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Original Research

Myxomycetes within the scope of the Island Biogeography Theory

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Abstract

Myxomycete data compiled from twelve different investigations on oceanic islands in different parts of the world were analyzed. The objective was to contextualize the potential application of some theoretical insights on the interpretation of the mechanisms responsible for the distribution of myxomycetes. Results presented herein suggest that island age could be a factor of importance in the distribution of myxomycetes, as proposed by current models of island biogeography. In general, tropical/ subtropical islands have a more similar myxobiota than islands in temperate/ subantarctic environments, which can be related to the high dispersal capability of common morphospecies and greater availability of substrate types in the tropical ecosystems. The observed species-to-genus ratios were highly overestimated by comparison with a known probabilistic model, which may support the idea of long-distance dispersal on islands as a primary mechanism of colonization.

Keywords: Amoebozoa, Distribution, Ecology, High-dispersal, Migration

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Introduction

Islands occupy about 3.5 % of the total global land surface but support a disproportionate number of global terrestrial species, currently thought to be between 15–20 % (Matthews & Triantis, 2021). Islands have been consistently called "natural laboratories" for the study of ecological and evolutionary processes. For a long time, islands have attracted the attention of scientists, and some believe that the most influential theoretical work within the field of biogeography was the theory of island biogeography (TIB) developed by Robert H. MacArthur and Edward O. Wilson in the 1960s (Whittaker et al., 2008).

Despite some limitations that have been addressed in recent decades (Whittaker et al., 2008), the foundational ideas of the TIB still stand (Matthews & Triantis, 2021), and it is widely believed that the dynamics among speciation, migration, extinction, and island attributes are the fundamental sculptors of insular populations. The accumulation of biological data since the 1960s has allowed an increased number of biological groups to be investigated under the scope of the TIB. Recently, alternative mathematical modelling has been developed (Fattorini, 2009), and data suggest that factors such as body size could affect the dynamics of biological groups on islands.

The idea of an island has been used not only in the case of real landmasses surrounded by water and isolated from other land surfaces but also regarding fragmented landscapes where there are "islands" of one type of ecosystem surrounded by a matrix of a different type (Matthews, 2021). However, it is now recognized that the lands surrounding habitat fragments are much more permeable than the water surrounding true islands (Matthews & Triantis, 2021) and that the TIB may not be as powerful to explain population dynamics in these instances. The myriads of properties associated with matrix types surrounding these islands is a current line of research.

Myxomycetes have been studied on islands previously (e.g., Stephenson et al., 2007), but there have not been attempts to address the patterns of myxomycete occurrence on islands under the scope of the TIB concepts (Schnittler et al., 2022). This is not surprising since myxomycetes are amoeboid organisms mostly studied under taxonomic approaches and whose ecology has been studied systematically only in the last 40 years or so. In the frame of the TIB, there are still no robust data to quantify speciation or extinction rates in myxomycetes, but it seems that the first process could be determined in the future (see Janik et al., 2022). Extinction is a harder process to determine with such an elusive group of organisms because the historical determination of occurrence is based on reproductive structures, which provide only partial data. The idea of migration has been more documented, and it is believed to primarily take place via long-distance spore dispersal (Schnittler et al., 2022), whose effectiveness is limited by historical factors of the colonized areas (Estrada-Torres et al., 2012). However, very broadly, myxomycetes have colonized every ecosystem on the planet studied thus far (Rollins & Stephenson, 2011), and their fossils are almost exact morphological copies of the forms observed today (Rikkinen et al., 2019), suggesting that the versatility to colonize the planet has been present in the group for millions of years.

The present study had the objective of developing an initial analysis of myxomycete biodiversity, within the frame of the TIB, in selected true islands around the world. The data used herein are the product of years of research and were not necessarily generated with the purpose of establishing comparisons but are useful to strengthen our understanding of the global ecology and biogeography of myxomycetes. Since these organisms have a particular life cycle, they can be relevant for global analysis of biodiversity in the context of modern phenomena such as climate change. However, newly designed studies and analyses of collected data are both important to continue addressing specific topics and developing information on the group. The present analysis was conceived with those ideas in mind.

2. Materials and methods

From the numerous studies carried out over the years to document the biodiversity of myxomycetes in understudied areas, a total of 12 datasets, all from true oceanic islands, were selected in different parts of the world. All these studies contained robust information, both from the methodological design and the identification component, and are comparable for the purposes of this investigation. Most of those datasets were generated using a combination of field collection and moist chamber protocols (MM), but a few were generated with only field collection methods (FC).

The datasets were obtained from studies carried out in the Hawaiian Islands (Eliasson, 2004), the Galapagos (Eliasson & Nannenga-Bremekamp, 1983), Cocos Island (Rojas & Stephenson, 2008), the Aldabra Atoll (Ing & Hnatiuk, 1981), Malta (Mifsud, 2020), Stewart Island (Stephenson et al., 2012), Macquarie Island (Stephenson et al., 2007; Stephenson, 2020), Ascension Island (Stephenson, 2009), La Réunion (Adamonyte et al., 2011), Christmas Island (Stephenson & Stephenson, 2019; Stephenson, 2020), the Seychelles (Kryvomaz et al., 2020a; 2020b) and Norfolk Island (Stephenson & Stephenson, 2020).

A species list was created for each one of these islands and curated using the current nomenclatural treatment of Lado (2005–2025). Those lists were used to evaluate the usefulness of two models of island biogeography for understanding the dynamics of myxomycete assemblages on islands. First, the proposal of Whittaker et al. (2008), commonly known as the logATT^2 model, was used. These authors recognized that one missing element from the original TIB model was the age of the island, which is important to understand the dynamics of the underlying mechanisms of migration, speciation, and extinction at an evolutionary scale. In this model, in addition to the size of the island, its age is considered a second attribute of importance to explain island biogeography patterns. This model takes the form:

$$S = a + bt + ct^2 + d\log A \qquad (1)$$

Where S = species richness, t = island age, A = island size and a, b, c, and d are constants that are particular to each case.

A second proposal, known as the powerATT^2 model, suggested by Fattorini (2009) as an alternative to the logATT^2 model, was also used. This model has been argued to be more useful in those cases where the relationship between the dynamics of biological groups and islands is different than expected by the TIB (due to the size of the organisms, for instance). This model takes the form:

$$S = aA^d + bt + ct^2 \qquad (2)$$

Where all the variables are the same as in (1), but the exponential form associated with the island size functions as a scaling factor modulating the species-area relationship.

In both cases, island size and age are more relevant than distance from the mainland, an original attribute of the TIB, because they were observed to be more significant after the original release of the theory. In this work, the distance between the studied islands and respective continental masses was obtained, but only for informative and contextual purposes.

To the best of our knowledge, neither the logATT^2 nor the powerATT^2 model has been used to study myxomycetes in the context of the TIB. As such, both models were used to calculate the parameter S, or the species richness, of each island. For this, a system of equations methodology was used to calculate the values of constants, and both the island size and age were obtained from the literature. After that step, the value of S was recalculated and then a coefficient of determination (R^2) between the sets of predicted and observed values was calculated for both models in a similar manner to both Whittaker et al. (2008) and Fattorini (2009).

To contextualize the approach of using those models for the calculation of species richness of myxomycetes from oceanic islands, a secondary comparison was carried out. Since vascular plants are one of the best-studied groups of organisms on islands, it is well known that adjusted R^2 values for this group of organisms are in the 0.83−0.94 range for the logATT^2 model (Whittaker et al., 2008). To take advantage of this information, a parallel calculation of species richness was carried out using the known number of vascular plants on each of the studied islands. In this case, to test the hypothesis that the results of vascular plants presented herein were not different from those published in the literature, a series of five coefficients of determination were calculated using a randomly selected five-island subset from the overall 12 study cases. Then, the resulting coefficients were compared with published values using a Mann-Whitney test, for which an alpha value of 0.05 was used to reject the null hypothesis.

In addition, the presence-absence data from all islands was used to construct a binary matrix for the calculation of the Simpson Similarity Index (SSI). In the same manner as other similar indices, this metric oscillates between 0 and 1, with the highest value being a complete overlap in assemblage composition. The SSI is adequate for comparisons where large differences are expected among assemblages since the value of the denominator is small. Because of the formulation, resulting values of similarity are higher than those from other common indices such as Jaccard or Sørensen, making it more useful to interpret in the case of dissimilar assemblages. With the SSI, a cluster of all the islands was constructed to visualize the relationship among them in terms of the similarities of their respective myxomycete assemblages. A secondary calculation of similarity was carried out using the coefficient of community as used by Stephenson et al. (1993) to contextualize the comparisons described herein.

Finally, as explained by Simberloff (1970), the linear relationship between the number of records and the mean value for mean species per genus (hereby referred to as *E*) can be useful to understand the dynamics of island biotas. It is known that the number of genera – *b* – increases as a function of the number of species – *a* – but in some cases the observed *a/b* ratio is higher than expected in terms of *E*. Such deviations may be explained by chance alone or may have mechanistic explanations that are related to the biology of the groups under study, as noted by Simberloff (1970) and Jarvinen (1982). For this reason, and with a mere exploratory intention, the parameter *E* was calculated using the formula:

$$E = \frac{(N-1)(\left(\frac{a}{b}\right)-1)}{a-1} + 1 \qquad (3)$$

Where *N* = number of records, a = number of species, and b = number of genera

After the calculation of *E*, made for each of the islands studied herein, the resulting values were compared with the observed values, from the species lists, and all deltas (i.e., the numerical difference) were obtained with the formula:

$$\Delta = Observed\ a/b - E \qquad (4)$$

All delta values were analyzed and discussed in the context of the theoretical ideas of Simberloff (1970) and Tjørve et al. (2018) and myxomycete studies using *a/b* ratios after the work of Stephenson et al. (1993).

3. Results

A total of 247 morphospecies were found to be present on the 12 islands considered herein (Supplementary Table 1). From that total, the highest species richness value was observed for the Seychelles, with 133 morphospecies, whereas the island with the lowest value was Macquarie Island, with only 27 identified morphospecies (Table 1). Island distance from the mainland and island age were not correlated with species richness, but island size was shown to be moderately correlated (r = 0.65) with the latter.

Table 1. Contextual information about the studied islands and number of recorded myxomycete and vascular plant species in each case (my, millions of years; FC, field collections only; MM, mixed methodology including field collections and moist chamber evaluations)

Insular territory	Island size (km^2)	Island age (my)	Distance from mainland (km)	Morphospecies of myxomycetes	Species of vascular plants
Hawaiian Islands (FC)	28311	5	3540	101	2264
Galápagos (FC)	8010	3	965	56	1425
Cocos Island (MM)	23.52	2.1	885	49	296
Malta (FC)	246	35	284	91	1100
Aldabra Atoll (FC)	155.4	2	726	55	178
Stewart Island (MM)	1748	85	30	50	800
The Seychelles (MM)	455	47	2864	133	900
Macquarie Island (MM)	128	25	2414	27	45
Ascension Island (MM)	88	6	1600	35	228
La Réunion Island (MM)	2512	2	730	89	1730
Christmas Island (MM)	135	60	420	65	411
Norfolk Island (MM)	34.6	3	1000	53	1000

Both the logATT^2 and powerATT^2 models showed good performance when predicting the species richness of myxomycetes on islands (Fig. 1, Table 2), but the coefficient of determination was higher for the powerATT^2 ($R^2 = 0.97$) than for the logATT^2 model ($R^2 = 0.62$). Neither model discriminated the predicted value based on the collecting methodology ($z = 0.25$, $P = 0.79$ and $z = 0.08$, $P = 0.93$ for the logATT^2 and power ATT^2 models, respectively). The plant data showed higher coefficients of determination in both cases, with values of 0.88 and 0.98 for the logATT^2 and powerATT^2 models, respectively. In this second case, the median value of the R^2 index was 0.94 for the five runs made with subsets of data from the islands studied herein and 0.91 for the data reported in the literature. The comparison of values did not show any significant differences ($z = 1.05$, $P = 0.29$).

The cluster analysis based on the SSI showed that the highest similarity was observed in the case of the myxomycete assemblages from the Seychelles and the Aldabra Atoll (Fig. 2). At a second level, myxomycetes from these islands also resemble those from Ascension and the Hawaiian Islands. Interestingly, the complete cluster of all those islands, along with La Reunion, Galapagos and Christmas Island, showed a similarity higher than 0.6 on the respective scale. Contrastingly, the myxomycetes from Malta and both Macquarie and Stewart islands were the most dissimilar in the complete analysis. The coefficient of community values reflected the same pattern (Table 3), with the Seychelles showing the highest values of similarity (average = 0.45) for pairwise comparisons with any other islands, and Macquarie Island showing the lowest values of similarity (average = 0.17).

Table 2. Observed and predicted species richness (SR) of myxomycetes in the twelve islands considered herein

Insular territory	**Observed SR**	**Predicted SR**	
		logATT^2	**powerATT^2**
Hawaiian Islands	101	107	106
Galápagos	56	47	64
Cocos Island	41	28	55
Malta	91	62	101
Aldabra Atoll	55	24	58
Stewart Island	50	95	52
The Seychelles	133	161	142
Macquarie Island	27	38	36
Ascension Island	35	65	36
La Réunion Island	89	83	106
Christmas Island	65	67	70
Norfolk Island	53	24	55

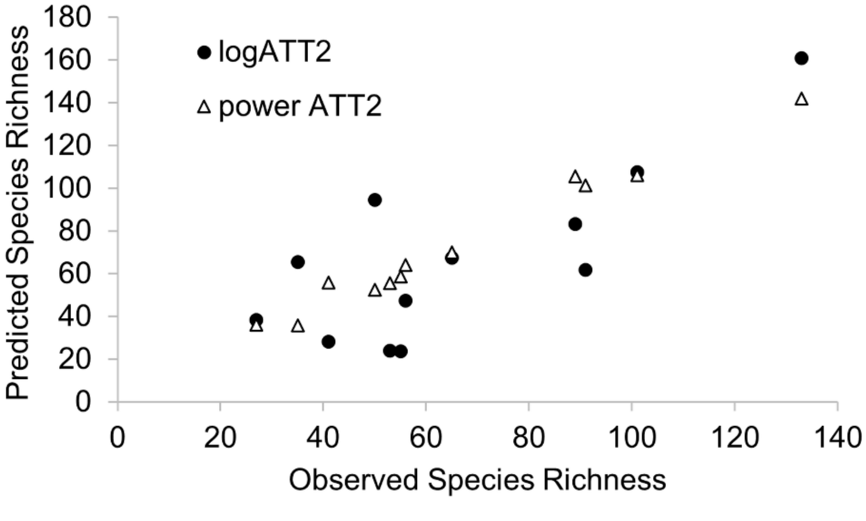

Fig. 1 - Relationship between the species richness of myxomycetes compiled from the literature and the predicted value for each of the two models used herein

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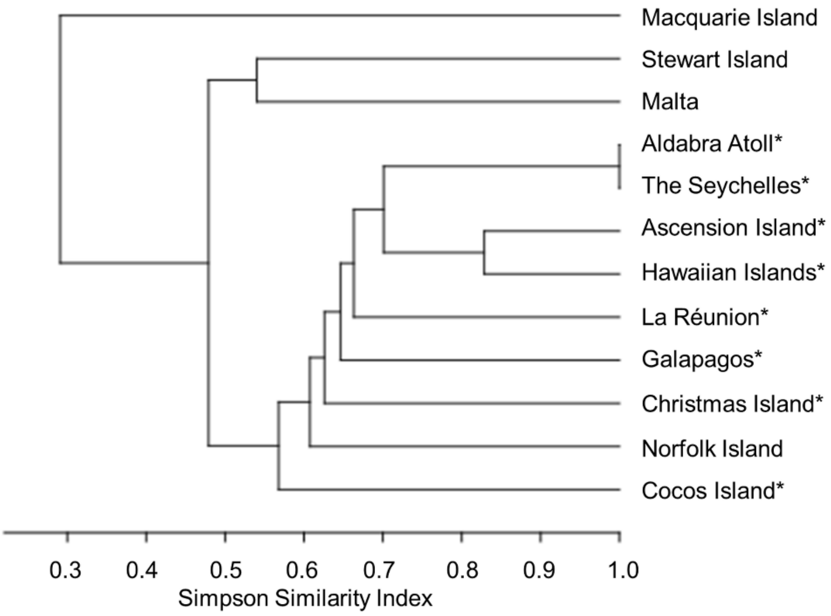

Fig. 2 - Cluster diagram of the similarities among the assemblages of myxomycetes based on the Simpson Similarity Index. The names with an asterisk highlight island with a tropical-subtropical climate

Table 3. Coefficient of community values for the pairwise comparisons of columns and rows associated with the myxomycete assemblages and islands considered herein (HI, Hawaiian Islands; GA, Galapagos; CI. Cocos Island; MA, Malta; AA, Aldabra Atoll; SI, Stewart Island; TS, The Seychelles; MI, Macquarie Island; AI, Ascension Island; LR, La Réunion; CH, Christmas Island; NI, Norfolk Island)

	HI	GA	CI	MA	AA	SI	TS	MI	AI	LR	CH	NI
HI	1.00											
GA	0.54	1.00										
CI	0.34	0.35	1.00									
MA	0.44	0.41	0.35	1.00								
AA	0.47	0.52	0.35	0.40	1.00							
SI	0.44	0.34	0.22	0.38	0.38	1.00						
TS	0.61	0.49	0.39	0.44	0.59	0.36	1.00					
MI	0.11	0.17	0.18	0.15	0.12	0.23	0.13	1.00				
AI	0.43	0.42	0.50	0.30	0.42	0.28	0.37	0.19	1.00			
LR	0.57	0.46	0.42	0.43	0.47	0.43	0.59	0.17	0.39	1.00		
CH	0.49	0.50	0.45	0.40	0.48	0.40	0.55	0.20	0.42	0.53	1.00	
NI	0.43	0.48	0.45	0.35	0.41	0.33	0.48	0.20	0.50	0.49	0.53	1.00

The average species-to-genus ratio for all islands was 2.58 (Table 4), with the highest value of 4.03 observed in the dataset from the Seychelles and the lowest value of 1.75 in the dataset from Ascension Island. In comparison, the average value of the parameter *E* was 1.54, with a range between 0.72–3.00, for the same islands. The observed ratio was higher than the expected parameter *E* in all cases, and the average value of D was 1.03, representing an average overestimation of 42.6 %. The range in this case was observed to be between 25.6–58.9 %.

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Table 4. Observed and expected ratios of species to genera (*a/b*), both from compiled datasets and using the parameter *E* along with the values corresponding to D and its percentual overestimation

Insular territory	***a/b* ratios**		**Overestimation**	
	Observed	**From *E***	**D value**	**% D value**
Hawaiian Islands	2.81	1.78	1.03	36.55
Galápagos	2.07	1.05	1.02	49.38
Cocos Island	2.05	0.99	1.06	51.71
Malta	3.14	2.11	1.03	32.76
Aldabra Atoll	3.24	2.19	1.05	32.31
Stewart Island	1.92	0.90	1.02	53.20
The Seychelles	4.03	3.00	1.03	25.56
Macquarie Island	1.93	0.89	1.04	53.85
Ascension Island	1.75	0.72	1.03	58.86
La Réunion	2.87	1.84	1.03	35.91
Christmas Island	2.71	1.68	1.03	37.97
Norfolk Island	2.41	1.38	1.03	42.72
Minimum value	1.75	0.72	1.02	25.56
Maximum value	4.03	3.00	1.06	58.86
Average value	2.58	1.54	1.03	42.56

4. Discussion

The results presented herein clearly suggest that island biogeography in myxomycetes warrants additional study. The distribution models used previously for macroscopic organisms demonstrated potential for analyzing spatial patterns of myxomycete distribution. In this study, the results observed for plants were essentially the same as already documented in the literature (Whittaker et al., 2008), suggesting the analysis was equivalent to previous investigations. In this manner, the values of the coefficient of determination in the myxomycete analysis seemed valid as well. In this context, interesting factors, such as the age of the island, appeared as a prominent variable that would be pertinent to explore more carefully in future investigations.

As noted, the associations between observed and predicted species richness values presented in Fig. 1 resulted in coefficients of determination that were very similar to published values. The higher fit of the powerATT^2 model was not surprising because it has been previously reported that models with exponential components perform better than others (Carey, 2020). Even though the use of the logarithmic term seems more appropriate for broader use (i.e., different groups of organisms), the exponential adjustment in the model seems to be more fitting in specific cases, particularly when body size can be an important factor controlling species richness per unit area (Fattorini, 2009). In myxomycetes, body size is obviously an important factor to consider, particularly for the migratory aspects, and the relationship between their size (either myxamoebae, sporocarps or plasmodia) and the area occupied by species is not very well understood (Rollins & Stephenson, 2012).

In this manner, it seems plausible that the low endemism observed in myxomycetes (Schnittler et al., 2022), which may be related to their high dispersal abilities and a mostly non-heterothallic lifestyle, is also influenced by the dynamics of population establishment (Borregaard et al., 2015). However, for a better understanding of these dynamics, a clear taxonomy of the group is necessary. Recent evaluations using molecular data, for instance, have demonstrated alternative patterns of endemicity (Janik et al., 2022) that cannot be established on morphospecies only. Accordingly, this could be the reason why already common morphospecies such as *Arcyria cinerea*, *Didymium squamulosum*, *Physarum compressum*, and *Stemonitis fusca* were present on almost all islands. If one adheres to the concept that “the most successful strategy is success” (Williams, 1964), one would anticipate that common taxa will likely be common on most islands. In other words, the presence of common morphospecies on islands can be simply explained by probabilistic theory rather than by ecological strategies, as pointed out for other organisms by Simberloff (1970).

The pairwise comparisons using SSI and the coefficient of community showed both expected and unexpected results. The high similarity between the Seychelles and the Aldabra Atoll makes sense, especially considering that the atoll is politically part of the former country (Claudino-Sales, 2018). In the present study, the two names were used for different islands based on climate (Farrow, 1971), but in terms of myxomycete assemblages, they were clearly part of one system. Also, the general dissimilarity of Malta and both Macquarie and Stewart Island also makes sense, considering that they are not tropical/ subtropical systems, as most of the other islands. However, based on the analysis, Norfolk and Cocos Island are more enigmatic since, in these cases, results showed more dissimilarities than similarities with other islands. One would have expected Norfolk Island to be closer to the other non-tropical islands and Cocos Island closer to Galapagos or even Hawaii. However, Cocos Island has been observed to have a more “continental” biota than other similar islands, and this has been argued to be the product of more frequent migratory events and lower levels of speciation (Igea et al., 2015). Also, the observed similarity between Ascension and the Hawaiian Islands is interesting but might be more related to the introduction of numerous non-endemic plants (e.g., Moulton & Pimm, 1986) that generate more similar myxomycete results. This is especially true for Ascension Island, where most of the present flora was derived from other parts of the world (Duffey, 1964). Similarly, conifers make up a major component of the vegetation on Norfolk Island, which is not the case for any of the other islands considered in the present study, and Macquarie Island would have been expected to be the most dissimilar because of the extreme high-latitude environment. Based on all these precedents, the complete picture of comparisons between islands seems highly dependent on specificities of each insular system, supporting the idea that contextual elements of islands are relevant for the application of TIB ideas to explain species distribution.

The species-to-genus ratios coincide with published literature in the sense that observed values are higher than those expected by calculating the parameter E (Simberloff, 1970). However, most documented overestimations have been computed between 10–20 % and in the present study they were up to 60 %. For islands, these differences have been explained mainly in terms of higher-than-expected dispersal capabilities and lower ecological requirements than observed in larger organisms (Jarvinen, 1982). If we use the same arguments for island dynamics, the high overestimations suggest extremely high dispersal ability in myxomycetes, at least in terms of the species collected as sporocarps. There are more species and fewer genera than expected by a probabilistic model, although this pattern is already known on islands (Tjørve, 2018; Gotelli & Coldwell, 2001). From a mechanistic point of view, the observation in myxomycetes sustains the results obtained in the model analysis and seems to support what is known of myxomycete dispersal (Schnittler et al., 2022). Long-distance dispersal across the group is promoted by the rather uniform size of myxomycete spores, usually between 7 and 12 mm (Tesmer & Schnittler, 2007) and simulations have shown that a windy storm can take a spore up to 500 km away from the geographical source (Schnittler et al., 2006).

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5. Outlook

In general, as expected, myxomycete data from islands are highly stimulating for interpreting the mechanisms responsible for their distribution. Islands are fantastic systems to examine the limits of species or taxonomic groups and deserve further study in the case of myxomycetes. Future projects targeting specific biogeographical questions with molecular data would be interesting for understanding specific mechanisms, but the general ideas of the TIB, which remain intact from a conceptual point of view, also deserve some time and effort. As mentioned earlier, speciation, migration and extinction processes are key elements of biogeography and each one of them could be examined in more detail in future myxomycete investigations. What seems clear as well, is that the attributes of islands are very important too, and among the many characteristics, their age seems also relevant to modulate what can be observed using sporocarp data of myxomycetes.

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