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Wind and small mammals are complementary fungal dispersers

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Abstract

Following a disturbance, dispersal shapes community composition as well as ecosystem structure and function. For fungi, dispersal is often wind or mammal facilitated, but it is unclear whether these pathways are complementary or redundant in the taxa they disperse and the ecosystem functions they provide. Here, we compare the diversity and morphology of fungi dispersed by wind and three rodent species in recently harvested forests using a combination of microscopy and Illumina sequencing. We demonstrate that fungal communities dispersed by wind and small mammals differ in richness and composition. Most wind-dispersed fungi are wood saprotrophs, litter saprotrophs, and plant pathogens, whereas fungi dispersed in mammal scat are primarily mycorrhizal, soil saprotrophs, and unspecified saprotrophs. We note substantial dispersal of truffles and agaricoid mushrooms by small mammals, and dispersal of agaricoid mushrooms, crusts, and polypores by wind. In addition, we find mammal-dispersed spores are larger than wind-dispersed spores. Our findings suggest that wind- and small-mammal-facilitated dispersal are complementary processes and highlight the role of small mammals in dispersing mycorrhizal fungi, particularly following disturbances such as timber harvest.

KEYWORDS
arbuscular mycorrhizae, dispersal complementarity, ectomycorrhizae, endozoochory, forest disturbance, saprotroph, spore morphology, wind dispersal

INTRODUCTION

Dispersal is a fundamental component of species life history and shapes community composition and ecosystem dynamics (Baguette et al., 2012). Dispersal of sessile species, particularly plants and fungi, is often passive and thus requires transport mechanisms such as wind, water, or animals (Halbwachs & Bässler, 2015; van der Pijl, 1969). Interspecific differences in dispersal mode can have far-reaching effects on community assembly and ecosystem function. This is of particular consequence following disturbance, as dispersal mode may mediate species' resilience to disturbance if propagules differ in their ability to relocate to more favorable conditions. Plants are relatively

well studied in this regard, with substantial literature investigating both pollen and seed dispersal following disturbance (Robledo-Arnuncio et al., 2014). Knowledge of fungal dispersal lags behind, despite the profound impact that fungi have on ecosystem structure and function via ecosystem processes including decomposition, nutrient cycling, host–pathogen interactions, and plant community composition via the establishment of mycorrhizal symbionts (Ostry & Laflamme, 2008; van der Heijden et al., 2008).

Fungi are dispersed by a variety of biotic and abiotic mechanisms. Wind- and animal-facilitated transport are two commonly cited dispersal modes (e.g., Halbwachs & Bässler, 2015), and the degree to which they represent complementary dispersal modes could shape spatiotemporal distributions and have important implications for fungal community assemblage and ecosystem function. Many fungi, particularly those that fruit aboveground (mushrooms), are ostensibly dependent on wind for dispersal. Some taxa have evolved adaptations that enhance spore dispersal into the airstream, such as the ability to generate convection currents that pull spores from beneath the mushroom cap and into the air (Dressaire et al., 2016) or fruitbody structures that forcibly expel spores upward (Halbwachs & Bässler, 2015). Spore dispersal by wind is influenced by a variety of factors such as habitat type and aridity, particularly for larger spores that are most likely to become airborne in loose, dusty soils (Egan et al., 2014). Wind speed also plays a role in dispersal, with intermediate or high wind speeds providing the most effective transport (Norros et al., 2014). Forest canopy structure and complexity (Norros et al., 2014) as well as topography (Amend et al., 2010) also impact dispersal distance. Thus, landscape conditions can have varying effects on distance, speed, and likelihood of wind dispersal for fungal spores. Changes in landscape structure through disturbance, such as timber harvest, may therefore hamper or enhance certain species' ability to disperse by wind.

Animal-facilitated dispersal is common for both mushrooms and truffles (belowground fruiting bodies) (Vašutová et al., 2019). Although some animals facilitate transport when spores attach to their body (e.g., Lilleskov & Bruns, 2005), dispersal via fungivory (the consumption of fungi) is better documented. Many animals consume and disperse fungal spores (directly or by consuming other fungivorous animals), including invertebrates (e.g., Harinikumar & Bagyarai, 1994) and vertebrates such as birds (Caiafa et al., 2021), herptiles (Lilleskov & Bruns, 2005), and mammals (Elliott et al., 2022). In some instances, fungal fruiting bodies such as truffles have evolved to release pungent volatile compounds to attract animal consumers including insects (Johnson & Jürgens, 2010) and small mammals

(Stephens et al., 2020). Because of their ubiquity and high population densities in forests, small mammals may serve as a particularly important spore dispersal pathway in these ecosystems and are known to consume both saprotrophic (Spooner, 2007) as well as arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) fungi (Vašutová et al., 2019). Diverse small mammal communities support the dispersal of a broad range of fungi (Nuske et al., 2017), including mycorrhizal fungi that assist in the establishment of tree seedlings following disturbance (Cázares & Trappe, 1994).

The degree to which wind- and small mammal-facilitated dispersal is redundant or complementary is poorly understood but has important implications for forest establishment and growth. If wind- and small mammal-facilitated dispersal are complementary, this indicates that small mammals play a role in dispersing fungi with limited potential for wind dispersal. Differences may be reflected in physical characteristics, such as spore melanization involved in UV protection (Deveautour et al., 2020), spore ornamentation to assist with lift in the air and/or retention in digestive tracks (Halbwachs & Bässler, 2015), and size that can affect whether spores become airborne (Chaudhary et al. 2020; Norros et al., 2014). Comparisons of dispersal mechanism and physical characteristics might reveal adaptive strategies among various fungal lineages or functional types that can impact the regrowth and composition of a forest.

In this study, we compared fungal communities dispersed by wind and three locally important species of small mammals in recently disturbed and adjacent intact temperate forests. We coupled small mammal field surveys with aerial spore trapping, and integrated microscopy and DNA sequencing to address the following questions: (1) Do wind and small mammals disperse taxonomically and functionally complementary fungal communities into disturbed areas? (2) Do physical differences in fruiting bodies and spores reflect differences in dispersal mechanisms? Fungi are important mediators of forest processes following disturbance (Policeli et al., 2020), and our study will show for one of the first times how taxonomically and functionally divergent fungi disperse following disturbance.

MATERIALS AND METHODS

Study site

Our study occurred in a northern mixed hardwood forest at the Second College Grant, a 10,800 ha property in Coos County, New Hampshire, USA (Appendix S1: Figure S1). Dominant tree species include sugar maple (*Acer saccharum*; AM associated), yellow birch (*Betula*

alleghaniensis; ECM associated), and American beech (*Fagus grandifolia*; ECM associated). Sampling occurred in eight experimental harvest gaps (0.4 ha) and adjacent, undisturbed forests. Cuts were established between August and December 2017 as part of the Adaptive Silviculture for Climate Change network (Nagel et al., 2017). Cuts were created by hand-felling of all but one or two seed trees and saplings. Branches were left as downed woody material. Harvest gaps contained young aspen (*Populus* spp.), red raspberry (*Rubus idaeus*), and pin cherry (*Prunus pensylvanica*), in addition to various grasses (Poaceae) and sedges (Cyperaceae).

Field surveys

Mammal trapping and scat collection

To compare wind- and mammal-dispersed fungal communities, we live-trapped small mammals (rodents and shrews) and installed spore traps in all eight harvest gaps and surrounding forests in August 2019. At each harvest gap, we surveyed small mammals using a trapping web design consisting of eight radially arranged 60 m transects (starting 30 m deep in the cut—close to the center—and extending 30 m into the adjacent forest), each with seven traps spaced 10 m apart for a total of 56 trap stations per site (Appendix S1: Figure S1). Trapping occurred during a 2-week period, with three nights of trapping (168 trap nights) conducted at each site. We captured small mammals using Sherman live traps (H. B. Sherman Company), and animals were uniquely marked (see Stephens et al., 2021b for details). Scat was collected from traps upon capturing an individual for the first time and frozen (−20°C) immediately. Traps that contained animals were replaced with clean traps to prevent cross-contamination of scat.

We focused on eastern chipmunks (*Tamias striatus*), southern red-backed voles (*Myodes gapperi*), and woodland jumping mice (*Napaeozapus insignis*) because of their high local abundance and documented dispersal of fungi in this region (see Stephens et al., 2021b; the present study uses the same study sites and scat samples). Previous work has suggested that *N. insignis* consumes large volumes of AM fungi, whereas *T. striatus* and *M. gapperi* consume substantial amounts of ECM fungi (Stephens et al., 2021b). We also calculated home range estimates for all three species as a proxy for spore dispersal potential (Appendix S1: Section S1). For our comparison of wind- and small mammal-dispersed spore communities, we selected ~20 scat samples per species across all sites (20 *T. striatus*; 19 *M. gapperi*; 20 *N. insignis*, for a total of 59 samples) from August 2019 to coincide with the timing of spore trapping. Variability in mammal population size among sites necessitated slight differences in the number of scat samples sourced per site (mean 7.4 ± 1.4 samples). Although our home range analysis (Appendix S1: Figure S2) demonstrated that individuals from each species used both intact forest and forest gaps (suggesting the exact location of scat collection would not influence fungal community), we sourced scat samples roughly equally from the forest (28) and gaps (31). Samples were freeze dried and homogenized into a powder for molecular and microscopic analyses.

Aerial spore traps

To measure spore deposition by wind, we deployed six spore traps at each of the eight study sites for 2 weeks in August 2019. We selected this period to coincide with the approximate peak fruiting of mushrooms (Borgmann-Winter et al., 2021) and truffles (Stephens et al., 2017) in this region, as well as to capitalize on the occurrence of both early- and late-season fruiters during this period. Spore traps were placed 12 m apart, along a 60 m transect extending 30 m into the harvest gap and 30 m into the forest. Although not dispersed as broadly as our mammal traps, it was expected that these traps would readily collect spores from fruiting fungi across the site, as it is well documented that airborne spores often travel tens to hundreds of meters (Halbwachs & Bässler, 2015). Each trap (modified from Peay et al., 2012) consisted of one funnel (10.2 cm diameter), mouth facing upward, secured with duct tape and sealed with parafilm to a 1 L bottle anchored in the soil (Appendix S1: Figure S3). Each bottle contained 200 mL of 95% ethanol as a preservative. Pilot trials indicated that little evaporation occurred after 2 weeks in full sun. Tops of funnels were located ~15 cm above the soil surface. The base of each funnel contained a piece of 125 μm screen to prevent large particles and insects from entering the traps. Although a limited number of AM spores exceed 125 μm (Vašutová et al., 2019), wind-dispersed AM spores typically do not (Chaudhary et al., 2020). Traps collected spores passively via wind-driven deposition or rain events. One trap was damaged and excluded from analysis, but the remaining traps ($n = 47$) were collected at the end of the 2-week sampling period by rinsing funnels with distilled water and securing bottle lids for transport. Spores were strained onto 0.45-μm filter paper using vacuum filtration and frozen at −20°C. Each piece of filter paper was cut in half; one half was used for molecular analyses and the other half for microscopy.

Microscopic analysis

Spore occurrence

Scat samples were prepared for microscopy following procedures outlined in Stephens et al. (2021b). Spore isolates were spread onto a 22×22 mm section of a glass slide, cleared with Visikol (Phytosys LLC, New Brunswick, New Jersey, USA), stained with iodine, and sealed with Flo-Texx Mounting Medium (Avantor, Radnor, Pennsylvania, USA).

Spore trap samples were prepared for microscopy by scraping the spore-bearing side of the filter paper into a vial with 500 µl of 95% ethanol and vortexed to homogenize. Initial trials indicated this method dislodged nearly all spores. Samples were then centrifuged and 450 µl of supernatant was decanted. Samples were vortexed again to resuspend spore material in the remaining 50 µl. The spore-bearing solution was then spread onto a 12×12 mm section of a glass slide, cleared with Visikol, stained with iodine, and sealed with Flo-Texx Mounting Medium.

We examined spore composition on each slide using 25 nonoverlapping fields of view at ×400 magnification (1% of the slide; combined area of 4.15 mm^2) for scat samples, and 20 nonoverlapping fields of view at ×400 (2% of the slide; combined area of 3.32 mm^2) for spore traps. Spores were assigned to morphotypes based on size, ornamentation, and coloration. Within each field of view, we counted the number of each morphotype present. To detect taxa with large spores (typically AM spores), we scanned each slide at ×100 magnification. For scat samples, we scanned 121 mm^2 (25%) of the slide. For spore trap samples, we scanned the entire slide due to the extremely low density of spores. Spores were identified to genus or species when possible, using such references as Castellano (1989), Kuo (2021) and reference spores from sporocarps collected in the field (Castellano & Stephens, 2017; Stephens et al., 2017), but in some cases (particularly in spore traps and for nonmycorrhizal species) taxonomy was not determined.

Spore trait data collection

We scored all spore morphotypes for three traits: greatest length (or diameter for round spores), ornamentation, and degree of melanization. The greatest length was measured using AMScope software (AMScope, Irvine, California, USA). Ornamentation was assessed on a presence–absence basis with ornamentation type noted, and melanization was characterized using a 1–5 rank, with 1 representing nonmelanized, hyaline spores, and 5 representing heavily melanized, dark brown spores. We tested for differences in these physical characteristics between wind-dispersed spores and mammal-dispersed spores.

Molecular analysis

Samples for DNA extraction were isolated from spore trap filter papers and scat samples (10 mg). We extracted DNA from all samples (scat and spore trap) using the DNeasy Powersoil Kit (Qiagen, Hilden, Germany) according to a standard protocol. We ran polymerase chain reactions (PCR) in duplicate alongside negative controls to amplify fungal DNA in the ITS2 region. Primers contained Illumina TruSeq adapter sequences, an 8-bp pad sequence, and a 2-bp linker sequence. For forward primers, we used a 1:1 ratio of fITS7 (Ihrmark et al., 2012) for general fungal amplification and ITS7o (Kohout et al., 2014) for slightly enhanced AM amplification (Lekberg et al., 2018). We used ITS4 (White et al., 1990) as a reverse primer. In addition to these primers, reactions used Phusion High Fidelity polymerase, a 49°C annealing temperature, and 35 PCR cycles, as developed by Kohout et al. (2014). Although these primers are somewhat biased against AM fungi, they capture similar patterns in AM fungal community structure as Glomeromycotina-specific primers while simultaneously allowing analysis across the fungal kingdom (Lekberg et al., 2018), which was the aim of the present study. Libraries were sequenced on a NovaSeq 6000 platform (Illumina, San Diego, California, USA) using 2×250 bp chemistry at the Hubbard Center for Genome Studies at the University of New Hampshire.

Bioinformatics

We first extracted the ITS2 region using ITSxpress in QIIME2 to remove chimeras and secondary structures, and to accurately align sequences (Bolyen et al., 2019). ITS-extracted sequences were processed using a modified DADA2 (v1.8) pipeline (Callahan et al., 2016). Next, we truncated reads at the first instance of Phred score <2, removed low-quality sequences with >2 expected errors, removed short sequences (<100 bp), merged forward and reverse reads, computed amplicon sequence variants (ASVs), and removed chimeras. Taxonomy was assigned by comparing sequences with the UNITE database (dynamic release 10.05.2021, Nilsson et al., 2019). ASVs were also assigned to functional type (e.g., ectomycorrhizal, AM) and fruitbody type (e.g., gasteroid) based on the FungalTraits database (Põlme et al., 2020).

Statistical analysis

Community analyses

We compared taxonomic richness (using ASVs) between scat (all mammals combined) and spore trap samples for all fungi, macrofungi only, AM fungi, and ECM fungi using two-sampled *t*-tests. Comparisons of richness were run on data rarefied to 1000 reads per sample. We also compared fungal functional types dispersed by wind, *M. gapperi*, *N. insignis*, and *T. striatus*. This comparison was conducted separately for each disperser type by comparing the mean overall proportion of reads that belonged to each of eight major functional types, including AM (Glomeromycota), ECM, litter saprotroph, mycoparasite, plant pathogen, soil saprotroph, unspecified saprotroph, and wood saprotroph. For macrofungi only, we calculated the proportion of reads in every sample that belonged to each of eight common fruitbody types: agaricoid (mushroom; inclusive of a wide variety of fruiting styles beyond typical "stalk and cap"), clavarioid (coral), corticioid (crust), gasteroid (puffball), gasteroid hypogeous (truffle), polyporoid (conk), tremelloid (jelly), and AM fungi (Glomeromycota). AM fungi were included as a category because many produce small fruiting structures that are consumed and dispersed by small mammals (e.g., Stephens et al., 2021b). We tested for differences in functional and fruiting types within each disperser category using linear mixed effects models ("lme" in the *nlme* package; Pineiro & Bates, 2023) including site and forest condition (harvest gap or intact forest) as random effects. All proportional data were arcsine transformed. Pairwise comparisons were conducted using the *emmeans* package (Lenth, 2021).

To evaluate the similarity between macrofungal communities dispersed by wind and each mammal species, we used a Bray–Curtis dissimilarity matrix based on ASVs and the reads for each scat and spore trap sample. This matrix was based on data rarefied to 500 reads and seven samples with <500 reads were removed (four from mammals and three from spore traps). To visualize trends in compositional structure between community types we used nonmetric multidimensional scaling (NMDS) in the R package *vegan* (Oksanen et al., 2019). To compare relative taxonomic community concordance (dispersion about the median) between mammal-dispersed and wind-dispersed samples, we used the "betadisper" function in *vegan*. To quantify the impact of the dispersal mechanism (wind versus scat) on community composition, we used a permutation-based analysis of variance (PERMANOVA), using 1000 randomized datasets with site as a stratum and forest condition as a covariate. To compare wind-dispersed fungal communities between cleared and intact forest, we used PERMANOVA with site as a stratum. To compare dispersed fungal communities among small mammal species, we used PERMANOVA with site as a stratum and forest condition as a covariate, as well as pairwise PERMANOVA (Arbizu et al., 2021) with a Bonferroni correction as a post hoc test. All permutation-based analyses were performed on ASV sequence proportions converted to Bray–Curtis dissimilarities.

Morphological comparisons

We compared three traits (melanization, length, and ornamentation) between spore morphotypes present in mammal scat and spore traps. To compare the degree of melanization, we used the Cochran–Armitage trend test, a test designed for comparisons of categorical and ordinal variables, in the R package *CATT* (Du & Hao, 2017). To compare spore length, we used a two-sample *t*-test. To compare the presence or absence of ornamentation, we used a χ^2 test of independence. We describe differences in ornamentation types (e.g., spikes, tapered attachments, bumps) between dispersal mechanisms, but due to small sample sizes, no statistical comparisons were made. Comparisons of melanization, ornamentation, and length between mammal scat and spore traps were also conducted specifically for AM morphotypes using the same analyses as described above. We did not conduct separate tests for ECM morphotypes due to an insufficient number of identified wind-dispersed ECM morphotypes. All statistical analyses were conducted in R version 3.6.3 (R Core Team, 2021).

RESULTS

Fungal identification and community analysis

Sequencing revealed 9679 unique ASVs (including 1573 described species) in spore traps and 7896 unique fungal ASVs (including 1222 described species) in mammal scat. Approximately 16% of all ASVs occurred in both mammal scat and spore traps. ASVs from spore traps represented 405 known families belonging to 147 known orders, and ASVs from mammal scat represented 374 known fungal families belonging to 139 known orders. Approximately 29% of ASVs were unidentified at the family level. Most ASVs were present in only a single sample (Appendix S1: Figure S4) for both spore traps (65%) and scat (80%). Spore trap samples were approximately one and a half times more ASV rich than scat samples ($t_{86.619} = 4.782$, $p < 0.0001$; Figure 1; Appendix S1: Table S1).

Approximately 21% of ASVs belonged to macrofungi (such as mushrooms, truffles, and polypores) and the remaining 79% belonged to fungi that produce microscopic or no known fruiting structures. When looking specifically at macrofungi, spore traps were more than twice as rich as scat samples ($t_{85.017} = 6.381$, $p < 0.0001$;
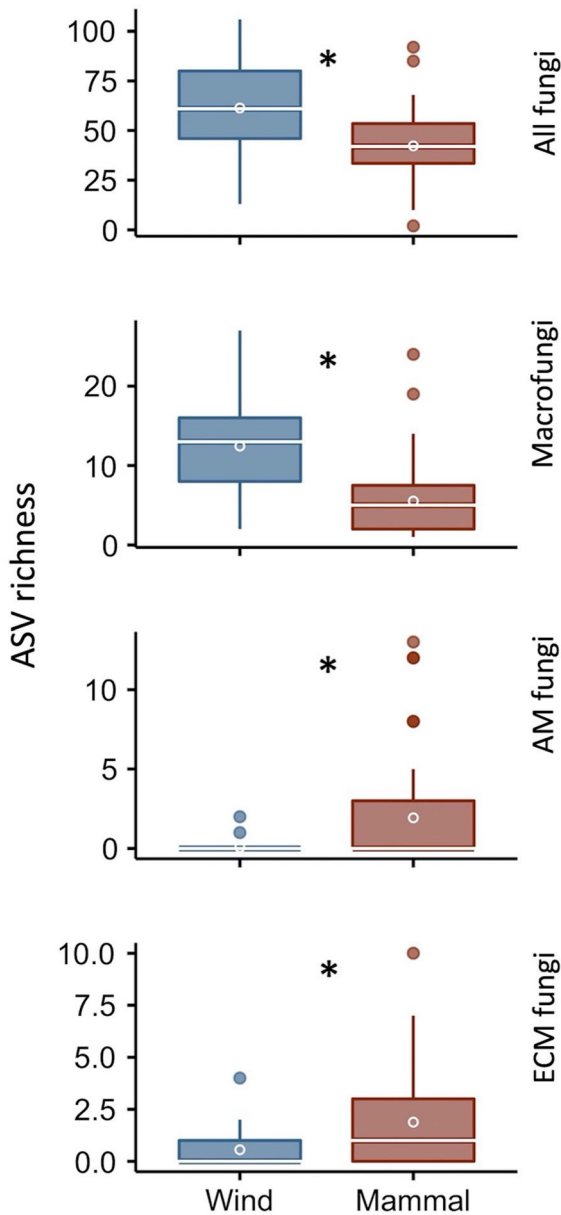
Figure 1). ECM taxa represented 3.2% of all ASVs detected, and AM taxa represented 1.7% of ASVs. Scat samples were roughly three times richer than spore traps for ECM taxa ($t_{79.788} = 4.375$, $p < 0.0001$) and nearly
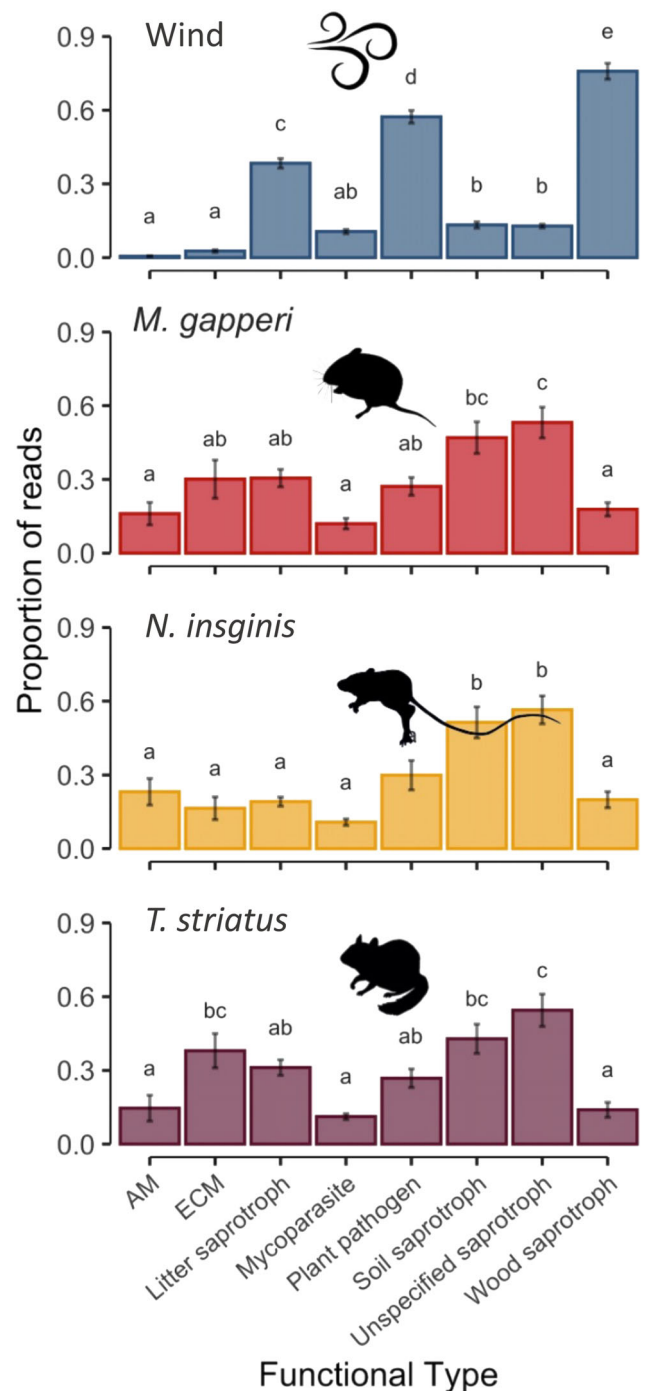

FIGURE 1 Comparison of taxonomic richness (based on amplicon sequence variants [ASVs]) of all fungi, macrofungi, arbuscular mycorrhizal fungi (AM), and ectomycorrhizal fungi (ECM) between spore traps and small mammal scat. Richness calculations are based on sample data rarefied to 1000 reads. All differences are statistically significant (Appendix S1: Table S1). Boxplots show 25th, 50th (median; white bar), and 75th percentiles. Whiskers represent the lowest and highest value within the 1.5 interquartile range. White circles denote mean values.

FIGURE 2 Proportion of reads per sample (mean ± standard error) for several common fungal functional types. Proportions were based on all present fungal amplicon sequence variants [ASVs] with known functional types. Within a panel, functional types with different letters are significantly different (Appendix S1: Tables S2–S6). [Correction added on 17 May 2023, after first online publication: Figure 2 has been replaced in this version to include panel labels.]

30 times richer for AM taxa ($t_{58.423} = 4.482$, $p < 0.0001$; Figure 1).

Spore traps and scat samples also contained complementary communities of fungi when compared by proportions of reads per functional type. Spore traps contained high proportions of litter saprotrophs, plant pathogens, and wood saprotrophs compared with other functional types and contained particularly low proportions of AM and ECM fungi (Figure 2, Appendix S1: Tables S2–S6). Although mycorrhizal taxa represented only a small proportion of reads in spore traps, a select few mycorrhizal genera occurred frequently in spore traps, including *Tomentella*, *Inocybe*, and *Ramaria* (Appendix S1: Table S7). In contrast, mammal scat samples contained comparatively high proportions of ECM and AM fungi as well as unspecified and soil saprotrophs (Figure 2). Commonly occurring mycorrhizal genera in mammal scat included *Russula*, *Cenococcum*, *Cortinarius*, *Elaphomyces*, and *Melanogaster* (Appendix S1: Table S8).

Macrofungal communities in spore traps and mammal scat were distinct (PERMANOVA: $F = 15.41_{(1,102)}$, $p = 0.001$; Appendix S1: Table S9). Mammal-dispersed communities were more variable than wind-dispersed communities, with a 30% greater dispersion about the median, a measure of beta diversity (Betadisper; $F = 162.05_{(1,103)}$, $p = 0.001$; Figure 3). Among spore trap samples, macrofungal communities differed between harvest gaps and intact forest (PERMANOVA; $F = 6.24_{(1,45)}$, $p = 0.001$; Appendix S1: Table S10). Among scat samples, spore communities did not differ between harvest gaps and forests (Appendix S1: Table S11). However, mammal-dispersed spore communities differed between *N. insignis* and both *M. gapperi* (pairwise PERMANOVA; $F = 1.69_{(1,37)}$, $p_{adj.} = 0.003$) and

T. striatus (pairwise PERMANOVA; $F = 1.39_{(1,38)}$, $p_{adj.} = 0.036$). Fungal communities did not differ between *T. striatus* and *M. gapperi* scat samples.

Complementarity was also observed when comparing macrofungal fruiting styles in spore traps and scat
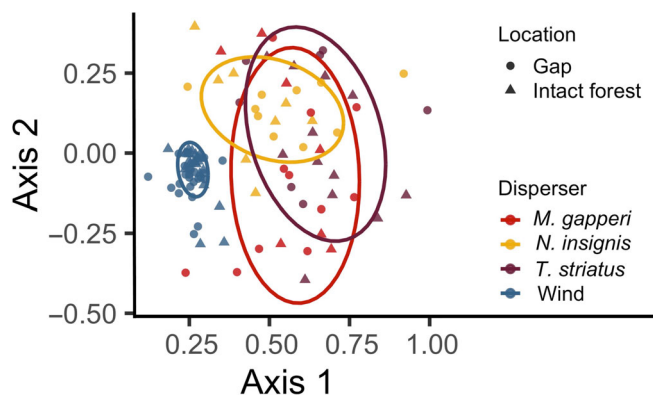

FIGURE 4 Proportion of reads per sample (mean ± standard error) as they relate to all detected macrofungal fruiting body types. Proportions were based on all present macrofungal amplicon sequence variants (ASVs). Within a panel, fruiting body types with different letters are significantly different (Appendix S1: Tables S12–S16).

FIGURE 3 Nonmetric multidimensional scaling (NMDS) ordination of macrofungal spore communities in spore traps and scat samples (final stress = 0.10). Ellipses represent 90% CIs around the centroid, and ellipse size approximates relative community concordance. Ordination was conducted on community data rarefied to 500 reads.
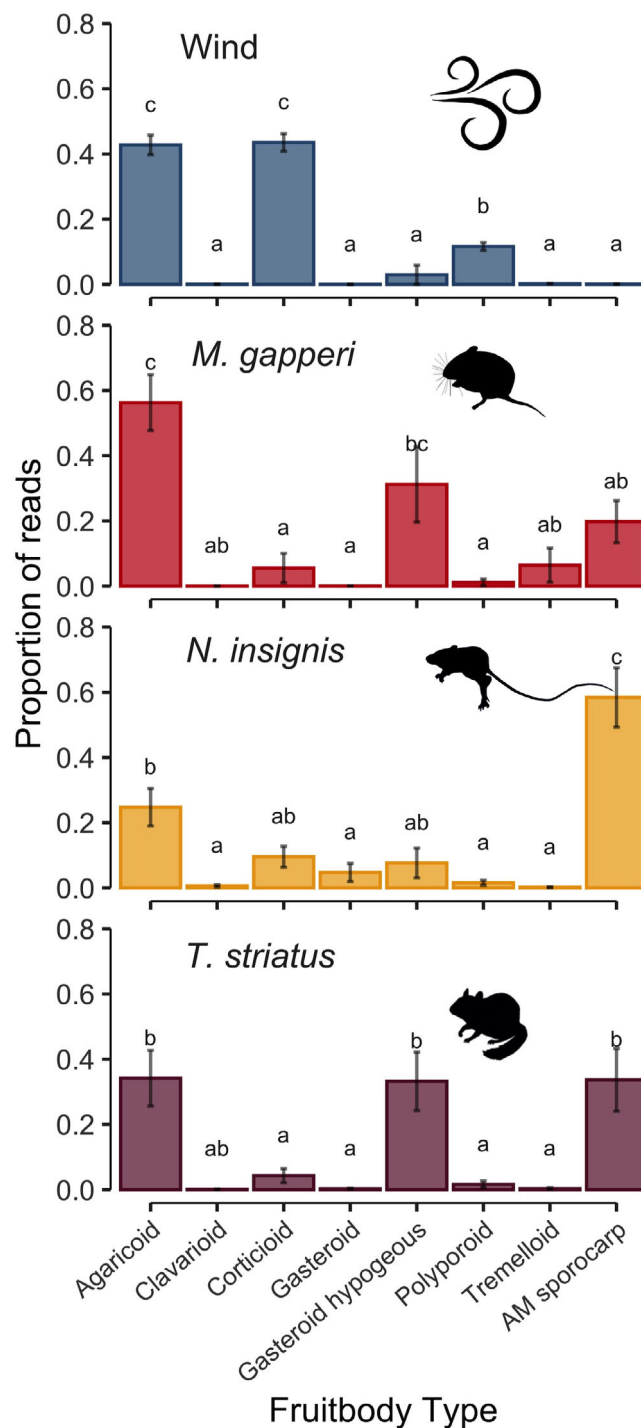
samples (Figure 4; Appendix S1: Tables S12–S16). Spore traps contained high proportions of taxa that produce agaricoid, corticioid, and polyporoid sporocarps. Scat samples contained high proportions of agaricoid, hypogeous gasteroid, and AM taxa.

Spore Morphotype occurrence and morphology

We identified 25 distinct spore morphotypes in mammal scat, 30 distinct morphotypes in spore traps, and two morphotypes present in both scat and spore traps. Most spore morphotypes occurred infrequently, mirroring results in the molecular dataset. Among wind-dispersed morphotypes, 67% (20 of 30) occurred in fewer than half of all samples. In mammal scat, 96% of all morphotypes (24 of 25) occurred in fewer than half of the individuals. Among the 13 morphotypes assigned to AM fungi, six were detected in spore traps and seven in scat. Among the 18 morphotypes of ECM fungi, 15 were detected in scat only, two were detected in spore traps only, and a single morphotype was detected in both.

Spore morphotypes exhibited a range of physical characteristics, including ornamentation types (such as spikes, wings, ridges, and bumps), melanization levels (from entirely unmelanized to highly melanized), and lengths (3.6–121.3 μm). Across all spores, we detected no difference in presence of ornamentation or degree of melanization between wind- and mammal-dispersed spores. Indeed, mean ($\pm$SE) melanization scores (from 1 to 5) were almost identical for spores dispersed by wind (2.83 $\pm$ 0.21) and small mammals (2.93 $\pm$ 0.24). Spores present in mammal scat were on average greater in length than spores present in spore traps (37.70 $\pm$ 6.60 μm versus 18.17 $\pm$ 3.25 μm; $t_{53} = 2.65$, $p = 0.0118$; Appendix S1: Figure S5). We noted a bimodal size distribution among spores dispersed via both mechanisms, with larger spores typically belonging to AM species, and smaller spores belonging to both AM and ECM as well as nonmycorrhizal species. There was no difference in ornamentation rate or degree of melanization between AM spores found in scat and those found in spore traps. Mammal-dispersed AM spores were nearly twice the length of wind-dispersed AM spores (82.74 $\pm$ 7.98 μm vs. 48.71 $\pm$ 11.64 μm; $t_{10} = 2.50$, $p = 0.0312$).

Although we did not detect a difference in the presence of ornamentation between wind-dispersed and mammal-dispersed spore morphotypes, we did identify some interesting patterns when looking at ornamentation types (e.g., spikes, bumps, ridges, tapered attachments). For instance, unornamented morphotypes comprised 50% of wind-dispersed spores but only 25% of mammal-dispersed morphotypes. Among wind-dispersed morphotypes, 35% exhibited some degree of spikiness, and all other ornamentation types were relatively uncommon. No one ornamentation type was dominant among mammal-dispersed morphotypes.

DISCUSSION

Our work is among the first to directly compare spore dispersal mechanisms using both genetic analyses and spore microscopy. Our findings indicate that mammal-driven dispersal is complementary to wind-driven dispersal, suggesting that both dispersal modes play important and distinct roles in ecosystem function. Complementarity was evident when comparing fungal community diversity in addition to functional and fruiting body types. Results from spore microscopy indicate that for some fungi, differences in dispersal strategy may be linked to differences in spore size. Overall, our results highlight the potential for small mammals to transport fungi within forest systems, including into disturbed areas undergoing regeneration.

Fungal community

We found differences in fungal ASVs, functional types, and fruiting types between wind- and mammal-dispersed communities. Taxonomic differences were evident not only in distinct ordination clustering and significant PERMANOVA results, but also based on the minimal overlap of ASVs (16%) and spore morphotypes (two out of 57) between dispersal modes. These findings underscore the unique value of small mammals as fungal spore dispersers and add to a growing literature documenting their importance for both ECM (e.g., Jacobs & Luoma, 2007; Nuske et al., 2017; Stephens et al., 2020) and AM taxa (e.g., Fracchia et al., 2011; Mangan & Adler, 2000).

We found that fungal functional types dispersed by wind and small mammals are complementary. Litter saprotrophs, plant pathogens, and wood saprotrophs dominated spore traps, whereas unspecified saprotrophs (perhaps gut fungi), soil saprotrophs, and mycorrhizal taxa were most abundant in scat samples. Despite substantially greater overall taxonomic richness in spore traps, scat samples were significantly richer for both AM and ECM taxa. These findings suggest an outsized mammalian role in mycorrhizal spore dispersal. Variation in the dispersal of functional types was also evident among mammal species, with AM fungi occurring in high abundance in *N. insignis* scat, and prolific ECM in *M. gapperi* and *T striatus* scat.

We also found that wind and small mammals disperse spores belonging to macrofungi with different fruiting body

types. Spore traps contained higher proportions of reads from fungi with agaricoid (including boletoid), corticioid, and polyporoid fruiting styles. In contrast, mammal scat contained higher proportions of gasteroid hypogeous taxa and AM fungi (particularly for *N. insignis*), likely to be attributable to the release of attractive volatile organic compounds (Stephens et al., 2020; Vašutová et al., 2019). The additional presence of considerable agaricoid material in scat supports previous findings (e.g., Stephens & Rowe, 2020) that small mammal consumption and potential dispersal of mushroom-forming taxa is substantial.

Sequencing unsurprisingly detected dramatically more taxa than morphotyping, but both approaches showed a low overlap in fungal communities dispersed by wind and mammals. It is also important to acknowledge that fungal DNA in our samples was not solely derived from mature spores (Chaudhary et al., 2020). Underdeveloped spores, colonized root tips, and hyphal chunks were likely to be present in scat and spore trap samples. The extent to which this fungal material facilitates dispersal is understudied, but recent literature suggests that hyphal chunks and mycelial spread effectively colonize new substrates (Bueno & Moora, 2019).

Spore morphology

Spore size generally relates to dispersal strategy for a variety of fungal taxa and functional types (e.g., Halbwachs & Bässler, 2015), and small spores are reported to travel farther via wind dispersal than larger spores (Dighton & White, 2017; Norros et al., 2014). Mammal-dispersed spores were twice as long as wind-dispersed spores (Appendix S1: Figure S5), with an average length of $37.70 \pm 6.60 \,\mu m$ compared with $18.17 \pm 3.25 \,\mu m$ for wind-dispersed spores. This pattern was likely to have been driven by the larger size of AM fungal spores detected in the scat ($82.74 \pm 7.98 \,\mu m$ vs. $48.71 \pm 11.64 \,\mu m$). Chaudhary et al. (2020) observed a similar pattern in wind-dispersed AM spores in an urban setting, reporting that most were $<70 \,\mu m$ in diameter, even though many known AM spores are much larger. The similarity of our findings suggests that large AM spore size may inhibit wind dispersal, with larger spores dispersing via other means, such as fungivory. Our use of a 125-μm filter during the preparation of both scat and spore trap samples precluded large spore morphotypes from our samples; however, the lack of any spores $>75 \,\mu m$ in our spore traps suggests that our filter design did not substantially alter results.

We found no differences in melanization between wind- and mammal-dispersed spores. Other studies have found melanization to be a poor predictor of dispersal strategy (windborne vs. nonwindborne) or life history types (saprotroph vs. ectomycorrhizal) (Chaudhary et al. 2020; Halbwachs et al., 2015). Although melanin can protect spores from prolonged exposure to ultraviolet radiation expected in airborne dispersal (Singaravelan et al., 2008), it can also protect spores from harsh conditions in mammalian digestive tracts (Dighton & White, 2017).

Previous studies have suggested that the presence and type of spore ornamentation in fungi may reflect a variety of dispersal strategies including both wind dispersal and fungivory (Halbwachs et al., 2015; Pringle et al., 2015). Although we noted a lower rate of ornamentation in wind-dispersed morphotypes, this analysis was underpowered and the difference was not statistically significant. Further work with greater sampling effort is needed to assess whether ornamentation is lower in wind- versus mammal-dispersed spores and/or if certain ornamentation types are beneficial for multiple dispersal pathways.

Dispersal potential

Our data suggest differences in dispersal potential for wind and small mammals. We found distinct wind-dispersed macrofungal spore communities between harvest gaps and adjacent intact forests. Although we did not directly measure wind dispersal distances, this community discordance suggests that spore dispersal may be distance limited for many taxa at the scale of tens of meters, and that wind-driven spore dispersal into disturbed areas may only be effective for some forest macrofungi. Our data are consistent with findings from diverse habitat types including scrublands (Peay et al., 2010), boreal forests (Norros et al., 2012), and coastal dunes (Galante et al., 2011), all of which demonstrated that, for some species, the probability of spore dispersal by wind declines over a scale of tens to hundreds of meters from the fruiting body.

Spore dispersal via small mammals is limited by movement ability. Reported rodent home range sizes are similar to our findings (0.36–2.29 ha; see Appendix S1: Figure S6), suggesting that dispersal by small mammals may on occasion be up to 200 m. Because all target species were frequently captured in both the forest and the harvest gaps, small mammals may play a role in returning forest fungi (particularly AM/ECM taxa), to disturbed areas. This conclusion is bolstered by our finding that macrofungal spore communities did not differ between scat samples collected in forests and harvest gaps, even though previous work from this site indicated that the macrofungal fruiting community itself did differ (Borgmann-Winter et al., 2021).

In addition to dispersal distance, it is important to consider the concentration of spores dispersed by wind

and small mammals because individual spores rarely germinate and colonize a new substrate. For ECM taxa, high (>50%) rates of seedling colonization require hundreds to thousands of spores (Peay et al., 2012), a pattern true for at least some nonmycorrhizal taxa as well (Nix-Stohr et al., 2008). Indeed, for hymenomycetes (including agaricoid, polyporoid, and tremelloid fungi), roughly one in one billion spores may become established (Burnett, 2003). Although it would not be meaningful to make direct statistical comparisons of spore concentrations between wind and mammals using our data, spore density estimates may provide the context for the relative importance of these two dispersal pathways for different fungal species. For instance, we noted that the mean density values for *Glomus* (AM) spores appeared more skewed toward mammal dispersal (1210–6500 spores/fecal pellet vs. <900 spores/m^2/day in spore traps) than bolete (ECM) dispersal did (8–7350 spores/fecal pellet vs. 7900 spores/m^2/day). Overall, spore traps collected hundreds of thousands of spores/m^2/day. Spore densities in scat varied substantially by species, with individual *N. insignis* pellets containing tens of thousands of spores, *M. gapperi* containing hundreds of thousands of spores, and *T. striatus* containing more than 1 million spores per pellet (Appendix S1: Table S17). The high concentration of spores in fecal pellets highlights the potential of scat as a dispersal pathway, particularly given the fact that that small mammals produce tens to hundreds of fecal pellets per day. Such concentrated spore loads are likely to be deposited in sheltered locations as mammals navigate the landscape, and may promote successful mycorrhizal colonization of tree seedlings (Stephens et al., 2021b).

Although our work does not demonstrate the viability of spores dispersed by small mammals, numerous studies have documented the survival of dispersed macrofungal spores (particularly mycorrhizal taxa) through gut passage, including many of the most commonly occurring genera in our scat samples (*Russula*, *Melanogaster*, *Elaphomyces*, *Glomus*, and *Tomentella*) (Elliott et al., 2022). In some cases, gut passage has been even reported to enhance spore viability. Therefore, it is likely that many fungal taxa in small mammal scat, particularly those with the highest spore density, are indeed dispersed as viable spores and contribute to the spore bank.

CONCLUSIONS

Our study suggests that wind- and small mammal-facilitated spore dispersal are complementary processes. Substantial taxonomic and functional differences in fungal communities dispersed by each mechanism underscore the important and distinct role that each mode plays in fungal dispersal and subsequently ecosystem function. Our results also indicate that small mammals play an important role as spore dispersers for both AM and ECM taxa. Overall, we found that small mammals are likely to play an important role in dispersing forest-associated fungi into a recently disturbed forest, thereby assisting in the regeneration of canopy species.

CONFLICT OF INTEREST STATEMENT
The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT
Microscopy data from fecal pellets (Stephens et al., 2021a) are available in Dryad at https://doi.org/10.5061/dryad.q83bk3jhz. All other data (Borgmann-Winter et al., 2023) are available in Figshare at https://doi.org/10.6084/m9.figshare.21201950.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.