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Fungal Fruiting and Dispersal Following Timber Harvest

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FUNGAL FRUITING AND DISPERSAL FOLLOWING TIMBER HARVEST

BY

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THESIS

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DEDICATION

To my parents, Karin and John, who introduced me to the joy of exploration.

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ABSTRACT

FUNGAL FRUITING AND DISPERSAL FOLLOWING TIMBER HARVEST

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Forest-dwelling fungi are critical to ecosystem function in their roles as decomposers and nutrient cyclers, food sources, pathogens, and mycorrhizal symbionts. In northern New England, a region with a substantial timber industry, the degree to which fungal communities are resilient to timber harvest, as well as their ability to recolonize post-disturbance, may impact ecosystem function and forest regeneration. In this thesis, we investigate the impacts of (1) timber harvest on fungal fruiting, an important element of fungal reproduction, and (2) the dispersal mechanisms by which fungi may re-colonize harvested areas.

In Chapter 1, we investigate the impact of timber harvest on epigeous fungal fruiting patterns. Fruiting has important impacts on fungal reproduction and ecosystem function. Forest disturbances such as timber harvest impact moisture, host availability, and substrate availability, which in turn may drive changes in fungal fruiting patterns and community structure. We surveyed mushrooms in 0.4-ha patch cuts (18 months post-harvest) and adjacent intact hardwood forest in northern New Hampshire, USA, to document the effects of timber harvest on summer fruiting richness, biomass, diversity, and community structure of ectomycorrhizal, parasitic, and

saprobic mushroom taxa. Fungal fruiting richness, diversity, and community heterogeneity were greater in intact forests than patch cuts. Among functional groups, ectomycorrhizal fruiting richness, diversity, and biomass were greater in unharvested areas than in the patch cuts, but parasitic and saprobic fruiting did not differ statistically between the two forest conditions. Our findings suggest that timber harvest simplifies fungal fruiting communities shortly after harvest, in particular triggering declines in ectomycorrhizal taxa which are important symbionts facilitating tree establishment and regeneration. Multi-aged silvicultural practices that maintain mature forest conditions adjacent to and throughout harvested areas through deliberate retention of overstory trees and downed woody material may promote fungal fruiting diversity in regenerating stands.

In Chapter 2, we compare fungal spore dispersal between wind and small mammals. Spore dispersal has important impacts on fungal diversity and ecosystem function. Dispersal can occur via several mechanisms, but wind is perhaps the best-studied and is often assumed to be the primary dispersal mechanism for most aboveground fungi. Mycophagy is another commonly reported dispersal mechanism, particularly as performed by small mammals, which are often speciose and abundant in forested systems. Few studies directly compare wind- and mammal-facilitated spore dispersal. Thus, it is unclear whether these pathways are complementary or redundant in the taxa they disperse and the ecosystem functions they provision. Here we compare the diversity and morphology of fungi dispersed by wind and three species of small mammals (*Myodes gapperi*, *Napaeozapus insignis*, and *Tamias striatus*) in recently harvested patch cuts using a combination of microscopy and Illumina sequencing. We demonstrate that fungal communities dispersed by wind and small mammals differ in taxonomy and species

richness, as well as functional group membership. A large proportion of wind-dispersed spores belong to wood saprotrophs, litter saprotrophs, mycoparasites, and plant pathogens, whereas most spores dispersed in mammal scat come from mycorrhizal and unspecified saprotrophic taxa. We note substantial dispersal of truffles, mushrooms, AM sporocarps, jellies, and crusts by small mammals. In addition, we find that mammal-dispersed spores are larger on average than wind-dispersed spores, but do not differ in melanization or the presence of ornamentation. We quantify dispersal distances of small mammals by modeling home range and core area size using kernel density estimators from mark-recapture survey data, finding the distance to be comparable to those reported in the literature for wind-based dispersal. Our findings suggest that wind- and small mammal-facilitated dispersal are complementary processes, which highlights the importance of maintaining robust small mammal communities, particularly following timber harvest.

CHAPTER 1

EFFECTS OF TIMBER HARVEST ON EPIGEOUS FUNGAL FRUITING PATTERNS AND COMMUNITY STRUCTURE IN A NORTHERN HARDWOOD ECOSYSTEM[1]

INTRODUCTION

Epigeous fungal sporocarps (mushrooms) play a critical role in fungal reproduction (Brown and Casselton 2001) and have secondary impacts on food webs (e.g., Orledge and Reynolds 2005), forest health (Ostry and Laflamme 2008), and nutrient cycling (Clemmensen et al. 2015). The abundance and spatial distribution of mushroom fruiting depend on several factors, including moisture (Sato et al. 2012), temperature (Kauserud et al. 2011), and host or substrate composition (Krah et al. 2018). Forest disturbances, including timber harvest, alter each of these factors. Timber harvest may decrease soil depth and moisture by causing erosion and compaction (Solgi and Najafi 2014), increase soil and substrate temperature by reducing canopy cover (Ballard 2000), and alter host and substrate availability by removing living trees while simultaneously increasing woody material in the form of slash. Consequently, timber harvest drives changes in mushroom fruiting patterns (Tomao et al. 2020).

Effects of timber harvest on mushroom fruiting have been examined at the species level, with reports of increased (Bonet et al. 2012) or decreased (Parladé et al. 2017) fruiting post-harvest. An alternate approach is to look more broadly at the responses among ectomycorrhizal, parasitic, or saprobic functional groups (e.g., Fernández-Toirán et al. 2006). For instance,

[1] Borgmann-Winter, B., Stephens, R.B., D'Amato, A.W., Frey, S.D., Rowe, R.J. 2021 *Canadian Journal of Forest Research* 52(1): 51-58

ectomycorrhizal fungi, which are symbionts of many tree species, have been shown to exhibit lower mushroom richness after timber harvest (Durall et al. 2006). Composition of belowground ectomycorrhizal communities also change after timber harvest (Jones et al. 2003), an effect that is magnified at increasing distances from adjacent intact forest (Durall et al. 1999). Removal of host trees may be detrimental to the survival and fruiting of ectomycorrhizal mushrooms as a group, which may in turn decrease the ability of ectomycorrhizal fungi to disperse to new tree seedlings, particularly in large cutblocks (Hagerman et al. 1999). By contrast, mushrooms of saprobes (decay taxa) and parasites (pathotrophic fungi that attack trees, insects, or other fungi) show a mixed response to forest harvest. Some saprobic and parasitic species (perhaps light or temperature-responsive species) increase fruiting abundance in response to canopy openings, whereas other species fruit less (Siitonen et al. 2005). Response may also differ based on host availability for parasitic taxa, or on substrate requirements, such as between humicolous and lignicolous saprobes (Fernández-Toirán et al. 2006). Whereas the humus layer required by humicolous saprobes is often thin in recently harvested forest due to disturbance by harvesting operations, the woody material required by wood-decay (lignicolous) saprobes may be abundant after forest harvest. Certain lignicolous saprobes have been shown to increase fruiting in cleared areas when there is sufficient slash left behind (Ylisirniö et al. 2012), and diversity of this group may increase when different sizes of woody material are available (Brazee et al. 2014). Due to the availability of large amounts of woody material following timber harvest, the speed with which wood-decaying saprobes proliferate has important implications for nutrient cycling and carbon storage.

This study documents patterns of fungal fruiting very early in the process of forest recovery (approximately 18 months post-harvest). The short-term effects of timber harvest on

mushroom fruiting patterns and early fungal succession are little-documented, as most studies are conducted at least four years post-harvest (e,g., Durall et al. 2006; Brazee et al. 2014), once forest regeneration is well underway. It is important to document fruiting patterns in the years immediately following forest harvest, as these patterns offer insight into both the resilience of previously established taxa to shifting biotic and abiotic conditions, and the ability of existing or newly established taxa to quickly capitalize on freshly available resources. This is especially the case in northern New England, USA, where timber harvest is a common form of disturbance (Kittredge et al. 2003) and is likely to increase due to salvage operations associated with climate change-induced disturbances such as invasive insect outbreaks and increasingly frequent windthrow and ice events (Dale et al. 2001). The vigor of mushroom fruiting in the immediate aftermath of forest disturbance, particularly at the functional scale (ectomycorrhizal, parasitic, saprobic), likely precipitates numerous downstream effects on nutrient cycling, trophic interactions, and the establishment of mycorrhizal mutualisms that impact forest community structure for decades. As such, documenting these early patterns is critical to informing an understanding of the role post-disturbance fungal fruiting has in driving long-term patterns in key forest ecosystem processes and dynamics.

MATERIALS AND METHODS

Study Site

Fieldwork was conducted at ten study plots located at the Second College Grant, a 10,800 ha forested property owned by Dartmouth College, in Coos County, New Hampshire, USA. This is a temperate, mixed forest system subject to warm summers and cool, snowy winters. Mean annual precipitation and temperature in the region are 1179 mm and 3.2°C, respectively

(Petrenko and Friedland 2015). Each plot consisted of a circular, 0.4 ha patch cut surrounded by a lightly harvested forest matrix last thinned between 1996 and 2000 (Jevon et al. 2019). All patch cuts were harvested between August and December 2017, and eight were harvested in association with the Adaptive Silviculture for Climate Change project, an international network of studies testing different approaches to forest adaptation in the face of climate change and shifting disturbance regimes (Nagel et al. 2017). Experimental harvests were created by hand-felling of all overstory stems with the exception of the deliberate retention of 3 to 4 legacy trees per patch for ecological and adaptation objectives. Felled trees were delimbed in the forest with tops left on site and merchantable bolewood removed by cable skidders that accessed patches using pre-designated skid trails. Basal area ranged from 25.7-27.0 m^2/ha prior to harvest and canopy trees were approximately 80-90 years old.

All plots were located in northern hardwood stands, ranging from 84-100% hardwood by basal area. Dominant canopy species (asterisks indicate ectomycorrhizal associates following Brundrett 2009) included sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia**), and yellow birch (*Betula alleghaniensis**), with smaller components of red maple (*Acer rubrum*), white birch (*Betula papyrifera**), red spruce (*Picea rubens**), quaking aspen (*Populus tremuloides**), and bigtooth aspen (*Populus grandidentata**). Composition of all unharvested forest was approximately 40% ectomycorrhizal canopy species by basal area, and 60% non-ectomycorrhizal species. Dominant woody understory species included striped maple (*Acer pensylvanicum*), hobblebush (*Viburnum lantanoides*), and American beech saplings. In the harvested areas, regenerating vegetation was dominated by a patchwork of aspen spp. and pin cherry (*Prunus pensylvanica*) saplings, red elderberry (*Sambucus racemosa*), red raspberry (*Rubus idaeus*), common hemp-nettle (*Galeopsis tetrahit*), and various grasses (Poaceae). Mean

proportional ground cover of woody material was approximately twice as high per unit area in the patch cuts (14.35 ± 0.95%; mean ± standard error of the mean) as it was in the nearby forest (6.78 ± 0.65%).

Mushroom collection and identification

To document differences in summer fruiting patterns between the recent patch cuts and adjacent forest, we surveyed epigeous sporocarps (mushrooms) at each of the ten plots in both July and August 2019. This was approximately 18 months after harvest which allowed one growing season for fungal communities to adjust to new environmental conditions and for fungal colonization of new woody material to begin. Surveys were conducted along two 60 m (2 m wide) belt transects, for a total of 240 m^2 surveyed per plot each month. Each transect began in the center of the patch cut, extended 30 m to the edge of the cut, and then continued an additional 30 m into the adjacent forest. Transects were located on opposite sides of each cut.

All mushrooms greater than 0.5 cm in width were counted within each belt transect, and substrate and location were recorded. Specimens not identified in the field were assigned to a temporary "morphotype" based on substrate, growth habit, coloration, and other physical characteristics, and later identified in the lab. Each mushroom was photographed *in situ* and up to three representative specimens per taxon or morphotype were harvested per plot each month. Specimens were dried in a dehydrator within 24 hours of collection and stored for later identification and analysis.

In the lab, unknown mushrooms were identified to genus (or species where possible; approximately 70%). Identification was based on a combination of microscopic analysis of morphological features and macroscopic analysis of dried specimens, photographs of fresh

specimens, staining, spore print color (when available), and field notes on growth habit and substrate. A variety of resources were used for specimen identification, including Baroni (2017), Barron (1999), Beug et al. (2014), Kuo (2021), and Lincoff (1981). Approximately 1% of mushrooms, accounting for 0.03% of total surveyed biomass, were not successfully identified to genus and were excluded from analysis.

The mass of all dehydrated mushroom specimens collected during field surveys was recorded. For each plot, the total fruiting biomass of each taxon was calculated by multiplying the mean dry mass of all collected specimens by the number of mushrooms of that taxon detected within the plot. In instances where frequently recurring taxa were not collected from every location on a transect (only three representative specimens were collected per plot), we assigned an estimated biomass value, calculated as the mean dry biomass of all other specimens of that taxon from the same plot and survey.

Mushrooms were also assigned to one of three functional groups based on taxonomy (genus) and substrate: ectomycorrhizal, parasitic, or saprobic. Functional groups were assigned using the FUNGuild database query tool (http://www.funguild.org, accessed 19 Nov 2020). For any genera listed in this database as including species from multiple functional groups, we assigned the functional group of the specific taxa occurring at our plots. For instance, the genus *Entoloma* contains species reported to belong to all three functional groups, but each of the species we identified as occurring at our study plots (e.g., *E. quadratum*) is believed to be saprobic, so the genus *Entoloma* was treated as saprobic in analyses. Parasitic mushrooms included both true parasites and taxa that may exhibit both parasitic and saprobic function throughout their life cycles, such as the genera *Fomitopsis* and *Ganoderma*. Taxa with poorly understood functionality (e.g., *Hygrocybe*; Lodge et al. 2014) and unidentified morphotypes

were not assigned to a functional group. These taxa accounted for approximately 1% of fruiting bodies. Representative voucher specimens were deposited in the fungarium of the Natural History Museum of Utah (Salt Lake City, Utah).

Analysis

To ensure a robust comparison of fruiting patterns in the patch cuts relative to the intact forest, we filtered out edge effects by excluding data recorded within 10 m of the patch cut-forest edge in either direction. July and August data were combined to represent summer fruiting patterns. In order to avoid double-counting of fruiting bodies between the study periods, conks and other long-lasting fruiting bodies were not counted in the August surveys when they matched the location and description of fruiting bodies observed in the July surveys.

At the genus level, we compared the number of individual fruiting bodies observed in the patch cut to the number observed in the forest using a Wilcoxon signed-rank test [*wilcox.exact*] in the R package "exactRankTests" (Hothorn and Hornik 2019). At the functional group level, we compared fruiting between the patch cut and the forest for all three functional categories using several metrics: genus richness, dry biomass, and Shannon-Weiner diversity index. Biomass was chosen over fruiting abundance at the functional group scale to avoid biasing results in favor of fungal taxa that produced numerous small fruiting bodies over taxa that produced individual, large fruiting bodies. Mean genus richness and mean dry biomass were compared using the Wilcoxon signed-rank test. To evaluate the effect of patch cuts on fungal fruiting composition, we used a Bray-Curtis dissimilarity matrix generated from biomass data for all genera detected at more than one study plot. To visualize trends in compositional similarity among plots we used non-metric multidimensional scaling (NMDS) in the R package "vegan"

(Oksanen et al. 2019). One patch cut was excluded from community analyses because it only contained one mushroom taxon detected at other plots. To quantify the role of timber harvest on community composition, we used PERMANOVA (multivariate repeated-measures analysis of variance – function [*adonis*] in vegan), applying the repeated measures by using 1000 randomized datasets. To test for homogeneity of dispersion between communities in the patch cuts and forests, we used the betadisperser function in vegan. All statistical analyses were conducted in R version 3.6.2 (R Core Team 2019).

RESULTS

We detected over 3,000 mushrooms belonging to at least 63 genera, including 11 ectomycorrhizal genera, 6 parasitic genera, and 42 saprobic genera (Table A1). Of these taxa, six (10%) were detected only in patch cuts, 38 (60%) were detected only in forests, and 19 (30%) were detected in both forests and patch cuts. Additionally, 40 genera (63%) were detected at only one of the ten study locations. This reflects the diversity and ephemerality of the fruiting body community and suggests that only a fraction of present taxa were detected in our single-year study, a pattern observed elsewhere even over many consecutive years of study (Straatsma et al. 2001). Likely due to small sample sizes, only three genera were found to fruit significantly more in either the patch cuts or the forests. Fruiting bodies of the genus *Schizophyllum* were more abundant in the patch cuts ($z = -2.93$, $p = 0.008$), and the genera *Hygrocybe* ($z = -2.48$, $p = 0.040$) and *Entoloma* ($z = -2.49$, $p = 0.040$) fruited more abundantly in the forests.

At the functional group level, several differences in mushroom fruiting were observed between the patch cuts and forests. Mean fruiting richness of all genera combined, including those not assigned to a functional group, was greater in the forests than in the patch cuts (z =

-2.35, $p = 0.010$; Fig. 1.1). Mean richness was also greater in the forest for fruiting bodies of ectomycorrhizal taxa specifically ($z = -2.36$, $p = 0.024$), and ectomycorrhizal fruiting body biomass in the forest was approximately ten times greater than in the patch cuts ($z = -2.15$, $p = 0.043$). In contrast, saprobic and parasitic fruiting body richness and biomass did not vary significantly between the patch cuts and forests. Fruiting biomass for all functional groups combined also did not differ. Shannon-Weiner diversity values were higher in the forest than in the patch cut, both for all taxa combined and for each individual functional category.

PERMANOVA indicated that fungal fruiting body community composition was significantly different between patch cuts and the forest ($F_{1,19} = 1.65$, adj. $p = 0.042$). The degree of fruiting community concordance was also significantly greater in patch cuts than in forests ($p = 0.014$). These relationships were apparent in the NMDS ordination (based on 25 genera that occurred at two or more plots), with slight separation between the two groups of communities along the horizontal axis, and a notably smaller ellipse spread around the centroid for fungal communities in patch cuts (Fig. 1.2).

DISCUSSION

Forest harvest resulted in lower overall mushroom richness and diversity 18 months post-harvest. Although approximately one third of genera were present in both patch cuts and surrounding forests, results from our betadisperser test and NMDS ordination indicate that there was less heterogeneity in fungal communities associated with harvested areas relative to intact forest communities. This greater community homogeneity is suggestive of structural simplification of the fungal community after harvest driven by the loss of many ectomycorrhizal and saprobic taxa, a pattern previously observed in a number of other regions (Tomao et al.

2020). Shifts in community concordance may also be attributable to abundant fruiting of early decay taxa colonizing slash in the patch cuts.

Indeed, a number of wood-decaying saprobic taxa were particularly abundant on slash in the patch cuts. One such taxon, *Schizophyllum*, was represented entirely by the species *S. commune*, and was the most commonly detected taxon in this study (Table A1). On average, fruiting bodies of *S. commune* were over seven times more abundant in the patch cuts than in the forest. Fruiting of this species may be enhanced by high density of slash, as there was approximately twice as much woody cover in the patch cuts as there was in the forests. Other taxa that were abundant on fresh slash included several species of the genus *Trametes*, as well as the genera *Irpex* (represented entirely by *I. lacteus*) and *Trichaptum* (represented by *T. biforme*), although none of these were statistically more abundant in the patch cuts than in the intact forest. Our findings are similar to those of a study in the midwestern United States, which reported no difference in abundance of *T. biforme* and *I. lacteus* between small gap cuts and forest habitat, although significantly higher abundance of three different species of *Trametes* was detected in the cuts (Brazee et al. 2014). Differences in quantity, size class, and decay stage of available deadwood in harvested areas may impact the degree and rapidity with which these early decay saprobes fruit in recent cuts.

Fruiting patterns observed in saprobes may also depend on how recently timber harvests occurred. Slightly older cuts (up to 10 years post-harvest) with abundant saplings are reported to contain higher species richness of wood-inhabiting fungi than any later successional stage (Junninen et al. 2006). This may be caused by a greater diversity of woody material size and decay class, due to a combination of fresh woody material from harvest activity and existing woody material remaining from the pre-harvest period. Although our study did not analyze

wood-inhabiting fungi as a group separately from other saprobic taxa, our analyses of saprobic and parasitic fungi overall do not suggest that patch cuts 18 months post-harvest are particularly taxonomically diverse. This discrepancy in findings may be caused by a combination of factors, including the differing stages of succession between the two studies. Greater time since harvest may result in greater sapling coverage and canopy cover which may result in woody substrates with higher moisture content, generally assumed to correlate positively with fungal fruiting. Additionally, the younger age of deadwood in our study (slash was <2 years old, as opposed to <10 years old) may limit saprobe richness, as older deadwood appears to decay heterogeneously and play host to a greater variety of wood-inhabiting species than fresh deadwood (Tomao et al. 2020). If young patch cuts do indeed provide habitat for only a limited suite of common saprobes, taxonomic richness and habitat for uncommon species may be improved by efforts that retain or minimize disturbance to key biological legacies contributing to saprobe diversity. This may include leaving patches of understory shrubs and advance regeneration, a variety of woody material size and age classes (Brazee et al. 2014), or even whole dead trees (Heilmann-Clausen and Christensen 2004), during harvest.

Parasitic fungi, including both polyporoid conk fungi that often parasites living trees (e.g*., Ganoderma*) and parasites of fungi (e.g., *Tremella*) and insects (e.g., *Cordyceps*), were frequently detected in the forests but were entirely absent from the patch cuts. This is likely because hosts were removed or displaced during timber harvest. The removal of large-diameter host trees and any overall decrease in large-diameter deadwood (another important substrate for many polypores; Toivanen et al. 2012), should decrease the fruiting of parasitic polypores, by far the most abundant class of parasites detected in our surveys. Timber harvest may also impact the availability of hosts for non-polyporoid parasites. For instance, the saprobic genus *Stereum*, host

to the parasitic fungus *Tremella aurantia*, was found almost exclusively in intact forest (Table A1). Similarly, forest harvest typically disrupts communities of moths and butterflies (Summerville and Crist 2002), important hosts of the parasite *Coryceps militaris* (Shrestha et al. 2016). Taken together, logging-induced declines in various host taxa would likely decrease the fruiting of parasitic mushrooms as a group. Yet, parasitic fungi were so highly variable in abundance, often due to dense clusters of conk fungi on individual trees, that no statistical difference in biomass or richness was detected between patch cuts and forests.

Ectomycorrhizal fruiting decreased sharply in response to timber harvest, with declines evident in richness and diversity of genera along with mean biomass of fruiting bodies. Similar trends have been documented in western North America, suggesting that forest harvest consistently decreases the fruiting of ectomycorrhizal mushrooms as a group (Durall et al. 2006). While this decrease in fruiting is not necessarily indicative of a similar loss of ectomycorrhizal taxa belowground (Gardes and Bruns 1996), several studies suggest that timber harvest alters belowground ectomycorrhizal communities as well (Byrd et al. 2000; Jones et al. 2003; Parladé et al. 2019). Shifts in ectomycorrhizal communities and fruiting patterns may be driven by increased soil temperatures, decreased moisture availability due to harvest disturbance of the forest floor, or otherwise inhospitable environmental conditions post-harvest, in addition to the direct losses of host trees. Perhaps importantly, much of the regenerating woody vegetation in the patch cuts was dominated by non-ectomycorrhizal plant species, such as red elderberry and pin cherry. Dominance of these non-ectomycorrhizal species could conceivably reduce abundance of ectomycorrhizal fungal taxa in the immediate aftermath of timber harvest. Root tip colonization of new seedlings steadily decreases at increasing distances from live trees, with the lowest colonization rates occurring beyond 15 m from live trees (Dickie and Reich 2005).

Moreover, ectomycorrhizal fruiting richness is reported to decrease exponentially with increasing cutblock size (Durall 1999), an effect that can be partially offset by the retention of mature trees in harvested areas (Luoma et al. 2004). This suggests that intact forests, as well as mature retention trees, play an important role in maintaining ectomycorrhizal communities belowground, which (coupled with other environmental variables) would help to explain the marked difference in ectomycorrhizal mushroom fruiting that we observed between patch cuts and nearby forest.

It is worth noting that some ectomycorrhizal taxa are sensitive even to low-intensity timber harvest regimes (Leski et al. 2019). These sensitive taxa may not be represented in our surveys due to the history of light thinning in the intact forest. Nevertheless, the absence of additional ectomycorrhizal taxa in the forest stands is unlikely to have biased our comparison of fruiting between patch cuts and intact forest.

Timber harvest may reduce opportunities for direct and indirect ectomycorrhizal spore dispersal to potential seedling symbionts. For instance, declines in mushroom fruiting caused by timber harvest likely decrease the quantity of spores dispersed locally by wind. Many ectomycorrhizal taxa also rely on fungivorous mammal and invertebrate species for indirect dispersal (Halbwachs and Bässler 2015), including several small mammal species known to consume and disperse large quantities of ectomycorrhizal mushrooms in this region (Stephens and Rowe 2020). Harvest-induced changes in canopy and ground cover coupled with declines in fruiting likely alter habitat suitability or movement patterns of these dispersers and thus reduce spore dispersal. Dietary shifts in small mammals and invertebrates driven by declines in ectomycorrhizal mushrooms may also have cascading impacts on forest food web structure and function.

Our functional group findings are likely representative of broader trends beyond the one year of sampling. Fruiting of individual ephemeral species is often inconsistent and difficult to predict in any given year (Straatsma et al. 2001); however, interannual fruiting patterns are more predictable by functional type. Mycorrhizal and saprobic mushroom fruiting abundance appear to fluctuate in concert from year to year (Straatsma and Krisai-Greilhuber 2003), even while exhibiting high variability at the species level and years of high and low fruiting overall. The vast majority of parasitic and many saprobic taxa documented in this study form fruiting bodies over the course of several years, so it is unlikely that patch cut-forest differences in fruiting abundance in these functional groups would vary greatly from year to year. Taking all of this into account, we suggest that the fruiting patterns we observed at the functional level are broadly representative of differences in epigeous fungal fruiting between patch cuts and intact forests in the years immediately following harvest. If relative differences in fruiting abundance at the functional level between patch cut and forest shifted among years, this would likely be indicative of directional change in fungal fruiting communities (succession) rather than interannual fluctuation in fruiting patterns. Furthermore, limiting sampling to summer months is unlikely to have biased the trends detected in this study. While it is plausible that seasonal differences in moisture and temperature could result in fruiting differences in patch cuts relative to forests, other studies that have sampled during a broader temporal window including both the spring and fall seasons (e.g., Durall et al. 2006) have documented similar trends to those observed here. Continued monitoring of these cuts over the coming years would confirm whether long-term trends mirror those of immediate response windows.

We demonstrate that timber harvest led to stark differences in fungal fruiting patterns in the second summer following harvest. These differences were particularly evident at the

community level, with lower richness and diversity, as well as greater community concordance, in the patch cuts than in the surrounding forest. Among functional groups, ectomycorrhizal fungi were most impacted by timber harvest with decreased fruiting richness, biomass, and diversity in the patch cuts. Changes in fungal fruiting abundance and community structure at this early point following timber harvest have downstream implications for fungal population connectivity, ecosystem health, nutrient cycling, and forest regeneration. In northern New England, where large parcels are commonly managed for timber production (Daigle et al., 2012), silvicultural strategies that incorporate impacts on fungal taxa may in turn enhance forest regeneration by supporting the ectomycorrhizal fungal communities critical for nutrient acquisition by trees. Strategies of particular interest may include retention of downed woody material and live overstory and understory trees, particularly ectomycorrhizal tree species such as *Betula* spp., as well as strategies that prioritize recolonization of harvested areas specifically by ectomycorrhizal tree seedlings. Such practices, aimed at maintaining mature forest conditions adjacent to and throughout harvested areas, may preserve mycorrhizal communities and soil conditions requisite for fungal fruiting, thereby promoting more diverse fungal fruiting communities.

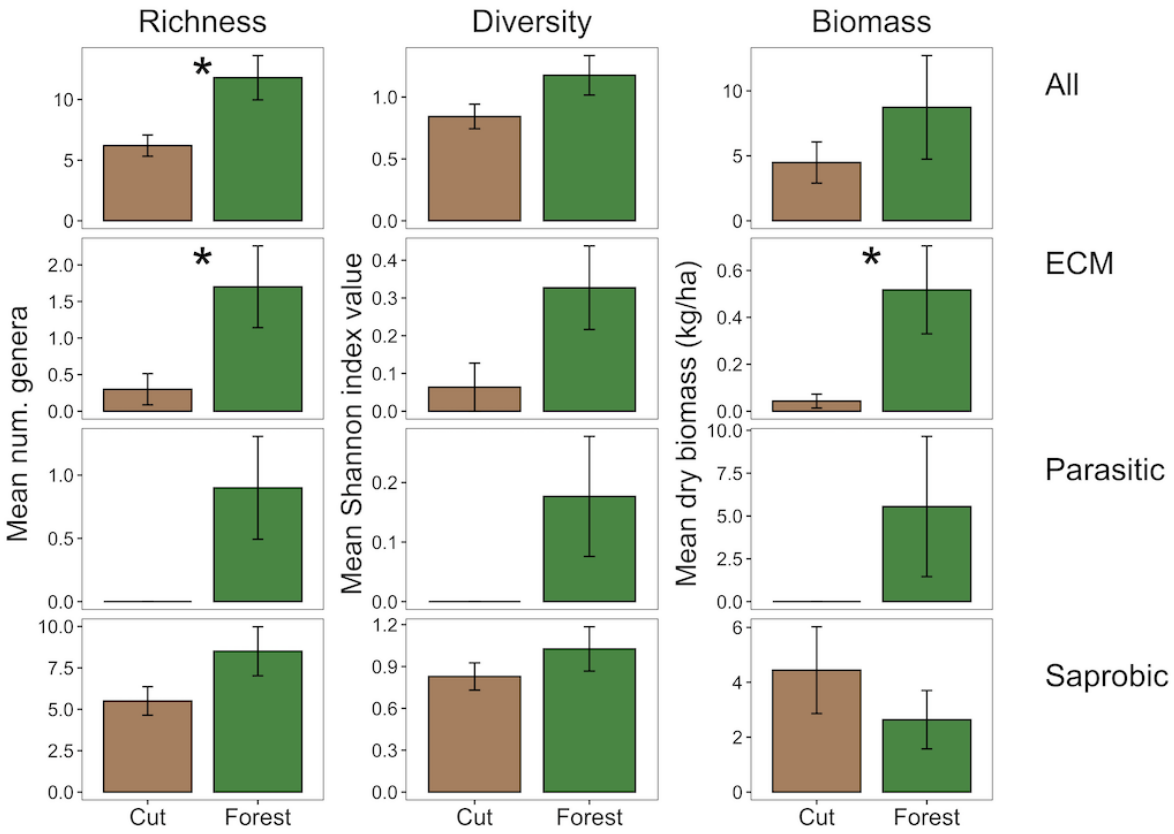

Figure 1.1. Values (means ± standard error of the mean) for genus richness, Shannon-Weiner diversity index (also at the genus level), and dry biomass of fruiting bodies per survey for all functional groups combined and for ectomycorrhizal (ECM), parasitic, and saprobic groups individually. Asterisks indicate significance ($p < 0.05$). Note that y-axes are scaled independently.

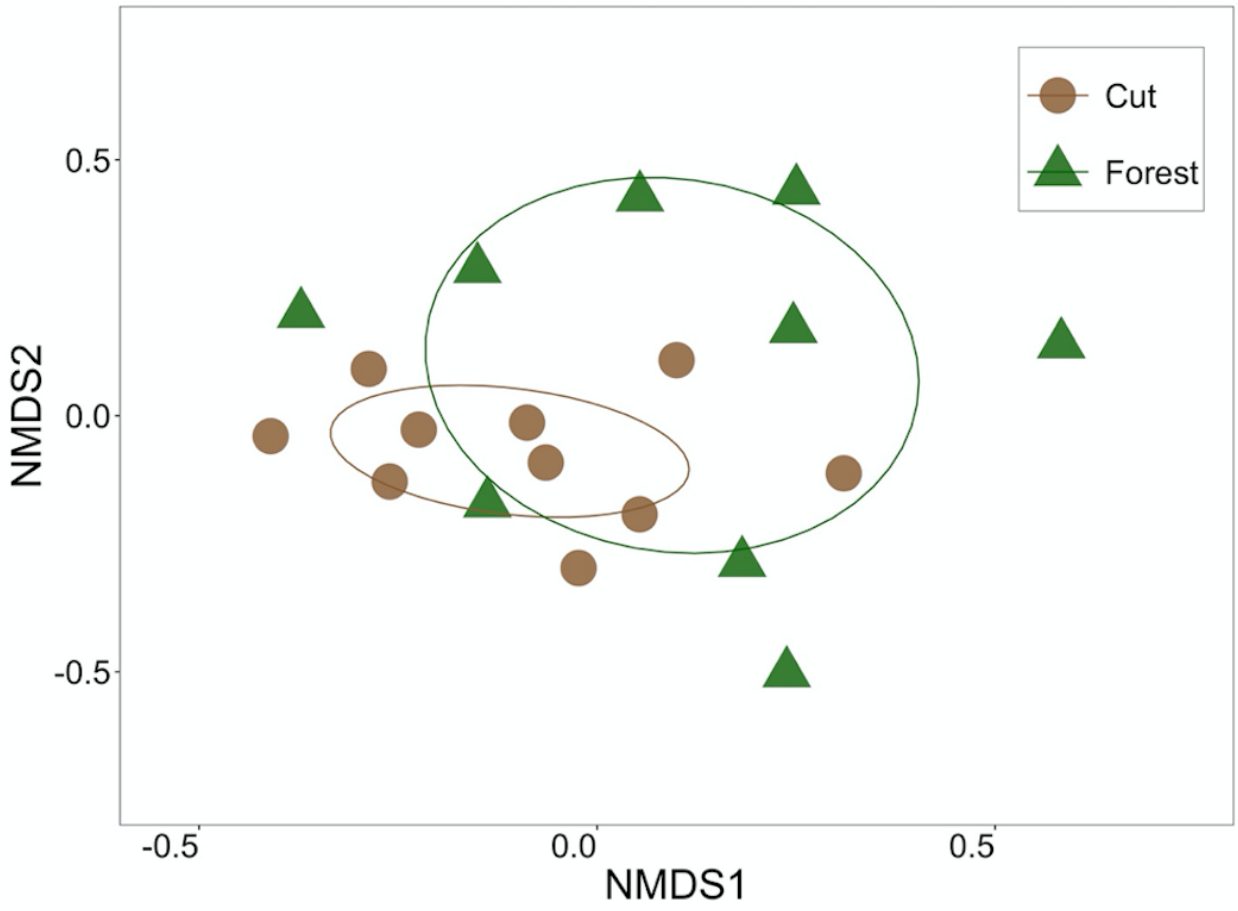

Figure 1.2. Two-dimensional nonmetric multidimensional scaling (NMDS) ordination (final stress = 0.15) of mushroom communities in patch cuts (circles, n = 10) and forests (triangles, n = 9). Greater pairwise distance between markers indicates decreased similarity in community composition. Ellipses represent 50% confidence intervals around the centroid, and ellipse size approximates relative community concordance.

CHAPTER 2

WIND VERSUS SMALL MAMMAL-FACILITATED FUNGAL SPORE DISPERSAL

INTRODUCTION

Fungal spore dispersal is a complex ecological process with profound impacts on ecosystem structure and function. Spore dispersal shapes community composition and genetic diversity of fungi responsible for a variety of ecosystem processes including decomposition and nutrient cycling (Clemmensen et al. 2015) and host-pathogen interactions (Ostry and Laflamme 2008). Spore dispersal also influences plant community composition (Van Der Heijden et al. 2008) and drought resilience (Parke et al. 1983) by driving establishment of arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) fungal symbionts, which exchange water and soil nutrients for carbohydrates (Smith and Read 1997). In forested systems, small mammals consume and disperse fungal spores (Stephens and Rowe 2020), but little is known about the impact of small mammal dispersal compared to other mechanisms such as wind (Vašutová et al. 2019).

Fungal spores disperse through a variety of mechanisms, including water, wind, and animal-facilitated transport. Many fungi, particularly those that fruit aboveground, are often presumed to be highly dependent on wind dispersal. Fungal taxa often possess adaptations that enhance spore dispersal into the airstream, such as the ability to generate convection currents that pull spores from beneath the cap and into the air (Dressaire et al. 2016). Animal-facilitated transport is a common fungal dispersal pathway both for aboveground (mushroom) and belowground (truffle) fruiters (Vašutová et al. 2019). While some animals facilitate transport

when spores attach to their body (e.g., Lilleskov and Bruns 2005), mycophagy (the consumption of fungal material) is better documented. In some instances, fungi have evolved to attract animal consumers by releasing pungent volatile compounds (Johnson and Jürgens 2010; Stephens et al. 2020). Many animal taxa are believed to consume and disperse fungal spores (either directly or by consuming other mycophagus animals), including invertebrates such as beetles (Park et al. 2014), worms (Harinikumar and Bagyaraj 1994), and flies (Chen et al. 2014), as well as vertebrates including birds (Caiafa et al. 2021), ungulates (Lekberg et al. 2011), herptiles (Lilleskov and Bruns 2005), mammalian carnivores (Aguirre et al. 2021), marsupials (Nuske et al. 2017), and small mammals (rodents and shrews). Small mammals, by nature of their ubiquity and high population densities, may serve as a particularly important spore dispersal mechanism (Johnson 1996), and are known to consume both saprotrophic (Spooner 2007) as well as AM and ECM fungi (Vašutová et al. 2019; Paz et al. 2021).

Small mammal-facilitated dispersal of fungal spores (particularly mycorrhizal species) may assist in the establishment of tree seedlings following disturbances as diverse as volcanic eruptions (Allen et al. 1992), glacial recession (Cázares and Trappe 1994), and timber harvest (Stephens et al. 2021). In some cases, exotic small mammals even facilitate invasion of exotic terrestrial plants by dispersing associated fungi (Adler et al. 2018). Similarly, absence of small mammals may preclude seedling establishment (Terwilliger and Pastor 1999). Importantly, not all small mammal species disperse the same fungal taxa, even within the same locality. Thus, diverse small mammal communities support dispersal of a broader range of fungi (Nuske et al. 2017; Stephens et al. 2021).

The degree to which small mammal-facilitated dispersal is redundant with or complementary to wind-driven dispersal is not well understood. Complementarity would indicate

that small mammals play a crucial role in dispersing ecosystem-altering fungi that have limited ability to disperse by other means. If small mammal- and wind-facilitated dispersal are indeed complementary, then there may be identifiable physical differences between the fungal taxa that each mechanism disperses. For instance, spores might display melanization for enhanced UV protection (Deveautour et al. 2020), specific ornamentation to assist with either lift or gut retention (Halbwachs and Bässler 2015), and size differences, which could reflect the relative likelihood of becoming airborne (Norros et al. 2014). Comparisons of dispersal mechanism and physical characteristics might reveal adaptive strategies of various fungal lineages or functional types.

In this study, we compare fungal dispersal by wind and three species of small mammals in recently harvested patch cuts and adjacent intact forest in northern New Hampshire, USA. We couple field surveys for spores and small mammals and integrate microscopy and Illumina sequencing to address the following questions: (1) Do wind and small mammals disperse similar or different communities of spores into disturbed areas following timber harvest? And, (2) Do physical differences in spores reflect differences in dispersal mechanisms?

MATERIALS AND METHODS

Study Site

Our study was conducted at the Dartmouth Second College Grant, a 10,800 ha forested property in Coos County, New Hampshire, USA. Sampling took place in eight experimental patch cuts (0.4 ha) and adjacent northern hardwood forest matrix last thinned approximately 20 years prior (Jevon et al. 2019). Dominant tree species include sugar maple (*Acer saccharum*; AM associated), yellow birch (*Betula alleghaniensis*; ECM associated), and American beech (*Fagus*

grandifolia; ECM associated). All patch cuts were harvested between August and December 2017 as part of the Adaptive Silviculture for Climate Change network to test forest adaptation strategies to climate change and shifting disturbance regimes (Nagel et al. 2017). Patch cuts were created by hand-felling trees except for one or two large diameter seed trees and young saplings. All tops and branches were left as downed woody material. Regenerating patch cuts contained 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 & Scat Collection

To quantify small mammal home ranges and collect spore-bearing scat, we live-trapped small mammals (rodents and shrews) during the summers of 2018, 2019, and 2020. Each year, trapping occurred at each of the eight patch cuts for three consecutive nights once a month from June-August (July-August in 2020 due to delays caused by COVID-19).

We surveyed small mammals using a trapping web design which contained eight 60 m transects, each with seven traps spaced 10 m apart for a total of 56 trap stations. Each transect began 30 m deep in the cut (close to the center of the cut) and extended 30 m into the adjacent forest (Fig. 2.1). Live trapping was conducted using Sherman live traps (H. B. Sherman Company) containing birdseed for bait and synthetic cotton to provide insulation. All captured rodents were marked with uniquely numbered ear tags (model 1005-1; National Band and Tag Company). Voles were tagged with an additional passive integrated transponder (model HPT9; Biomark) in case of ear tag loss. Scat was collected from traps upon capturing an individual for the first time each month and frozen (-20°C) immediately upon collection. Traps that contained

animals were washed and replaced with clean traps to prevent cross-contamination of scat samples.

For this study, we focused on eastern chipmunks (*Tamias striatus*), southern red-backed voles (*Myodes gapperi*), and woodland jumping mice (*Napaeozapus insignis*). These three rodent species were chosen both for their high local abundance and for their documented propensity to consume and disperse fungal material in this region (Stephens and Rowe 2020). For each target species, we selected approximately 20 scat samples (20 *T. striatus*; 17 *M. gapperi*; 23 *N.* insignis, for a total of 60 samples) from August 2019 (to coincide with the timing of spore trapping; see below). Each sample was freeze-dried and ground into a fine powder for molecular and microscopic analyses. We interpreted scat contents as an indicator of fungal spore dispersal; although presence of spores in scat does not prove spore viability *per se*, numerous studies have demonstrated that fungal spores remain viable after passage through small mammal digestive tracts (Paz et al. 2021, Castillo-Guevara et al. 2011).

Spore Traps

To measure spore deposition and dispersal by wind, we deployed six spore traps at each of the eight study sites for two weeks during August 2019. We selected this period due to the relative increase in abundance of fungal fruiting bodies in this region during late summer (e.g., Stephens et al. 2017, Borgmann-Winter et al. 2021). Spore traps were placed 12 m apart, along a 60 m transect extending from 30 m deep in the patch cut to 30 m deep in the forest. Each trap consisted of one funnel (10.2 cm diameter), mouth facing upward, anchored into a 1 L, ethanol-containing water bottle anchored approximately 15 cm into the soil. Each funnel contained a piece of 125µm filter paper to prevent large particles from entering the traps. It is worth noting

that the size of filter paper prevented the occurrence of any spores greater than 125µm in our traps. A limited number of AM spores are known to exceed this size (Vašutová et al. 2019) but there is evidence that wind-dispersed AM spores tend to be smaller (Chaudhary et al. 2020), so it is likely that our trapping captured all wind-borne AM spores. Traps collected spores passively via wind-driven deposition or rain events. One spore trap was damaged in the field and excluded from analysis, but the remaining spore traps (n = 47) were collected at the end of the two-week sampling period. Spores were strained onto 0.45µm 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

Powdered scat samples were prepared for microscopic analysis procedures outlined in Stephens et al. (2017). Spore isolates were spread onto a 22 x 22 mm section of a glass slide, cleared with Visikol (a chloral hydrate substitute; 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 sample into a vial with 1mL of 95% ethanol. Samples were then centrifuged to collect spore material at the bottom of each vial, and 900µl of ethanol was decanted. The remaining 100µl of sample was vortexed to homogenize. The entire spore-bearing solution was then spread onto a 12 x 12 mm section of a glass slide, cleared with Visikol, and sealed with Flo-Texx Mounting Medium.

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

Spore Trait Data Collection

We scored all spore morphotypes for three traits: greatest length, ornamentation, and degree of melanization. Greatest length was measured directly using the measuring tool in the software program AMScope (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 non-melanized, hyaline spores, and 5 representing heavily melanized, dark brown spores. We used these rankings to test for differences in physical characteristics between wind-dispersed spores and mammal-dispersed spores.

Molecular Analysis

The spore-bearing side of every remaining filter paper segment was scraped into a unique vial using a sterilized razor blade. We extracted genomic DNA from all samples (scat and spore trap) using the DNeasy Powersoil Kit (Qiagen, Hilden, Germany) according to standard protocol. We conducted polymerase chain reactions (PCR) in duplicate to amplify fungal DNA in the ITS region. Primers contained Illumina TruSeq adaptor 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 were conducted using Phusion High Fidelity polymerase, a 49ºC annealing temperature, and 35 PCR cycles, as developed by Kohout et al. (2014). Although these primers are somewhat biased against AM fungi, they have been shown to perform well at detecting community-scale differences (Lekberg et al. 2018), which was the aim of the present study. Illumina sequencing was conducted using a NovaSeq 6000 platform (Illumina, San Diego, California, USA) with 2 x 250 bp chemistry at the Hubbard Center for Genome Studies at the University of New Hampshire (Durham, New Hampshire, USA).

Bioinformatic Analysis

We extracted the ITS2 region sequences using ITSxpress in QIIME2. Merged sequences were assigned to amplicon sequence variants (ASVs) using the DADA2 protocol v1.8 (Callahan et al. 2016). We trimmed primers and sequences and removed chimeras. To increase quality, sequences were truncated at the first quality score of two, and sequences less than 100 bases were discarded. Taxonomy was assigned by comparing ASV sequences to the UNITE database

(Nilsson et al. 2019). ASVs were also assigned to trophic type (e.g., ectomycorrhizal) and fruitbody type (e.g., gasteroid) based on the FungalTraits database (Põlme et al. 2020).

Statistical Analysis

Home range analysis

We used mark-recapture data from all three years to model home range and core area for *T. striatus*, *M. gapperi*, and *N. insignis*. Home range, defined here as the area in which an individual is likely to occur at any given point in time (Worton 1989), reflects a species' resource requirements as they relate to local environmental factors including distribution of food and habitat resources (Burt 1943; Tisell et al. 2019). We treated home ranges as the maximum probable area estimate for spore dispersal potential, whereas core areas (zones of intense use within home ranges where individuals spend the majority of their time) served as a probable estimate for concentrated spore dispersal potential. To model home range, we used a utilization distribution (UD) kernel density model (Anderson 1983; Worton 1989) in the R package "adehabitatHR" (Calenge 2006). Models were calculated for each adult male and female captured at least five times in one summer on a given trapping web. Home ranges were calculated at the 95% UD isopleth to eliminate outliers. Core areas were calculated according to Vander Wal and Rodgers (2012) by plotting UD area against volume and identifying the point at which the slope of the fitted line was equal to one. Core area was the area before the slope equaled one, in which proportional home range use increased at a greater rate than proportional home range area. Home ranges and core areas were projected into QGIS3.4, where we measured area and maximum distance traveled into the patch cut for each individual.

We generated home range and core area estimates for both sexes of all three target species. For each species, home range and core area estimates were compared between sexes using two-sampled t-tests. Maximum linear dispersal distance was determined for males and females of each species by measuring the greatest length of each home range polygon in QGIS 3.4. For each species, maximum dispersal distance was compared between sexes using a two-sampled t-test.

Community analyses

We used sequencing data to compare fungal communities dispersed by wind and small mammals. We also tested for fungal community differences among the three mammal species. To identify the fungal functional groups dispersed by different mechanisms (wind, *M. gapperi*, *N. insignis*, or *T. striatus)*, we compared the overall proportion of reads within each sample that belonged to each of eight major functional types: AM (Glomeromycota), ECM, litter saprotroph, mycoparasite, plant pathogen, soil saprotroph, unspecified saprotroph, and wood saprotroph. This comparison was conducted separately for wind dispersal and each mammal species.

To identify macrofungal fruiting body types dispersed by different mechanisms, we calculated the proportion of macrofungal reads in each sample that belonged to each of eight fruiting template types. Macrofungal fruiting types were agaricoid (mushroom), clavarioid (coral), corticioid (crust), gasteroid (puffball), gasteroid hypogeous (truffle), polyporoid (conk), tremelloid (jelly), and AM sporocarp (all taxa in the genus *Glomus*). We tested for differences in functional groups and fruiting types within each disperser type using ANOVA and Tukey's Test of Honest Significant Difference.

For all further community analyses, reads were rarefied to 1000 reads per sample to weight all samples equally, and three samples with fewer than 1000 reads were removed from analysis. We used these rarefied data to compare taxonomic richness (using ASVs) between scat and spore trap samples for all fungi, AM fungi, ECM fungi, and all macrofungi using two-sampled t-tests. To evaluate similarity between fungal communities dispersed by different mechanisms, we used a Bray-Curtis dissimilarity matrix based on ASVs and the reads for each scat sample and spore trap sample. In this matrix, we included taxa that were present in at least 5% of samples. To visualize trends in compositional structure between community types we used non-metric 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 test in vegan. To quantify the impact of dispersal mechanism on community composition, we used a multivariate repeated-measures analysis of variance (PERMANOVA), using 1000 randomized datasets. We used PERMANOVA to compare spore trap and scat communities overall and location of sample (forest or patch cut) for spore trap and scat communities separately. We used pairwise PERMANOVA (Arbizu et al. 2021) with a Bonferroni correction as a post hoc test for differences in communities dispersed by the three mammal species.

Morphological comparisons

We compared three morphological characteristics between spore morphotypes detected only in mammal scat and morphotypes detected only in spore traps. To compare degree of melanization, we used the Cochran-Armitage trend test, a parametric test designed for comparisons of categorical and ordinal variables, in the R package "CATT" (Du and Hao 2017).

To compare overall spore length, we used a two sampled t-test. To compare the presence or absence of ornamentation, we used a chi-square test of independence. We conducted a qualitative comparison of various ornamentation types (e.g., spikes, tapered attachments, bumps) between dispersal mechanisms, as a relatively small sample size for each ornamentation type precluded statistical comparisons. Comparisons of melanization, ornamentation, and length between mammal scat and spore traps were also conducted specifically for AM morphotypes using the same statistical tests. We did not conduct separate tests for ECM morphotypes due to an insufficient number of wind-dispersed ECM taxa. All statistical analyses were conducted in R version 3.6.3 (R Core Team 2021).

RESULTS

Home Range

All three target species were frequently captured in both the patch cuts (~40%) and the intact forest (~60%). From 2018-2020, we captured a total of 202 individual *M. gapperi*, 271 individual *N. insignis*, and 137 individual *T. striatus*. Of these individuals, we captured 24 *M. gapperi* ($n_{male} = 7$, $n_{female} = 17$), five *N. insignis* ($n_{male} = 1$, $n_{female} = 4$), and 42 *T. striatus* ($n_{male} = 17$, $n_{female} = 25$) at least five times, which we used to model home range and core area for each species (Fig. 2.2). Male *M. gapperi* had significantly larger home ranges (2.29 ± 0.65 ha versus 0.36 ± 0.06 ha; t = 4.64, df = 22, p = 0.0001), and core areas (0.79 ± 0.23 ha versus 0.12 ± 0.02 ha; t = 4.52, df = 22, p = 0.0002) than females (Fig. 2.3). Similarly, male *T. striatus* had significantly larger home ranges (1.36 ± 0.29 ha versus 0.68 ± 0.08 ha; t = 2.65, df = 40, p = 0.0115) and core areas (0.45 ± 0.09 ha versus 0.23 ± 0.03 ha; t = 2.49, df = 40, p = 0.0172) than females. For *N. insignis*, average home range size was 1.89 ± 0.68 ha and core area was 0.62 ±

0.25 ha, but small sample sizes precluded a comparison between sexes. For all three small mammal species, core areas were on average 33% of the larger home range area. As a result of sex-driven differences in home range and core area size, male *M. gapperi* also had significantly longer potential dispersal distances than females (188.6 ± 27.1 m versus 80.2 ± 7.4 m; $t = 5.29$, $df = 22$, $p < 0.0001$). Similarly, male *T. striatus* had longer maximum dispersal distances than females (152.5 ± 17.6 versus 106.9 ± 8.0 m; $t = 2.64$, $df = 40$, $p = 0.0116$). *N. insignis* maximum dispersal distance (males and females combined) was 164.7 ± 36.1 m.

Genetic Analyses

Sequencing revealed 7,970 unique fungal ASVs (including 1,233 described species) in mammal scat and 9,484 unique ASVs (including 1,559 described species) in spore traps. Approximately 16% of all ASVs occurred in both mammal scat and spore traps. ASVs from mammal scat represented 377 known fungal families belonging to 140 known orders, and ASVs from spore traps represented 402 known families belonging to 147 known orders. A total of 4,335 ASVs were unidentified at the family level, and of these, 2,764 were unidentified to order. For both spore traps and scat samples, approximately 65% of ASVs were present in only a single sample (Fig. 2.4). Spore trap samples were approximately one and a half times more species rich than scat samples ($t = 5.25$, $df = 76.97$, $p < 0.0001$; Fig. 2.5)

ECM taxa represented 3.3% of all ASVs detected, and AM taxa represented 1.8% of ASVs. Scat samples were slightly more species rich than spore traps for ECM taxa ($t = 2.84$, $df = 74.93$, $p = 0.006$) and nearly five times more species rich for AM taxa ($t = 5.21$, $df = 23.749$, $p < 0.0001$; Fig. 2.5). For both AM and ECM taxa, over 99% of all reads occurred in scat samples rather than spore traps.

Approximately 30% of ASVs belonged to macrofungi (such as mushrooms, truffles, and polypores) and the remaining 70% belonged to fungi that produce microscopic or no known fruiting structures. When looking specifically at macrofungi, spore traps were nearly five times more taxon-rich than scat samples ($t = 11.15$, $df = 52.41$, $p < 0.0001$; Fig. 2.5).

The taxonomic community present in spore traps was distinct from the community present in mammal scat. This was evident in the NMDS ordination (Fig. 2.6), with right-left separation between spore trap samples and the three small mammal species. PERMANOVA results indicate that wind-dispersed and mammal-dispersed communities were significantly different ($F = 32.23$, $df = 105$, $p = 0.001$). Mammal-dispersed communities had significantly greater dispersion about the median (Betadisper; average distance to median 0.544 vs. 0.433) than wind-dispersed communities (Permutest; $F = 20.378$, $df = 105$, $p = 0.001$). Among spore trap samples only, communities differed between patch cuts and forest (PERMANOVA; $F = 3.77$, $df = 45$, $p = 0.001$), a pattern which is also evident in the NMDS ordination. Among scat samples, spore communities did not differ between patch cuts and forest. Mammal-dispersed spore communities did however differ between *T. striatus* and both *M. gapperi* (Pairwise PERMANOVA; $F = 3.55$, $p_{adj.} = 0.003$) and *N. insignis* (Pairwise PERMANOVA; $F = 4.22$, $p_{adj.} = 0.003$). Fungal communities did not differ between *M. gapperi and N. insignis* scat samples. Sex did not significantly affect species richness in scat samples for any of the three mammal species.

Spore traps and scat samples also contained complementary communities of fungi when compared by functional type. For instance, spore traps contained elevated proportions of litter saprotrophs, mycoparasites, plant pathogens, and wood saprotrophs compared to other functional types and contained particularly low proportions of AM and ECM fungi (Fig. 2.7). In contrast,

small mammal scat samples contained comparatively high proportions of ECM and AM fungi, as well as unspecified saprotrophs.

Similar complementarity was observed when comparing fruiting styles of macrofungi in spore traps and scat samples (Fig. 2.8). Spore traps contained high proportions of taxa that produce agaricoid (mushroom), corticioid (crust), and polyporoid (conk) sporocarps. Scat samples contained high proportions of agaricoid, hypogeous gasteroid (truffle) and AM sporocarp-producing taxa. *M. gapperi* samples also contained elevated levels of tremelloid (jelly) taxa, and *N. insignis* contained elevated levels of corticioid taxa.

Spore Morphotype Occurrence and Morphology

We identified 25 distinct spore morphotypes in mammal scat and 30 distinct morphotypes in our spore traps. Two additional morphotypes were present in both mammal scat and spore traps. Independent of dispersal method, most spore morphotypes occurred infrequently. Among wind-dispersed morphotypes, 67% of morphotypes (20 of 30) occurred in fewer than half (23 of 47) of all samples. In mammal scat, 96% of all morphotypes (24 of 25) occurred in fewer than half (30 of 60) of individuals. Among the 12 spore morphotypes believed to belong to AM fungi, five were detected exclusively in spore traps and seven were detected exclusively in mammal scat. Among the 16 spore morphotypes believed to belong to ECM fungi, 15 were detected exclusively in mammal scat and a single morphotype was detected exclusively in spore traps.

Spore morphotypes exhibited a range of physical characteristics, including a variety of ornamentation types (such as spikes, wings, ridges, and bumps), melanization levels (from entirely unmelanized to highly melanized) and lengths (3.6 µm-121.3µm). Across all spores, we

detected no difference in presence of ornamentation or degree of melanization between wind- and mammal-dispersed spores. Indeed, mean (±SE) melanization scores (from 1-5) were almost identical for spores dispersed by wind (2.83 ± 0.21) and small mammals (2.93 ± 0.24). Spores present in mammal scat were on average greater in length than spores present in spore traps (37.70 ± 6.60 μm versus 18.17 ± 3.25 μm; $t = 2.65$, $df = 53$, $p = 0.0118$; Fig. 2.9). We noted a bimodal size distribution among spores dispersed via both mechanisms, with larger spores typically belonging only to AM species, and smaller spores belonging to both AM and ECM species.

There was no difference in ornamentation rate or degree of melanization between AM spores found in mammal scat and those found in spore traps. Mammal-dispersed AM spores were greater in length than wind-dispersed AM spores (82.74 ±7.98 μm versus 48.71 ± 11.64 μm; $t = 2.50$, $df = 10$, $p = 0.0312$). The small sample size of wind-dispersed ECM fungi prohibited comparisons of ECM spores between scat and spore trap samples.

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 specific ornamentation types (i.e., spikes, bumps, ridges, tapered attachments). For instance, unornamented morphotypes comprised 50% of wind-dispersed spores, whereas only 25% of mammal-dispersed morphotypes were unornamented. 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

We detected differences between wind-dispersed and mammal-dispersed spore communities, indicating that these mechanisms play complementary roles in fungal spore dispersal and thus ecosystem function. We found that different small mammal species dispersed different fungal communities, implying that diverse mammal communities enhance fungal diversity following disturbance. We also found that small mammals appeared to import spores from the forest into the patch cuts more consistently than wind, suggesting that small mammals play an important role in facilitating regeneration of forests communities. Results from spore microscopy indicate that differences in dispersal strategy are linked to differences in spore size.

Fungal Community

We detected differences in fungal taxonomy, functional type, and fruiting body styles between wind and mammal-dispersed spore communities. Taxonomic differences were evident not only in distinct NMDS ordination clustering and significant PERMANOVA results, but also based on the minimal overlap of ASVs (16%) and spore morphotypes (two out of 57) between the two dispersal mechanisms. These findings underscore the importance of small mammals as spore dispersers and add to growing literature documenting their role as dispersers for ECM taxa (e.g., Jacobs and Luoma 2007; Frank et al. 2008; Nuske et al. 2019, Stephens et al. 2020) and AM taxa (e.g., Mangan and Adler 2000; Fracchia et a. 2011; Adler et al. 2018). Our work builds on such studies by providing a clear, side-by-side comparison of dispersal mechanisms and demonstrates that mammal-driven dispersal is complementary to wind-driven dispersal. This is, to our knowledge, the first time that spore communities dispersed by wind and mammals have been directly compared using genetic analyses (but see Warner et al. 1987 for an AM-only comparison using microscopy).

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 mycorrhizal taxa and unspecified saprotrophs were most abundant in mammal samples. Scat samples were significantly more species-rich than spore traps for both AM and ECM taxa, despite substantially greater overall taxonomic richness in spore traps. This indicates that mammals play an outsized role in mycorrhizal spore dispersal.

Variation in dispersal of functional types was also evident among mammal species. All three mammal species appeared to be relatively strong AM dispersers, whereas *M. gapperi* and *T. striatus* also appeared to be strong ECM dispersers—findings that align with other recent work in this region (Stephens et al. 2021). Thus, dispersal complementarity exists not only between wind and small mammals, but also among small mammal species.

We also found that wind and small mammals disperse spores belonging to fungi with different fruiting body types. Spore traps contained high levels of agaricoid (including boletoid), corticioid, and polyporoid fruiters. In contrast, mammal scat contained substantial amounts of gasteroid hypogeous taxa and AM sporocarps (particularly for *N. insignis*), a finding that matches quite well with existing literature (Vašutová et al. 2019). The additional presence of substantial agaricoid material in small mammal scat supports previous findings (e.g., Stephens and Rowe 2020) that suggest small mammal consumption and potential dispersal of mushroom-bearing taxa should not be underestimated. Somewhat surprisingly, *M. gapperi* appeared to consume tremelloid (jelly) fungi, a behavior that is not well documented in the literature. Also surprising was the relatively high proportion of corticioid (crust) fungi present in *N. insignis* scat.

Spore Morphology

Mammal-dispersed spores were, on average, significantly greater in length (or diameter, for round spores) than wind-dispersed spores. This pattern held true both for all spores combined and specifically for AM spores. Spore size is generally assumed to relate to dispersal strategies for a variety of fungal taxa and functional types (Kauserud et al. 2008, Halbwachs and Bässler 2015), and small spores have been reported to travel farther via wind dispersal than larger spores (Norros et al. 2014, Dighton and White 2017).

For AM spores specifically, wind-dispersed spore length ranged from 16 to 75 µm, with an average length of 50 µm (compared to an average of 82 µm for mammal-dispersed). Chaudhary et al. (2020) observed a similar pattern in wind-dispersed AM spores, reporting that the majority were <70 µm 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 mycophagy (Stephens et al. 2021). The filter paper used in our spore traps limited collection of airborne spores to <125 µm, but the lack of any spores >75µm in our spore traps suggests that our filter design did not bias our results.

We found no differences in melanization between wind and mammal-dispersed spores. Other studies have also found melanization to be a poor predictor of dispersal strategy (windborne versus non-windborne) or life history (saprotroph versus ectomycorrhizal) (Halbwachs et al. 2015, Chaudhary et al. 2020). This may be because melanin is able to protect spores both from the prolonged exposure to ultraviolet radiation expected in airborne dispersal (Singaravelan et al. 2008), and from the harsh conditions present in digestive tracts of mycophagous animal species (Dighton and 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 mycophagy

(Halbwachs and Bässler 2015, Pringle et al. 2015). Although we noted a lower rate of ornamentation in wind-dispersed morphotypes, this difference was not statistically significant, although that may partly reflect a relatively small sample size. In mammal-dispersed morphotypes, we observed a high rate of ornamentation and a diversity of ornamentation styles. It is possible that differences in ornamentation between wind and mammal-dispersed spores exist and that a presence-absence approach is insufficient to detect these differences. It is also possible that certain ornamentation types are capable of taking advantage of multiple dispersal pathways (i.e. both wind and mycophagy), as is the case in some instances of seed dispersal (e.g., der Weduwen and Ruxton 2019).

Dispersal Potential

Wind- and mammal-facilitated spore dispersal are local-scale processes. Although we did not directly measure wind dispersal distances, we found different wind-dispersed spore communities between patch cuts and adjacent intact forest. This community discordance suggests that spore dispersal for many fungal taxa may be distance-limited at the scale of tens of meters, and that wind-driven spore dispersal into deforested areas may not be highly effective for many forest fungal taxa. Reported distances of wind dispersal vary substantially. Our findings are consistent with other findings that demonstrate dispersal is limited to the scale of tens to hundreds of meters from the fruiting body (Peay et al. 2010, Norros et al. 2012) or perhaps even closer for some ECM taxa (Galante et al. 2011), although there is some evidence of much greater long-distance dispersal (e.g., Geml et al. 2011).

Spore dispersal distances for small mammals are limited by movement ability which is highly correlated with body size. Maximum dispersal distance estimates for rodents such as the

Eurasian wood mouse (*Apodemus sylvaticus*) and bank vole (*Clethrionymys glareolus*) range from 20-50m (Halbwachs and Bässler 2015) and are similar to our findings for rodents. Male small mammals often have larger home ranges than females (e.g. Feldhamer 1979), as a biproduct of differing reproductive strategies between sexes (e.g., Tisell et al. 2019), and thus males are more likely to disperse spores over greater distances. Because all three target species were frequently captured in both the forest and the patch cuts, small mammals may play an important role in transporting forest fungi, particularly mycorrhizal taxa, into regenerating patch cuts.

In addition to dispersal distance, it is important to consider concentration of spores dispersed by wind and small mammals because individual spores rarely germinate and colonize a new substrate. For ectomycorrhizal taxa, high (>50%) rates of seedling colonization require hundreds to thousands of spores (Peay et al. 2012), a pattern that appears true for at least some non-mycorrhizal 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). Thus, for fungal species with particularly low rates of establishment, the diffuse nature of wind dispersal may provide only very limited establishment potential. In contrast, individual small mammal fecal pellets contained an average of tens to hundreds of thousands of spores. Such concentrated spore loads, likely deposited in sheltered locations as mammals navigate the landscape, may provide ample spores for successful colonization. This has particularly important implications for mycorrhizal taxa that colonize tree seedlings, as small mammals such as *M. gapperi* are likely to use downed woody material (Stephens et al. 2021), which has substantial value as a substrate for seedling establishment (Bolton and D'Amato 2011) and simultaneously retains moisture (Pichler et al. 2012), which would favor fungal

establishment. By linking rodent dispersers, seedlings, and mycorrhizal symbionts, pieces of downed woody material may serve as “hotspots” for forest regeneration.

Pairing Sequencing with Microscopy

The overall findings of our genetic analyses aligned closely with our microscopy results. However, sequencing did detect substantially greater numbers of fungal taxa (an approximately 100-fold difference). Similar discrepancies between spore microscopy and sequencing have been documented before in airborne AM taxa, (Chaudhary et al. 2020), although the differences in our own study are much greater. These differences may reflect difficulty of using microscopy to identify spores to the species level, as well as the extreme rarity of many taxa in our samples. It is also likely that fungal DNA in our samples was not solely derived from mature spores (Chaudhary et al. 2020). Underdeveloped spores, colonized fine-root tips, and hyphal chunks were almost certainly present in scat and spore trap samples. The extent to which this additional fungal material may or may not serve as an alternative pathway for dispersal is understudied, but recent literature suggests that hyphal chunks in particular may effectively colonize new substrates (Bueno and Moora 2019). Our findings highlight the value of conducting microscopic and genetic analyses in tandem; sequencing results suggest great diversity of fungal taxa, while the limited morphotypes detected via microscopy suggest that many of the detected taxa were present but not as spores.

Conclusions

Our study suggests that wind- and small mammal-facilitated spore dispersal are complementary ecological processes. Substantial differences in spore communities (both taxonomic and functional) dispersed by each mechanism indicate that fungal dispersal strategies

are highly divergent, a pattern that is at least partially reflected in spore morphology, with wind-borne spores exhibiting smaller overall size than mammal-dispersed spores. Our results also indicate that small mammals play an important role as spore dispersers for both AM and ECM taxa, which were overwhelmingly more abundant in scat samples than in spore traps. Overall, our findings suggest that small mammals play an important role in dispersing forest-associated fungi (particularly mycorrhizal species) into recently harvested forest, thereby assisting in the regeneration of forest canopy species.

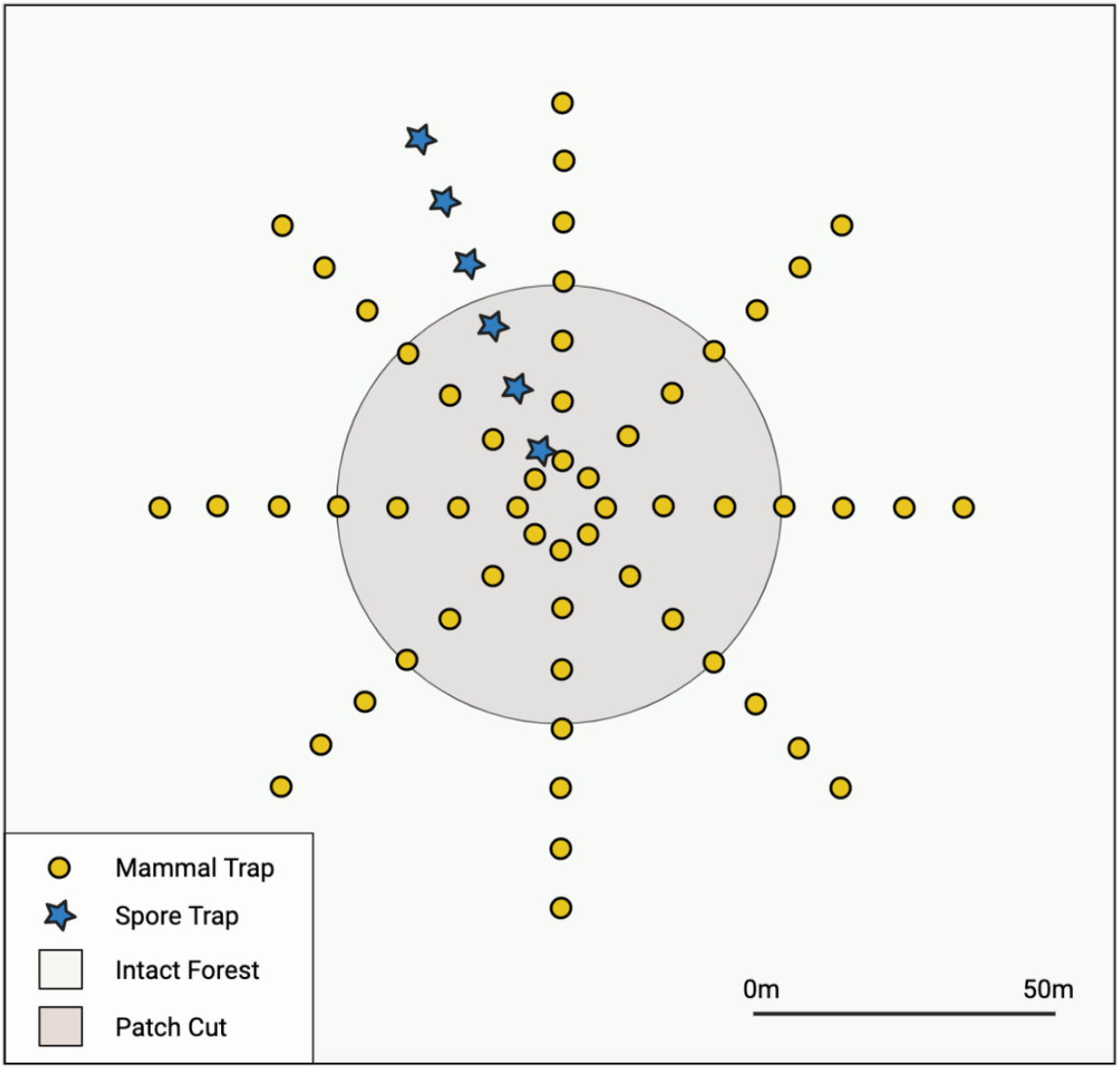

Figure 2.1. Schematic diagram of one of the eight study webs utilized in this study. Light green background indicates mature forest; light brown indicates patch cut. Yellow circles represent small mammal trap stations (n = 56), and blue stars represent traps for airborne spores (n = 6).

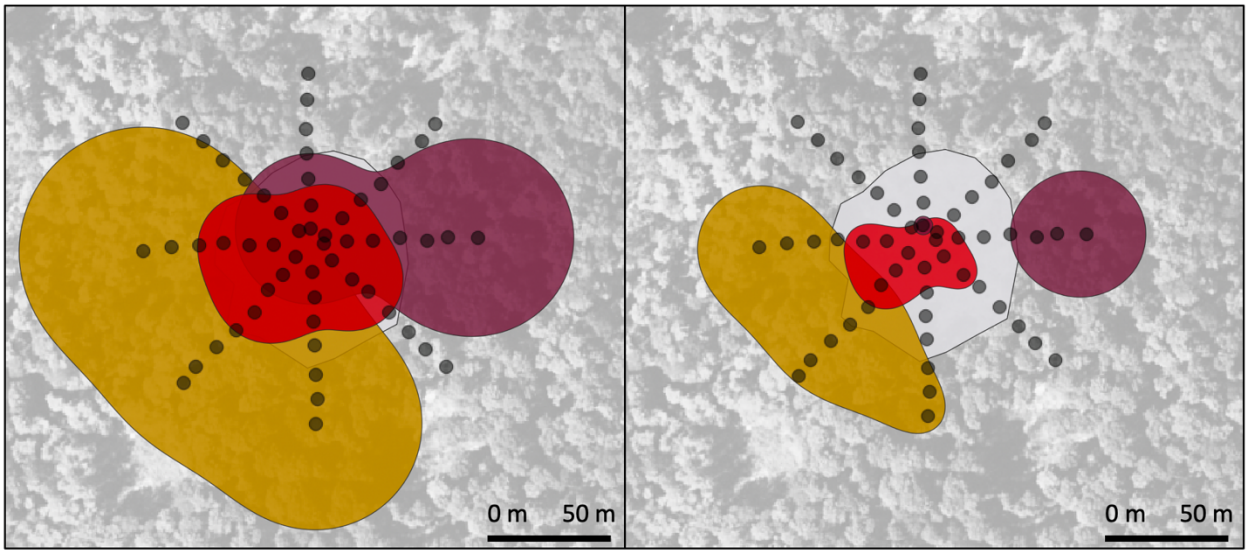

Figure 2.2. Representative home ranges (left) and core areas (right) of female *Myodes gapperi* (red), *Napaeozapus insignis* (gold), and *Tamias striatus* (purple). Black circles represent trap stations. Gray polygon denotes patch cut boundary.

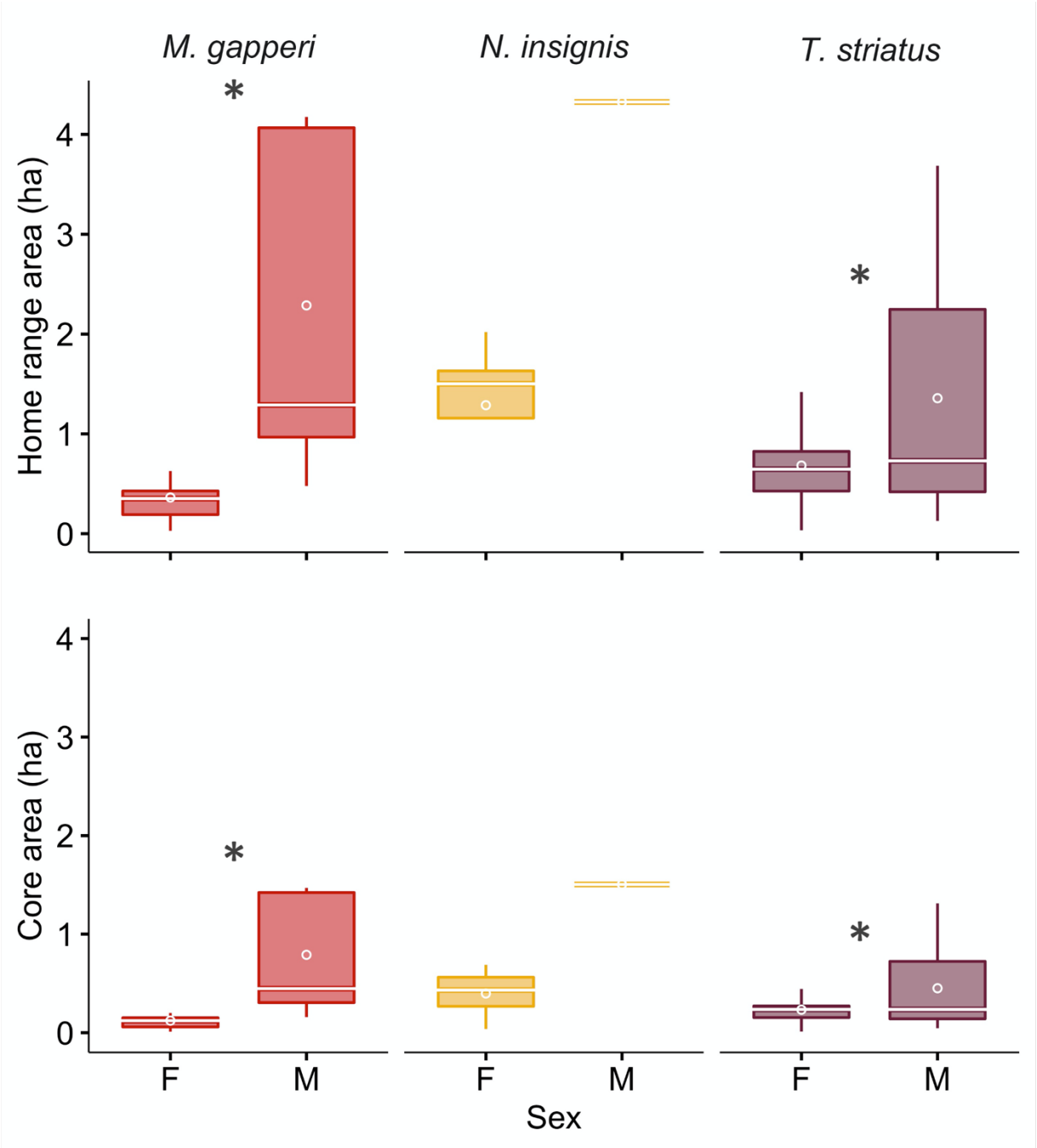

Figure 2.3. Home range (left) and core area (right) for male and female *Myodes gapperi* (n_{male} = 7, n_{female} = 17), *Napaeozapus insignis* (n_{male} = 1, n_{female} = 4), and *Tamias striatus* (n_{male} = 17, n_{female} = 25). Boxplots show 25th, 50th (median; white bar), and 75th percentiles. White circles denote mean values. Whiskers represent the lowest and highest value within the 1.5 interquartile range. Asterisks indicate statistically significant differences ($p < 0.05$) between sexes.

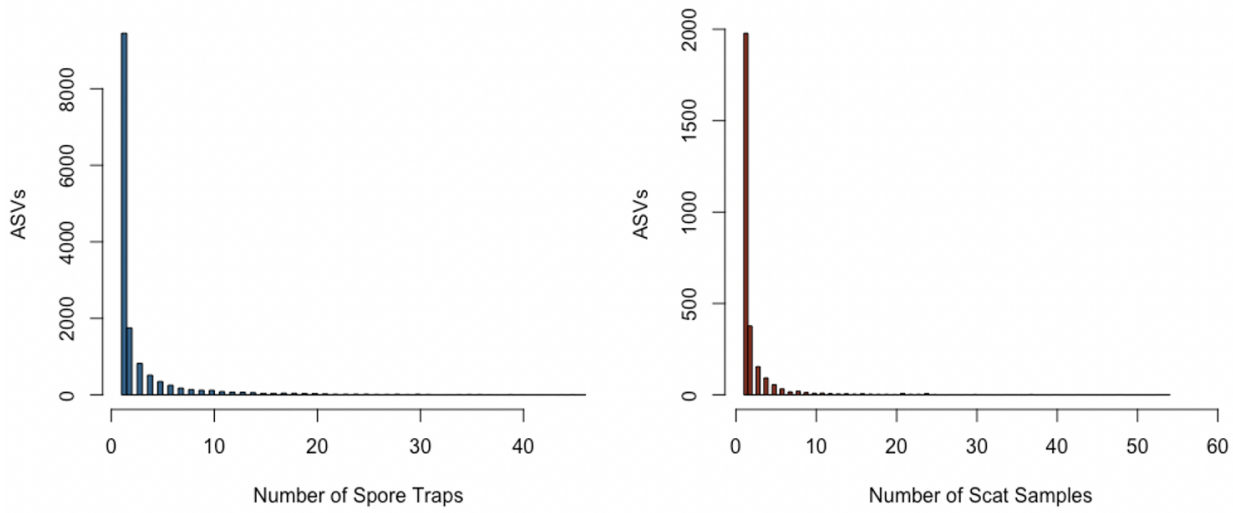

Figure 2.4. Frequency distribution depicting occurrences of amplicon sequence variants (ASVs) in spore traps (left) and scat samples (right). Occurrence is based on number of samples where an ASV was detected. Note that y-axes scale independently.

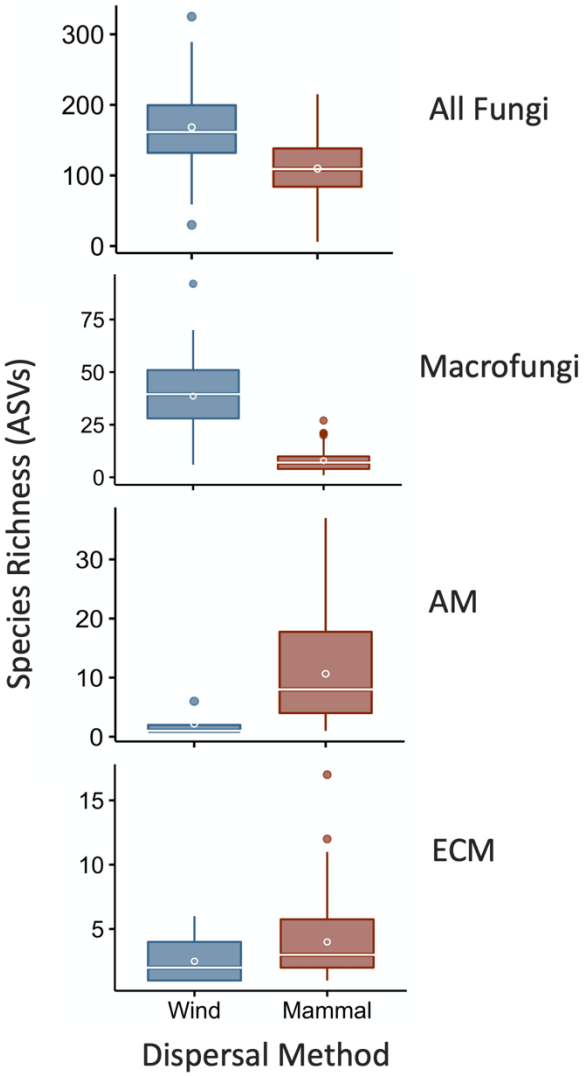

Figure 2.5. Comparison of taxonomic richness (based on ASVs) of all fungi, macrofungi only, arbuscular mycorrhizal fungi, and ectomycorrhizal fungi between spore traps and small mammal scat. Richness calculations are based on sample data rarefied to 1000 reads. All differences are statistically significant ($p < 0.05$). 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. Note y-axis scales independently.

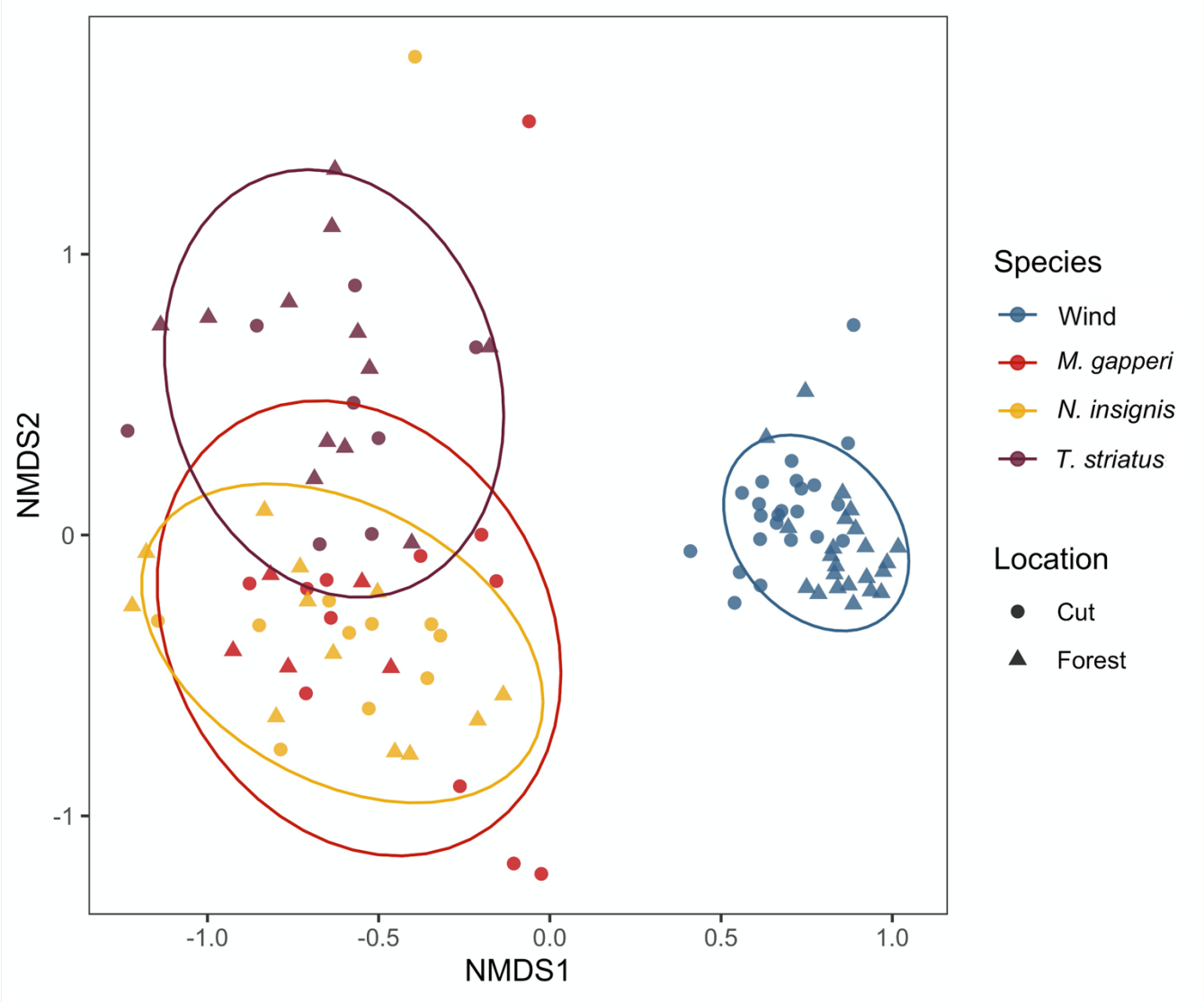

Figure 2.6. Two-dimensional nonmetric multidimensional scaling (NMDS) ordination (final stress = 0.19) of fungal spore communities of spore trap and scat samples. Color corresponds to mammal species or spore trap. Shape corresponds to location (patch cut or forest) of sample collection. Greater pairwise distance between markers indicates larger differences in community composition. Ellipses represent 90% confidence intervals around the centroid, and ellipse size approximates relative community concordance. Ordination was conducted on community data rarefied to 1000 reads.

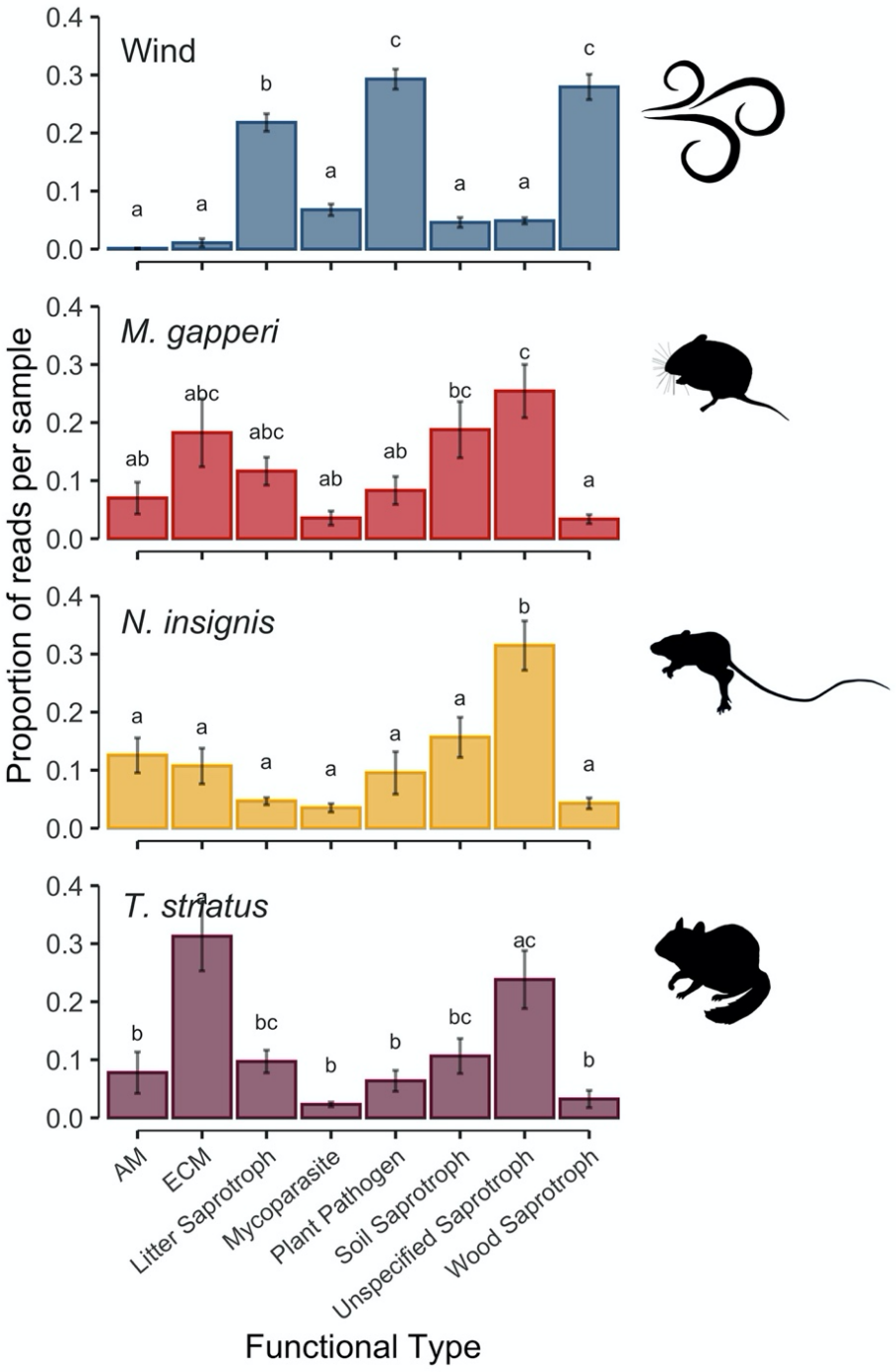

Figure 2.7. Proportion of reads per sample (mean ± standard error) belonging to several common fungal functional types. Proportions were based on all present ASVs with known functional types. Within a panel, functional types with different letters are significantly different ($p < 0.05$).

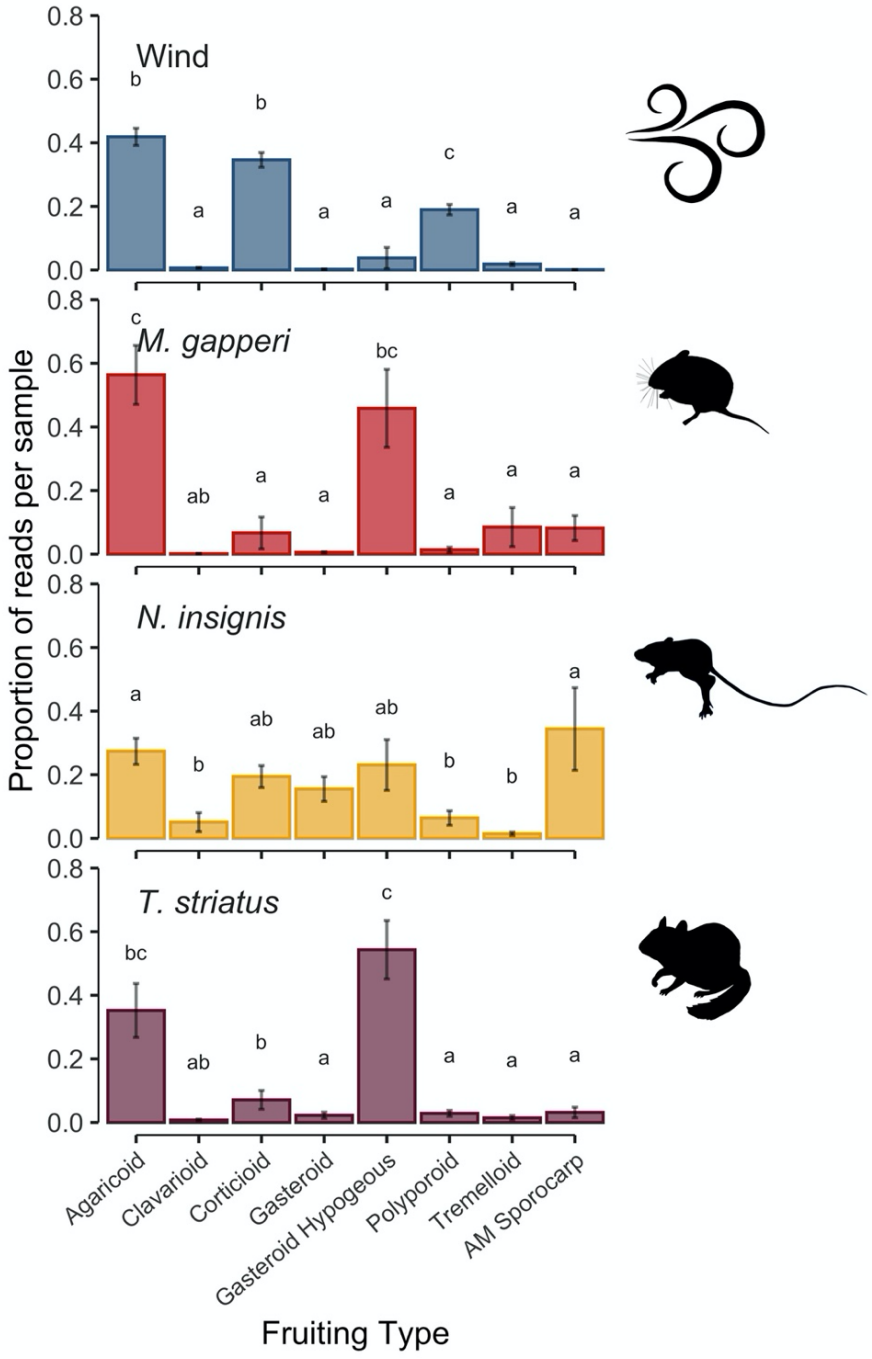

Figure 2.8. Proportion of reads per sample (mean ± standard error) as they relate to all detected macrofungal fruiting body types. Proportions were based on all present macrofungal ASVs. Within a panel, fruiting body types with different letters are significantly different ($p < 0.05$).

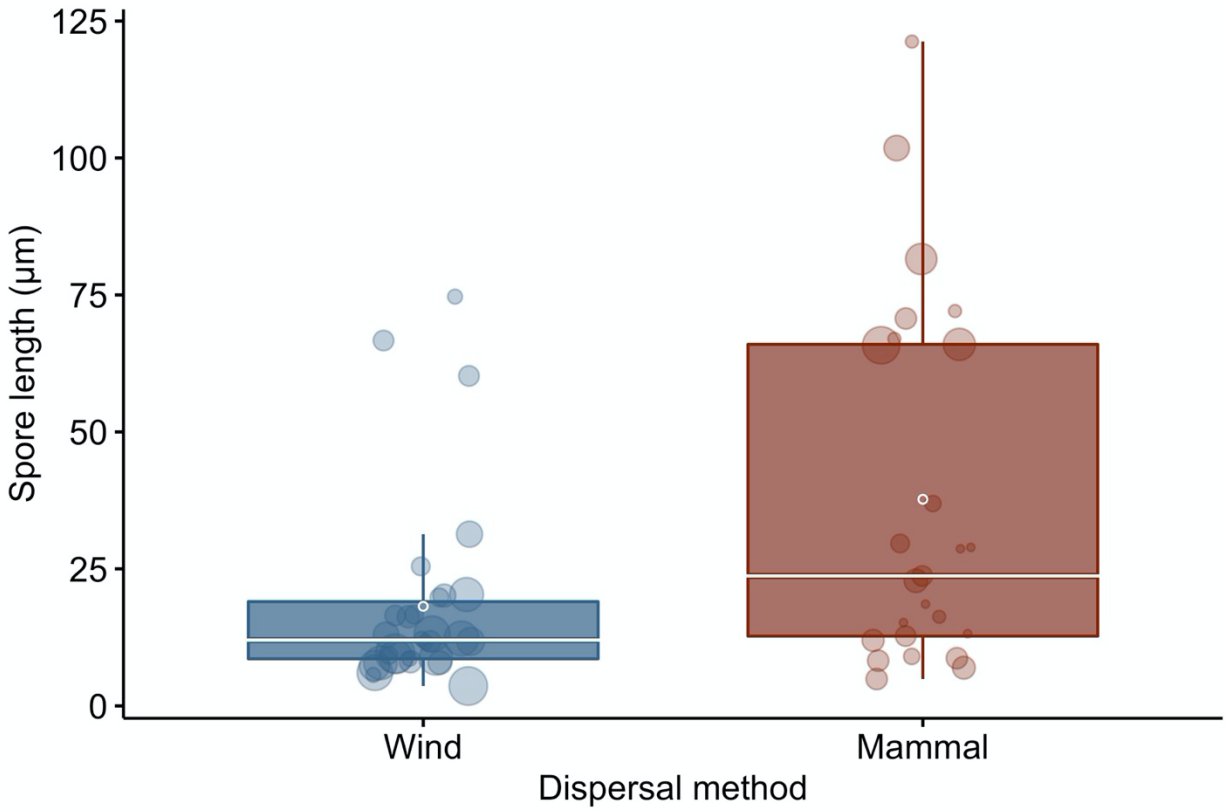

Figure 2.9. Maximum length of spores dispersed by mammals and wind. Boxplots show 25th, 50th (median; white bar), and 75th percentiles. Whiskers represent the lowest and highest value within the 1.5 interquartile range. White circles denote mean values. Each data point represents an individual morphotype; point diameter represents relative occurrence frequency (i.e., morphotypes present in many samples are assigned larger points).

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APPENDIX

Table A1. Observed fruiting bodies and abundance by genus (organized by functional type). Nomenclature based on Index Fungorum taxonomy (http://www.IndexFungorum.org, accessed 5 Nov. 2020). The genus *Clavulinopsis* was categorized as ectomycorrhizal following Birkebak et al. (2013). Note that many taxa were detected in only one stand (i.e., plot).

Genus	**Number of plots detected (*n* = 10)**	**Total found in forest**	**Total found in cut**	**Functional group**
Amanita	3	2	3	Ectomycorrhizal
Boletus	2	2	0	Ectomycorrhizal
Clavulina	1	49	0	Ectomycorrhizal
Clavulinopsis	2	5	0	Ectomycorrhizal
Cortinarius	1	1	0	Ectomycorrhizal
Inocybe	2	3	0	Ectomycorrhizal
Leccinum	1	1	0	Ectomycorrhizal
Russula	4	3	2	Ectomycorrhizal
Scleroderma	1	4	0	Ectomycorrhizal
Suillus	2	2	0	Ectomycorrhizal
Tricholoma	1	1	0	Ectomycorrhizal
Cordyceps	1	1	0	Parasitic
Fomes	2	38	0	Parasitic
Fomitopsis	2	8	0	Parasitic
Ganoderma	2	4	0	Parasitic
Phellinus	1	1	0	Parasitic
Tremella	1	7	0	Parasitic
Agrocybe	1	2	0	Saprobic
Apioperdon	1	1	0	Saprobic
Bisporella	3	10	1	Saprobic
Calocera	1	18	0	Saprobic
Camarops	1	0	5	Saprobic
Cerioporus	3	5	1	Saprobic
Clitocybe	1	5	0	Saprobic
Collybia	1	1	0	Saprobic
Crepidotus	2	8	1	Saprobic
Cudonia	1	1	0	Saprobic
Dacrymyces	1	7	0	Saprobic
Daedaleopsis	1	0	4	Saprobic
Entoloma	3	17	0	Saprobic

Galerina	1	1	0	Saprobic
Gymnopilus	1	0	2	Saprobic
Gymnopus	2	4	0	Saprobic
Hymenochaete	2	53	0	Saprobic
Hypoxylon	2	252	0	Saprobic
Inocephalus	1	0	2	Saprobic
Irpex	4	3	59	Saprobic
Marasmiellus	1	2	0	Saprobic
Marasmius	7	34	173	Saprobic
Megacollybia	5	13	1	Saprobic
Mycena	6	12	24	Saprobic
Neobulgaria	1	22	0	Saprobic
Neofavolus	1	3	0	Saprobic
Panellus	1	20	0	Saprobic
Peziza	3	2	3	Saprobic
Phlebia	2	2	0	Saprobic
Plicaturopsis	2	303	32	Saprobic
Pluteus	5	3	3	Saprobic
Psilocybe	6	13	8	Saprobic
Pycnoporus	4	0	18	Saprobic
Schizophyllum	9	100	1110	Saprobic
Scutellinia	4	18	13	Saprobic
Steccherinum	1	20	0	Saprobic
Stereum	4	322	6	Saprobic
Tatraea	1	1	0	Saprobic
Trametes	9	274	556	Saprobic
Trichaptum	3	28	196	Saprobic
Tyromyces	4	27	10	Saprobic
Xylaria	2	2	0	Saprobic
Gliophorus	1	3	0	Unknown
Helvella	1	1	0	Unknown
Hygrocybe	5	20	0	Unknown
Rickenella	1	0	7	Unknown

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23-Mar-2018

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Natural Resources & the Environment
James Hall Rm 136
Durham, NH 03824-2601

IACUC #: 180301
Project: Linking Small Mammals and Mycorrhizal Fungi to Forest Regeneration
Approval Date: 22-Mar-2018

The Institutional Animal Care and Use Committee (IACUC) reviewed and approved the protocol submitted for this study under pain or distress category D - *Animal use activities that involve accompanying pain or distress to the animals for which appropriate anesthetic, analgesic, tranquilizing drugs or other methods for relieving pain or distress are used.*

Approval is granted for a period of three years from the approval date above. Continued approval throughout the three year period is contingent upon completion of annual reports on the use of animals. At the end of the three year approval period you may submit a new application and request for extension to continue this project. Requests for extension must be filed prior to the expiration of the original approval.

Please Note:
1. All cage, pen, or other animal identification records must include your IACUC # listed above.
2. Use of animals in research and instruction is approved contingent upon participation in the UNH Occupational Health Program for persons handling animals. Participation is mandatory for all principal investigators and their affiliated personnel, employees of the University and students alike. Information about the program, including forms, is available at http://unh.edu/research/occupational-health-program-animal-handlers.

If you have any questions, please contact either Dean Elder at 862-4629 or Julie Simpson at 862-2003.

For the IACUC,

Jessica A. Bolker, Ph.D.
Chair

cc: File