

# Assemblages of myxomycetes associated with three different substrates affected by forest wildfires

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**Background and aims** – In late November and early December of 2016, forest wildfires occurred over portions of the Great Smoky Mountains National Park (USA) and more than 4 000 ha were affected. Previous studies have shown that myxomycete assemblages can be greatly impacted as a result of this type of disturbance; after which, the recovery of the forest determines the availability of substrates for new colonisation. The objective of the project reported herein was to assess the impact of wildfires on the recovery of the assemblages of myxomycetes associated with three different substrates (forest floor leaf litter, the bark of living trees, and woody twigs) in two areas with different fire intensity.

**Material and methods** – Two study areas subjected to different fire intensity were selected and sampled 30 months after the wildfires. Myxomycetes were studied using the moist chamber culture technique as it applies to these organisms. Satellite imagery was used to determine forest recovery and similarity indices were used to compare experimental myxomycete assemblages among study areas and substrates. Historical data were used as a reference to contextualise the results.

**Key results** – A total of 38 species of myxomycetes representing 17 different genera were recorded from the two study areas. Samples from the lower intensity burn area yielded more myxomycetes than samples from the higher intensity burn area, with values of 84% and 59%, respectively. This same pattern was also observed for the number of recorded specimens (133 and 93, respectively). The comparison of experimental assemblages with previous data suggested that ground litter assemblages were still in early stages of recovery, whereas the assemblages associated with bark and twigs had recovered much faster.

**Conclusion** – The relatively higher intensity fire had more of an effect on myxomycetes than the relatively lower intensity fire. Myxomycete assemblages are resilient to wildfires and they recover differentially depending on the substrate they grow on.

**Keywords** – Disturbance; ecological recovery; forest ecology; Great Smoky Mountains National Park; North Carolina; slime molds; Tennessee.

## INTRODUCTION

Myxomycetes (plasmodial slime molds or myxogastriids) are a group of amoebozoans associated with dead plant material in virtually every type of terrestrial ecosystem investigated to date, with approximately 1000 species known worldwide

(Lado 2005–2020). The myxomycete biota of the Great Smoky Mountains National Park (USA) is especially well known, largely as a result of surveys carried out in the context of the All Taxa Biodiversity Inventory project (Stephenson et al. 2001; Stephenson & Landolt 2009). More than 220 species have been recorded from the park. This total is as

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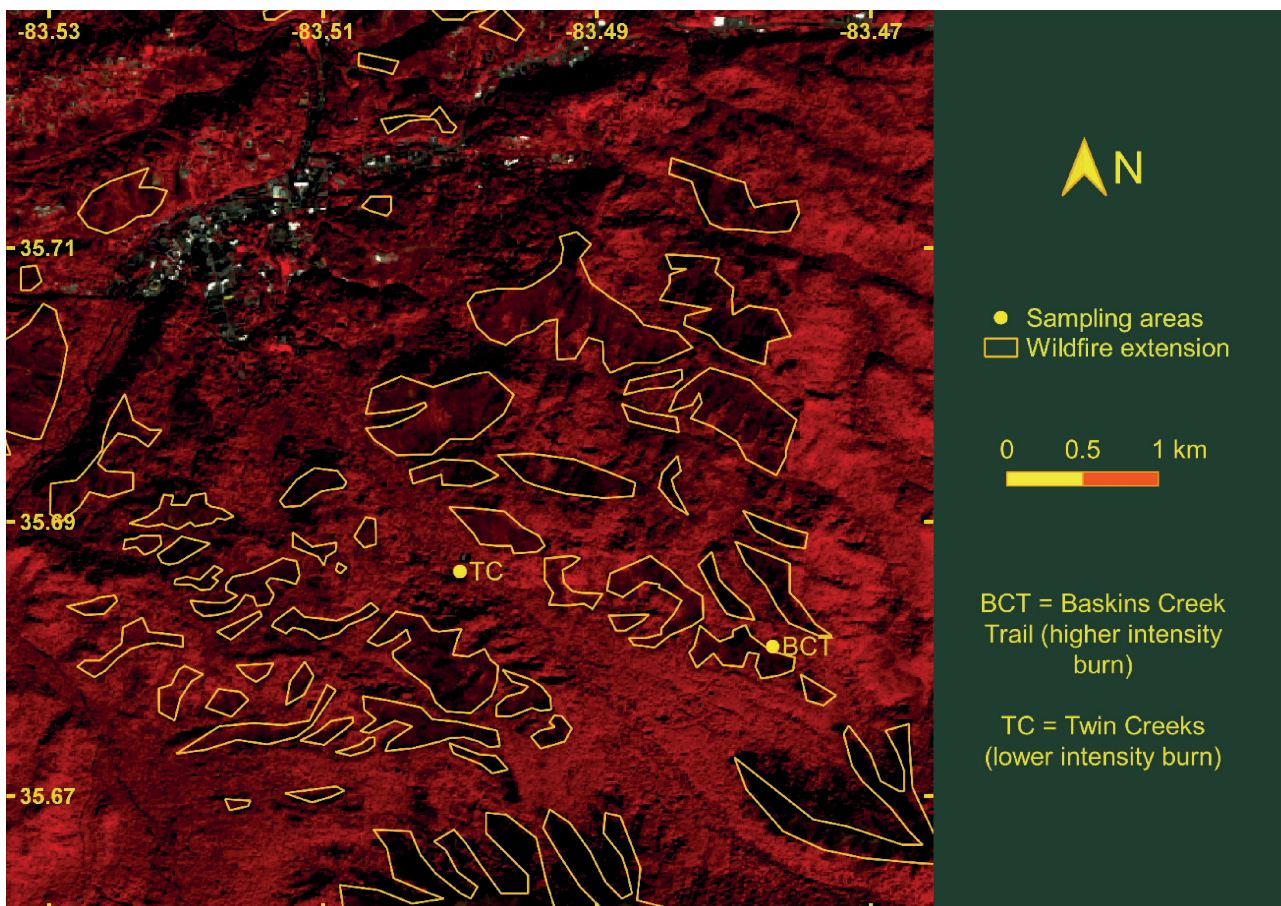
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high as or higher than those recorded for any comparable area of North America.

In temperate forests, myxomycetes are associated with a number of different substrates. These include relatively large pieces of coarse woody debris (e.g. stumps and fallen logs) on the forest floor, woody twigs typically with a diameter of no more than a centimetre, the bark surface of living trees, forest floor leaf litter (also known as ground litter), the dung of herbivorous animals, and aerial portions of dead but still standing herbaceous plants. Each of these substrates tends to be characterised by a distinct assemblage of species (Stephenson 1988, 1989, 2011; Stephenson & Stempen 1994). The myxomycetes associated with the bark surface of living trees, forest floor litter, and twigs are consistently present and often abundant, but many of the species involved are rather inconspicuous or sporadic in their occurrence and thus difficult to detect in the field. However, the moist chamber culture technique as it applies to myxomycetes (Gilbert & Martin 1933) provides a convenient and often very productive method for studying these substrates. Since its introduction, the technique has been used with considerable success by numerous researchers (e.g. Härkönen 1977; Blackwell & Gilbertson 1980; Stephenson 1989).

In late November and early December of 2016, forest wildfires occurred over portions of the Great Smoky Mountains National Park. More than 4000 ha were affected by these events. Some areas were subjected to intense fires that consumed most of the vegetation, whereas the fires in other areas were less intense. Recent studies carried out in these areas show that microbial dynamics and functional guilds were greatly impacted (Brown et al. 2019) and that after two years, some microbial communities were in early stages of their recovery process (Harpe et al. 2019). It is well known that wildfires are among the most impactful disturbance factors in forest ecosystems (Ahlgren & Ahlgren 1960) and their negative impact on the ecological dynamics of ground-level organisms is strong (Merino et al. 2018; Bowd et al. 2019; Dove et al. 2020). Due to the fact that some myxomycetes occur in association with substrates on the ground, wildfires can have a strong effect on the assemblage of species present (see Adamonytė et al. 2016).

In that context, the present study was the result of two circumstances. The general area impacted by such wildfires in the Great Smoky Mountains had been investigated previously for myxomycetes and there are limited studies showing the effect of wildfires on these organisms (e.g. Novozhilov et al. 2007; Gabel et al. 2010). The overall



**Figure 1** – Infrared False Color Composite image (Sentinel Bands 2,3,8 from October 2018, courtesy of the European Space Agency-ESA) showing the areas affected by the 2016 wildfires around the city of Gatlinburg, TN. The location of the two study areas relative to the burned sections of forest is shown. This type of image allows a clearer delimitation of burned vs non-burned areas based on the reflectance signatures of living vegetation in the infrared section of the electromagnetic spectrum.

objective of the project reported herein was to assess the impact of wildfire on the assemblages of myxomycetes associated with the three different substrates in two areas subjected to different fire intensities. As such, this study contributes to the knowledge of wildfire effects on microbial systems and their ecological recovery.

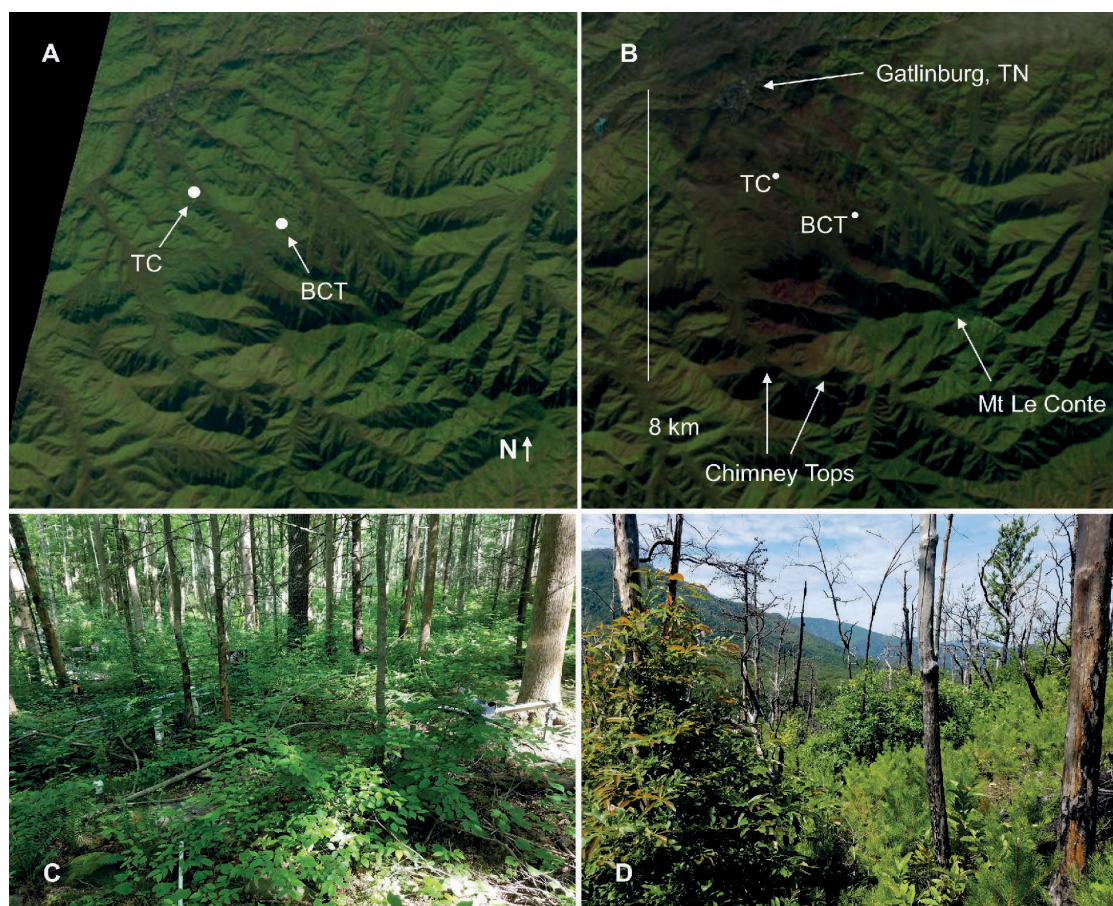
## MATERIAL AND METHODS

The present study was carried out in the Great Smoky Mountains National Park, a federally managed forest encompassing an area of 2113 km<sup>2</sup> in western North Carolina and eastern Tennessee in the United States. The park is located at 35°36'N, 83°29'W, with elevations ranging from approximately 270 to 2000 m above sea level.

Based on satellite imagery (Sentinel-2, courtesy of the European Space Agency, ESA) as well as public information, two study areas in the vicinity of Gatlinburg, Tennessee, were selected on the basis of fire intensity during the 2016 events (figs 1, 2). A relatively lower intensity burn study area (fig. 2C) was designated on a slope with a west-northwest aspect at the Twin Creeks All Taxa Biodiversity Inventory site (35°41'11"N, 83°29'60"W, 595 m; referred to as TC), and a relatively higher intensity burn study area (fig.

2D) was selected on a slope with a west-southwest aspect along the Baskins Creek Trail (35°40'45"N, 83°28'38"W, 865 m; referred to as BCT). Prior to the wildfires, TC was characterised by a second-growth mixed hardwood cove forest with a great laurel (*Rhododendron maximum* L.) understory and BCT encompassed a second-growth mixed oak-hardwood forest. Both areas have been under natural regeneration after the wildfires.

Thirty months after the wildfires, on 28 Jun. 2019, samples of twigs (T), forest floor leaf litter (GL), and bark (B) were collected at regular intervals along walking transects that extended through the two study areas being considered. Those substrates would have been depleted during the wildfires in both study areas, and the assemblages of myxomycetes associated with them at the time of sampling were considered to be the result of new colonisation. In this manner, ten samples were collected from each of the three types of substrates in each of the two study areas, for a total of 60 samples. Each sample was placed in an individual paper bag and the latter numbered and marked with the type of substrate. The entire set of samples was returned to the Eumycetozoa Laboratory at the University of Arkansas for processing.



**Figure 2** – Landscape-level (Landsat 8, courtesy of the U.S. Geological Survey) and ground-level images of the study areas selected for this investigation. **A.** Pre-wildfire satellite view of the general area obtained on 12 Nov. 2016. **B.** Post-wildfire satellite view obtained on 21 Dec. 2016 showing the extension affected by fire. **C.** View of the forest in Jun. 2019 in TC. **D.** View of the forest in Jun. 2019 in BCT. Photographs by Will Kuhn.

At the University of Arkansas, the samples were used to prepare moist chamber cultures. These were prepared in the manner described by Stephenson & Stempen (1994) and consisted of plastic disposable Petri dishes (90 mm diameter) lined with filter paper. Three Petri dishes were prepared from each sample, for a total of 30 for each type of substrate, 90 for each study area, and a total of 180 for the entire project. Enough sample material was placed in each dish to cover most of the bottom, and the material was moistened with distilled water. After a period of approximately 24 hours, the pH of each culture was determined with a portable pH meter and then excess water in the Petri dish was poured off. Moist chamber cultures were placed out of direct sunlight and maintained at room temperature. Water was added to these cultures when necessary to maintain moist conditions, and the cultures were checked at least twice each week for evidence (either plasmodia or fruiting bodies) of myxomycetes over a period of approximately three months. When fruiting bodies were observed, they were recorded, removed from the moist chamber culture, air-dried, and placed in small pasteboard boxes for long-term storage and identification. A specimen was defined as a record of the occurrence of one or more fruiting bodies of a particular species of myxomycete in a single culture. Some specimens consisted of only a single fruiting body, whereas others consisted of numerous fruiting bodies. With the information obtained from the moist chambers, a database of species, records, and pH values was created for the three different substrates at the two study areas.

Using Landsat 8 images (courtesy of the U.S. Geological Survey) from each season from winter 2016 (the time of the wildfires) to the summer of 2019 (the time of sampling), a forest recovery progression was recreated for 20 hectares associated with each of the two study areas. For this, the Soil Adjusted Vegetation Index (SAVI), an estimator of vegetation health similar to the NDVI but with a correction based on soil variables (Huete 1988), was used. This estimator is useful to analyze normal seasonal vegetation dynamics as well as abnormal events and is based on the formula:

$$SAVI = \frac{(1 + L)(NIR - Red)}{(NIR + Red + L)}$$

where *NIR* is the spectral data between 850–880 nm, *Red* represents the spectral data between 640–670 nm, and *L* is a canopy background adjustment factor, for which a value of 0.5 was used herein.

SAVI values oscillate between -1 and 1. Negative values are associated with lack of vegetation, heavy disturbance, or non-forested areas; values close to 0 are associated with bare soil and disturbance; and positive values are associated with vegetation cover and biomass presence, even during the winter. Values closer to 1 are interpreted as complex and healthy vegetation cover, usually associated with forested areas during the peak of the growing season.

In a similar manner, for the winter seasons of 2016, 2017, and 2018, a calculation of land surface temperature for a 20-hectare polygon was carried out using Landsat 8 information. This approach was used to analyse if the

wildfires had affected the temperature values of the study areas during 2016 (immediately post-fire) more drastically than normal oscillations in relation with non-burned areas of the general landscape. Based on the work of Adamonytė et al. (2016), more intense fires (that can be determined on the basis of temperature) have a stronger impact on myxomycete communities. The calculations of land surface temperature are complex and were based on a scheme similar to that of Avdan & Jovanovska (2016) using Band 10 for the thermal infrared spectral analysis.

With the myxomycete moist chamber data, the number of species and records as well as the Shannon's Index of Diversity and Evenness values were calculated for each substrate in each of the study areas. Also, the Chao1 estimator associated with the maximum number of species expected with the methods used in the present study was calculated using the formula:

$$Chao1 = a + \frac{b^2}{2c}$$

where *a* is the total number of species in the dataset, *b* is the number of singletons (species with a single occurrence in the sample), and *c* the number of doubletons (species with double occurrences in the sample).

Also, the assemblages of species recorded from the different substrates and the two study areas were compared by pairwise calculation of the coefficient of community (also known as Bray-Curtis Index) using the formula shown below (Mueller-Dombois & Ellenberg 1974):

$$\text{Coefficient of community (CC)} = \frac{2d}{e + f}$$

where *e* represents the total number of species present in the first study area or dataset being considered, *f* represents the total number of species in the second study area or dataset being considered, and *d* represents the common species present between two study areas or datasets being considered. The value of CC ranges from 0 to 1, where 0 indicates no common species shared between two study areas or datasets and 1 indicates that all species are common to both study areas or datasets.

In addition, all datasets recorded herein were compared with previous information using a species assemblage approach. For this, a pre-wildfire dataset of myxomycete records for the Great Smoky Mountains National Park collected as part of the All Taxa Biodiversity Inventory (ATBI) project, was used. This task was carried out only with the assemblages of species that were associated with the three substrates studied as part of the present investigation. For this, a cluster analysis using the Bray-Curtis algorithm was performed and both the numbers of unique and common species were calculated for each branching. This approach was used to determine the relative complexity of species assemblages associated with the three substrates and the two study areas.

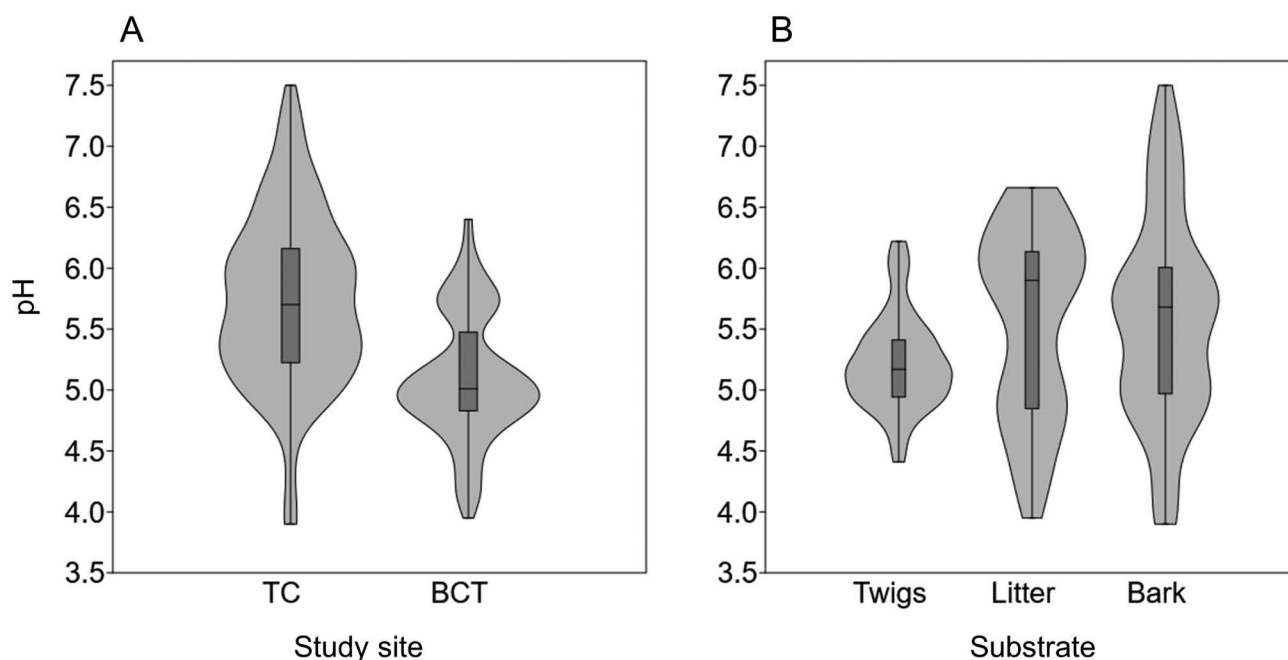
## RESULTS

A total of 38 species representing 17 genera were recorded from the 226 specimens appearing in the 180 moist chamber cultures prepared in the present study (table 1, supplementary file 1). The vast majority (> 97%) of all specimens could be identified to species, but a few were poorly developed or aberrant and could be referred only to genus. The only exception was one specimen of *Trichia* that was well developed but could not be placed in any species of which the senior author is aware and thus will need further examination. It was left as *Trichia* sp. in table 1. Myxomycete data previously obtained in the general area showed about 99 species on the same substrates studied herein. With such figure, the present study recorded about 40% of the known biodiversity in the area. Interestingly, *Didymium ochroideum* G.Lister, *Perichaena pedata* (Lister & G.Lister) G.Lister ex E.Jahn, and *Physarum auriscalpium* Cooke had not yet been recorded.

The most diverse genus was *Physarum*, with seven species. The single most common species was *Arcyria cinerea* (Bull.) Pers., which was represented by 46 specimens. It was the only species recorded from all three substrates in both of the study areas. Historical data (using information generated by the first author during the period 1999–2003 with support from Discover Life in America and the All Taxa Biodiversity Inventory project) showed that *Didymium melanospermum* (Pers.) T.Macbr., *Leocarpus fragilis* (Dicks.) Rostaf., and *Physarum viride* (Bull.) Pers. are fairly common on all three substrates, but the results from the present study were not consistent with that observation. The next most common species was *Echinostelium minutum* de Bary (27 specimens), followed by *Stemonitis fusca* var. *nigrescens* (Rex) Torrend

(22), *Perichaena vermicularis* (Schwein.) Rostaf. (16), and *Perichaena chrysosperma* (Curr.) Lister (14). The numbers of species associated with the three different substrates ranged from only six (litter for BCT) to 20 (bark for TC). In BCT, bark was also the most productive substrate, with 14 species. Historical data showed that ground litter was the substrate with the highest number of both species and records in the area. When the totals for the same type of substrate in the two study areas were compared, the most appreciable difference existed for litter. Sixteen species were recorded for TC, which was appreciably higher than the total (six, as noted above) for BCT. These results showed that, in comparison with the 67 historically recorded species on litter, only 28% of them were recorded in the present study.

The coefficient of community indices calculated for the possible pairwise comparisons of the three different substrates, based on pooled data from both study areas, were 0.37 (bark and litter, 6 common species), 0.49 (bark and twigs, 8 common species), and 0.47 (litter and twigs, 10 common species). These values suggest that the assemblages of myxomycetes associated with bark and litter are the least similar, whereas those associated with bark and twigs are the most similar. With this index, litter was the most distinct substrate. However, these patterns were not necessarily reflected in the values obtained for pairwise comparisons calculated for substrates in just one of the two study areas. For TC, the values were 0.39 (bark and twigs, 5 common species), 0.42 (bark and litter, 6 common species), and 0.38 (litter and twigs, 8 common species), whereas for BCT they were 0.32 (litter and twigs, 3 common species), 0.29 (bark and litter, 3 common species), and 0.50 (bark and twigs, 6 common species).



**Figure 3** – Violin charts and boxplots of the pH value profiles recorded in the study sites (A) and substrates (B) evaluated in the present investigation.

**Table 1** – Occurrence of myxomycetes in the three different substrates in the two different study areas. Also provided is a summary of values (with the highest shown in bold) obtained for the assemblage of species associated with each substrate.

Myxomycete species	Historical data			Baskins Creek Trail			Twin Creeks		
	B	L	T	B	L	T	B	L	T
<i>Arcyria affinis</i> Rostaf.	2								
<i>Arcyria cinerea</i> (Bull.) Pers.	17	70	5	5	1	13	7	1	19
<i>Arcyria denudata</i> (L.) Wettst.	1	2							
<i>Arcyria major</i> (G.Lister) Ing	1								
<i>Arcyria pomiformis</i> (Leers) Rostaf.	1	1							
<i>Arcyria stipata</i> (Schwein.) Lister		3							
<i>Badhamia affinis</i> Rostaf.	1		1						
<i>Badhamia goniospora</i> Meyl.	1								
<i>Badhamia macrocarpa</i> (Ces.) Rostaf.			1						
<i>Badhamia papaveracea</i> Berk. & Ravenel	1								
<i>Badhamia versicolor</i> Lister	1								
<i>Badhamiopsis ainoae</i> (Yamash.) T.E.Brooks & H.W.Keller	3								
<i>Ceratiomyxa fruticulosa</i> (O.F.Müll.) T.Macbr.		2							
<i>Clastoderma debaryanum</i> A.Blytt		9		3			1		1
<i>Collaria arcyrionema</i> (Rostaf.) Nann.-Bremek. ex Lado	1			2			1		
<i>Collaria lurida</i> (Lister) Nann.-Bremek.		9							
<i>Colloderma oculatum</i> (C.Lippert) G.Lister	3	3							
<i>Comatricha elegans</i> (Racib.) G.Lister			1	1					
<i>Comatricha laxa</i> Rostaf.	1	1	1						
<i>Comatricha nigra</i> (Pers. ex J.F.Gmel.) J.Schröt.	8		4				2		
<i>Comatricha pulchella</i> (C.Bab.) Rostaf.			1	2			2		
<i>Comatricha</i> sp.					1				1
<i>Comatricha tenerrima</i> (M.A.Curtis) G.Lister							3		
<i>Craterium minutum</i> (Leers) Fr.	3	2	1						
<i>Craterium obovatum</i> Peck		1							
<i>Cribraria cancellata</i> (Batsch) Nann.-Bremek.		1							
<i>Cribraria confusa</i> Nann.-Bremek. & Y.Yamam.	4								
<i>Cribraria intricata</i> Schrad.	3	4							
<i>Cribraria microcarpa</i> (Schrad.) Pers.		3			2	1	3		
<i>Cribraria purpurea</i> Schrad.		1							
<i>Cribraria rufa</i> (Roth) Rostaf.		2							
<i>Cribraria violacea</i> Rex	1						4		
<i>Diachea subsessilis</i> Peck		1							
<i>Diacheopsis insessa</i> (G.Lister) Ing	1								
<i>Dictydiaethalium plumbeum</i> (Schumach.) Rostaf.	4								
<i>Diderma effusum</i> (Schwein.) Morgan	1	11			1		2	2	1
<i>Diderma hemisphaericum</i> (Bull.) Hornem.		2						1	1
<i>Diderma roanense</i> (Rex) T.Macbr.	1	6							
<i>Diderma spumarioides</i> (Fr. & Palmquist) Fr.		2							
<i>Diderma testaceum</i> (Schrad.) Pers.		12						3	
<i>Didymium anellus</i> Morgan		4							
<i>Didymium clavus</i> (Alb. & Schwein.) Rabenh.		1							
<i>Didymium difforme</i> (Pers.) Gray		7							

**Table 1 (continued)** – Occurrence of myxomycetes in the three different substrates in the two different study areas. Also provided is a summary of values (with the highest shown in bold) obtained for the assemblage of species associated with each substrate.

Myxomycete species	Historical data			Baskins Creek Trail			Twin Creeks		
	B	L	T	B	L	T	B	L	T
<i>Didymium iridis</i> (Ditmar) Fr.	1	7							
<i>Didymium melanospermum</i> (Pers.) T.Macbr.	15	18	4						
<i>Didymium minus</i> (Lister) Morgan		2							
<i>Didymium nigripes</i> (Link) Fr.		4							
<i>Didymium ochroideum</i> G.Lister								1	
<i>Didymium squamulosum</i> (Alb. & Schwein.) Fr. & Palmquist	1	4							
<i>Echinostelium minutum</i> de Bary	5	3		8		7	4		8
<i>Enerthenema papillatum</i> (Pers.) Rostaf.	3								
<i>Fuligo septica</i> (L.) F.H.Wigg.	6	4							
<i>Hemitrichia calyculata</i> (Speg.) M.L.Farr	5	4							
<i>Hemitrichia minor</i> G.Lister	2						1		
<i>Hemitrichia serpula</i> (Scop.) Rostaf. ex Lister	2	6				1			
<i>Lamproderma columbinum</i> (Pers.) Rostaf.		3							
<i>Lamproderma scintillans</i> (Berk. & Broome) Morgan				1					
<i>Leocarpus fragilis</i> (Dicks.) Rostaf.	2	2	5						
<i>Lepidoderma tigrinum</i> (Schrad.) Rostaf.		3							
<i>Licea minima</i> Fr.	4	1		3	1	1	1	1	
<i>Licea operculata</i> (Wingate) G.W.Martin	6		1				3		
<i>Licea parasitica</i> (Zukal) G.W.Martin	1								
<i>Licea pedicellata</i> (H.C.Gilbert) H.C.Gilbert	1								
<i>Licea</i> sp.								1	
<i>Lycogala epidendrum</i> (L.) Fr.	3	5						2	
<i>Metatrichia floriformis</i> (Schwein.) Nann.-Bremek.		1							
<i>Metatrichia vesparia</i> (Batsch) Nann.-Bremek. ex G.W.Martin & Alexop.	6	3							
<i>Perichaena chrysosperma</i> (Curr.) Lister		9		3		3	6	1	1
<i>Perichaena depressa</i> Lib.		6		1					
<i>Perichaena pedata</i> (Lister & G.Lister) G.Lister ex E.Jahn								4	1
<i>Perichaena</i> sp.								1	1
<i>Perichaena vermicularis</i> (Schwein.) Rostaf.		5		6		3	1		6
<i>Physarum album</i> (Bull.) Chevall.	21	9							1
<i>Physarum auriscalpium</i> Cooke						1		1	
<i>Physarum bethelii</i> T.Macbr. ex G.Lister	1								
<i>Physarum bivalve</i> Pers.		16						1	2
<i>Physarum cinereum</i> (Batsch) Pers.		4						2	
<i>Physarum compressum</i> Alb. & Schwein.		5							
<i>Physarum contextum</i> (Pers.) Pers.	1								
<i>Physarum crateriforme</i> Petch	3								
<i>Physarum decipiens</i> M.A.Curtis	1					1			
<i>Physarum galbeum</i> Wingate		2							
<i>Physarum</i> cf. <i>hongkongense</i> Chao H.Chung									1
<i>Physarum leucophaeum</i> Fr. & Palmquist	1	1							
<i>Physarum nucleatum</i> Rex				1		1			

**Table 1 (continued)** – Occurrence of myxomycetes in the three different substrates in the two different study areas. Also provided is a summary of values (with the highest shown in bold) obtained for the assemblage of species associated with each substrate.

Myxomycete species	Historical data			Baskins Creek Trail			Twin Creeks		
	B	L	T	B	L	T	B	L	T
<i>Physarum penetrale</i> Rex	1								
<i>Physarum psittacinum</i> Ditmar		1							
<i>Physarum pusillum</i> (Berk. & M.A.Curtis) G.Lister		2	1						
<i>Physarum viride</i> (Bull.) Pers.	12	9	3			1	1		2
<i>Stemonitis axifera</i> (Bull.) T.Macbr.	2	4							
<i>Stemonitis flavogenita</i> E.Jahn	1						3		
<i>Stemonitis fusca</i> var. <i>nigrescens</i> (Rex) Torrend	3	2		4		9			9
<i>Stemonitis herbatica</i> Peck		1							
<i>Stemonitopsis hyperopta</i> (Meyl.) Nann.-Bremek.	2	2	1						
<i>Stemonitopsis typhina</i> (F.H.Wigg.) Nann.-Bremek.		1							
<i>Symphytocarpus herbaticus</i> Ing		1							
<i>Trichia botrytis</i> (J.F.Gmel.) Pers.		1		1	1				
<i>Trichia contorta</i> (Ditmar) Rostaf.	1								
<i>Trichia decipiens</i> (Pers.) T.Macbr.	2	3							
<i>Trichia erecta</i> Rex	4	2							
<i>Trichia favoginea</i> (Batsch) Pers.	8	15				1	2	1	
<i>Trichia munda</i> (Lister) Meyl.	1	1							
<i>Trichia persimilis</i> P.Karst.	3								
<i>Trichia</i> sp.								1	
<i>Trichia subfusca</i> Rex	3	4					1	4	
<i>Tubifera ferruginosa</i> (Batsch) J.F.Gmel.		3	1						
<i>Willkommlangea reticulata</i> (Alb. & Schwein.) Kuntze						3			2
<b>Number of species</b>	58	67	15	14	6	13	<b>20</b>	16	16
<b>Number of records</b>	198	340	31	41	7	45	50	26	<b>57</b>
<b>Chao1 Maximum number of species</b>	96	77	60	17	11	<b>34</b>	23	<b>34</b>	25
<b>Shannon Index of Diversity</b>	3.6	3.5	2.4	2.4	1.8	2.1	<b>2.8</b>	2.6	2.1
<b>Shannon Evenness</b>	0.6	0.5	0.7	0.8	<b>0.9</b>	0.6	0.8	0.8	0.5

Many of the species represented by three or more specimens displayed a preference for one type of substrate. For example, 18 of the 22 records of *Stemonitis fusca* var. *nigrescens* were from twigs, whereas all five records of *Willkommlangea reticulata* (Alb. & Schwein.) Kuntze were from this substrate. Species displaying an apparent affinity for bark were *Comatricha tenerrima* (M.A.Curtis) G.Lister, *Cribraria violacea* Rex, *Licea minima* Fr., *L. operculata* (Wingate) G.W.Martin, and *Stemonitis flavogenita* E.Jahn. Only a very few species were represented by at least four records on litter, but two of these (*Perichaena pedata* and *Trichia subfusca* Rex) appeared to display an affinity for this substrate. In the historical records, there was not a clear preference of species for twigs or bark, but *Clastoderma debaryanum* A.Blytt, *Cribraria microcarpa* (Schrad.) Pers., *Diderma hemisphaericum* (Bull.) Hornem., *D. testaceum* (Schrad.) Pers., *Perichaena chrysosperma* (Curr.) Lister, *P. depressa* Lib., *Physarum bivalve* Pers., *Ph. cinereum*

(Batsch) Pers., and *Perichaena vermicularis* had only been recorded on litter.

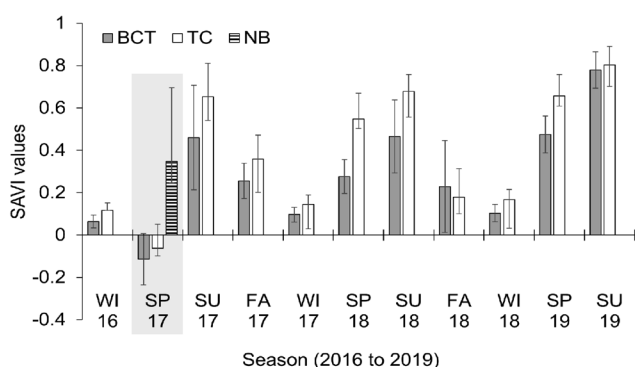
Collectively, 72% of all moist chamber cultures yielded some evidence (either fruiting bodies or plasmodia) of myxomycetes. Two or more species appearing in a single culture was not unusual, and a few cultures yielded four or more species. However, the set of cultures prepared with samples from TC (84%) was more productive than the set prepared with samples from BCT (59%). Moreover, the former set of cultures yielded a total of 133 specimens, whereas the latter produced only 93 specimens.

The median value of pH for all 180 moist chamber cultures was 5.3, with a maximum value of 7.5 and a minimum value of 3.9 (fig. 3). Cultures prepared with twigs were the most acidic (median = 5.1 with a range of 4.4 to 6.2), whereas those prepared with bark were the least acidic (median = 5.9 with a range of 3.9 to 7.5). Values of pH also

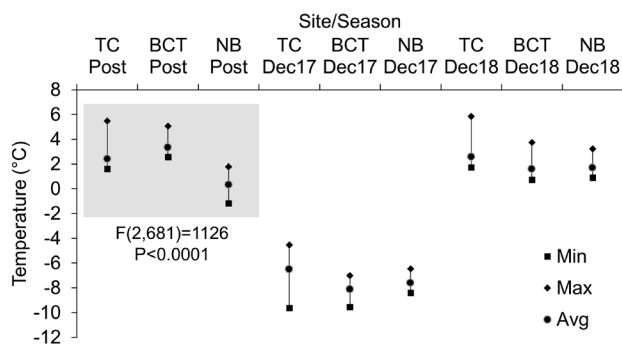


differed between study areas, with a median value of 5.0 (range of 3.9 to 6.4) for BCT, and a median of 5.7 (range of 3.9 to 7.5) for TC.

Satellite imagery showed that both study areas were affected by the wildfires and that the first growing season, in the spring of 2017, was the most disturbed in terms of deviation from normal dynamics (fig. 4). The average SAVI value for the springs of 2017 and 2018 was 0.48, and the non-burned control plot during the spring of 2017 showed an average value of 0.34. In contrast, the average value for the burned study areas was -0.08, thus demonstrating the strong effect of the wildfires. Even the winter seasons of 2017 and 2018 showed a higher average value of 0.13. This imagery also showed that the forest was in recovery during the 30 months after the wildfires, with a cover of vegetation already present in the summer of 2017. Such recovery has been more accelerated in TC than in BCT, which also tended to have milder winter surface temperatures (see fig. 5), presumably affecting myxomycete dynamics indirectly by allowing vegetation to recover faster and modifying the



**Figure 4** – Soil Adjusted Vegetation Index (SAVI) values for each season and study area (TC and BCT) between the winter of 2016 and the summer of 2019. The values for TC and BCT during the spring of 2017 were compared with a control non-burned (NB) area. WI = winter, SP = spring, SU = summer, FA = fall.



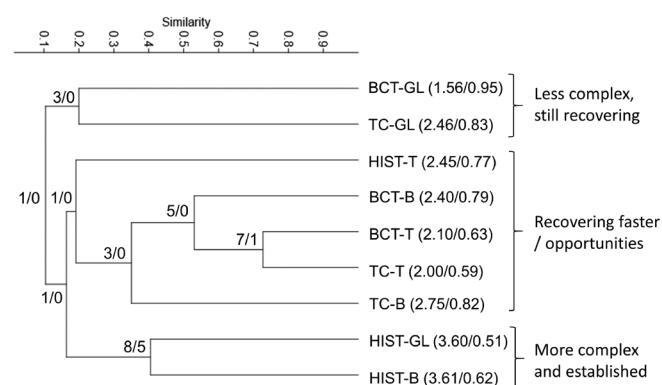
**Figure 5** – Maximum (Max), minimum (Min), and average (Avg) temperature values (in °C) calculated for the winters of 2016–2018 from Landsat 8 images for 20 hectares associated with both study areas (TC and BCT) as well as non-burned (NB) control areas. 2016 is abbreviated as Post, for being the immediate post-fire season.

microhabitat conditions. Interestingly, of the three winter seasons evaluated, only during the winter of 2016, surface temperatures associated with the two study areas were significantly different from those from non-burned areas. This analysis also showed, as expected based on the reported fire intensity, that temperatures in BCT were higher than in TC, demonstrating a stronger effect from the fire.

Finally, when the species assemblages associated with the three substrates and two study areas were compared with previous data from the Great Smoky Mountains National Park, the results did not show many differences between study areas (fig. 6). All beta diversity values using the Whittaker estimator were higher than 0.65. Albeit the latter, approximately 65 species previously recorded in the area were not observed in the present survey. Interestingly, clear differences in assemblage recovery were observed for ground litter, with less complex assemblages (i.e. simpler in terms of diversity and evenness) in comparison with historical data. This observation also supports the results obtained from the coefficient of community comparison discussed earlier. For litter, the remarkably high evenness values demonstrated numerically the simplicity in the structure of the assemblage in comparison with the other substrates, instead of assemblage maturity. Both twigs and bark, in both study areas, showed an intermediate stage of recovery in relation to previous information. Taking the Shannon's Index of Diversity and Evenness values, it is also apparent that historical data represented more complex and established assemblages, as expected.

### Annotated list of species

In the list that follows, species of myxomycetes recorded in the present study were arranged alphabetically by genus and then species. Information was provided on the number of specimens recorded, the range of pH values of the culture(s) in which the specimen appeared, and the substrate(s)



**Figure 6** – Cluster analysis of similarity (Bray-Curtis algorithm) showing the relationships among assemblages of myxomycetes recorded on substrates (GL, T, and B) and in study sites (TC and BCT). The historical records (HIST) obtained for the same general area of the Great Smoky Mountains National Park for the same substrates were included. The numbers of unique and shared species are shown in the branches and the Shannon's Index of Diversity as well as Evenness values are shown next to each subdataset label.

with which records were associated. Numbers given in parentheses are collecting numbers of the first author.

***Arcyria cinerea*** (Bull.) Pers.

Represented by 46 specimens (including 33761, 33808, and 34102) and associated with all three substrates in both study areas. However, it was most common (32 specimens) on twigs. The cultures in which this species appeared ranged in pH from 3.9 to 7.1.

***Clastoderma debaryanum*** A.Blytt

Represented by five specimens (including 33960 and 33962) and recorded from both study areas. The majority of specimens (four) were recorded on bark (pH 5.4 to 6.1).

***Collaria arcyronema*** (Rostaf.) Nann.-Bremek. ex Lado

Represented by three specimens (including 34008 and 34010), all of which were recorded on bark (pH 5.7 to 6.7). This species was recorded from both study areas.

***Comatricha elegans*** (Racib.) G.Lister

Represented by a single specimen (33770) recorded on bark (pH 6.4) from BCT.

***Comatricha nigra*** (Pers. ex J.F.Gmel.) J.Schröt.

Represented by two specimens (including 33771), both on bark (pH 7.3 and 7.5) from TC.

***Comatricha pulchella*** (C.Bab.) Rostaf.

Represented by four specimens (including 33840 and 33988), all on bark (pH 5.0 to 5.9). Two specimens were recorded from both BCT and TC.

***Comatricha tenerrima*** (M.A.Curtis) G.Lister

Represented by three specimens (34131 and 34194) on bark (pH 7.1 and 6.9), both from TC.

***Cribraria microcarpa*** (Schrad.) Pers.

Represented by six specimens (including 33812 and 33856), three on bark (pH 4.1 to 5.7), two on litter (pH 4.1 and 5.0), and one on twigs (pH 5.1). This species was recorded from both study areas.

***Cribraria violacea*** Rex

Represented by four specimens (including 33809 and 34137), all on bark (pH 6.1 to 6.7) from TC.

***Diderma effusum*** (Schwein.) Morgan

Represented by six specimens (including 33762 and 33939), with three on litter (pH 5.8 to 6.6), two on bark (pH 5.7 and 6.7) and one on twigs (pH 5.6). This species was recorded from both study areas. It is typically associated with litter (Martin & Alexopoulos 1969).

***Diderma hemisphaericum*** (Bull.) Hornem.

Represented by two specimens, the first (33946) recorded on litter (pH 6.1) and the second on bark (pH 5.0). Both specimens were recorded from TC.

***Diderma testaceum*** (Schrad.) Pers.

Represented by three specimens (34040 and 34041) on litter (pH 5.9 for both) from TC.

***Didymium ochroideum*** G.Lister

Represented by a single specimen (33963) recorded on litter (pH 6.6) from TC.

***Echinostelium minutum*** de Bary

Represented by 27 specimens (including 33769, 33855 and 33954), with 15 recorded on twigs (pH 4.4 to 5.9) and 12 recorded on bark (pH 3.9 to 5.9).

***Hemitrichia minor*** G.Lister

Represented by a single specimen (34180) on bark (pH 6.7) from TC. In earlier taxonomic treatments of the myxomycetes, this species was listed as *Perichaena minor* (G.Lister) Hagelst.

***Hemitrichia serpula*** (Scop.) Rostaf. ex Lister

Represented by a single specimen (34211) on twigs (pH 4.9) from BCT. This species is only occasionally recorded from moist chamber cultures, but the specimen on which this record is based was well-developed.

***Lamproderma scintillans*** (Berk. & Broome) Morgan

Represented by a single specimen (observed but not collected) recorded on bark (pH 5.9) from BCT.

***Licea minima*** Fr.

Represented by seven specimens (including 33841 and 34228), recorded from both study areas. Four specimens were recorded on bark (pH 4.1 and 5.8), one on twigs (pH 5.0 and 5.2) and two on litter (pH 4.8). Litter is an unusual substrate for this species.

***Licea operculata*** (Wingate) G.W.Martin

Represented by three specimens (including 33846 and 34095), all recorded on bark (pH 5.0 to 5.1) from TC.

***Lycogala epidendrum*** (L.) Fr.

Represented by two specimens (including 33848) recorded on bark (both pH 5.0) from TC. This species is very rarely recorded from moist chamber cultures. The two aethalia obtained in the present study were unusually small but otherwise typical in overall morphology.

***Perichaena chrysosperma*** (Curr.) Lister

Represented by 14 specimens (including 33961, 34109, and 34117) recorded on bark (pH 5.6 to 7.0), litter (pH 6.1), and twigs (pH 5.2 to 5.6) from both study areas.

***Perichaena depressa*** Lib.

Represented by a single specimen (34278) consisting of only three sporocarps on bark (pH 5.8) from BCT. This is a distinctive species because of the consciously flattened sporocarps.

***Perichaena pedata*** (Lister & G.Lister) G.Lister ex E.Jahn

Represented by five specimens (including 34097 and 34108), with four on litter (pH 5.9 to 6.1) on one on twigs (pH 5.2) from TC.

***Perichaena vermicularis*** (Schwein.) Rostaf.

Represented by 16 specimens (including 33814 and 33942), with six from bark (pH 5.1 to 6.4), nine from twigs (pH 5.2 to 6.2), and one from litter (pH 5.9). This species was recorded from both study areas.

***Physarum album*** (Bull.) Chevall.

Represented by a single specimen (34229) on twigs (pH 5.4) from TC. This specimen consisted of a single but well-developed fruiting body.

***Physarum auriscalpium*** Cooke

Represented by two specimens (34207 and 34233), one from a twig (pH 5.0) from BCT and one from litter (pH 6.1) from TC.

***Physarum bivalve*** Pers.

Represented by three specimens (34138 and 34139), both from TC. One was on litter (pH 5.9) and the other two were from twigs (pH 5.2).

***Physarum cinereum*** (Batsch) Pers.

Represented by two specimens (34091 and 34192) recorded on litter (pH 6.0 and 6.4) from TC. This species typically occurs in large fruiting, but the specimens recorded in the present study consisted of only a few sporocarps.

***Physarum cf. hongkongense*** Chao H.Chung

Represented by a single specimen (34321) on twigs (pH 5.4) from TC. This species was described originally from Asia but has since been reported from scattered localities throughout the world. It is not common.

***Physarum nucleatum*** Rex

Represented by two specimens (34007 and 34132), with one on twigs (pH 5.2) and one on bark (pH 5.7).

***Physarum viride*** (Bull.) Pers.

Represented by four specimens (including 34302), with three on twigs (pH 4.9 and 5.2) and one (pH 5.9) on bark. This species was recorded from both study areas.

***Stemonitis flavogenita*** E.Jahn

Represented by three specimens (including 33903 and 33941) on bark (pH 5.0 for all three) from TC.

***Stemonitis fusca*** Roth

Represented by 22 specimens (including 33890 and 33948), with 18 on twigs (pH 4.5 to 5.9) and four from bark (pH 5.7 to 5.9). This species was recovered from both study areas. Specimens obtained from moist chamber cultures, as was the case in the present study, appear to represent the variety *nigrescens*, which is sometimes recognised as the distinct species *Stemonitis nigrescens* Rex (Martin & Alexopoulos 1969).

***Trichia botrytis*** (J.F.Gmel.) Pers.

Represented by two specimens (including 34107), both from BCT. One was on litter (pH 4.2) and the other was on bark (pH 4.6).

***Trichia favoginea*** (Batsch) Pers.

Represented by four specimens (including 33780 and 34184), with two on bark (pH 5.6 and 5.7) and one each on litter (pH 6.7) and twigs (pH 5.0). This species was recorded from both study areas.

***Trichia subfusca*** Rex

Represented by five specimens, all recorded from TC. Four (including 34090 and 34129) were on litter (pH 5.4 to 6.2) and one was on bark (pH 5.2 and 6.7).

***Trichia sp.***

Represented by a single specimen (34197) on litter (pH 6.1) from TC. This specimen could not be assigned to any species of which the first author is aware. However, it was clearly different from the other species of *Trichia* obtained in the present study.

***Willkommlangea reticulata*** (Alb. & Schwein.) Kuntze

Represented by five specimens (including 34053 and 34210), all of which were recorded on twigs (pH 4.9 to 5.1) from both study areas. It has been suggested (Stephenson et al. 2008) that twigs represent the primary substrate for this species.

## DISCUSSION

When a forest community is subjected to fire, the first thing that burns is the litter layer (consisting mostly of dead leaves) on the forest floor. Mixed in with this litter layer are woody twigs that have fallen from trees. Both the litter layer and the twigs can be consumed almost completely by surface fires. These same fires can cause charring of the outer bark on the lower trunks of trees in the forest. However, the outer bark is already dead, and unless the tree is a species with very thin bark, it is likely to survive. More intense fires can kill the tree and consume even relatively large pieces of coarse woody debris (e.g. fallen logs).

Many of the woody twigs and probably all of the dead leaves processed in the present study would be expected to have fallen to the forest floor well after the fires that took place 30 months earlier. None of the samples of litter and only a few of the samples of twigs displayed any evidence that they had been subjected (at least directly) to fire. This was not the same for the samples of bark, many of which

did show some evidence of charring. This was the case for both the TC and BCT study areas and was expected based on the clear strong effect of the wildfires, as quantified through satellite imagery.

There have been very few studies that have examined the effects of fire on myxomycetes. Novozhilov et al. (2007) compared the assemblages of myxomycetes associated with bark and litter in a series of burned and control (i.e. unburned) sites in a study area located north of Fairbanks in central Alaska. They reported that the numbers of species recorded for these two substrates were fairly comparable. It should be noted that no distinction was made between fallen leaves and small woody twigs in this study. Gabel et al. (2010) collected myxomycetes both before and after what they described as a devastating fire at a study site in South Dakota. They recorded 13 species before the fire and 14 species after the fire, with four species represented in both sets of collections. Adamonytė et al. (2016) examined the effects of crown fire and surface fire on the myxomycetes associated with pine plantations in Lithuania. Their study extended over a period of three years, and they reported that both types of fire had a major impact on the assemblages of myxomycetes present. Both the assemblages present in plantations subjected to fire and those which were not proved to be equally diverse, but they were quantitatively very different with respect to the species of myxomycetes present. Interestingly, particular species tended to switch to different substrates during the course of post-wildfire succession. The results obtained in both of these studies suggest that myxomycetes associated with particular localities recolonise the area rather quickly after a fire, but the structure of the assemblages present may undergo appreciable changes. In the present study, such detailed documentation was not possible because the exact locations had not been examined with the same techniques and effort prior to the fires, but when data was compared with historical records, results also suggest changes in species assemblages.

It has been reported (Mataix-Solera et al. 2009) that an intense fire accompanied by high temperatures can result in complete sterilisation of the soil microbiota. There is no reason to suggest that the same would not be the case for the microbiota (including myxomycetes) associated with litter, woody twigs, and bark. In the same general study areas as the present study, strong effects on that microbiota have been reported (Brown et al. 2019), and at least based on surface temperatures during the 2016 winter, significant differences existed between the study areas and non-burned portions of the forest. However, many species of myxomycetes are known to have a high dispersal potential (Stephenson 2011), so once substrates suitable for their growth and development have become available again following the fire, a new assemblage of species would become established. This certainly appears to be the case in the present study, since the structure of the assemblages associated with the three substrates is somewhat different from previous data. In particular, it is remarkable that the number of shared species among substrates/study areas was very low, suggesting that such colonisation process was still very active.

The coefficient of community values from both study areas indicated that the assemblages of species of

myxomycetes associated with bark and litter were the least similar, whereas the assemblages associated with litter and twigs were the most similar. Based on what is known about the ecological distribution of particular species of myxomycetes, these results might have been anticipated. The species associated with bark (which are commonly referred to as corticolous species) tend to be different than those associated with litter, based on the results obtained in numerous studies (e.g. Stephenson 1989). Moreover, the litter substrate and the twig substrate occur together on the forest floor, so some overlap in species might be expected. At least some of the overlap in species composition that occurred between bark and twigs is almost surely the result of the fact that most twigs still had their bark (albeit very thin) still intact. However, it is interesting that ground litter showed the most distinct (and simple) species assemblage in the present study but the most complex assemblage in the historical data. This result suggests a stronger effect of the fire on that substrate, in comparison with twigs and bark. However, it should be noted that the historical records considered herein were obtained in the larger region of the Great Smoky Mountains National Park and are simply a point of reference for analysis.

It has long been known that pH is a major factor contributing to the distribution of myxomycetes in nature (Stephenson 2011). However, pH did not appear to be important for the three types of substrates examined, since there was a high degree of overall similarity in the values recorded for the sets of cultures. Nevertheless, the wide range of values (3.9 to 7.5 when all cultures are considered) probably has some impact on the occurrence of certain species. The difference in pH values between study areas was interesting, showing more acidic substrates in BCT than in TC. Although these were not significant differences, they may have accounted for some differences in species composition between the two sites. For instance, of the 13 recorded species within the genera *Physarum*, *Diderma*, and *Didymium*, all of which produce fruiting bodies with lime (calcium carbonate) present, 62% were not recorded from BCT. Records from these genera at TC were observed at an average pH of 5.9 in comparison with a value of 5.3 for BCT.

In summary, the wildfires that took place in 2016 appear to have had a strong effect on the assemblages of myxomycetes associated with the three substrates in the two study areas, since several levels of ecological analysis differed from previous data. This effect seems to have been less pronounced in TC than in BCT, as expected. As such, our data suggest that the relatively higher intensity burn had more of an effect on myxomycetes than the relatively lower intensity burn. Remarkably, even though the assemblages of species present have largely recovered 30 months after the two study areas were subjected to burning, such recovery is still an ongoing process. It is likely that the assemblages of species associated with substrates in the areas affected by the wildfires were different from those found before this event. Historical data pointed in that direction. It would seem worthwhile to carry out future studies in the same study areas in order to follow up on the present investigation.

## SUPPLEMENTARY FILE

**Supplementary file 1** – Complete list of myxomycete specimens recorded in the present study along with information on substrate, pH values, and the study site where they were observed.

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