**INTRODUCTION**

The Madrean Sky Island Archipelago in southern Arizona supports diverse ecosystems unique from the Sonoran Desert. Hosting a heterogeneous landscape spanning grasslands to coniferous forests at the summit, these biodiversity hot spots bridge the flora and fauna of the northern temperate Rocky Mts. with that of the southern subtropical Sierra Madre Mts. (citation). Communities of ectomycorrhizal (EM) fungi isolated within these montane forests play an important supportive role within forest ecosystems, assisting with water and nutrient uptake, seedling establishment, plant heath, and soil characteristics (Smith & Read, 2008). While their unique location and ecology makes these communities of considerable research interest, it also makes these montane islands sensitive to disturbances, such as drought, wildfire, and climate change.

Periodic wildfires are an integral component of ecosystems playing an important role in shaping community structure, soil characteristics, and ecosystem processes (citation). Increasing global temperatures, reoccurring drought, and long-term wildfire suppression across forests within the United States has altered fire regimes, increasing the occurrence of large, high intensity wildfires (citations). Forests maladapted to the frequency of these intense wildfires are undergoing unprecedented changes including within their microbial communities (citations). EM fungi undergo significant changes under fire disturbance that vary based on both frequency and intensity of wildfires (citation). Research into EM community resistance (i.e. the extent to which a community is displaced by disturbance) and resilience (i.e. the rate of recovery following a disturbance) can elucidate how forest ecosystems are likely to be affected in the future (Pimm 1984; Attiwill 1994; Kipfer *et al.,* 2011)

To date, communities of EM fungi have been poorly studied within Arizona with the exception of one study within the Santa Catalina Mts. (Bowman & Arnold, 2008).

Diversity has been shown to both increase and decrease post fire depending on fire intensity (i.e. temperature and length of fire) and fire frequency (citations). Following the intermediate disturbance hypothesis, evidence indicates that with low or high intensity fires diversity decreases (Wilkinson, 1999; Dahlberg *et al.* 2001; Peay *et al*. 2009), but at intermediate levels fires can increase diversity by opening resources for competitively inferior species thereby increasing diversity (Peay *et al.* 2019). Increasing frequency of fires can impact the composition and diversity of EM communities

How is this research distinct?

No research in SW on fire.

No comparison of geographically distinct but environmentally similar areas to assess the importance of comm. composition versus stochastic processes. (Can I say this as we did not examine the spore community?)

The isolated forests of the Madrean Sky Islands are unique enclaves of biodiversity which have yet to be fully explored.

In our study, we examined the long-term effects (approx. 15 years) of fire on the EM community associated with Ponderosa pine in order to determine how fire affects EM communities, and if similar patterns are seen in two geographically distinct but environmentally similar montane forests in southern Arizona. To answer these questions, we conducted an observational study pairing sites burned in forests fires (fire-affected, FA) with sites that were not burned (fire-unaffected, FU). We predicted that 1) EM species richness and diversity would increase in FA communities, 2) EM community structure and taxonomic composition in FA sites would be distinct from that found in FU sites, and 3) similar processes would be seen in both mountain ranges.

**METHODS**

**Study sites**

We conducted this study in the Santa Catalina Mountains (SCM) and the Pinaleno Mountains (PM) of southern Arizona, USA. The ranges are located at approximately the same latitude and are separated by approximately 150 km distance (Figure 1; Table 1) (Shreve 1919). They have similar orientations, are composed predominantly of gneiss and granite, and have similar plant communities (Shreve 1919; Shreve 1922). Portions of both ranges experienced severe wildfires between 2002 and 2004. In the SCM, the 2002 Bullock fire and the 2003 Aspen fire burned 123.7 km2 and 343 km2, respectively (Iniguez et al. 2008). In the PM, the 2004 Nuttail-Gibson complex burned the northern and southern portion of the range affecting a total of 120.29 km2. In 1996, the Clark peak fire burned 26 km2 in an adjacent area (USDA Forest Service, 2013). Historically, the mean fire interval was infrequent within the SCM occurring approximately every 11.6 years (Iniguez *et al.*, 2008), whereas in the PM low severity fires were frequent, occurring at a fire interval of approximately 4.2 years (Grissino-Mayer et al. 1995). These shared traits make the ranges optimal for a comparison study of the effects of a recent fire history on EM communities associated with *Pinus ponderosa*.

We selected sites that had experienced a low- to intermediate-intensity burn with Ponderosa pine trees still standing. FU and FA sites were assessed using a combination of visual cues (e.g. presence of burn scares on trees, charcoal layer within soil horizon) and burn maps from Monitoring Trends in Burn Severity (MTBS) (accessed online , 2017). We identified two FA and two FU sites in each range (total 8 sites). In the SCM, we sampled two FU sites in 2014 (six trees per site; total 12 trees) and two FA sites in 2016 (five trees per site; total 10 trees) (Table 1). Based on species accumulation curves from previous sampling, we reduced sampling in the SCM FA sites and both the FA and FU sites in the PM to five trees per site (Bowman and Arnold, 2018).

**Sample collection**

We collected three root cores (5 cm diameter; 15 cm depth) at the canopy dripline of each sampled tree corresponding to uphill, parallel, and downhill of the tree (SCM: 66 root cores; PM: 60 root cores). Prior to coring, we removed the litter layer and then transported roots in plastic bags in a cooler back to the lab. Roots were stored at -20°C before processing.

We collected soil cores from three trees per site (total 24 soil cores, 12 per range) and stored samples at 4°C for processing within 72 hrs after collection. Each sample was sieved over a 2 mm mesh and dried at room temperature for 72 hrs. Motzz Laboratories (Phoenix, AZ, USA: http://www.motzzlaboratory.com/) performed chemical analyses.

**Sample processing**

We gently cleaned roots with tap water over a 2 mm sieve. Examining roots under a dissecting microscope, we collected root tips with evidence of EM fungal colonization. To verify host identification of roots collected in forests with Douglas Fir (*Pseudotsuga menziesii*) and/or oak (*Quercus* sp.) (Table 1), we evaluated roots as described in Bowman and Arnold (2018).

Briefly, we sorted EM root tips from *P. ponderosa* to morphotypes based on physical characteristics of the EM mantle (Agerer, 1995). The number of live root tips per morphotype was recorded for each soil core. One or two representatives of each morphotype per core were chosen haphazardly for DNA extraction. All other root tips were stored in cetyltrimethyl ammonium bromide (CTAB) at -80 °C. The remaining root samples were then air dried for 5-7 days, and their dry weight was recorded.

We extracted total genomic DNA from root tips immediately after sorting using the RedExtract-N-Amp plant PCR kit (Sigma-Aldrich, St. Louis, Missouri, USA) following the manufacturer’s instructions. The internal transcribed spacer region (ITSrDNA, including ITS1, ITS2, and 5.8S rDNA) was PCR-amplified using primers ITS1F and LR3. We did not use primer ITS4B because of the prevalence of EM belong to Ascomycota in preliminary surveys (Bowman & Arnold, 2018).

We visualized PCR products with SYBR green following electrophoresis on a 1% agarose gel in 1% TAE buffer. We cleaned samples that amplified using ExoSAP-IT (Affymetrix, Santa Clara, California, USA). Bidirectional Sanger sequencing was performed by the University of Arizona Genetics Core using the Applied Biosystems Big Dye Chemistry Terminator v. 3.1 cycle sequencing kit. We assembled sequences, scored bases, and assigned quality scores with *phred* and *phrap* in Mesquite v. 2.01+ (Maddison and Maddison, 2011; Ewing and Green, 1998; Ewing et al., 1998). We manually edited assembled sequences in Sequencher v. 4.10.1 (GeneCodes Corporation). Sequences were classified to family/genus using UNITE and NCBI to ensure that amplified DNA was from EM species rather than soil fungi or root endophytes.

We isolated 9,844 root tips from 132 root cores. Of these, 514 were selected from individual morphotype groups for sequencing of which 442 (86%) were sequenced successfully. We assembled operational taxonomic units (OTUs) in the web-based Mobyle SNAP Workbench using the sanger\_otu\_clustering\_workflow (Monacell and Carbone, 2014; U’Ren et al., 2014). The assembly pipeline used removed chimeric sequences (Edgar et al., 2011); automatically trimmed the small subunit ribosomal DNA (SSUrDNA), large subunit DNA (LSUrDNA), and 5.8S sequences; and removed sequences lacking either the ITS1 or ITS2 region. Sequences were clustered into OTUs at 97% sequence similarity resulting in a total of 116 OTUs (Izzo et al., 2005; Smith et al., 2007). Of the 116 OTUs, 54 (47%) were singletons and 20 (17%) were doubletons.

**Analysis**

Mean annual precipitation (mm) and maximum annual temperature (°C) (Table 1) were correlated (linear regression; F1,39 = 117.10, p-value < 0.001, R2 = 0.74), Therefore we used mean annual precipitation to represent climate in our analyses as it showed a significant difference between ranges, while max annual temperature did not (Fig. S1). We analyzed climate variables using a mixed effects model as part of an analysis of variance (ANOVA) in which range and fire history were fixed factors and site was treated as a random factor.

We conducted a PCA of the soil characteristics, which differed between ranges and as a function of fire histories (Table 2). PCA axis 1, which explained 50.22% of the variation, was used as the response variable in a mixed effects model ANOVA in which range and fire history were fixed factors and both site and tree were treated as random factors. Our analysis showed that soil did not vary significantly between ranges nor between sites with differing fire histories (Fig. S2). We, therefore, did not include soil in future analyses.

*Species richness and diversity*

Diversity was analyzed as Fisher’s alpha and Shannon’s diversity (Fisher et al., 1943). Fisher’s alpha is robust to variable sample sizes and is used for communities that generally follow a logarithmic series distribution, as is common microbial communities. To complement Fisher’s alpha diversity index, diversity was also calculated using Shannon’s diversity index as it is a non-parametric diversity measure (Shannon, 1948). Diversity and species richness were calculated per tree with the ‘vegan’ package in R (Supplementary table S1) (Oksanen, 2018). Data were assessed for normality and heterogeneity of variance prior to analysis (data not shown). Species richness and diversity were normally distributed. We removed outliers from the Fisher’s alpha analysis where the species richness was equal to the community abundance as this falsely inflated the Fisher’s alpha value (Supplementary table S1). We assessed differences between FA and FU sites within each range for species richness, Fisher’s alpha, and Shannon’s diversity using a t-test. All analyses were carried out using R (R Core Team, 2018).

*Community composition*

Community composition of EM communities was analyzed based on fire history, both within each range and across both ranges, using an analysis of similarity (ANOSIM). Patterns were assessed visually using non-metric multidimensional scaling (NMDS). To assess community differences, we used two different similarity indices: Jaccard (a presence/absence measure) and Morisitia-Horn (an abundance measure) (Magurran 2004). Data were assessed for normality and equal variance prior to ANOSIM (data not shown). The datasets that failed to meet the assumptions required for ANOSIM were analyzed with PERMANOVA.

*Taxonomy*

Sequences were assigned taxonomically with the NCBI and the UNITE databases (UNITE community). Taxonomy was assessed with a chi-square analysis at the class level and genus level as a function of fire history within each range. Rare genera (those with fewer than four occurrences across all sites) were removed prior to analysis. As certain genera and species are known to increase in abundance in fire disturbed sites, we used indicator species analysis to assess whether particular taxonomic groups were more prevalent within FA or FU sites. The analysis was implemented using the ‘indicspecies’ package in R (De Cáceres & Legendre, 2009).

**RESULTS**

Overall, we found species richness and diversity did not vary based on fire history. Species richness (Fig. 2A) and Fisher’s alpha (Fig. 2B) were greater in FA sites than in FU sites, and this trend was reflected in both ranges. Shannon’s diversity showed a similar pattern (Supplementary figure S3). Average Fisher’s alpha across all sites was 15.0 (± 7.9) with FA sites having 17.3 (± 8.0) and FU sites having 13.2 (± 7.5).

*Community composition*

Community composition in FA differed from FU sites, with overall more variation in the PM than the SCM (Fig. 3). EM communities in sites without recent burn history (FU sites) show slight overlap, while sites with a recent fire history (FA sites) in both ranges are completely distinct with no overlap in community composition (Fig. 4 and S4).

*Taxonomy*

We found that EM taxonomy differed between FA and FU sites (Fig. 5 & 6). The most abundant genera were *Cenococcum*, *Russula*, *Tomentella*, and *Lactarius* (Fig. 6)*.* FA sites within the SCM were characterized by a species of questionable EM status, *Sistotrema* (Table S2). In the PM, FU sites were characterized by a species of *Lactarius*, an EM genus, and *Phialocephala*, a dark septate endophyte (DSE) (Table S2).

**DISCUSSION**

In this study, we aimed to determine whether 1) EM community diversity and composition would differ in FA and FU sites 15 years post-fire and 2) if similar patterns would be observed in geographically distinct, but environmentally similar forests. We found no difference in species richness or diversity based on fire history, but community composition differed in FA sites compared to paired FU sites. Overall, we found similar patterns in both ranges. This finding demonstrates that even in geographically distinct forests hosting unique EM communities, EM species diversity and community composition undergo similar changes post fire disturbance.

Whereas EM communities across both ranges differed between FA and FU sites, EM communities in the SCM and PM showed no similarity in FA sites (Fig. 4B) compared to a higher level of similarity in FU sites (Fig. 4A). Although care was taken to ensure that both environment and fire conditions across sites were similar, the distinct communities present in FA sites of each range could reflect unknown factors. Alternatively, these differences could indicate that changes in taxonomic composition are governed more by non-disturbance processes, such as historical contingency. We also observed that the taxonomic composition of EM communities within the two ranges showed contrasting patterns, supporting the latter hypothesis. These differences indicates that the direction of the change in disturbed areas was dependent on the initial EM community pool.

Studies in which EM communities were assessed immediately post-fire have found that both diversity and species richness can increase compared to pre-fire status (Stendell *et al.* 1999; Baar *et al.* 2002). The slightly higher species richness and diversity we found in FA compared to FU sites could indicate these sites are continuing recovery to pre-fire conditions. A study in which recovery of sites post-fire was assessed found that approximately 15 years was sufficient for EM community recovery to near pre-fire diversity status (Treseder *et al.* 2004), although other studies have indicated that substantially longer is required for communities to fully stabilize post-fire (Visser 1995). Factors that could affect levels of species richness and diversity pre- and post-fire are the severity of the fire, that is temperature of fire and depth of soil horizons affected (Stendell *et al*. 1999; Dahlberg *et al.* 2001; Baar *et al.* 2002; Glassman *et al.* 2016). Although we were unable to measure these factors in our observational study, visual indicators and fire severity maps indicate that our FA sites probably underwent a low-severity fire which would have lower temperatures and low level penetration of soil horizons. Low level disturbances such as this can leave the EM spore bank and portions of the hyphal community intact decreasing recovery time (Dahlberg *et al.* 2001; Baar *et al.* 2002; Glassman *et al.*2016).

While the spore community was not assessed here, studies looking at disturbance of EM communities have shown that the dormant spore community serves as the initial inoculum post-fire (Dahlberg *et al.* 2001; Baar *et al.* 2002; Glassman *et al.*2016). Common genera associated with the spore bank are *Rhizopogon,* *Wilcoxina*, and *Tomentella* among others (Baar *et al.* 2002). While *Rhizopogon* and *Tomentella* were present in FA sites, these genera were also in FU sites and overall relative abundance was very low possibly supporting the recovery of FA sites to pre-fire conditions.

A major concern of this study was the temporal difference in sampling (Table 1). EM communities are known to undergo community shifts over relatively short time scales (i.e. seasonal), but year-to-year within the same season there can be little to no changes within the community (Koide *et al.* 2005; O’Hanlon 2012). Additionally, there is evidence that temporal shifts within EM communities is stronger in extraradical hyphae and less pronounced in root colonized EM (Koide *et al.* 2005). As we sampled within the same season of different years and only sampled EM colonized roots, the temporal effect on sampling should be minimal.

The findings outlined here support previous findings in studies of the effect of fire on EM communities, but also demonstrate that the pre-fire community is an important factor in determining how these communities will respond to fire disturbance. While not assessed here, this could have important implications for speed and ability of forests to recover based on pre-fire diversity and composition of the EM community.

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**Figures**

Figure 1: Map of the Santa Catalina Mts. and sampling sites.

Figure 2: Species richness (A) and Fisher’s alpha diversity (B) as a function of both fire history and range. A. T-test, PM: T17.90=1.76, p-value=0.10; SCM: T18.68=1.81, p-value=0.09. B. T-test, PM: T7.09=1.87, p-value=0.10; SCM: T16.44=0.39, p-value=0.70. FA = fire affected, FU = fire unaffected.

Figure 3: NMDS of EM community across fire unaffected (FA) and fire unaffected (FU) sites in the Pinaleno Mts. (A) and Santa Catalina Mts (B) based on Morisita Horn similarity index. A. PM, stress=0.16, ANOSIM: R=0.54, p=value=0.001; B. SCM, stress=0.20, PERMANOVA: F=1.96, R2=0.09, p-value=0.02. Green = FU, black = FA; circles = SCM, squares = PM.

Figure 4: NMDS of EM community across fire affected (FA; A) and fire unaffected (FU; B) based on Morisita Horn similarity index . A. FA, stress=0.19, ANOSIM: R=0.33, p-value=0.001; B. FU, stress=0.15, PERMANOVA: F=3.23, R2=0.16, p=value=0.001. Green = FU, black = FA; circles = SCM, squares = PM.

Figure 5: Class level taxonomy of EM communities as a function of fire history. Each range assessed individually. A. PM, X26=22.48, p-value<0.001; B. SCM, X26=16.314, p-value=0.003. FU = fire unaffected, FA = fire affected.

Figure 6: Genus level taxonomy of EM communities as a function of fire history. Each range assessed individually. A. PM, X29=37.62, p-value<0.001; B. SCM, X213=34.61, p-value=0.001. FU = fire unaffected, FA = fire affected.

**Supplementary Figures:**

Figure S1: Average annual precipitation (mm) as a function of both range and fire history. ANOVA with site as a random factor, range: F1,4 = 99.21, p-value = 0.001; burn history: F1,4 = 3.59, p-value = 0.13; range:burn history: F1,4 = 7.67, p-value = 0.05. FA = fire affected; FU = fire unaffected.

Figure S2: PCA of soil characteristics as a function of both range and fire history. ANOVA with site as a random factor, range: F1,4 = 7.20, p-value = 0.06; burn history: F1,4 = 6.32, p-value = 0.07; range:burn history: F1,4 = 0.003, p-value = 0.96. FA = fire affected; FU = fire unaffected.

Figure S3 Shannon’s diversity as a function of fire history and range. T-test, PM.: T18.41=1.83, p-value = 0.08; SCM: T13.48=2.06, p-value =0.06.

Figure S4: NMDS of EM community across fire affected (FA; A) and fire unaffected (FU; B) based on Jaccard similarity index. A. FA, stress=0.19, PERMANOVA: F=2.92, R2=0.14, p-value=0.001; B. FU, stress=0.13, PERMANOVA: F=2.41, R2=0.12, p=value=0.002. Black = FA, Green = FU; circles = SCM, squares = PM.

Figure S5: NMDS of EM community across FA and FU sites in the PM (A) and SCM (B) based on Jaccard similarity index. A. PM, stress=0.15, ANOSIM: R=0.53, p=value=0.001; B. SCM, stress=0.21, ANOSIM: R=0.11, p-value=0.06. Black = FA, green = FU; circles = SCM, squares = PM.