Ecology Letters

WILEY

ECOLOGY LETTERS

LETTER

Beyond Predators: Carnivores as Secondary Dispersers of Mycorrhizal Fungi

Ryan B. Stephens[1] | Remington J. Moll[2] | Amanda M. McGraw[3] | Marcos V. Caiafa[4] | Matthew E. Smith[4] | Deahn M. Donner[5] | Alexis R. Grinde[6] | Michael J. Joyce[6]

[1]Department of Biological Sciences, East Tennessee State University, Johnson City, Tennessee, USA | [2]Natural Resources and the Environment, University of New Hampshire, Durham, New Hampshire, USA | [3]Wisconsin Department of Natural Resources, Rhinelander, Wisconsin, USA | [4]Department of Plant Pathology, University of Florida, Gainesville, Florida, USA | [5]USDA Forest Service Northern Research Station, Rhinelander, Wisconsin, USA | [6]Natural Resources Research Institute, University of Minnesota, Duluth, Minnesota, USA

Correspondence: Ryan B. Stephens (stephensrb@etsu.edu)

Received: 9 July 2025 | **Revised:** 4 November 2025 | **Accepted:** 5 November 2025

Editor: Juan Manuel Morales

Keywords: carnivore ecology | diploendozoochory | dispersal effectiveness | fungal dispersal | indirect dispersal | secondary dispersal

ABSTRACT

Primary dispersers of seeds and spores play critical roles in structuring the distributions of species, yet the role of predators as secondary dispersers remains largely unknown. This is especially true of mycorrhizal fungi, which often rely on small mammals to consume and disperse spores. We investigated how predator size, diet, and movement influence secondary spore dispersal in a terrestrial carnivore community by quantifying spore loads in scats (dispersal quantity) and integrating movement rates with gut passage time to determine dispersal distance (dispersal quality). Spores in carnivore scats increased with consumption of small mammals and transport of spores closely tracked home range movements. Larger carnivores deposited fewer spores but moved them farther from their source, creating a continuum between the quantity and quality of dispersal effectiveness. Our findings highlight the importance of carnivores as long-distance dispersers of mycorrhizal fungi and reveal how trophic interactions contribute to ecosystem functioning through secondary dispersal.

1 | Introduction

Animals are important dispersal vectors of propagules (seeds and spores) for many plant and fungal species (Nathan et al. 2008; Golan and Pringle 2017). Endozoochory, or primary dispersal, where fruiting bodies are consumed by animals and propagules passed through the digestive tract and dispersed following excretion, has been well documented for a wide range of plant (Nathan et al. 2008) and fungal taxa (Vašutová et al. 2019). However, trophic interactions can alter dispersal dynamics and growing evidence suggests that diploendozoochory (hereafter secondary dispersal)—where propagules are ingested by a primary consumer which in turn is predated upon by a secondary consumer—represents an important yet understudied dispersal mechanism (Hämäläinen et al. 2017; Elliott et al. 2023). Predators may serve as highly effective dispersal vectors, capable of transporting large quantities of propagules orders of magnitude farther than their prey (Nogales et al. 2002). These longer distance movements may be particularly important given shifting climatic niches and increasingly fragmented landscapes (Hämäläinen et al. 2017). Although secondary dispersal of seeds has been observed in a range of vertebrates (reviewed by Hämäläinen et al. 2017), the role predators play in dispersing mycorrhizal fungi has received little attention.

Mycorrhizal fungi form symbiotic relationships with most plant species, giving plant roots improved access to water and soil nutrients (Smith and Read 1997). These fungi can shape ecosystem

dynamics by affecting plant establishment, growth, productivity, and resiliency to drought along with controlling soil carbon storage dynamics (Terwilliger and Pastor 1999; Anthony et al. 2022, 2024; Luo et al. 2023). Across ecological scales, dispersal limitation of mycorrhizal fungi can strongly influence fungal community composition (Peay et al. 2010; Peay and Bruns 2014). To facilitate dispersal, many mycorrhizal fungi produce spores within mushrooms (epigeous) or truffles (sequestrate and hypogeous). Although mushroom spores can be dispersed by abiotic factors such as wind (but see Li 2005, Galante et al. 2011), truffles cannot forcibly discharge spores and require animal vectors for spore liberation and movement (Johnson 1996). Small mammals play a key role as primary consumers of truffles, often dispersing more diverse mycorrhizal fungal communities than wind (Stephens and Rowe 2020; Borgmann-Winter et al. 2023). However, spore dispersal by primary fungal consumers is typically limited to distances of tens to a few hundred metres because home ranges for most small mammals are less than a few hectares (Swihart et al. 1988). Spore dispersal distance may increase by several orders of magnitude when carnivores prey on primary fungal consumers (Elliott et al. 2023), but the relative importance of this secondary dispersal depends on how frequently carnivores consume small mammals and how far they move. Additionally, some studies have suggested that carnivores may directly consume sporocarps (Zielinski et al. 1999; Aguirre et al. 2021), although it is unclear if direct consumption or multitrophic interactions are the primary mode of fungal spore transmission. Identifying the factors that influence fungal spore consumption and movement by carnivores is crucial for understanding the role these species play in shaping fungal dispersal dynamics across spatial scales. This, in turn, has important implications for broader ecosystem functioning, including nutrient cycling, plant community composition, and the resilience of ecosystems to environmental changes (Baldrian et al. 2023).

The dispersal effectiveness of an animal vector is often divided into the quantitative (number of propagules) and qualitative (distance moved and location deposited) components of dispersal (Schupp et al. 2017). Because body mass is related to both diet and movement of carnivore species, it may play a key role in structuring both components of secondary dispersal effectiveness (Draper et al. 2022) (Figure 1). Body size in terrestrial carnivores is positively correlated with prey size (Vézina 1985). Because fungi are a major food source for small mammals (particularly rodents; Elliott et al. 2022), smaller predators that consume more small mammals may deposit scats with more fungal spores, compared to larger predators that consume larger prey that rarely consume fungi (Figure 1a). Carnivore body mass is also positively correlated with both gut retention time (Hernot et al. 2005; Draper et al. 2022) and home range size (Swihart et al. 1988). Accordingly, after consuming spores, larger carnivores likely retain spores longer in their digestive tracts and move farther during home range movements, together allowing them to disperse spores longer distances compared to smaller carnivores (Figure 1b).

To determine the role of predators as secondary dispersers, we evaluated five carnivore species in northern temperate forests that vary in body size by nearly an order of magnitude (4.1–31.2 kg; Figure 2). We combined microscopy and sequencing of fungal spores with diet analysis to determine how consumption

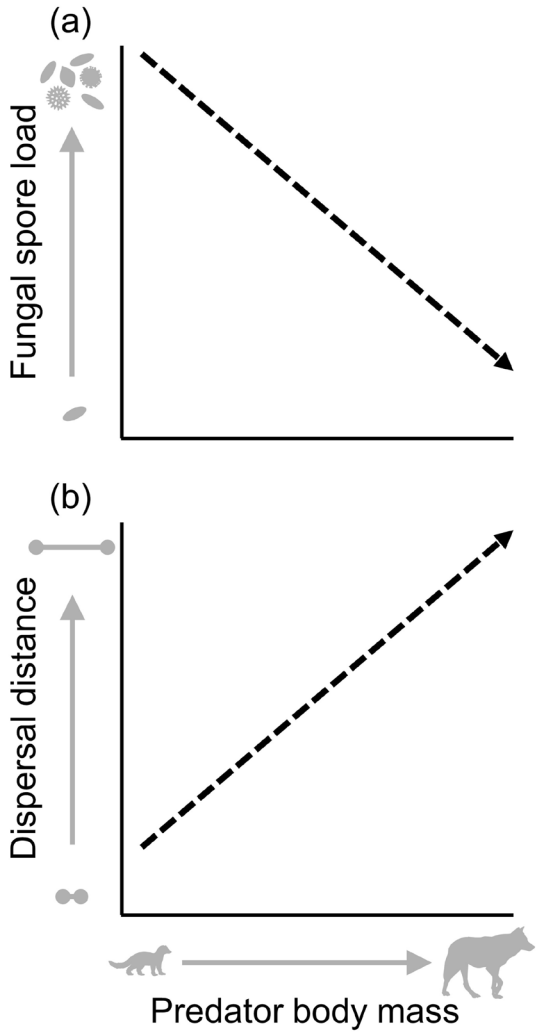

FIGURE 1 | Predictions of how predator body mass relates to the (a) quantity of spores in scat and (b) distance that spores are dispersed. Smaller predators generally eat smaller prey (such as rodents which regularly consume fungi), resulting in scats with more spores compared to larger predators which eat larger prey that consume less fungi. Body mass is related to home range size and gut passage time such that smaller predators move shorter distances and retain spores for a shorter duration compared to larger predators that can disperse spores farther. Fisher silhouette by Gabriela Palomo-Munoz and wolf silhouette by Margot Michaud.

of small mammals relates to fungal spore composition in carnivore scats. Additionally, we integrated movement rates and gut passage time of carnivores to predict the distance over which each carnivore species disperses spores. We then assessed how the quantitative (spore abundance) and qualitative (movement) components of dispersal relate to body mass and integrated these two components to generate a spore dispersal effectiveness landscape. We predicted that spore dispersal would be strongly related to carnivore body mass, but that the qualitative and quantitative axes of spore dispersal would covary (Figure 1). Specifically, we expected that predator body mass would be negatively correlated with spore abundance and positively correlated with movement distance, creating a general continuum of dispersal effectiveness with a tradeoff between the quantity and quality of spore dispersal that carnivore species provide.

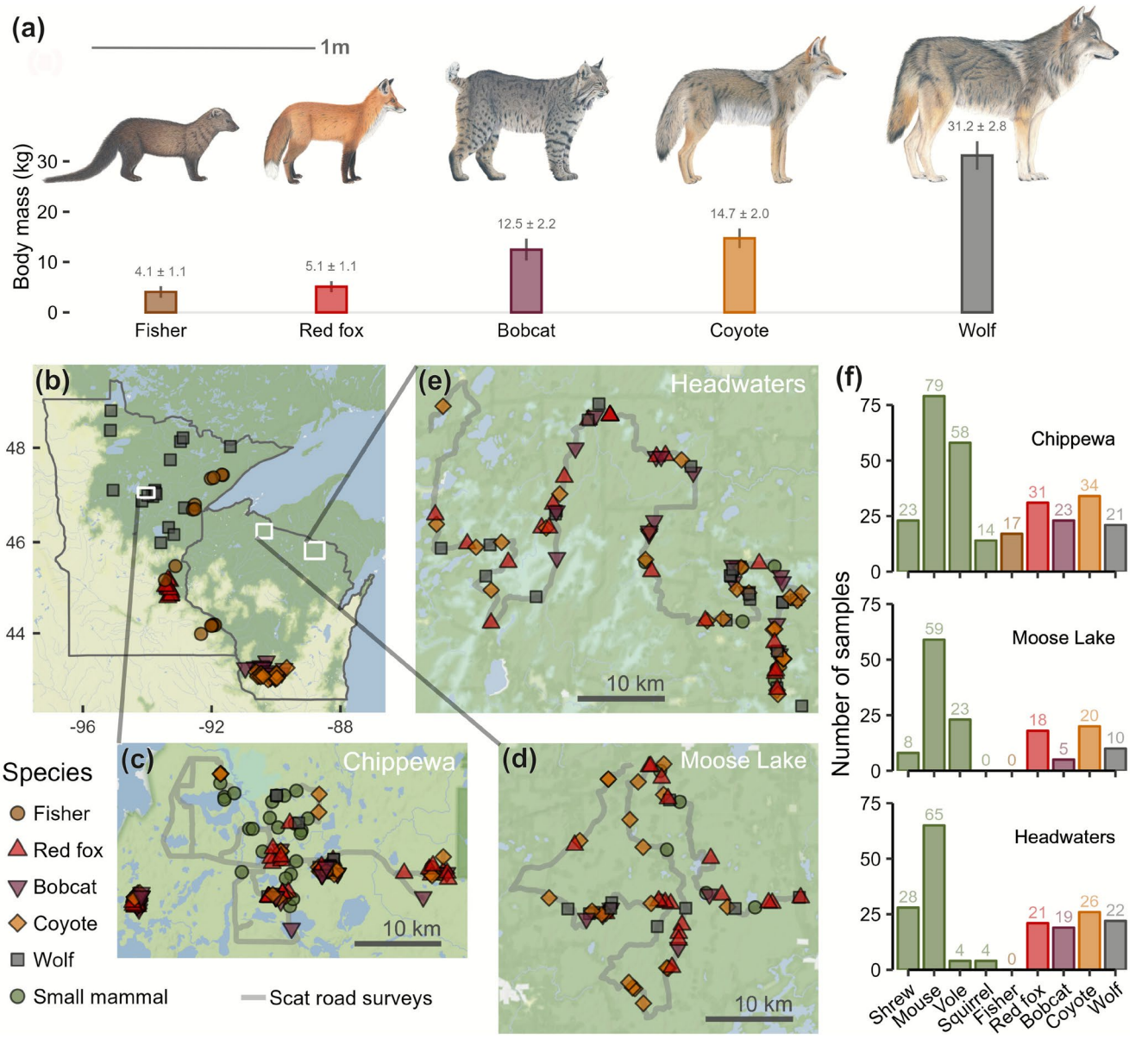

FIGURE 2 | The (a) focal carnivore species ranged in mean body mass (±SD) by nearly an order of magnitude from fisher (4.1 kg) to wolf (31.2 kg). Within Minnesota and Wisconsin, (b) collar fix data from individuals (shapes represent centroids of movements) were used to estimate spore dispersal distance and (c–e) carnivore scat collection (road survey and scat detection dogs) and small mammal trapping were conducted across three study areas (Chippewa, Headwaters, Moose Lake) yielding a total of (f) 365 small mammal and 267 carnivore scats for fungal spore assessment. Carnivore illustrations by Ryan Stephens.

2 | Materials and Methods

2.1 | Study System

We focused on five carnivore species that co-occur in forests of the upper midwestern USA and range in body mass by nearly an order of magnitude: fisher (*Pekania pennanti*), red fox (*Vulpes vulpes*), bobcat (*Lynx rufus*), coyote (*Canis latrans*), and grey wolf (*Canis lupus*; Figure 2a). For analyses, we used carnivore movement data collected in eastern Minnesota and southern Wisconsin (Figure 2b) and fungal spore data (from small mammals and carnivore scats) sampled within the Chippewa National Forest in Minnesota (hereafter Chippewa; Figure 2c) along with sites near the Moose Lake State Natural Area (hereafter Moose Lake; Figure 2d) and Headwaters Wilderness Area (hereafter Headwaters; Figure 2e) in Wisconsin. We sampled dominant forest communities including northern hardwood, upland mixedwood, upland softwood, and lowland softwood forests (for site-specific details see Data S1).

2.2 | Small Mammal Sampling

We trapped small mammals to characterise fungal spore consumption by the prey base. In 2020, we surveyed 26 sites at Chippewa (9 upland hardwood, 9 upland mixedwood, 8 upland softwood) and 7 sites each at Moose Lake and Headwaters (3 upland hardwood and 4 lowland softwood). We sampled each of the 40 sites for three consecutive days (October 1–19) using

two parallel 80 m transects with 5 trap stations. Each trap station had 2 mouse snap traps (20 traps per site) plus 5 rat traps placed on transects to target squirrels. For fungal spore analyses, we randomly selected up to 20 individuals of each species in each forest type and study area (Figure 2f). Individuals were prepared as vouchers and deposited in the Yale Peabody Museum of Natural History, New Haven, Connecticut. During preparation, contents from the large intestine and cecum (last 10 cm of intestine for shrews) were transferred to a microcentrifuge tube and lyophilised for spore analyses. Sampling protocols were approved by Animal Care and Use Committees of University of Minnesota (Protocol #2008-38344A) and Wisconsin Department of Natural Resources (Protocol #20-01) and followed guidelines for use of wild mammals in research (Sikes 2016).

2.3 | Carnivore Scat Sampling and Processing

To determine prey and fungal spore consumption by carnivores, we collected scats using road surveys, live trapping, detection dogs, and active searches near resting sites of collared individuals between 2020 and 2022. At each study area, we collected scats along ca. 160 km road survey route (Figure 2c–e). Routes were cleared 1 week before the first collection and driven (24–40 km/h) four times, approximately 1 week apart at Chippewa (October 1–23, 2020) along with Moose Lake and Headwaters (October 5–29, 2020, October 11—November 9, 2021). To collect additional scats at Chippewa, we captured carnivores using 37 Tomahawk live traps (model 108—checked daily for 11 days within suitable habitat along scat routes). However, despite considerable road survey and trapping efforts, there were only 18 usable scats from Chippewa in 2020. To increase sample sizes, we used a scat detection dog (Rogue Detection Teams, Rice, Washington) to conduct five surveys that each covered approximately 2.6 km^2 per day in 2021. During each survey, we systematically targeted areas with features that facilitate carnivore activity or funnel movement (e.g., roads, trails, edges, topographic features). Results from detection dog surveys indicated that fishers were present but that scats were not deposited on roads. As fishers are an important part of carnivore communities in Minnesota and Wisconsin (Pauli et al. 2022), we supplemented our dataset with fisher scats ($n = 13$) collected between 7 September and 18 October 2022 from resting sites of collared animals in Superior National Forest, Minnesota (Data S2).

Carnivore scats were identified to species using either morphology (fox and wolf) or DNA (National Genomics Center for Wildlife and Fish Conservation; Missoula, MT, USA; Data S3). After identification, carnivore scats were weighed, broken into pieces, hydrated in water, and washed through a 500 μm screen to recover undigested prey remains (e.g., bones, teeth, claws, hair). Prey items were identified to the lowest possible taxonomic level using a reference collection and taxonomic keys (Adorjan and Kolenosky 1969; Hazard 1982). Additionally, we retained 0.5–2.0 g of scat subsamples (collected throughout the scat) for fungal spore analysis. The pieces were soaked in warm water and homogenised to create 50 mL of scat slurry. The slurry was filtered through a 500 μm screen three times to isolate fine particles. Scat filtrate was mixed with 95% EtOH to a volume of 5 mL and the remaining large particles were added to undigested prey for diet assessments.

2.4 | Fungal Spore Analysis

We used microscopy to quantify the types and abundance of fungal spores in small mammal intestines and carnivore scats (see Stephens et al. 2017). Spores were isolated from samples (20 mg of freeze-dried small mammal intestinal material or 500 μL of carnivore scat filtrate) by filtering through a 125 μm screen with 40 mL of distilled water. For each sample, 100 μL of concentrated spore isolate (precipitate mixed with 95% ethanol) was spread onto a 22 × 22 mm area of a glass slide, cleared, and sealed with a cover slip. For each slide (one per small mammal and two per carnivore sample), we counted the number of spores of each fungal taxon in 20 fields of view at 400× magnification and enumerated larger and less numerous spores by scanning a 121 mm^2 area at 100×. We used spore counts, spore isolate volume and total material extracted from cecums and large intestines of small mammals to quantify spore abundance in each small mammal as a proxy for the number of spores that a carnivore would ingest when consuming prey. Similarly, we used spore counts, spore isolate volume, filtrate volume, and scat weight to calculate the total number of spores for each carnivore scat. Spores were categorised into morphotypes based on size, shape, wall thickness, colour, and ornamentation. Truffles were identified to the lowest possible taxonomic unit (genus or species) and mushrooms as spore morphotypes. Additionally, to confirm truffle identifications and assign taxonomy (genus or family) to mushroom-producing taxa, all carnivore scats with spores were amplified in the rDNA internal transcribed spacer region 2 (ITS2) using primers ITS4-fun and 5.8 s-fun and sequenced using Illumina MiSeq (Data S4). Many arbuscular mycorrhizal species are sporocarpric and consumed by small mammals (Janos et al. 1995), but are difficult to identify based on spores and ITS2 sequencing. For arbuscular mycorrhizal fungal spores, we assigned morphotypes to family Glomeraceae. Our analyses were likely unaffected by soil contamination as autumn leaf senescence provided a barrier between scats and soil. Additionally, focusing on spores eliminated any influence of hyphal contamination. However, because carnivore scats could have been contaminated from mushrooms, in analyses we only included truffle taxa (rarely disperse via wind; Borgmann-Winter et al. 2023) or mushrooms that were present in small mammal digestive tracts.

We assessed fungal community similarity among study areas and between carnivore scats and small mammals using permutational multivariate analysis of variance (PerMANOVA) in R package 'Vegan' (Oksanen et al. 2014) on a Bray–Curtis dissimilarity matrix. We visualised patterns in fungal composition among samples using non-metric multidimensional scaling (NMDS) in R package 'Vegan' using the same dissimilarity matrix. Prior to analyses, we relativised spore data by scaling across all samples within a fungal taxon and removing fungal taxa that occurred in < 2% of samples.

We compared fungal richness and spore loads (1) within each carnivore species when small mammal remains were present

and absent and (2) among carnivore species when either small mammal remains were present or absent using generalised linear models analysed in a Bayesian framework. For fungal richness we used a negative binomial error distribution and for spore loads we used a gamma distribution (for Bayesian modelling details see Data S5). We further qualitatively compared spore richness and loads in carnivore scats to those in shrews (*Blarina brevicauda*, *Sorex cinereus*, *S. arcticus*), mice (*Peromyscus leucopus*, *P. maniculatus*), voles (*Myodes gapperi*) and squirrels (*Glaucomys volans*, *G. sabrinus*, *Tamiasciurus hudsonicus*, *Tamias striatus*). Spore loads were adjusted for differences in spore production among fungal taxa by using an index calculated as the sum of scaled spore abundances of fungal taxa within a sample (scaled 0 to 1 within a taxon across small mammal and carnivore samples) (Stephens et al. 2021). Spore load values ranged from 0 (no spores) to the richness of the scat sample (i.e., indicating that all identified fungal taxa were present at their highest observed abundances).

To assess if spores in carnivore scat were related to the frequency of small mammal prey consumption, we compared fungal richness and spore loads to the frequency at which a carnivore species consumed small mammals (based on diet assessment) using linear regression that propagated uncertainty across the modelling steps in a Bayesian framework (Data S5). We used a bipartite network to visualize interaction frequencies based on count data between carnivore species and arbuscular mycorrhizal and ectomycorrhizal fungi. To assess the magnitude of spore dispersal, we calculated spore abundance in scats for the most common fungal taxa (present in ≥ 10 carnivore scats).

2.5 | Spore Dispersal Distance

We modelled spore dispersal distance for each carnivore species by integrating movement data from collared individuals with gut passage time from the literature. Movement data came from four GPS collar studies with telemetry fixes every 1–11 h during the fall or early winter. We obtained movement data from Minnesota and Wisconsin for female and male individuals, respectively, from fishers ($n = 7$, 7), red foxes ($n = 6$, 8), bobcats ($n = 8$, 10), coyotes ($n = 6$, 9; Margenau et al. 2023), and wolves ($n = 9$, 9; Erb et al. 2015, Chakrabarti et al. 2022) (Figure 2b; Data S6). Because we were interested in regular home-range movements, dispersing individuals were excluded. We used collar movement data to quantify displacement as the net distance (m) moved from a starting location over a five-day period. Within an individual, sequence start times were staggered such that displacements were calculated over all times of the day. We modelled mean net displacement as a function of time using a non-linear saturation model (Michaelis–Menten formulation) assuming gamma-distributed errors (Rehm et al. 2019):

$$\mu_i = \frac{\alpha_{j|sex} \times time_i}{\beta_{j|sex} + time_i}$$

where μ_i is the mean displacement for the ith observation, $\alpha_{j|sex}$ are asymptotes for the jth individual drawn from sex-specific Gaussian hyperdistributions, and $\beta_{j|sex}$ are half-saturation constants drawn from sex-specific Gamma hyperdistributions. Thus, the model accounted for repeated measures from individuals and differences in displacement due to sex, enabling species-level predictions averaged across sexes.

We modelled gut passage time using data collected from a literature review of 20 studies tracking the passage of seeds or seed-like particles (e.g., plastic beads) in 18 species from focal carnivore families (Canidae, Felidae, Mustelidae). For each study, we extracted data on the timing and corresponding cumulative proportion of particles that passed through since ingestion (when graphic, data were extracted using GetData Graph Digitizer; version 2.26). We translated these proportions into estimated seed numbers using a benchmark of 100 seeds per trial, which is conservative given that the mean number of seeds in trials, when reported, was 240.6 (SD = 123.9, range 93–384). We then modelled the number of seeds deposited as a function of time, taxa, and body mass using a binomial logistic regression with a random intercept indexed by study. Due to low sample size for felid observations (9 gut passage times from two studies), we combined Felidae and Canidae into a single category. Using a natural log transformation of the time covariate provided a superior model fit (Data S5). We used model posteriors to predict gut passage time for each species based on body mass and family. We then estimated spore shadows of species by using the posteriors to replace the time variable in the gut passage time model with the associated predicted distances from the displacement model.

2.6 | Body Mass and Dispersal Effectiveness

To determine how carnivore body mass influences spore dispersal, we used a linear regression with a Gaussian error distribution to assess the relationship between carnivore body mass and both the quantitative (spore load index) and qualitative (distance) components of spore dispersal. As above, we propagated uncertainty across modelling steps in a Bayesian framework (Data S5). To assess our prediction that there is a tradeoff between the quantity and quality of spore dispersal, we constructed an effectiveness landscape where spore dispersal effectiveness = quantity × quality (Schupp et al. 2010, 2017).

With the exception of PerMANOVA, we analysed all models in a Bayesian framework using Markov chain Monte Carlo simulations in JAGS and R (Plummer 2003; R Core Team 2021).

3 | Results

3.1 | Spore Community Composition and Abundance

We analysed 365 small mammal samples and 267 carnivore scats for fungal spores across the three study areas (Figure 2f). We detected fungal spores in 87% of small mammal samples (shrew = 68%, mouse = 85%, vole and squirrel = 100%) and 67% of the carnivore scats (fisher = 77%, red fox = 84%, bobcat = 62%, coyote = 65%, wolf = 49%). Overall, there was high

overlap in fungal community composition between small mammals and carnivore scats with trophic level (prey vs. carnivore) only explaining 0.8% of variation ($F_{1,477} = 2.02$, $p < 0.001$) and study area 1.4% ($F_{2,477} = 3.21$, $p < 0.001$) based on PerMANOVA (Figure 3a).

Within a carnivore species, spore richness (Figure 3b) and spore loads (Figure 3c) in scats were higher when small mammal remains were present compared to when they were absent. Further, when small mammal remains were present, all carnivore species had similar spore richness and spore loads (Figure 3b,c). However, at the species level, carnivores that had a higher frequency of small mammal consumption had both higher spore loads and spore richness (fishers having the highest values and wolves having the lowest), although this relationship was stronger for spore richness than spore

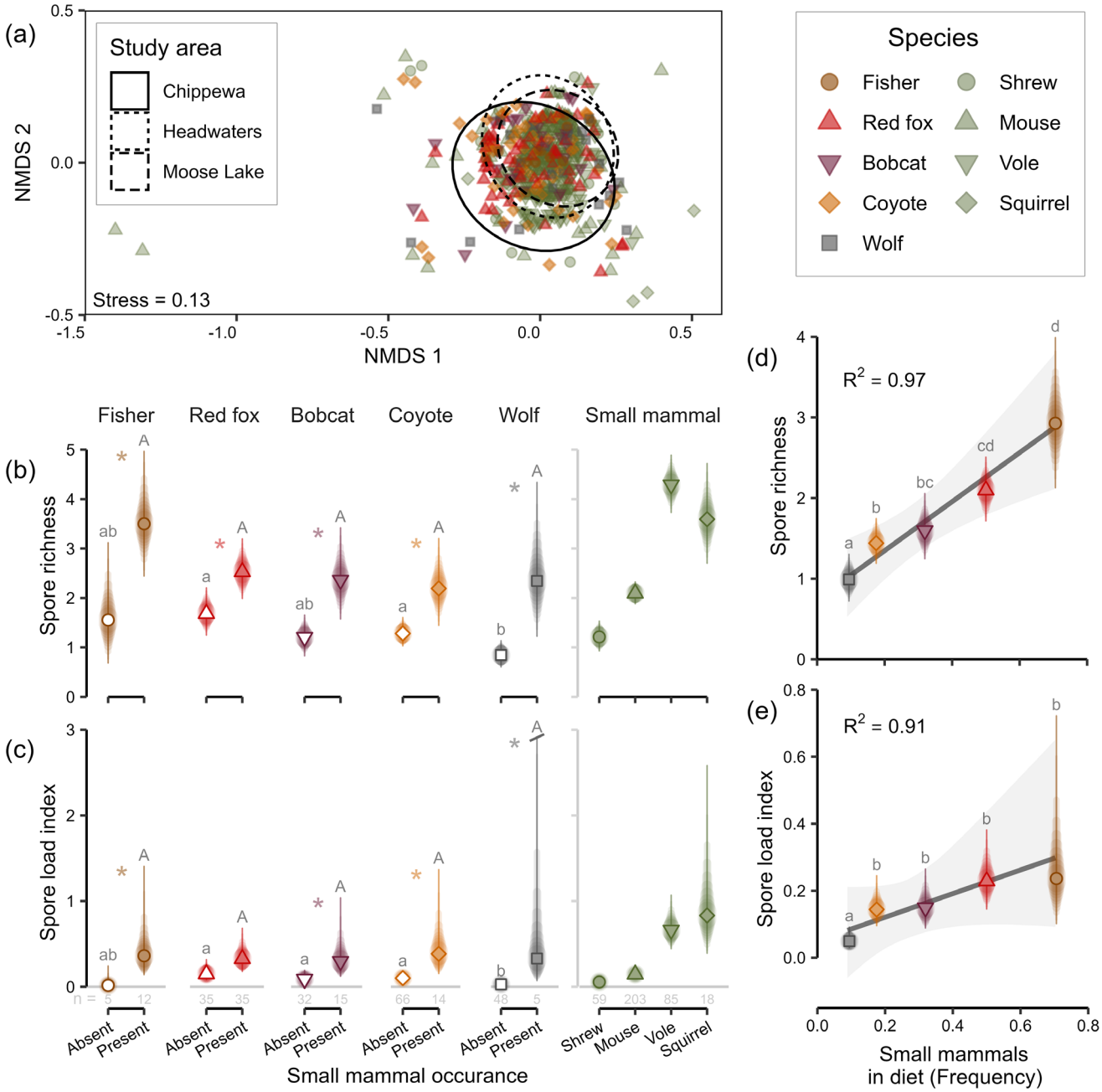

FIGURE 3 | (a) Nonmetric multidimensional scaling (NMDS) ordination indicating similar fungal spore community composition between small mammals and carnivore scats. Comparison of (b) spore richness and (c) spore loads in carnivore scats when small mammals are absent (open shapes) or present (closed shapes); small mammals provided for reference (spore loads represent all gut contents). Relationship between small mammal frequency in carnivore diets and (d) spore richness and (e) spore loads in carnivore scats. For spore richness and spore loads, symbols represent medians and thin solid lines are 95% credible intervals with increasing transparent line size indicating credible intervals from 90% to 10% (increments of 10). Asterisks denote significant differences within a species and different letters signify differences between species. For panels d and e, Bayesian linear regressions are indicated with grey lines and shaded 95% credible intervals. Note that the 95% credible interval for wolf spore loads with small mammals present extends to 5.1 and was truncated for better visualisation of trends.

loads (Figure 3d,e). Overall, carnivores interacted with both arbuscular mycorrhizal and ectomycorrhizal fungi and dispersed at least 32 fungal taxa based on spore morphotypes with confirmation from sequencing, most of which were truffles (Figure 4a). Sequencing only picked up 22% of spores detected in microscopy (likely due to saprobic dung-associated fungi dominating sequence reads), making it impossible to use operational taxonomic units (OTUs) to parse many of the genus-level identifications across samples. When a fungal taxon was present, spore abundance ranged from around 100 to over a billion, with median abundance values around 10,000 spores per scat (Figure 4b).

3.2 | Spore Dispersal Distance

Displacement varied among the carnivore species with red foxes moving the shortest distance, followed by coyotes, fishers, and wolves (with consistent trends after 10 h as assessed by overlap of 95% credible intervals; Figure 5a). Bobcat movements had high uncertainty, likely due to differences between sexes, but they tended to move farther than red foxes and coyotes (Figure 5a). Mean gut passage time increased with carnivore size with fishers having the shortest (9.1 h) and wolves having the longest (16.6 h) transit times (Figure 5b). Spore dispersal roughly tracked movement with red fox dispersing

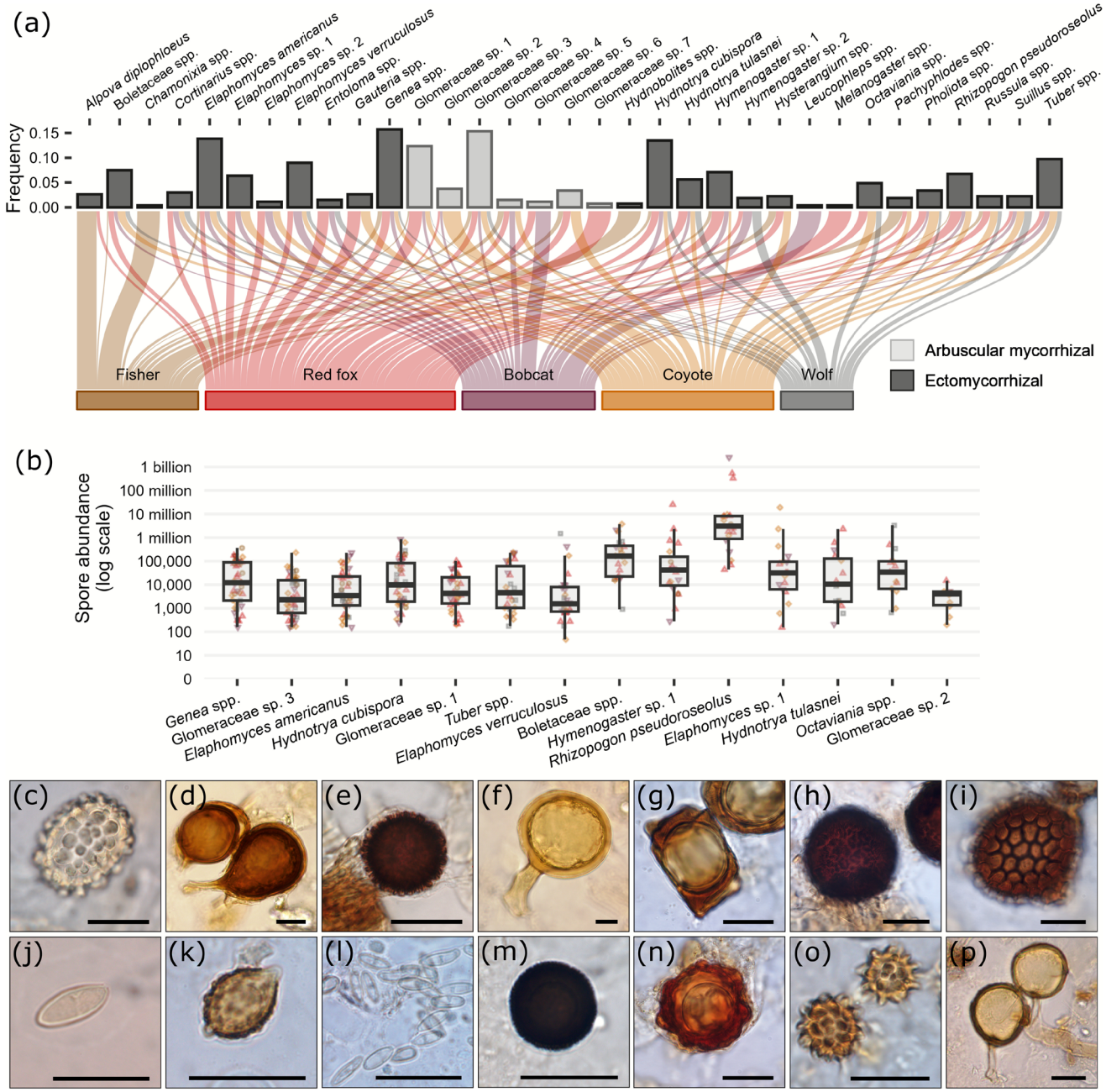

FIGURE 4 | (a) Bipartite network representing interaction frequency between carnivore species and mycorrhizal fungi (vertical bars indicate interaction frequency for arbuscular mycorrhizal and ectomycorrhizal fungal taxa). (b) Boxplots of spore abundance for the most common fungal taxa in carnivore scats (present in 10 or more samples) including (c) *Genea* spp., (d) Glomeraceae sp. 3, (e) *Elaphomyces americanus*, (f) Glomeraceae sp. 1, (g) *Hydnotrya cubispora*, (h) *Elaphomyces verruculosus*, (i) *Tuber* spp. (j), Boletaceae spp., (k) *Hymenogaster* sp., (l) *Rhizopogon pseudoroseolus*, (m) *Elaphomyces* sp. 1, (n) *Hydnotra tulasnei*, (o) *Octaviania* spp., and (p) Glomeraceae sp. 2.

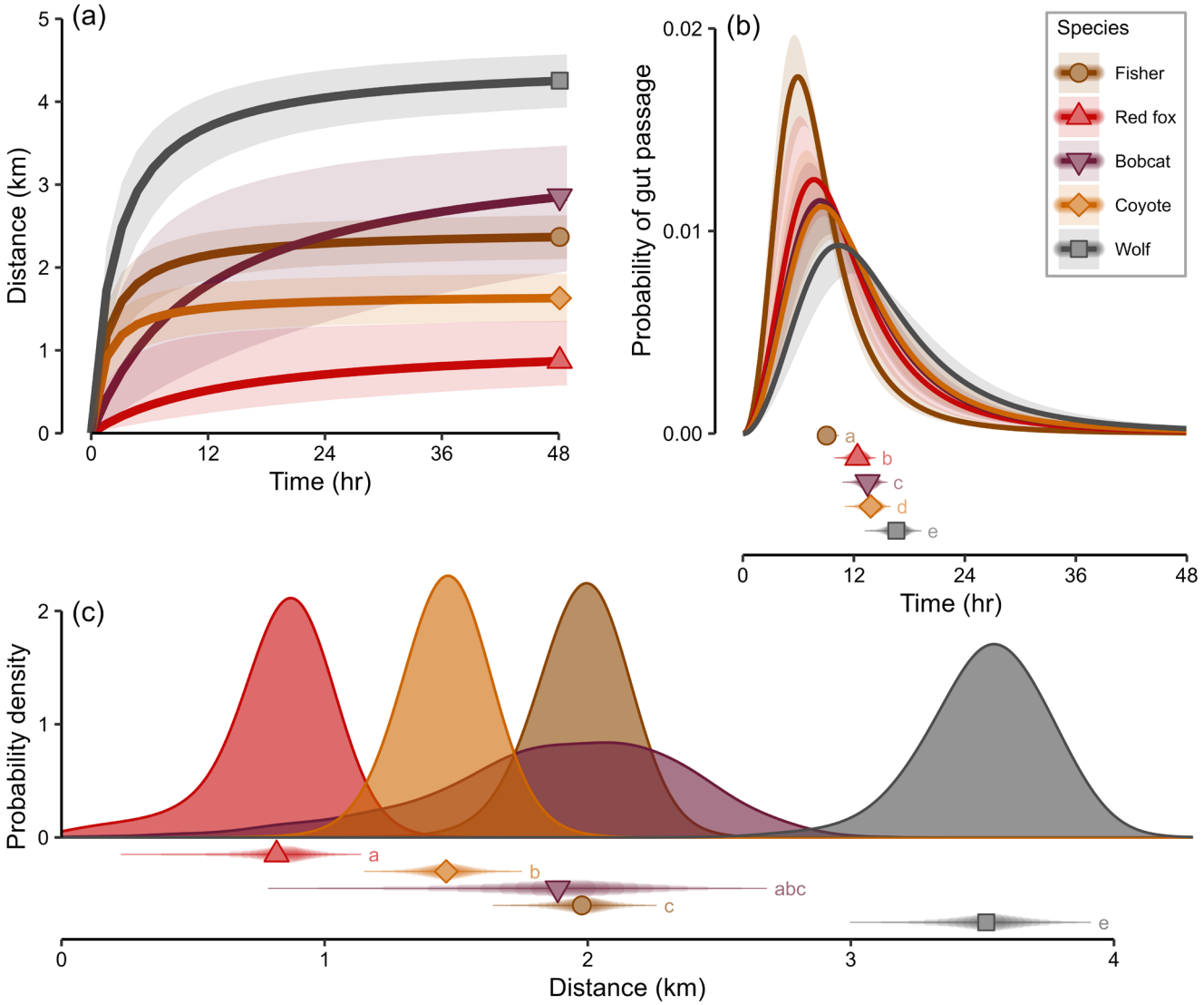

FIGURE 5 | Carnivore species differ in (a) distance moved over time (displacement), (b) gut passage time, and (c) spore dispersal distance (integrating displacement distance and gut passage). Shaded areas around lines for displacement and gut passage are 95% credible intervals. For mean gut passage time and spore dispersal distance (indicated by symbols), thin solid lines are 95% credible intervals with increasing transparent line size indicating credible intervals from 90% to 10% (increments of 10). For gut passage time and spore dispersal distance, different letters indicate significant differences between species.

spores the shortest mean distance (0.8 km), followed by coyote (1.5 km), fisher (2.0 km), and wolf (3.5 km) (Figure 5c). Bobcats (1.9 km) had similar mean dispersal distances as fishers but were variable and broadly overlapped with red fox and coyote (Figure 5c).

3.3 | Body Mass and Dispersal Effectiveness

Body mass was negatively correlated with spore loads ($R^2 = 0.92$) and positively correlated with dispersal distance ($R^2 = 0.70$) (Figure 6a,b). These tradeoffs in the quantity (spore abundance) and quality (movement distance) components of dispersal were reflected in dispersal effectiveness with similar values for red fox, coyote, and wolf; with the smaller carnivore (red fox) plotting higher on the quantity axis and the largest carnivore (wolf) plotting higher on the quality axis (Figure 6c). However, although there was some overlap, fisher and bobcat were 2.5 and 1.5 times more effective, respectively, compared to other carnivores, a pattern largely driven by their ability to disperse spores relatively far for their body sizes (Figure 6b,c).

4 | Discussion

We found that body mass and subsequent differences in diets and movement influence the relative role that carnivore species play as secondary dispersers of mycorrhizal fungi. Overall, smaller-bodied carnivores consumed more small mammals and dispersed higher spore loads but over shorter distances relative to larger-bodied carnivores that consumed fewer small mammals but moved longer distances. Our findings highlight the role of trophic interactions in contributing to ecosystem functioning and suggest that carnivores provide an important but largely overlooked mechanism of long-distance dispersal of mycorrhizal fungi.

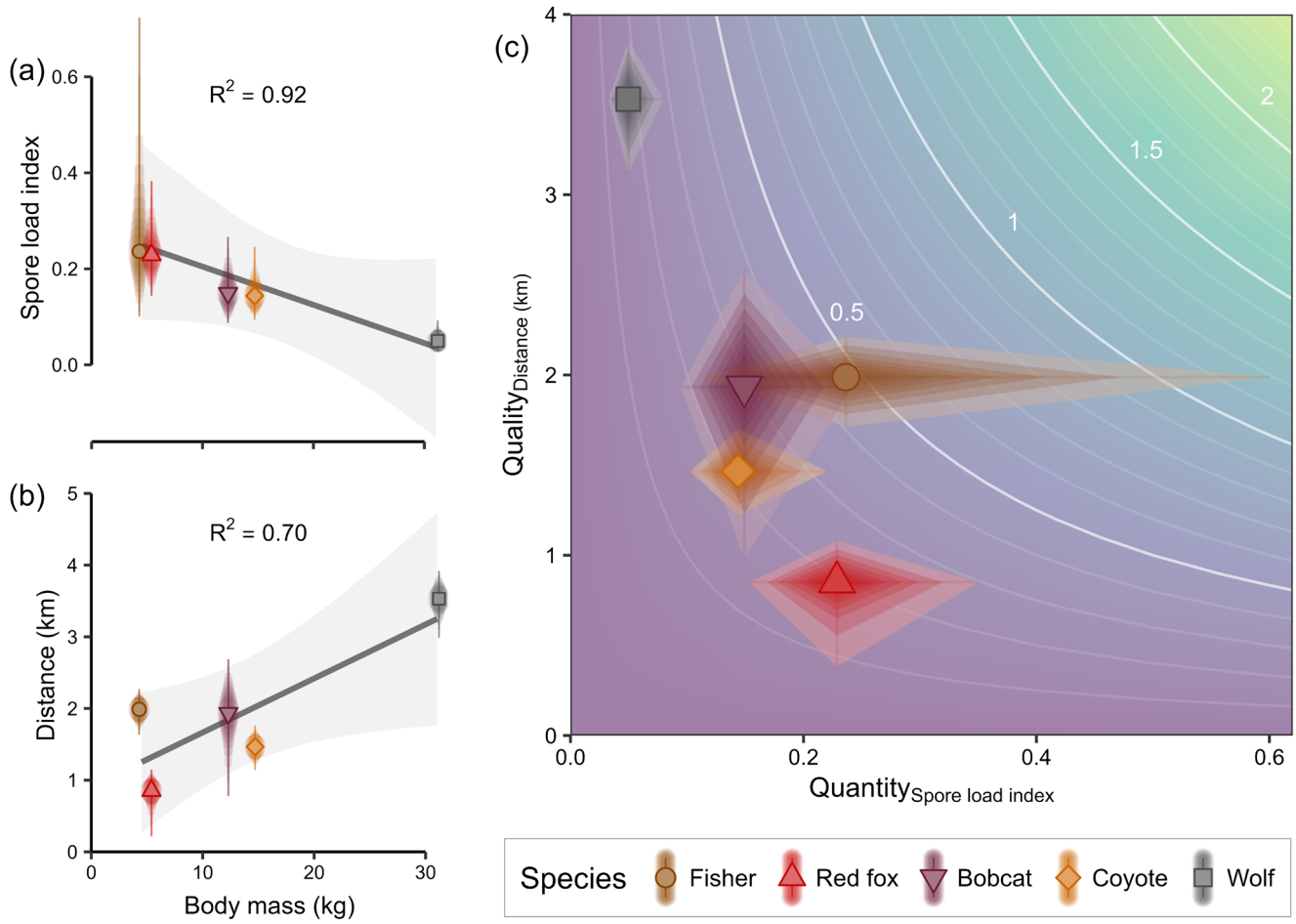

FIGURE 6 | Relationship between (a) spore loads and (b) spore dispersal distance as a function of body mass and (c) position of five carnivore species within the spore dispersal effectiveness landscape. Isoclines represent all combinations of quantity (spore loads) and quality (distance) that have the same spore dispersal effectiveness with increasing effectiveness from bottom left to top right. In all plots, shapes represent medians and solid lines indicate 95% credible intervals with increasing transparent line (or polygon) size indicating credible intervals from 90% to 10% (increments of 10). For panels a and b, Bayesian linear regressions are indicated with grey lines and shaded 95% credible intervals.

4.1 | Quantitative Component of Spore Dispersal

There is considerable variation in spore inoculum densities required for effective colonisation of roots, but many taxa can colonise roots with only a few hundred to several thousand spores (Parladé et al. 1996; Rincón et al. 2001; Klironomos and Hart 2002). Our results indicate that spore loads vary greatly but that carnivores can generally disperse sufficient numbers of mycorrhizal fungal spores to facilitate colonisation of plants (Figure 4b). Fungal spores have been previously detected in scats of fisher and pampas fox (Zielinski et al. 1999; Aguirre et al. 2021), although it has been unclear if spores are the result of primary or secondary consumption. When small mammal remains were present in carnivore scat, we observed more spores compared to when they were absent, indicating that spores are primarily from consuming prey. Many scats with no identified small mammal remains retained low levels of spores along with microscopic fragments of hair. As a small fraction of prey hair often passes after bones and teeth (Bowland and Rowland 1991), we suspect that many of these spores also originated from prey but are either slow to exit the gut or get caught with hair particles. Nevertheless, coyote and red fox scats often had high spore abundances of *Elaphomyces* and *Rhizopogon* (which produce relatively large sporocarps) with no trace of prey remains. This suggests that omnivorous predators may act as both primary and secondary dispersers of mycorrhizal fungi, although direct consumption may be limited to fungal taxa with relatively large sporocarps whereas secondary dispersal will likely reflect the wide array of sporocarp sizes that small mammals consume (Stephens et al. 2017).

Higher small mammal frequency in the diet increased overall fungal richness and spore loads in carnivore scats, although the relationship with spore loads was not as strong (Figure 3b,c). Spore loads include both richness and spore abundance, and although mid-sized carnivores such as bobcat and coyotes have relatively lower fungal richness, they have a high abundance of spores when taxa are present. This may be driven in part by the size of bobcat (15.2 ± 11.3 g) and coyote scats (13.4 ± 11.0 g), which are much larger than fisher (5.8 ± 3.9 g) or red fox (6.9 ± 6.8 g) scats.

4.2 | Qualitative Component of Spore Dispersal

Larger-bodied species have been shown to provide longer-distance propagule dispersal (Wotton and Kelly 2012; Rehm

et al. 2019). We generally observed this trend but found that there were considerable species-specific effects with fishers having the ability to disperse spores relatively long distances for their body size (Figure 6b). Similar to Rehm et al. (2019), we found that spore shadow distributions were primarily driven by movement rates rather than gut passage time, underscoring the importance of movement in dispersal distance. Thus, even smaller-bodied species with relatively fast gut passage times can provide long-distance dispersal if movement rates are high. Nevertheless, variability in gut retention time related to diet could still modulate dispersal distance. For example, shifts from a meat- to fruit-based diet can reduce gut retention time in grizzly bears by over 50% (Elfström et al. 2013). Also, given that small particles such as spores may persist at low levels in the gut longer than larger particles such as bones (Bowland and Rowland 1991), it is likely that gut passage time distributions have considerably longer tails than what we modeled from experimental studies using seeds (Figure 5b). Given the saturating nature of displacement kernels (Figure 5a), these longer tails would be unlikely to greatly increase dispersal distance for home range movements but could increase movement for dispersing individuals and broaden the deposition area of spores if they were deposited in more scats.

Our assessment of the qualitative component of dispersal was based on movement distance, but effects from gut passage on viability along with the location of deposition are also important aspects of dispersal quality (Schupp et al. 2010). Although freezing and alcohol emersion of samples prevented us from thoroughly assessing spore viability, most spores were intact (e.g., Figure 4c–p), suggesting that they were still viable. Further, seedlings have been successfully inoculated with fungal spores that passed through the digestive systems of both small mammals (reviewed in Elliott et al. 2022) and pampas foxes (*Lycalopex gymnocercus*; Aguirre et al. 2021), together suggesting that spores remain viable across trophic levels. However, overall spore viability may vary depending on gut retention time along with species-specific differences in animal stomach acidity and fungal spore traits such as wall thickness and melanization (Anderson 2025).

Most of our scats were collected from roads. Spores from these samples could ultimately be moved off the road by water or insects such as dung beetles (Milotić et al. 2019); however, roads are likely not an ideal habitat for colonising host plants. Based on dog surveys in our Chippewa study area, carnivores deposit scats in forested areas, but differences in habitat selection could lead to differences in microsite location deposition (García-Cervigón et al. 2018). For example, fishers primarily stay in mature forest whereas bobcats use both mature and regenerating forest (McNitt et al. 2020a; Pauli et al. 2022). Further, differences in tree community composition at the microsite, coupled with fungal species-specific host affinities, will strongly influence the ability of dispersed spores to colonise host plants. For example, most arbuscular mycorrhizal fungi have broad host associations whereas many ectomycorrhizal fungi are host specific such as *Rhizopogon* species that only associate with members of the family Pinaceae (Massicotte et al. 1994).

4.3 | Spore Dispersal Effectiveness

We found that all carnivore species dispersed spores, but that fishers were the most effective in terms of dispersing high spore loads over relatively long distances. Given the ubiquity of fungivory, especially by small mammals (Elliott et al. 2022), we suspect that secondary fungal dispersal by carnivores is a widespread phenomenon. Similar to fishers, other terrestrial mustelids are likely highly effective spore dispersers including martens (*Martes* spp.), which occur throughout the Holarctic and parts of Southeast Asia (Zhou et al. 2011). In addition, birds of prey—such as hawks and owls—that regularly hunt small mammals and traverse large areas may also play an important role in spore dispersal. Unlike many terrestrial carnivores, raptors are less constrained by roads and human infrastructure, potentially allowing them to disperse spores more broadly across fragmented landscapes.

Although we focused on interspecific variation in spore dispersal, intraspecific variation and seasonality may modulate the relative effectiveness of individuals. Specifically, individual variation in diet and movement associated with sex, age, and behaviour could change both the quantitative and qualitative components of dispersal effectiveness (Zwolak 2018), with the relative importance of these factors varying among species. For example, sex may drive movement for some species such as bobcats and fishers where males move considerably farther than females (McNitt et al. 2020b), but for pack animals such as wolves, sex has less influence. For social carnivores such as coyotes and wolves, behaviour associated with status may influence dispersal effectiveness as subordinate or transient individuals consume less large-bodied prey and move farther distances than dominant individuals (Bartel and Orrock 2022). Competition among carnivore species (Major and Sherburne 1987; Smith et al. 2023) and seasonality (Jensen et al. 2024) may further modify dispersal effectiveness by changing small mammal consumption rates along with movement and habitat selection. Seasonality may also play a role in structuring fungal spore composition in carnivore scats as small mammal diets shift with fungal fruiting phenology (Lehmkuhl et al. 2004).

5 | Conclusions

We found that carnivores differ in the qualitative and quantitative aspects of fungal spore dispersal, suggesting low ecological redundancy among species and highlighting the importance of maintaining carnivore communities to facilitate this ecosystem function across spatial scales. The ability of carnivores to move spores longer distances than their prey is especially important as fungi track changing climate windows and host plant distributions (Van Nuland et al. 2024). Additionally, because carnivores move across heterogeneous landscapes (Olson et al. 2024), and use disturbed areas such as burned or logged forest (Vanbianchi et al. 2017; Jones et al. 2024), they can maintain genetic connectivity of mycorrhizal fungi across fragmented habitat patches and establish new populations in regenerating areas. Together this long-distance dispersal across heterogeneous landscapes is especially important for truffle taxa which rely almost exclusively on animal vectors for dispersal.

Author Contributions

M.J.J. and R.B.S. conceived and designed the study. M.J.J. and A.M.M. collected field data and D.M.D. secured funding. M.J.J. processed carnivore scats and R.B.S. processed small mammal samples, conducted the literature review, performed microscopy, and analysed the data in conjunction with R.J.M. M.V.C. and M.E.S. performed genetic analyses. R.B.S. wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

Acknowledgements

R.B.S. greatly appreciates lab space provided by Rebecca Rowe and microscope access from Serita Frey during the sample processing stage of the project. We appreciate the help of technicians in collecting and processing carnivore scats, especially Anna Mangan and Teresa Pearson. We thank James Forester, Geoff Miller, John Erb, Carolin Humpal, Dave MacFarland, and Lydia Margenau for providing GPS collar data. Funding was provided by the University of Minnesota's Natural Resources Research Institute (M.J.J.), the Wisconsin Department of Natural Resources (A.M.M), US Forest Service Northern Research Station (joint venture agreement 21-JV-11242313-054; M.J.J. and D.M.D.), USDA NIFA McIntire-Stennis project FLA-PLP-006168 (M.E.S.), and Hatch project 1001991 (M.E.S.). Partial funding to collect and analyze fisher scats in the Superior National Forest was provided by the Minnesota Environmental and Natural Resource Trust Fund (M.J.J.).

Funding

This work was supported by USDA NIFA McIntire–Stennis project (FLA–PLP–006168), Northern Research Station, joint venture agreement 21-JV-11242313-054, Hatch project (1001991), Minnesota Environmental and Natural Resource Trust Fund, Wisconsin Department of Natural Resources, University of Minnesota's Natural Resources Research Institute.

Data Availability Statement

All data and code were archived in Figshare (https://doi.org/10.6084/m9.figshare.29519564.v1). Illumina MiSeq sequencing data were deposited at NCBI Sequence Read Archive under BioProject accession number PRJNA1236618.

Peer Review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.70282.

References

Adorjan, A. S., and G. B. Kolenosky. 1969. "A Manual for the Identification of Hairs of Selected Ontario Mammals." *Ontario Department of Lands and Forest Resources Report (Wildlife)* 90: 1–64.

Aguirre, F., E. Nouhra, and C. Urcelay. 2021. "Native and Non-Native Mammals Disperse Exotic Ectomycorrhizal Fungi at Long Distances From Pine Plantations." *Fungal Ecology* 49: 101012.

Anderson, J. 2025. "Raptors as Secondary Dispersers of Mycorrhizal Fungal Spores." Master's Thesis. East Tennessee State University.

Anthony, M. A., T. W. Crowther, S. Van Der Linde, et al. 2022. "Forest Tree Growth Is Linked to Mycorrhizal Fungal Composition and Function Across Europe." *ISME Journal* 16: 1327–1336.

Anthony, M. A., L. Tedersoo, B. De Vos, et al. 2024. "Fungal Community Composition Predicts Forest Carbon Storage at a Continental Scale." *Nature Communications* 15: 2385.

Baldrian, P., R. López-Mondéjar, and P. Kohout. 2023. "Forest Microbiome and Global Change." *Nature Reviews Microbiology* 21: 487–501.

Bartel, S. L., and J. L. Orrock. 2022. "The Important Role of Animal Social Status in Vertebrate Seed Dispersal." *Ecology Letters* 25: 1094–1109.

Borgmann-Winter, B. W., R. B. Stephens, M. A. Anthony, S. D. Frey, A. W. D'Amato, and R. J. Rowe. 2023. "Wind and Small Mammals Are Complementary Fungal Dispersers." *Ecology* 104: e4039.

Bowland, J. M., and A. E. Rowland. 1991. "Differential Passage Rates of Prey Components Through the Gut of Serval *Felis Serval* and Black-Backed Jackal *Canis mesomelas*." *Koedoe* 34: 37–39.

Chakrabarti, S., S. T. O'Neil, J. Erb, C. Humpal, and J. K. Bump. 2022. "Recent Trends in Survival and Mortality of Wolves in Minnesota, United States." *Frontiers in Ecology and Evolution* 10: 826358.

Draper, J. P., J. K. Young, E. W. Schupp, N. G. Beckman, and T. B. Atwood. 2022. "Frugivory and Seed Dispersal by Carnivorans." *Frontiers in Ecology and Evolution* 10: 864864. https://www.frontiersin.org/journals/ecology-and-evolution/articles/10.3389/fevo.2022.864864/full.

Elfström, M., O.-G. St⊘ en, A. Zedrosser, I. Warrington, and J. E. Swenson. 2013. "Gut Retention Time in Captive Brown Bears *Ursus arctos*." *Wildlife Biology* 19: 317–324.

Elliott, T. F., C. E. T. Paine, G.-A. Ballard, et al. 2023. "The Dingo (*Canis familiaris*) as a Secondary Disperser of Mycorrhizal Fungal Spores." *Wildlife Research* 51: WR22057.

Elliott, T. F., C. Truong, S. M. Jackson, C. L. Zúñiga, J. M. Trappe, and K. Vernes. 2022. "Mammalian Mycophagy: A Global Review of Ecosystem Interactions Between Mammals and Fungi." *Fungal Systematics and Evolution* 9: 99–159.

Erb, J., C. Humpal, and B. Sampson. 2015. *Minnesota Wolf Population Update 2015*. Minnesota Dept of Natural Resources.

Galante, T. E., T. R. Horton, and D. P. Swaney. 2011. "95% of Basidiospores Fall Within 1 m of the Cap: A Field- and Modeling-Based Study." *Mycologia* 103: 1175–1183.

García-Cervigón, A. I., M. Żywiec, M. Delibes, A. Suárez-Esteban, R. Perea, and J. M. Fedriani. 2018. "Microsites of Seed Arrival: Spatio-Temporal Variations in Complex Seed-Disperser Networks." *Oikos* 127: 1001–1013.

Golan, J. J., and A. Pringle. 2017. "Long-Distance Dispersal of Fungi." *Microbiology Spectrum* 5: 10–1128.

Hämäläinen, A., K. Broadley, A. Droghini, et al. 2017. "The Ecological Significance of Secondary Seed Dispersal by Carnivores." *Ecosphere* 8: e01685.

Hazard, E. B. 1982. *The Mammals of Minnesota*. University of Minnesota Press.

Hernot, D. C., V. C. Biourge, L. J. Martin, H. J. Dumon, and P. G. Nguyen. 2005. "Relationship Between Total Transit Time and Faecal Quality in Adult Dogs Differing in Body Size." *Journal of Animal Physiology and Animal Nutrition* 89: 189–193.

Janos, D. P., C. T. Sahley, and L. H. Emmons. 1995. "Rodent Dispersal of Vesicular-Arbuscular Mycorrhizal Fungi in Amazonian Peru." *Ecology* 76: 1852–1858.

Jensen, A. J., M. Muthersbaugh, C. R. Ruth, et al. 2024. "Resource Pulses Shape Seasonal and Individual Variation in the Diet of an Omnivorous Carnivore." *Ecology and Evolution* 14: e11632.

Johnson, C. N. 1996. "Interactions Between Mammals and Ectomycorrhizal Fungi." *Trends in Ecology & Evolution* 11: 503–507.

Jones, E. M., A. J. Koch, R. K. Hamede, and M. E. Jones. 2024. "A Systematic Global Review of Mammalian Carnivore Responses to Production Forests." *Mammal Review* 54: 133–149.

Klironomos, J. N., and M. M. Hart. 2002. "Colonization of Roots by Arbuscular Mycorrhizal Fungi Using Different Sources of Inoculum." *Mycorrhiza* 12: 181–184.

Lehmkuhl, J. F., L. E. Gould, E. Cázares, and D. R. Hosford. 2004. "Truffle Abundance and Mycophagy by Northern Flying Squirrels in Eastern Washington Forests." *Forest Ecology and Management* 200: 49–65.

Li, D.-W. 2005. "Release and Dispersal of Basidiospores From *Amanita muscaria* Var. *Alba* and Their Infiltration Into a Residence." *Mycological Research* 109: 1235–1242.

Luo, S., R. P. Phillips, I. Jo, et al. 2023. "Higher Productivity in Forests With Mixed Mycorrhizal Strategies." *Nature Communications* 14: 1377.

Major, J. T., and J. A. Sherburne. 1987. "Interspecific Relationships of Coyotes, Bobcats, and Red Foxes in Western Maine." *Journal of Wildlife Management* 51: 606–616.

Margenau, L. L. S., R. E. Russell, A. T. Hanrahan, N. M. Roberts, J. L. Price Tack, and D. J. Storm. 2023. "Survival and Cause-Specific Mortality of Coyotes in Wisconsin." *Journal of Mammalogy* 104: gyad033.

Massicotte, H. B., R. Molina, D. L. Luoma, and J. E. Smith. 1994. "Biology of the Ectomycorrhizal Genus, *Rhizopogon*: II. Patterns of Host-Fungus Specificity Following Spore Inoculation of Diverse Hosts Grown in Monoculture and Dual Culture." *New Phytologist* 126: 677–690.

McNitt, D. C., R. S. Alonso, M. J. Cherry, M. L. Fies, and M. J. Kelly. 2020a. "Influence of Forest Disturbance on Bobcat Resource Selection in the Central Appalachians." *Forest Ecology and Management* 465: 118066.

McNitt, D. C., R. S. Alonso, M. J. Cherry, M. L. Fies, and M. J. Kelly. 2020b. "Sex-Specific Effects of Reproductive Season on Bobcat Space Use, Movement, and Resource Selection in the Appalachian Mountains of Virginia." *PLoS One* 15: e0225355.

Milotić, T., C. Baltzinger, C. Eichberg, et al. 2019. "Functionally Richer Communities Improve Ecosystem Functioning: Dung Removal and Secondary Seed Dispersal by Dung Beetles in the Western Palaearctic." *Journal of Biogeography* 46: 70–82.

Nathan, R., F. M. Schurr, O. Spiegel, O. Steinitz, A. Trakhtenbrot, and A. Tsoar. 2008. "Mechanisms of Long-Distance Seed Dispersal." *Trends in Ecology & Evolution* 23: 638–647.

Nogales, M., V. Quilis, F. M. Medina, J. L. Mora, and L. S. Trigo. 2002. "Are Predatory Birds Effective Secondary Seed Dispersers?" *Biological Journal of the Linnean Society* 75: 345–352.

Oksanen, J., F. G. Blanchet, R. Kindt, et al. 2014. "Vegan:Community Ecology Package."

Olson, L. E., J. D. Sauder, P. A. Fekety, et al. 2024. "Fishers (*Pekania pennanti*) Are Forest Structure Specialists When Resting and Generalists When Moving: Behavior Influences Resource Selection in a Northern Rocky Mountain Fisher Population." *Movement Ecology* 12: 49.

Parladé, J., J. Pera, and I. F. Alvarez. 1996. "Inoculation of Containerized *Pseudotsuga menziesii* and *Pinus pinaster* Seedlings With Spores of Five Species of Ectomycorrhizal Fungi." *Mycorrhiza* 6: 237–245.

Pauli, J. N., P. J. Manlick, J. M. Tucker, G. B. Smith, P. G. Jensen, and J. T. Fisher. 2022. "Competitive Overlap Between Martens *Martes americana* and *Martes caurina* and Fishers *Pekania pennanti:* A Rangewide Perspective and Synthesis." *Mammal Review* 52: 392–409.

Peay, K. G., and T. D. Bruns. 2014. "Spore Dispersal of Basidiomycete Fungi at the Landscape Scale Is Driven by Stochastic and Deterministic Processes and Generates Variability in Plant–Fungal Interactions." *New Phytologist* 204: 180–191.

Peay, K. G., M. Garbelotto, and T. D. Bruns. 2010. "Evidence of Dispersal Limitation in Soil Microorganisms: Isolation Reduces Species Richness on Mycorrhizal Tree Islands." *Ecology* 91: 3631–3640.

Plummer, M. 2003. "JAGS: A Program for Analysis of Bayesian Graphical Models Using Gibbs Sampling." Page in K Hornik, F Leisch, and A Zeileis, editors. Proceedings of the 3rd International Workshop on Distributed Statistical Computing, Vienna, Austria.

R Core Team. 2021. *R: A Language and Environment for Statistical Computing Version 4.0.4*. R Foundation for Statistical Computing. http://www.R-project.org.

Rehm, E., E. Fricke, J. Bender, J. Savidge, and H. Rogers. 2019. "Animal Movement Drives Variation in Seed Dispersal Distance in a Plant-Animal Network." *Proceedings of the Royal Society B* 286: 20182007.

Rincón, A., I. F. Alvarez, and J. Pera. 2001. "Inoculation of Containerized *Pinus pinea* L. Seedlings With Seven Ectomycorrhizal Fungi." *Mycorrhiza* 11: 265–271.

Schupp, E. W., P. Jordano, and J. M. Gómez. 2010. "Seed Dispersal Effectiveness Revisited: A Conceptual Review." *New Phytologist* 188: 333–353.

Schupp, E. W., P. Jordano, and J. M. Gómez. 2017. "A General Framework for Effectiveness Concepts in Mutualisms." *Ecology Letters* 20: 577–590.

Sikes, R. S., and the Animal Care and Use Committee of the American Society of Mammalogists. 2016. "2016 Guidelines of the American Society of Mammalogists for the Use of Wild Mammals in Research and Education." *Journal of Mammalogy* 97: 663–688.

Smith, M. M., J. D. Erb, and J. N. Pauli. 2023. "Reciprocated Competition Between Two Forest Carnivores Drives Dietary Specialization." *Journal of Animal Ecology* 92: 1695–1706.

Smith, S. E., and D. J. Read. 1997. *Mycorrhizal Symbiosis*. 2nd ed. Academic Press.

Stephens, R. B., S. D. Frey, A. W. D'Amato, and R. J. Rowe. 2021. "Functional, Temporal and Spatial Complementarity in Mammal-Fungal Spore Networks Enhances Mycorrhizal Dispersal Following Forest Harvesting." *Functional Ecology* 35: 2072–2083.

Stephens, R. B., T. J. Remick, M. J. Ducey, and R. J. Rowe. 2017. "Drivers of Truffle Biomass, Community Composition, and Richness Among Forest Types in the Northeastern US." *Fungal Ecology* 29: 30–41.

Stephens, R. B., and R. J. Rowe. 2020. "The Underappreciated Role of Rodent Generalists in Fungal Spore Dispersal Networks." *Ecology* 101: e02972.

Swihart, R. K., N. A. Slade, and B. J. Bergstrom. 1988. "Relating Body Size to the Rate of Home Range Use in Mammals." *Ecology* 69: 393–399.

Terwilliger, J., and J. Pastor. 1999. "Small Mammals, Ectomycorrhizae, and Conifer Succession in Beaver Meadows." *Oikos* 85: 83–94.

Van Nuland, M. E., C. Qin, P. T. Pellitier, K. Zhu, and K. G. Peay. 2024. "Climate Mismatches With Ectomycorrhizal Fungi Contribute to Migration Lag in North American Tree Range Shifts." *Proceedings of the National Academy of Sciences of the United States of America* 121: e2308811121.

Vanbianchi, C. M., M. A. Murphy, and K. E. Hodges. 2017. "Canada Lynx Use of Burned Areas: Conservation Implications of Changing Fire Regimes." *Ecology and Evolution* 7: 2382–2394.

Vašutová, M., P. Mleczko, A. López-Garc'ia, et al. 2019. "Taxi Drivers: The Role of Animals in Transporting Mycorrhizal Fungi." *Mycorrhiza* 29: 413–434.

Vézina, A. F. 1985. "Empirical Relationships Between Predator and Prey Size Among Terrestrial Vertebrate Predators." *Oecologia* 67: 555–565.

Wotton, D. M., and D. Kelly. 2012. "Do Larger Frugivores Move Seeds Further? Body Size, Seed Dispersal Distance, and a Case Study of a Large, Sedentary Pigeon." *Journal of Biogeography* 39: 1973–1983.

Zhou, Y.-B., C. Newman, W.-T. Xu, et al. 2011. "Biogeographical Variation in the Diet of Holarctic Martens (Genus *Martes*, Mammalia: Carnivora: Mustelidae): Adaptive Foraging in Generalists." *Journal of Biogeography* 38: 137–147.

Zielinski, W. J., N. P. Duncan, E. C. Farmer, R. L. Truex, A. P. Clevenger, and R. H. Barrett. 1999. "Diet of Fishers (*Martes pennanti*) at the Southernmost Extent of Their Range." *Journal of Mammalogy* 80: 961–971.

Zwolak, R. 2018. "How Intraspecific Variation in Seed-Dispersing Animals Matters for Plants." *Biological Reviews* 93: 897–913.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** ele70282-sup-0001-Supinfo.docx.