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SUMMARY

Oceanic islands are available to bryophytes almost exclusively by long range air dispersal. The colonization of these islands is a long lasting and ongoing process, depending a great deal on the available amount of airborne propagules and on the size and distance of the donor and recipient areas. The flux density as expressed by the immigration index of MacArthur and Wilson and several other factors that influence successful colonization, such as competitive ability, the genetic properties and the saturation level of island biomes, are discussed in this context. Adaptive radiation has special significance in oceanic island evolution. Phylogeography, using DNA sequencing, parsimony and maximum likelihood analysis to obtain more exact data on the origin, evolutionary and migratory history of living organisms has introduced a new era in the study of island colonization. The author's own observations on the great significance of migration sequence for the colonization process are described and an equation to describe the relationship is proposed. The presence or lack of different taxonomic groups on different islands of the same archipelago can be explained most probably by migration sequence. The "antenna phenomenon", which is the importance of emergent, partly open habitats in capturing airborne propagules during the colonization process and the dissemination of taxa, is a new concept in island biogeography.

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Bryophyte colonization and speciation on oceanic islands: an overview

Tamás Pócs

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Oceanic islands are available to bryophytes almost exclusively by long range air dispersal. The colonization of these islands is a long lasting and ongoing process, depending a great deal on the available amount of airborne propagules and on the size and distance of the donor and recipient areas. The flux density as expressed by the immigration index of MacArthur and Wilson and several other factors that influence successful colonization, such as competitive ability, the genetic properties and the saturation level of island biomes, are discussed in this context. Adaptive radiation has special significance in oceanic island evolution. Phylogeography, using DNA sequencing, parsimony and maximum likelihood analysis to obtain more exact data on the origin, evolutionary and migratory history of living organisms has introduced a new era in the study of island colonization. The author's own observations on the great significance of migration sequence for the colonization process are described and an equation to describe the relationship is proposed. The presence or lack of different taxonomic groups on different islands of the same archipelago can be explained most probably by migration sequence. The "antenna phenomenon", which is the importance of emergent, partly open habitats in capturing airborne propagules during the colonization process and the dissemination of taxa, is a new concept in island biogeography.

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Two basic types of islands can be recognized in phytogeography. The first type are *continental islands*, which were once connected to a continent (such as Great Britain, Trinidad, or Zanzibar) and, with some restrictions (see Cook et al. 2002), isolated terrestrial habitats, such as inselbergs, patchlike alpine biomes or dry valleys surrounded by mountain ranges, or even forest areas surrounded by dry land. The second are *oceanic islands*, which were never connected to any land mass and thus are available for colonization by living organisms only by long range dispersal. These are primarily volcanic islands that develop over hot spots, such as the Galápagos, Hawaii or the Comoros and the Mascarenes or the higher, uplifted coral islands (like Aldabra) or low coral atolls and keys, like the Maldives or Chagos Islands. Some granitic islands may also be included here, such as the Seychelles, which are remnants of a larger subcontinent that has mostly been submerged.

My overview is based firstly on the literature, where I have selected examples from a range of disciplines, including phanerogamic botany and even zoology, as very few up to date investigations have been conducted on bryophytes in this field of study. Secondly, I will provide a short account of some of my own observations about the problems of bryophyte colonization, based on 15 years of work in the islands of the Indian Ocean.

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Review

True oceanic islands are available for bryophytes almost without exception through *long range air dispersal*. The conditions required for this have been discussed by Zanten and Pócs (1981). An estimation of the probability that propagules will reach oceanic islands is commonly made using the classic *immigration index* of MacArthur and Wilson (1967):

$$\mathbf{I} \mathbf{i} = \sum_{\substack{j=1\\j\neq i}}^{n} \mathbf{A}_{j}^{n} \times \mathbf{d} \mathbf{i} \mathbf{j}^{-1}$$

is often used, where I i = the relative flux density of propagules reaching region i from all other regions, Aj= the area of region j, dij = the distance between regions \mathbf{i} and \mathbf{j} , while \mathbf{n} is the number of regions. The index presumes that the proportion of propagules reaching region \mathbf{i} from region \mathbf{j} is directly proportional to the size of region \mathbf{j} and inversely proportional to the distance between them. It also assumes that the number of propagules is proportional to the population sizes of the individual species, and through this to the size of the region producing the propagules.

The *size adjusted version* of this equation is also used, where the index adjusts to the size of recipient island and assumes that the larger the island, the more likely it will intercept airborne propagules.

Accordingly the adjusted I then =
$$\sqrt{I}i \sum_{\substack{i=1\\i\neq j}}^{n} X \sum_{\substack{j=1\\i\neq j}} Iij$$



Fig. 1 (upper): The distribution of *Jaegerina luzonensis* Broth. (lower): The distribution of *Cololejeunea* raduliloba Steph. The square root of the recipient region \mathbf{i} is multiplied by the total propagule flux reaching region \mathbf{i} from all other regions. We used these equations and eight variables (Spence and Pócs 1989) when evaluating the species diversity and similarity of Afro alpine and Afro montane vegetation islands in East Africa.

MacArthur and Wilson (1963) predicted that equilibrium would be reached in the number of species, due to the increase of new immigrants and the extinction of previous residents. Although this has seemed to be the case on many islands that have been investigated, the inadequacy of the formula has become apparent from recent studies. Johnson et al. (2000) established a new model for island biogeography, estimating the rates of migration and extinction using *population genetic data*. This model predicts that populations on large islands and on distant islands should be genetically more divergent from the mainland source than those on islands of smaller size and closer to the mainland. Subsequent research also showed that the genetic diversity of immigrants plays a crucial role (Parrish 2002). Parrish and Maron et al. (2004) have even demonstrated the change of genetic diversity over the course of immigration to a new area. One might believe that the age of the island would be more decisive, but the *diversity of habitats* has turned out to be a more important factor (Spence and Pócs 1989, Pócs 1997).

Further investigation of continental and oceanic island examples has shown that the success of immigration greatly depends on the *competitive ability* of the incoming species and on their *community interactions* (Saxena 1991, Strasberg 1995, Thebaud et al. 2005) and, that competitive ability largely depends



Fig. 2 (upper): The distribution of *Cheilolejeunea ventricosa* (Schiffn.) X.L. (lower): The distribution of *Harpalejeunea filicuspis* (Steph.) Mizut.



Fig. 3: The distribution of *Frullania usambarica* Schiffn., which is rare in continental Africa and occurs on both typical "antenna" peaks of Mayotte Island.

on *ecophysiological factors*, such as the photosynthetic rate (Black et al. 1969, Dulai et al. 1998, 2003, DeWalt 2003), even in bryophytes (Molnár et al. 2003). Although most of these studies were done on invasive species, the results are also suitable for spontaneous immigrants, especially if they arrive from continents or major land masses or even from islands colonized much earlier than the recipient island. There, during their long evolutionary past, invasive species have developed a powerful competitive capacity through their higher vitality, quicker ontogenesis, more successful propagation strategy and better adaptability, which has enabled them to survive in very diverse plant communities with tremendous niche overlaps. Whenever they arrive in an unsaturated island biome they take advantage of their inherited stronger competitive ability and quickly fill the niche gaps or even occupy already settled niches occupied by less competitive island inhabitants. Of course, this is probably not the case if the propagules arrive from another island of a similar age.

During the speciation process in oceanic islands, *adaptive radiation* has turned out to be the basic evolutionary process (Porter, 1984), defined as "the evolution of divergent forms from single ancestral form, each adapted to a different niche or different habitat". Porter has demonstrated this process using the evolution history of many Galápagos endemics, including Darwin's finches or some species of Scalesia, an important endemic genus of Asteraceae trees. The higher number of endemics below species level suggests younger immigrants, and above species level less recently established arrivals. The adaptive radiation process in the case of insular bryophytes has been well demonstrated by Crosby (1969) using the distribution of the Caribbean mosses, as well as in Tixier's survey of some epiphyllous liverworts in the Indian Ocean islands and in Indomalesia (Tixier 1980, 1984, 1987). This process resulted in the evolution of 14 out of the 20 *Pilotrichum* (=*Callicosta*) species in the Caribbean islands, with two radiation centres, one from the Oriente of Cuba + Jamaica and the other from the north eastern Lesser Antilles (Crosby 1969). In the Indian Ocean islands, the main radiation centres were clearly mainland Africa and the similarly ancient, Gondwanean Madagascar, where a remarkable 4 endemic taxa of Diplasiolejeunea evolved. Tixier (1980) documented the step-by-step isolation on the island below the species level, starting with different inselbergs that were not too far from each other. From there they radiated to different mountain ranges within the island, where the evolution at species level took place. Later on the propagules arrived at the much younger, volcanic ocean islands by air dispersal, where further evolution occurred. The same is true for Cololejeunea, where secondary centres had also developed in the Réunion Island, where four endemics are found, and in the Comoro Islands, where there are three. The Réunion and Comoro endemics are clearly less isolated than the Madagascar ones, due to their more recent genesis. But the radiation centres in Indomalesia should not be overlooked. There, several clades gave birth to Indian Ocean island taxa, and, at the tips of these clades, secondary evolution has occurred.

The isolation of an island flora can be expressed simply by its rate of endemism. The top row of Table 1 shows the rate of endemism among the foliicolous bryophyta of different Indian Ocean islands, compared with that of the Usambara Mountains on the African mainland from an isolated location that is surrounded by the sea of dry savannah woodland.

The individuality of island bryofloras can also be compared by their species/genus ratio (Gradstein and Weber 1982, Pócs 1988), which is much lower on islands than on the mainland. The second row of Table 1 shows this, again comparing the same areas, as described above (after Pócs 1997).

Probably the most useful in this aspect is the Index of Insularity by Tyron (1979), which combines the

	Seychelles	Comoros	Madagascar	Réunion	Mauritius	All lands	Usambara Mt.
Rate of endemism	6	10	13	10	10	37.7	4
ratio	3.07	4.38	3.33	4.33	2,80	1.92	2.82
index (Tyron)	0.52	1.14	6.03	2.10	1.11	7.28	2.79

Table 1. The rate of isolation (insularity) among the epiphylls of Indian Ocean Islands, compared with the continental African Usambara Mountains (Based on Pócs 1997)

above two characters, the percent of endemism and the species/genus ratio in one (third row of Table 1). The greater the value of the index, the greater the "insularity"; in the case of mosses and liverworts, indices have been calculated to be 5.00 for the mosses and 3.12 for the liverworts of Cuba, 7.13 for the Galápagos Islands and 2.99 for the Seychelles liverworts, 1.14 for the Comoros and 6.3 for Madagascar epiphylls (Pócs 1988, 1997).

A new era started in island biogeography with DNA sequencing, in parallel with the development of morphological investigations using parsimony and maximum likelihood analyses (Emerson et al. 2001). A new science, *Phylogeography*, had arisen, combining the methods of chloroplast and mitochondrial DNA phylogeny and cladistics with biogeography, to obtain data on the origin and evolutionary and migratory history of living organisms. From our point of view it is interesting that phanerogam botanists, for example Mummenhoff et al. (2001) in *Lepidium*, Brassicaceae, Moore et al. (2002) in *Tolpis*, Asteraceae and a good number of other authors, have suc-

cessfully established immigration histories, including colonization and extinction processes, of the investigated genera. Warren et al. (2003) have conducted the most relevant study in my investigation area, the Indian Ocean islands, although this work was done on sunbirds (Nectaridinae). In this study, the authors collected a total of 1309 base pairs of mitochondrial sequence data from the island sunbird taxa, combined with those of continental sunbirds. Topological and branch length information combined with estimated divergence times served to establish hypotheses for the direction and sequence of the colonization process in relation to the geological history of these islands. They found that during the past 3.9 million years, two independent waves of colonization had taken place. By applying Bremer's cladistic method for ancestral areas (Bremer 1992), they found that the Comoros and the Seychelles Islands were the first centres of colonization from mainland Africa. Madagascar, where the higher species diversification took place, was later colonized by sunbirds from the Comoros. They established that migration from the



Fig. 4. The distribution of *Lejeunea pililoba* Spruce.



Fig. 5. The distribution of all *Plagiochila* (black dots) and of all *Frullania* species (triangles) on Mayotte Island. (Species of both genera are very common in mainland Africa and very rare on Mayotte Island).

mainland to the islands was easier than the occupation of the islands, which involved competing with the species that were already present on the islands. Using a molecular clock combined with the known age of the volcanic islands, they could also ascertain the divergence points in the time of the different clades.

Although in the field of bryology many recent investigations have been done on the molecular phylogeny and taxonomy of liverworts, relatively few of them have been phytogeographically oriented. Groth et al. (2004) traced the origin and very complex immigration history of genus Plagiochila. Heinrichs et al. (2004) and Lindner et al. (2004) dealt with the Afro-American intercontinental distribution of Plagiochila corrugata based on the nrDNA ITS sequences, while Heinrichs et al. (2005) investigated all African taxa in detail. This study provided a number of examples of long range dispersal from America to Africa. On the other hand, in the immigration history of the Vagae clade, which has recently dispersed both throughout the Neotropics and in the Palaeotropics, the East African islands proved to be the centre of evolution. So the recent African *Plagiochila* flora is a mixture of old elements and recent immigrants. Using the criteria of maximum parsimony and an analysis of the nuclear ribosomal DNA and the chloroplast DNA of the two widespread *Campylopus* species of Gondwanean origin, *C. pilifer* Brid. and *C. introflexus* (Hedw.) Brid., Stech and Dohrmann (2004) found two evolutionary lineages in the second species, one for the Old World and one for the New World. Shaw (2000) dealt with the cryptic speciation of *Mieliloferia* from a molecular phytogeographic point of view, while Shaw et al. (2003) discussed the intercontinental Mediterranean disjunction of pottioid mosses from a morphologic and molecular basis.

My observations

Strange immigrants - significance of first arrival

Different islands, even ones that belong to the same archipelago, such as the Comoros or Mascarenes, have remarkable differences in the composition of their flora. These striking differences are represented not only by their set of endemic species but also in their strange immigrants from distant land masses. These bryophyte species in many cases are not rarities, but play an important role in the bryovegetation. Several good examples of migrants that are quite common in their new locations are the Philippine-New Guinean Jaegerina luzonensis Broth. on Grand Comoro Island (known as J. plicata Cardot) (Fig. 1), or the East Asian Cololejeunea raduliloba Steph. (Fig. 1) or the Indomalesian Harpalejeunea filicuspis (Steph.) Mizut. on Mayotte Island (Fig. 2) (both in Comoro Archipelago), the Neotropical Phyllogonium species found on Réunion Island, Lejeunea pililoba Spruce on Mayotte Island (Fig. 4, 6) or the Indomalesian Cheilolejeunea ventricosa (Schiffn.) X.L.He on Mauritius (Fig. 2). I am quite convinced that this phenomenon can be explained only by the underestimated role of the *first incidental colonizers* in a certain habitat. Oceanic islands, as a result of their history, have had or still have many unsaturated niches. Whenever these niches are occupied, the colonizing species reproduces there, inhibiting colonization by any other species. Of course, much depends on the sexuality and competitive ability of occupants. To obtain the frequency rate of an immigrant species (F) in a certain habitat from the size adjusted version of MacArthur and Wilson index, I i (the relative flux density of propagules), should be multiplied by these factors, of which m is the number of already present taxa, s is the sequence serial number during the colonization of a certain habitat while c is a factor of competitive ability of the immigrant, compared to the species already present, among the conditions of the habitat. Thus the formula becomes:

$\mathbf{F} = \mathbf{I} \mathbf{i} (\mathbf{m} + 1 - \mathbf{s})^2 \times \mathbf{c}$

which accounts for the logarithmic nature of reproduction and the increasing difficulty in occupying a certain habitat on an island with respect to the question "which species was first?" and which species followed and in what sequence. Of course, this is a theoretical formula, as **c** is difficult to obtain, but even so it can help to reconstruct the sequence of occupation (**s**) or other unknown components of the above equation.

Lack of taxonomic groups – "antenna phenomenon"

Another interesting fact, previously described by Grolle (1978), is the *lack of important taxonomic* groups on certain oceanic islands. He documented the complete absence of these groups but did not suggest any reason why representatives of Marchantiales, *Lepidozia, Jungermannia* and *Porella* are missing on the Seychelles, even though these groups are common in Africa and in Asia in similar environmental conditions. I could add to these many more examples from other oceanic islands, for example the strong under-representation of *Frullania* (Fig. 5), *Plagiochila* (Fig. 5) and Lepidoziaceae on the Mayotte Islands in the Comoros.

I can explain this only by the fact that oceanic island colonization is a dynamic ongoing process. The missing groups may not yet have reached a relatively young volcanic island or have not been able to successfully fill all suitable niches yet. It is known that the immigration and colonization process lasts for millions of years, until all habitats and their niches are saturated (see for example the data of Moore et al. 2002). I observed the very special significance in this process on emergent, rocky summits with relative open vegetation (elfin forest or open bushes). On the Mayotte Islands these are the only habitats for the above mentioned, under-represented genera, which are known to be very widespread and common in other tropical areas with similar environmental conditions.

These emergent habitats act much like an aerial, and catch airborne propagules (a process I have called the "*antenna phenomenon*"). These habitats also allow for the later dissemination of species, which probably has not yet happened. This is the only possible explanation for why *Plagiochila* species, for exam-



Fig. 6. The distribution of *Lejeunea pililoba* Spruce (black dots) on Mayotte Island. This Neotropical species does not occur in mainland Africa but is very common on Mayotte Island (see also Fig. 4).

ple, do not occur in the widespread wet tropical habitats of Mayotte, which include primary and secondary rain forests or tree crop cultivations such as smallscale coffee trees, breadfruit cultures and naturalized mango stands. (There are other habitats, more open for colonization on the Mayotte Islands, like the huge coastal cliffs of Petite Terre or the dry deciduous forests with baobabs on the southern part of the Grand Terre or on Mbouzi Island, but these places are characterized by microclimatic conditions that are unsuitable for these groups). The absence of Frullania species on the greatest part of Mayotte is even more apparent, as a good number of them are more xerotolerant and belong to the commonest epiphytes of sole, remnant trees in cultivated areas or roadsides everywhere in the tropics. However, contrary to what might be predicted, the open elfin and cloud forests of the "antenna" summits of Choungi and of Bénara peaks have 5 species of Frullania (Fig. 3) and 3 species of *Plagiochila* that occur with great frequency, whereas in the other large and ecologically suitable wet tropical areas, only one occurrence of Plagiochila and one of the weedy Frullania ericoides has been

noted during a thorough, two-month collection foray, which involved visits to all forest reserves.

Expanded altitudinal range - unsaturated niches

There is a striking difference in the altitudinal distribution of many bryophyte species on the African mainland and on the oceanic islands. This can be explained only partly by the more oceanic climate of the islands. The altitudinal distribution of many species in the oceanic islands is conspicuously wider than that of the same species on the mainland. I explain this phenomenon as resulting from the unsaturated niches of the oceanic island habitats, where the flora consists of a smaller number of species than in a similar area of the large land masses, so that much less niche overlap occurs. Therefore the competition among species is reduced as compared to the mainland habitats. This also means that many species can realize more of their fundamental niches, which allows for an extended adaptation to the habitats of different altitudes. This is at the moment only a working theory, which has to be proven by precise observations and by their statistical evaluation.

In summary, we may conclude that the introduction of cladistics and gene sequencing methods in island biogeography and evolution, in parallel with other investigations, has initiated the beginning of a new era and a new branch of science: Phylogeography. It is hoped that this new discipline will someday be able to answer the intriguing questions that remain in explaining the very complex process of island colonization.

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