

Myxomycetes distribution along an elevational gradient on coniferous woody debris in the mountains of Central Japan

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Abstract: Although myxomycetes are globally distributed in terrestrial ecosystems, studies of their local distribution along an elevation gradient remain few and ambiguous. The present study was seasonally carried out with field surveys for collecting fruiting bodies in five coniferous forests at elevations ranging from 679 to 2135 m in a mountainous region of Central Japan. A total of 1254 records on coniferous dead wood represented 50 taxa belonging to 21 genera. Myxomycete diversity decreased with increasing elevation and was higher in summer than in autumn. Five communities at different elevation sites were ordinated using non-metric multidimensional scaling (NMDS). The four communities in lower elevation pine forests were associated with the elevational gradient and separated from a subalpine coniferous forest community. Four species, *Lamproderma columbinum*, *Cribraria macrocarpa*, *Physarum atroviolaceum*, and *Arcyria monticola*, specifically inhabited the subalpine in the autumn. The community structure of myxomycetes revealed elevational differences that affected species occurrence in a temperate local region of Central Japan.

Keywords: community structure, pine forests, subalpine, temperate

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Introduction

Myxomycetes are known to occur in all major ecosystems worldwide (Schnittler et al. 2022) and exhibit differential distribution patterns across ecologically distinct climate zones with more finite divisions associated with substrate properties such as decay wood, bark surface, litter, and soil in the forest ecosystem (Novozhilov et al. 2022). They are protistan amoebae whose life cycle includes the reproductive and spore-producing stages, involving sporangia development to hold the spores (Keller et al. 2017), and spreading mainly by wind (Kamono et al. 2009). Decayed dead wood abundantly furnishes most myxomycetes, referred to as lignicolous myxomycetes, which have been investigated by

identification of macroscopic production of fruiting bodies and the species present (Rollins and Stephenson 2011).

Recently, studies on the biogeographical patterns of myxomycetes have reported a pattern of decreasing diversity with increasing elevation in neotropical areas (Rojas and Stephenson 2007; Schnittler and Stephenson 2000) based on various substrates in broader elevation ranges across different elevational belts and vegetation units. The detailed response of myxomycete communities along elevational grades was suggested by investigations of transects in Costa Rica (Rojas et al. 2016) and transects in the lower elevational range of the Philippines (Dagamac et al. 2014). In their studies in tropical forests, elevational gradients involved complex fluctuations, such as temperature, precipitation, plant vegetation, and geographical site effects. The altitudinal pattern has been also studied in Kirishima Mountain of temperate Japan, where three different vegetation types along elevational gradients have identified distinctive myxomycete communities (Takahashi and Harakon 2010). Furthermore, myxomycete communities and species occurrence differ between foothill forests and subalpine forests in terms of coniferous dead wood (Takahashi and Harakon 2012). Geographical distribution of myxomycetes has been revealed to be associated with air temperature in the temperate region of the Japanese archipelago (Takahashi and Hada 2010).

However, the pattern of myxomycete distribution and diversity associated with an elevational grade is unclear on a regional scale. Better-designed studies on myxomycetes are required to explore the shape of ecological differences at different elevations in detail. A quantitative survey based on the frequent appearance of myxomycete sporangia on a substrate is needed to understand the influence of abiotic factors on myxomycetes in a local biota.

This study was carried out to clarify the myxomycete communities associated with an elevational gradient on decaying coniferous wood in a mountainous region of Central Japan. A comparison of seasonal surveys among five different coniferous forests along elevational grades aimed to reveal that elevation is an important factor accounting for the distribution of myxomycetes in a local region.

Materials and methods

Study sites

The Japanese archipelago has rich biodiversity because of the horizontal and vertical expansion of the environment despite its small land area (Yumoto 2010), where the Nagano Prefecture underlies a geographically undulating terrain with vast altitude differences of approximately 300–3000 m over an area of 13560 km² in Central Japan (Tsuchida and Suekuni 1987). The elevational and geographical differences in the region have created habitats and biodiversity in various vegetation. Five survey sites were selected in coniferous forests of Nagano Prefecture, within an 85 km radius from south-west to north-east, at elevations ranging from 600 m to 2100 m (Fig. 1, Table 1).

Based on the vegetation map of Nagano Prefecture, pine forests were developed as village-vicinity forests (Satoyama forests) in the lowlands (650–1300 m alt.), while the natural coniferous forest (2100 m alt.) was in the subalpine. Recently, pine wilt disease advanced in the 1980s in western Japan (Fujihara

1996) and extended to Nagano Prefecture (Nakamura 2020). Since these conifer forests have rotted logs of various decay states, it is possible to study the distribution of wood-inhabiting myxomycetes along elevation grades from the lowlands to the highlands.

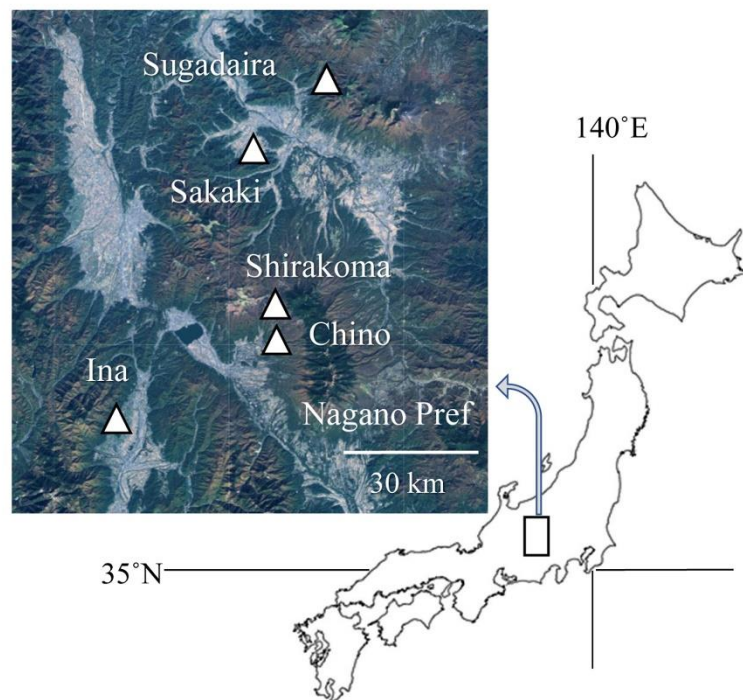


Figure 1. Five survey sites in Nagano prefecture of Central Japan.

Table 1. Survey site location, number of samples, wood hardness and diversity of myxomycete communities. SD: standard deviation of wood hardness.

Variable/Survey sites	Sakaki	Ina	Chino	Sugadaira	Shirakoma
Elevation (m)	679	925	1037	1332	2135
Latitude (N°)	36.42972	35.84527	36.022844	36.521557	36.047876
Longitude (E°)	138.1501	137.8978	138.22919	138.35106	138.36394
Samples					
Summer	142	146	121	124	136
Autumn	129	118	117	100	120
Wood hardness	18.9	16.6	20.4	21.0	20.4
SD	7.4	8.9	7.9	8.0	6.6
Myxomycetes					
Species richness	26	29	21	21	25
Species diversity	2.67	2.74	2.40	2.42	2.54
Equitability	0.82	0.81	0.79	0.80	0.79
Completeness (%)	73.6	86.1	73.7	91.3	64.1

Five survey sites were settled altitudinally at the following four locations in the pine forests and a subalpine coniferous forest for easy access and decay logs in abundance: Ina (925 m altitude, Yokoyama Ina-shi, 35.8452 °N, 137.8977 °E), Chino (1037 m altitude, Kohigashi, Chino-shi, 36.0228 °N, 138.2291 °E), Sakaki (679 m altitude, Sakaki-machi, Hanisina-gun, 36.429723 °N, 138.150067 °E), and Sugadaira (1332 m altitude, Sugadairakogen, Ueda-shi, 36.5215 °N, 138.3510 °E). These forests had many dead trees due to pine wilt disease (Fig. 2A), which has progressed to varying states of decay. The subalpine forest site was Shirakoma-ike (2132 m altitude, Koumi-machi, Minamisaku-gun, 36.0475 °N, 138.3640 °E) in Yatugatake Mountain, which is made up of old grown conifers, such as the dominant *Tsuga diversifolia* Mast, mixed *Abies veitchii* Lindley, and *Abies mariesii* Mast. All these sites had several fallen dead trees with decay at varying states (Fig. 2B) and were suitable for myxomycete growth.

Climate data were obtained from the Japanese Meteorological Agency (<https://www.data.jma.go.jp/>). Ina, the most southwestern site (35.500 °N, 137.300 °E, 633 m asl), had an annual precipitation of 1454 mm and a mean annual temperature of 11.7 °C, while the mean lowest temperature was 6.3 °C, and mean annual snow depth was 11 cm on January 2023. Sugadaira highland (36.900 °N, 138.500 °E, 1253 m asl), the most north-western site, had an annual precipitation of 1220.5 mm and a mean annual temperature of 6.6 °C, while the mean lowest temperature was 1.1 °C, and mean annual snow depth was 648 cm (1999–2020), and snowfall is expected to occur for approximately 6 months per year. The temperature difference between the upper and lower elevations was approximately 10.0 °C, based on the rate of temperature decrement of -0.69 °C/100 m along increasing elevation indicated by temperature decrement in Ina city of Nagano Pref (Suzuki 2000).

Data collection

Field surveys were carried out in summer and autumn at five sites simultaneously, as myxomycetes abundantly inhabiting pine decay wood occurred at the peak of summer and autumn in western Japan (Takahashi and Hada 2008)—comparisons of the myxomycete communities required survey results from the same time during peak seasons among different locations. Schnittler and Novozhilov (1996) suggested that repeated field collection surveys for at least two field seasons per year are necessary to ensure the phenological group records. Detectability increased among species and communities; the number of colonies of fruiting bodies provided a basic unit to estimate species richness and abundance in a community.

The search effort was made on approximately 200 or more fallen logs until at least 100 collections were found by naked eye observation and using a magnifying glass. Most logs randomly distributed and scattered on the floor. We sought and assessed logs of fallen dead trees with diameters ≥ 10 cm and lengths ≥ 1 m and identified portions of logs in which myxomycete fruiting bodies occurred. Every assessment was performed walking on each census route, which was approximately 800 m long at the longest distance in the forest. The wood hardness at which a fruiting colony occurred was pointed and measured using a soil hardness meter (No. 351; Fujiwara Scientific), which can indicate a depth of 1–40 mm in the decaying state. Field surveys were performed on July 23, 2017, July 25, 2018, October 28, 2018, and October 28, 2019. A survey required effort of approximately four hours every time.

A colony of fruiting bodies is considered to have emerged from the same plasmodium recorded as one sample following the methods used in previous studies (Eliasson 1981; Stephenson 1989). Myxomycete fruiting bodies were identified at the species level, and a piece of sporangia was glued to a specimen box to be examined under microscopic observation in the laboratory. The abundance of myxomycete species was recorded as a community by combining the number of colonies at specific sites and seasons as datasets. The nomenclature followed Yamamoto (2021) described and identified species based on morphological features using microscopic observations, whereas scientific names referred to the most recent literature (Lado 2005–2022). Species richness was regarded as a taxon, including varieties as species. Voucher specimens were deposited at the Tottori Museum Herbarium.



Figure 2. Survey forests and myxomycete fruiting bodies. A: Pine Forest in lowland, B: Subalpine coniferous forest in Mt. Yatugatake, C: Fruiting bodies of *Trichia decipiens*, D: Fruiting bodies of *Lamproderma columbinum*. E: Fruiting bodies of *Cribraia macrocarpa*, F: Fruiting bodies of *Physarum atroviolaceum*. Photographs of myxomycete sporangia, *L. columbinum*, and *C. macrocarpa* were provided by Ms. Kyouko Tateishi. Scale bars show 1 mm.

Data analysis

The number of colonies (abundance) in specific sites or seasons was used to assess the species diversity and structure of the myxomycete communities. The species composition of the community was indicated by the score of relative abundance of species [number of colonies for given species / total colonies \times 100 (%)]. Sampling adequacy (percentage of completeness) was assessed by dividing the number of taxa observed (Sobs) within the site by the estimated number of taxa (Sest) (Chao 1 (Chao 1984)) using the PAST software (Hammer *et al.* 2001) and the formula [Sobs / Sest \times 100 (%)]. The Shannon–Wiener diversity index H' (Shannon & Weaver 1963) and equitability index J' (Pielou 1966) were determined as described in previous studies (Stephenson 1989) to quantify the myxomycete diversity at each site.

The ordination in the five myxomycete communities was analyzed by non-metric multidimensional scaling (NMDS) using PAST software and ordered according to the first two axis scores. The software was used effectively in a similar previous study (Takahashi *et al.* 2018). NMDS was based on Bray-Curtis dissimilarities (Bray and Curtis 1957), where higher values (up to a maximum of 1.0) indicate more significant dissimilarity between communities for species composition and abundance. The scores of the first two NMDS axes were then assessed for correlations with environmental variables using correlation analysis performed with Excel Statistics (version 7.0; Esumi Co., Ltd., Tokyo, Japan) to estimate the association between myxomycete communities and elevational trends. Cluster analysis (paired group) was performed on the five myxomycete communities based on survey sites to make groups with a Jaccard similarity score of 0.60.

Species that appeared biased in a community at a given site were determined by their relative abundances using an independent t-test performed using ESUMI Excel Statistics 5.0 software (ESUMI Co. Ltd., Tokyo, Japan).

Results

Myxomycete communities

The fruiting of myxomycetes appeared in the wood hardness range of 16.6 ± 8.9 – 21.0 ± 8.0 mm depth (mean \pm standard deviation, Table 1) in an average of specific survey sites. Wood at lower sites was slightly softer than that at highland sites at Sugadaira and Yatugatake (Table 1), but there was no significant correlation between elevation and wood hardness ($r = 0.410$, $p = 0.256$).

A total of 1,253 colonies recorded were obtained from five different sites (Table 2) and were identified to 50 taxa belonging to 21 genera. The seasonal survey observed over a hundred or more samples (number of colonies) at a site (Table 1). Thirty-four taxa found in the summer were identified among 15–25 taxa sites, with a mean of 18.8 taxa per site, and 33 taxa were found in the autumn ranging from 11 to 16 taxa with a mean of 13.3 taxa. Individual sites provided 26 taxa at Sakaki (679 m), 29 taxa at Ina (925 m), 21 taxa at Chino (1037 m), 21 taxa at Sugadaira (1332 m), and 25 taxa at the Yatugatake subalpine forest (2135 m). The assessment's estimated completeness, which ranged from 64.1% to 91.3% among sites (Table 1), was 69.4% in the survey.

The most abundant species across the survey (Table 2) was *Trichia decipiens* (Pers.) T. Macbr. with a relative abundance of 20.8%, in decreasing order of *Physarum viride* (Bull.) Pers. 9.1%, and *Lycogala epidendrum* (L.) Fr. 8.9%, the remaining 26 taxa appeared in four samples or more (relative abundance of 0.3%). Furthermore, 21 species were found to have abundances of three or fewer. Five taxa were biased on the abundance in autumn, namely *Trichia decipiens* (Fig. 2C), *Lamproderma columbinum* (Pers.) Rostaf. (Fig. 2D), *Cribraria macrocarpa* Schrad. (Fig. 2E), *Trichia verrucosa* Berk., and *Arcyria ferruginea* Sauter. Eleven taxa were abundant in summer, such as *L. epidendrum* and *Stemonitis axifera* (Bull.) T. Macbr., *Ceratiomyxa fruticulosa* (O.F. Müll.) T. Macbr., and *Cribraria cancellata* (Batsch) Nann.-Bremek., followed by seven species in decreasing order.

Species abundance biased at the elevational gradient were four species at subalpine, i.e., *L. columbinum*, *C. macrocarpa*, *Physarum atroviolaceum* G. Moreno, and Y. Yamam. (Fig. 2F), & A. Castillo and *Arcyria monticola* Y. Yamam. & H. Hagiw. The mountainous pine forests contained characteristically biased species, i.e., four species in Sakaki; *Arcyria cinerea* (Bull.) Pers., *Arcyria obverata* (Oeder) Onsberg, *Stemonitis fusca* Roth, and *Cribraria minutissima* Schw., one species in Ina; *Cribraria tennella* Schrad., one species in Chino; *Ceratiomyxa fruticulosa* (Mueller) T. Macbr., and five species in Sugadaira; *S. axifera*, *Lamproderma arcyronema* Rostaf., *A. ferruginea*, *Physarum nutans* Pers., *Stemonitis tyhina* var. *similis* (G. Lister) Nann.-Bremek. & Y. Yamam. as indicated in Table 2.

Seasonally biased species were 11 in summer, abundant in order of *C. fruticulosa*, *S. axifera*, and *Lycogala epidendrum* (L.) Fr.; following eight species, and five species in autumn, abundant in order of *T. decipiens*, *L. columbinum*, and *C. macrocarpa*, of which both communities indicated Bray-Curtis dissimilarity index of 0.686.

Ordination of Myxomycete communities

The species diversities (H') and equitability of 10 myxomycete communities surveyed seasonally (Fig. 3) ranged from 1.58 to 2.68, higher in summer than autumn. Both indices tended to decrease with increasing elevation, with correlation coefficients of -0.597 in summer and -0.772 in autumn, similar to the equitability value decreasing. The diversity of species tended to be slightly lower as the elevation increased. The communities at a lower elevation of 925 m alt. had the greatest diversity. Equitability reached its highest at 679 m alt. in summer, while the lowest was at the subalpine forest at 2135 m alt. in autumn.

The ordination of myxomycete communities on five different elevational sites (Table 3) using NMDS analysis indicated distinct myxomycete assemblages across the gradients of elevation and wood hardness (Fig. 4). The arrangement of NMDS scores was significantly correlated with an elevational grade at axis one and with differences in wood hardness at axis 2 (Table 3). The oval with a dashed line in Fig. 4 separates two lowland groups by cluster analysis from the subalpine site. Forest vegetation between lowland pine forests and a subalpine conifer made the separation discontinuously different. Lower pine forests (<1000 m alt.) were dissimilar to highland pine forests (> 1000 m alt.), whose communities were further distant from subalpine. Myxomycete communities on coniferous dead wood were distributed along the elevation grade and formed different community structures in the mountain region of Central Japan.

Table 2. Myxomycete species and the number of colonies (abundances) recorded in five survey sites. Species arranged in order to relative abundance. **Characteristic species in the site using an independent T-test for four or more abundances, statistical significance $p < 0.01$

	Survey sites					Summer	Autumn		Total abundance	Relative abundance (%)	
	Sakaki	Ina	Chino	Sugadaira	Shirakoma						
Species recorded four or more abundances											
<i>Tricha decipiens</i> (Pers.) T. Macbr.	59	53	61	56	32	37	224	**	261	20.8	
<i>Physarum viride</i> (Bull.) Pers.	26	20	30	29	9	65	49		114	9.1	
<i>Lycogala epidendrum</i> (L.) Fr.	23	19	28	23	19	74	**	38	112	8.9	
<i>Stemonitis axifera</i> (Bull.) T. Macbr.	20	14	20	32	**	16	**	14	102	8.1	
<i>Ceratiomyxa fruticulosa</i> (Mueller) T. Macbr.	20	13	30	**	9	29	**	10	101	8.1	
<i>Cribraria cancellatum</i> (Batsch) Nann.-Bremek.	24	22	9	8	9	71	**	1	72	5.7	
<i>Lamproderma columbinum</i> (Pers.) Rostaf.		5	2		46	**		53	**	53	4.2
<i>Stemonitopsis hyperopta</i> (Maylan) Nann.-Bremek.	17	5	11	6	11	34		16	50	4.0	
<i>Cribraria macrocarpa</i> Schrad.					45	**		45	**	45	3.6
<i>Arcyria cinerea</i> (Bull.) Pers.	15	**	9	8	1	6		27	12	39	3.1
<i>Trichia verrucosa</i> Berk.		36						36	**	36	2.9
<i>Tubifera ferruginosa</i> (Batsch) J. F. Gmel.	1	17	9	3	6	30	**	6	36	2.9	
<i>Stemonitis axifera</i> var. <i>smithii</i> (T. Macbr.) Hagelst.	11	10	8	2	2	29	**	4	33	2.6	
<i>Lamproderma arcyrionema</i> Rostaf.	6	2	1	16	**	25	**		25	2.0	
<i>Arcyria ferruginea</i> Sauter			7	15	**			22	**	22	1.8
<i>Stemonitopsis gracilis</i> (G. Lister) Nann.-Bremek.	2	5	1	3	3	13	**	1	14	1.1	
<i>Lindbladia tuburina</i> Fr.	8	4	1			13	**		13	1.0	
<i>Fuligo septica</i> (L.) Wiggers	1	5	3		3	12	**		12	1.0	
<i>Arcyria obverata</i> (Oeder) Onsberg	10	**				7		3	10	0.8	
<i>Cribraria tenella</i> Schrad.	1	9	**			9		1	10	0.8	
<i>Stemonitis fusca</i> Roth	8	**	2			10	**		10	0.8	
<i>Comatricha nigra</i> (Pers.) Schroet.	1		3	4		1		7	8	0.6	
<i>Physarum nutans</i> Pers.	1	2		5	**	1		7	8	0.6	
<i>Lindbladia cribrarioides</i> (Emoto) Farr & Alexop.	4	2				6			6	0.5	
<i>Stemonitopsis tyhina</i> var. <i>similis</i> (G. Lister) Nann.-Bremek. & Y. Yamam.		1		4	**	1			6	0.5	
<i>Cribraria minutissima</i> Schw.	5	**						5	5	0.4	
<i>Physarum atroviolaceum</i> G. Moreno, Y. Yamam. & A. Castillo					5	**		5	5	0.4	
<i>Arcyria monticola</i> Y. Yamam. & H. Hagiw.					4	**		4	4	0.3	
<i>Physarum flavicomum</i> Berk.			1	2	1	2		2	4	0.3	

Species less than four abundances

<i>Clastoderma debaryanum</i> A. Blytt	1	1	1		3		3	0.2	
<i>Cribraria violacea</i> Rex	2				1		3	0.2	
<i>Diderma floriforme</i> var. <i>subfloriforme</i> (Candoussau & Nann.-Bremek.) Y. Yamam.					3		3	0.2	
<i>Enertenema papillatam</i> (Pers.) Rostaf.			3				3	0.2	
<i>Physarum globliferum</i> (Bull.) Pers.	2	1					3	0.2	
<i>Stemonitis pallida</i> Wingate	3						2	0.2	
<i>Trichia favoginea</i> (Batsch) Pers.				3			3	0.2	
<i>Arciria denudata</i> (L.) Wettst.		1					1	0.1	
<i>Cribraria intricata</i> Schrad.	1	1					2	0.2	
<i>Leocapus flagilis</i> (Dicks.) Rostaf.	1	1					2	0.2	
<i>Craterium dictyosporum</i> (Rostaf.) Neubert, Nowotny & Baumann		1					1	0.1	
<i>Cribraria atrofusca</i> G. Martin & Lovejoy					1		1	0.1	
<i>Cribraria ferruginea</i> Meylan					1		1	0.1	
<i>Cribraria intricata</i> var. <i>dictydioides</i> (Cooke & Balf.) Lister			1				1	0.1	
<i>Cribraria vulgaris</i> Schrad.					1		1	0.1	
<i>Elaeomyxa cerifera</i> (G. Lister) Hagelst.					1		1	0.1	
<i>Hemitrichia calyculata</i> Speg.				1			1	0.1	
<i>Physarum roseum</i> Berk. & Br.				1			1	0.1	
<i>Stemonaria laxiretis</i> Nann.-Bremek. & Y. Yamam.	1						1	0.1	
<i>Stemonitis verginiensis</i> Rex		1					1	0.1	
<i>Trichia subfusca</i> Rex					1		1	0.1	
Total	271	264	238	224	256	669	584	1253	100
Number of taxa	26	29	21	21	25	34	33	50	

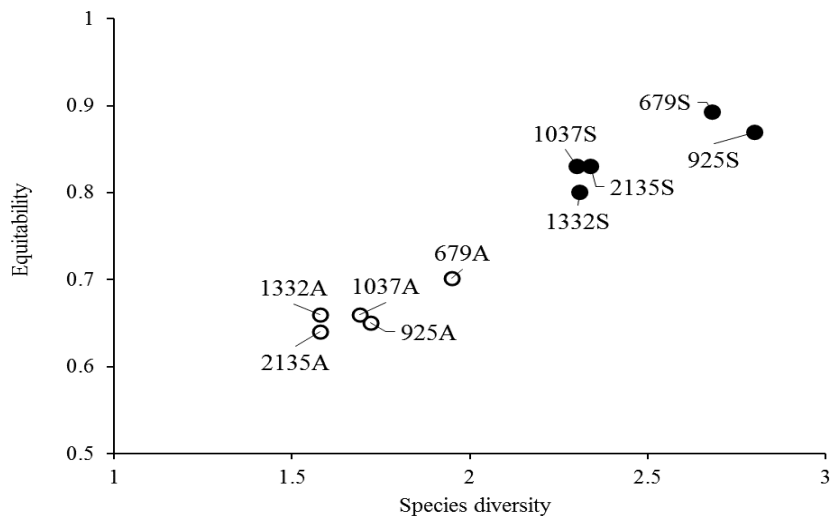


Figure 3. Comparing species diversity of myxomycete communities at five survey sites in summer and autumn according to species diversity index and equitability. ● in summer, ○ in autumn.

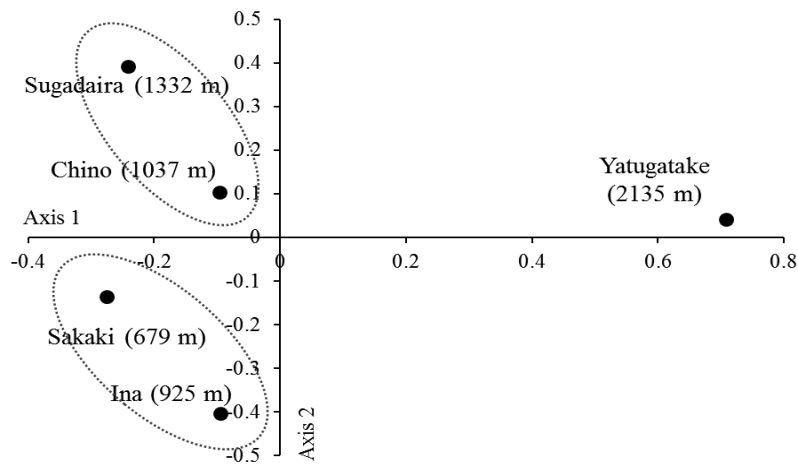


Figure 4. Ordination plot for five communities at survey sites using NMDS first two scores. Stress = 0, R^2 of Axis 1 = 0.708 and Axis 2 = 0.002. Ovals with dashed lines indicated groups according to the cluster analysis classification (paired group, Jaccard similarity value of 0.6, statistical reliability > 80%).

Table 3. Correlation coefficients between first two scores of NMDS of five different sites and environmental variables and myxomycete communities. *Significance $p < 0.05$.

Variables	Axis 1	Axis 2
Environmental variables		
Elevation (m)	0.897 *	0.385
Latitude (N°)	-0.425	0.627
Longitude (E°)	0.387	0.883
Wood hardness	0.218	0.941 *
Myxomycete communities		
Species richness	0.126	-0.923 *
Species diversity	-0.036	-0.902 *
Equitability	-0.477	-0.692

Discussion

The distribution of myxomycetes seems to be limited not only by climate and vegetation on a global scale but also by ecological differences in particular habitats, such as forest types and substrate types on a local scale (Stephenson *et al.* 2008). Several studies have shown that differences in vegetation types and moisture gradients affect myxomycetes' distribution along elevation gradients in tropics (Schnitler and Stephenson 2000; Dagamac *et al.* 2014; Rojas *et al.* 2016), subtropics (Novozhilov *et al.* 2018), and temperate zone (Takahashi and Harakon 2010). A similar trend of elevational and moisture gradient associations with decreasing species numbers and diversity was also observed for various substrates in northern boreal forests in Russia (Novozhilov *et al.* 2020). However, current studies have included the effects of multiple conditions on varied substrates of ground litter and used moist chamber cultures to affect the development of myxomycete communities under field conditions. There is a question regarding a firm distribution pattern and how elevation may not be an essential factor in shaping the distribution of myxomycetes in tropical forests in Costa Rica (Rojas *et al.* 2016). The present study specified substrate to coniferous decay wood locally and indicated that myxomycete communities' composition varied with elevation gradient and showed several species occurred most frequently within a given elevation band (Table 2). The elevational distribution pattern of bark living myxomycete was studied on *Cryptomeria japonica* tree and revealed changes in the community structures with increasing elevation, decreasing species richness, and species per tree in western Japan (Takahashi 2017). Elevational shift of ca. 1000 m affected the difference in myxomycete communities. Thus, myxomycetes distribution was also shaped on decay wood by the influence of elevational dynamics in a mountainous region of Central Japan.

Myxomycete seasonality was revealed on decaying pine wood in western Japan (Takahashi and Hada 2008). As species in autumn differed from those in summer, it was suggested that the communities seasonally sift on a woody substrate. Wood hardness resulting in wood decay indicated that myxomycetes preferred wood portions in a moderately decayed state. However, wood hardness was slightly softer in summer than in autumn (Table 1), which suggests that seasonal differences may have diversified the decaying state for myxomycete inhabitation. Otherwise, myxomycetes may use bait resources associated

with seasonally different supplies derived from different decay states throughout the year. communities were reflected by elevational site differences at two collection periods. The biogeography of myxomycetes was horizontally distributed according to air temperature in temperate Japan (Takahashi and Hada 2010), revealing that the average minimum temperature strongly influences the myxomycete community structure. Four pine sites were in high grade at 650 m alt., also associated with temperature grade and environmental differences. These elevational variables were sensitive to myxomycete community structures in pine forests, which may be affected by the temperature decrement of ca. 3.6 °C in a local area. On the bark of *Cryptomeria japonica* trees, which are endemic species of the Japanese archipelago, temperature and elevational differences are factors affecting the spatial inhabitation of myxomycetes in terms of abundance, occurrence, and species composition of the communities (Takahashi 2017; Takahashi et al. 2018; Takahashi et al. 2020). The present study found that the subalpine community in autumn was separated from other communities, i.e., several specified species appeared in higher elevation subalpine sites, such as *L. columbinum*, *C. macrocarpa*, *P. atroviolaceum*, and *A. monticola*. As such, temperature changes along elevational grade seems to be an important factor for myxomycete distribution.

Lamproderma columbinum appears to be restricted mainly to subalpine coniferous (Takahashi 2001; Stephenson 2004; Takahashi and Harakon, 2012) and boreal forests (Schnittler and Novozhilov 1996; Novozhilov et al. 2020) and rarely appears in late autumn at lower elevations of 440 m altitude in southwestern Japan (Takahashi 2010). *Cribraria macrocarpa* is abundant in subalpine areas in autumn, rare in highlands (Takahashi and Harakon 2012), and appears in boreal forests (Novozhilov et al. 2020). Furthermore, *Physarum atroviolaceum* and *Arcyria monticola*, also found in Hokkaido, northern Japan (Yajima et al. 2010), were explicitly found in the subalpine of Central Japan as a taxonomic type locality in autumn (Yamamoto 2021). Subalpine habitats are specified for myxomycetes in autumn, which may adapt to cold climates with ecological differences from lowland pine forests. Thus, these four species may be threatened by global warming. Influences from global warming are also presumed to affect the biodiversity and distribution of myxomycetes.

Myxomycete communities were delineated between subalpine (2100 m) and lowland pine forests (up to 1300 m alt.), which were ordered according to elevational gradient (Fig. 4). Interestingly, the myxomycete community adapted to the geographical environment along the elevation gradient. In the case of myxomycetes on the living bark of *Cryptomeria japonica* trees, community structure shifts with increasing elevation, with a slight decrease in species diversity on Yakushima Island in southwestern Japan (Takahashi 2017). In western Japan, two corticolous species were distributed with elevational grades *Cribraria microcarpa* (positively correlated) and *Diderma chondrioderma* (negatively correlated) (Takahashi et al. 2020). Although the present study was based on field surveys during wood decay after pine wilt disease and derived only from coniferous dead wood in central Japan, myxomycetes in mountains and subalpine areas show a defined distribution pattern, suggesting an association with elevational differences in different environments impacting myxomycete growth. Myxomycetes play a vital role in processing debris and humus in forest ecosystems; therefore, more studies are needed to elucidate the higher ecological complexity involving myxomycetes and the perspective of a forest ecosystem at a specific local spatial and temporal scale.

In conclusion, the intermediate decay state of coniferous coarse woody debris hosts many myxomycetes and their distribution patterns were documented to be associated with the elevation gradient across a local mountainous area of Central Japan. We discovered that myxomycete communities were clearly distributed on coniferous dead wood as decreasing species richness and diversity with rising the elevational gradient was observed in temperate regions, with some specified species occurring in subalpine environments.

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