2005) or hematoxylin (Castillo-Guevara et al. 2011). However, seemingly undamaged spores (Nakamori and Suzuki 2010) or spores containing oil drops (Kobayashi et al. 2017) may have already lost their viability (Urban 2016). There is evidence of different propagation strategies across AM fungal species and clades (Varela-Cervero et al. 2016). Indeed, many environmental sequences have never been matched with AM fungal sporulation, i.e., only about 315 species have been shown to sporulate under controlled conditions (Morton et al. 1995), while the species richness is estimated to be much larger,

Table 1 List of animal groups shown to successfully transport propagules of mycorrhizal fungi. More details in Online Resource 1 (Table S1)

Animals	Fungi	Habitat	Geography	Methodology	References
Invertebrates					
Mollusks: slugs	ECM	Pine forest	Italy	Observation of germinating spores in gut system and feces	Voglino (1895)
Earthworms	AM	Urban; rainforest; garden or not specified	USA, Australia, India	Bait plants inoculated with casts or spores and root fragments extracted from casts	McIlveen and Cole (1976), Redell and Spain (1991), Harinikumar and Bagyaraj (1994)
Ants	AM	Garden or not specified	India	Bait plant inoculated with spores extracted from casts	Harinikumar and Bagyaraj (1994)
Grasshoppers	AM	Coal mines	USA	Bait plants inoculated with crushed grasshoppers	Ponder (1980)
Millipedes	AM	Lab experiment	India	Spores extracted from feces. Vitality of spores examined by tetrazolium salts (MTT) staining	Ambarish and Sridhar (2014)
Isopods	AM	Lab experiment	USA	Bait plant inoculated with feces	Rabatin and Stinner (1988)
Springtails	AM	Lab experiments	Canada	Animals as vectors between mycorrhizal and nonmycorrhizal seedlings	Klironomos and Moutoglis (1999)
Mites, Flies, Beetles, Millipedes, Springtails, Mites, Centipedes	ECM	*Pinus muricata* forest	USA	Bait plants inoculated with spore suspension extracted from feces. Vitality of spores examined by DAPI staining	Lilleskov and Bruns (2005)
Vertebrates					
Rodents	AM	Coniferous, subtropical, sclerophyll and tropical forests; semiarid shrub-steppe; coal mine areas	USA, Panama, Argentina, Australia	(1) Bait plants inoculated by spores extracted from the digestive tract or from scat, with feces or hypogeous sporocarps, or with whole animals (2) Extraction of spores from the digestive tract; viability tested by germination	Trappe and Maser (1976), Rothwell and Holt (1978), Kotter and Farentinos (1984), Warner et al. (1987), Allen and MacMahon (1988), McGee and Baczocha (1994), Reddell et al. (1997), Mangan and Adler (2002), Fracchia et al. (2011)
Rodents	ECM	Subtropical vegetation, truffière	Australia, USA, Mexico	(1) Bait plants inoculated with spores extracted from feces (2) Spores extracted from feces and vitality stained with fluorescent diacetate (FDA) or tetrazolium salts (MTT) (3) Observation of germinating spores in feces	McGee and Baczocha (1994), Reddell et al. (1997), Terwilliger and Pastor (1999), Colgan and Claridge (2002), Castillo-Guevara et al. (2011), Ori et al. (2018)
Rabbits	AM	Coal mines	USA	Bait plants inoculated with feces	Ponder (1980)
Marsupials	AM	Subtropical and tropical vegetation	Australia	Bait plants inoculated with spores extracted from feces	McGee and Baczocha (1994), Reddell et al. (1997)
Marsupials	ECM	Sclerophyll forest; tropical lowland forest; tree plantation	Australia	Bait plants inoculated with feces or spores isolated from feces	Lamont et al. (1985), Claridge et al. (1992), McGee and Baczocha (1994), Reddell et al. (1997), Wood et al. (2015)
Ungulates	AM	Coniferous forests	USA	Bait plants inoculated with feces	Allen (1987), Lekberg et al. (2011)
Ungulates	ECM	Coniferous and deciduous forests	USA, Argentina, Italy, Israel, New Zealand	Bait plants inoculated with feces	Ashkannejhad and Horton (2006), Nuñez et al. (2013), Piattoni et al. (2014), Wood et al. (2015), Livne-Luzon et al. (2017)
Birds	AM	Urban; coniferous forests	USA, Portugal		

Animals	Fungi	Habitat	Geography	Methodology	References
Salamanders	ECM	Coniferous forests	USA	Bait plant inoculated with nest material or feces. Spores extracted from feces. Vitality of spores examined by DAPI staining	McIlveen and Cole (1976), Correia et al. (2018) Lilleskov and Bruns (2005)
Elephants	AM	Savannah	Burkina Faso	Bait plant inoculated with feces	Paugy et al. (2004)

Table 1 (continued)

approx. 1700–2700 species (Öpik et al. 2014). Although bait plant approaches can test for germination and colonization of ingested colonized roots and mycelia (Reddell and Spain 1991), spore viability tests can only be applied to sporulating AM fungi under environmental conditions. Although multiple taxa may simultaneously colonize roots of a single plant, only a small number of AM fungal taxa is known to grow in pot or in vitro root cultures (Ohsowski et al. 2014), thereby limiting viability tests of AM fungal propagules only to this subset of cultivable taxa that form spores.

Positive evidence for the successful transport of ECM fungi is mostly for hypogeous fungi, while there are almost no data about corticioid fungi (only *Tomentella*, *Amphinema*), pileate fungi (only *Suillus*, *Hebeloma*), and fungi with holothecia (only *Thelephora*). There is no evidence at all concerning Ascomycetes forming apothecia (e.g., *Helvella*, *Wilcoxina*). For AM fungi, the evidence is limited mostly to Glomeraceae. Only six of the publications in which successful transport was proven used molecular identification approaches, and from these, only one used high-throughput sequencing (Livne-Luzon et al. 2017) (see Table 1 for methods).

Most of the 33 published papers successfully proving dispersal by animals of mycorrhizal propagules focused on the role of mammals, especially rodents. These studies dealt with the endozoochory of hypogeous fungi, particularly AM fungi and truffle-like fungi (Table 1), while only a few studies have focused on invertebrates. Thus, the importance of animals as transporters of mycorrhizal fungal propagules for different fungal species and habitats is far from being covered. The potential of different animal groups to transport mycorrhizal fungi will be discussed in the following section. As there are indications that mycorrhizal fungi do not act uniformly (Klironomos and Moutoglis 1999; Castillo-Guevara et al. 2011), any generalizations naturally need to be taken with caution.

Animals important in mycorrhizal fungi dispersal

The most important role of animals in mycorrhizal fungal dispersal is probably played by fungal feeders (feeding on fruit bodies or mycelia with spores, Online resource 1—Table S3, Fig. 1) and animals sharing the environment with fungi. Our overview below is based on published mycological and zoological papers and books together with expert knowledge on different relevant zoological groups. This is summarized in Table 2 (with further details in Online resource 1—Table S2).

Invertebrates

Only meso- and macrofauna were considered in this review. Even though soil microfauna (protists and nematodes) have been observed eating fungal spores (Ekelund and Rønn 1994;

Fig. 1 a, b Pilei of *Boletus luridiformis* fruit bodies with marks of rodent (**a**) and slug (**b**) grazing
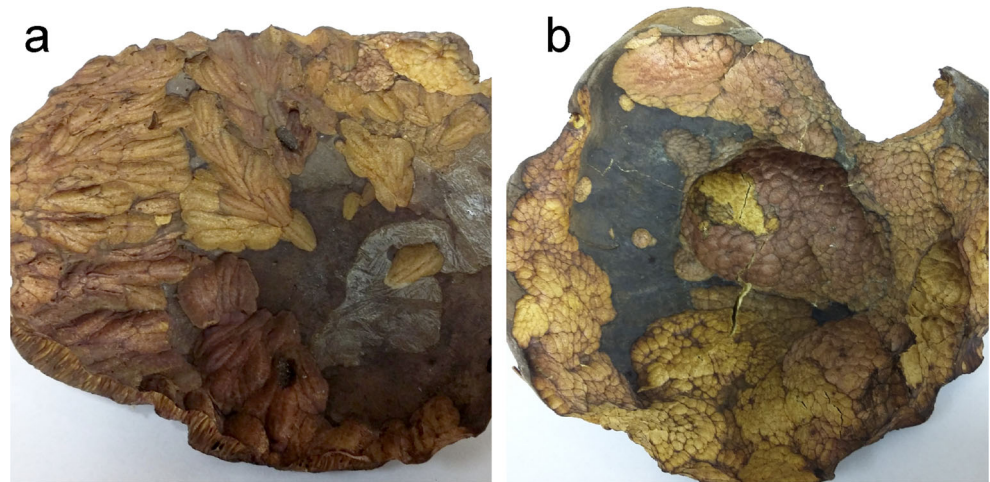
Geisen et al. 2018) and mycorrhizal fungal tissues (Riffle 1975; Giannakis and Sanders 1989), their ability to disperse fungi is likely very limited both because of their minute size and because they feed on these structures to digest them.

Soil mesofauna

Collembolans and oribatid mites are two common soil mesofaunal groups that can possibly impact mycorrhizal dispersal. Collembolans are considered to be mainly fungivorous and can occasionally consume entire ECM fruit bodies in enormous quantities (Yamashita and Hijii 2003), as well as also feeding on AM fungi (Rabatin and Stinner 1988; Klironomos et al. 1999; Gange 2000). However, endozoic dispersal by collembolans is questionable. Nakamori and Suzuki (2005) found that collembolans destroyed spores during gut passage. Later, they observed that spores of 18 ECM fungal species were completely damaged in the feces of *Ceratophysella denisiana*. Moreover, gut-passage time was much shorter than the duration of feeding, so most feces were deposited on the original fruiting body without any real contribution to dispersal (Nakamori and Suzuki 2010). Nevertheless, 7–8% of ingested *Tomentella* spores were found to be intact in collembolan guts (Lilleskov and Bruns 2005), which could indicate the chance for occasional dispersal. Intact spores were also found in the feces of collembolan species without molar plates (Nakano et al. 2017). In addition, Anslan et al. (2016) identified *Cortinarius* sequences in collembolan guts, but because of the molecular approach, it was not possible to test propagule viability. As indicated by Maaß et al. (2015), ectozoochory is probably the most important means of spore dispersal provided by this group, but there are few data (Lilleskov and Bruns 2005; Anslan et al. 2016). Klironomos and Moutoglis (1999) showed that *Folsomia candida* may aid in transporting AM mycorrhizas from already colonized plants to noncolonized neighbors, thereby decreasing the effect of distance on colonization ability.

Some collembolans are also known to move vertically in the soil (Krab et al. 2010), so they could potentially bring fungal propagules to roots.

Oribatid mites are a very abundant group of soil invertebrates (Maraun et al. 1998). They feed mostly on mycelia, including ECM (Schneider et al. 2005), and possibly also on ectomycorrhizas and resupinate fruit bodies. A high percentage of intact spores were found in the guts of mites found on *Tomentella sublilacina* (Lilleskov and Bruns 2005). Renker et al. (2005) analyzed fungi associated with four species of mites but found only saprotrophs and parasites. Menta and Pinto (2016) observed that oribatid mites can carry the spores of *Tuber* on their bodies.

Several other groups could potentially disperse mycorrhizal fungi, but there is no direct evidence about such transport. *Prostigmatid mites* (Treonis 2017) do not seem to be suitable for dispersing spores by endozoochory, because many of them prey on other microarthropods and nematodes (Coleman et al. 2004). However, external spore transport cannot be excluded because they share the environment with fungi. *Protura* (Hexapoda) have been found to feed on ectomycorrhizas (Sturm 1959). Their abundance significantly decreases after tree girdling (Malmström and Persson 2011), but nothing is known about their spore dispersal abilities. A similar lack of knowledge is apparent for *Pauropoda* (Myriapoda), except for records about "eating mycelia of molds" and that they live in the upper soil layers (Starling 1944). Their gut sometimes contained parts of hyphae (Rémy 1950). Generally, they are rather rare, and their distribution is patchy, being more frequent under logs and moss carpets. *Enchytraeidae* feed on decaying organic matter, litter, and roots. Hedlund and Augustsson (1995) proved that the enchytraeid species *Cognettia sphagnetorum* feed on fungi as well as an increased effect of worms both on the growth and respiration of the saprotrophic species *Mortierella isabellina*. Ponge (1991) found mycorrhizal hyphae in the fecal pellets of enchytraeids collected from Scots pine litter. These species could

Table 2 Overview of invertebrates supposed to transport mycorrhizal fungi. More details including lifestyle and references in Online Resource 1 (Table S2). Data without references are based on expert estimation of authors

Phylum	Groups—including commonly used names	Transfer of ectomycorrhizal fungi		Transfer of arbuscular mycorrhizal fungi		Possible horizontal dispersal distance	Possible vertical dispersal distance
		Endozoochory	Ectozoochory	Endozoochory	Ectozoochory		
Mollusca	Gastropoda—slugs, snails	Yes (Voglino 1895), feed on above-ground fruit bodies (Maunder and Voitk 2010) and roots (Wöllmer and Kottke 1990)	Possibly yes	Possibly yes	Possibly yes	Several meters (Arion rufus on average 4.4 m per day, max. 14.6 m, Türke et al. 2018)	Pest slugs up to 40 cm (Glen et al. 1990)
Annelida	Oligochaeta—earthworms	Possibly not—low frequencies of spores in casts comparing to AM (Redell and Spain 1991)	Possibly yes—mycelia and spores could be attached on the skin surface	Yes, spores can survive transport through the alimentary canal (Brown 1995)	Possibly yes, mycelia and spores could be attached on the skin surface	Several meters (depending on the ecological group of earthworm species)	Up to 2 m in depth (depending on the species)
Annelida	Oligochaeta, Enchytraeidae—potworms	No data	Possibly yes—mycelia and spores could be attached on the skin surface	Possibly yes (accidentally with consumed soil)	Possibly yes, mycelia and spores could be attached on the skin surface	Several centimeters (depending on size and lifestyle)	Mostly up to 10 cm, rarely 1 m deep (Dózsa-Farkas 1992)
Arthropoda	Insecta (Diptera)—flies	Possibly yes—found in the gut system (Lilleskov and Bruns 2005; Kitabayashi et al. 2016)	Yes, based on observations	No data	No data	Potentially several kilometers	Larvae occur maximum 20 cm below surface
Arthropoda	Insecta (Coleoptera)—beetles	Possibly yes, found in the gut system (Lilleskov and Bruns 2005)	Yes, based on observations (Lilleskov and Bruns 2005)	No data	No data	Usually several meters, potentially more	Possibly up to 50 cm below surface
Arthropoda	Insecta (Hymenoptera)	No data	Probably yes	No data	Probably yes	Potentially several kilometers	Probably not
Arthropoda	Insecta (Hymenoptera, Formicidae)—ants	Possibly yes (some found eating fungal fruit bodies, e.g., Epps and Penick 2018)	Possibly yes (can be in contact when eating fungal fruit bodies, or when removing soil in the case of Endogonales or hypogeous fungi)	No data	Yes but only indirect indications available (e.g., Friese and Allen 1991)	From several meters to hundreds of meters (depends of the foraging behavior of the species), even kilometers in the case of queens	Several centimeters up to few meters down the soil, and several tens of meters in the case of tree-climbing species
Arthropoda	Insecta (Orthoptera)—crickets, grasshoppers	No data	No data	Probably yes (Ponder 1980)	Probably yes (Ponder 1980)	Potentially several kilometers	Possibly up to 50 cm
Arthropoda	Diplopoda—millipedes	Found in the gut system (Lilleskov and Bruns 2005)	Yes, based on observations (Lilleskov and Bruns 2005)	No data	No data	Tens of meters (Lilleskov and Bruns 2005)	Assumed few centimeters
Arthropoda	Malacostraca (Isopoda)—woodlice	No data	No data	Yes (Rabatin and Stinner 1989)	No data	Several meters (Porcellio scaber, Armadillidium versicolor—about 4–6 m)	Hemilepistus reaumurii up to 50 cm (Shachak 1980)

Table 2 (continued)

Phylum	Groups—including commonly used names	Transfer of ectomycorrhizal fungi		Transfer of arbuscular mycorrhizal fungi		Possible horizontal dispersal distance	Possible vertical dispersal distance
		Endozoochory	Ectozoochory	Endozoochory	Ectozoochory		
						horizontally in 4–5 h, Pálková 2013	*Armadillidium vulgare* 16–24 cm (Frouz et al. 2004)
Arthropoda	Collembola—springtails	Limited—most of spores were destroyed (Lilleskov and Bruns 2005), undestroyed spores in the gut of collembola without molar plates (Nakano et al. 2017)	Yes, based on observations (Lilleskov and Bruns 2005), sequences from their legs (Anslan et al. 2016)	Yes (Klironomos and Moutoglis 1999)	Spores possibly not, because of their weight, maybe mycelia, no data	Up to 10 cm for edaphic species (Bengtsson et al. 1994; Hopkin 1997)	Mostly up to 10 cm (in litter and humus layer)
Arthropoda	Arachnida (Oribatida)—oribatid mites	Found in gut system (Lilleskov and Bruns 2005)	Yes, based on observations (Lilleskov and Bruns 2005)	Possibly not	Spores possibly not, because of their weight, maybe mycelia, no data	Few centimeters (Renker et al. 2005, 0.3–2.1 cm per day, Lehmitz et al. 2012)	Mostly up to 10 cm (in litter and humus layer)
Arthropoda	Chilopoda—centipedes	Found in the gut system (Lilleskov and Bruns 2005)	No data	No data	No data	Tens of meters (Barth and Broshears 1982)	Few tens of centimeters

potentially disperse AM and the spores of ECM fungi from resupinate fruit bodies, since they live in soil close to the surface. *Tardigrada* have also been suspected to participate in spore dispersal, although direct evidence is missing (Treonis 2017). However, their contribution to fungal dispersal is probably negligible, because of their adaptation to liquid food and limited movements. In any case, the large differences in spore size across ECM and AM fungi, sometimes by orders of magnitude, make it more likely that any potential transport by mesofauna will be of ECM than AM fungal propagules.

Spore dispersal by soil mesofauna may be both by endozoochory and ectozoochory and can be important for short distances, especially by vertical transport. As shown by an experiment in which cystidia of *Russula* were destroyed (Nakamori and Suzuki 2007), fungal fruit body traits (cystidia, crystals, setae, milk) may influence the degree by which they are consumed and hence affect the probability of propagule transport. Therefore, associated animal communities will probably differ among fungal species and influence their dispersal abilities. The influence of predation on dispersal effectiveness via mesofauna has not yet been sufficiently studied.

Soil macrofauna

Macrofauna most likely play a much larger role in dispersing mycorrhizal fungi. *Earthworms* are believed to be important vectors of AM fungi. Several studies (Online resource 1, Table S2) have shown that earthworm casts contain higher numbers of spores and infective propagules than nearby field soil. AM fungal spores can survive the ingestion process by earthworms (Brown 1995). Furthermore, Harinikumar et al. (1994) found that AM fungal propagules can survive in dried earthworm casts and hence become important inoculant sources for plants. Nevertheless, contradictory results make it difficult to generalize about the importance of earthworms as dispersers of AM fungi. For instance, Harinikumar et al. (1994) found that *Lumbricus terrestris* (an anecic species, i.e., moving vertically from the surface to deeper soil layers) can greatly contribute to the dissemination of AM fungi, as can also the endogeic *Aporrectodea trapezoides* (Redell and Spain 1991). In contrast, Pattinson et al. (1997) did not find any effect of *Aporrectodea trapezoides* on the dispersal of the AM fungus *Glomus intraradices*, while Gormsen et al. (2004) did not find any influence of the epigeic *Lumbricus rubellus* earthworm on the dispersal of AM fungi, even though they stimulated the growth of AM fungal mycelium. The numbers of ECM fungal spores in earthworm casts were extremely low in comparison to those of ECM spores found in more specialized vectors (e.g., rodents) (Redell and Spain 1991). Still, Montecchio et al. (2015) found *Suillus grevillei* and *Xerocomus badius* in the casts of earthworms previously placed in sterile soil inoculated by their mycelia; however, these fungi were not viable based on culture tests, although

this could be caused by their symbiotic lifestyle. Based on mesocosm experiments, earthworms were found to have no influence on ECM fungal species composition of white spruce seedlings (Cameron et al. 2012). Since many ECM fungi form resupinate fruit bodies in litter and on branches lying on the ground, both of which are accessible to epigeic earthworms, direct observation together with manipulative experiments could determine if earthworms play any role in ECM dispersal.

Isopoda (Oniscidea) are key system regulators of decomposition and nutrient recycling. Mainly, the endogeic, surface- and litter-dwelling ecomorphological forms feed on soil, fungi, litter, and its microbiota and contribute to the dispersal of microbial propagules (Brereton 1957; Hassall et al. 1987). They are often found near fungal fruit bodies, but it is not known whether fungal spores, especially those of ECM fungi, are consumed and transported by isopods. Rabatin and Stinner (1985) found AM fungal spores in the gut of several pitfall trapped woodlice. Because their digestive efficiency is rather low (Hornung 1981), spores leave their digestive tract unaffected, acting as passive travelers within fecal pellets, thereby inoculating new surfaces. For example, more than half of AM fungal spores in the gut of woodlice seem to be viable (Rabatin and Stinner 1988). The gut content of *Porcellio scaber* was found to contain 5–20% fungi depending on season, while that of juveniles reached 33% (Soma and Saito 1983). Most of these species are active in the uppermost levels of the soil horizon in a depth profile of 5–15 cm (Rudy et al. 2018) (Fig. 2). Nevertheless, some species can move up to 80 m per day horizontally (den Boer 1961) and up to 50 cm vertically (Rendoš et al. 2016), so they could potentially be very effective transporters of propagules. In arid ecosystems, active borrow digging species, such as *Hemilepistus*, can dig 60–90 cm deep in the soil causing high soil turnover and mixing (Shachak 1980).

A high percentage of intact spores of *Tomentella* (ECM fungus) were found in the gut of the millipede *Harpaphe haydeniana* (Lilleskov and Bruns 2005), and unidentified fungal spores were found also in feces of the pill millipede *Glomeris hexasticha* (Tajovský 1992). AM fungal spores were found in the feces of the julid millipedes *Ophyiulus pilosus* and *Cylindroiulus caeruleocinctus* (Rabatin and Stinner 1988) and feces of giant pill-millipedes of the genus *Arthrosphaera* (Ambarish and Sridhar 2014). There are also specialized feeders of fruit bodies among millipedes. Probably, all members of the order Platydesmida (62 described species) eat fruit bodies of saprotrophic fungi, e.g., *Irpex* and *Trametopsis* (Wong 2017), *Merulius* (Rockefeller 2012), and *Peniophora* (Gardner 1974), while consumption of fruit bodies of mycorrhizal species has not been reported yet.

ECM fungal spores with intact nuclei have been found in the gut contents and feces (20%) of soil-dwelling predators such as *centipedes* (Lilleskov and Bruns 2005), although it is

not clear if they consumed the fungi directly, or if they consumed other invertebrates with spores in their gut. Because of their rather fast movement (1–3 cm/s), their potential for fungal dispersal may be significant.

The use of high-throughput sequencing of their gut content could help illuminate the role of soil macrofauna in transporting mycorrhizal propagules. Mesocosm experiments and manipulative experiments in natural conditions are necessary to support such studies.

Invertebrates with mostly an aboveground lifestyle

Any field mycologist would recognize that ECM fungal fruit bodies are eaten by *slugs* (Buller 1909; Elliott 1922), *snails* (Wolf and Wolf 1939), and *dipteran larvae*. The vast majority of terrestrial mollusks (snails and slugs) are detritivores, feeding on decaying plant material and fungal hyphae (Barker and Efford 2004). Still, we have a surprisingly limited knowledge on the exact diet of many of these species. The available information is both based on field (e.g., Maunder and Voitk 2010 and references therein) and laboratory observations (e.g., Gain 1891; Capinera 2017). While larger bodied slugs and snails are often found on fruit bodies, smaller, forest-dwelling groups, such as Clausiliidae (door snails), might feed directly on hyphae (Welter-Schultes 2012). Voglino (1895) observed that spores of some ECM species found in the gut system and feces of unidentified slugs can germinate and hypothesized that slugs are important for the dispersal of *Russula* and *Lactarius* species. No later study verified his observation and no data on the identity of the slug species

are available. McGraw et al. (2002) found many spores of ECM hypogeous fungi and AM fungi from the Glomeraceae family in feces of two *Prophysaon* species, but without evidence of their viability. Recently, slugs were proven to be dispersal vectors of lichens (Boch et al. 2011). Also, propagules as well as the hyphae of *Phytophthora* spp. (Oomycota) can survive inside the digestive system of slugs (Telfer et al. 2015). Türke et al. (2018) showed that slugs are able to transport live oribatid mites by endozoochory and that they survived gut passage. It is likely that the whole soil microecosystem, including bacteria, fungi, nematodes, etc., is then also dispersed. Because slugs are known to feed on ECM roots (Wölmer and Kottke 1990), they could be important in the vertical transport of these fungi as well.

Various species of *Diptera* (Mycetophilidae and other ca. 26 families, cf. Jakovlev 1994; Ševčík 2010) use fruit bodies as a food source and place for development of their larvae. It is well known that long-living polypore fruit bodies are associated with specific insects (Ševčík 2003; Schigel 2009; Jakovlev 2012; Roháček and Ševčík 2013). In contrast, most Diptera species growing in ephemeral fruit bodies of ECM fungal species seem to be oligophagous to polyphagous (e.g., Jakovlev 2012; Põldmaa et al. 2016; Koskinen et al. 2019). There are only a few examples of a strict association between Diptera and ECM fungal species, including, e.g., *Bolitophila hybrida* (Bolitophilidae) to *Paxillus* spp., *Mycetophila blanda* (Mycetophilidae) to *Lactarius* spp., *Mycetophila alea* (Mycetophilidae) to *Russula nigricans* and related species, and *Cheilosia scutellata* (Syrphidae) to *Boletus* spp. and *Leccinum* spp. (cf. Chandler 2010;

Fig. 2 Maximum dispersal ranges for the movement of animal groups for which evidence of successful transport exists (Table 1). The animal groups are classified by the magnitude of length units in which they move (i.e., habitat range). Beetles are not included in the figure due to the wide diversity in habitat conditions and morphologies in Coleoptera
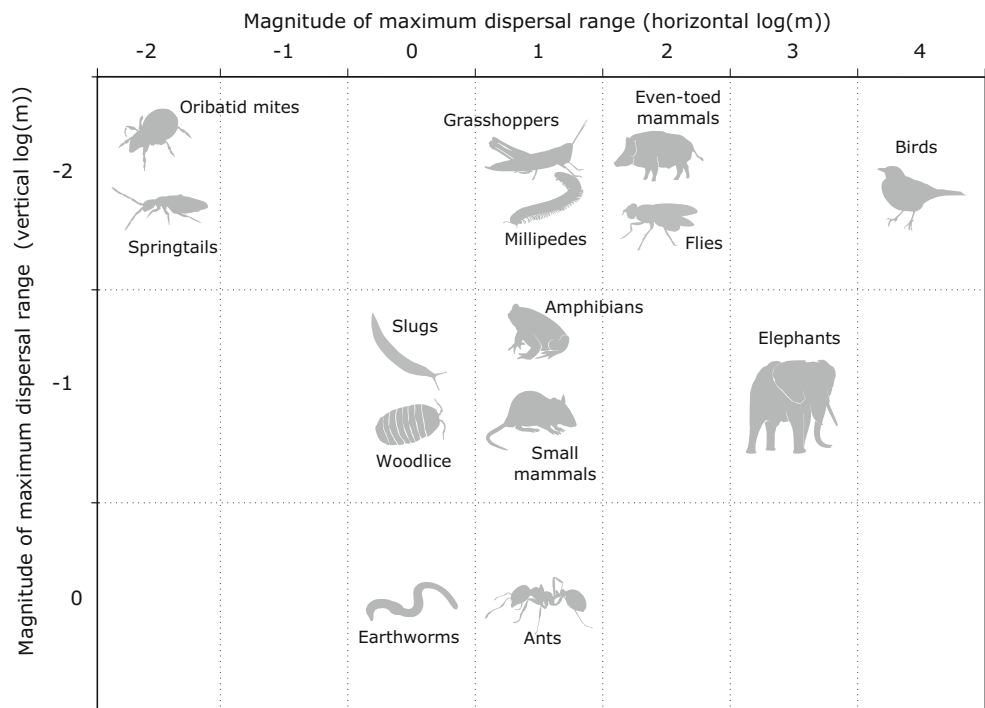
Jakovlev 2012; Ševčík 2010). The adult flies visit fungal fruit bodies to lay their eggs (usually between the gills/pores) and mate on the surface of a fruit body. The larvae are either endomycophagous or surface feeders. The surface feeders may be predaceous (e.g., Keroplatidae) or spore-feeding (some Mycetophilidae). In most of these cases, the larvae or the adults can accidentally transfer the spores, the adults from one fruit body to another and the larvae from the fruit body into the ground. Pupation takes place either in the fruit body, if this is solid enough (e.g., some *Lactarius* or *Russula*), or in the ground (soft agarics). Lilleskov and Bruns (2005) observed a high proportion of undestroyed spores in the guts of Diptera. Later, Kitabayashi et al. (2016) found a high percentage of vital spores in the digestive tract of dipteran larvae, while Kobayashi et al. (2017) observed that the colorless spores of *Russula* and *Amanita* in dipteran guts were mostly damaged, whereas the colored spores of *Suillus*, *Boletellus*, and *Cortinarius* were not. Experimentally spore-fed drosophilid flies excreted numerous spores within 12 h of feeding (Kobayashi et al. 2017), which could possibly prevent the transfer of the spores through the guts of the larvae into the ground, in the case of larval development lasting longer than 1 or 2 days. *Hymenoptera* could also be potential dispersal agents, because, as parasites of Diptera, they often occur on fruit bodies of ECM fungi. Hymenopteran parasitoids of fungivorous Diptera, Coleoptera, and other insects belong mainly to the families Ichneumonidae, Diapriidae, Proctotrupidae, and Braconidae (cf. Ševčík 2010). *Ants* were found to transport AM fungi (Harinikumar and Bagyaraj 1994). Their feeding on the fruit bodies of the saprotrophic *Pleurotus ostreatus* (Epps and Penick 2018) indicates a potential to transport spores from ECM fungal fruit bodies.

Several groups of *Coleoptera* are associated with hypogeous ECM fungi (e.g., Fogel and Peck 1975), whereas most fungivorous beetles are associated with wood-decaying fungi (cf. Shigel 2009; Ševčík 2003). Viable spores of hypogeous fungi (*Scleroderma*, *Amarrendia*, *Hysterangium*) and AM fungi were observed in feces of ten Coleoptera species from the genera *Blackbolbus* and *Bolborhachium* (Houston and Bogher 2010). Similarly, AM fungal spores were found in the gut systems of Carabidae and Scarabaeidae beetles (Rabatin and Stinner 1988). Jacobsen et al. (2017) proved the ability of Coleoptera species to carry spores of lignicolous saprotrophs to new substrates. Such transport could also be important for the distribution of ECM fungal species which form fruit bodies on logs. Coprophilous beetles are most likely important for transporting spores of mycorrhizal fungi from the feces of fungal feeders to soil/roots.

Also, *grasshoppers* were found to be AM fungal vectors promoting a succession of vegetation on former coal mine sites (Ponder 1980). However, Allen (1987) and Warner et al. (1987) reported that AM spores from grasshoppers did not germinate. *Cicades* were observed to have AM spores on

their bodies (Allen et al. 1997). Also, several species of *Thysanoptera* feed on fungi (Ruess and Lussenhop 2005) but have rarely been observed on fungal fruit bodies, e.g., *Hoplothrips fungi* has been reared from the fruit bodies of the saprotrophic *Stereum hirsutum* (Ševčík 2003) and *Haplothrips flavipes* from *Stereum*, *Ganoderma*, *Polyporus*, and *Pleurotus* fruit bodies (Judd 1957). Their possible co-occurrence with AM or ECM corticioid or hypogeous fruit bodies is still questionable.

Other possible ground-living vectors include *aphids*, which were reported to feed on ectomycorrhizas (Zak 1965); however, they are not assumed to distribute them, because they usually suck on sap, using the stylets with tiny lumen. In addition, Nakamori and Suzuki (2012) observed terrestrial flatworms of the family *Rhynchodemidae* to carry ECM fungal spores on their body and inside the bodies of their collembolan prey. However, their occurrence on fruit bodies is rather low.

To summarize, the importance of slugs, snails, dipterans, and coleopterans for the distribution of fungal propagules is largely unknown. Dipterans are possibly important only for ECM fungi, whereas the other groups of animals may disperse both ECM and AM fungi. To our knowledge, no recent experiments have proven spores to be viable after digestion by mollusks, nor any possible adaptations of mycorrhizal fungal propagules to passage through the mollusk gut.

Vertebrates

Mammals

Many mammal groups, including marsupials, rodents, shrews, even-toed ungulates, carnivores, and primates, are known to consume ECM fungal fruit bodies (reviewed by Luoma et al. 2003; Claridge and Trappe 2005; Urban 2016; Zambonelli et al. 2017; Online resource 1—Table S3). Most vertebrates, including mammals, can be classified as preferential, opportunistic, or accidental fungivores (Claridge and Trappe 2005). Examples of *obligate mycophagy*, though rare (Claridge and Trappe 2005), include the interaction between hypogeous fungi and the Californian red-backed vole (*Myodes californicus*) and California vole (*Microtus californicus*) in North America and two rat-kangaroos, long-footed potoroo (*Potorous longipes*) and Gilbert's potoroo (*Potorous gilbertii*) in Australia (Maser et al. 1978; Bougher et al. 1998; Green et al. 1999; Urban 2016). *Preferential consumption* of fungi has been noted mostly in North American members of Sciuridae, Cricetidae, and Australian marsupials from the family Potoroidae, although some other marsupial and murid species, like the swamp wallaby (*Wallabia bicolor*), long-nosed bandicoot (*Perameles nasuta*), and bush rat (*Rattus fuscipes*), are also known to consume a comparable diversity and quantity of fungi (Claridge and Trappe 2005; Urban 2016;

Nuske et al. 2017; Zambonelli et al. 2017). In Australia, over 50 mammal species across nine families were found to consume fungi, with the majority classified as *opportunistic* or casual mycophagists (Nuske et al. 2017). Claridge and Trappe (2005) noted that many southern and northern hemisphere rodents, which can also be assigned to these groups, occasionally consume fungi in considerable quantities. This kind of mycophagy is characteristic also for larger mammals, such as even-toed ungulates, carnivores, and primates (Luoma et al. 2003; Claridge and Trappe 2005). Most mammals, especially obligate and preferential mycophagists, consume a range of fungal species present in the area of their occurrence (Claridge and Trappe 2005). However, specificity to different degrees was also noted by some authors. Schickmann et al. (2012) found that the diet of rodents and shrews in the forests of the Eastern Alps consisted of at least 20 ECM species, both epigeous and hypogeous, but noted a weak trend for preferential consumption of *Tuber* cf. *puberulum* by shrews. However, the preference of southern red-backed vole for *Hydnotrya variiformis* and northern flying squirrels for *Rhizopogon* spp. was much stronger (Dubay et al. 2008). Also, *Mesophellia* and *Castoreum* fungi were preferentially eaten by Tasmanian bettong, which presumably caused the domination of these fungi in the hypogeous fungal community (Johnson 1994). The differential consumption of hypogeous fungi by two bandicoot species, the southern brown bandicoot (*Isoodon obesculus*) and long-nosed bandicoot (*Parameles nasuta*), inhabiting the same area but utilizing different niches, clearly resulted in different dispersal patterns of fungi (Claridge 2002).

Accidental dispersal of spores from fruit bodies by mycophagous mammals has also been noted. Squirrels and other animals were found to eat only the peridium of *Elaphomyces*, *Radiigera*, and *Pyrenogaster*, discarding the powdery spore mass that is then spread around (Ingold 1973; Trappe and Masser 1977). Also, long-nosed potoroos consume the central columellae of fruit bodies of Mesophelliaceae species discarding the spores that are released to the air or adhere to animal fur (Lamont et al. 1985; Claridge et al. 2001). Caching fungi, practiced by some small mammals (*Myodes* spp., *Sorex* spp., *Glaucomys sabrinus*), may extend the fungal spore dispersal range especially in the case of pilferage and recaching, e.g., by birds or other mammals (Vernes and Poirier 2007; Maser et al. 2008). This is also true for the drying of fungi, which is practiced by some squirrels and pack rats (*Neotoma* spp.) (Maser et al. 2008; Claridge and Trappe 2005). Generally, any visitor to a fruit body has the potential to disperse spores, regardless of whether it consumes it or hunts for fungivores.

AM fungi are also dispersed by mammals. The elephant (*Loxodonta africana*) and bison (*Bison bison*) are *the largest species*, which had viable AM fungi in their feces. Bison has been shown to be an important AM fungal dispersal vector in

Yellowstone National Park (see Table 1, Online resource 1—Table S1; Paugy et al. 2004; Lekberg et al. 2011). Apart from these, only the elk (*Cervus elaphus*) has been reported as an important vector of AM fungal dispersal, with their activities possibly aiding in the recolonization of the volcanic area formed after the eruption of Mount St. Helens (Allen 1987). *Rodents* are also vectors of AM fungal spores and sporocarps especially in tropical ecosystems and in the southern hemisphere (see Table 1, Online resource 1—Table S1). AM fungal transport by marsupials was reported by Vernes et al. (2015).

Mammals play a crucial role in transporting fungal spores mostly as consumers of ECM fungi with different degrees of mycophagy. Although primarily nonspecific consumers of fungal species, they may also show some preferences; however, this phenomenon and its role in shaping fungal populations needs further study. Although mycophagy has been well documented in the case of several species, there are still many mammals that have not yet been studied in this respect.

Birds and reptiles

Outside of mammals, very little is known about the dispersal potential of other vertebrates. Birds and reptiles have been reported to feed on ECM fruit bodies (Miller and Halls 1969; Simpson 1998, 2000; Medway 2000; Cooper and Vernes 2011). Recently, Beever and Lebel (2014) hypothesized that birds, especially forest-inhabiting flightless, but now, extinct species, were important factors enabling the spread and diversification of the New Zealand hypogeous ECM fungal biota. The AM fungal communities colonizing the artificial island Peberholm between Denmark and Sweden appeared to be a subset of the much older neighboring island, which points to a high colonization potential of certain early successional AM fungi, likely assisted by migratory *birds* such as geese (Nielsen et al. 2016). McIlveen and Cole (1976) reported the presence of AM fungal spores and their successful colonization of bait plants from the nest material of robins and swallows. Recently, Correia et al. (2018) showed the joint transport of *Rubus* seeds and AM fungus by robins and warblers. Though accidentally, predatory birds may move AM or ECM fungi many kilometers when a fungivorous mice, vole, or squirrel is caught (see next section).

Food webs including mycophagous animals

Similar to seed dispersal (Hämäläinen et al. 2017), spores of mycorrhizal fungi can also be dispersed via food webs that include fungivores and their predators; however, this issue has been very poorly studied (Luoma et al. 2003; Trappe and Claridge 2005; Zambonelli et al. 2017). Trappe and Claridge (2005) hypothesized that fungal spores can be dispersed over long distances by the northern spotted owl (*Strix occidentalis caurina*) hunting the northern flying squirrel, which feeds

predominantly on hypogeous fungi (Verner et al. 1992; Hallet et al. 2003). The same may be true for many species of birds of prey as well as other carnivores, such as foxes and martens, but the evidence for this is missing or scarce (Trappe and Claridge 2005; Zambonelli et al. 2017). Zielinski et al. (1999) found spores of at least six species of hypogeous fungi in the feces of North American fishers (*Pecania pennati*) together with the remains of many mycophagous rodents. Although the presence of intact basidia implied direct mycophagy by fishers, the intake of spores together with the intestinal systems of small mammals was a more likely reason. Many invertebrates feeding on fungi are members of food webs together with their invertebrate and vertebrate predators (Neutel et al. 2002). Voglino (1895) found germinating spores in the guts of toads, though these were more damaged compared to their fungivorous snail prey. Lilleskov and Bruns (2005) found *Tomentella lilacina* spores in food webs including mycophagous invertebrates and their predators: centipedes (Chilopoda), Pacific newt, *Taricha* sp. (Salamandridae), and California slender salamander, *Batrachoseps attenuatus* (Plethontidae). Despite a decreased survival rate of spores after passage through a predator's gut system, these authors regarded this food web interaction as an important mechanism for long-distance dispersal of spores, especially in the case of large spore loads.

Fungal traits associated with dispersal

Spores and other propagules

Spores are thought to be the most important propagules of fungi. External ornamentations like spines, ridges, hooks, etc. are supposed to facilitate ectozoochory, while thick walls and pigmentation are important for endozoochory (Halbwachs et al. 2015; Calhim et al. 2018) and prolong their vitality (Nguyen 2018). For example, Kobayashi et al. (2017) found that colored spores isolated from the guts of drosophilids found on fruit bodies were less damaged than colorless ones. Also, spore hydrophobicity seems to be important in transport via ectozoochory (Ruddick and Williams 1972; Halbwachs and Bässler 2015). Spore traits are probably both the least plastic and, at the same time, the best recorded traits across the fungal tree of life. Systematic analysis similar to Halbwachs et al. (2015) between mycorrhizal species known to be dispersed either by ectozoochory or endozoochory should therefore be relatively straightforward. Also, experiments to test the functionality of, e.g., spore ornamentation in ectozoochory are also doable and needed as it is relatively easy to collect enough spores from many fungal species for animal trials.

There are considerably less data on the importance of other propagules for dispersal. Some ECM fungi, mostly members of Boletales, e.g., the genera *Austropaxillus*, *Boletus*, *Gyrodon*, *Leccinum*, *Paxillus*, *Pisolithus*, and *Suillus*, produce sclerotia (Smith et al. 2015). The best known example of sclerotia-forming ECM fungus is *Cenococcum geophilum*, a cosmopolitan species that spreads exclusively as mycelium, sclerotia, and possibly detached ectomycorrhizas (Taylor and Sinsabaugh 2015). Avis and Charvat (2005) proved that *Russula* and *Cortinarius* ectomycorrhizas could serve as propagules under natural conditions. Saprotrophic Agaricales species, e.g., *Psilocybe*, *Coprinopsis*, *Hypholoma*, and *Pholiota*, are known to produce asexual spores (Walther et al. 2005), but it is not known if this is also the case for Agaricales ECM species. In contrast, most Ascomycota species produce conidia, including ECM species, e.g., *Tuber* spp. (Urban et al. 2004), which perhaps serve as a spermatia. However, their role in dispersal is largely unknown.

There is no information about if fragments of ECM fungal mycelia or rhizomorphs can be successfully dispersed by animals. Culturable fungi are easily maintained and transferred, and in principle, dispersal of mycelial fragments could potentially be more widespread in nature than normally thought, although probably mainly at a local scale. If so, then the question is by which mechanism hyphal fragments are dispersed, e.g., can hyphae survive conditions in the gut system, are there any functional differences between thin- and thick-walled hyphae, the importance of rhizomorphs, etc.? For AM fungi, although new colonization can initiate from both spores and mycelium (Klironomos and Hart 2002; Varela-Cervero et al. 2016), it seems more likely that spores can survive longer in the environment (López-García et al. 2014). But there are probably differences across fungal taxa (Chagnon et al. 2013) that need to be studied more. All AM fungal spores are more or less globose and smooth, but size differs by an order of magnitude (from 50 to 500 μm). Other things being equal, smaller spores disperse by wind easier than larger ones (Allen et al. 1993; Egan et al. 2014), but on the other hand, smaller spores also have a ten times larger surface/volume ratio and this may provide less resistance to environmental stressors, etc. (Calhim et al. 2018).

During passage through the digestive tract, spores are affected by the gut environment, including digestive enzymes, acids, higher than ambient temperatures, and the gut microbiome. This can potentially affect the survival, activity, and germination ability of spores (Fogel and Trappe 1978). There is evidence that spores of mycorrhizal fungi survive the passage through invertebrate and vertebrate gut systems and are able to successfully initiate symbiosis with plant roots (Table 1). However, detailed studies on the nature of actions in the gut environment on spores are rare. The factors acting in the digestive tract may modify both spore wall structure and morphology, which can influence spore germination. Piattoni et al. (2014) showed that the ornamentation of *Tuber aestivum* spores was clearly corroded after passage through the gut of the pot-bellied pig. These authors regarded these changes as the main factors responsible for the higher

germination rate of spores from pigs' feces and, thus, the higher percentage of ECM colonization of *Pseudotsuga menziesii* and *Pinus ponderosa* seedlings compared to seedlings inoculated with undigested spores. Similarly, Ori et al. (2018) showed, by examination in a scanning electron microscope (SEM), the degradation and disfiguration of the ornamentation of *T. aestivum* spores retrieved from the crested porcupine feces and germination of spores. Claridge et al. (1992) observed a lack of amyloid reaction of *Zelleromyces* spores that were eaten by the long-nosed potoroo, and suggested that this was due to passage through the gut system. Also, the physiological activity of spores may be altered by the gut environment. Castillo-Guevara et al. (2011) showed that, although the percentage of spores with intact nuclei (hematoxylin staining) of *Suillus tomentosus* slightly decreased after passing through the gut system of two rodent species, the percentage of active spores (MTT staining) increased. Data about the effect of passage through the gut system on AM spore modifications are largely missing. The influence of gut passage on spore structure and physiology requires further research including a wide range of animal species, both vertebrate and invertebrate, and fungal taxa.

Future experimental studies are needed to determine the survival rates of spores after endozoochory and the frequency of spores attached to invertebrates.

Fungal fruit bodies

Generally, two main fruit body types can be distinguished: epigeous with active spore discharge adapted mainly to wind dispersal and hypogeous without active spore discharge and spore dispersal mostly by animals or soil/water movement. Hypogeous fungi have mostly arisen repeatedly from epigeous ancestors many times during evolution both within the Ascomycota and Basidiomycota (Trappe et al. 2009), e.g., at least ten times within the Pezizales (Tedersoo et al. 2006). Even within epigeous fruit bodies, there are several types that do not appear to be well adapted to wind dispersal, e.g., clavarioid and resupinate forms, especially if these occur on the lower side of branches near to or on the soil. Indeed, as shown by Lilleskov and Bruns (2005), viable spores of the resupinate *Tomentella sublilacina* can be transported by animals, especially by soil mesofauna (see Table 1). Thus, we could expect a gradient from wind to animal dispersal depending on the height of sporulation above the soil surface.

Some species of AM fungi can also produce sporocarps which cluster spores sometimes even embedded in a peridium (e.g., genera *Glomus*, *Sclerocystis*, *Diversispora*, *Redeckera*) (Oehl et al. 2011), vary from a millimeter up to a few centimeters in diameter, e.g., like *Glomus megalocarpum* which forms structures 38 mm long (Redecker et al. 2007). These are mostly born hypogeous, as with most other AM fungal species, but some species are known to produce sporocarps at the soil surface (e.g., *Glomus epigeum*, Bonfante-Fasolo and Vian 1984).

Forming a fruit body is a costly process and several mechanisms have evolved to protect them against fungivores. Mechanisms include secondary metabolites (Kempken and Rohlfs 2010), lactiferous hyphae (*Lactarius*), cystidia, crystals, etc. As suggested by Urban (2016), the lack of toxin production by truffles is closely linked to the transition from epigeous to hypogeous fruiting within the Discinaceae and Helvellaceae (Pezizales). This is most likely an adaptation for spore dispersal by animals, but the opposite can also occur, i.e., adaptation of animal vectors, as shown by some Diptera that evolved mechanisms to overcome the toxicity of α-amanitin when feeding on *Amanita* species (Bunyard 2018).

For AM fungi, fruit body formation by itself could be a trait associated with dependency on animal dispersal, since some studies have noted out the preference of some rodent species for feeding on AM fungi which produce sporocarps (Janos et al. 1995; Mangan and Adler 2002).

Volatile compounds

Volatile organic compounds (VOC) emitted by fruit bodies, mycelia, and spores probably play a key role in the interaction between fungi and animals. However, most evidence was obtained from experiments with saprotrophic species, mainly polypores (Kües et al. 2018). Other evidence for the role of VOCs has also come from the very few studies that have used hypogeous fruit bodies of the ECM genera, including the ones on *Tuber* (Pacioni et al. 1991; D'Auria et al. 2014), *Gautieria*, *Hymenogaster*, *Melanogaster*, *Octaviania*, and *Pachyphloeus* (D'Auria et al. 2014) and the epigeous *Tricholoma matsutake* (Sawahata et al. 2008). Volatile compounds were also measured in vitro in cultures of *Laccaria*, *Paxillus*, and *Hebeloma* (Müller et al. 2013; Ditengou et al. 2015). It is thought that polyphagous animals are attracted to fruit bodies by emission of 1-octen-3-ol (typical mushroom odor), whereas species-specific interactions are mediated by unique cocktails of VOCs, mainly terpenoids. These latter compounds may also indicate the age of the fruit body as well as other conditions including the actual populations of invertebrates (Kües et al. 2018). Pacioni et al. (1991) demonstrated that 3-methyl-butanal and dimethyl sulfide, produced by many truffles, attracted mycophagous insects in general; however, only dimethyl sulfide clearly attracted the beetle *Leiodes cinnamomea*, a species feeding strictly on hypogeous fungi. Although some information is known for the groups of fungi forming ECM, no studies have been conducted regarding possible volatile compounds associated with AM sporocarps or spores, although they could play a key role in facilitating animal encounters. Much technical advancement has occurred in this field, so that now it is perfectly feasible to conduct high-throughput sampling and analysis of both fungal fruit bodies

in the field as well as in fungal culture collections. We therefore foresee a huge increase in available data in the coming years which will allow a thorough mapping of odors emitted across the fungal tree of life. Again, this will not be done with mapping only but will also require attraction/repulsion tests with specific VOCs/animals.

Importance of transport of mycorrhizal fungi propagules by animals in ecosystems

Horizontal transport

Horizontal transport via animals naturally influences community and population structure of the transported fungal taxa (Douhan et al. 2011). This could be more pronounced in the case of specific interactions like hypogeous fungi with rodents and marsupials or pileate fruit bodies and dipterans.

The dispersal distance depends on the home range of the species, the area occupied by a single individual, and potential migration patterns. Generally, small animals can actively carry spores only at relatively small distances, whereas larger animals, especially those more opportunistic in habitat use, such as deer, reindeer, elk, mountain goat, bear, and wild boar in the Northern Hemisphere (Online resource 1, Table S3), wallabies in Australia (Claridge et al. 2001), or elephants in Africa (Paugy et al. 2004), can carry spores over long distances (Tables 2, Online resource 1—Table S2, Fig. 2).

Based on molecular data, Nielsen et al. (2016) suggested that geese may facilitate the movement of AM fungi between islands. The influence of animal migration routes on the population/community structure of fungi and the consequences of their disruption have never been studied.

A key factor influencing the successful dispersal of fungal propagules via animals is the retention time of spores in their gut systems (Danks 2012; Urban 2016). Cork and Kenagy (1989) found the mean retention time of *Elaphomyces* spores in the Cascade golden-mantled ground squirrel (*Spermophilus saturatus*) and the deer mouse (*Peromyscus maniculatus*) to be 24.8 ± 3.6 and 12.0 ± 2.4 h, respectively. Furthermore, they showed that excretion of 95% of the ingested spores required 52.0 ± 12 h in the latter species. In addition, the mean retention time in the gut system of swamp wallaby (*Wallabia bicolor*) was found to be 26.9–35.1 h; however, spores were still found in feces after 69 h from intake (Danks 2012). The spores of *Pisolithus arrhizus* passed within 48.4 ± 6.0 h through the digestive system of the giant white-tailed rat (*Uromys caudimaculatus*) (Comport and Hume 1998). The distance scale can be further magnified if the animal is captured by a predator. However, horizontal transport distances in relation to species-specific traits,

connected environmental factors, and food web interactions still require detailed studies.

Vertical transport

The importance of vertical transport lies in the need of mycorrhizal fungal species to (1) reach the soil surface to enable transport to new habitats and (2) find new roots to colonize. Animals may facilitate the vertical movement of propagules; thus, their activity can be important in bringing spores to the soil surface for other means of dispersal, e.g., ant hills and badger mounds (Allen et al. 1997). Animal species that forage in the hymenophore, but also spend part of their life underground, could serve as effective spore vectors to roots (e.g., dipteran larvae, Kitabayashi et al. unpubl., slugs and potentially isopods). Spores released with feces can be distributed either by water (Burges 1950) or coprophilous animals such as dung beetles and other insects (Claridge et al. 1992). While with normal agricultural practices mechanical soil mixing of the upper soil layers is common, animals can be crucial to disperse spores vertically in no tillage or natural ecosystems (Friese and Allen 1991). Mesocosm designs, as already suggested by Halbwachs and Bässler (2015), would be a promising approach for obtaining more data about the importance of water and invertebrates in the vertical dispersal of spores. Also, experiments with exotic, but still closely related, species with either easily distinguishable spore morphologies or DNA profiles can be used to follow the transport from aboveground to roots.

Maintaining fungal communities and ecosystems

The degree of mycophagy practiced by many widespread animals is supposed to largely influence fungal community structure and the co-occurrence of fungal species. However, this conclusion is based more on field observation than detailed studies. Nuske et al. (2018) found that the ECM community in a north-east Australian woodland was dominated by truffle-like species. Nearly 90% of these fungal taxa were also found in the diet of the fungal specialist, *Bettongia tropica*, but only slightly over 50% were consumed by generalist mammals. These authors concluded that the loss of the fungal specialist in the area could cause changes in the ECM community structure. Also, unmanaged forest sites after windthrow were found to harbor significantly more hypogeous fungi than managed sites, possibly due to the presence of suitable cover for small mammals (Vašutová et al. 2018).

Almost nothing is known concerning the dispersal mode of rare ECM species (Molina et al. 2011; Sugiyama et al. 2019), nor about species with a high affinity to naturalness. Knowledge of their biology and associated organisms are necessary to develop effective conservation strategies for their survival. It is important to determine if they are dispersed by

Table 3 Critical questions for future research on animal transport of mycorrhizal fungi

Question or knowledge gap	Comments and suggestions for future research
Animals	
How can we extend our knowledge on animal-mediated fungal dispersal from anecdotal evidence to an extensive mapping of fungal–animal interactions?	High-throughput sequencing makes an excellent starting point for broad screenings of animals of different trophic levels—feces or body parts of larger animals, whole smaller animals (invertebrates) using relevant primer combinations (Koskinen et al. 2019).
	After this, promising interactions can be further evaluated and proved by bait plant or vitality assays (see "Experimental evidence" section).
	Especially morphological observation of gut contents and observation of surfaces of insufficiently known groups, e.g., of Protura, Pauropoda, Enchytraeidae, are needed. Also, testing if Mollusca and Isopoda are able to transport viable propagules of ECM fungi and test of epizoochory of oribatid mites and collembolans. Similarly, find if some isopods or millipedes occur in the vicinity of ECM fruit bodies and observation/analyses of their feces and surfaces. Also, analyses of millipede gut systems for presence of AM fungi.
How do fungal spores or other propagules survive in the food web?	Analysis of the gut system or scat of predators of known spore transporters (predatory mites–oribatid mites, robins or moles–earthworms, predatory birds or larger mammals–small mammals) will extend our knowledge on importance of food webs for fungal dispersal.
How long are spores retained in gut systems of different animals?	This question should be approached in manipulative lab experiments where animals would be fed with inorganic markers and fungal spores.
How wide are the effective habitat ranges of the different animals?	In combination with the previous question, gut transport timing studies should be combined with studies on the movements of animals in the habitats and even with ethological studies to quantify the distances and conditions at which animals can release fungal propagules. Information on animal sex and age structure should be included as factors affecting animal movement range.
How important are earthworms for the dispersal of ECM and AM fungi? Do the abundance and diversity/life forms of earthworms significantly impact AM fungal communities?	Detailed analysis of the AM fungal communities associated with epigeic, endogeic, and anecic earthworm species is needed. Sites which differ in earthworm populations, e.g., intensive versus no-till agriculture or areas where earthworms are invasive or not, should be carefully selected and earthworm and AM fungal community structure co-analyzed. Observation and experiments with epigeic earthworms and resupinate fruit bodies of ECM fungi.
Do opportunistic mycophagists have preferences for specific mycorrhizal fungi, and if so, do they influence fungal communities?	Analysis of stomach or feces, large-scale comparison of fungal communities with/without presence of animals.
What is the potential fungivory of mammals which have not been studied yet (e.g., carnivores—bears, badgers etc.; even-toed ungulates (other than wild boars)? How important are vertebrates for the distribution of AM fungi forming fruit bodies?	Analysis of stomach or feces. Use of specific primers (universal or group specific).
Fungi	
Which fungal propagules/structures survive transport in the gut systems, e.g., spores, mycelial fragments, sclerotia, ECM mantles, etc.?	Fungal species invest differently in distinct structures. To identify fungal dispersal strategies, select fungi where different structures are available and easy to identify and mesocosm experimental testing of animals fed with different fungal propagules/structures.
How can we use already published trait lists, e.g., from fungus, etc. to formulate/verify hypotheses?	Especially information on spore size, shape, and ornamentation are readily available and can be used for hypothesis-driven questions on fungal dispersal.
How to assess the importance of animal dispersal compared to other dispersal methods for specific fungal–animal interactions? Especially AM fungal species forming fruit bodies are understudied in this respect.	Air versus animal transport can be evaluated by combining the use of spore traps and animal or scat analysis within the same geographic area. This will be critical in order to understand the impact of (animal) species loss on fungal diversity (especially in the case of rare fungal species)—see "Maintaining fungal communities and ecosystems" section.
Interactions	
How to identify specific evolutionary adaptations of fungi to be dispersed by animal vectors?	If fungi depend on being taxied, specific traits must have evolved during evolution. These could be morphological or anatomical adaptations or the occurrence/loss of special taste/smell/toxic substances.

Table 3 (continued)

Question or knowledge gap	Comments and suggestions for future research
	In addition, mirrored co-evolution between fungal and animal species would be a strong indication.
How can we disentangle/explore and interpret the total network of interactions between fungi and animal groups at specific sites?	Network analysis would be a powerful tool, e.g., to link species of animals and mycorrhizal fungi present in their guts or scats of a particular site. Different parameters of the structure of these bipartite interaction networks, such as nestedness or modularity, will shed light onto the specificity (species–species) of dispersal strategies and the resilience of networks facing species loss.
How do animals influence fungal population structure?	Selection of fungal species with known and contrasting dispersal modes, e.g., wind versus animal, and comparison of the population structure by using genetic markers.
Ecosystems	
How do animals influence vertical spore movement?	Establishment of mesocosm experiments with and without fungal fed animals (e.g., collembolans, oribatid mites, earthworms, isopods, slugs) and analyze the potential for downward movement using bait techniques.
How important are animals in the establishment of invasive ECM species?	Analyses of invasive ECM fruit body consumers in pristine areas.
Methodology	
How to validate different methods for evaluating the success of fungal propagules being dispersed especially after endozooic transfer?	Comparison of different vitality tests ("Experimental evidence" section) in parallel experiments. For this, selection of fungal species, for which the bait plant approach is possible to use, is necessary.

rare specialists, which may also be threatened with extinction, or generalists and how to support their spreading to new localities.

Because of the symbiotic lifestyle of mycorrhizal fungi, interactions between fungi and animals also affect plant communities. Allen and MacMahon (1988) demonstrated the potential of pocket gophers to disperse AM fungi across a recent volcanic area thereby facilitating plant succession. Similarly, deer were proved to transport *Suillus* spores to coastal sand dunes (Ashkannejhad and Horton 2006). Vernes and Dunn (2009) reported that the composition of the bush rat (*Rattus fuscipes*) diet changed significantly from woodland and open forest (ECM) to rainforest (AM). It was hypothesized that the bush rats could transport spores between contrasting habitats and so influence their plant composition. Lastly, interactions between fungi and animals could also be crucial in the spread of invasive species. For example, wild boars seem to have played a key role in the invasions of pine into South America (Nuñez et al. 2013).

There are almost no data concerning which dispersal mode of mycorrhizal communities dominates across different biotopes or landscapes. Allen (1988) hypothesized that wind is the dominant vector in arid lands and animals in mesic lands. However, no larger-scale studies have been conducted on this topic, and experimental data on the dispersal mode of particular fungal species are also missing. Ecosystems dominated by plants associated with mycorrhizal fungi which heavily depend on animal transport could be more threatened by extinctions or niche changes of key animal species (Nuske et al. 2019).

Therefore, additional knowledge gaps include the tripartite interactions between mycophagous animals, mycorrhizal fungal communities and associated vegetation, and the importance of mycorrhizal fungi dispersal via animals in ecosystems. Both phenomena (invasion and extinction) might have important impacts on the gene flow and dispersal range of mycorrhizal fungi through food web connections among specific animal and fungal taxa. It is likely that these connections will most probably change in the future resulting in biogeographical redistribution of organisms, biodiversity loss, and global change.

Conclusion and future research

Mycorrhizal fungi are integral parts of most terrestrial ecosystems and contribute to a range of ecosystem services such as nutrient capturing, soil aggregation, C-sequestration, and maintaining plant diversity. Maintaining a diverse palette of mycorrhizal fungal species in ecosystems is therefore an important aspect of habitat conservation.

In contrast to wind dispersal, which is mostly limited to the close vicinity of the fruit body (Galante et al. 2011) or is also highly unpredictable, animals could bring a sufficient amount of spores to an appropriate place and "fertilize" them. They may disperse fungi purposefully in highly developed fungal–animal interactions or accidentally through their activities or via unspecific feeding on fungal structures. The importance of different groups of animals as fungal "taxi drivers" is difficult to assess, because only 33 studies showing successful transport have been

published so far, most on mammals and hypogeous ECM fungi. Most fungal–animal relationships are species dependent and any conclusions across broader groups must be done with caution.

In Table 3, we have summarized the main knowledge gaps including insufficient information on invertebrates and their role in fungal dispersion, the way fungal propagules pass through food webs, and the mechanisms of vertical dispersal. We have suggested future research directions to overcome these knowledge gaps. Two steadily evolving methods, High-throughput sequencing and VOC analysis, are especially promising for future research. High-throughput sequencing could facilitate the broad screening of feces and gut systems of animals. Such studies could indicate their potential for dispersal of mycorrhizal fungi (Koskinen et al. 2019). However, detailed and manipulative lab studies are necessary to provide more evidence of successful transport. Similarly, classical taxonomic knowledge and collaborative work between mycologists and zoologists will enable detailed observational studies on animals and fungal propagules in situ as well as in the lab.

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