Does Huxley's Line Apply to Myxomycetes?

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Does Huxley's Line Apply to Myxomycetes?[1]

Sittie Aisha B. Macabago,[2,4] *and Steven L. Stephenson*[3]

Abstract: This paper considers whether Huxley's modification of the Wallace line represents a regional boundary affecting distribution in myxomycetes, using patterns of species composition from the territories of Borneo, Palawan, and the remainder of the Philippine archipelago. With a total of 30 species of myxomycetes belonging to 16 genera (taxonomic diversity index, TDI = 1.88), Borneo recorded the highest taxonomic diversity compared to Palawan with 56 species (TDI = 2.67) and the oceanic Philippines with 159 species (TDI = 4.18). Based on species composition, Borneo is more similar to Palawan (coefficient of community, CC = 0.395) than it is to the oceanic Philippines (0.254). However, Palawan is more similar to oceanic Philippines (0.502) than it is to Borneo. This suggests that Borneo and Palawan have a certain affinity in terms of species composition of myxomycetes, but Palawan still seems to have a higher community similarity to the remainder of the Philippine archipelago when compared to Borneo. Therefore, in terms of species composition alone, myxomycetes do not appear to concur with the biogeographic region delineated by Huxley's line.

Keywords: Wallace's line, Wallacea, Sunda, slime molds, biogeography, paleotropics

Biogeographic studies in the Philippines have been limited to a relatively few taxa. The Philippines, an archipelago of more than 7,100 islands in the Western Pacific has three major island groupings—Luzon, Visayan, and Mindanao—which are all part of the Philippine biodiversity hotspot (Heaney 1998). The position of this region in "Wallacea" (*sensu* Dickerson et al. [1928] and defined below) remains a subject for biogeographical debate (Vallejo 2011). The greater islands of Luzon and Mindanao were formed during the Pleistocene. Islands such as Mindoro, Palawan, Sibuyan, Romblon, Tablas, Camiguin, the Batanes Islands, and the Babuyan Islands have never been connected to Luzon, Mindanao, or other Visayan islands (Vallejo 2011). These islands are oceanic islands, except for Mindoro and Palawan.

The Palawan group of islands represents a fragment of the continental crust which became separated during the formation of the basin of the South China Sea. The tectonic histories of the Philippine islands have been described by Hall (1996, 1998) and Yumul et al. (2008), and the Visayan islands by Dimalanta et al. (2006) and Yumul et al. (2000). The evolution of the archipelago began in the Mesozoic when a fragment of the Asian continent separated, giving rise to Palawan. Continued seafloor spreading and formation of oceanic crust in the Oligocene and the Miocene gave rise to the South China Sea (Vallejo 2011). There is tectonic evidence that Palawan was connected to Borneo

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(Heaney 1998) for a time. Earlier studies and descriptions of the tectonic history of the Philippine islands suggest that this region could be a key to the basic concepts inherent in the biogeography of Wallacea.

Regarded as a relatively underdeveloped faunal transition zone in the Asian and Australian regions (Wallace 1880, Mayr 1976) and characterized by a notable degree of endemism, Wallacea is delimited as the region between Weber's Line to the east and Wallace's line to the west (Figure 1). Huxley modified Wallace's line by including all the oceanic islands of the Philippines east of the line (Mayr 1976, Simpson 1977). Huxley (1868) supported Wallace's designation of Selat Lombok as the regional boundary in the lesser Sundas but extended the line as shown in Figure 1—northward between Kalimantan and the Sulu Archipelago, through the Mindoro Strait between Mindoro and the Calamian Group including Palawan, which is a part of the Philippines but generally agreed by researchers to be Asiatic in fauna, then stretching between the Philippine Batan Islands and Taiwan into the Pacific. Wallace never accepted the northern extension of this line; thus, it is more properly referred to as "Huxley's Line," as was done by Scrivenor et al. (1943). The main point relevant to this paper is that it assigns the Philippines (except for Calamian, Palawan, and adjacent small islands) either to the Australian Region or to a separate region between the Oriental and Australian. According to Simpson (1977), Huxley's line when readjusted to coincide

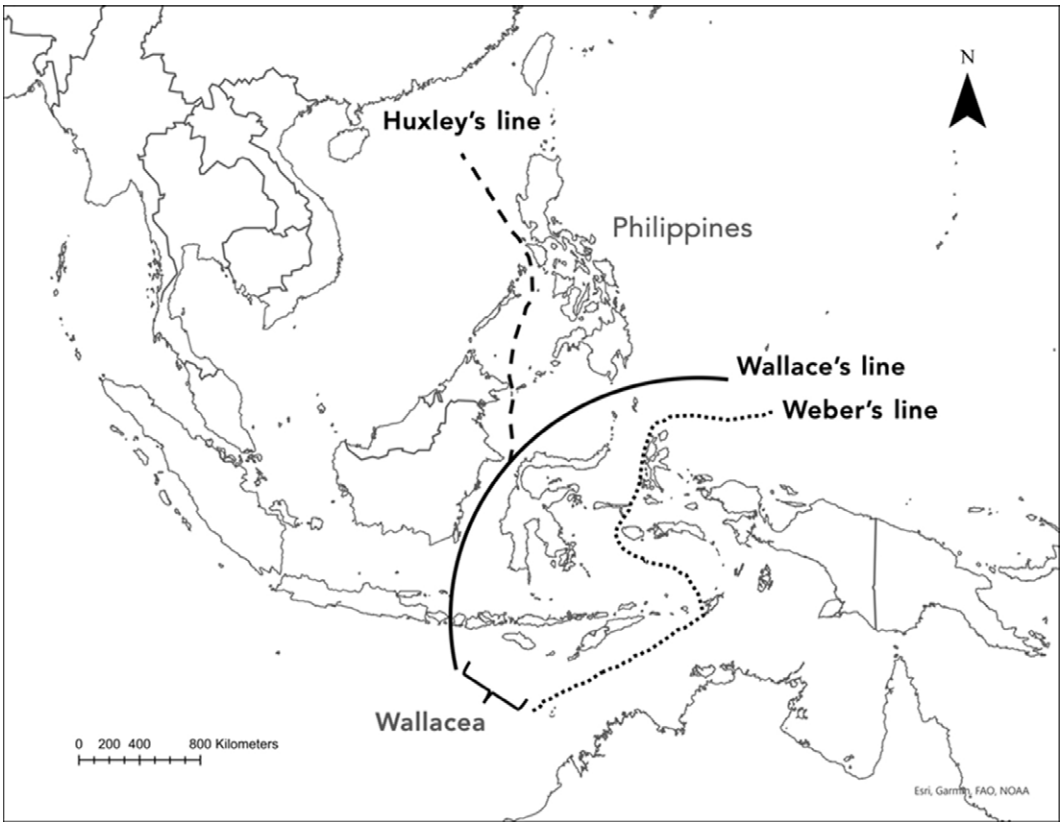

FIGURE 1. Map showing the Philippines relative to some biogeographical boundaries/lines in the Southeast Asian region. Image generated using the software ArcGIS Pro.

with the edge of the Sunda shelf is a clear-cut boundary such that all faunas and islands to the west of that line definitely belong to the Oriental Region.

Earlier biogeographical studies are in agreement that Palawan served as an Asian corridor to the Philippines (Vallejo 2011). The Palawan group of islands is situated on the Sunda Shelf, separated from Borneo by a channel less than 150 m deep and from Mindoro by a channel more than 400 m deep. A number of researchers (e.g., Delacour and Mayr 1946, Heaney 1986) suggested that the Palawan group is faunistically a part of Borneo. There have been several organisms studied to illustrate patterns of species distribution in this region, but never myxomycetes.

Myxomycetes are eukaryotic amoebozoans that give rise to fruiting bodies, which are often visible to the naked eye and capable of producing spores that could be dispersed to potentially long distances. Studies by Kamono et al. (2009) and Ronikier and Lado (2015) have supported the long-distance dispersal of myxomycetes, even suggesting that cross continental dispersal events can take place (Stephenson et al. 2008, Dagamac et al. 2017*a*). Furthermore, studies on isolated islands show the lack of endemism due to dispersal in the Galapagos (Eliasson and Nannenga-Bremekamp 1983), Hawaii (Eliasson 1991), Macquarie Island (Stephenson et al. 2007), and Bohol (Macabago et al. 2017), to name a few. Throughout a few decades of often widely interrupted myxomycete surveys carried out in the Philippines, only a handful have included the islands of Palawan. Similarly, in Borneo there have only been two published studies recording myxomycetes prior to 1998.

The present study attempted to determine if regional boundaries occur in known assemblages of myxomycetes relative to Huxley's modification of the Wallace line by way of assessing distributional patterns, including similarities and disparities in species composition among the assemblages of myxomycetes in three different localities—Palawan, Borneo, and the oceanic Philippines.

MATERIALS AND METHODS

Collection of Data

A combination of published and digitally sourced data was used in this study. These sources were tallied separately for each of the three localities considered (Figure 2): Borneo, the Palawan group of islands (or sometimes referred to as Palawan in the succeeding text), and the oceanic Philippines (i.e., the Philippine archipelago excluding the islands of Palawan).

Borneo

There were three major sources of data for Bornean myxomycetes. These were a published paper by Ing and Spooner (1998), the Global Biodiversity Information Facility (www.gbif.org), and the Malaysian Borneo website (http://www.fungiofmalaysianborneo.com/). The paper by Ing and Spooner (1998) cross-referenced two other studies that added to the list of myxomycetes from Borneo—a study by Peregrine and Kassim bin Ahmad (1982) that noted three species presumably associated with plant diseases and Pegler (1997) noting two myxomycetes, one of which was identified only to the genus level and the other reported previously. These three studies listed a total of 28 species of myxomycetes. The virtual repositories of the Planetary Biodiversity Inventory Eumycetozoan Database (1994) through the Global Biodiversity Information Facility (www.gbif.org) noted the occurrence of *Paradiachea cylindrica*, and the personal website: http://www.fungiofmalaysianborneo.com/ added *Lycogala epidendrum* to the list of 30 Bornean myxomycetes.

Palawan

The papers that were the sources of data for Palawan were Reynolds (1981), with the first 26 species of myxomycetes including collections from previous studies, Pecundo et al. (2017), which added 22 species, and Macabago et al. (2020*a*), with eight more species, for a total of 56 species of myxomycetes.

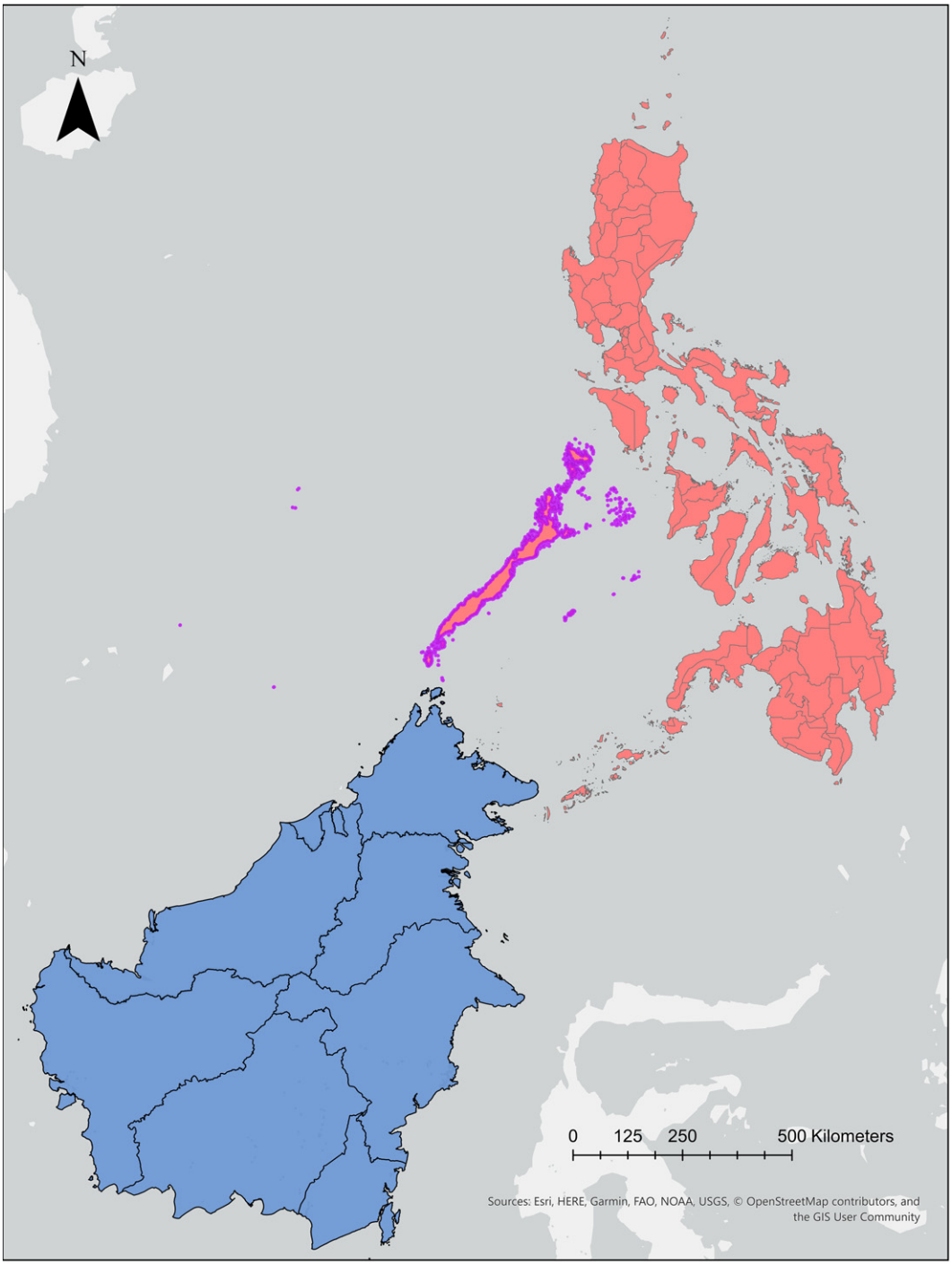

FIGURE 2. Map showing the respective positions of Borneo (blue, lower left) and the Philippines (red, upper right), including the Palawan group of islands (lined in purple, mid-frame). Image generated using the software ArcGIS Pro.

Oceanic Philippines

There were four major papers used as sources. These were Dagamac and dela Cruz (2015), in which the authors summarized 149 species from previous studies, Macabago et al. (2017, 2020*b*), with nine new records of myxomycetes, and Bernardo et al. (2018), with one addition, for a total of 159 species. The combination of collections from Palawan and oceanic Philippines totaled 161 species for the entire Philippines.

Analysis of Data

A list of all known or recorded species of myxomycetes for each locality was compiled by collating the various sources mentioned above. These lists included both natural field collections and moist chamber culture collections. Whether a myxomycete record from every source was associated with a certain substrate (specific plant material or other organic microhabitats) or with other parameters considered in the specific independent research and/or digital repository was not taken into account in this study because of the evident disparities either in sampling technique or overall data gathered in most, if not all, sources. These lists were then used as a basis for comparisons of species composition and taxonomic diversity, and also to analyze the similarities in the assemblages of myxomycetes in the three localities.

The taxonomic diversity index (TDI), also known as the S/G ratio, was computed by obtaining the ratio of the number of species to the number of genera (Stephenson et al. 1993). The value of this ratio is inversely proportional to the taxonomic diversity, where a lower ratio indicates a more diverse biota.

Pairwise comparisons of myxomycete assemblages were performed using Sorensen's coefficient of community (CC) index as described by Stephenson (1989). The CC index is based on the presence or absence of species in the two communities being compared, with values ranging from 0 to 1, where lower CC values imply less similar communities.

RESULTS

A list of myxomycetes exclusively present in each locality and shared by two or all three localities are illustrated in Figure 3. Table 1 shows the total number of species collected thus far from all the territories.

In terms of taxonomic diversity, Borneo recorded a higher TDI value than Palawan or the remainder of the Philippines (Table 1), which indicates that although Borneo has the fewest number of species (30), these are distributed in relatively more diverse genera (16) than in either of the other regions.

A total of 167 species were collectively recorded for all three localities (Borneo, Palawan, and the oceanic Philippines). Seventeen of these species (10.2% of total number listed) were shared among the three localities as shown on the intersection of all three circles in the Venn Diagram (Figure 3). These were *Arcyria cinerea*, *Arcyria denudata*, *Ceratiomyxa fruticulosa*, *Comatricha nigra*, *Cribraria cancellata*, *Cribraria microcarpa*, *Diderma effusum*, *Hemitrichia serpula*, *Lycogala epidendrum*, *Perichaena depressa*, *Physarum cinereum*, *Physarum compressum*, *Physarum pusillum*, *Physarum stellatum*, *Physarum viride*, *Stemonitis splendens*, and *Stemonitopsis typhina*. These are the same species shared between Borneo and Palawan (24.6% of the total 69 species), which means there are no myxomycetes present exclusively in both Borneo and Palawan that are not recorded in oceanic Philippines.

However, between Borneo and oceanic Philippines there are more species shared (24, or 14.5% of 165 total). These were the seventeen that were present in all three localities plus *Didymium megalosporum*, *Didymium melanospermum*, *Fuligo septica*, *Physarella oblonga*, *Physarum flavicommum*, *Physarum globuliferum*, and *Physarum tenerum*. These were the same species shared between Borneo and the Philippines as a whole (14.4% of the 167 total).

In contrast, Palawan shared 54 species (33.5% of 161 total) of myxomycetes with the oceanic Philippines. These were the seventeen shared by all three above and the 37 shared exclusively by Palawan and oceanic Philippines (see Figure 3).

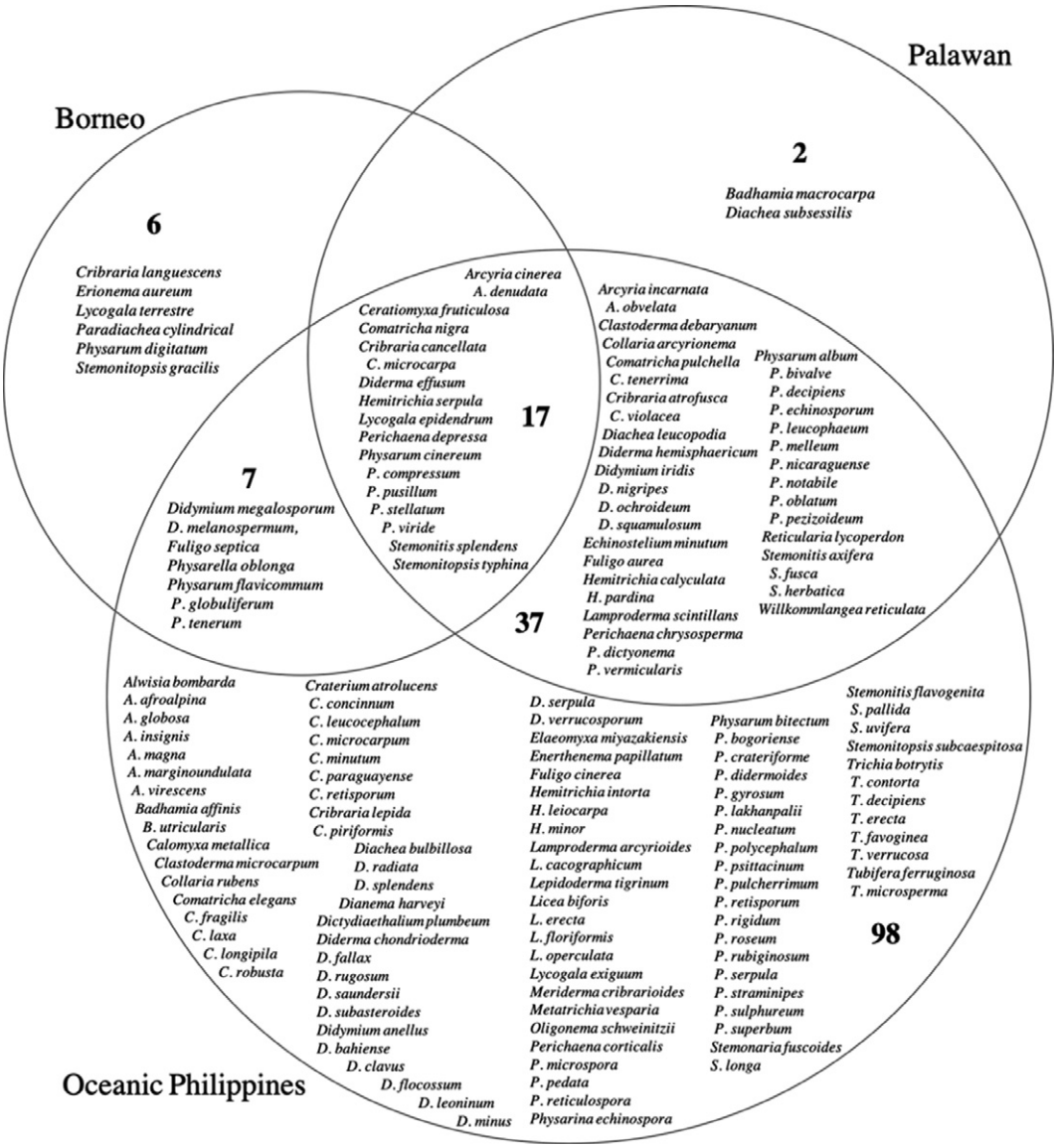

FIGURE 3. Venn diagram showing the occurrences of myxomycetes in each locality. Shared species are shown where the circles intersect.

Six species of myxomycetes (20% of species listed for Borneo) were recorded exclusively from Borneo. These were *Cribraria languescens*, *Erionema aureum*, *Lycogala terrestre*, *Paradiachea cylindrica*, *Physarum digitatum*, and *Stemonitopsis gracilis*. Two species (3.6% of species listed thus far for Palawan) were recorded only for Palawan. These were *Badhamia macrocarpa* and *Diachea subsessilis*. Ninety-eight (61.6%) of the total species listed for the oceanic Philippines were unique to this locality, meaning they were not found

TABLE 1

Taxonomic Diversity Index (TDI) Values for the Localities being Studied, where the Number of Species was Divided Among the Number of Genera (S/G)

	Species	Genera	TDI
Borneo	30	16	1.88
Palawan	56	21	2.67
Oceanic Philippines	159	38	4.18
Philippines	161	38	4.24

A higher value for TDI indicates a lower taxonomic diversity.

TABLE 2

Sorensen's Coefficient of Community (CC) Values Showing Similarities in Community Composition, where the Number Closest to 1 Shows the Highest Similarity

Localities	CC
Borneo – Palawan	0.395
Palawan – Oceanic Philippines (oPH)	0.502
Borneo – Oceanic Philippines (oPH)	0.254
Borneo – Philippines (PH)	0.251

in either Borneo or Palawan, while 137 (85.1%) species were found only in the Philippines but not in Borneo.

In order to more intuitively measure similarities in the assemblages of myxomycetes in each locality, the Sorensen's coefficient of community (CC) was used. Since CC considers the species of myxomycetes common to both communities being compared relative to the total number of species occurring in both, this calculation is appropriate for a presence/absence data such as the one used in this study. The communities displaying CC values closest to 1 indicate higher similarity. Taking into consideration the records for each locality and the species they share with the other localities, CC values revealed that the assemblage of myxomycetes in Borneo is more similar to Palawan (Table 2) than it is to oceanic Philippines or the remainder of the Philippines (including Palawan). However, Palawan is more similar to the oceanic Philippines than it is to Borneo.

DISCUSSION

The Philippines has a largely Sunda biotic component with notable Wallacean, New Guinea, and Australian elements (Vallejo 2011) in its biota. The apparent and at times conflicting interpretations from previous studies that mostly featured macro-organisms (i.e., animals and plants) concur with the seemingly debatable and unsettled place of the Philippines in Wallacea. A study on mosses by Tan (1996) indicated that the Palawan moss flora is mainly an extension of the flora of the Philippines, with some affinity with Java and the lesser Sundas, while showing little influence from Borneo. Likewise, earlier studies by Holloway and Jardine (1986) and Holloway (1987) showed through a phenetic study of Indo-Australian butterflies that Palawan did not exclusively cluster with Borneo (or even the Greater Sundas). Instead, it grouped together with the collective Greater and Lesser Sunda islands like Burma (now Myanmar), Indochina, and Malaya. These coincide with Cracraft's (1988) conclusion that Palawan lacked a "special" relationship with Borneo, but was instead a peripheral part of Sundaland. On the contrary, a study by Schuh and Stonedahl (1986) presented an area cladogram, based on the distributions of various members of the order Hemiptera, wherein some parts of southern Philippines are shown linking with North Borneo before linking with northern Philippines (Vane-Wright 1990). In addition, Tan (1998) stated that some areas of Borneo and Palawan possessing an assemblage of uncommon moss taxa sharing similar ecological preferences and same pattern of distribution have been interpreted as a refugium for species in the Tertiary moist and the Quaternary dry forests (Meijer 1982, Tan 1996).

Based on the results obtained in the present study, the myxomycetes show an extent of similarity between Borneo and Palawan, but not one that exhibits convincing endemism. This could very well be a provisional statement due to the intricate nature of fruiting for myxomycetes (Schnittler et al. 2017), such that when conditions are deemed inapt, they

can, in theory, exist in other forms (i.e., amoeboid) that will inhibit morphological identification of existing species. Borg Dahl et al. (2018) showed that there is greater diversity of myxomycetes in the soil than the fructifications show. They also provided evidence that fruiting success of nivicolous myxomycetes depended on previous temperature and snow regime. In a biogeographic study of protosteloid amoebae, Aguilar and Lado (2012) also displayed that differences in climatic conditions and microhabitat preferences caused variations in species composition and structure of assemblages from one area to another.

Despite the shared geologic history of Palawan and Borneo there is evidence of disjunction in species composition between these two territories. Whether or not the Philippines' Palawan is faunistically and/or floristically Bornean, or its islands more likely served as a refugia of Sundaland species, it is possible that subsequent climate changes after the Pleistocene have led to habitat, vegetation, abiotic and biotic environment differences, and possible vicariant speciation events contributing to the variances in species composition and diversity in this area. A phylogeographic study of a myxomycete population (Dagamac et al. 2017*b*) showed limited gene flow that may lead to allopatric speciation because of geographical barriers and reproductive isolation between ribotypes, and ultimately displaying an evidence of an on-going speciation.

Considering the size of Palawan, it has been proven to be rich in plant and animal species while still being explored more in terms of extant myxomycetes and other microscopic taxa. Based on this study alone Borneo seems to have a stronger affinity to Palawan than the rest of the Philippines; however, it does not seem to show Palawan as the northern limit to a regional boundary, such as the Huxley's modification of Wallace's line. To conclude that the known biogeographic region delineated by Huxley's line does or does not apply to myxomycetes is not yet substantiated at this point. Initial studies, such as this, allows for the conception of more relevant approaches in answering biogeographic questions. Although myxomycetes are microorganisms and are likely capable of long-distance dispersal, which would in theory render oceans ineffective as barriers, the results here suggest that more intricate methods such as environmental niche modeling (e.g., Aguilar et al. 2014, Rojas et al. 2015) and other more indicative protocols, such as phylogeographic endeavors (see Dagamac et al. 2017*b*) discerning if myxomycete species are restricted by ecological/environmental conditions or by geographic barriers, are needed to reach conclusive results. Clearly, this is a subject that warrants additional study. What could prove to be useful in this endeavor is to include metadata of Australian and Papuan biota and other Oriental/Asian territories to demonstrate if indeed islands to the west of Huxley's line, like Palawan and Borneo, cluster with the oriental (Simpson 1977) region and in the process, provide explanation on the factors driving species diversification or lack thereof.

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