Diversity of myxomycetes in typhoon-prone areas: a case study in beach and inland forests of Aurora and Quezon Province, Philippines

Enrico M. Cabutaje^{1,2}, Melissa H. Pecundo² & Thomas Edison E. dela Cruz^{1,2,3,*}

¹ The Graduate School,

² Fungal Biodiversity, Ecogenomics, and Systematics (FBeS) Group, Research Center for the Natural and Applied Sciences, and ³ Department of Biological Sciences, College of Science, University of Santo Tomas, España Blvd. 1008 Manila, Philippines

* e-mail: tedelacruz@ust.edu.ph

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Field specimens of myxomycetes and substrates were collected seven months after a typhoon hit Aurora Province and a month after a typhoon hit Quezon Province in Eastern Philippines. A total of 720 moist chambers were prepared from aerial leaf litter, ground leaf litter and twigs that were randomly collected within the two forest types in the two provinces. Myxomycete records from the field and moist chambers resulted to the identification of 42 species belonging to 18 genera in Aurora, and 48 species belonging to 19 genera in Quezon. Comparing the two forest types, inland forests had higher species diversity, richness, and evenness, but the beach forests were more taxonomically diverse. Community analysis showed similarities in myxomycete species composition between the beach and inland forests in Aurora and Quezon provinces. Relating the output with typhoons, a higher number of species was observed in Quezon where field and substrate collections were conducted one month after a typhoon than in Aurora where longer period (= 7 months) has already elapsed before field and substrate collections. Our results suggested that potential impact of typhoon on myxomycetes.

Keywords: fruiting body, natural disturbance, species diversity, tropical forest, typhoon.

Forests are considered as the most biologically diverse and complex areas on earth. They provide watershed protection, prevent soil erosion, mitigate climate change, and serve as habitat for a vast array of flora and fauna. Thus, forests are essential for the earth's biodiversity. However, forest ecosystems are still facing different problems that have critically affected their vitality. One of these problems is the several natural and man-made disturbances. These disturbances have been associated with changes in biodiversity within forest ecosystems (Yao et al. 2015) and can potentially have long-term consequences in forest structure (Parmesan 2006, Allen et al. 2010). One of the most devastating natural disturbances forests ever face are typhoons. A tropical typhoon is characterized by strong wind and heavy rainfall which can lead to landslide, high sea waves, and flood. Plant communities are greatly influenced by the disturbance caused by typhoons. Typhoon modifies plant community structure in forests and could be a major factor for species migration among animals. Typhoon could also affect microscopic organisms. For instance, Tsai et al. (2007) studied the

cant decrease in microbial biomass carbon values was observed in seasons with typhoons than in seasons without typhoons, but such differences were not observed in the following year. The effects of typhoon to phytoplankton responses was also analysed in the study of Ko et al. (2015) which showed an increased phytoplankton response, i.e., chlorophyll-a concentration, primary production and turnover rate, in the semi-closed reservoir freshwater ecosystem during the typhoon-period as compared with the non-typhoon period. Recently, the long-lasting effects of typhoon disturbance on saproxylic fungi, bryophytes, and on seedling regeneration on coarse woody debris were studied by Fukasawa et al. (2019), who suggested that typhoon disturbance that occurred 55 years ago had no longlasting effects on current wood decay fungal communities, but the disturbance together with the wood decay type provided significant impacts on bryophytes communites and seedling density. Despite these, documented studies on the potential

effects of typhoon disturbance on the activities of

soil microbes and found out that in 2004, a signifi-

impact of typhoons on other microorganisms, particularly myxomycetes, are nil to very scarce. In this study, we believe that any modification in plant communities in forests brought by typhoon disturbance might directly or indirectly affect myxomycete communities since they grow on these materials and use it as their microhabitats. Thus, any site with rich vegetation and hit by natural disturbance such as typhoon might have higher myxomycete diversity as this provides more plant debris on forest floor suitable for myxomycete propagation.

Myxomycetes or plasmodial slime molds, also known as myxogastrids, are a group of fungus-like protists that are widely dispersed in terrestrial habitats. The life cycle of myxomycetes includes the unicellular, multinucleate plasmodium and the spore-bearing fruiting body. The fruiting bodies hold spores which are dispersible by air and sometimes by animal vectors. The released spores germinate and give rise to amoeboflagellate cells which later develop into the plasmodium. Interestingly, myxomycetes distribution could also be affected by different factors in the environment. Factors such as temperature (Stephenson & Stempen 1994), pH (Kilgore et al. 2009) and elevation (Rojas et al. 2016) have been evaluated in previous studies. This unusual characteristic of myxomycetes life cycle and the potential impact of environmental conditions to their life cycle make myxomycetes an ideal model organism to study many biological processes and even impacts of man-made and natural disturbances.

The Philippines is considered as the most exposed country to tropical cyclones (Brown 2013). In fact, approximately 20 tropical cyclones enter the Philippine Area of Responsibility (PAR) yearly (Dela Cruz 2016). The islands of Eastern Visayas, and the eastern sides of the Bicol region and Northern and Southern Luzon such as the coastal provinces of Aurora and Quezon are often where typhoons make landfall. In October 2016, the province of Aurora was hit by typhoon "Karen" (International name: Sarika). The Philippine Atmospheric Geophysical and Astronomical Services Administration (PAGASA) described typhoon "Karen" as having a moderate to heavy rainfall and strong winds within the 500-kilometer diameter, with a maximum wind of 150 kph and gustiness of 210 kph. Typhoon signal no. 3 was raised in Aurora province during typhoon "Karen" which resulted to toppled trees, ripped off roofs, and destroyed houses. On the other hand, the Quezon province experienced typhoon "Maring" (International name: Doksuri) on September 2017. This typhoon had a maximum wind of 85 kph and gustiness of 105 kph. Quezon Province was declared under typhoon signal no. 1, but experienced heavy rains that alerted the province against possible landslide and flash floods. Thus, typhoon "Karen" and "Maring" left the provinces of Aurora and Quezon disturbed and damaged. To test our hypothesis that typhoon can impact the communities of myxomycetes, this study looked at the diversity and assemblages of myxomycetes in two forest habitats, beach and inland forests, in these two provinces following these typhoons, albeit no records of myxomycetes were reported for the study sites prior to this study.

Materials and methods

Study sites

A total of 12 collection sites which include three beach and three inland forests in Aurora and three beach and three inland forests in Quezon were selected for the collection of fruiting bodies and substrata. The geographical coordinates and elevations of the collection sites are presented in Tab. 1. Beach forest refers to the forested areas located in coastal areas, or specifically along the beach apart from a mangrove ecosystem. Primavera & Sadaba (2012) considered beach forest as a narrow strip of land along the sea. In our study, beach forests are composed of less heterogeneous plant community which includes the species of Terminalia cattapa L. and Barringtonia asiatica (L.) Kurtz. Populations of coconut trees (Cocos nucifera L.) were also observed in this forest site. On the other hand, inland forest refers to the forested areas situated away from the coastline. Unlike beach forests, inland forests were observed with high heterogeneous plant communities and usually dominated by dipterocarp trees. See Fig. 1 for the map of study sites and photographs of the two forest types.

Field and substrate collection

The collection of field specimens and substrata were conducted in Aurora seven months following typhoon "Karen". On the other hand, field and substrate collections in Quezon were done one month following typhoon "Maring". Myxomycete fruiting bodies were collected within a 25×25 meter quadrat in each collection site. Additionally, 20 samples each of aerial leaf litter (AL), ground leaf litter (GL), and twigs (TW) were randomly collected within the 625 m² plot in each collection site. The collected substrata were placed in brown paper bags and properly labelled with collection site, sub-

Study site	Forest type	Latitude (N)	Longitude (E)	Elevation (m asl)
	Beach Forest	16° 4' 25.0716"	121° 44' 55.7556"	14.0
Aurora	Beach Forest	$15^{\circ} 54' 39.816''$	$121^{\circ} \ 33' \ 57.564''$	14.5
	Beach Forest	$15^{\circ} 45' 14.148''$	$121^{\circ} 35' 19.212''$	12.0
	Inland Forest	15° 47' 44.772"	121° 28' 37.128"	37.3
	Inland Forest	$15^{\circ} 57' 20.88''$	$121^{\circ} \ 35' \ 26.232''$	93.7
	Inland Forest	$15^{\circ} \ 43' \ 59.856''$	$121^{\circ} \ 36' \ 44.568''$	66.8
Quezon	Beach Forest	13° 59' 22.38"	$121^{\circ} 56' 41.424''$	12.2
	Beach Forest	$14^{\circ} \ 10' \ 32.88"$	$121^{\circ} \ 43' \ 57.972''$	23.1
	Beach Forest	$14^{\circ} \ 35' \ 26.664''$	$121^{\circ} \ 37' \ 3.504"$	4.9
	Inland Forest	13°59'36.3"	121°49'27.2"	255.5
	Inland Forest	$14^{\circ} 8' 24.864''$	$121^{\circ} \ 34' \ 52.212''$	451.9
	Inland Forest	$14^{\circ} \ 32' \ 4.596"$	$121^{\circ} 34' 44.832''$	294.0

Tab. 1. Geographic coordinates and elevation of the 12 collection sites in Aurora and Quezon Province.

strate type, and collection date. These were transferred to the laboratory, with wet samples air-dried for at least a week prior the preparation of moistchamber cultures.

Preparation of moist chamber

An excellent technique to evaluate the diversity of myxomycetes in a specific substrate and study site has been reported with the use of moist chamber (Novozhilov et al. 2000). In this study, moist chamber technique was used. This set-up includes a disposable petri dish lined with a paper towel. A total of 720 moist chambers were prepared. For the AL and GL, about 8–10 pieces of dried leaves were cut into small size and were placed in moist chamber set-up. Correspondingly, TW were cut into small length, about 2–3 inches, to fit inside the petri dish. The moist-chamber set-ups were flooded with distilled water and were soaked for 24 hours. After soaking, pH was measured, and the water was poured out from the moist chambers. All the moist chambers were incubated at room temperature (23-26 °C) under normal sunlight (Snell & Keller 2003) and were checked two to three times a week for the presence of myxomycetes' plasmodia and fruiting bodies. The presence of fruiting bodies/plasmodia in a moist chamber was regarded as positive collection, otherwise was considered as negative.

Characterization and identification of myxomycetes

All the myxomycete specimens from the field collections and moist chambers were observed using a compound light microscope. Each of the myxomycete specimens was photographed using a DSLR camera. Following the protocol of Lado (2001), identification of myxomycetes was done by observing the morphological characteristics of the fruiting body. The description of each fruiting body was noted. These include but are not limited to the type and size of fruiting body, shape of sporotheca, appearance of the stalk and peridium, and presence of lime on sporotheca and stalk. Furthermore, the spores from the fruiting bodies were also observed. The spores were mounted first in a clean glass slide with the use of distilled water as mounting medium (Keller et al. 2008). The branching pattern of capillitial threads and the color and ornamentation of the mature spores were observed. The detailed structure of the spores was also noted. Finally, all the data gathered were used to identify the myxomycetes using published literature, e.g. nomenclature protocol of Martin & Alexopoulus (1969) and Lado (2005-2020) and web-based and electronic identification keys, such as the Eumycetozoan Project (http://slimemold.uark.edu/). The names of all identified myxomycetes were verified using an online nomenclatural database for the eumycetozoans (http://nomen.eumycetozoa.com).

Ecological analysis

The productivity of moist chambers for each of the forest type in the two provinces (post-typhoon exposure) was computed separately. Percent yield was computed in which the total positive collections were divided by the total number of moist chambers prepared multiplied by 100. The occur-



Fig. 1. Map of the study sites generated by DIVA-GIS Version 7.5.0: circle = inland forests, star = beach forests, and photographs of two forest types. A–B Inland forest, C–D beach forest.

rence of each species was also determined based on its relative abundance (RA). The abundance index (AI) was computed in which the total number of each myxomycetes species in each of the two forest types in the two provinces was divided by the total number of collections. The AI of each species was also computed for the overall collections in this study. Then, each species was ranked based on different categories following the description of Stephenson et al. (1993): (1) abundant, if the RA value is equal or more than 3 %, (2) common, if the RA value is between 3 % and 1.5 %, (3) occasional, if the RA value falls between 1.5 % and 0.5 %, and (4) rare, if the RA value is less than 0.5 % of the total number of collections. An annotated list of all myxomycetes species reported in this study is also presented in this paper.

In this study, a series of rarefaction curves was plotted for the assessment of the completeness of the sampling effort. This was formulated using the setting of the downloadable program EstimateS Version 9.0, with 100 randomizations (Colwell 2013). The Chao 2 estimator was used as similarly described in the study of Alfaro et al. (2015). The Chao 2 estimator is a non-parametric incidencebased estimation of species richness and ecological pattern of species as noted in Unterseher et al. (2008). The percentage of completeness for the study was thereby computed by dividing the actual number of recorded species by the mean number of expected species as estimated by the Chao 2 estimator. Individual Species Accumulation Curve (SAC) was prepared for the pooled data in Aurora and pooled data in Quezon. In addition, separate SAC was also computed for the two forest types in the two provinces. Lastly, rarefaction curves for the pooled data of Aurora, pooled data of Quezon, and data for each of the two forest types in the two provinces were constructed using the Coleman Rarefaction values to compare the richness of species.

Taxonomic diversity was also computed as the ratio of the number of species to the number of genera (S/G ratio). The number of species and genera were recorded for each substrate type and forest type in the two provinces. Lastly, different diversity indices, i.e., Shannon Index of Diversity [HS], Gleason Index of Species Richness [HG], Pielou's Index of Species Evenness [E]), Fisher's Alpha Index [FAI] and Simpson Index [SI], were computed for the various datasets, e.g. between substrate types and forest types in the two provinces (past typhoon exposure) as described by Stephenson (1989) and Dagamac et al. (2012). This was done for the quantification of species diversity. HS, HG, and E were com-

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puted using Microsoft Excel based on published formula (Magurran 2004) while the FAI and SID were calculated using the software SPADE or Species Prediction and Diversity Estimation (http:// chao.stat.nthu.edu.tw) by generating the maximum likelihood estimator. To test if the species diversity values between beach and inland forests in Aurora and Quezon (past typhoon exposure) were significantly different, diversity t-test was performed at 0.01 and 0.05 levels of significance using the software PAST (Hammer et al. 2001; http://folk.uio.no/ ohammer/past).

Community analysis

Similarities of myxomycete communities between the two kinds of forest habitat (beach forest vs inland forest) and between substrate types (AL vs GL vs TW) per habitat types in relation to past typhoon exposures (Aurora vs Quezon) were also analysed. In this part, Sorensen's coefficient of community (CC) and the Percentage Similarity (PS) indices were calculated as described by Stephenson (1989). The presence or absence of species between the two communities was considered in the coefficient of community (CC). The CC values ranges from 0 (when no species are present in both communities) to 1 (when all species are present in both communities). The PS considers both the presence or absence of species and their relative abundance (Stephenson 1988, Stephenson 1989). These two types of community analysis have been extensively used in other biodiversity and ecological studies (Stephenson et al. 2000, Dagamac et al. 2012). Venn diagrams were also constructed to present the distribution and the similarities of myxomycete species between beach and inland forests. Furthermore, a cluster analysis was generated using the software PAST based on the Morisita index of similarity. This was done to visualize the pattern of similarities in myxomycete species composition between the two forest types in the two provinces.

Results

Moist chamber productivity

A total of 720 moist chambers were prepared from substrates that were randomly collected in beach and inland forests of Aurora, and in beach and inland forests of Quezon. A total of 180 bags were collected each from the two forest types comprising of 60 AL, 60 GL, and 60 TW. From the moist chamber cultures prepared in Aurora, 286 or 79 % yielded positive growth for myxomycetes, either as plasmodia (23 %) or fruiting bodies (57 %). On the other hand, moist chamber cultures prepared in Quezon resulted to 279 or 78 % positive growth for myxomycetes as either plasmodia (29 %) or fruiting bodies (48 %). When the percent yield of myxomycetes between the two forest types was computed, 149 or 83 % moist chambers were noted as positive in beach forest while 137 or 76 % moist chambers were computed as positive in inland forests in Aurora. In Quezon, 140 or 78 % moist chambers were positive for myxomycetes in beach forest while 139 or 77 % moist chambers were observed as positive in inland forest.

Species listing and distribution

A total of 62 species belonging to 21 genera were identified from the field collection and moist chamber cultures of substrates collected in beach and inland forests of Aurora and Quezon Province. Forty-two species belonging to 18 genera were recorded in Aurora (the province hit by typhoon "Karen/ Sarika" seven months before field and substrate collections), whereas 48 species belonging to 19 genera were recorded in Quezon (the province hit by typhoon "Maring/Doksuri" a month before field and substrate collections). Beach forest in Aurora vielded a total of 29 species and 15 genera while inland forest gathered 33 species representing 15 genera. On the other hand, 30 species belonging to 16 genera were documented in beach forest while 41 species belonging to 17 genera were noted in inland forest of Quezon. An annotated list of all the myxomycete species obtained from the field collections and moist chambers are provided below with images of representative species (Fig. 4). After each species name, the number of records was noted as either collected from Aurora Province (AP) or Quezon Province (QP) and recovered either from field collections (FC) or moist chamber (MC). These numbers were also distributed as either from beach forest (BF) or inland forest (IF). The type of substrates (AL, GL, TW) where such species was collected was also indicated along with the overall AI ranking (A, C, O, R). Finally, all species recorded for the first time in the country in this study are highlighted in bold and a short description and images are provided (Fig. 5). Majority of the specimens were identified up to species level. However, five specimens were only assigned to genus level due to their uncommon morphology resulting to the difficulty of further classifying them. The list is alphabetically arranged according to taxonomic order, genus, and species.

Ceratiomyxales

Ceratiomyxa fruticolosa (O.F. Müll.) T. Macbr. [QP: FC (6) = IF: decayed logs (6)] – O

Echinosteliales

- Clastoderma debaryanum A. Blytt [AP: MC (1) = IF: TW (1)] R
- *Echinostelium minutum* de Bary [AP: MC (1) = BF: TW (1)] [QP: MC (2) = IF: AL (1), BF: TW (1)] – R

Liceales

- Cribraria cancellata (Batsch) Nann.-Bremek. [QP: FC (1) = BF: decayed log (1)] R
- Cribraria violacea Rex [AP: MC (5) = IF: TW (2), BF: GL (1), TW (2)] [QP: FC (2) = BF: decayed log (2) / MC (1) = IF: TW (1)] – O
- Licea biforis Morgan [AP: MC (1) = IF: TW (1)] [QP: MC (2) = BF: AL (1), TW (1)] R

Physarales

- Craterium minutum (Leers) Fr. [QP: MC (2) = IF: TW (2)] R
- Craterium sp. [QP: MC(2) = BF: GL(2)] R.
- Craterium leucocephalum (Pers. ex J.F. Gmel.) Ditmar [QP: FC (4) = IF: leaf litter (4)] – R
- Diachea bulbillosa (Berk. & Broome) Lister [AP: MC (3) = IF: AL (1), GL (2)] R
- Diachea leucopodia (Bull.) Rostaf. [AP: MC (12) = IF: AL (2), TW (1), BF: AL (1), GL (7), TW (1)] [QP: FC (6) = BF: leaf litter (6) / MC (15) = IF: AL (1), BF: (AL (6), GL (8)] - A
- **Diachea megalospora** K.S. Thind & Manocha [AP: MC(1) = IF: GL(1)] R.
- Sporothecae globose, 0.6 mm diam., crystal like. Characterized by light orange stalk expanded at the base and tapered upward. With black sporemass and brown irregular shape spores with warts forming reticulation. Previously reported in Australia (Hosokawa et al. 2018)
- Diachea splendens Peck [QP: FC (1) = IF: leaf litter (1)] R
- Diachea subsessilis Peck [AP: MC (8) = IF: AL (5), GL (3)] O
- Diderma effusum (Schwein.) Morgan [AP: MC (2) = IF: GL (2)] [QP: FC (3) = IF: leaf litter (2), BF: leaf litter (1) / MC (8) = IF: GL (1), TW (1), BF: AL (3), GL (1), TW (2)] - C
- Diderma hemisphaericum (Bull.) Hornem. [AP: FC (1) = BF: coconut inflorescence sheath (1) / MC (27) = IF: AL (10), GL (3), BF: AL (8), GL (6)] [QP: MC (20) = IF: AL (6), GL (6), TW (1), BF: AL (6), GL (1)] – A

Diderma sp. [QP: FC (1) = IF: leaf litter (1)] – R

- $Didymium \ bahiense \ Gottsb. [QP: FC (3) = IF: leaf litter (1), BF: leaf litter (2)] R$
- *Didymium clavus* (Alb. & Schwein.) Rabenh. [QP: FC (1) = IF: leaf litter (1)] R
- **Didymium eximium** Peck [QP: FC (1) = IF: leaf litter (1)] R.
- Sporocarp 1.5 mm high. Sporotheca umbilicate, pale gray. Stalk pale orange above, darker towards the base. Spores pale brown with evenly distributed warts. Also reported in Central Chile (Lado et al. 2012).
- Didymium iridis (Ditmar) Fr. [QP: FC (1) = IF: leaf litter (1)] R
- **Didymium listeri** Massee [AP: MC (1) = BF: GL (1)] R.
- Naturally occurring on leaf litter, plasmodiocarps pulvinate, 0.3 mm high, spore-mass black to brown with minutely warted spore ornamentation. Previously reported in the mountain area of Taiwan (Liu & Chen 1998).
- Didymium melanospermum (Pers.) T. Macbr. [QP: FC (1) = BF: leaf litter (1)] – R
- Didymium minus (Lister) Morgan [QP: FC (1) = BF: leaf litter (1) / MC (1) = IF: GL (1)] – R
- Didymium nigripes (Link) Fr. [AP: MC (2) = IF: AL (1), BF: TW (1)] [QP: FC (3) = BF: leaf litter (3) / MC (3) = IF: AL (1), TW (1), BF: GL (1)] – O
- Didymium sp. [AP: MC (1) = IF: GL (1)] R
- Didymium squamulosum (Alb. & Schwein.) Fr. & Palmquist [AP: FC (1) = IF: ground leaf litter (1) / MC (27) = IF: AL (9), GL (9), TW(1), BF: AL (5), GL (2), TW (1)] [QP: FC (2) = IF: leaf litter (1), BF: leaf litter (1) / MC (15) = IF: AL (6), GL (1), BF: AL (8)] – A
- *Physarella oblonga* (Berk. & M.A. Curtis) Morgan [AP: MC (1) = IF: GL (1)] [QP: MC (1) = IF: AL (1)] - R
- *Physarum auriscalpium* Cooke [AP: MC (1) = IF: AL (1)] R.
- Naturally occurring on leaf litter. Sporocarp globose to sub-globose with orange to brown stalk. Lime scales on sporocarps. Spore-mass black, spores minutely warted. Recorded from mangrove leaves in Brazil (Cavalcanti et al. 2016).
- *Physarum compressum* Alb. & Schwein. [QP: MC (8) = IF: AL (2), TW (4), BF: AL (1), GL (1)] – O
- Physarum decipiens M.A. Curtis [AP: MC (21) = IF: GL (1), TW (5), BF: AL (1), GL (1), TW (13)] [QP: MC (5) = IF: TW (3), BF: AL (1), TW (1)] A
- *Physarum echinosporum* Lister [AP: MC (2) = BF: GL (2)] [QP: FC (2) = BF: twig (2) / MC (14) = BF: AL (1), GL (13)] - C

- Physarum melleum (Berk. & Broome) Massee [AP: MC (5) = IF: AL (2), TW (1), BF: GL (1), TW (1)] [QP: FC (9) = IF: leaf litter (8), BF: leaf litter (1) / MC (2) = IF: AL (2)] - C
- Physarum oblatum T. Macbr. [AP: MC (6) = IF: GL (1), TW (2), BF: AL (1), TW (2)] [QP: FC (3) = BF: leaf litter (2), coconut inflorescence sheath (1) / MC (3) = IF: TW (1), BF: AL (1), TW (1)] - C
- Physarum roseum Berk. & Broome [QP: FC (1) = IF: twig (1)] – R
- Physarum stellatum (Massee) G.W. Martin [AP: FC (1) = IF: decayed log (1)] – R
- Physarum viride (Bull.) Pers. [AP: FC (4) = IF: ground leaf litter (1), BF: ground leaf litter (3)] - O

Stemonitales

- Collaria arcyrionema (Rostaf.) Nann.-Bremek. ex Lado [AP: MC (11) = IF: AL (2), GL (3), TW (1), BF: AL (1), GL (1), TW (3)] [QP: FC (3) = IF: leaf litter (1), twig (1), BF: leaf litter (1) / MC (8) = IF: TW (1), BF: AL (3), GL (1), TW (3)] - C
- Comatricha nigra (Pers. ex J.F. Gmel.) J. Schröt. [AP: MC (3) = IF: GL (1), TW (1), BF: TW (1)] – R
- $\begin{array}{l} Comatricha \; pulchella \; (C. \; Bab.) \; Rostaf. \; [AP: \; MC \; (1) \\ = IF: \; AL \; (1)] \; [QP: \; MC \; (2) = IF: \; TW \; (2)] R \end{array}$
- Comatricha sp. [AP: MC (1) = BF: TW (1)] R
- Comatricha tenerrima (M.A. Curtis) G. Lister [AP: MC (11) = IF: TW (2), BF: TW (9)] [QP: FC (1) = IF: twig (1) / MC (9) = IF: TW (4), BF: TW (5)] - C
- Lamproderma scintillans (Berk. & Broome) Morgan [AP: FC (1) = IF: decayed log(1) / MC (10) = IF: AL (1), GL (3), TW (2), BF: AL (2), TW (2)] [QP: FC (2) = IF: leaf litter (2) / MC (10) = IF: TW (5), BF: AL (1), TW (4)] – A
- Lycogala exiguum Morgan [AP: FC (1) = BF: decayed log (1)] [QP: FC (1) = IF: decayed log (1)] – R
- Stemonaria fuscoides Nann.-Bremek. & Y. Yamam. [QP: MC (1) = BF: TW (1)] – R
- *Stemonitis axifera* (Bull.) T. Macbr. [AP: MC (1) = IF: TW (1)] [QP: FC (1) = IF: twig (1)] – R
- Stemonitis fusca Roth [AP: MC (7) = IF: AL (1), TW (1), BF: GL (2), TW (3)] [QP: MC (8) = IF: TW (5), BF: AL (1), TW (2)] C
- Stemonitis herbatica Peck [AP: MC (2) = BF: TW (2)] [QP: MC (1) = IF: TW (1)] - R
- Stemonitis pallida Wingate [QP: MC (1) = IF: TW (1)] R
- Stemonitis virginiensis Rex [AP: MC (1) = IF: TW (1)] R.
- Naturally occurring on twigs. Sporocarps on a common hypothallus and 6–8 mm high. Sporotheca blackish to brown, slightly acuminate above,

spores pale brown and reticulated. Reported also in mangrove forest in Brazil (Cavalacanti et al. 2016).

Trichiales

- Arcyria cinerea (Bull.) Pers. [AP: FC (1) = IF: coconut inflorescence sheath (1) / MC (133) = IF: AL (19), GL (14), TW (15), BF: AL (32), GL (21), TW (32)] [QP: FC (6) = BF: coconut inflorescence sheath (3), leaf litter (3) / MC (104) = IF: AL (15), GL (5), TW (12), BF: AL (22), GL (18), TW (32)] – A
- Arcyria denudata (L.) Wettst. [AP: FC (4) = IF: decayed log (2), BF: decayed log (2) / MC (3) = BF: AL (1), TW (2)] [QP: FC (4) = IF: twigs (2), BF: leaf litter (1), woody twig (1) / MC (2) = BF: TW (2)] - C
- $\begin{array}{l} Arcyria \ globosa \ Schwein. \ [AP: MC (6) = BF: AL (4), \\ GL(1), TW (1)] \ [QP: MC (2) = IF: AL (1), GL (1)] O \end{array}$

Arcyria sp. [QP: MC (2) = BF: TW (2)] - R

- Hemitrichia calyculata (Speg.) M.L. Farr [QP: FC (2) = IF: decayed log (1), BF: twig (1)] - R
- Hemitrichia serpula (Scop.) Rostaf. ex Lister [AP: FC (2) = IF: decayed log (1), BF: decayed log(1) / MC (1) = BF: AL (1)] [QP: FC (3) = IF: decayed log (1), BF: decayed log (2)] - O
- Metatrichia vesparia (Batsch) Nann.-Bremek. ex G.W. Martin & Alexop. [AP: FC (2) = IF: decayed log (2) / MC (1) = IF: GL (1)] – R
- Perichaena chrysosperma (Curr.) Lister [AP: MC (19) = IF: AL (1), TW (4), BF: AL (4), GL (3), TW (7)] [QP: MC (18) = IF: AL (3), GL (1), TW (8), BF: AL (4), GL (1), TW (1)] A
- $\begin{array}{l} Perichaena \ corticalis \ (Batsch) \ Rostaf. \ [AP: MC \ (1) = \\ BF: \ AL \ (1)] R \end{array}$
- Perichaena depressa Lib. [AP: MC (24) = IF: TW (2), BF: AL (4), GL (9), TW (9)] [QP: FC (1) = BF: coconut inflorescence sheath (1) / MC (28) = IF: AL (2), TW (3), BF: AL (4), GL (3), TW (16)] - A
- Perichaena pedata (Lister & G. Lister) G. Lister ex
 E. Jahn [AP: MC (5) = IF: AL (1), GL (1), BF: GL (1), TW (2)] [QP: MC (1) = IF: TW (1)] O

Species relative abundance

The AI used in this study was based on the ranking of Stephenson et al. (1993). From the 29 species identified in beach forest of Aurora (= seven months after a typhoon), eight species were reported as abundant, five species were common, eight species were occasional, and eight species were rare. In inland forest, eight species were also reported as abundant, five species as common, and 20 species as rare from the 33 identified species. On the other hand, in Quezon (= one month after typhoon), eight species were reported as abundant, six species were common, eight species were occasional, and eight species were rare from the 30 species identified in beach forest, while 11 species were reported as abundant, four species as common, and 26 species as rare from the 41 species identified in inland forest. Taking all counts into consideration, of the 62 species reported in this study eight species were abundant, eight species were common, and nine species were occasional with 37 species as rare.

Sampling efforts and species accumulation curve

To provide evidences on the extensiveness and exhaustiveness of the sampling efforts, SAC was computed. The number of records and species in the field and moist chambers were included in the analysis. SAC was plotted to determine whether the recorded number of species reflects the total number of myxomycetes that can be present in the collection sites. In this study, 82.35 % and 85.71 % sampling efforts were computed for Aurora and Quezon, respectively (Fig. 2). The individual sampling effort for the two forest types in Aurora and Quezon was also computed. In Aurora, 87.87 % in beach forest and 86.84 % in inland forest were the computed sampling efforts (Fig. 2). Moreover, 93.75 % and 68.33 % sampling efforts were computed for beach and inland forests in Quezon, respectively (Fig. 2).

Taxonomic and species diversity

Taxonomic diversity between forest types in the two study sites (post typhoon exposure) was assessed. Taxonomic diversity was computed as the ratio of the number of species to the number of genera (S/G ratio) to provide an overview of the myxomycete diversity in the study areas. Beach forests had the highest taxonomic diversity (S/G=1.93 in Aurora; S/G=1.88 in Quezon) as compared to inland forests (S/G=2.20 in Aurora; S/G=2.41 in Quezon) (Tab. 2). In terms of substrate type, AL in both beach forest (S/G=1.56) and inland forest (S/G=1.50) had the highest taxonomic diversity in Aurora while TW in beach forest (S/G=1.36) and AL in inland forest (S/G=1.63) had the highest taxonomic diversity in Quezon. Note that the actual diversity of the myxomycetes is not reflected only in the taxonomic diversity values and thus, species diversity was also assessed based on the richness, abundance, and evenness of the myxomycetes. In this part, occurrence data from field and moist chamber collections were both included. Between the two forest types, inland forest had higher values in terms of species diversity (HS, FAI), richness (HG), and evenness (E, SID) as compared to beach forest (Tab. 2). Rarefac-

Study site	Time of collection	Forest type	Species diversity ^a				Taxonomic diversity			
			HS	HG	Е	FAI	SID	S/G ratio	Species	Genera
Aurora	7 months after a typhoon	Beach Forest	1.08	5.15	0.46	8.78	0.17	1.93	29	15
		Inland Forest	1.17	6.33	0.53	12.75	0.13	2.20	33	15
		Pooled Data	1.17	6.88	0.45	11.98	0.15	2.33	42	18
Quezon	1 month after a typhoon	Beach Forest	1.10	5.36	0.47	9.31	0.15	1.88	30	16
		Inland Forest	1.35	7.94	0.62	18.27	0.08	2.41	41	17
		Pooled Data	1.28	7.92	0.50	14.57	0.11	2.53	48	19

Tab. 2. Taxonomic and species diversity of myxomycetes collected seven months after a typhoon in Aurora and one month after a typhoon in Quezon in relation to forest types.

^a Diversity t test showed significant difference between pooled data from Aurora and Quezon at p < 0.05. Significant differences at p < 0.01 were also observed between the two forest types in Quezon but not in Aurora. Similarly, significant differences at p < 0.01 was noted between the inland forest in Quezon and either of the two forest types in Aurora but not between the beach forest in Quezon and either of the two forest types in Aurora.

tion curve constructed from Coleman rarefaction values generated using EstimateS also showed similar findings (Fig. 3). This trend was observed in both provinces. In fact, looking again at the number of species obtained in the present study, a higher number of species was obtained in inland forest (33 species in Aurora; 41 species in Quezon) as compared to beach forest (29 species in Aurora; 30 species in Quezon). In terms of substrate types, highest values of species diversity, richness, and evenness were observed in TW in beach forest and GL in inland forest in Aurora (Tab. 3). In Quezon, highest values for species diversity, richness, and evenness were computed in AL in beach forest and TW in inland forest.

Community analysis

The similarities in myxomycete assemblages between beach and inland forests were evaluated using Sorensen's CC and PS. In this part, a CC value of 0.65 and a PS value of 0.66 were obtained between beach and inland forests in Aurora, and a CC value of 0.65 and a PS value of 0.54 were obtained between the two forest types in Quezon (Fig. 6). Looking at the two similar forest habitats in relation to past typhoon exposure, a CC value of 0.64 and a PS value of 0.73 were obtained between beach forests of Aurora and Quezon. On the other hand, community analysis between inland forest of Aurora and inland forest of Quezon revealed a CC value of 0.59 and a PS value of 0.60 (Fig. 6). Cluster analysis based on the Morisita index of similarity generated using the PAST software also showed a high degree of similarities in terms of myxomycete community composition between the beach forests in Aurora and Quezon (Fig. 7). In terms of substrate type, highest CC value in Aurora was computed between GL and TW in beach forest (0.65) suggesting about 60 % of myxomycete species obtained in GL were also found in TW. In fact, 12 species were found common between the two substrates. However, when the abundance was considered in the computation, highest similarity value was obtained between similar substrate type, that is, TW in beach and inland forests (PS = 0.74). This indicates that the myxomycete species common in TW between the two forest types had an almost equal abundance. In Quezon, the highest similarity was obtained between AL and GL (CC = 0.69) in beach forest, with 9 species common to both substrate types. Interestingly, the highest PS value was obtained between same substrate type - AL in beach and inland forests (PS = 0.72).

Discussion

Moist-chamber productivity and myxomycete composition in Aurora and Quezon provinces

In this study, the presence of myxomycetes' fruiting bodies or plasmodia in moist chamber signifies



Fig. 2. Species accumulation curve generated for the collected myxomycetes species: A Aurora (pooled), B Quezon (pooled), C beach forest in Aurora, D beach forest in Quezon, E inland forest in Aurora, and F inland forest in Quezon.

one positive collection, otherwise considered as negative. Among the positive collections, fruiting bodies were observed more often than plasmodia, which implied that many of the plasmodia had developed into recognizable fruiting bodies. The result was similarly observed in the study of Macabago et al. (2016) where the percentage of fruiting bodies was higher than plasmodia. Despite the dif-

Study site	Forest type	Substrate type	HS	HG	E	FAI	SID
		AL	0.81	3.10	0.44	5.44	0.27
	Beach forest	GL	0.92	3.43	0.52	6.49	0.18
		TW	1.04	4.59	0.52	8.87	0.15
Aurora		AL	0.91	3.46	0.52	6.64	0.18
	Inland forest	GL	1.02	4.13	0.61	9.39	0.14
		TW	0.99	4.01	0.61	9.43	0.17
		AL	0.95	3.38	0.53	6.23	0.17
	Beach forest	GL	0.77	2.56	0.55	4.36	0.23
0		TW	0.83	3.25	0.44	5.68	0.25
Quezon	Inland forest	AL	0.90	3.21	0.56	6.45	0.18
		GL	0.69	2.16	0.58	4.75	0.26
		TW	1.12	4.04	0.64	9.98	0.10

Tab. 3. Species diversity of myxomycetes collected seven months after a typhoon in Aurora and one month after a typhoon in Quezon in relation to substrate types.



Fig. 3. Rarefaction curve constructed from Coleman Rarefaction values generated using Estimate S.

ferences in collections done after typhoon, both beach and inland forests in the two provinces showed high moist chamber productivity (78–79 %) as evidently observed in the number of positive collections for myxomycetes. The productivity of the moist chamber in this study was comparable to the other forest types so far studied in the country such as the lowland tropical forest in the Bicol Peninsula (74 %, Dagamac et al. 2015a), the karst forest in Quezon province (82 %, Dagamac et al. 2015c), and the limestone forest in Palawan (73 %, Pecundo et al. 2017) but relatively higher than the productivity reported in the lowland mountain forest and agricultural plantations in Negros Occidental (27 %, Alfaro et al. 2015), the island forest in Pangasinan (55 %, Kuhn et al. 2013), and the forested ecopark in Quezon City (51 %, Macabago et al. 2010).

Most of the myxomycete species during field collection in inland forests were recovered from decayed logs and leaf litter collected several days after a typhoon hit the collection sites. These substrates had been proven as best microhabitats for myxomycetes in the natural environment (Stephenson 1989). In addition, woody substrates have high surface area that supports bacteria and other microorganisms upon which the myxomycetes feed (Eliasson & Nannenga-Bremekamp 1983, Madelin 1984). The myxomycetes species collected directly from inland forests included A. cinerea, A. denudata, C. fruticulosa, C. arcyrionema, C. tenerrima, C. leucocephalum, D. splendens, D. effusum, Diderma sp., D. bahiense, D. clavus, D. eximium, D. iridis, D. squamulosum, H. calyculata, H. serpula, L. scintillans, L. exiguum, M. vesparia, P. melleum, P. roseum, P. stellatum, P. viride, and S. axifera. On the other hand, myxomycete species from beach forests were recovered mostly from coconut husks. Coconut husks have sufficient water-holding capacity providing ideal moist condition favourable for the growth of myxomycetes. In fact, myxomycetes that thrive in coastal areas can be found mostly in old, rotting piles of coconut husks and nuts (Ing & Hnatiuk 1981). Similarly, majority of the field specimens collected in the study of Dagamac et al. (2015b) in the coastal forest in Oriental Mindoro, Philippines were recovered from coconut husks. The myxomycete species collected directly



Fig. 4. Photographs of selected myxomycetes species reported in this study: A Craterium leucocephalum, B Didymium clavus, C Metatrichia vesparia, D Physarum echinosporum, E P. roseum, F Stemonaria fuscoides.

from beach forests were A. cinerea, A. denudata, C. arcyrionema, C. cancellata, C. violacea, D. leucopodia, D. hemisphaericum, D. effusum, D. bahiense, D. melanospermum, D. minus, D. nigripes, D. squamulosum, H. calyculata, H. serpula L. exiguum, P. depressa, P. echinosporum, P. melleum, P. oblatum, and P. viride. As expected, most myxomycete species documented in this study were recovered from the moist chambers rather than from the field, suggesting that moist chamber technique can support different myxomycete assemblages. In fact, certain myxomycete species can be found only in moist chamber cultures such as Echinostelium elachiston, Echinostelium cribrariodes, Licea pedicellata, Comatricha synsporos, Macbrideola scintillans, and Physarum dictyosporum (Martin & Alexopoulus, 1969). Myxomycetes identified from moist chambers herewith included species under the genera Arcyria, Clastoderma, Collaria, Comatricha, Craterium, Cribraria, Diachea, Diderma, Didymium, Echinostelium, Hemitrichia, Lamproderma, Licea, Metatrichia, Perichaena, Physarella, Physarum, Stemonaria, and Stemonitis. Interestingly, four species recovered from moist chambers in Aurora, namely, Diachea megalospora (inland forest), Didymium listeri (beach forest), Physarum auriscalpium (inland forest), and Stemonitis virginiensis (inland forest) are new records for the Philippines (Fig. 5). In addition, one species, Didymium eximium (inland forest) collected from the field in Quezon was also noted as a new record. In totality, five species were reported in this study as new records for the country which increased the number of reported myxomycete species for the



Fig. 5. The five new records of myxomycetes for the Philippines: A Diachea megalospora, B–C Spores of D. megalospora, D Didymium eximium, E–F Spores of D. eximium, G Didymium listeri, H–I Spores of D. listeria, J Physarum auriscalpium, K–L Spores of P. auriscalpium, M Stemonitis virginiensis, N–O Spores of S. virginiensis.



Fig. 6. Venn diagram showing the similarities in myxomycete species composition between collection done 7 months after a typhoon in Aurora and collection done 1 month after a typhoon in Quezon: a Aurora (seven months after typhoon), b Quezon (one month after typhoon), c between beach forests, d between inland forests; CC Coefficient of Community, PS Percentage Similarity.

Philippines from 159 (Dagamac & dela Cruz 2019) to 164. The term "new record" here refers to the first report of a previously identified myxomycete species in the Philippine Island.

Overall, this present study documented 62 species of myxomycetes which was comparable with the number of species recorded in the tropics, e.g. 77 species in the cloud forest in Ecuador (Schnittler et al. 2002), 70 species in agricultural and forest sites in Thailand (Tran et al. 2008), and 60 species in the Amazon forest in Peru (Rojas & Stephenson 2012). This report was higher than the number of myxomycete species documented in other sites in the Philippines, e.g. from the seven different vegetation types in Bohol Island (54 species, Macabago et al. 2017), the coastal, mountain, and community forests in Oriental Mindoro (42 species, Dagamac et al. 2015b), the coastal and mountain forests in Occidental Mindoro (44 species, Macabago et al. 2016), the ultramafic and volcanic forests in Luzon Island (40 species, Rea-Maminta et al. 2015), and the mountain forests in Pampanga (30 species, Dagamac et al., 2014). This suggests that the number of myxomycetes vary in different forest types and ecoregions in the Philippines. It would be interesting to further study the intrinsic and extrinsic factors that may have contributed to this variation in species composition.

Abundance, SAC, and sampling efforts

Myxomycetes are widely distributed in different terrestrial habitats and their presence in the environment is reported to be significantly influenced by their microhabitat (Stephenson 1989). Each microhabitat is known to host unique or different sets of myxomycetes (Stephenson et al. 1993). From the 62 species identified in this study, eight species were abundant, eight species were common, and nine species were occasionally occurring with most recorded species, i.e. 37 as rare or reported from one or very few collections. Among these, A. cinerea remained as the most single abundant species with 244 collections and was observed in all substrates collected in the beach and inland forests of Aurora and Quezon provinces. The cosmopolitan species A. cinerea had been extensively recorded in tropical (Rojas et al. 2012) and temperate regions (Stephenson 1988), and was reportedly inhabiting a wide array of substrata including special microhabitats such as decayed inflorescence (Schnittler & Stephenson 2002), grass litter (Carascal et al. 2017), barks and dung (Stephenson, 1989). Aside from A. cinerea, other species that were also reported as abundant here were D. leucopodia, D. hemisphaericum, D. squamulosum, L. scintillans, P. chrysosperma, P. depressa, and P. decipiens. These myxomycetes species were also reported in other myxomycete studies conducted in the Philippines, e.g. in Puerto Galera, Oriental Mindoro (D. hemisphaerium, D. squamulosum, and L. scintillans, Dagamac et al. 2015b), in Bohol Islands (P. chrysosperma and P. depressa, Macabago et al. 2017), and in Bataan, Pangasinan, and Zambales (D. leucopodia, Rea-Maminta et al. 2015). It is interesting to note that one species, *P. decipiens*, was reported in this study as abundant. This species was first reported in the Philippine island by Kuhn et al. (2013), and since then, was rarely reported as abundant species. Macabago et al. (2017) reported this species as rare while Dagamac et al. (2015c) reported it as occasionally occurring. This observation was supported by the study of Eliasson and Nannenga-Bermekamp (1983) which stated that variation among myxomycetes tends to occur from one place to another in terms of their relative abundance.

Species accumulation curve showed that more than 80 % of the estimated possible myxomycetes within the collection sites in the respective provinces were recorded in this study. As shown, 42 species (Chao 2 mean: 51) and 48 species (Chao 2 mean: 56) were identified in Aurora and Quezon, respectively. The relatively high numbers of sampling ef-



Fig. 7. Cluster analysis of myxomycetes communities based on Morisita index of similarity between beach and inland forests in Aurora and Quezon provinces.

fort was evident for both the forest types in Aurora and Quezon since the number of species recorded in each of the forest types in the two provinces were almost near the expected number of species represented by the Chao 2 mean. The result suggested that majority of the expected number of species in the collection sites were recorded in this study. The extent of sampling efforts reported herein was similarly observed in the study conducted in the coastal, mountain and community forests in Puerto Galera, Oriental Mindoro with 89 % sampling efforts (Dagamac et al. 2015b).

Diversity of myxomycetes in beach and inland forests in Aurora and Quezon provinces

The measurement of taxonomic diversity represents how the number of species is distributed to the number of genera, and thus, a biota in which the species are divided among many genera is more "intuitively" diverse in a taxonomic sense than in a biota which the species belong to a few genera (Stephenson et al. 1993). A low S/G value implies higher taxonomic diversity. In this study, beach forest was observed to be more taxonomically diverse than inland forest. This was evident in both Aurora and Quezon provinces. Similarly, Dagamac et al. (2015b) reported the highest taxonomic diversity in coastal forest (situated near the seacoast) among the three forest types surveyed in their study. Conversely, Macabago et al. (2016) reported a higher taxonomic diversity in mountain forest or the site that is situated away from the seacoast than the one situated

near the seacoast. In terms of substrate type, AL in both beach and inland forests in Aurora were more taxonomically diverse as compared with GL and TW in the two forest types, while TW (as compared with AL and GL) in beach forest and AL (as compared with GL and TW) in inland forest were observed to be more taxonomically diverse in Quezon. Stephenson et al. (2000) stressed that the taxonomic diversity values for the myxobiota in temperate and tropical areas vary. In terms of species diversity, inland forest had higher species diversity than beach forest, both observed in the two provinces when the computed diversity values were considered (Tab. 2). This is further supported by a higher number of species recorded in inland forest (33 species in Aurora; 41 species in Quezon) as compared to beach forest (29 species in Aurora; 30 species in Quezon). This is congruent with the rarefaction curves constructed using the Coleman Rarefaction values (Fig. 3). Statistical analysis using the diversity t-test showed significant differences at p <0.01 only between the two forest types in Quezon but not in Aurora and between the inland forest in Quezon and any of the two forest types in Aurora. Comparing the pooled data between the two sampling areas, we also observed a significant difference (p < 0.05) between Quezon (= 1 month after the typhoon) and Aurora (= 7 months after the typhoon). Nevertheless, the higher number of species in inland forest could be attributed to the heterogeneity and rich vegetation of the area where a higher species of plants and trees are evident, and thereby providing microhabitats for myxomycetes. In the Philippines, Alfaro et al. (2015) found out that a lowland montane forest yielded higher number of myxomycete species than the monotypic agricultural plantations, suggesting that forested areas with heterogeneous plant communities supported a higher number of myxomycete species than areas with a homogenous vegetation. Hence, myxomycetes diversity is higher in a site with rich vegetation. On the other hand, in beach forest, few species of trees are present such as *B. asiatica* and *T. cattapa*, the usual dominating species in beach forest (Primavera & Sadaba 2012), with the presence of some coconut trees and, thus represented limited possible microhabitats for myxomycetes. A slightly higher number of species in inland forests might also suggest that the general environmental condition in inland forest is more favorable for the growth and development of myxomycetes than in beach forest. The geographical locations of the two forest types could also have great impact as a similar trend was observed in the study of Macabago et al. (2016) where the mountain forest which was situated away from the seacoast had a higher number of myxomycete species than the coastal forest. In line with this observation, it would also be interesting to study further how various environmental conditions along the coastal areas, e.g. exposure to salty air brought about by wind blowing from the sea or high soil salinity, affect myxomycetes growth and development.

Community analysis between beach and inland forests of Aurora and Quezon

There were high similarities among myxomycete species composition between the beach and inland forests in Aurora, and between the same forest types in Quezon (Fig. 6). Of the 42 species identified in Aurora, 20 species were found common to the two forest types. These species were A. cinerea, A. denudata, C. arcyrionema, C. nigra, C. tenerrima, C. violacea, D. leucopodia, D. hemisphaericum, D. nirgipes, D. squamulosum, H. serpula, L. scintillans, P. chrysosperma, P. depressa, P. pedata, P. decipiens, P. melleum, P. oblatum, P. viride, and S. fusca. On the other hand, from the 48 species recorded in Quezon, 23 species were recorded in the two forest types. These species were A. cinerea, A. denudata, C. arcyrionema, C. tenerrima, C. violacea, D. leucopodia, D. effusum, D. hemisphaericum, D. bahiense, D. minus, D. nigripes, D. squamulosum, E. minutum, H. calyculata, H. serpula, L. scintillans, P chrysosperma, P. depressa, P. compressum, P. decipiens, P. melleum, P. oblatum, and S. fusca. Interestingly, the result was also observed in other myxomycete studies where two different forest habitats harboured almost similar species. The study of Dagamac et al. (2015b) noted 17 species of myxomycetes that are common to coastal forests and inland forests (mountain and community forests) in Puerto Galera, Occidental Mindoro. Similarly, 29 species were reported common to coastal and mountain forests in the study of Macabago et al. (2016) in Lubang Island, Occidental Mindoro. Moreover, the computed PS value between beach and inland forests in Aurora and Quezon suggested that the similar myxomycete species present in the two forest types almost had an equal abundance. Comparable result was also reported in the study of Macabago et al. (2016) between coastal and mountain forests with 0.76 CC value, albeit showed a lower PS value (0.31) contrary to the present study. In terms of substrate type, a higher degree of similarity (CC value based on presence or absence of species) between two different substrates present in the same forest habitat was observed. But the incorporation of abundance with the presence or absence of species in computing similarities showed a higher similarity (PS value) between two similar substrate types from different forest habitats. This observation is supported by the Venn diagram shown in Fig. 6. This pattern was in contrast to the study of Macabago et al. (2016) where the highest PS value was obtained between two different substrates from the same forest habitat.

Impacts of typhoon on myxomycete diversity

The province of Aurora and Quezon in the eastern side of the Philippines are frequently exposed to typhoons originating from the Pacific Ocean. These frequent typhoons may have resulted to regular damage and modification in plant community structure among its beach and inland forests. It has been previously reported that typhoons strongly influenced the structure of the forest with effects that persisted for decades or even longer (Boose et al. 2001, Yao et al. 2015). In addition, typhoon disturbance also had significant impacts on the biogeochemical processes (Marler & Ferreras 2014) and litter fall rates (Wang et al. 2013). As baseline taxonomic and diversity data from the two typhoonprone provinces prior to typhoon exposure is lacking, it is still speculative to say that typhoon disturbance directly affected the diversity of myxomycetes in the two forest habitats in the presented study. However, our research provided some key findings that may contribute to our understanding of the possible impact of natural disturbance on myxomycetes, i.e. by increasing the possible microhabitats on the forest floor for myxomycete colonization and by facilitating spore dispersal leading to a higher species diversity. As stated by Sousa (1984), disturbance damages one or more individuals (or colonies) in an area but may create an opportunity for a new group of individuals to become established. As the disturbance caused by typhoon may have resulted to an increase of plant materials on the forest floor such as leaf litter, twigs and logs, the dispersed myxomycete spores likewise may have been given the opportunity to grow, develop and be more established due to the availability of these highly favourable substrata. Therefore, the heterogeneous plant compositions in inland forests in Quezon and Aurora and the resulted increase of available microhabitats for myxomycetes brought about by typhoon disturbance are factors that may have contributed to a slightly higher number of collected species from inland forests in this study. Previous report stated that the actual distribution of most myxomycetes species is usually determined by the availability of suitable microhabitats for their establishment, growth, and development (Schnittler & Mitchell 2000). In addition, different environmental factors associated with typhoon such as strong winds and heavy rains may serve as agents of dispersal which transferred myxomycetes spores from one habitat type to another. It could also potentially transfer the actual plant materials between forest sites, thereby increasing possible microhabitats for myxomycetes.

Past disturbance had a significant impact on the diversity of species in an area (Grime 1977). Takafumi & Hiura (2008) further stated that disturbance history can explain the variation in richness of forest vegetation, even long after the disturbance had occurred, e.g. 50 years after the typhoon, and that the effects of disturbance could remain for 20 to 80 years. In the present study, a Category 1 typhoon, "Maring" (Doksuri), hit the province of Quezon in 2017 with a maximum wind of 85 kph and a gustiness of 105 kph. After the province experienced this typhoon, the effect of disturbance was still evidently observed on the forest floor due to the presence of snags and logs and of numerous plant debris. A Category 3 typhoon, "Karen" (Sarika), also hit the province of Aurora in 2016 with a maximum wind of 150 kph and gustiness of 210 kph. This typhoon also resulted in the toppling of many trees. Carreno-Rocabado et al. (2012) studied the impact of levels of disturbances on trees in tropical forests within a period of eight years and found that high over moderate disturbance could highly influence the diversity and the functional state of trees. As with the case of the present study, it can be speculated that the intensity of the two typhoons that hit Aurora and Quezon provinces before our field and substrate collections may have caused physical and functional changes in forest community, and resulted in the accumulation of fallen leaves and branches on the forest floor and in the toppling of trees leading to log formation. These scenarios may have increased the potential microhabitats of myxomycetes, thereby may explain the high taxonomic and species diversity reported in this study. Additionally, the strong wind associated with the above-mentioned typhoons could have served as excellent agent of spore dispersal that blew the myxomycete spores over a significant distance and/or from one habitat type to another. Myxomycetes spores are easily dispersed by wind (Kamono et al. 2009), with even a slight breeze can cause myxomycetes spore dispersal at a significant distance of ~1.8 km (Schnittler et al. 2006). This may explain the high similarity of assemblages of myxomycetes between the two forest types and even between the two typhoon-prone provinces.

Disturbances can have both positive and negative effects on biodiversity. As typhoon disturbance can negatively influence the plant communities in a forest, it could otherwise increase the available resources for othr organisms. Holt (2008) stressed that one of the consequences of resource pulses brought about by a disturbance was that a given community could increase the number of its individuals. It is interesting to note that in our study a significantly higher species richness and diversity was observed from Quezon a month after a typhoon hit its inland and beach forests as compared to the two forest sites in Aurora which was hit by the typhoon seven months before our field and substrate collections. We hypothesized that myxomycetes could have increase its assemblages immediately after typhoon disturbance but may have returned to its "typical" community structure as the forests recover. However, a more detailed investigation is suggested to prove this hypothesis.

In summary, our study provided relevant baseline information on the possible impacts of typhoon on the diversity of myxomycetes in beach and inland forests of Aurora and Quezon, Philippines. The forest sites with heterogeneous and richer vegetation when disturbed by a typhoon could provide more suitable microhabitats for myxomycetes, and thus resulted in a higher number of myxomycetes than forest sites with lesser vegetation. The easy dispersal of myxomycete spores as triggered by typhoon winds could also contribute to the observed species diversity and similarities in myxomycetes communities between the two different forest habitats. Time-dependent differences in species assemblages could also be observed following a typhoon disturbance and maybe related with forest recovery. However, to further establish these hypotheses and the main findings on the impact of typhoons on myxomycetes, a more comprehensive field and sampling collection and an evaluation of plant communities in the study sites should be conducted before and after a typhoon.

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References

- Alfaro J.R.D., Alcayde D.L.I.M., Agbulos J.B., Dagamac N.H.A., dela Cruz T.E.E. (2015) The occurrence of myxomycetes from a lowland montane forest and agricultural plantations of Negros Occidental, Western Visayas, Philippines. *Fine Focus* 1: 7–20.
- Allen C.D., Macalady A.K., Chenchouni H., Bachelet D., Mc-Dowell N., Vennertier M., Kitzberger T., Ridling A., Breshears, D.D., Cobb N. (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management* 259: 660–684.
- Boose E.R., Chamberlin K.E., Foster D.R. (2001) Landscape and regional impacts of hurricanes in New England. *Ecological Monographs* 71:27–48.
- Brown S. (2013) The Philippines is the most storm-exposed country on earth. In: https://world.time.com/2013/11/11/ the-philippines-is-the-most-storm-exposed-country-on-earth (accessed 02 Mar 2018).
- Carascal M.B., Rea M.A.D., Dagamac N.H.A., dela Cruz T.E.E. (2017) Myxomycetes associated with grassland litter in the Philippines. *Current Research in Environmental & Applied Mycology* 7: 56–63.
- Carreno-Rocabado G., Pena-Claros M., Bongers F., Alarcon A., Licona J.C., Poorter L. (2012) Effects of disturbance intensity on species and functional diversity in a tropical forest. *Journal of Ecology* 100: 1453–1463.
- Cavalcanti L.H., Damasceno G., Costa A.A.A., Bezerra A.C.C. (2016) Myxomycetes in Brazilian mangroves: species associated with Avicennia nitida, Laguncularia racemosa and Rhizophora mangle. Marine Biodiversity Records 9: 31. doi: 10.1186/s41200-016-0035-4.
- Colwell R.K. (2013) EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. User's Guide and application; http://viceroy.eeb.uconn. edu/estimates (accessed 10 Mar 2018).
- Dagamac N.H.A, Dela Cruz T.E.E. (2019) The Philippine slime molds after Dogma's 1975 list – How far have we been? *Philippine Journal of Systematic Biology* 13(2): 58–65.
- Dagamac N.H.A., Dela Cruz T.E.E., Rea-Maminta M.A.D., Aril-dela Cruz J.V., Schnittler M. (2015a) Rapid assessment of myxomycetes diversity in Bicol Peninsula. *Nova Hedwigia* 104 (1–3): 31–46.
- Dagamac N.H.A., Rea-Maminta M.A.D., Batungbacal N.S., Jung S.H., Bulang C.R.T., Cayago A.G.R., dela Cruz T.E.E. (2015b) Diversity of plasmodial slime molds (myxomycet-

es) in coastal, mountain, and community forests of Puerto Galera, Oriental Mindoro, the Philippines. *Journal of Asia-Pacific Biodiversity* 8: 322–329.

- Dagamac N.H.A., Rea-Maminta M.A.D., dela Cruz T.E.E. (2015c) Plasmodial slime molds of a tropical karst forest, Quezon National Park, the Philippines. *Pacific Science* 69(3): 407–418.
- Dagamac N.H.A., Stephenson S.L., dela Cruz T.E.E. (2014) The occurrence of litter Myxomycetes at different elevations in Mt. Arayat National Park, Pampanga, Philippines. Nova Hedwigia 98: 187–196.
- Dagamac N.H.A., Stephenson S., dela Cruz T.E.E. (2012) Occurrence, distribution and diversity of myxomycetes (plasmodial slime moulds) along two transects in Mt. Arayat National Park, Pampanga, Philippines. *Mycology* 3(2): 119–126.
- Dela Cruz G. (2016). "IN NUMBERS: Typhoons in the Philippines and the 2016 polls". https://www.rappler.com/moveph/issues/disasters/126001-typhoons-enter-philippinesfast-facts (accessed 02 Mar 2018).
- Eliasson U., Nannenga-Bremekamp N.E. (1983) Myxomycetes of the Scalesia Forest, Galapagos Islands. Mycology Proceedings C 86: 148–153.
- Fukasawa Y., Ando Y., Oishi Y., Suzuki S., Matsukura K., Okano K., Song Z. (2019) Does typhoon disturbance in subalpine forest have long-lasting impacts on saproxylic fungi, bryophytes, and seedling regeneration on coarse woody debris? *Forest Ecology and Management* 432: 309–318.
- Grime J.P. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111: 1169–1194.
- Hammer O., Harper D.A.T., Ryan P.D. (2001). PAST: Paleontological Statistics Software Package for Education and Data Analysis. http://folk.uio.no/ohammer/past (accessed 10 Mar 2018).
- Holt R. D. (2008) Theoretical perspectives on resource pulses. Ecology 89: 671–681.
- Hosokawa A., Reid C.R., Latty T. (2018) Slimes in the city: The diversity of myxomycetes from inner-city and semi-urban parks in Sydney, Australia. *Fungal Ecology* 39: 37–44.
- Ing B., Hnatiuk R. (1981) Myxomycetes of Aldabra atoll. *Atoll Research Bulletin* 249: 1–10.
- Kamono A., Kojima H., Matsumoto J., Kawamura K., Fukui M. (2009) Airborne myxomycete spores: detection using molecular techniques. *Naturwissenschaften* 96: 47–151.
- Keller H.W., Kilgore C.M., Everheart S.E., Carmack G.J., Crabtfree C.D., Scarborough A.R. (2008) Myxomycete plasmodia and fruiting bodies: unusual occurrences and user-friendly study techniques. *Fungi* 1: 24–37.
- Kilgore C.M., Keller H.W., Ely J.S. (2009) Aerial reproductive parts of vascular plants as a microhabitat for myxomycetes. *Mycologia* 101: 305–319.
- Ko C., Lai C., Chen T., Hsu H., Shiah F. (2015) Typhoon effects on phytoplankton responses in a semi-closed freshwater ecosystem. *Marine and Freshwater Research* 67: 546–555.
- Kuhn R.V., Javier A.O.M., Rodillas C.P., Parra C.M., Corpuz L.H.M, Moron L.S., dela Cruz T.E.E. (2013) Diversity of plasmodial myxomycetes from Anda island, Pangasinan, Philippines. *Biotropia* 20: 1–9.
- Lado C. (2001) A nomenclature taxabase of Myxomycetes. Cuadernos de trabajo de flora micológia Iberica 16: 1–224.
- Lado C. (2005-2020) An online nomenclatural information system of Eumycetozoa. Real Jardín Botánico, CSIC. Madrid, Spain; http://www.nomen.eumycetozoa.com (accessed 11 Mar 2018).

- Lado C., Wrigley de Basanta D., Estrada-Torres A., Stephenson S. L. (2012) The biodiversity of myxomycetes in Central Chile. *Fungal Diversity* 59: 3–32.
- Liu C., Chen Y. (1998) Myxomycetes of Taiwan X. Three new records of *Didymium*. *Taiwania* 43: 177–184.
- Macabago S.A.B., Dagamac N.H.A., dela Cruz T.E.E. (2010) Diversity and distribution of plasmodial myxomycetes (slime molds) from La Mesa Ecopark, Quezon City, Philippines. *Biotropia* 17(2): 51–61.
- Macabago S.A.B., Dagamac N.H.A., dela Cruz T.E.E., Stephenson S.L. (2017) Implications of the role of dispersal on the occurrence of litter-inhabiting myxomycetes in different vegetation types after a disturbance: a case study in Bohol Islands, Philippines. *Nova Hedwigia* 104 (1–3): 221– 236.
- Macabago S.A.B., Stephenson S.L., dela Cruz T.E.E. (2016) Diversity and distribution of myxomycetes in coastal and mountain forests of Lubang Island, Occidental Mindoro, Philippines. *Mycosphere* 7: 18–29.
- Madelin M.F. (1984) Myxomycetes, microorganisms and animals: a model of diversity in animal-microbial interactions. In: Anderson J.N., Rayner A.D.A., Walton D.W.H. (eds.) Invertebrate-microbial interactions. Cambridge University Press, New York, pp. 1–33.
- Magurran A.E. (2004) *Measuring biological diversity*. Blackwell Publishing, USA.
- Marler T.E., Ferrera U. (2014) Differential leaflet mortality may influence biogeochemical cycling following tropical cyclones. *Communicative & Integrative Biology* 7(2): e27924, doi: 10.4161/cib.27924.
- Martin G., Alexopoulus C. (1969) *The myxomycetes*. University of Iowa Press, Iowa City.
- Novozhilov Y.K, Schnittler M., Rollins A.W., Stephenson S.L. (2000) Myxomycetes from different forest types in Puerto Rico. *Mycotaxon* 77: 285–299.
- Parmesan C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* 37: 637–669.
- Pecundo M.H.P., Dagamac N.H.A., Stephenson S.L., Dela Cruz T.E.E. (2017) First myxomycete survey in the limestone forest of Puerto Princesa Subterranean River National Park, Palawan, Philippines. *Nova Hedwigia* 104(1–3): 129– 141.
- Primavera J.H., Sadaba R.B. (2012) Beach forest species and mangrove associates in the Philippines. SEAFDEC Aquaculture Department, Tigbauan, Iloilo.
- Rea-Maminta M.A.D., Dagamac N.H.A, Huyop F.Z., Wahab R.A., dela Cruz T.E.E. (2015) Comparative diversity and heavy metal biosorption of myxomycetes from forest patches on ultramafic and volcanic soils. *Chemistry and Ecology* 31: 741–753.
- Rojas C., Stephenson S.L. (2012) Rapid assessment of the distribution of mycomycetes in a southwestern Amazon forest. *Fungal Ecology* 5(6): 726–733.
- Rojas C., Stephenson S.L., Valverde R., Estrada-Torres A. (2012) A biogeographical evaluation of high-elevation myxomycetes assemblages in the northern Neotropics. *Fungal Ecology* 5: 99–113.
- Rojas C., Valverde R., Calvo E. (2016) Does elevation influence the distributional patterns of tropical myxomycetes? A case study in Costa Rica. *Mycology* 7: 45–52.
- Schnittler M., Lado C., Stephenson S.L. (2002) Rapid biodiversity assessment of a tropical myxomycete assemblage – Maquipucuna Cloud Forest Reserve, Ecuador. *Fungal Diversity* 9: 135–167.

- Schnittler M., Mitchell D.W. (2000) Species diversity in myxomycetes based on the morphological species concept - A critical examination. *Stapfia* 73: 55–61.
- Schnittler M., Stephenson S.L. (2002) Inflorescence of neotropical herbs as a newly discovered microhabitat for myxomycetes. *Mycologia* 94: 6–20.
- Schnittler M., Unterseher M., Tesmer J. (2006) Species richness and ecological characterization of myxomycetes and myxomycetes-like organisms in the canopy of a temperate deciduous forest. *Mycologia* 98: 223–232.
- Snell K.L., Keller H.W. (2003) Vertical distribution and assemblage of corticolous myxomycetes on five tree species in the Great Smoky Mountains National Park. *Mycologia* 95: 565–576.
- Sousa W.P. (1984) The role of disturbance in natural communities. Annual Review of Ecology and Systematics 15: 353– 391.
- Stephenson S.L. (1988) Distribution and ecology of myxomycetes in temperate forests, I. Patterns of occurrence in the upland forests of southwestern Virginia. *Canadian Journal* of Botany 66: 2187–2207.
- Stephenson S.L. (1989) Distribution of myxomycetes in temperate forests, II. Patterns of occurrence of bark surface of living trees, leaf litter, and dung. *Mycologia* 81: 608–621.
- Stephenson S.L., Novozhilov Y.K., Schnittler M. (2000) Distribution and ecology of myxomycetes in high latitude regions of the Northern Hemisphere. *Journal of Biogeography* 27: 741–754.
- Stephenson S.L., Kalyanasundaram I., Lakhanpal T.N. (1993) A comparative biogeographical study of myxomycetes in the mid-Appalachians of eastern North America and two regions of India. *Journal of Biogeography* 20: 645–657.

- Stephenson S.L., Stempen H. (1994) Myxomycetes: A handbook of slime molds. Timber Press, Portland, Oregon.
- Takafumi H., Hiura T. (2008) Effects of disturbance history and environmental factors on the diversity and productivity of understory vegetation in a cool-temperate forest in Japan. *Forest Ecology and Management* 257: 843–857.
- Tran H., Stephenson S., Hyde K., Mongkolporn, O. (2008) Distribution and occurrence of myxomycetes on agricultural ground litter and forest floor litter in Thailand. *Mycologia* 100(2): 181–190.
- Tsai C., Liao J., Wang H., Hseu Z. (2007) Effects of typhoon disturbances on soil microbial activities in an uplifted coral reef tropical forest, Southern Taiwan. *Taiwan Journal of Forest Science* 22(3): 265–279.
- Unterseher M., Schnittler M., Dormann C., Sickert A. (2008) Application of species richness estimators for the assessment of fungal diversity. *FEMS Microbiology Letters* 282: 205–213.
- Wang H.C., Wang S.F., Lin K.C., Lee P.J.S., Lin, T.C. (2013) Litterfall and element fluxes in a natural hardwood forest and a Chinese-fir plantation experiencing frequent typhoon disturbance in central Taiwan. *Biotropica* 45: 541– 548.
- Yao A., Chiang J., McEwan R., Lin T. (2015) The effect of typhoon-related defoliation on the ecology of gap dynamics in a subtropical rain forest of Taiwan. *Journal of Vegetation Science* 26: 145–154.

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