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Functional, temporal and spatial complementarity in mammal-fungal spore networks enhances mycorrhizal dispersal following forest harvesting

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Abstract

1. Animals that disperse plant or fungal propagules following forest disturbances, including timber harvests, play an important role during forest regeneration by dispersing seeds or spores from intact communities to disturbed sites. Determining how complementary or redundant animal species are as dispersers of propagules is key to understanding the stability of dispersal dynamics and informing management practices.
2. Here we examine the functional, temporal and spatial components of mycorrhizal fungal spore dispersal by small mammals (rodents and shrews) following timber harvest. We tracked the interactions of seven mammal species and 34 fungal taxa composed of two mycorrhizal functional types, arbuscular mycorrhizae (AM) and ectomycorrhizae (ECM), in 11 patch cuts (0.4 ha) distributed across hardwood and mixedwood forest in the north-eastern United States. Over a 2-year period directly following harvests, we measured the relative contribution of mammal species to spore dispersal using networks that integrated mammal abundance with spore loads in scat. We also measured species-specific microhabitat associations.
3. Mammals were complementary in their dispersal of AM and ECM fungal spores. However, within AM dispersal networks, mammals were redundant, with asynchrony in mammal population fluctuations among years leading to changes in the relative importance of mammal species. Comparatively, ECM fungal spore consumption and dispersal was primarily provided by one rodent species (*Myodes gapperi*), resulting in dispersal networks that were highly specialized. This indicates that AM spore dispersal is more robust to changes in mammal community turnover compared to ECM spore dispersal.
4. Mammal species varied from having no microhabitat associations to associating with a variety of different forest structure and ground cover conditions, indicating that species play different roles from broadcasting spores widely to depositing spores in discrete locations. By preserving microhabitat characteristics that are associated with small mammals in harvested areas, particularly downed wood and patches of pre-harvest vegetation, forest managers can help maintain dispersal of mycorrhizal fungi.

KEYWORDS
functional complementarity, fungal dispersal, mutualistic network, species interactions, timber harvest

1 | INTRODUCTION

The dispersal of plant seeds and fungal spores is a vital process that influences the structure and composition of communities during forest regeneration (Boeraeve et al., 2018; Tabarelli & Peres, 2002). In many systems, animals provide critical directional dispersal of propagules from intact forest to disturbed areas, and the composition of animal communities can shape the biodiversity of the regenerating community (Carlo & Morales, 2016; Wunderle, 1997). For example, in seed dispersal networks, animal species are often complementary in the ecosystem functions they provide—playing different roles depending on the types of seeds they eat or the locations at which they are deposited (García-Cervigón et al., 2018; Morán-López et al., 2020). Determining the mechanisms that underlie how complementary or redundant species are within dispersal networks is key to understanding how stable dispersal dynamics are and how to maintain these interactions in managed systems (Schleuning et al., 2015).

In forested systems, mammals are important dispersers of mycorrhizal fungi (Schickmann et al., 2012; Stephens & Rowe, 2020), although the factors that shape a species importance within mammal-fungal networks and how stable interactions are in recently cleared areas have been little explored. Mycorrhizal fungi are mutualists that colonize roots and allow plants to access water and soil nutrients in exchange for sugars derived from photosynthesis (Smith & Read, 1997). In temperate forests, nearly all tree species form a symbiotic relationship with either arbuscular mycorrhizal (AM) or ectomycorrhizal (ECM) fungi, and the community composition of these fungal associates can affect the diversity and community dynamics of plants and influence ecosystem functioning (Van Der Heijden et al., 2008). For some tree species, colonization by mycorrhizal fungi directly following establishment can be more important for growth than competition with herbaceous vegetation, and maintaining diverse mycorrhizal communities can increase seedling productivity (Jonsson et al., 2001; Peay, 2018). Following timber harvests, however, mycorrhizal fungal diversity is reduced as host trees die, resulting in precipitous declines in mycorrhizal colonization rates of regenerating seedlings away from the forest edge (Dickie & Reich, 2005; Jones et al., 2003).

Mammals that consume above-ground (mushrooms) and below-ground (truffles) fruiting bodies of mycorrhizal fungi can disperse spores which subsequently colonize plant roots (Caldwell et al., 2005; Trappe & Maser, 1976). Mammal-dispersed fungi are often among the first taxa to colonize trees growing away from the forest edge (Cázares & Trappe, 1994), suggesting that mammals play an important role in forest regeneration by directionally dispersing spores into cleared areas. As such, understanding how functionally, temporally and spatially complementary or redundant mammal species are in terms of fungal spore dispersal is important for informing forest management strategies that maintain this ecosystem function.

During tree seedling establishment, successful mycorrhizal colonization from dispersal depends on the presence of spores from the correct mycorrhizal associate (AM or ECM) and the spores being abundant enough to colonize roots (Peay et al., 2012). Additionally, although some tree species are able to establish in open areas, many require microsites where downed woody material or vegetative cover provide shade or protection (Gray & Spies, 1997), making spore dispersal to these microsites particularly important. Thus, for effective spore dispersal by mammals to occur, they must disperse fungal spores of the correct functional type, in sufficient quantities, and to appropriate microsite locations. Small mammals (rodents and shrews) are important dispersers of mycorrhizal fungal spores, particularly for truffle taxa (Maser et al., 1978). Although small mammals that eat fungi as their main food source are often considered the most important dispersers of spores, species that consume relatively small amounts of fungi can be important when their populations are high (Stephens & Rowe, 2020). Because small mammal species frequently have large year-to-year population fluctuations (Krebs & Myers, 1974), the role of species in dispersing fungi may be temporally variable. The stability of spore dispersal will be tied to how redundant species are in terms of the type of fungi they eat and the asynchrony of their population dynamics. The ability of an animal species to effectively disperse propagules at quality sites is tied to its microhabitat associations, with generalist species broadcasting propagules widely and those with strong associations providing dispersal to specific microsites (García-Cervigón et al., 2018; Schleuning et al., 2015).

To examine the functional, temporal and spatial components of spore dispersal by small mammals in regenerating forest, we measured small mammal-fungal interactions over a 2-year period directly following patch cut harvests in northern New Hampshire, USA. The region is actively managed for timber production and has a diverse small mammal community with species that commonly consume fungi (Jevon et al., 2019; Stephens, Hocking, et al., 2017; Stephens & Rowe, 2020). We integrated AM and ECM spore loads in scat with mammal abundance to build mammal-fungal networks for both years of the study and among three forest types. We assessed microhabitat affinities of mammal species to further determine locations that spores are deposited. From these data, we address the following questions: (a) How do fungal consumption and population fluctuations affect the complementarity and redundancy of small mammal species in the dispersal of AM and ECM fungi, and are species roles stable among years and forest types?; and (b) do small mammal species broadcast spores widely or are their activities associated with specific microhabitat locations? We predicted that both small mammals that consume large amounts of spores and those that are abundant would be important dispersers (Stephens & Rowe, 2020). We also predicted that some mammal species would associate with microhabitats that are essential for seedling recruitment, making them particularly important to forest regeneration (Morán-López et al., 2020).

2 | MATERIALS AND METHODS

2.1 | Study system

We conducted our study at the Dartmouth College Second College Grant in northern New Hampshire, USA, which has been actively managed for timber since 1808 (Jevon et al., 2019). Early timber harvests largely targeting softwood tree species, leading to stands that were historically mixedwoods to become dominated by hardwood species, although current management strategies focus on maintaining a range of compositional conditions (Jevon et al., 2019). Our sampling took place in 11 patch cuts (0.4 ha), eight of which were in northern hardwood forest as part of replicated, operational-scale treatments installed through the Adaptive Silviculture for Climate Change network (Nagel et al., 2017). Four of these treatments were located on sites with enriched soils (Alder Brook) with another four located on sites with unenriched soils that historically supporting mixedwood conditions (Merrill Brook; Figure 1a). In addition, three replicates were established in nearby mixedwood forests (Figure 1a). All patch cuts were harvested between August and December 2017. With the exception of one or two large-diameter seed trees and non-merchantable saplings, all trees were removed from the patch cuts with tops and branches left as downed woody material. The forest surrounding the patch cuts also received light thinning (see Appendix S1 in Supporting Information for details on thinning and understorey regeneration).

Although both the northern hardwood sites were dominated by sugar maple (*Acer saccharum*—AM associated) with a lesser component of American beech (*Fagus grandifolia*—ECM associated) and yellow birch (*Betula alleghaniensis*—ECM associated), the soils at Alder Brook were more fertile than those at Merrill Brook (Jevon et al., 2019), and hereafter we treat them as separate forest types 'enriched hardwood' and 'unenriched hardwood' respectively (Figure 1a). The adjacent mixedwood sites had soils that were less productive than the other two sites and were dominated by red spruce (*Picea rubens*—ECM associated), balsam fir (*Abies balsamea*—ECM associated), yellow birch and red maple (*A. rubrum*—AM associated).

2.2 | Small mammal and microhabitat sampling

We sampled small mammals and microhabitat characteristics in patch cuts and surrounding forest at 56 stations arranged in a web array (Figure 1a,b). Webs consisted of eight 60-m transects (seven stations spaced 10 m apart) starting 30 m in the cut (near the centre) and extending 30 m into the forest (Figure 1b), yielding 24 stations in the cut, eight at the edge and 24 in the forest. We focused on seven small mammal species that are common in the north-eastern USA (Stephens, Hocking, et al., 2017) and together represented over 97% of unique captures in our study (Figure 2). These species consistently use regenerating forest, with *Microtus pennsylvanicus* and *Zapus hudsonius* preferring the early successional structure provided by timber harvest over mature forest (Zwolak, 2009). Although *Myodes gapperi* primarily consumes fungi (often 60% or more of diet), the other species consume fungi as a smaller portion of their diet (13% to 22%; Ovaska & Herman, 1986; Stephens & Rowe, 2020; Whitaker, 1962).

At each web, we measured small mammal abundance using a Sherman live trap (H. B. Sherman Company) set within 1.5 m of each station for three consecutive nights in June, July and August of 2018 and 2019. Traps were baited with birdseed and provisioned with polyester batting for insulation. Rodents were marked with numbered ear tags (model 1005-1; National Band and Tag Company) with voles (*M. gapperi* and *M. pennsylvanicus*) also receiving a passive integrated transponder (model HPT9; Biomark). Shrews *Blarina brevicauda* were toe-clipped. We collected scat from traps upon first capture of an individual within a month. Scat was frozen after collection and all traps with captures were washed and replaced with clean traps.

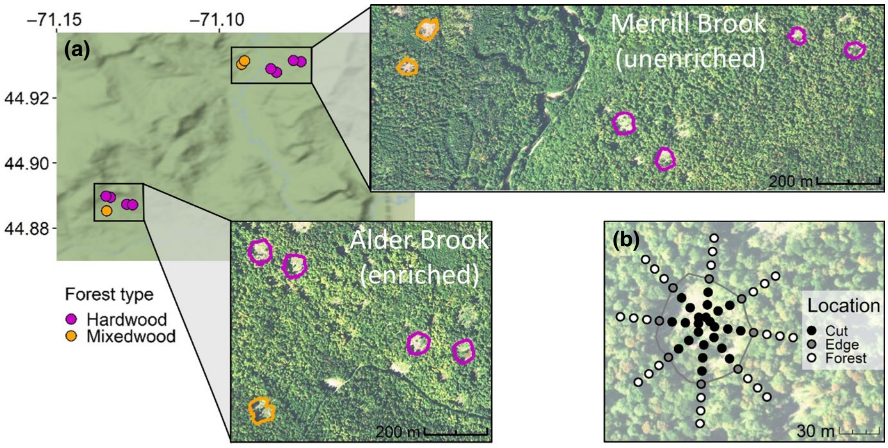

FIGURE 1 Locations of (a) patch cuts at Second College Grant and (b) web design used to sample small mammals and microhabitat variables at patch cuts

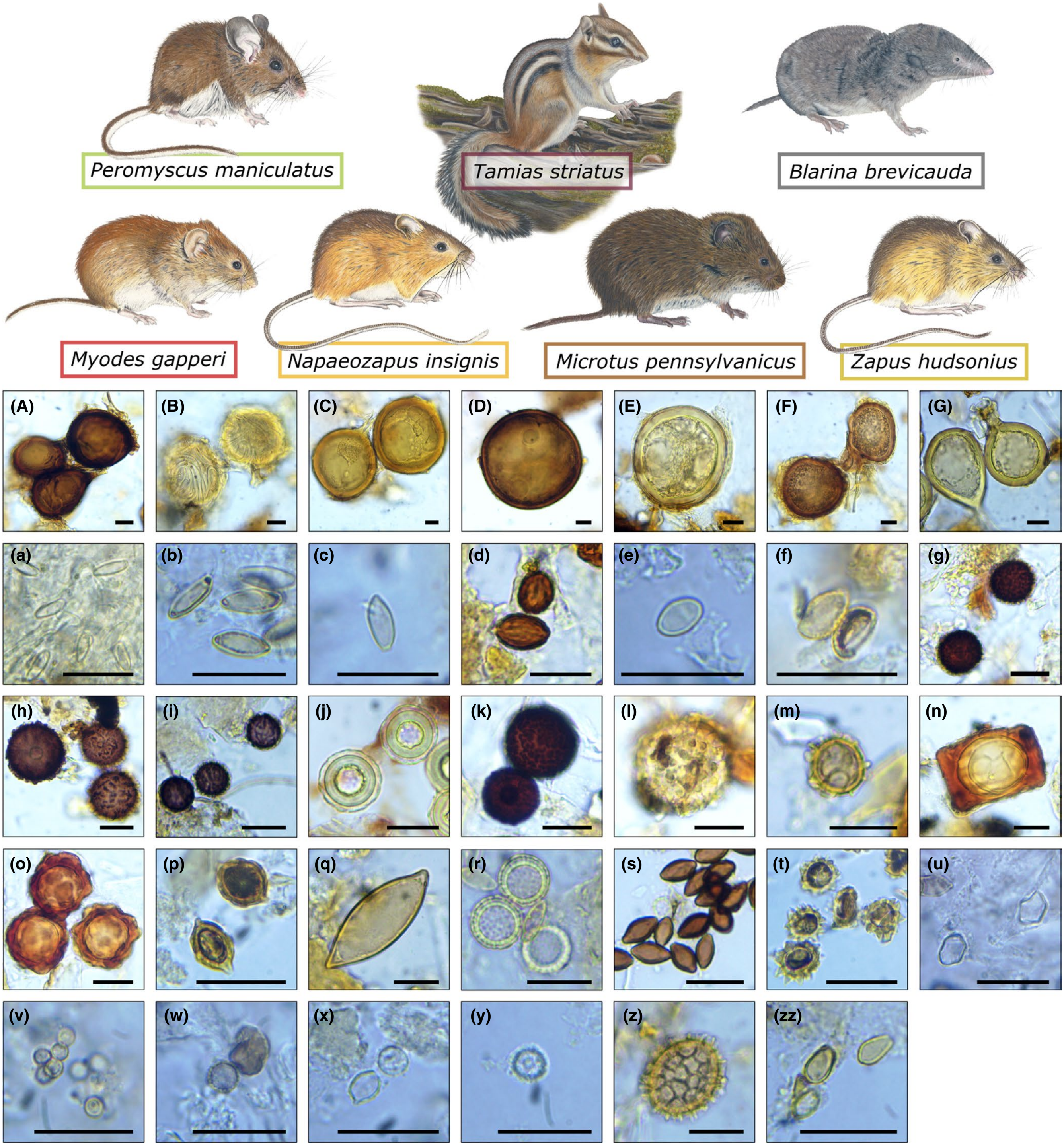

FIGURE 2 (Top) Common small mammals captured in patch cuts at Second College Grant and (Bottom) the spore morphotypes they disperse belonging to AM fungi (A–G) and ECM fungi (a) Boletaceae 1, (b) Boletaceae 2, (c) Boletaceae 3, (d) *Chamonixia* spp., (e) unknown mushroom 1, (f) *Cortinarius* spp., (g) *Elaphomyces americanus*, (h) *Elaphomyces macrosporus*, (i) *Elaphomyces* spp., (j) *Elaphomyces remickii*, (k) *Elaphomyces verruculosus*, (l) *Genea* spp., (m) *Hydnobolites* spp., (n) *Hydnotrya cubispora*, (o) *Hydnotrya tulasnei*, (p) *Hymenogaster* spp., (q) *Leucangium* spp., (r) *Leucophleps* spp., (s) *Melanogaster* spp., (t) *Octaviania* spp., (u) *Entoloma* spp., (v) unknown mushroom 2, (w) Russulaceae 1, (x) Russulaceae 2, (y) Russulaceae 3, (z) *Tuber* spp. and (zz) unknown mushroom 3. Scale bars are 20 µm. Mammal illustrations and spore images by R. Stephens

We used the number of unique individuals captured within a patch cut (stations 10–30 m in cuts) on each web as an index of small mammal abundance. We used mixed effects models ('lme' in the R package 'NLME'; Pinheiro et al., 2012) to determine if small mammal abundance differed by species, year and forest type. Main effects in models were species, year and forest type along with their three-way interaction. To account for repeated measurements among years, we included a random intercept for the web. We used post hoc tests with Tukey's correction for multiple comparisons (R package 'EMMEANS', Lenth, 2018) to test for (a) differences among species within a forest type and year, (b) differences among forest types (within a species and year) and (c) and differences between years (within a species and forest type).

To characterize microhabitat, we collected station-level data on tree species composition and structure (basal area and stem density) along with percent cover of downed woody material and vegetation. Within a 4-m radius of each station, we measured DBH (1.3 m height) on trees ≥10 cm and calculated basal area (m^2/ha) of AM- and ECM-associated trees. As a measure of mid-story forest structure and cover, we calculate stem density (stems per ha) by tallying tree stems and shrubs <10 cm at DBH. We estimated vegetative and downed woody cover below DBH as the mean of two measurements from 1-m^2 quadrats on either side of the trap station. Whereas downed woody material stayed stable over the 2 years, vegetative cover increased from 2018 to 2019. We were unable to conduct vegetation surveys in 2018 and instead measured vegetative cover in June (shortly after leaf-out) and August 2019 and used June data as a proxy for 2018. Despite not surveying vegetation in 2018, photographs and data collected in a complementary plot network indicated that vegetation conditions in July and August 2018 were similar to those documented in June 2019, thus capturing trends in increasing vegetative cover between years.

2.3 | Fungal spore analysis

Because fungal sporocarp production and consumption by small mammals is highest in the summer and early fall in the region (Stephens, Remick, et al., 2017), we used scat samples from July and August to identify mammal-fungal interactions. For each of the small mammal species, we analysed up to 20 scat samples in each forest type per year. We randomly selected scats as evenly as possible among webs and stratified selection so that samples were from the forest (~40%), patch cuts (~40%) and edge (~20%). When we had fewer than 20 scat samples for a species within a forest type and year, we analysed all available samples. For community analysis we used a resampling procedure to account for sample size differences (see Section 2.4). Following methods outlined by Stephens, Remick, et al. (2017), the spore isolate was extracted from approximately 15 mg of freeze-dried scat and permanently mounted onto a 22 mm × 22 mm area of a glass slide. For each slide, we counted the number of spores of each fungal taxon in 25 fields of view at 400× magnification and enumerated larger and less numerous spores (particularly Glomeromycota taxa) not detected at 400× by scanning a 121-mm^2 area at 100×. We used spore counts, spore isolate volume and scat weight to calculate the total spore abundance per taxon (spore load) in 1 g of scat. AM spores (Figure 2A–G) were grouped into morphotypes based on size, cell wall thickness and colour but were not assigned to a taxonomic designation. ECM spores (Figure 2a–zz) were identified to the lowest possible taxonomic unit (usually genus or species) using Castellano et al. (1989) and regional references (Stephens & Rowe, 2020). We acknowledge that using spore morphology may limit the taxonomic breadth for some taxa with similar morphology, particularly mushrooms. Nevertheless, using morphology gave us the distinct advantage of being able to quantify spore abundance in scat rather than DNA barcoding, which may detect DNA that is not from spores (see Appendix S2 for further discussion on our use of spore morphology).

To assess the relative consumption of AM and ECM fungi among mammal species, we compared spore richness and a spore load index (that incorporated richness and number of spores). For the spore load index, we used square-root transformed spore abundance data to reduce overdispersion from samples with extremely high spore loads. We relativized spore abundance data by scaling across all scat samples within a fungal taxon such that individual sample values for a given fungal taxon ranged from 0 to 1. Within a scat sample, we calculated the spore load index by summing the scaled abundances of fungal taxa, giving values that ranged from 0 (no spores of any fungal taxa) to the richness value of the scat sample (i.e. all fungal taxa in the sample have the highest spore loads). Following the same procedures as outlined for mammal abundance, we used mixed effects models to determine if spore richness or spore loads differed among mammal species, forest type, year and location (forest, edge, cut) for both AM and ECM fungi. We also included the interaction between mammal species × forest type, mammal species × year and mammal species × location. To assess significant differences between main effects and interactions, we used post hoc tests with *p*-values adjusted with Tukey's correction for multiple comparisons.

2.4 | Network construction and analysis

We assessed dynamics in mammal-fungal interactions by using networks constructed with a resampling technique that incorporated the mean spore loads in a given mammal species' scat with its abundance in the patch cuts (Stephens & Rowe, 2020). Specifically, we aggregated data within a forest type and year (i.e. across sampling webs) and drew inference from 100 iterations in which we calculated mean taxon-specific spore loads (square-root transformed) from seven randomly selected scat samples from each small mammal species. Each of these spore means was multiplied by a species-specific abundance estimate drawn from a probability distribution from the live-trapping data (mean and standard deviation of the sampling webs within a forest type and year), yielding abundance-adjusted spore means. This approach allowed us to build a given network with relatively similar scat sample sizes for each mammal species. Because location (forest, edge or cut) did not influence spore loads for either AM or ECM fungi (see Results section), we used scat samples collected at all trap stations to construct networks but only used mammal abundance data from patch cuts. Scat sample sizes for a given small mammal species within a given year and forest type ranged from 0 to 20 (mean ± *SD* = 10.1 ± 7.6; Table S1). For small mammal species with less than seven scat samples in a given year and forest type, we used all available samples for each iteration. Although scat samples from these species were static in iterations, variation was incorporated with mammal abundance. Within a fungal taxon, we relativized abundance-adjusted spore means by scaling across iterations from all species, years and forest types which made it possible to compare networks in different forest types and years. Scaled spore loads of species were then aggregated by iteration number to construct 100 mammal-fungal interaction communities for each forest type and year.

We visualized network dynamics among forest types and years by averaging the 100 scaled mammal-fungal interactions and plotting them with the 'geom_parallel_sets' function in the R package 'GGFORCE' (Pedersen, 2019). To quantitatively assess changes in species importance and network dynamics, we analysed networks with the R package 'BIPARTITE' (version 2.15; Dormann et al., 2008). We used species strength (hereafter 'importance'), which is the sum of dependencies of all fungal taxa for a small mammal species (Bascompte et al., 2006), to assess the importance of a small mammal species at dispersing fungal spores within a network and year. To describe the overall fungal dispersal at the network level, we used generality of fungal taxa, or the mean effective number of fungal taxa weighted to account for sample size (Tylianakis et al., 2007). We quantified network specialization with the standardized two-dimensional Shannon entropy index (H_2'), with lower values indicating high functional redundancy (close to 0—fungal taxa are dispersed by a broad range of mammals) and higher values indicating specialization (close to 1—fungal taxa are dispersed by only few mammals; Blüthgen et al., 2006). Using the resampled networks, we determined significant differences in small mammal importance (within a year, forest type and fungal type), fungal generality (among years and forest types within a fungal type) and H_2' (between AM and ECM fungi for each forest type and year) using permutational ANOVA (R package 'COIN'; Zeileis et al., 2008). We followed significant ANOVAs with pairwise permutation tests with *p*-values adjusted with Bonferroni correction for multiple comparisons ('pairwisePermutationTest' in the R package 'RCOMPANION'; Mangiafico, 2020).

2.5 | Microhabitat associations

We assessed associations between small mammal activity and microhabitat variables (basal area of AM- and ECM-associated trees, stem density, vegetative cover and downed woody cover) with GLMMs (R package 'GLMMTMB'; Brooks et al., 2017). We used the number of captures within a year at a trap station as an indication of activity for a given mammal species. We were unable to fit models for *B. brevicauda* due to too few captures. We used data from all trap stations and used microhabitat variables along with year as fixed effects. Basal area, stem density and downed woody cover were log-transformed to improve normality and all continuous variables were z-standardized. To assess how small mammals may have used ground cover variables differently between years, as regeneration progressed, we assessed the interactions between year and stem density, vegetative cover and downed woody cover. We did not include the interaction terms for *Z. hudsonius* due to extremely low captures in 2018 (Figure 3). We included trap station nested within the web as a random effect and sequentially fit models using a Poisson distribution, negative binomial distribution (to account for overdispersion) and the inclusion of a term for zero inflation. We used the R package 'BBMLE' (Bolker, 2020) to select the best fitting model based on AICc and the R package 'DHARMA' (Hartig, 2020) to test for under and overdispersion along with zero inflation. The R package 'PERFORMANCE' (Lüdecke et al., 2020) was used to calculate the marginal R^2 (i.e. proportion of variance explained by the fixed effects).

All statistical analyses were conducted in R version 4.0.4 (R Core Team, 2021).

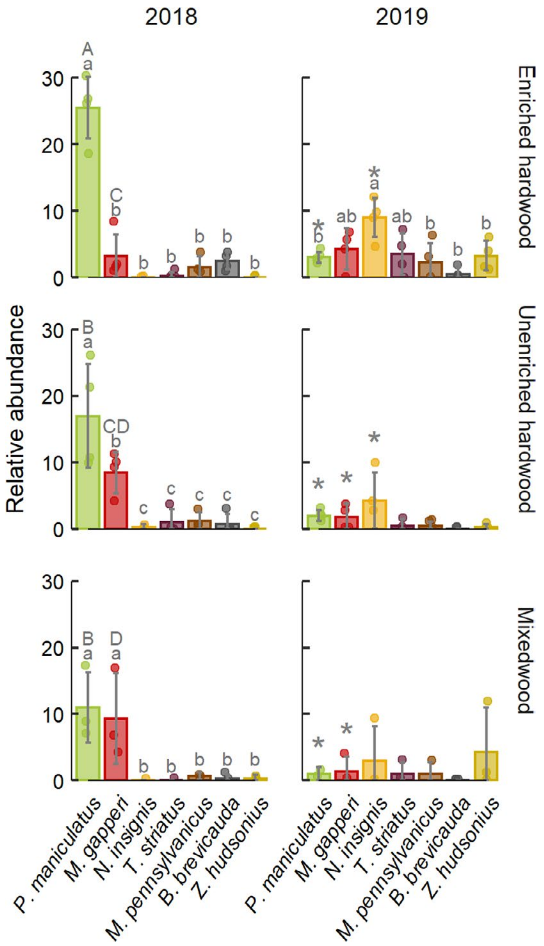

FIGURE 3 Abundance of small mammal species among forest type and between years. Bars are mean abundance across webs (±*SD*) with points representing individual web values. Lowercase letters denote significant differences among mammal species within a forest type and year and uppercase letters denote significant differences for a species among forest types within a year, with the same letters indicating no significant differences. Asterisks above bars in 2019 indicate a significant change in abundance from 2018 within a forest type

3 | RESULTS

3.1 | Mammal abundance

Mammal abundance in patch cuts varied by species and among forest type and years (Figure 3; Table S2). In 2018, *Peromyscus maniculatus* dominated all forest types, reaching its highest abundance in enriched hardwoods. *Myodes gapperi* was also abundant in unenriched hardwood forest and was co-dominant with *P. maniculatus* in mixedwood forest. In the following year, populations of *P. maniculatus* drastically declined across forest types along with *M. gapperi* in the unenriched hardwood and mixedwood forest, while *Napaeozapus insignis* increased in abundance in both the unenriched and enriched hardwood forests. Although not significant, *Tamias striatus* ($p = 0.089$) and *Z. hudsonius* ($p = 0.089$) showed a trend of increasing abundance in enriched hardwood sites between the 2 years as did *Z. hudsonius* ($p = 0.070$) in mixedwood forest. All other species had similar abundances between years and forest types.

3.2 | Spores in scat

In 424 scat samples from seven small mammal species (106 *P. maniculatus*, 101 *M. gapperi*, 60 *N. insignis*, 70 *T. striatus*, 33 *M. pennsylvanicus*, 33 *B. brevicauda* and 21 *Z. hudsonius*), we detected 34 fungal spore morphotypes (7 AM and 27 ECM) and observed 1,484 individual mammal species-fungal taxon interactions (875 for AM fungi and 609 for ECM fungi). Overall, 96% of scat samples contained fungal spores (89% contained AM spores and 71% contained ECM spores). Spore richness and spore load index differed by species, year and forest type but not location (Figure 4; Tables S3 and S4; Figures S1–S3). *Napaeozapus insignis* had the highest levels of AM spores (both richness and spore load index) and *P. maniculatus*, *M. gapperi* and *T. striatus* had the lowest levels, with the other mammal species being intermediate (Figure 4). However, despite these significant differences, all species consistently carried AM fungal spores. Comparatively, *M. gapperi* and *T. striatus* were the only species to have high levels of ECM spores with all other species having very low levels, particularly for the spore load index (Figure 4). *Peromyscus maniculatus* and *N. insignis* had significantly lower AM spore richness in 2019 compared to 2018 (Figure S1). *Peromyscus maniculatus* also had lower AM spore loads in 2019, whereas *M. gapperi* showed the opposite pattern (Figure S1). Only *M. gapperi* showed significant differences in spore metrics among forest types, with ECM spore richness and spore loads being lowest in unenriched hardwood and mixedwood sites (Figure S2).

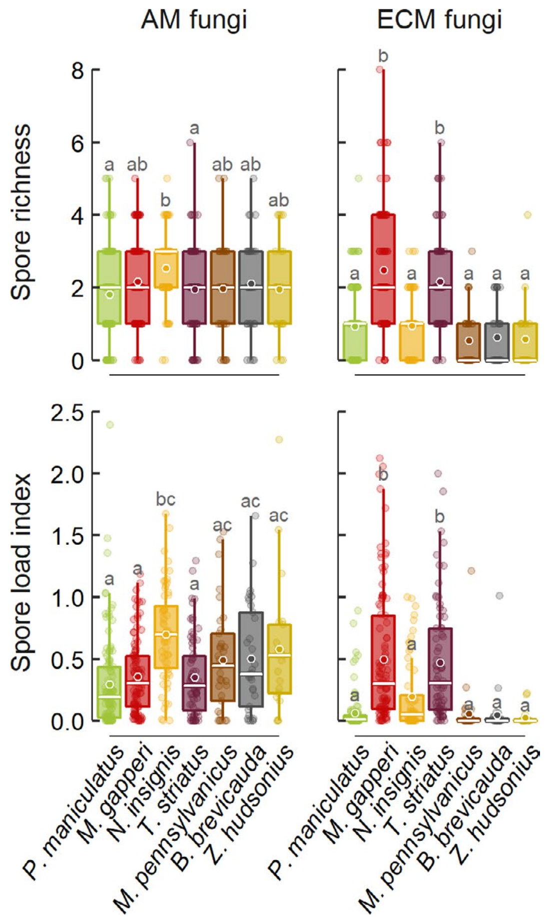

FIGURE 4 Boxplots of fungal spore type richness and spore load index for AM and ECM fungi in mammal scat. Medians and means are indicated by horizontal white bars and white circles respectively. Mammals within a metric and fungal type with the same letters are not significantly different. Box limits are the first and third distributional quartiles and whiskers extend to the most extreme data point within 1.5 times the interquartile range. The full data range is plotted with outlier points extending beyond whiskers

3.3 | Spore dispersal networks

For both AM and ECM fungi and in both years, spore dispersal declined from enriched hardwood forest to unenriched hardwood to mixedwood forest (Figure 5; Figure S4). In 2019, spore dispersal declined from 2018 across forest types with the exception of enriched hardwood sites which had similar ECM spore dispersal in both years and mixedwood forest sites which had higher AM spore dispersal in 2019 (Figure 5; Figure S4). Within each forest type and year, AM fungal-mammal networks were generalized ($H_2' = 0.16–0.51$) indicating high functional redundancy among mammals compared to ECM fungal-mammal networks that were highly specialized ($H_2' = 0.72–0.94$) suggesting that species were providing unique spore dispersal (Figure S5). The importance of small mammal species at dispersing fungal spores in patch cuts differed between fungal types and years (Figure 5; Figure S6). For AM spores, disperser importance was strongly tied to abundance (Figure 3), with *P. maniculatus* being the most important in both hardwood forest types and co-important with *M. gapperi* in mixedwood forest in 2018. Following population crashes of *P. maniculatus* and increases in *N. insignis* in 2019, *N. insignis* became the most important disperser of AM spores in both hardwood forest types and *Z. hudsonius* was important in mixedwood forest. Comparatively, for ECM spores, *M. gapperi* was consistently the most important disperser across forest types, even at low abundance.

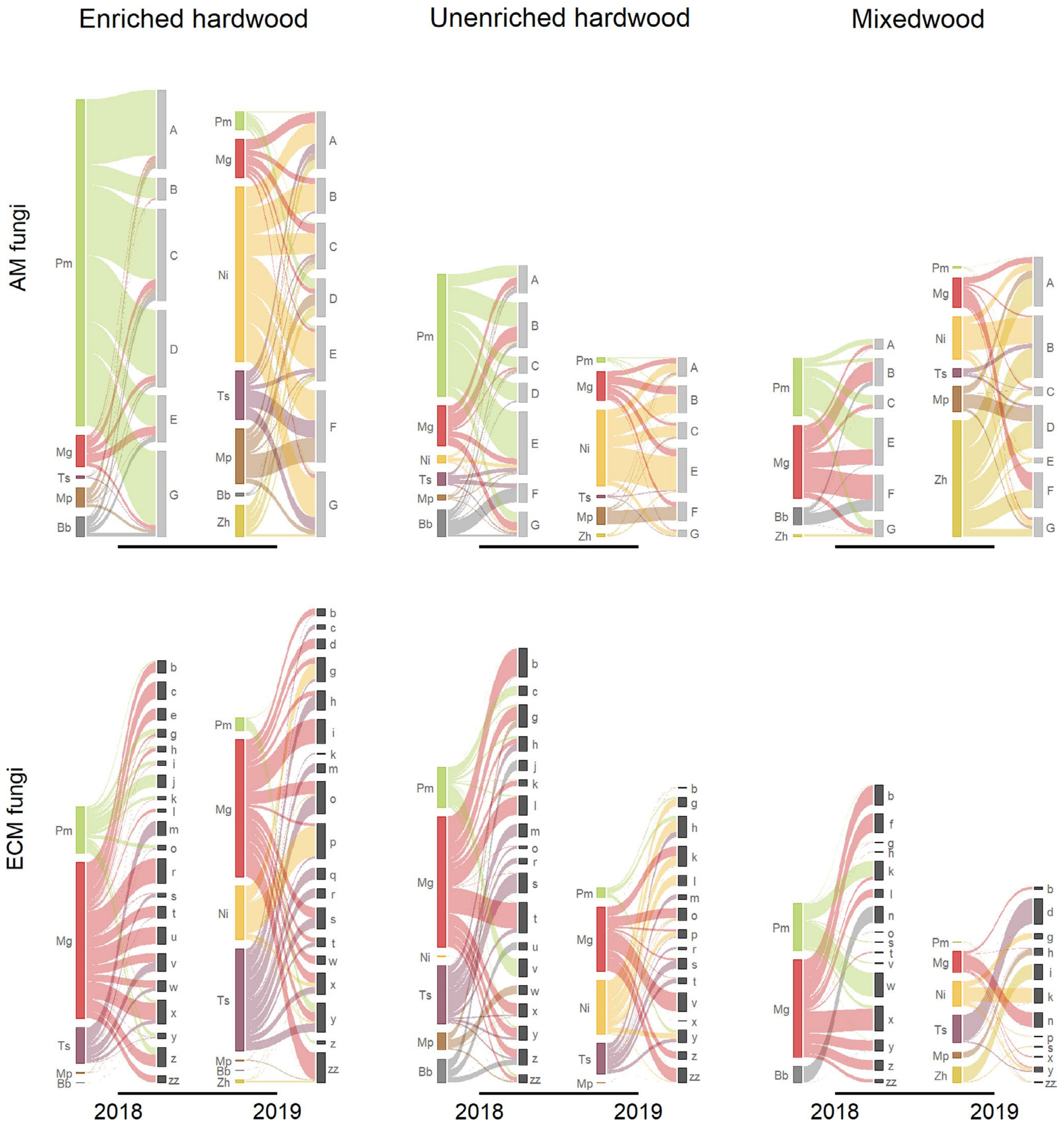

FIGURE 5 Mammal-fungal networks representing spore dispersal of AM and ECM fungal spores in patch cuts among forest types and between years. For a given fungal spore type, total spores are a product of the mean spore loads carried by a mammal species and its relative abundance. Spore abundance of a taxon is scaled across networks (forest type and year) such that fungal taxon bar height indicates relative dispersal. Mammal bars represent total contribution to spore dispersal. Abbreviations for mammal species are the first letter of the genus and species and letters for fungi are distinct morphotypes as shown in Figure 2

3.4 | Microhabitat associations

With the exception of *T. striatus* (R^2 = 0.20), microhabitat variables and year explained between 47% and 81% of the variation in small mammal activity (Figure 6). As would be expected with interannual changes in small mammal abundance (Figure 3), year was a significant predictor of activity for all species except *M. pennsylvanicus* (Figure 6). The basal area of ECM- and AM-associated trees was positively correlated with the activity of *M. gapperi* and *N. insignis* respectively. In contrast, the basal area of AM-associated trees was negatively correlated with the activity of *M. pennsylvanicus*. With the exception of *P. maniculatus*, mammal species were significantly more

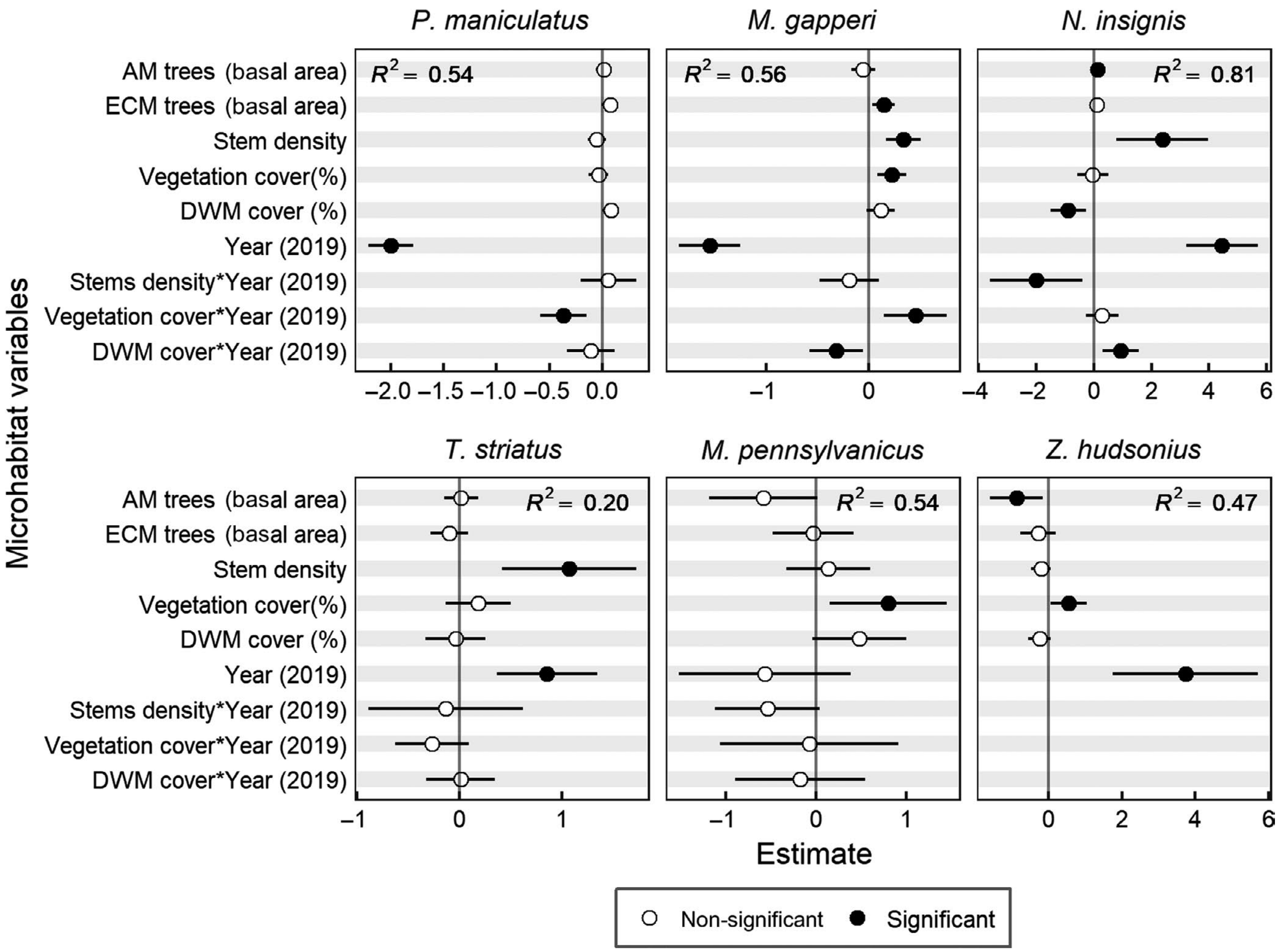

FIGURE 6 Results of GLMMs indicating the influence of microhabitat variables and year on trap-level activity of small mammals. Circles represent model estimates and lines are 95% confidence intervals. Open circles are non-significant and closed circles are significant. Estimates above zero positively influence small mammal activity and those below zero negatively influence activity. Marginal R^2 values are shown in the upper portion of the plots for each species. DWM, downed woody material

active with greater levels of stem density or vegetative cover. With regeneration, *M. gapperi* switched from using downed woody cover in the first year to vegetative cover in the second year. Both *N. insignis* and *M. pennsylvanicus* showed similar patterns with less reliance on areas with high stem density in the second year.

4 | DISCUSSION

As a result of species-specific differences in fungal consumption and population dynamics, we found that mammals played complementary roles in terms of the type of mycorrhizal fungi they dispersed. For AM fungi, mammal species were more redundant at providing dispersal, with asynchrony in mammal population fluctuations among years leading to changes in the relative importance of mammal species. Comparatively, only two mammal species regularly consumed ECM fungi, resulting in dispersal networks that were highly specialized. These differences in network structure between AM and ECM fungi have important implications for how changes in the mammal community influence the stability of mycorrhizal spore dispersal following forest disturbances. Mammals also varied from having no microhabitat associations to being strongly associated with forest structure and ground cover variables, suggesting that species deposit spores in different microsites associated with regenerating seedlings.

4.1 | Functional complementarity and temporal stability

By integrating data on fungal spore consumption and abundance of small mammal species, we were able to determine the mechanisms that shape the functional role of species and assess the stability of AM and ECM fungal dispersal. Compared to ECM fungi, all mammal species commonly ingested AM fungal spores (Figure 4). The consumption of AM fungi may be direct, as *N. insignis* regularly eat AM sporocarps (Whitaker, 1962), or indirect from eating arthropods that consumed AM spores (Rabatin & Stinner, 1988). Such secondary dispersal may be the case for *B. brevicauda*, which is an insectivore but commonly has AM fungal spores in its scat (Ovaska & Herman, 1986). This combination of direct and indirect spore ingestion likely increases the overall probability that a given small mammal will consume AM spores. Because all mammal species commonly carried AM fungal spores, mammal abundance, which changed among years, primarily drove the importance of species within networks. Although masting events (where trees produce large seed crops) cause synchronous population fluctuations of small mammal species, *N. insignis* often increases in abundance when other species decline (likely due to their ability to hibernate; Stephens, Hocking, et al., 2017). This asynchrony in population fluctuations, particularly between *P. maniculatus* and *N. insignis*, appears to help maintain temporal stability of AM spore dispersal despite changes in mammal community composition (Figure 5).

Compared to AM fungi, ECM spore dispersal networks were highly specialized, making them sensitive to changes in community composition, especially the loss or declines in key dispersers (Schleuning et al., 2015). Only two species (*M. gapperi* and *T. striatus*) regularly consumed ECM spores and most of the dispersal was provided by *M. gapperi*, which more consistently used patch cuts. We had expected that abundant species would be important ECM dispersers (Stephens & Rowe, 2020). However, most other species consumed low levels of ECM spores, making them poor dispersers relative to *M. gapperi*, even after accounting for abundance. Interestingly, we also found that the consumption of spores by *M. gapperi* declined across the nutrient gradient from enriched hardwood sites to mixedwood forest. This may be due to less sporocarp production, as fruiting body surveys indicated extremely low production at our mixedwood sites (unpublished data). Lower levels of consumption coupled with population declines of *M. gapperi* resulted in little ECM dispersal in unenriched hardwood and mixedwood forests in 2019. Because mycorrhizal fungi are particularly important for plant productivity at sites with low nutrient availability (Jonsson et al., 2001), managing for habitat characteristics that support the occurrence and movement of important dispersers, such as *M. gapperi*, following timber harvest will help maintain ECM spore dispersal (Jacobs & Luoma, 2008; Schickmann et al., 2012; see next section).

4.2 | Microhabitat associations

We found that small mammal species used different microhabitats. Such complementary microhabitat use plays an important role in maintaining spatial coverage in the dispersal of propagules (Morán-López et al., 2020; Schleuning et al., 2015). Habitat generalists such as *P. maniculatus*, that use a wide variety of habitats and have weak microhabitats associations, can be important for dispersing propagules to areas that other species often avoid, such as open areas (Carlo & Morales, 2016; Morán-López et al., 2020). Most of the other mammal species were associated with either stem density or vegetative cover (Figure 6). The dispersal of spores to areas of high stem density may increase fungal diversity to these trees. Within the harvested areas, the majority of plants composing our measure of vegetative cover (e.g. grasses, herbaceous plants and maple seedlings) were AM associated and may benefit from AM spores dispersed by mammals. Only two mammal species were positively associated with the basal area of trees, with *M. gapperi* and *N. insignis* associated with ECM and AM trees respectively. These associations may represent the areas where fungal sporocarps were foraged from since *M. gapperi* and *N. insignis* commonly consumed ECM and AM sporocarps respectively. The relatively small size of the patch cuts (0.4 ha) likely allowed these species to consume sporocarps in the forest and move them into the cuts during activities within their home range, the average size of which is between 0.4 and nearly 4 ha (Tisell et al., 2019). Interestingly, both open habitat associates (*M. pennsylvanicus* and *Z. hudsonius*) consumed AM fungi but were almost never captured in the forest, suggesting that they may be foraging sporocarps inside the cut. Thus, they may play a unique role in moving fungi around the cut as their activities are associated with vegetative cover, but they likely do not bring fungi in from the surrounding forest.

For some species, microhabitat associations changed with regeneration. Notably, *M. gapperi* used more downed woody cover in the first year when patch cuts were relatively open and switched to using vegetative cover in the second year as regeneration progressed. This suggests that downed woody material provides an important source of cover for *M. gapperi* directly after timber harvest when vegetative cover is lacking. Although we measured downed woody cover as both slash from recently harvested trees, along with pre-existing logs in the later stages of decomposition, *M. gapperi* are known to use woody cover in both forms (Bowman et al., 2000; Sullivan et al., 2011). Slash and decomposed wood are also important for the establishment of many tree seedlings, particularly those associated with ECM fungi. Slash provides shade and protection from ungulate browsing (Gray & Spies, 1997; Palik et al., 2015), and logs in the later stages of decomposition are important for the regeneration of small-seeded tree species, including yellow birch, eastern hemlock *Tsuga canadensis* and red spruce (Bolton & D'Amato, 2011; Weaver et al., 2009). Thus, *M. gapperi*, which carries high ECM spore loads in its scat, may provide critical dispersal of ECM fungal inoculum to seedlings at prime microsite locations and directly following establishment, a time when colonization is critical (Peay, 2018).

5 | CONCLUSIONS

Our results indicate that, following timber harvests, individual small mammal species play complementary roles in dispersing AM and ECM fungi. This suggests that maintaining a diverse small mammal community in recently harvested forests will help maintain this important ecosystem function. We found that the driver of a mammal species importance at dispersing spores differed between fungal functional types, with the most abundant mammal species providing AM spore dispersal, whereas only *M. gapperi*, which consumes fungi as a main part of its diet, provided consistent ECM dispersal. Members of the genus *Myodes* are distributed throughout the northern hemisphere and are often the most important dispersers of ECM fungi within the mammal community (Jacobs & Luoma, 2008; Schickmann et al., 2012). We also found that the activity of most small mammal species was associated with one or more microhabitat variables, many of which are strongly influenced by forest harvesting activities (Palik et al., 2020). Thus, similar to recommendations made in other regions, silviculture strategies focused on retention of downed woody material and existing patches of vegetation may serve to maintain a diversity of spore dispersal mechanisms in managed forests (Jacobs & Luoma, 2008; Schickmann et al., 2012).

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AUTHORS' CONTRIBUTIONS

R.B.S. collected the data, analysed the data and wrote the first draft of the manuscript. All the authors conceived the ideas, designed the methodology, contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.q83bk3jhz (Stephens et al., 2021).

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SUPPORTING INFORMATION

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