



Wood-colonizing fungal community response to forest restoration thinnings in a *Pinus tabuliformis* plantation in northern China



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ABSTRACT

Forest restoration thinning in Chinese pine (*Pinus tabuliformis*) plantations can alter stand structure and soil abiotic properties, which have the potential to change biotic properties such as wood-inhabiting fungal community structure. Therefore, three thinning treatments (30%, 41% and 53% of the standing biomass removed) and an unthinned control stand were established at stand age 35 to determine the effects on surface and mineral soil wood-inhabiting fungi. Chinese pine, loblolly pine (*Pinus taeda*), and trembling aspen (*Populus tremuloides*) wood stakes were placed horizontally on the soil surface and inserted vertically into the mineral soil and sampled over 3 years. Fungal species were identified using high-throughput amplicon sequencing (HTAS) of DNA barcode regions. Across all wood stake species on the soil surface, operational taxonomic unit (OTU) richness averaged 138 OTUs per thinning treatment. Significantly greater OTU richness ($p < 0.01$) on both surface pine species stakes was observed in the unthinned control as compared to the moderate and heavily thinned plots. In the mineral soil, wood stakes averaged only 91 OTUs, with no clear OTU pattern for thinning treatment or sampling time for richness. However, aspen stakes had significantly lower ($p < 0.01$) OTU richness than both pine species stakes on the surface and in mineral soil. Although richness was not strongly affected, fungal community composition in the mineral soil was significantly altered by thinning treatments, wood stake species, and sampling time. This study extends our knowledge of the long-term effects of stand thinning on fungal communities' richness and composition.

1. Introduction

To meet increasing demands for timber and restore ecosystem services (e.g. C sequestration, water and soil conservation), forest thinning operations are increasing in China and it is critical to understand how they may affect fungal community structural changes (Chen et al., 2015). Since fungi are major contributors to forest site organic matter (OM) decomposition, particularly the more recalcitrant fractions (e.g., woody residues; de Boer et al., 2008), understanding the effects of forest land management on fungal community structure is important for ecosystem functions such as seedling establishment, plant diversity, nutrient cycling, and water uptake. Chinese pine (*Pinus tabuliformis* Carrière) is endemic to northern China and plays an important role in

biodiversity, reforestation, and nutrient cycling (Ma et al., 2005). Chinese pine forests also contribute numerous ecosystem services, such as increasing water storage and soil conservation, valued at nearly \$8000 USD ha⁻¹ year⁻¹ (Guo et al., 2008). However, due to high stand densities many ecosystem services (e.g., water storage, infiltration) are at risk for wildfire or insect and disease outbreaks. In China, these stands are intensively managed and thinning is often used to increase stem-level productivity (Ma et al. 2005; Carey 2003; Page-Dumroese et al., 2010; D'Amato et al., 2013; Chen et al., 2015), lower the risk of wildfire, or reduce pest incidence if trees are not damaged during harvest operations (Maloney et al., 2008). Ecosystem changes associated with thinning operations, however, could result in changes to fungal diversity and ecosystem functions (Kerr, 1999; Bengtsson et al.,

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2000).

Forest thinning can leave a significant amount of C on the soil surface in the form of delimited or topped trees (Polagye et al., 2007) which alters both C and N pools on the soil surface and in the mineral soil (Sherman et al., 2018). Changes in canopy coverage can also alter vegetation species composition and distribution (Schulp et al., 2008; Overby et al., 2015) by creating canopy openings that have the potential to alter belowground fungal biodiversity by altering the amount of sunlight reaching the soil surface (Colgan et al., 1999; Wang and Liu, 2011; Thibodeau et al., 2000; Brooks and Kyker-Snowman, 2008). In a Chinese pine plantation thinned at age 20 to heavy, moderate, and light intensities, soil respiration increased 8–21% in the two years following thinning as compared to unthinned control plots and thinning affected soil temperature, but not moisture across the treatments (Cheng et al., 2014). In Oregon, USA, repeated thinning over four decades in a ponderosa pine (*Pinus ponderosa*) forest decreased litter cover but increased fungal abundance and diversity and altered community structure (Overby et al., 2015). In some stands, low intensity thinning in temperate forests has increased soil microbial functional diversity, structure, and fungal biomass when measured by phospholipid fatty acid analysis (PLFA; Cookson et al., 2008; Chen et al., 2015) or DNA fingerprinting (Thakuria et al., 2008). Other studies have shown no effect of forest thinning on microbial biomass carbon (C), soil respiration, or enzyme activity (Grayston and Rennenberg, 2006; Maassen et al., 2006). Furthermore, aspect was an important factor in a beech (*Fagus sylvatica*) forest in central Europe, where microbial biomass was reduced after forest thinning on a cool-moist site but increased on a warm-dry site (Grayston and Rennenberg, 2006). Harvest operations have also resulted in an overall reduction in fungal species richness of wood-inhabiting and ectomycorrhizal fungi in both broadleaf and conifer forests (Smith et al., 2005; Lindner et al., 2006; Nordén et al., 2008). These divergent results of harvest impacts on microbial diversity, function, and community structure highlight the need for site-specific data examining the role of forest management and site.

Substrate quality affects both fungal community composition as well as decomposition rate. Wood is decomposed primarily by basidiomycete fungi in brown and white rot functional groups (Blanchette, 1984). These two groups differ in their ability to degrade lignin (Rayner and Boddy, 1988; Floudas et al., 2012) and different fungal groups are associated with different woody species. For example, broadleaved trees are generally decomposed at a faster rate than conifers in both temperate and boreal forests due to lower C:N and lignin concentrations (Cornwell et al., 2009; Strukej et al., 2013). The LIDET (Long-Term Intersite Decomposition Experiment), used wood dowels and demonstrated that pine wood decomposes slower than broadleaf wood, supporting the notion that substrate quality controls decomposition rates, and highlights that microbes may have a “home-field advantage” in a given environment (Gholz et al., 2000). Additionally, Wang et al. (2019) noted that wood quality significantly affects decomposition rates in a Chinese pine stand in northern China.

In addition to substrate quality, the location of wood (on or in the soil) can affect both the type of microbial community and decomposition rate (Lindahl et al., 2007; Preston et al., 2012; Voříšková et al., 2014). For example, the vertical distribution of the fungal community in boreal and temperate forests reflects soil stratification: saprotrophic taxa are more abundant close to the surface of the forest floor where most C is mineralized, whereas mycorrhizal fungi increase in abundance with soil depth (O'Brien et al., 2005; Lindahl et al., 2007). Wood decomposition and soil depth relationships appear to be implicitly tied to local site and soil climatic conditions which govern wood and soil moisture contents, soil temperature fluctuations, fungal activity, and ultimately forest C cycling (Voříšková et al., 2014). Greater wood stake decomposition was found deeper (15 cm v. 5 cm) in the soil profile after a wildfire in Montana, USA (Page-Dumroese et al., 2019), but not in the cooler Swiss Alps (Risch et al., 2013). Therefore, similar to thinning impacts, how fungal communities regulate wood decomposition within

the soil profile is likely site-specific.

Soil saprotrophic fungi are major drivers of terrestrial biogeochemical cycling through their roles in the breakdown and recycling of OM (Read and Perez-Moreno, 2003). Forest changes (e.g. thinning, soil OM, C) may alter the diversity and distribution of fungi and their responses to forest management activities and alter the balance among pathogenic, symbiotic and saprophytic microbes (Vandenkoornhuysen et al., 2015; van der Wal et al., 2015).

Few studies have investigated the relationship between forest management and long-term changes in the diversity and composition of the fungal community associated with wood decomposition in the field (e.g., Heilmann-Clausen, 2001; Lindner et al., 2011; Brazeo et al., 2014). Since forest management does alter soil conditions, it would be expected that soil microbial populations may be altered. However, because fungi are variable within a given stand, results may be site- or soil-specific (Ayres et al., 2009). As such, our field trial is a unique opportunity to characterize three years of wood-inhabiting fungal community changes associated with wood stakes of three tree species: native Chinese pine, non-native loblolly pine (*Pinus taeda* L.) and trembling aspen (*Populus tremuloides* Michx.). Both loblolly pine and aspen stakes are used as part of multiple global wood decomposition studies (e.g., Jurgensen et al., 2006; Risch et al., 2013; Finér et al., 2016; Jurgensen et al., 2019; Page-Dumroese et al., 2019; Wang et al., 2019). These three species of wood stakes encompass a range lignin, cellulose, and N concentrations, which could favor the development of different wood-decomposing microbial communities (Blanchette, 1984; Wang et al., 2018). Consequently, our goals were to assess fungal community composition and richness in wood stakes: (1) on the soil surface and in the mineral soil, (2) for three tree species, (3) in different thinning treatments, and (4) over time.

2. Materials and methods

2.1. Study site

This study was conducted in a 35-year old Chinese pine plantation located in Pingquan county, Hebei province (118°40'E, 41°13'N), China, at an elevation of 700–800 m. The area has a semi-humid, continental monsoon climate, with a mean annual temperature of 7.3 °C (min. –24.7 °C and max. 41.5 °C) and an average frost-free period of 135 days during the study. Precipitation per annum was 542 mm. Soil texture was sandy loam derived from granitic parent material and the surface 0–15 cm soil had a pH of 6.7, OM concentration was 1.66%, and total N concentration was 0.053% (Wang et al., 2019). The dominant understory vegetation species were *Elsholtzia stauntoni* L., *Spiraea salicifolia* L., *Rosa multiflora* L., *Carex lanceolata* Boott L., *Potentilla tanacetifolia* L. and *Caragana sinica* L.

The plantation was established in 1976 from seed with 5000 trees/ha of initial stand density, and had an average tree diameter of 7.2 cm and a height of 5.1 m before being thinned in 2011. Thinning was conducted to improve forest health conditions by reducing fire risk and potential insect and disease outbreaks. As such, the cutting was considered a restoration thinning. The slopes at this site are steep (33.1°–39.6°) and therefore, trees were cut by hand. All woody biomass was immediately removed from the site. Each thinning treatment was replicated three times, but because two replicates were shallow to bedrock (< 10 cm deep mineral soil), only one of the thinned replicates was used and two subplots at each end of the plot were installed. Study plots [20 m × 20 m (0.04 ha)] were randomly assigned across the slope and separated from each other by a 5 m buffer. Plots were thinned to three stand densities: low (30%), moderate (41%), and high (53%) amounts of overstory removal, and an adjacent portion of the plantation was left unthinned as a control (4700 trees/ha).

Table 1
Results of the ANOVA identifying single factors and three-way interactions for surface and mineral OTUs richness.

Factor	Surface total OTU richness			Mineral total OTU richness		
	DF	F value	P	DF	F value	P
Year	2	0.01	0.99	2	5.36	0.01
Treatment	3	6.99	< 0.01	3	3.20	0.03
Species of stakes	2	29.38	< 0.01	2	11.75	< 0.01
Year × Species of stakes	4	0.18	0.95	4	0.51	0.73
Year × Treatment	6	1.04	0.42	6	7.07	< 0.01
Treatment × Species of stakes	6	1.17	0.34	6	2.56	0.02
Treatment × Species of stakes × Year	12	1.57	0.14	12	1.57	0.11

2.2. Wood stakes and fungal samples

Aspen, loblolly pine, and Chinese pine wood stakes were cut from kiln-dried, knot-free sapwood. Two aspen and loblolly pine surface stakes (2.5 × 2.5 × 15 cm) were cut from a longer 40 cm stake, and two mineral stakes (2.5 × 2.5 × 20 cm) were cut from a longer 50 cm stake. The remaining 10 cm center section was used as a laboratory control (time = 0) to determine mass loss of the two surface and mineral soil stakes after they were sampled (Wang et al., 2019). Since wood for Chinese pine stakes was limited, both surface and mineral soil stakes were 15 cm long, but a 10 cm control was also kept in the laboratory. The upper end of each mineral stake was treated with a wood sealer to reduce moisture loss from the cut surface after installation (see Jurgensen et al., 2006).

In May 2012, two subplots consisting of twenty-five surface stakes of each species were placed on top of the litter (< 0.50 cm thick) in each thinned treatment plot and the unthinned control and secured with a stainless steel landscape staple. An additional 25 stakes of aspen and loblolly pine were inserted vertically to a depth of 20 cm in the mineral soil in each plot. Chinese pine mineral stakes were only 15 cm long and, therefore, inserted to a soil depth of 15 cm. To minimize changing soil physical properties surrounding the mineral stakes and to limit damage to stakes during installation, the surface litter was pushed aside and a 2.5 cm² hole was made in the soil with a metal coring tool to the appropriate depth for each stake. Stakes were inserted into the hole and the litter replaced. During stake insertion into the mineral soil, we ensured that the top of each mineral stake was level with the top of the mineral soil. A total of 360 surface and 360 mineral stakes were installed (4 treatments × 2 stake locations × 2 replicates × 3 wood species × 15 stakes). In May of 2013, 2014, and 2015, five surface and five mineral stakes of each species were removed from each plot and weighed in the field to obtain stake moisture content.

Stakes were kept cool after extraction from the soil and within 24 h we collected wood shavings from each stake for fungal DNA analysis. Before collecting the wood shavings, both ends of each stake were cleaned with a sterile razor blade to remove loose soil. For both surface and mineral soil stakes, each end of the stake was drilled with sterile drill bits and, for each stake, the two shaving samples were composited into one individual sample. Shavings were placed in 2 ml strip tubes in 96-well format, covered with filter-sterilized cell lysis solution (CLS; Lindner and Banik, 2009) and sent to the Center for Forest Mycology Research (Madison, WI, USA) for fungal community analysis. All fungal samples were frozen at -80 °C until DNA was extracted.

2.3. Sequencing fungal ITS sequences isolated directly from wood samples

Fungi inhabiting the wood stakes were identified using DNA-based methods. For stakes on the surface and in mineral soil, only four of the five stakes in each subplot were sampled for DNA analyses due to funding and time constraints (the four stakes to be sampled were chosen at random). The samples from the four stakes were pooled by subplot prior to genomic DNA extraction, and DNA extraction followed the methods in Lindner and Banik (2009).

We followed the procedures for high-throughput amplicon sequencing (HTAS) using the Ion Torrent platform (Ion PGM™; Thermo Fisher Scientific, Madison, WI, USA), following the methods in Palmer et al. (2018). Briefly, we used primers fITS7 (Ihrmark et al., 2012) and ITS4 (White et al., 1990) for our PCR reactions. Both primers were modified with Ion Torrent specific adapters, and the fITS7 primers were also appended with a unique barcode sequence. Following PCR amplification, Zymo Research's Select A-Size DNA Clean & Concentrator spin columns (Zymo Research, Irvine, CA, USA) were used to clean the resulting PCR products. The products were then quantified with a qubit 2.0 fluorometer with the high-sensitivity DNA quantification kit (Thermo Fisher Scientific, Madison, WI, USA) and equilibrated with a synthetic mock community (SynMock; Palmer et al., 2018) of single-copy nonbiological sequences to parameterize our bioinformatics. Sequencing was performed following manufacturer's recommendations. Bioinformatic processing of the sequence reads was performed with AMPtk (version 0.8.5; Palmer et al., 2018).

2.4. Fungal community analysis

DNA-based studies of microbial communities typically cluster sequences into Operational Taxonomic Units (OTUs) based on percent sequence similarity because the relationship between DNA sequences and species is not always known. OTU accumulation curves were generated to plot OTU richness across thinning treatments with the 'specaccum' function. Three-way ANOVAs were used to test OTU richness among thinning treatments, stake species and sampling time (Table 1). OTU counts were transformed to presence/absence data, and plot bars were created to visualize the relative abundance of different taxa by thinning treatments, stake species, stake locations (top and bottom), and sampling times. Fungal community analyses were conducted in the vegan package (Oksanen et al., 2017) of R Statistical Software (R Core Team, 2017). To visualize the fungal communities in ordination space, we performed non-parametric multidimensional scaling (NMDS) using the metaMDS function with the modified Raup-Crick dissimilarity metric described by Chase et al. (2011), calculated by the raupcrick function. To assess whether thinning treatments (unthinned control, light, moderate and heavy thinning), or stake species (aspen, Chinese pine, loblolly pine), or sampling time (1, 2, and 3 years after installation) were related to fungal community structure, nonparametric permutational multivariate ANOVA (PERMANOVA) tests (Anderson, 2001) were performed by the adonis function. To assess the effects of multivariate dispersion on these same variables, multivariate homogeneity of group dispersion tests was performed with the betadisper function.

3. Results

3.1. Total OTU richness

Overall, 1133 OTUs were detected, with 20.9% classified to species, 34.7% classified to genus, 34.7% classified to family, 54.3% classified to order, 70.4% classified to class, and 85.4% classified to phylum.

For surface stakes, OTU richness did not differ across years (Table 1

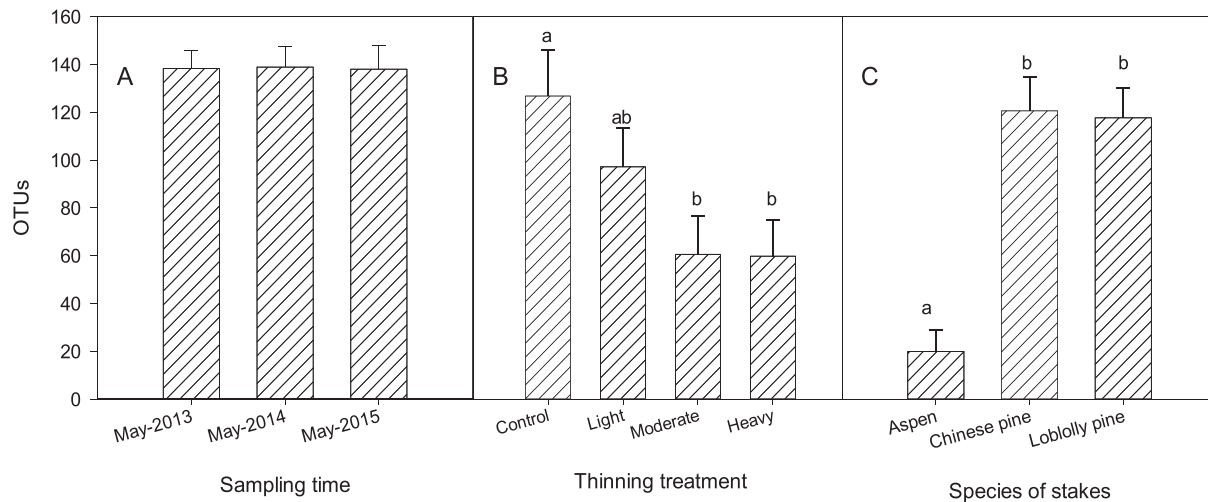


Fig. 1. Surface stake total OTU richness for (A) year sampled, (B) thinning treatment, and (C) wood stake species.

and Fig. 1), with an average of 138.3 ± 7.5 , 138.9 ± 8.7 , and 138.0 ± 9.9 OTUs found in 2013, 2014, and 2015, respectively. OTU richness was significantly lower in moderately (124.1 ± 9.0) and heavily (123.6 ± 8.5) thinned plots compared to unthinned control plots (161.3 ± 10.8 ; Fig. 1). OTU richness in light intensity thinned plots (144.7 ± 9.1) did not differ significantly from the moderate and heavily thinned plots or from the control. Significantly greater OTU richness was found on pine stakes (156.2 ± 6.9 and 157.8 ± 8.1 for loblolly and Chinese pines, respectively) compared to aspen stakes (101.2 ± 5.1 ; Fig. 1).

For mineral stakes, OTU richness was significantly lower than in surface wood stakes (Fig. 2). Thinning treatment interacted with both year and species of wood stake (Table 1). In 2013, there was no difference in OTU richness across treatments, but in 2014, OTU richness was significantly lower in light intensity thinned plots (57.1 ± 7.5) compared to moderately thinned plots (106.5 ± 12.1) and control plots (118.9 ± 12.5). In 2015, OTU richness was significantly lower in light (93.6 ± 10.9) and moderate intensity (68.7 ± 8.1) thinned plots compared to heavily thinned plots (141.2 ± 12.7 ; Fig. 2). For aspen stakes, significantly greater OTU richness was found in unthinned control plots (100.0 ± 15.1) than in light intensity or heavily thinned plots (57.2 ± 8.3 and 57.5 ± 4.9 , respectively). While there was no significant difference in OTU richness across thinning treatments on Chinese pine stakes, OTU richness was significantly greater on loblolly

pine stakes in control plots (134.0 ± 10.3) compared to all thinning treatments (89.9 ± 10.7 , 100.0 ± 12.5 and 102.5 ± 10.2 in light, moderate, and heavily thinned plots, respectively; Fig. 3). In addition, OTU richness was significantly higher in surface wood stakes than the mineral stakes.

3.2. Community composition

For the purposes of graphical illustration, the top 10 genera in each variable of interest were identified (Fig. 4). The composition of the top 10 genera changed after thinning. For example, *Cladophialophora* was the most abundant genus in unthinned control (13.0%) and light plots (13.4%), but 12.7% and 11.4% in moderate and heavy plots, respectively. *Exophiala* was higher after moderate (12.9%), heavy (12.9%) and light (13.2%) thinning as compared with the unthinned plots (11.8%). *Aequabiliella* and *Cryptococcus* were the two genera identified endemic to the unthinned plots, accounting for 8.7% and 8.5%, respectively. The relative percentage of *Coniochaeta* and *Exophiala* increased after thinning. For species of wood stakes, *Exophiala* and *Cladophialophora* were the two most abundant genera in all three wood species stakes, while *Alternaria* and *Knufia* were only identified in aspen stakes. Similarly, *Penicillium* and *Rhinochadiella* were only identified in Chinese pine, while *Aequabiliella* was the only genus within the top 10 genera that identified in loblolly pine. The composition of the top 10 abundant genera changed with sampling time. For example, *Aequabiliella* decreased from 2013 (9.2%) to 2014 (7.4%) and in 2015 it was not included in the top ten genera. However, a different pattern was found in *Cladophialophora*, which was similar for all three years with 12.1% in 2013, 12.5% in 2014 and 12.7% in 2015. There was also a large difference in fungal composition among surface and mineral wood stakes. Only 4 of the top 10 genera (*Exophiala*, *Cladophialophora*, *Devriesia* and *Rhexodenticula*) were identified in both surface and mineral stakes. Meanwhile, the relative percentage of *Devriesia* and *Rhexodenticula* both decreased for the two stake locations.

Multivariate analyses indicate that fungal community composition on both surface and mineral stakes differed across years, thinning treatments, and wood stake species. Whereas, there were significant differences in multivariate dispersion among year and wood stake species only for surface stakes (Table 2).

Both surface and mineral stake fungal community composition in control plots was most similar to those in heavily thinned plots, followed by moderate and light intensity thinned plots (Figs. 5 and 6). For surface stakes, community composition visualized with ordination, indicated that Chinese pine stakes were more similar to the communities

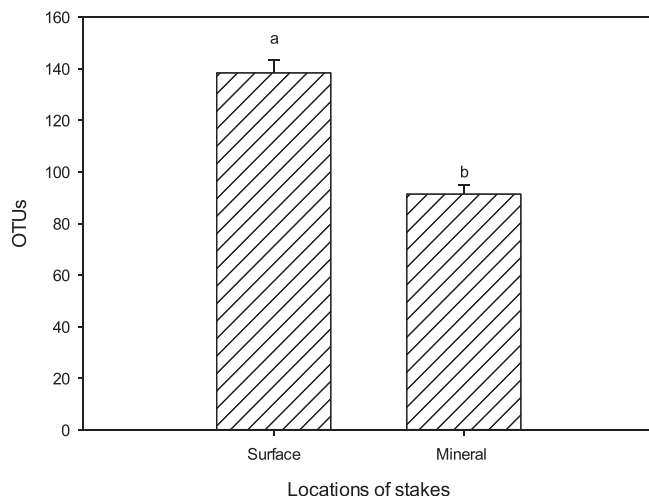


Fig. 2. Total OTU richness for soil surface and mineral soil stakes.

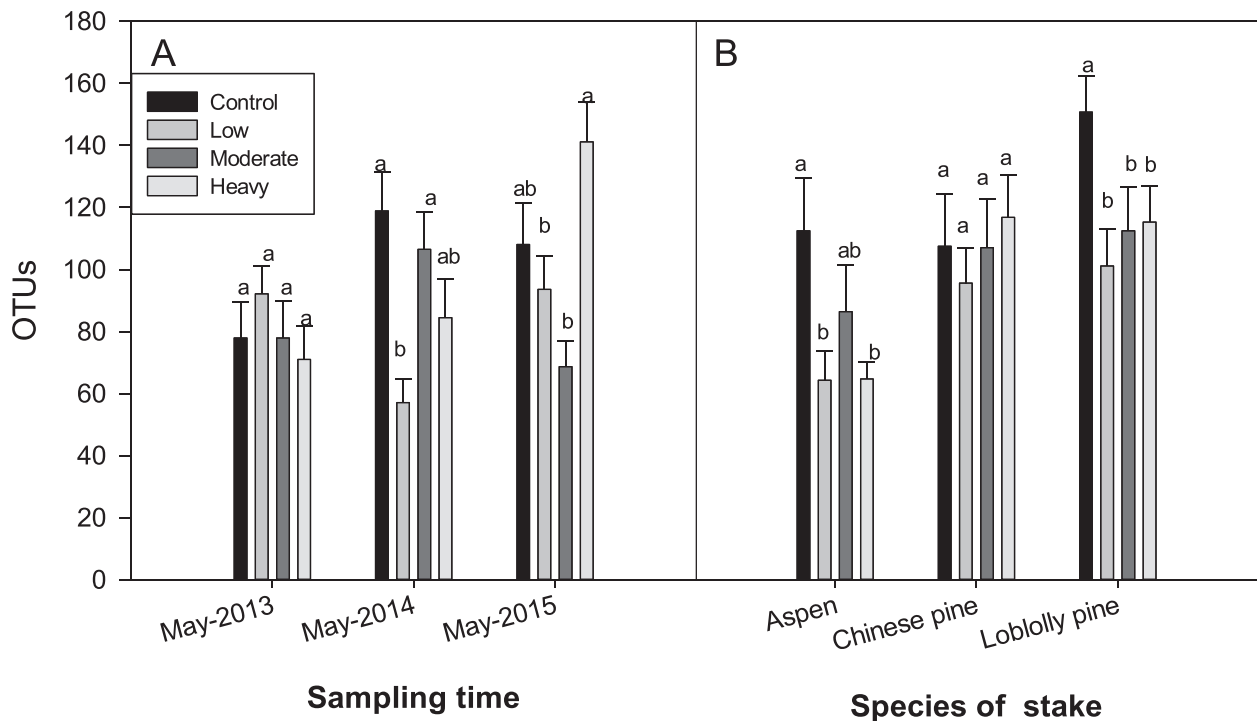


Fig. 3. Mineral soil stakes total OTU richness for (A) each sampling date within each thinning treatment, and (B) stake species within each thinning treatments. Different letters indicate significant differences within sampling time and species of stake ($p = 0.05$).

present on loblolly pine stakes than to the communities present on aspen stakes. However, this clear separation of fungal communities present on pine versus aspen is less pronounced with the mineral stakes. For both surface and mineral stakes, community composition in 2013 was more similar to the communities detected in 2014 than to those detected in 2015.

4. Discussion

Our analyses indicate that restoration thinning in Chinese pine plantations altered fungal community assemblage and OTU richness and the results varied depending on the species of stake (aspen, loblolly pine and Chinese pine), the year (1, 2, and 3 years after decomposed), and the stake location (soil surface vs. mineral soil). Although OTU richness was lower on aspen than on pines, there is likely a continuum of fungal species that are degrading the lignin, cellulose, and hemicellulose on each stake (Riley et al., 2014). Impacts on microbial communities have been evaluated immediately after thinning or for a short period after thinning (Giai and Boerner, 2007; Baena et al., 2013; Bolat, 2014), but our 3-year study shows that impacts may be detectable in and on the soil for a longer period of time and that the substrate (stake species) can influence microbial assessments in this Chinese pine plantation. In addition, OTU richness was higher on surface stakes than in the mineral stakes potentially influencing their wood decomposition rates differently (Lindahl et al., 2007; Wang et al., 2019). Stand thinning may be the most important factor in altering fungi because it can alter water and nutrient availability, soil temperature and moisture, dead root biomass, and understory and overstory stand structure.

4.1. Thinning effects

4.1.1. Surface stakes

On the soil surface, richness of wood-inhabiting fungal communities was significantly lower in moderately and heavily thinned plots compared to unthinned control plots. The unthinned control plots had the highest OTU richness, which is consistent with results from studies of

thinned Douglas-fir (*Pseudotsuga mensiesii*) stands (Colgan et al., 1999; Gomez et al., 2005). The possible reason could be the increased mean air temperature after thinning (average temperature of growth season was 19.1 °C in control plots, 19.4 °C in light thinned plots, 19.9 °C in moderately thinned plots and 20.5 °C in heavily thinned plots, unpublished data) decreased fungal richness (Pietsch et al., 2019). It has been shown that both crop residues (Chatterjee et al., 2008) and forest litter (Palviainen et al., 2004) decompose faster after canopy removal. Furthermore, removal of more of the canopy likely resulted in greater swings in these conditions. Thinning to restore forest stand structure is a major form of forest disturbance, and is widely used to decrease fire risk and increase resistance to pests and supply biofuels or other bio-products (Maloney et al., 2008; Verschuyf et al., 2011).

In addition, there are some data that indicate that more diverse fungal populations result in greater mass loss of woody substrates. For example, high fungal diversity enhanced decomposition rates in boreal forest wood (Tiunov and Scheu, 2005). In a microcosm study, fungal species richness had no influence on the OM content of humus, and functional redundancy in decomposer fungi may influence decay rates (Setälä and McLean, 2004). In a thinned Mediterranean forest, however, there were no differences in fungal community composition or structure (Castaño et al., 2018). The OTU richness of surface stakes in the light intensity thinned plots did not differ significantly from control plots but the composition of fungal communities was less similar between the control and light level of thinning than that between control and heavily thinned plots. A long-term soil productivity study indicated that changes fungal communities from harvesting were relatively minor in comparison to the variability between soil layers and among geographic regions (Wilhelm et al., 2017). It is unknown why the unthinned control and heavily thinned plots have fungal communities that are similar, but it could be related to understory vegetation, proximity of the wood stakes to trees, or soil microsite properties that were not measured in this study.

4.1.2. Mineral soil stakes

For wood stakes placed in the mineral soil, thinning treatment

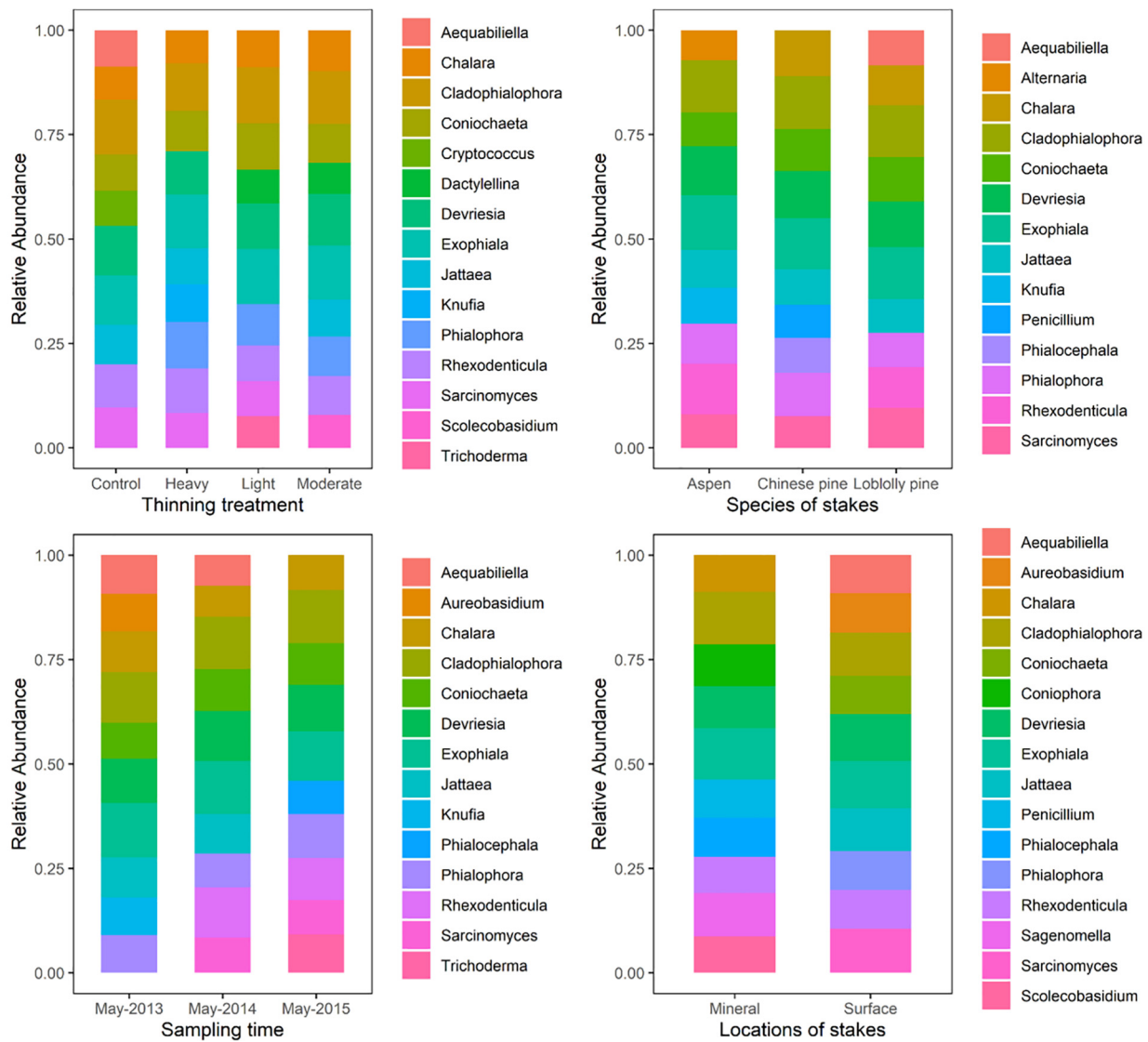


Fig. 4. The top 10 fungal genera under (A) thinning treatments (B) wood species (C) sampling time and (D) stake locations.

effects on OTU richness were not detected in the first year. Differences in OTU richness were detected in years 2 and 3 and likely became evident once the stakes had absorbed enough moisture to be a favorable habitat for fungal colonization (Banu et al. 2004; Bani et al., 2018). Mineral soil stakes are less prone to daily fluctuations in temperature and moisture than surface stakes and, as the stakes decompose, they also increase in moisture content and become more favorable for fungal colonization. All species of stakes in the mineral soil in all the thinning treatments had greater moisture content than stakes in the unthinned control stand (Wang et al., 2019) and is likely one reason for increased OTU richness over time. Moisture in the substrate also played a key role in Sitka spruce (*Picea sitchensis*) stumps where optimum colonization occurred when wood moisture content was 30–70% of saturation

(Bendz-Hellgren and Stenlid, 1998).

Thiobodeau et al. (2000) found thinning increased both soil temperature and moisture leading to increased microbial biomass in a thinned balsam fir (*Abies balsamea*) stand. Conversely, increasing harvest intensity in an aspen forest decreased microbial biomass (Hassett and Zak, 2005). In Finland, clearcut harvesting accelerated wood stake decomposition in the mineral soil due to increased soil temperature (Finér et al., 2016). Clearly site conditions and climatic regimes drive soil and microbial responses to stand management. In addition, soil conditions such as compaction, OM content, live roots, textural changes with soil depth, and rock-fragment content all affect temperature and moisture conditions near the wood stakes. These soil attributes can be highly variable in forest soils and lead to small-scale differences in both

Table 2

Results of the PERMANOVA identifying single factors and betadisper test for surface and mineral OTU composition.

Factor\Method	Surface				Betadisper		Mineral				Betadisper	
	PERMANOVA DF	F	r ²	P	F	P	PERMANOVA DF	F	r ²	P	F	P
Year	2	42.0	0.49	< 0.01	22.6	< 0.01	2	38.8	0.36	< 0.01	0.6	0.57
Treatment	3	16.5	0.43	< 0.01	2.1	0.11	3	26.3	0.36	< 0.01	1.5	0.20
Species of stakes	2	34.7	0.51	< 0.01	6.9	0.01	2	21.3	0.23	< 0.01	2.2	0.12

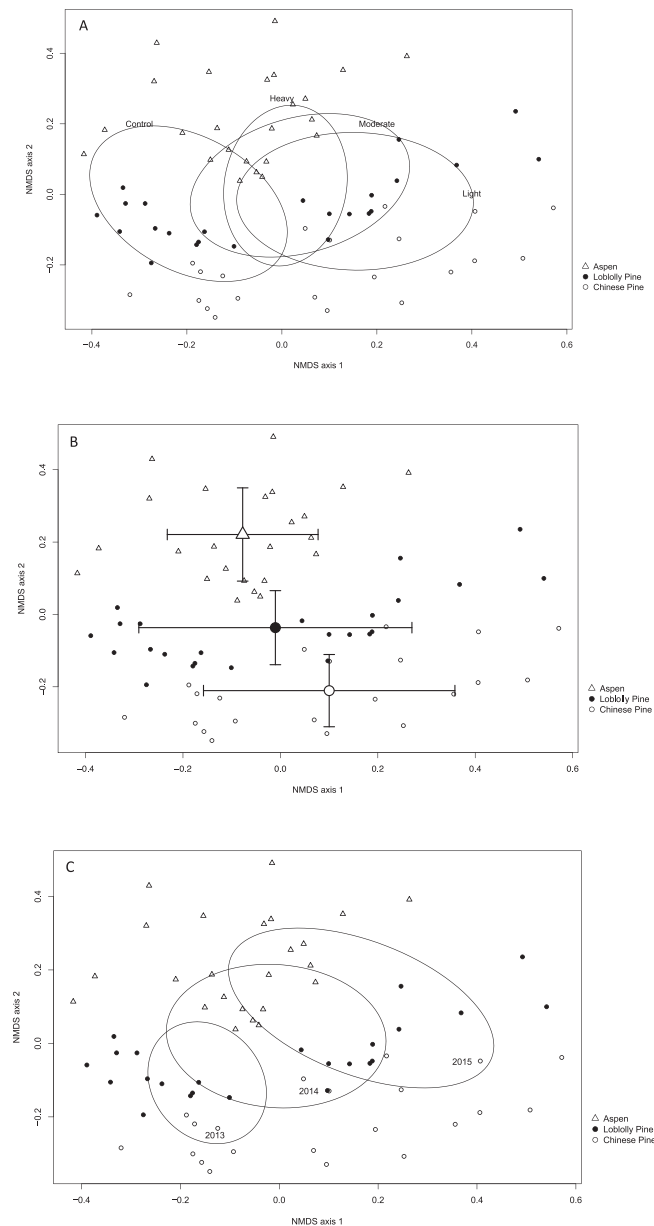


Fig. 5. Surface stake fungal communities differed significantly by (A) thinning treatment (control, heavy, moderate, and light), (B) stake species (aspen, loblolly pine, and Chinese pine) and among (C) years (2013–2015).

wood decomposition (Page-Dumroese et al. 2010) and likely play a role in fungal diversity and structure.

An increase in fungal diversity enhances decomposition relative to one-species systems (Robinson et al., 1993; Setälä and McLean, 2004). In addition, high species diversity could insure that during sustained drought or high temperatures fungi would be present or survive the harsh environmental conditions (Huston, 1997). Increased fungal diversity may also increase wood decomposition because different fungi could attack different substrates (Fukasawa et al., 2011). By the end of our study, the heavily thinned plots had the greatest OTU richness and, therefore, may be more resilient after disturbance.

4.1.3. Stake species

Within both the surface and the mineral soil, OTU richness on aspen stakes was significantly lower than OTU richness on both species of pine stakes. However, within the mineral soil, this result varied across thinning treatments. Aspen stakes have lower lignin content than both

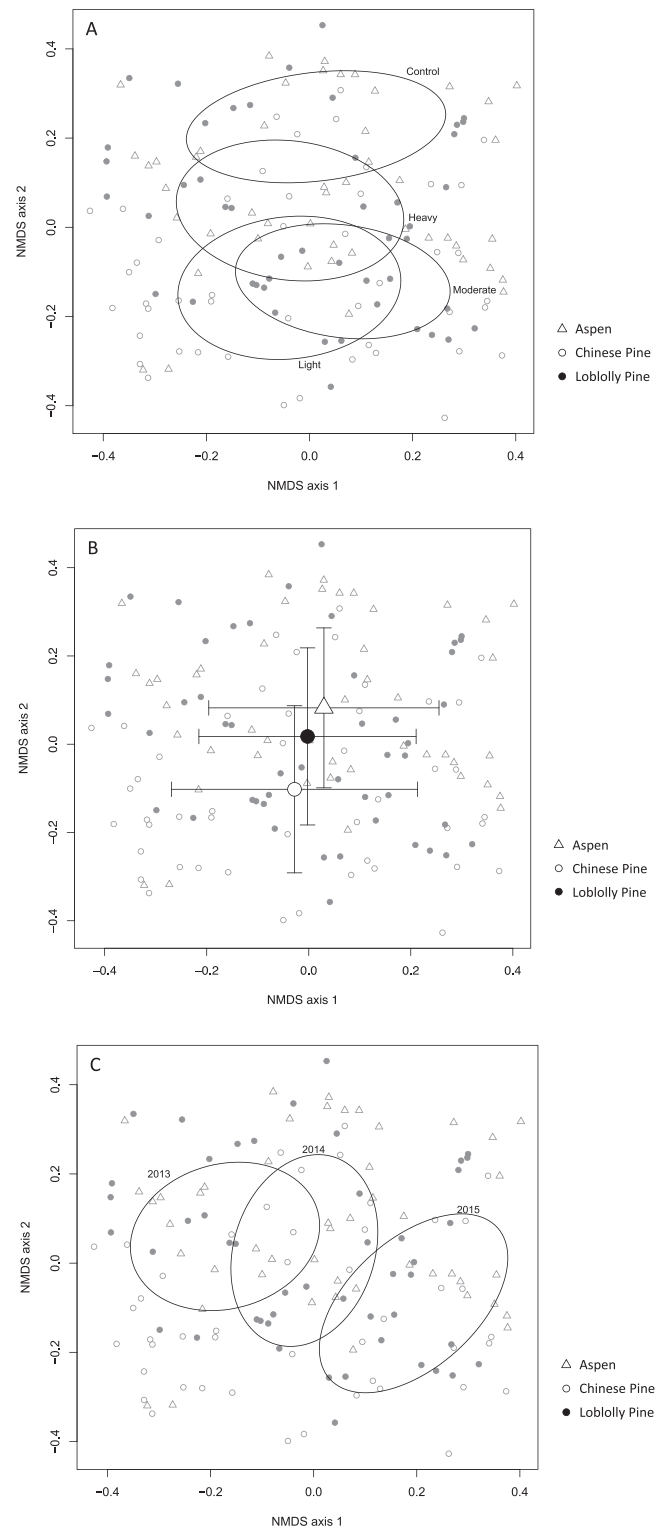


Fig. 6. Stakes in the mineral soil fungal communities differed significantly by (A) thinning treatment (control, heavy, moderate, and light), (B) stake species (aspen, loblolly pine, and Chinese pine) and among (C) years (2013–2015).

loblolly and Chinese pine, leading to greater mass loss of aspen stakes (Wang et al., 2019) which may lead to less OTU richness. White-rot fungi preferentially degrade wood from deciduous trees (Tuor et al., 1995), but recently this paradigm for wood decay has been challenged because of the diversity of species present in natural systems (Riley et al., 2014). Although OTU richness was lower on aspen than on pine, there is likely a continuum of fungal species that are degrading the

lignin, cellulose, and hemicellulose (Riley et al., 2014).

Both pine stake species had similar OTU richness, with the Chinese pine stakes also having significantly greater mass loss than loblolly pine (Wang et al., 2019). A home-field advantage (local substrates will decompose faster than non-local material; Veen et al., 2015) may be occurring. However, since aspen stakes with significantly lower OTU richness had a similar mass loss to the Chinese pine stakes (Wang et al., 2019), home-field advantage may not be occurring or wood quality may be more important (Hättenschwiler et al., 2011; Veen et al., 2015). Forest tree species (Tedersoo et al., 2008a), management (Erland and Taylor, 2002), and soil microsite heterogeneity (Tedersoo et al., 2008b) all affect fungal communities structure and diversity. Specifically, tree species influences litter quality and soil microclimates. Over the long-term trees could promote fungal species that are better able to decompose the wood they encounter most within the soil (Chomel et al., 2015) and, therefore, it is not surprising that the pine stakes had greater OTU richness than the non-native aspen stakes.

4.2. Fungal succession

Succession of fungi on wood occurs by the sequential occupation of the same site by either different fungi or different associations of fungi (Rayner and Todd, 1980). Our wood stakes were kiln dried and had no fungi on them when they were inserted into or laid on top of the soil. After one year in the soil, we were able to detect OTU differences among treatments and stake species. Within the first two years, fungal richness on mineral stakes in the heavily thinned treatments was lower than that found on stakes in the unthinned control. However, by the third year (May 2015), the heavily thinned plots had significantly more fungal OTUs as compared with the low or moderately thinned plots, suggesting a change in stake moisture or a movement of nitrogen into the stake by fungi (Jurgensen et al., 2006) may be responsible for increased OTU richness. It is likely that as the lignocellulosic bonds were broken down, more fungal species were able to access the wood stakes. There has been work that highlights the interspecific interactions of fungi and their role in determining community composition (Connell and Slatyer, 1977; Drake, 1991; Chase, 2003) and indicates that fungi in the soil at the beginning of our study likely played an important role in the subsequent success and growth of fungal species on our wood stakes. Although abiotic factors play an important role in decomposition, fungi also play a role by altering the chemical and physical properties of the wood (Stokland et al., 2012). Lindner et al. (2011) noted that when Norway spruce (*Picea abies*) logs were either inoculated with white rot or brown rot fungi or were left to be naturally colonized, the initial colonizer affected both species richness and wood mass loss. For surface stake communities, the species composition changed from year to year, even though there was no significant difference in OTU richness in the fungal community from year to year.

5. Conclusion

In our study, thinning had a significant effect on fungal community composition and richness after 3 years, both on the soil surface and in the mineral soil, indicating that fungal communities respond to above-ground vegetation changes in temperate forests of northern China. This work has important implications for addressing stand disturbance effects on surface below-ground fungal communities. Further research should address ecosystem processes such as nutrient cycling, C sequestration, CO₂ flux, and understory species interactions with fungal community structure and function. Our work provides needed baseline data on the impacts of thinning on wood colonizing fungal communities over time in a Chinese pine forest, but thinning effects on microbial populations should also be assessed in other forest types and climatic regimes. This data can be used to develop management tools to predict and model the effects of forest thinning gradients on fungal communities and ecosystem processes. Changes in the richness and species

composition of wood-inhabiting fungi could impact the health and productivity of forest sites by affecting key rates of nutrient cycling, although the results of our study are limited to this particular site and soil type. We detected changes in fungal community and OTU richness (for the mineral stakes), but more work is needed to understand whether these changes have functional implications for nutrient cycling or C sequestration.

CRedit authorship contribution statement

Weiwei Wang: Conceptualization, Formal analysis, Visualization, Writing - original draft. **Daniel L. Lindner:** Conceptualization, Supervision, Validation, Writing - review & editing. **Michelle A. Jusino:** Methodology, Formal analysis, Methodology, Writing - review & editing. **Deborah Page-Dumroese:** Conceptualization, Funding acquisition, Supervision, Writing - review & editing. **Jonathan M. Palmer:** Formal analysis, Methodology, Software, Writing - review & editing. **Mark T. Banik:** Formal analysis, Methodology, Software, Writing - review & editing. **Martin Jurgensen:** Conceptualization, Supervision, Writing - review & editing. **Kymerly Draeger:** Formal analysis, Methodology, Software, Writing - review & editing. **Yong Liu:** Conceptualization, Project administration, Supervision, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data accessibility

Raw Ion Torrent sequence data are available in the Short Read Archive of the National Center for Biotechnology Information under BioProject accession PRJNA632840. Data are presented in the supplementary materials and/or will be made available upon request from the corresponding author.

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