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# CELEBRATING DARWIN

*Proceedings of the Symposium*
*"Darwin´s Mistake and what we are doing to correct it"*

Ponta Delgada, São Miguel, Açores
September 19-22, 2009

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# CONTEÚDO / CONTENTS

Perched upon the Mid Atlantic Ridge, specks of land amidst the vastness of a deep ocean, physically and politically ultra-peripheral, the Azores could easily be missed, were it not for their natural centrality. At the very hinge of the Eurasian, African and American tectonic plates, the warmth of the Earth's core breathes upon the islands during the plates' calmer cycles and the convulsions of their relentless movements have stirred peoples' imagination with rumours of Atlantis. At the crossroads of winds and sea-currents, they enjoy mild yet moody weather, although its global meteorological framing unwillingly spreads the misconception that the Azores should have as bad a reputation as its anticyclone has in European mainland. At the interface of the temperate and subtropical realms, they treasure the remnants of what the ice has destroyed thousands of years ago on the mainland. Meeting point of bio-travellers in their continuous colonization wanderings, they provide shelter and hospitality to many a visitor; the result is a mixed biota characteristic of a mild environment where, sometimes unfortunately, any newcomer thrives well and successfully.

Technical sailing constraints of Darwin's time led him to stop in the Azores on his way home. After almost five years at sea, the young scientist did not abate his enthusiasm for knowing nor skipped his duty to record everything of interest he could find. However, a surprise lurked far inland when, upon ear say that there was an active crater beyond the mountain, Darwin set foot to find it, only to be disillusioned at the sight of but a dozen of holes in the ground spewing clouds of vapour. Then, with the simplicity of a scientist reporting the fact, he wrote in his memories that (in)famous phrase:

*"I enjoyed my day's ride, though I did not find much worth seeing".*

We took that sentence out of context, we know, when choosing a title for the symposium. However, we were in some way right to do so, for we do have a lot worth seeing. And Darwin himself suspected it when, 45 years later, he wrote to Francisco d'Arruda Furtado:

> *"I consider it a fortunate event for science, that a man like yourself [...] should inhabit a group of oceanic islands. [...] You have a splendid field for observation and I do not doubt but that your researches will be very valuable"*.

What more could be said of a place that has not much worth seeing?

We are here now precisely to rectify that idea and to honour Darwin as the great man he was. We will do that by listening to those who have reached the stratosphere of science yet still walk with us in a down-to-earth friendly way; some have been with us for decades, shaping our students and delighting us with their friendship. But we will do that also by showing that, through our effort, we yearn to be worthy of those words that Darwin wrote to our own d'Arruda Furtado: *"your researches will be very valuable"*.

The magnanimous and gentle Darwin also wrote in his memories of the "*Voyage*", about the Azoreans:

> *"It seems a great pity that so fine a population should be compelled to leave a land of plenty, where every article of food is exceedingly cheap and most abundant: but the labourer finds his labour of proportionally little value."*

Again I beg to disagree, not exactly because of the price of food, but because we are confident that our labour is worth seeing; after all, we learned from the best.

Now, your very presence here makes us feel that the Azores are at the very centre of the world.

I thank you all for joining us. We will strive to make these four days unforgettable so that you will long to return. Let us, then, celebrate Darwin.

António M. de Frias Martins

Opening words at the Symposium

*"Darwin´s Mistake and what we are doing to correct it"*

September 19-22, 2009, Ponta Delgada, São Miguel, Azores

Darwin wrote in his memories of the "*Voyage of the Beagle*", when he stopped by the Azores on his way home and visited Terceira Island, September 20th, 1836:

"*I enjoyed my day's ride, though I did not find much worth seeing*".

Yet, about fifty years later, when corresponding with the Azorean malacologist Francisco d'Arruda Furtado, he wrote: "*I consider it a fortunate event for science, that a man like yourself [...] should inhabit a group of oceanic islands. [...] You have a splendid field for observation and I do not doubt but that your researches will be very valuable*" (Letter from C. Darwin to F. d'Arruda Furtado, July 3, 1881). As Azoreans, scientists, we secretly wish this comment will one day be applicable to us!

We were part of the worldwide commemorations of Darwin and his "*On the Origin of Species*", for Darwin was here and species are presently being originated here. For this reason – and to rectify Darwin's first impression – we prepared this symposium, in the Azores, September 19-22, the very days Darwin had visited these islands 173 years before.

DAY 1 – *The way we were* – Although geologically young, the Azores have one of the few examples of neogene subtidal of oceanic islands and we have been digging it. We possibly hold an important key to the understanding of the effects of glaciations on the North Atlantic biota. Moreover, our hot-springs harbour archaic microbes that encrypt within the very secrets of life. **Paulyn Cartwright**, who searches for consistency for the evolutionary patterns in the fluidity of medusozoans, has kindly granted us the honour of this day's opening address. **Brian Morton**, a long time honorary Azorean, set the general tone to the symposium by addressing the relationship Darwin/Azores.

DAY 2. – *The dynamics of colonization* – Isolated in the middle of the North Atlantic, at the crossroads of currents and winds, at the hinge of the temperate/subtropical realm, the Azores epitomise a biogeographical paradigm: against winds and currents, they are European! **Peter Grant**, who unravelled the interdependence of biotic/abiotic factors associated with the diversity of the Galápagos finches, kindly granted us the honour of this day's opening address. **Paulo Borges** and **Jeremy McNeil** showed how, in the Azores, arthropods could answer Darwin's quest for the dynamics of dispersion and colonization.

DAY 3. – *The dynamics of evolution* – Terrestrial molluscs are the Azorean "finches"; half of them are endemic and speciation can really be caught red-handed here. We are convinced that punctuated equilibrium is seen alive in our snails. **Bruce Lieberman**, who learned from the fathers of punctuated equilibrium and has tracked evolution from deep time, has kindly granted us the honour of this day's opening address. **A. Frias Martins** and **Thierry Backeljau** showed that land snails are prime subjects for the study of evolution in this natural laboratory.

– *Darwin and Society* – Darwin's work profoundly influenced the world, far beyond the realm of science; it touched the very roots of people's lives, their social agreements, their religious believes. Here, reason and heart often have clouded the desire for a much needed mutual understanding. **Eugenie C. Scott**, who has devoted her carrier to promote the understanding and separation of science and faith, has kindly granted us the honour of this session's opening address.

DAY 4. – *The dynamics of conservation* – It is here (and we aren't proud of it!) that lives the most endangered bird of Europe, the Azorean chaffinch *Pyrrhula murina*. It is also here that a prize-winning project to protect it is being developed. **Rosemary Grant**, who, with Peter, was here in the 70's looking at our finches, has kindly granted us the honour of this day's opening address. **Joaquim Teodósio** showed how we have saved our own, endemic finch.

## THE PROGRAMME

Sept. 19 – ***The way we were***

- Cartwright, P. - *The origin and diversification of life's earliest metazoans*
- Morton, B. - *Charles Darwin and the evolution of the Atlantic Ocean and the Açores*

Sept. 20 – ***The dynamics of Colonization***

- Grant, P., & R. Grant - *Colonization of Islands*
- Borges, P. - *Patterns of colonization and dispersal in Azorean arthropods: diversification, rarity and extinction*
- Cardoso, P., M.A. Arnedo, K.A. Triantis & P.A.V. Borges - *Diversity drivers of Macaronesian spiders and the role of species extinctions*
- Rodrigues, T., S.V. Drovetski, R.M. Zink, V. Neves & D. Gonçalves - *Could competitive exclusion among closely related colonists play a role in constraining island biodiversity?*
- Silva, L., & C. Daheler - *Are biogeographic factors affecting indigenous and non-indigenous island floras the same?*
- Moura, C.J., F.M. Porteiro, N.E. Peralta, M.R. Cunha & A.D. Rogers - *Cryptic biodiversity, phylogeographical and evolutionary patterns of shallow and deep-water* Nemertesia *(Cnidaria: Hydrozoa) from the north-eastern Atlantic and western Mediterranean*
- McNeil, J. - *Studying the cost of migration: a comparison of* Pseudaletia unipuncta *populations from Canada and the Azores*
- Leonardo, M., & M.F. Medeiros - *Preliminary data about the breeding cycle and diurnal activity of the Azorean bat (*Nyctalus azoreum*)*
- Parente, M.I., F.O. Costa & G.W. Saunders - *Assessing biodiversity of Azorean brown algae under a molecular lens*
- Gabriel, D., A.I. Neto & S. Fredericq - *Biodiversity of the Nemastomatales (Rhodophyta): new insights and future perspectives*
- Gabriel, R. - *Azorean Rare Bryophytes: Ecological Preferences and Distribution*

Sept. 21 – ***The dynamics of Evolution***

- Lieberman, B. - *Macroevolution and Palaeontology: Expanding Darwinism*
- Martins, A.F.M. - *When the "finches" are snails*

- Aguiar, P. - *Living fossils among us?*
- Marcelino, J.A.P., R. Giordano, F. Soto-Adames, P. Garcia, R. Resendes, L. Silva, E. Weber & A.O. Soares - *Unobserved diversity in Darwin's appraisal of the Azores*
- Silva, L., R. Elias, M. Moura & E. Dias - *Intraspecific variation, the raw material for evolution: the example of the Azorean Juniper*
- Chorão, A., S.V. Drovetski, S.J.M. Davis, R. Godinho & D. Gonçalves - *Some morphological and molecular evidence for speciation in the Azorean quail (*Coturnix c. conturbans*)*
- Backeljau, T. - *Evolution alive and kicking... or how Azorean endemic snails fooled taxonomy*
- Calado, G., & J. Cruz - *Testing Vermeij's Hypothesis - contributions from the NW Atlantic*
- Raposeiro, P., A.C. Costa, S.J. Hughes & V. Gonçalves - *Azorean lotic systems biodiversity and conservation: targets for environmental management*

- ***Darwin and Society***
- Scott, E.C. - *Evolution is fundamental. Why is it so controversial?*
- *Round table* - Chair: Magda Costa Carvalho
  With Eugenie C. Scott, M. Patrão Neves, A.M. de Frias Martins, André Levy and Helena Abreu.

Sept. 22 – ***The dynamics of Conservation***

- Grant, R., & P. Grant. - *Evolution of Darwin's Finches*
- Teodósio, J. - *Priolo, the finch that Darwin missed*
- Calado, H., & A. Gil - *SMARTPARKS - new concepts on nature conservation and management*
- Rodrigues, P., & R. Tristão da Cunha - *Azorean birds - a natural heritage*
- Martins, M., L. Silva, M. Moura, G. Maciel & R. Corvelo - *Azorean vascular plants: threats and conservation challenges*
- Ávila, S.P. - *The economical value of the fossils of Santa Maria Island: 10 years of research*
- Botelho, A.Z., A.C. Costa & H. Calado - *Biodiversity, Conservation and Marine Spatial planning*

**POSTERS:**

- Cunha, A., A.C. Costa & J. Xavier - *Porifera from Flores Island (Azores)*
- Ferreira, A., A. Rodrigues, R. Tristão da Cunha & A.M.F. Martins - *Reproductive cycle of three species of* Drouetia *from the Azores*
- Lourenço, P., T. Backeljau & M.A. Ventura - *Low genetic differentiation among* Chrysoperla carnea *s.l. (Neuroptera: Chrysopidae) populations from Azores*
- Pinheiro, A., A.C. Costa & L. Silva - *Conservation satuts of the coastal flora in São Miguel Island (Azores)*
- Tristão da Cunha, R., P. Rodrigues & A.M.F. Martins - *Azorean terrestrial malacofauna - a biogeographical snap-shot*

Aware of our insignificance but strategically perched upon the shoulders of the tallest in the world of science, we proudly present you the Proceedings of the Symposium and invite you to visit and enjoy the Azores and the science herein developed.


Can individuals discriminate on the basis of beak shape and body size in the absence of vocal cues?
CONCLUSIONS-
FUNDAMENTAL TIE-IN BE
EARTH HISTORY CHANGE
EVOLUTION


STOP

CELEBRATING DARWIN

# *The way we were*

AÇOREANA, 2011, 7: 15-38

# MACROEVOLUTIONARY PATTERNS AND PROCESSES DURING THE CAMBRIAN RADIATION: INTEGRATING EVIDENCE FROM FOSSILS AND MOLECULES

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## ABSTRACT

The Cambrian radiation represents a key episode in the history of life when most of the major animal lineages appeared and diversified in the fossil record. Unravelling the patterns and processes driving the Cambrian radiation has proven challenging. We discuss several lines of evidence that provide additional understanding about the Cambrian radiation including trilobite phylogeny and biogeography, cnidarian fossils and phylogenies, metazoan phylogenies and the molecular clock, genomics and evolutionary development, and palaeoecology. We argue that by integrating these disparate lines of evidence, a more comprehensive view of the Cambrian radiation emerges.

## RESUMO

A radiação Câmbrica representa um episódio-chave na história da vida, quando a maior parte das linhagens animais apareceu e se diversificou no registo fóssil. Descobrir os padrões e os processos que conduziram a radiação Câmbrica tem-se mostrado um desafio. Discutimos aqui várias linhas de evidência que proporcionam entendimento adicional sobre a radiação Câmbrica incluindo filogenia e biogeografia das trilobites, fósseis e filogenias de cnidários, filogenias e relógio molecular dos metazoários, genómica e desenvolvimento evolutivo, e paleoecologia. Argumentamos que, integrando essas linhas de evidência variadas, emerge uma visão mais abrangente da radiação Câmbrica.

## INTRODUCTION

Macroevolution is the study of the patterns and processes relating to the birth, death, and persistence of species. As such, a special aspect of the study of macroevolution has been a focus on investigating key episodes in the history of life that involve differential proliferation or extinction of species. The fossil record is our one true repository of species' births and deaths. One of the most important episodes in the history of life, at least in terms of its placement in time and phylogenetic space, was the Cambrian radiation. Consideration of the evolutionary significance of this key episode dates back at least to Darwin (1859), and it will be the focus of our contribution. Since there is such a long history of study, scientists' conclusions about the episode and its significance have changed through time (see Lieberman, 1999a, 2003a; Knoll, 2003; Valentine, 2004; Brasier, 2009). Originally this radiation was held to be largely synonymous with the origins and diversification of animals. However, more recently, a nuanced view has emerged, and now it is more typically treated as the initial appearance and proliferation of abundant metazoan remains in the fossil record (Knoll, 2003; Lieberman, 2003a; Valentine, 2004; Brasier, 2009). Part of the transition to this more nuanced view has involved increasing phylogenetic precision about the taxa involved. For instance, it is now recognized that several animal phyla proliferated well before the start of the Cambrian including sponges and the Ediacaran biota, which likely contains some stem group cnidarians, or their relatives. However, establishing strong phylogenetic links between elements of the Ediacaran biota and *bilaterian* animal phyla has proven more difficult.

Darwin's (1859) perspective on the Cambrian radiation is worth considering. Notably, Darwin argued that the major groups of taxa that appeared in the fossil record at this time must have evolved well back into the pre-Cambrian. It appears now that Darwin may have been partly inaccurate to the extent that he claimed the roots of Cambrian radiation taxa extended way back into the pre-Cambrian, but he was right to suggest that the Cambrian radiation was not solely an explosive evolutionary event writ large in the fossil record. Instead, the Cambrian radiation had some pre-Cambrian fuse, where the taxa had originated and started evolving (a lit fuse) before the explosive radiation (the bang) appeared on the scene. Because of this, a key question now is how long before the radiation did the component taxa actually evolve. This is fundamental because it determines whether the Cambrian radiation really is a key episode in the history of life, from an evolutionary perspective, and does indeed represent a dramatic evolutionary proliferation or radiation, or instead marks some set of changing ecological or environmental conditions that allowed already extant organisms to become more visible in the fossil record, either through increases in abundance or size or changes in fossilization potential. Here we consider this issue in greater detail, marshalling various lines of evidence from the fossil record and the extant biota. Then we consider the specific set of changes, genetic and environmental, that may have caused the radiation to happen. We conclude with some discussion on how to forge a synthesis between disparate lines of evidence, from trilobite phylogenies to genetic toolkits, and approaches, from palaeontology to evo-devo, to come up with a broader view of macroevolution both in general and during the Cambrian radiation interval in particular.

Information from palaeontology and development in some respects played an important role in the formulation of what is referred to as the Neo-Darwinian synthesis (e.g., Simpson, 1944; de Beer, 1940) as practitioners from these areas were involved in what is treated as a hallmark event in evolutionary biology. However, by the same token it could be argued that when it came to incorporating actual data or theoretical outlooks, neither of these disciplines was well represented in the body of evolutionary theory that is associated with that synthesis (see Eldredge, 1985; Gould, 2002). Major advances in evolutionary biology have come, and are apt to continue to come, from more fully incorporating information from palaeontology and comparative development.

One important aspect of studying any interval in the history of life is having information about the pattern of evolution during that time period. Thus, phylogenies are a prerequisite for any study that aims to adduce evolutionary processes or mechanisms operating at the grand scale. This is because

> *"the most important connection between (pattern and process) …*

*involves the comparison of both intrinsic and extrinsic features of organisms predicted from theories of process, with those actually found in nature"* (Eldredge and Cracraft, 1980, p. 4).

Fortunately, a number of phylogenetic hypotheses for different groups are available that can prove useful in teasing apart the nature of the Cambrian radiation. One set of phylogenies comes from Cambrian organisms themselves, specifically trilobites (e.g., Lieberman, 1998, 1999b, 2001a, 2002); these are in many respects the hallmark Cambrian fossils in terms of the abundance and diversity in Cambrian strata. Another set of phylogenies comes from molecular systematic analysis of an early diverging animal group, the phylum Cnidaria (Collins *et al.*, 2006; Cartwright *et al.*, 2008). These phylogenies, taken in concert with the stratigraphic distribution of various cnidarian fossils, can inform us about the evolutionary nature of the Cambrian radiation (Cartwright & Collins, 2007). Finally, our knowledge of metazoan phylogeny, based on molecular systematic analyses of extant phyla, helps us recognize when and how the different parts of the genetic toolkit evolved (Putnam *et al.*, 2007; Chapman *et al.*, 2010).

## THE TEMPO AND MODE OF EVOLUTION DURING THE CAMBRIAN RADIATION

### *Trilobite phylogeny, biogeography, and the timing of the Cambrian radiation.*

The earliest trilobites appear in the fossil record in the latter part of the Lower Cambrian, roughly 525 Ma (Lieberman & Karim, 2010). When they appear it is effectively simultaneously on several different continents. Moreover, from their earliest appearance they show signs of significant biogeographic differentiation (Fortey *et al.*, 1996; Lieberman, 1999a). This early biogeographic differentiation provides cogent evidence that trilobites may have been evolving for some period of time before they actually appeared in the fossil record. A key question of course is how long were trilobites around before their appearance in the fossil record? Phylogenetic biogeographic analysis provides a means of quantifying the duration of this hidden evolutionary history. In particular, phylogenetic biogeographic analysis can be used to determine if there were any major tectonic events that may have influenced the early evolution of trilobites, through their effects on patterns of speciation. If there is evidence for congruent biogeographic differentiation that might be related to such tectonic events, and further, if these tectonic events can be dated, it provides a minimum age for the timing of biogeographic differentiation and thus evolutionary origins of the group (Lieberman, 2003a).

Phylogenetic biogeographic analysis on basal trilobite lineages suggests that patterns of early trilobite evolution show an episode of vicariance associated with the breakup of a supercontinent that occurred somewhere in the interval 550-600 Ma (Meert & Lieberman, 2004). (The method of biogeographic analysis employed by Meert & Lieberman, 2004 makes it possible to consider patterns of dispersal and does not simply assume vicariance. In the particular case of these Cambrian trilobites no evidence for dispersal was uncovered. Thus, the biogeographic patterns cannot be explained by a subsequent dispersal event that postdated the breakup of the supercontinent. Of course this does not imply that *no* Cambrian trilobites ever dispersed before, during, or after 550-600 Ma; the biogeographic history of the majority of Cambrian, and other trilobite groups, has unfortunately not yet been investigated in a phylogenetic framework. Still, based on available evidence it does appear that for the key basal trilobite groups congruent dispersal was absent and their diversification was most prominently influenced by vicariance that occurred sometime between 550-600 Ma. Additional information about the biogeographic method used is provided in Lieberman, 2000). This was a time of major geological changes and for a long time it had been generally recognized that there was some association between these and the major biological changes that were occurring, but phylogenetic biogeographic analysis provides a means of more rigorously demonstrating that correlation. In particular and foremost, consider the fact that biogeographic patterns reveal the prominent stamp of vicariance recorded in congruent biogeographic patterns. This suggests that earth history events exerted a significant control on this key episode in the history of life and influenced the early evolution of a major group of organisms, the trilobites (Meert & Lieberman, 2004). This provides evidence not only that the radiation is in some ways linked to changes in the abiotic environment but that it was the opportunities for geographic isolation that continental fragmentation afforded that helped spur speciation and the radiation (Lieberman, 2003a, b).

A second key aspect of the biogeographic patterns is that they suggest that the origin of trilobites occurred roughly 20-70 million years before their first appearance in the fossil record. Given that trilobites are at least modestly derived euarthropods, and arthropods are in turn a relatively derived bilaterian phylum, it suggests considerable metazoan, and even bilaterian, divergence must have occurred before the start of the Cambrian. The meaning of these results is clear: the Cambrian radiation had a significant fuse (Lieberman, 2003c; Meert & Lieberman, 2004).

What happened during the Cambrian radiation reflects a more general pattern associated with other evolutionary radiations in the fossil record. In particular, many radiations appear in the fossil record fully formed, and after the bulk of diversification has occurred (Lieberman *et al.*, 2007; Abe & Lieberman, 2009). For instance, the "Cenozoic" radiation of mammals has roots extending tens of millions of years back into the Cretaceous (Archibald, 1996). (Further, pre-Cenozoic mammals are much rarer than their Cenozoic brethren, typically small, and on the whole morphologically homogeneous.) On the surface this could simply imply an incomplete fossil record, but on closer inspection this pattern could actually be revealing something about the nature of evolutionary radiations in general. (Notably, Simpson, 1944 and Eldredge & Gould, 1972 also argued that the relatively rapid appearance of higher taxa or species in the fossil record told us something important about the nature of the evolutionary process.) The very conditions that encourage evolutionary radiations may also make groups less likely to be commonly retrieved as fossils. This gains special meaning when considered in light of punctuated equilibria (Eldredge & Gould, 1972); this theory posits that the very conditions that encourage speciation, rarity and a restriction to marginal environments, are likely to conspire to make actual speciation events difficult to recover. Perhaps it should not be surprising then that groups undergoing rapid speciation would do so under conditions that make them less likely to become palaeontologically emergent. Once groups do become commonplace and distributed across a range of environmental settings they are likely to fossilize but the engine of evolutionary radiation will mostly be shut off. Further, it is also worth noting that in the case of the Cambrian trilobites, although we may be missing part of their radiation in the fossil record, the signature of that radiation is still preserved.

*Tempo of trilobite evolution during the Cambrian radiation*.

Information from trilobite phylogenies can also be used to consider how rapidly speciation was occurring during the radiation. It has been suggested (e.g., Gould, 1989) that evolution at this time was operating unusually rapidly, but results from analyses of stochastic models suggest that, at least in the case of trilobites, rates of speciation cannot be statistically distinguished from rates in other groups and at other time periods (Lieberman, 2001b, 2003c). The rate of speciation was found to be high during the Cambrian radiation in the trilobite groups considered by Lieberman (2001b), but it was not found to be beyond the pale of evolutionary rates witnessed at other times in the history of life. However, an important aspect of rapid evolution is not just the speed with which speciation transpires but also the amount of change that occurs at each speciation event. Indeed, an important aspect of Gould's (1989) arguments about the pace of Cambrian evolution have centered on the amount of morphological change occurring then and the greater genetic flexibility of Cambrian faunas. At least in the case of basal Early Cambrian trilobites for which phylogenetic information exists, however, there does not seem to be any statistical change in the amount of morphological change occurring at speciation events before and after the Cambrian radiation interval (Smith & Lieberman, 1999). This is not to suggest that greater genetic flexibility plays no role in explaining what was unique about the Cambrian radiation, and we will consider this issue more fully below, but such processes either did not leave their signature upon basal trilobite speciation or the change in genetic flexibility did not occur until some time after the Cambrian radiation.

*Metazoan phylogenies and the molecular clock.*

Molecular phylogenies of extant metazoan phyla can provide important information with regard to patterns of evolution between phyla and the relative timing of their origination and diversification. By densely sampling representatives from all major phylum (Paps *et al.*, 2009) and applying phylogenomic techniques to sample DNA sequences from hundreds of genes (Dunn *et al.*, 2008; Hejnol *et al.*, 2009), a consensus is emerging regarding the phylogenetic relationships between major metazoan lineages. We summarize this consensus here. In particular, choanoflagellates are the sister taxon to all Metazoa. Acoelomorpha (acoels + nemertodermatids) is the sister clade to Bilateria. Protostomia comprises two major clades: the Lophotrochozoa, which includes molluscs, annelids, flatworms and bryozoans; and the Ecdysozoa, which includes arthropods, nematodes, tardigrades and kinorhynchs. Within Deuterostomia, the echinoderms and hemichordates form a clade that is sister to the chordates. Less certainty is the relative placement of several early diverging metazoan lineages. For instance, Porifera is generally thought to be paraphyletic (Borchiellini *et al.*, 2001; Medina *et al.*, 2001), although a recent phylogenomic study has recovered a monophyletic Porifera (Philippe *et al.*, 2009). The pattern of divergence between Ctenophora, Porifera and Cnidaria is also controversial. Most molecular phylogenies support Porifera as the earliest diverging lineage (Glenner *et al.*, 2004; Philippe *et al.*, 2009), whereas other recent phylogenomic studies support Ctenophora as sister to the rest of the Metazoa (Dunn *et al.*, 2008; Hejnol *et al.*, 2009). There is little consensus on the placement of Placozoa, although most evidence indicates they are an early diverging metazoan (Dellaporta *et al.*, 2006; Hejnol *et al.*, 2009; Philippe *et al.*, 2009). There exist two conflicting hypotheses on the placement of the parasitic myxozoans: they could be derived cnidarians or the sister to Bilateria (discussed in Evans *et* *al.*, 2010). Finally, the enigmatic *Xenoturbella* has been placed as the earliest diverging deuterostome (Philippe *et al.*, 2009) or as sister to Acoelomorpha at the base of Bilateria (Hejnol *et al.*, 2009). Over the next few years, through the application of genomic technologies, there will be dramatic increases in molecular sequence data from a diverse sampling of metazoan taxa. These new data will help to resolve many of the remaining questions in metazoan phylogeny.

Detailed molecular phylogenies, in conjunction with the fossil record, can be useful for estimating dates of the origin of major metazoan lineages. It is well documented, however, that molecules do not actually evolve in a "clock-like" fashion and therefore dates from molecular clocks are highly dependent on the model of molecular evolution used and on the fossil calibrations used to mark minimum and maximum time boundaries at multiple nodes on the tree. Cartwright & Collins (2007) reviewed the literature on some of the earliest fossils representatives of major metazoan lineages and Table 1 summarizes some of the key fossil dates. These fossil dates were used as calibration points on relevant nodes of a molecular phylogeny of Metazoa (Cartwright *&* Collins, 2007). Specifically, the crown group lineages were used to date the minimum age of the clade that includes that fossil taxon. In addition, sponge biomarker, cnidarian stem fossil and bilaterian trace-fossil evidence were used to assign a maximum-age dates (Table 1). A penalized likelihood model that uses a semi-parametric approach to relax the stringency of a clock was employed (Sanderson, 2002). The results of some of the dates recovered in the molecular clock analysis of Cartwright & Collins (2007) are shown in Table 2. Although the dates of these analyses should be viewed with an appropriate degree of skepticism given that they are highly dependent on both the model of molecular evolution and the accuracy of the fossil calibration, it is interesting to note that although metazoan origins are indicated to extend way back (this is likely a problem related to the available choices to root the tree), most of the major metazoan clades (Cnidaria, Deuterostomia, Ecdysozoa and Lophotrochozoa) are predicted to have originated either towards

TABLE 1. Earliest Fossil Representative of Major Metazoan clades

| **Earliest Fossil representative** | **Date (Ma) Formation** | **Stem/ Crown** | **Reference** |
|---|---|---|---|
| Porifera,<br>Silicea | 710<br>(Biomarkers) | Stem | Love *et al.*, 2006 |
| Porifera<br>*Paleophragmodictya* | 560 | Crown | Gehling & Rigby, 1996 |
| Cnidaria | 570 | Stem | Xiao *et al.*, 2000 |
| Scyphozoa,<br>Semaestome | 500<br>Marjum | Crown | Cartwright *et al.*, 2007 |
| Scyphozoa,<br>Coronate | 500<br>Marjum | Crown | Cartwright *et al.*, 2007 |
| Hydrozoa,<br>Narcomedusae | 500<br>Marjum | Crown | Cartwright *et al.*, 2007 |
| Hydrozoa,<br>Filifera | 500<br>Marjum | Crown | Cartwright *et al.*, 2007 |
| Cubozoa,<br>*Tripedalia* | 500<br>Marjum | Crown | Cartwright *et al.*, 2007 |
| Ctenophora<br>*Fasciculus* | 500<br>Burgess | Stem | Conway Morris & Collins, 1996 |
| Bilateria | 560 | Stem | Narbonne & Aitken, 1990 |
| Arthropoda<br>*Anomalocaris* | 530 | Stem | Collins, 1996 |
| Brachiopoda | 525<br>cosmopolitan | Crown | |
| Urochordate<br>*Shankaouclava* | 525<br>Chengjaing | Stem | Chen *et al.*, 2003 |
| Chordate<br>*Yunnanozoan*<br>*Haikouichthys* | 525<br>Chenjiang | Stem | Chen *et al.*, 1995; Shu *et al.*, 1999 |
| Chordata<br>Agnathan | 495<br>many | Crown | |

the very end of the pre-Cambrian (late Neoproteorozoic) or even in the Early Cambrian. Thus, the Cambrian radiation, according to the molecular clock analyses, does appear to approximate the time when major metazoan lineages start to appear and/or diversify in the fossil record. This introduces a bit of a disconnect

TABLE 2. Results of molecular-clock analysis for estimated dates of origin of several metazoan lineages from Cartwright & Collins (2007)

| Taxon | Estimated date of origin |
|---|---|
| Metazoa | 1147 |
| Choanoflagellates | 837 |
| Ctenophores | 390 |
| Silicea | 710 |
| Cnidarians | 570 |
| Bilaterians | 560 |
| Deuterostomes | 540 |
| Hemichordates | 361 |
| Chordates | 495 |
| Protostomes | 543 |
| Ecdysozoa | 530 |
| Lophotrochozoa | 537 |

relative to the trilobite results already discussed, and we are not sure yet how to square these two disparate data sets. In particular, the patterns from trilobite biogeography suggested that this euarthropod clade had begun to diversify by 550-600 Ma. By contrast, the molecular clock results suggest that Ecdysozoa, which is down the tree relative to Euarthropoda, originated at 530 Ma. This discrepancy illustrates the inherent problems with molecular clock analyses. While these analyses provide insight into the relative timing of the origin of these lineages, there is likely a fair amount of error in the estimation of actual dates, because of the dependency on a model of molecular evolution and accuracy in fossil calibrations. Ultimately, synthesis in science in general, and evolutionary biology in particular, will come not from deciding which result is right, but explaining how and why there are differences between the two.

## MEDUSOZOAN FOSSILS AND PHYLOGENIES AND THEIR BEARING ON THE CAMBRIAN RADIATION

Cnidarians are an important metazoan group because of their exceptional diversity, their prominent role in marine ecosystems and their place as one of the earliest diverging animal lineages. Thus, understanding their evolutionary history, and also their distribution in the fossil record, can provide important clues about the nature of evolutionary patterns and processes, especially during the Cambrian radiation interval. Associated with the Cnidarian Tree of Life project (http://cnidtol.com/)

there have been significant advances in our understanding of cnidarian phylogeny (McFadden *et al*., 2006; Cartwright *et al*., 2008; Collins *et al*., 2008; Daly *et al*., 2008; Evans *et al*., 2008; Bentlage *et al*., 2010; Nawrocki *et al*., 2010). A summary of our current understanding of cnidarian relationships is shown in Figure 1. This information, along with newly discovered cnidarian fossils from the Cambrian, can be put together to provide a picture of evolution at this time, and to add to the perspective from trilobites already presented.

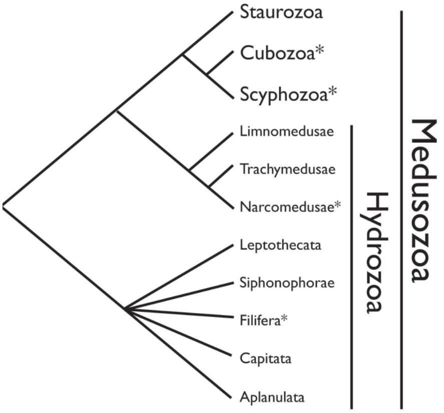

FIGURE 1. Medusozoan phylogeny summarizing our current understanding of cnidarian relationships based on Collins *et al*. (2006), Cartwright *et al*. (2008), Collins *et al*. (2008), and Evans *et al*. (2008). Those taxa with Middle Cambrian fossil representatives are denoted by an "*".

One difficulty with interpreting early cnidarian fossils, especially those belonging to the Medusozoa, which includes those with a medusae stage (jellyfish) in their life cycle, comprising the classes Cubozoa, Scyphozoa, Staurozoa and Hydrozoa (Daly *et al*., 2007) is that they are often poorly preserved. Sometimes the "synapomorphy" used to identify a medusozoan basically amounted to "rounded blob", and often with early putative medusozoan fossils that is all that is visible (Hagadorn *et al*., 2002). Although such an assignment may in general be valid, it makes it difficult to say much more about these sorts of fossils and especially to determine whether or not they represent stem or crown medusozoans.

Recently, we were fortunate enough to be able to study and describe new and exquisitely detailed Middle Cambrian medusozoan fossils (Cartwright *et al*., 2007). One of these fossils is shown in Figure 2. These fossils provided enough character data to allow them to be assigned not only to extant medusozoan classes but also to extant orders, families, and in one case a genus. One of these genera, the

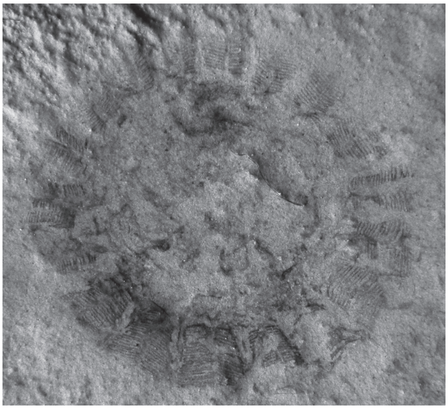

FIGURE 2. Fossil cnidarian identified as a crown group scyphozoan jellyfish that belongs to the extant order Semaeostomae. The fossil is from the Middle Cambrium Marjum Formation (approximately 500 million years old) in Utah, U. S. A.; see Cartwright *et al*. (2007) for additional details.

cubozoan *Tripedalia*, today has an advanced visual system and complex reproductive behavior. Although these structures are not visible on the Cambrian fossils, phylogenetic evidence indicates that the character complexes associated with these would have also originated back in the Cambrian.

In Figure 1, the medusozoan taxa that have Middle Cambrian fossil representatives are depicted with an asterisk. As illustrated in this figure, nearly the entire breadth of medusozoan phylogenetic diversity was present by the Middle Cambrian. This implies that not only all of the extant medusozoan higher taxa, but even many of the extant orders and perhaps families and genera had begun to diversify by the Middle Cambrian, shortly after the Cambrian radiation. The implications seem clear, and are akin to what was discovered with the trilobites: it is likely that the early Cambrian represents an interval of rapid diversification.

The record from fossils and phylogeny is also informative about the nature of Cambrian ecosystems. For a long time it was thought that these were relatively simple, but the presence of a diverse variety of pelagic organisms provides a cautionary tale. Today jellyfish are dominant predatory forms (and also prey items) in open ocean environments. Their presence and diversity back in the Cambrian suggests that these environments were occupied; furthermore, there must have been prey for the jellyfish to feed on in the pelagic environments. It appears that Cambrian ecosystems were not as simple as once thought and in particular pelagic ecosystems were occupied by a diverse array of taxa.

## ANCESTRAL GENETIC TOOLKITS AND EVOLUTIONARY DEVELOPMENT IN RELATION TO THE CAMBRIAN RADIATION

Recently, entire genomes have been sequenced from a diverse array of metazoan taxa. Most notably for our discussion here, the first complete, assembled genome from the sea anemone *Nematostella vectensis* (Putnam *et al.*, 2007) and the hydrozoan *Hydra magnipapillata* have been published (Chapman *et al.*, 2010). In addition, genome sequencing projects from the demosponge *Amphimedon queenslandica*, the placozoan *Trichoplax*, the ctenophore *Mnemiopsis leidyi* and the coral *Acropora millepora* are expected to be released in the near future. Comparisons of cnidarian genomes with those of bilaterians have revealed unexpected insights into the genetic makeup of early-diverging animals. Prior to the availability of genomic data in non-bilaterian animals, it was thought that many of the complex, signaling pathways were unique to vertebrates, because the model organisms *Drosophila* and *Caenorhabditis elegans* lacked these genes. However, it is now known that both *Hydra* and *Nematostella* possess a complex genome that contains many developmental regulatory genes/gene families previously thought to be specific to vertebrates (Ball *et al.*, 2004; Kusserow *et al.*, 2005; Technau *et al.*, 2005; Ryan *et al.*, 2006; Chapman *et al.*, 2010) (meaning that these genes were lost in *Drosophila* and *Caenorhabditis*). Prominent signaling pathways shared between bilaterians and cnidarians include Hedgehog, the receptor for tyrosine kinase, Notch, transforming growth factor-B and Wnt (Technau *et al.*, 2005; Chapman *et al.*, 2010). Thus, the ancestor to cnidarians and bilaterians must have been equipped with a diverse genomic toolkit necessary for the specification of complex body plans. It is likely that before the evolution of multicellular animals, many of these genes were performing entirely different functions, and were subsequently co-opted for signaling the development of complex and diverse metazoan body plans. For example, the cellular adhesion gene family cadherins that is important for mediating cell-cell signaling in metazoans, is present in single celled protists such as the choanoflagellates (King *et* *al*., 2003; Abedin & King, 2008). The increased availability of genomes from other early-diverging lineages will allow for a more precise reconstruction of the metazoan ancestral genome. Thus far, evidence from genomics indicates that the ancestral metazoan genetic toolkit was complex and enabled the rapid diversification of body plans during the Cambrian radiation.

Although the complex metazoan ancestral genomic toolkit can in part explain rapid diversification of animal body plans, it cannot explain why these body plans appear to become more canalized through time. Peterson *et al.* (2009) proposed that the evolution of microRNAs, because of their key role in transcriptional regulation, may explain the increasing morphological conservativism of body plans through time. Specifically, Peterson *et al*. (2009) note that the evolution of additional microRNA gene families through time means that development becomes more tightly regulated. While this hypothesis is conceivable, it seems a bit premature as very little is known about the role of the diverse microRNA families that exist in metazoans. In addition, although microRNA gene families become more diverse through time, the total number of microRNAs does not. That is, there is no correlation between the number of total microRNAs and morphological complexity in extant metazoan taxa. For example, Peterson *et al*. (2009) reports that the sea anemone *Nematostella* has 29 total microRNAs, whereas mouse has only 16. Moreover, pattern and process could be conflated in Peterson *et al.*'s (2009) argument because of the existence of a "left wall" *sensu* Gould (1996). That is to say, the number of microRNA families start out low and through time has to increase because the only direction available for change is for the number to increase (gene families that went extinct and were eliminated could not be sampled). This argument was originally developed by Gould (1996) to explain why apparent biological complexity increases through time. However, any time there is a trend that occurs in a system that involves an originally minimal value that increases through time, one has to be careful not to prematurely invoke a driven trend; the pattern could just involve a random walk, with passive diffusion away from a reflecting barrier or minimum value. Moreover, diversification of gene families through time is not unique to microRNAs. Hox genes also show gene duplications and diversification in many separate lineages. (The same "left wall" argument might explain some of these patterns as well.) In summation, it is likely that there is no single explanation for the canalization of body plans in metazoans, but instead it was due to a number of complex changes both in the genomes themselves and in the regulations and interactions amongst the different signaling pathways.

## CHANGES IN THE ABIOTIC ENVIRONMENT AND THE TIMING OF THE RADIATION

As we have already described, there is some evidence that changes in the abiotic environment at least partly triggered the Cambrian radiation. In particular, the geological changes at the end of the Proterozoic associated with the fragmentation of a supercontinent expanded the opportunities for vicariant differentiation and allopatric speciation, thereby increased the tempo of evolution at the time (Lieberman, 2003a; Meert & Lieberman, 2004). These were not, however, the only profound set of environmental changes transpiring at the time. During the very end of the Proterozoic there were also a series of major climatic changes, informally grouped under the rubric of the Snowball Earth (Hoffman *et al.*, 1998). There may have been as many as four episodes when the Earth experienced near total glaciation, being completely encased in ice; the intervening intervals also witnessed extreme environments as the ice melted away only to be followed by episodes of near broiling warmth where global temperatures hovered at close to 50 °C. Given the inhospitable environments, at least for large multicellular organisms, it may be no surprise that it was only after these conditions ameliorated that such organisms evolved (Hoffman *et al.*, 1998; Knoll, 2003). In this case, environmental conditions might well have served as a check on evolution, with environmental moderation creating fodder for evolutionary change.

Another critical aspect in the abiotic environment and evolutionary equation, at least regarding large organisms, are oxygen concentrations. These seem to have been generally increasing towards the end of the Proterozoic, perhaps then reaching 10% of present atmospheric levels (Fike *et al.*, 2006; Canfield *et al.*, 2007; Li *et al.*, 2010). This might have been an important threshold especially for the generation of key proteins found in many organisms, such as collagen, and also facilitating the building of rigid exoskeletons that make organisms more likely to fossilize (Schopf & Klein, 1992; Bengtson *et al.*, 1994). It also would have facilitated the evolution of large body size because of the issue of surface area to volume constraints (see Bonner, 1988). Again, these environmental changes involve removing a constraint that would have kept a lid on the evolution of animals. The changes do appear to have occurred some time before animals actually are found in the fossil record. Thus, the changes might not have precipitated evolution instantaneously. However, it is worth adding that this difference in timing lessens when one takes into account the evidence from trilobites, which indicates evolution might have significantly preceded first appearance in the fossil record.

In addition, the biotic environment as manifest in ecological interactions in the Proterozoic world would have been impoverished relative to those that prevail today, or even relative to those that prevailed by the late Cambrian. There is some general sense that minimal competition early in the history of animal life in the Proterozoic might have served to facilitate the evolution of animals early on. As competition inevitably increased with increasing diversity in the Phanerozoic, evolution might have later become constrained. However, the evolutionary mechanisms whereby these ecological differences would become translated, specifically from the ecological to the genealogical hierarchies, are not as yet clear and must remain nebulous at this time (Lieberman, 2008).

## CONCLUSIONS

Unravelling the patterns and processes involved in the Cambrian radiation is one of the grand challenges in evolution because these events occurred rapidly and in deep time. A comprehensive understanding of the origin and diversification of major metazoan lineages will likely come from the integration of several fields of inquiry, including a careful study of diversification in the fossil record, detailed paleobiogeographic analyses, paleoecological studies, molecular phylogenetic studies, and studies of genomics and evolutionary development. We predict that from these disparate lines of evidence a macroevolutionary synthesis will emerge where paleontology, phylogenetics and evolutionary development are the key areas of study for understanding this important episode (as well as other important episodes) in the history of life.

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# CHARLES DARWIN AND THE EVOLUTION OF THE ATLANTIC OCEAN, THE MACARONESIAN ISLANDS, AND THE AÇORES

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Darwin wrote in his notes for the *Voyage of the Beagle* when he stopped off at Terceira on 20 September 1836 on his way back to England:
*'I enjoyed my day's ride, though I did not find much worth seeing'*.

## ABSTRACT

The first stop on 16 January 1832 on the voyage of H.M.S. *Beagle* was the island of Santiago in the Cape Verde Archipelago. While there, Darwin, only 22 years old and with a Cambridge degree in theology, examined an uplifted layer of fossiliferous sandy breccia sandwiched between lava flows. These first observations eventually played an historic role in his and our understanding of ocean genesis and the colonization and subsequent evolution of island floras and faunas.

The English botanist Joseph Hooker had noted floristic similarities between the Falkland Islands and Iceland, neither having hardly any indigenous species, and South America and Europe, respectively. To explain this, the English malacologist Edward Forbes proposed in 1846 that a great land mass had existed in the Miocene encompassing northern Europe and Spain, and extending out from the Mediterranean far westwards into the Atlantic Ocean virtually to the coast of North America. On his return to England, Darwin became skeptical of Forbes's lost land and sent seeds of the Western Atlantic fabaceans *Entada gigas* and *Mucuna urens* from Açorean beaches to the Royal Botanic Gardens at Kew where they were planted, germinated and produced healthy, mature, vines. Subsequently, Darwin set up his own experiments in the glasshouse at Down House where he immersed the seeds of 87 species of common plants in seawater for a month. He then tried to germinate them and found that over half (64) had survived. By his own calculations, ocean currents could thus have taken such seeds well over half way across the Atlantic Ocean. He undertook similar work on dried muds collected from the feet of migrating birds and concluded that no Forbesian landmass was necessary to explain Hooker's biogeographic similarities.

The observations of Darwin on Santiago eventually led on Cocos-Keeling in the Pacific to his concept of oceanic islands having either risen or sunk, or of sea levels falling and rising, respectively, or both. Darwin thus set in place an alternative, and more plausible, theory to that of Forbes, which suggested that newly-emergent islands could be colonized naturally by plants and animals from other locations and that, through natural selection, such isolated individuals could evolve into distinct species.

Thus, although Darwin stayed but a few days in the Açores, the islands subsequently played a critical role in his understanding of the evolution of islands and life upon them. Terrestrially, the Açorean flora and fauna have been much modified by the hand of man. This is also true of the few low-lying wetlands, but the islands remain, because of their Atlantic isolation, one of the best places to test Darwin's hypotheses about island colonization and to effect Macaronesian marine conservation.

## RESUMO

A primeira paragem em 16 de Janeiro de 1832 na viagem do H.M.S *Beagle* foi a ilha de Santiago no Arquipélago de Cabo Verde. Enquanto ali, Darwin, com apenas 22 anos de idade e graduado em teologia por Cambridge, examinou uma camada erguida de breccia arenosa fossilífera entalada entre derrames de lava. Estas primeiras observações eventualmente tiveram um papel histórico no seu e nosso entendimento da génese do oceano e da colonização e subsequente evolução das floras e faunas das ilhas.

O botânico Inglês Joseph Hooker notou semelhanças florísticas entre as Ilhas Falkland e a Islândia, nenhuma possuindo praticamente espécies indígenas, e a América do Sul e a Europa, respectivamente. Para explicar isso, o malacólogo Inglês Edward Forbes propôs em 1846 que uma grande massa de terra existiria no Mioceno abrangendo a Europa do Norte e a Espanha, e estendendo-se para fora do Mediterrâneo muito para oeste Oceano Atlântico adentro virtualmente até à América do Norte. No seu regresso à Inglaterra, Darwin tornou-se céptico quanto à terra perdida de Forbes e enviou sementes de fabáceas do Atlântico Oeste *Entada gigas* e *Mucuna urens* das praias Açorianas para os Royal Botanical Gardens em Kew onde foram plantadas, germinaram e produziram trepadeiras

saudáveis, maturas. Subsequentemente, Darwin preparou as suas próprias experiências na estufa em Down House onde imergiu em água do mar durante um mês as sementes de 87 espécies de plantas comuns. Experimentou então germiná-las e descobriu que mais de metade (64) haviam sobrevivido. Por seus próprios cálculos, as correntes oceânicas poderiam pois ter trazido tais sementes bem mais do que metade do caminho através do Oceano Atlântico. Ele fez trabalho semelhante com lamas secas recolhidas das patas de aves migradoras e concluiu que não seria necessária a massa de terra Forbesiana para explicar as similaridades biogeográficas de Hooker.

As observações de Darwin em Santiago levaram eventualmente, em Cocos-Keeling no Pacífico, ao seu conceito de ilhas oceânicas haverem subido ou afundado, ou de mares descendo e subindo, respectivamente, ou a ambas as situações. Darwin então colocou uma teoria alternativa à de Forbes, e mais plausível, que sugeria que ilhas recém-emersas poderiam ser colonizadas naturalmente por plantas e animais de outras localidades e que, através da selecção natural, esses indivíduos isolados puderam evoluir em espécies distintas.

Assim, embora Darwin tenha permanecido nos Açores apenas alguns dias, as ilhas subsequentemente desempenharam um papel crítico na sua compreensão da evolução das ilhas e da vida nelas existente. Em terra, a flora e a fauna Açorianas têm sido muito alteradas pela mão do homem. Tal é verdade acerca das poucas zonas húmidas baixas mas, devido ao seu isolamento no Atlântico, as ilhas permanecem um dos melhores lugares para testar as hipóteses de Darwin acerca da colonização das ilhas e para levar a cabo a conservação marinha da Macaronésia.

## INTRODUCTION

Charles Darwin was born on 12 February 1809. One of the greatest influences in his early life was his paternal grandfather Erasmus Darwin (1731-1802) who recognized and described 'biological evolution'. In 1825 (aged 16), Darwin arrived at the University of Edinburgh to read medicine. This lasted for but two years and in 1828 (aged 19), Darwin enrolled at the University of Cambridge to read divinity. Unsuccessfully, as it transpired. Here, however he came under the influence of two great men – the geologist Adam

Sedgwick (1785-1873), who had become Woodwardian Professor of Geology at Cambridge in 1818, and the botanist John Stevens Henslow (1796-1861), who had been appointed Professor of Botany at Cambridge contemporaneously with Darwin in 1825. Darwin left Cambridge in 1931, not a clergyman, but with a B.A. in Theology, Euclid and Classics. He is now, however, with training by Sedgwick and Henslow an enthusiastic, albeit, amateur geologist and botanist.  On 24 August 1831, Henslow informed Darwin that there is a space for him on H.M.S. *Beagle* as naturalist companion to Captain Robert FitzRoy (1805-1865).  Darwin accepted the invitation and on 27 December 1831 (aged 22), he and the *Beagle* departed on her second voyage, principally to conduct a hydrographic survey of the coast of South America. The expedition was not to return to England until 2 October 1836, almost five years after it had set sail.  In Cambridge, Darwin had become much influenced by the writings of Charles Lyell (1797-1875), author of *Principles of Geology* and took Volume I with him on the voyage and received Volume II on route.It has to be said that Darwin was not an outstanding student, indeed his father 'despaired of him' but, today, there is a statue of Charles Darwin as a young man in the gardens of Christ's College, Cambridge (Figure 1). On the steering wheel of H.M.S. *Beagle*, however, were carved the words of Nelson's exhortation to his men at Trafalgar: '*England expects every man to do*

FIGURE 1.  The statue of Charles Darwin as a young man in the gardens of Christ's College, Cambridge. '*I believe that I was considered by all*… [to be] *an ordinary boy well below the common standard of intellect*'. Charles Darwin, 1876.

*his duty*'. Such a daily reminder of his duty must have kept him working throughout the long periods of boredom, tedium, seasickness and homesickness that he endured for the 58 months of the voyage.

The *Beagle*'s last stop on its five year voyage was the Açores. Although Charles Darwin was singularly unimpressed by the islands on his visits to Terceira and São Miguel in 1836, the archipelago, along with other macaronesian ones would eventually play an important role in his understanding of biogeography and the evolution of island isolated floras and faunas. The first stop of the *Beagle* in 1832 was to be the Canaries. The island's Spanish authorities, however, had heard that cholera was rampant in England and so forbade any landing. Instead, therefore, the first stop of H.M.S. *Beagle* was the Portuguese colony of the Cape Verde Islands.

## THE CAPE VERDE ISLANDS

The Cape Verde Islands are located 450 kilometres off the coast of West Africa (Senegal) and were discovered in 1456. Colonized by the Portuguese in 1462, they became important as a stopping off point for the trans-Atlantic slave trade. Subsequently, the importance of the islands declined. Darwin arrived at the capital, Porto Praya (Praia), on the island of St Jago (Santiago) on the 16 January 1832 (the *Beagle*'s first stop) and described his surroundings as wearing a 'desolate aspect' (Darwin, 1845).

At the time of Darwin's visit to Santiago, the Christian church still believed in the cosmogony of James Ussher (1581-1656), Archbishop of Armagh, Primate of All Ireland, and Vice-Chancellor of Trinity College, Dublin, who had identified creation as starting on Sunday 23 October 4004 B.C. Such a view had the important support of Sir John Lightfoot (1602-1675), Vice Chancellor of Cambridge University, who even added an exact time - 9 a.m. - to the prescribed date. Having established the first day of creation, Ussher calculated the dates of other biblical events, concluding, for example, that Adam and Eve were driven from Paradise on Monday 10 November 4004 B.C.

Charles Lyell, however, did not believe any of this. Rather, he believed the Earth to be billions of years old. In addition to the debate regarding the Earth's age, however, the scientific world was similarly divided as to whether the geological record was (i), best interpreted as a series of catastrophic events, the most recent being equated with the deluge of Noah's flood with the ark touching down on Mount Ararat, according to Ussher, on Wednesday 5 May 2348 B.C. (thereby achieving convergence between geology and scripture) or (ii), as Lyell believed, slowly acting processes of formation, erosion, deposition and deformation. The Temple of Serapis, at Pozzuoli, Naples, actually provided evidence of the latter, even then. Here, date mussels, *Lithophaga lithophaga* (*dattero di mare*) have made holes in the 2nd century columns, at a height of ~5.7 metres showing that they were originally uncovered, then covered and now, again, uncovered by the sea – attesting, because the columns were undisturbed, slow, gradual, changes in sea level over historical time. The temple and its date mussel artifacts were so important to Charles Lyell that an illustration of it (Figure 2) was used as a frontispiece to his book '*Principles of Geology*' (Lyell, 1830-1833).

When Darwin arrived on the Cape Verde Islands – as desolate today through over-grazing, as they were then, his mind was debating the conflicting views in relation to creation, and the arguments about catastrophe *versus* gradualism. Captain FitzRoy, who was a devout creationist, not just believing in the literal truth of Genesis but condemning Lyell as a heretic too,

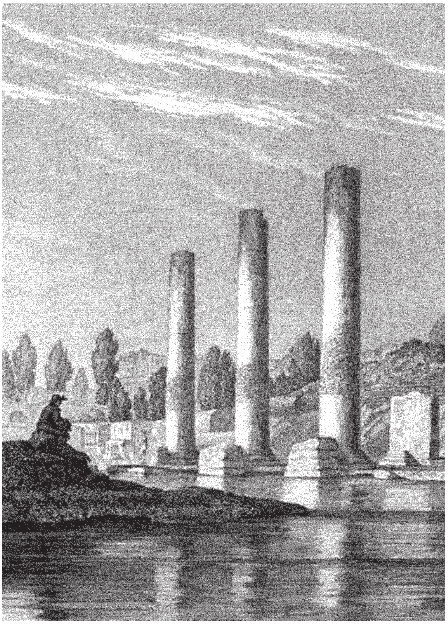

FIGURE 2. The Temple of Serapis, at Pozzuoli, Naples, where date mussels, *Lithophaga lithophaga* (dattero di mare) have made holes in the 2nd century columns, at a height (today) of ~5.7 metres. The frontispiece to Charles Lyell's *Principles of Geology* (1830-1833).

would be of little help to him in this debate.

But the harbour at Praia on Santiago held a secret that Darwin discovered. Here, on Quail Island (now Ilhéu de Santa Maria) he noted the presence of a horizontal white band running through the rocks, about 30 feet (~10 metres) above sea-level (Figure 3). It was composed of a sandy breccia, made of compressed shells and 'corals' (actually maerl) and continued as far as the eye could see. Figure 4A shows some of the fossils collected by this author from Darwin's stratum on Quail Island in 2009. The breccia matrix contains patellid and fissurellid limpets, other gastropod fragments, venerid, donacid, glycymerid and chamid (upper) shell valves, crab 'fingers' and maerl fragments, attesting to its origin. That is, an uplifted shallow, tropical, seabed composed of large sand grains, with a surface cover of calcareous maerl nodules (Darwin's 'coral'), attesting to gentle surface wavelets, and a mixture of organic fragments of, mostly, mollusc shells derived from rocky and sandy inshore and soft offshore habitats. The fossils obviously suggest that the whole area had once been under water but, for Darwin, the question was: why not now?

The geology of the Cape Verde Archipelago has been described by Mitchell-Thomé (1972) and Figure 5 is the only detailed map of the geology of the

FIGURE 3. On Quail Island (now Ilhéu de Santa Maria) at Santiago in the Cape Verde Islands, Darwin noted the presence of a horizontal white band (arrow) running through the rocks about 30 feet (~10 metres) above sea-level. (Photo: B. Morton).

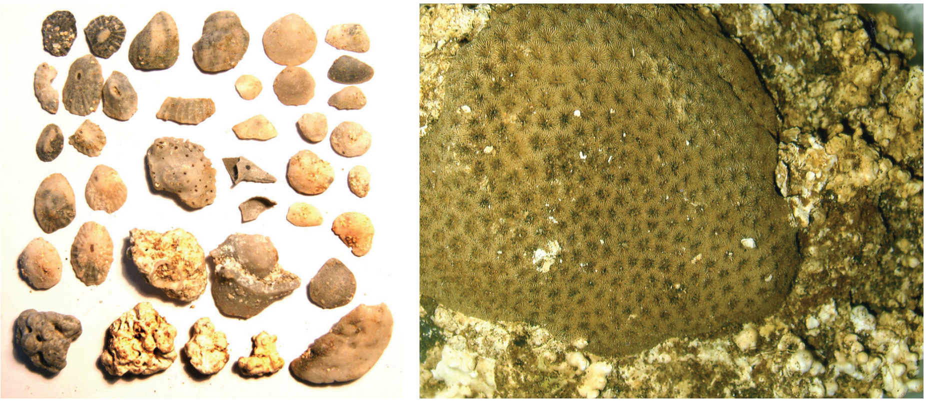

FIGURE 4. A, Some of the fossils collected by this author from the limestone of Quail Island in 2009. The breccia matrix contains patellid and fissurellid limpets, other gastropod fragments, venerid, donacid, glycymerid and chamid (upper) shell valves, crab 'fingers' and maerl fragments. B, The coral *Siderastrea radians* attached to a piece of Darwin's fossiliferous limestone collected from the beach at San Tome on Santiago. (Photo's: B. Morton).

twelve islands and shows that they represent a within-plate archipelago located some 500 kilometres west of Senegal. The archipelago probably dates back some 180 Ma and the islands are made up mostly of Tertiary and younger volcanics. The oldest rocks on Maio are Mesozoic limestone but most are Cenozoic (<65 Ma) and the most recent, as on the northwestern-most tip of Santiago at Tarrafal are raised beach deposits. For Darwin, the Quail Island limestone stratum was highly significant and he made a woodcut illustration of it (Figure 6: after Darwin, 1844, p. 9) in which he showed how it dips locally below sea level in an asymmetrical fashion. In Figure 6, A represents the sea; B, ancient volcanic rocks; C, upper basaltic lava and arrowed is a thin layer of white limestone between them.

Four years later on into the voyage, H.M.S. *Beagle* stopped at the Cocos-Keeling islands for but one day on 2 April 1836. This stop was, however, also significant because his book '*The Structure and Distribution of Coral Reefs*' (Darwin, 1842), illustrated how various kinds of coral islands may be formed by either subsidence of the land or rises in sea level (or both) and eventually

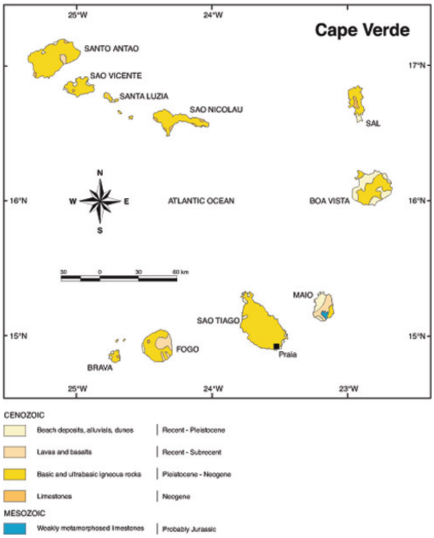

FIGURE 5. The only geological map of the of the Cape Verde Islands showing that the 12 islands represent a within-plate archipelago located some 500 kilometres west of Senegal. (Courtesy of Dr Lyall Anderson, University of Cambridge).

lost to the depths still holds true today, attesting not only to his remarkable insight, but also to the significance of Quail Island in the Cape Verde's. For here, he believed the maerl was 'coral' and, in fact, corals do occur in the shallow subtidal of the Cape Verde's, for example *Siderastrea radians* here attached to a piece of limestone (Figure 4B), so that this must have been the first time he contemplated how such coral islands evolve.

Also on Santiago, however, Darwin discovered an African baobab tree (*Adansonia*). His plant is no longer alive (Pearson & Nicholas, 2007), but there is still a pair of trees to be found on the island in the valley extending north from the original capital, Cidade Velha, on the south coast of Santiago. The male tree illustrated (Figure 7, note the man standing beside it), and the female, are bigger than Darwin's and must have been mature when he visited the island. Darwin also knew

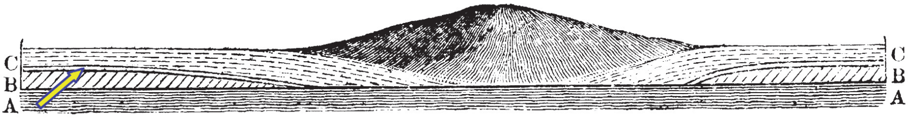

FIGURE 6. The woodcut Darwin made of the limestone stratum on Quail Island, Cape Verde, in which he shows how it dips locally below sea level in an asymmetrical fashion. A represents the sea, B, ancient volcanic rocks; C upper basaltic lava with a thin layer of white limestone (arrowed), between them. (After Darwin, 1844, p. 9.)

FIGURE 7. An African baobab tree (*Adansonia*) today, on Santiago, Cape Verde Islands. (Note the man standing beside it.) (Photo: B. Morton).

that the largest baobab trees could attain a great age of 6,000 years. Could this therefore, be evidence for a lost landmass that had once connected Africa with these Atlantic islands? If so, his baobab must have sprouted in the first week of creation, but only if one believed in Bishop Ussher's account of Biblical chronology. But how, therefore, could this tree be older than the Quail Island fossils? The truth is, however, much more prosaic: the trees were probably taken to the Cape Verde Islands, as seeds, by either slaves or their traders just a few hundred years previously. But, at the time, Darwin was not to know that. Nevertheless, Darwin's sojourn on Santiago was significant in a number of ways but, most importantly, because here his first thoughts on oceanic island formation were born and he began to question the accepted, literal, truth of creation.

## FORBES'S LOST LAND

At the time of Darwin's visit to Cape Verde, the English naturalist, malacologist, geologist, palaeontologist and Professor of Natural Philosophy at Edinbugh University, Edward Forbes (1815-1854), and therefore an eminent person, had proposed (Forbes, 1846) that a great land had existed in the Miocene (7-26 Ma) encompassing northern Europe and Spain, and extending out from the Mediterranean, past the Açores (and thus way beyond the Canaries and Cape Verde), as far out into the Atlantic as the Sargasso Sea. That is, virtually to the coast of North America (Figure 8). Such a land largely filled the Atlantic Ocean. Hence, as far as Forbes's theory was concerned, Darwin's baobab would simply be a remnant of a time when the Cape Verde's had been joined to Africa by this, now sunken, inter-connecting landmass.The English botanist Joseph Dalton Hooker (1817-1911), at 22 (the

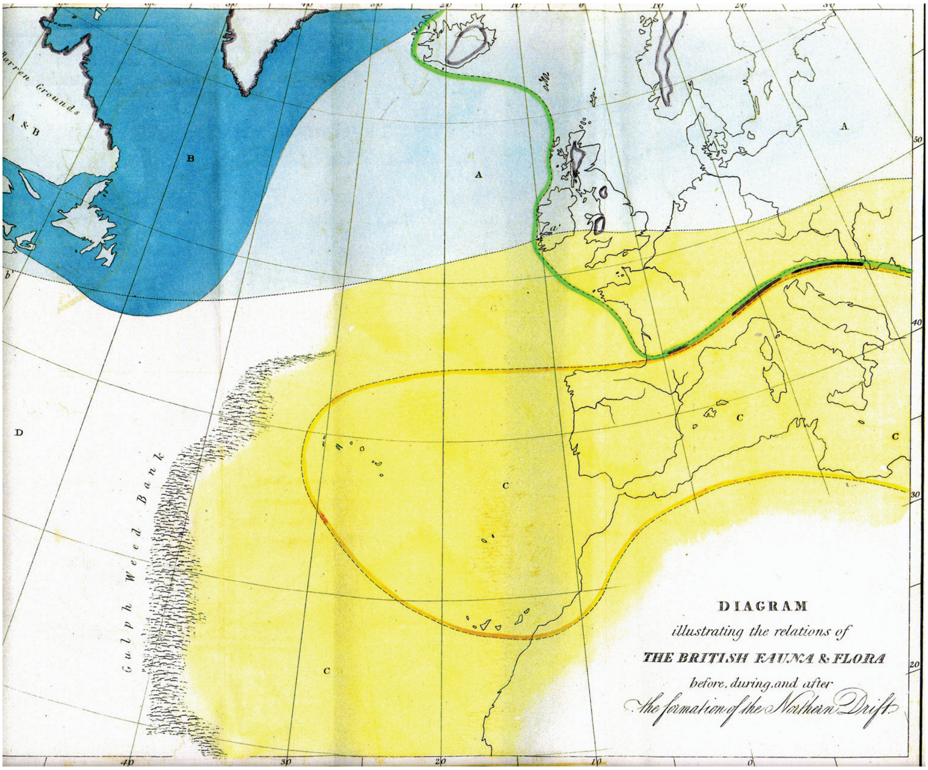

FIGURE 8. Forbes concept of a land that largely filled the Atlantic Ocean, thereby accounting for Hooker's similarities in the plant and animal fossils of Europe and North America. (From Forbes, 1846).

same age as Darwin when he joined H.M.S. *Beagle*), enlisted on Captain James Clark Ross's Expedition to Antarctica (1839-1843). Subsequently, Hooker noted the floristic similarities between the Falkland Islands and Iceland, neither of which had hardly anything indigenous, and South America and Europe, respectively. One well-known example at the time was the beach pea (*Lathyrus japonicus*), illustrated in Figure 9, which was then thought to have a North American and rare British occurrence and thus provide evidence of a formerly contiguous Atlantic distribution. Edward Forbes's lost landmass also explained this, thereby further accounting for similarities

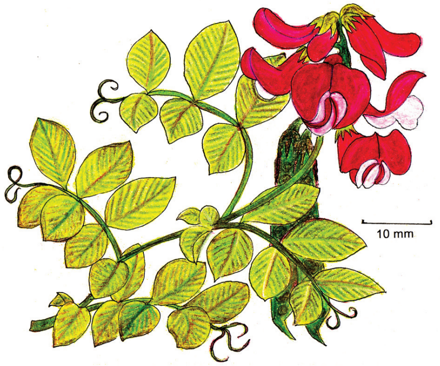

FIGURE 9. The beach pea, *Lathyrus japonicus.* (B. Morton).

in the plant and animal fossils of Europe and North America. It is now known that the beach pea, whose seeds can survive many months in seawater, has a circum-polar distribution. Later, Darwin, after looking at seed dispersal more scientifically, would offer an alternative hypothesis to that of Forbes.

Forbes had also dredged in the Aegean from 1841-42 aboard H.M.S. *Beacon* giving rise to his second, Azoic (or Lifeless), theory, that no life existed below a depth of ~500 metres. This view, too, would later be challenged by Charles Wyville Thompson (1830-1882) who succeeded Forbes as Professor of Natural Philosophy at Edinburgh University. Thompson aimed to disprove the Azoic Theory and did so on H.M.S. *Challenger* that, on its famous, pioneering, voyage between 1872-1876, found life at 9,000 metres. *Challenger*, like the *Beagle,* put into Porto Praia on St Iago (Santiago), Cape Verde Islands, and Henry Nottidge Moseley (1844-1891), one of the naturalists on board, was keen to see the rocks described by Darwin - so significant had they become.

Forbes died at an early age of 39, his theories, though interesting, all subsequently shown to be wrong. But the Challenger Expedition did more – its 50 volumes of research findings, largely edited by John Murray (1841-1914), who had been Wyville-Thompson's assistant on the voyage and who took over the editing and publishing of the expedition's results (completed in 1896), effectively, laid the foundations for the modern science of oceanography. Murray, for example, was the first person to note the existence of the Mid-Atlantic Ridge and ocean trenches and, indeed, coined the word 'oceanography'. And, for continuing and refining this newest of sciences, we have to thank the researches of three other 20th century physical oceanographers.

## ALFRED WEGENER, EDWARD BULLARD AND FREDERICK VINE

Forbes' view of a sunken land bridge across the Atlantic persisted into the 20th century and it was not until 1911 that the German meteorologist Alfred Wegener (1880-1930), noticing that the fossils of identical plants and animals could be found on opposite sides of the Atlantic, suggested that the continents were 'drifting' apart.

Orthodox science, that is, those believing Forbes, at the time explained this by postulating that land bridges, now sunk, had once connected far-flung continents. Wegener also, however, noted the close fit between the coastlines of South America and Africa and wondered whether the continents might not have been joined at one time. He argued the continents could drift about, laying down the groundwork for the 1950's palaeomagnetism research that reconstructed the world's historical geology in terms of a unified theory of continental drift. Figure 10 shows the maps in the 1966 edition of Wegener's book illustrating continental drift for three epochs. Edward Crisp Bullard (1907-1980), who became professor of Geodesy and Geophysics at Cambridge University, later produced a computer fit of the continents that Wegener had called 'Pangaea', showing just how the continents do actually fit very closely into a jigsaw-like picture.

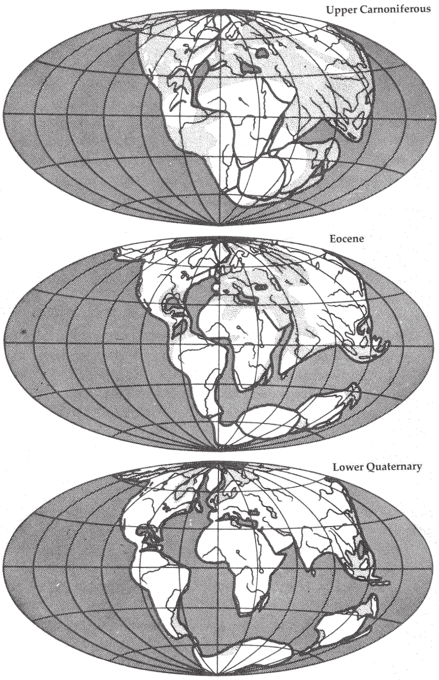

FIGURE 10. The maps in the 1966 edition of A. Wegener's book illustrating continental drift for three epochs.

In 1963, the Cambridge geophysicist Frederick Vine (born 1939) proved the concept of sea-floor spreading by studying the reversals in the polarity of the Earth's magnetic field. Vine showed that the parallel bands of palaeomagnetic anomalies on either side of oceanic mountain ridges resulted from the combined effects of reversals in the polarity of Earth's magnetic fields and the generation of new floor along the axes of the ridges. Today, through the science of geomagnetism, we can interpret the evolution of the earth's continents and oceans over time, explaining why similar fossils occur on different continents. Through the pioneering work of Wegener, Bullard and Vine, we now know an enormous amount about the Earth's seabed, including its age(s) and about the plates that form the continents and are separated from each other by the mid-oceanic ridges. The Açores Archipelago sits on the Mid-Atlantic Ridge.

## DARWIN'S EXPERIMENTS

Upon his return to England, Darwin became skeptical of Forbes's lost land and after receiving several seeds of the Western Atlantic *Entada gigas* and *Mucuna urens* from Açorean beaches, sent them to the Royal Botanic Gardens at Kew where they were planted, germinated and produced healthy mature vines. Clearly, these and, indeed other seeds of several species of sea beans are capable of surviving Gulf Stream transport from the tropical Western Atlantic to the Açores, including *Mucuna urens* as well as *M. sloanei* and *M. fawcetti*. The seeds of these three species of coastal leguminous vines share the characteristic of a darkly pigmented hilum encircling five-sixths of the margin of each. The embryo within the seed is protected by a thick, resistant, exocarp capable of prolonged exposure to seawater (Gunn *et al*., 1976).

In fact, the Açores receives a variety of seeds and vegetative dissemules, many of which originate from the tropical Western Atlantic (Table 1). The sea heart, *Entada gigas*, is the most common disseminule on Açorean beaches, delivered by Gulf Stream currents from Caribbean shores. *Entada gigas* is a large, climbing, tropical, coastal, vine producing large chocolate-brown seeds up to six centimetres in diameter and some two centimetres thick. The seeds are buoyant and can remain afloat at sea for at least two years (Gunn *et al*., 1976). Veríssimo (1989) suggested that

TABLE 1. Plant disseminules recorded from Açorean beaches (after Gunn *et al*., 1976).

| **Disseminule** | **Common name** | **Family** | **Source, habit and habitat** |
|---|---|---|---|
| *Astrocaryum* sp. | Starnut palm | Palmaceae | Caribbean; wet lowland forest tree |
| *Calocarpum mammosum* | Egg fruit | Sapotaceae | Tropical America; tree |
| *Crescentia cujete* | Calabash tree | Bignoniaceae | New World tropics; tree |
| *Dioclea reflexa* | Sea purse | Leguminoseae | Asia; vine |
| *Entada gigas* | Sea heart | Leguminoseae | Caribbean; climbing vine |
| *Manicaria saccifera* | Sea coconut | Palmaceae | American tropics; coastal tree |
| *Merremia discoidosperma* | Many's bean | Convolvulaceae | Central America; woody, wet forest |
| *Mucuna sloanei* | True sea bean | Leguminoseae | Caribbean vine |
| *Sacoglottis amazonica* | Cojon de burro | Humiriaceae | South America; lowland forest tree |
| *Sapindus sapinaria* | Black pearl/Soapberry | Sapindaceae | American tropics; tree |

Christopher Columbus (1451-1506), upon finding *E. gigas* seeds along the shores of either Porto Santo or Madeira during his residence on the islands between ~1479-1482, used the observation to support his argument for, an as yet undiscovered (then in ignorance of Viking achievements and the evidence thereof on Newfoundland), westward land – the Americas – or, rather, as he thought, Asia.

As a consequence of the results of the Kew experiments, Darwin set up his own in the Old Laboratory and Greenhouse in the grounds of Down House where he immersed the seeds of 87 species of common plants in seawater for a month. He then tried to germinate them and, to his surprise, 64 subsequently germinated after an immersion period of 28 days and a few survived immersions of 137 days. Nine legumes were tried and, with one exception, all died, including the common pea (*Pisum sativum*) although, as noted above, it is known that the sea pea occurs in North America and along the southeast coast of England, for example on the Dungeness shingle banks, on the southeast coast of England, and has a circum-polar distribution.

Darwin also noted that many of the seeds, without either the capsule or fruit, sank within a few days and could not, therefore, have survived a long sea voyage. Later, he tried larger fruits and capsules and eventually to dry and then try the stems and branches of 94 plants with ripe fruits. The majority sank quickly, including fresh cuttings whereas dried ones floated for longer. For example, ripe hazelnuts sank immediately whereas dried ones floated for 90 days and subsequently germinated, as did the ripe seeds of *Helosciadium* (water parsnip) and an asparagus-plant (*Asparagus officinalis*) with ripe berries (85 days). Of the 94 dried plants, 18 floated for >18 days. Darwin consulted '*Johnston's Physical Atlas*' wherein it was stated that the average rate of several Atlantic currents is 33 miles·day-1, with some running at 60 miles·day-1, and concluded that 14 out of 100 (14%) plants might be floated across 924 miles of sea and if blown to a favourable spot, would germinate. By his own calculations, therefore, ocean currents could thus have taken such seeds well over half way across the Atlantic, that is, easily, to the Açores.

Darwin's experiments thus set in place an alternative, more plausible, theory to that of Forbes and which suggested that newly emergent islands could be colonized by plants and animals from other locations and that through natural selection such isolated individuals could come to evolve into distinct species. Thus, Darwin's interpretation of the stratum on Quail Island initially stimulated him to think about how oceanic islands are formed, but his experiments on seed dispersal also demonstrated to him how such new entities might be colonized. This latter observation ultimately led to his great theory about the evolution of life itself.

## THE AÇORES

The Açores archipelago is located on the Mid-Atlantic Ridge on its only triple junction. The discovery of the Açores, according to 14th century Genoese maps, the Portulanos, seems to have taken place between 1317 and 1339 (Bento, 1994) but the Portuguese navigator Diogo de Silves is credited with the discovery of the islands in 1427. Portuguese settlers first colonized the islands permanently beginning with Santa Maria in 1432, São Miguel in 1439 and the other seven subsequently. Darwin and the *Beagle* stopped off in the Açores (the last stop) for six days on the way back to England and visited Terceira on 20 September 1836 and São Miguel subsequently, although he probably did not disembark the ship at the latter. His comment about Terceira (Darwin, 1845) was:

> '*I enjoyed my day'sride, though I did not find much worth seeing*'.

We have to remember, however, that Darwin was terribly homesick, indeed had been for many months. He even dismissed Australia as uninteresting! There, he did not even see a kangaroo! As we now know, however, the Açorean islands are extremely interesting, especially geologically. Santa Maria is the oldest island of the Açores and arose from the sea in the Late Miocene ~7 million years ago. It is the only one of the nine Açorean islands to have a sedimentary cover and has a rich fossil record dating from the Late Miocene-Early Pliocene to the Pleistocene (Madeira *et al.*, 2007). As on Santiago in the Cape Verde Islands, there is on Santa Maria an uplifted Early Pliocene fossiliferous stratum and Janssen *et al*. (2008, figure 3) illustrate an accumulation of *Cavolinia marginata* in a crustacean burrow from the Lower Pliocene of Cré, on this island. Ages of fossil molluscs recovered from Santa Maria range from 10.03 to 2.24 Ma (Kirby *et al.*, 2007).

Similarly, to the rear of the long expanse of sandy beach on the southern shore of Porto Santo, one of the Madeiran islands, there is a raised beach of offshore sand (Figure 11) not unlike that seen on the coast at Tarrafal on Santiago (Cape Verde Islands). Hence, throughout Macaronesia, there is ample evidence of uplifted marine sediments attesting not only to active vulcanism over relatively recent time but to the insight of Darwin in recognizing this very early on during his voyage with the *Beagle*.

FIGURE 11. A raised beach towards the rear of the long sandy beach on the south coast of Porto Santo, Madeira. (Photo: B. Morton).

We also know that sometime between 3.1-3.6 million years

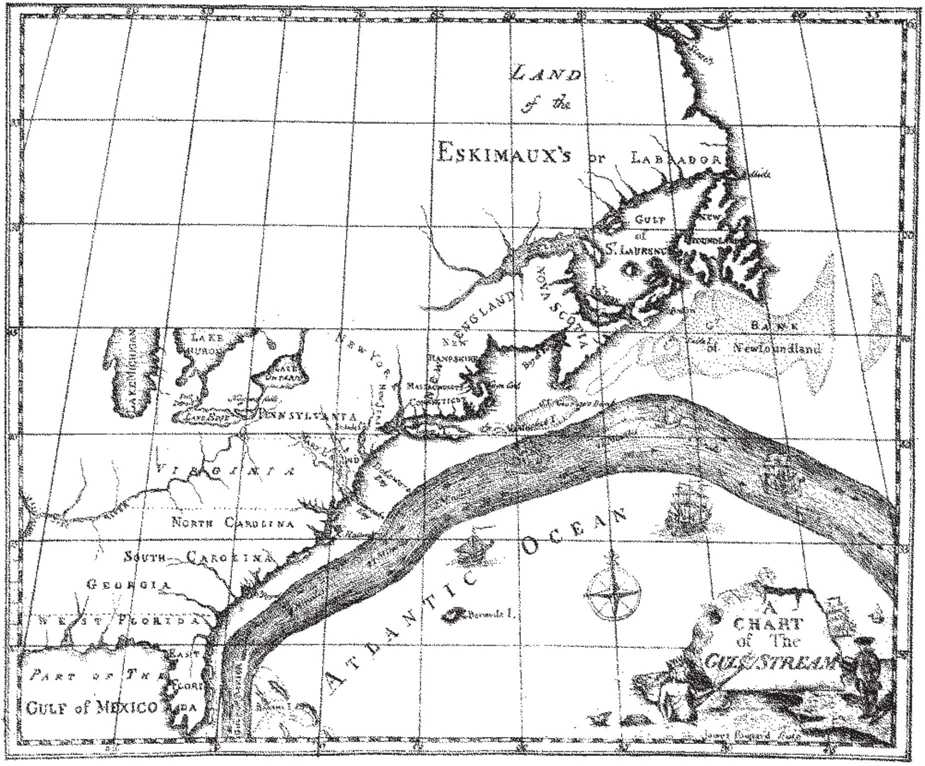

FIGURE 12. The map of the Gulf Stream created by Benjamin Franklin on 2 May 1775. He thought of it as a river.

ago, after the Middle Pliocene uplift of the Central American Seaway, the connection between the Pacific and Atlantic Oceans was closed at the approximate position of modern Panama (Vermeij & Rosenberg, 1993), isolating coral reefs in the Caribbean and creating the modern pattern of circulation of both oceans, but importantly for the Atlantic – the Gulf Stream –, first mapped by Benjamin Franklin (1706-1790), who was postmaster general of the American colony at the time, during a voyage from England to the soon to become United States in 1775 (Figure 12). He recorded that the current was some 3.5 °C warmer than the surrounding sea and by taking regular temperature readings could trace its course. It is this current which allows the Azores to be colonized sporadically by species with long-lived larvae from the Caribbean, such as the taenioglossan tonnoidean gastropod *Charonia variegata* (Lamarck, 1816) recorded only once from Faial at 15 metres depth (Gofas & Beu (2002). Also in the early Pliocene, the Bering Strait between Alaska and Siberia opened and cool-temperate and polar marine species were able to move between the North Pacific and the Arctic-Atlantic basins (Vermeij, 1991).

Such relatively recent historical events have been responsible for not just the Atlantic circulation pattern we see today, but also for the species of marine plants and animals found on the shores and shallow subtidal waters of the Macaronesian, including Açorean, islands as they arose successively either prior or subsequent to these major events (Morton & Britton, 2000a). We, therefore, know much about the circulation of the Atlantic Ocean and how it has evolved and in broad terms how and when the marine biota of the Açorean islands arrived. That the islands emerged either before or after these events, however, make them a chronometer for the testing of theories related to island colonization times and routes but also marine biogeography.

Today, the Açorean islands are influenced by the North Atlantic Current at the surface and by water arriving from the Mediterranean at mid-water depths. The variety of currents influencing the islands at different depths thus has the potential therefore to create in the Açores a meeting place of marine plants and animals from different locations (Morton *et al.*, 1997). It should therefore be possible to monitor past and present colonization (and spreading) events to not just test Darwin's theory of island and biological evolution but to expand it into a programme that tests current ideas about the human-assisted introduction of exotic species (Morton & Britton, 2000b).

The above-described variety of ocean currents is predominantly responsible for the historical import onto the Açorean islands' shores of its characteristic marine flora and fauna (Morton & Britton, 2000a). Just as Darwin showed with plant seeds, Dinesen (pers. comm.) has suggested that the planktonic larvae of many marine invertebrates may spend up to four weeks in the upper water mass where current speeds of ~1.8 km $h^{-1}$ are common. Such larvae, again as with Darwin's seeds, could thus be transported ~1,200 kilometres from their spawning site and hence easily reach Açorean waters. Subsequently, such larvae may travel for up to three weeks in near-bottom waters before settling is required for post-metamorphic survival. During this time, at a common speed for near bottom advection of 0.18 kilometres hour-1 (50 mm second-1), the larvae could be transported horizontally for a further 90 kilometres, during which time settlement-inducing cues could be encountered. Hence, it is not surprising and despite their isolation, that the marine environment of the Açorean islands comprises communities, which contain species that are largely encountered elsewhere, notably in the Mediterranean (Morton & Britton, 2000a) and that are transported to them in surface ocean currents.

Thus, both algae and animals may have arrived at the Açores with ocean currents, or through rafting on mats of floating vegetation or wood and *via* human interventions although, in the latter case, as the islands have been colonized since the early part of the 15th century, the origins and routes of such introductions have been lost in time. Morton & Britton (2000b) have reviewed this subject.

## AÇOREAN BIOTIC ENDEMICITY

The terrestrial environment of the Açores has been much modified by man since the initial colonization of the islands in the early part of the 15th century. Thus, of the ~3,000 species of vascular plants found on the Açores, only 72 [68 according to Borges & Gabriel, 2009] are endemic (the Açorean enigma; Carine & Schaefer, 2009) and, even so, some 52 of these are considered threatened. Borges & Gabriel (2009) have catalogued the terrestrial taxa of the Açores and identified a total of 4,515 species. Of these, 420 are considered to be endemic: that is, 267 arthropods, 68 spermatophytes, 12 lichens, 9 bryophytes, 49 gastropods, 3 nematodes and 13 chordates. Some endemic terrestrial biodiversity may have been lost because it is estimated that, overall, but 2% of natural forest remains on the islands.

This has had readily identifiable consequences for some species and in the past, the status of the endemic Açorean bullfinch – the priolo – (*Pyrrhula murina*) was considered threatened although it is possibly making a recovery in some locations. Interestingly, this species is today restricted to the eastern end, Nordeste, of the island of São Miguel. In Darwin's time, however, it would have had a much wider distribution on this island and thus if he had landed on São Miguel, he may well have seen it, easily recognized it as subtly different from the European bullfinch (*Pyrrhula pyrrhula*) and, thereby, not only considered the Açores to be more interesting than he did, but obtaining a clear example of island endemicity. We have to remember, moreover, that Darwin did not discover the significance of the Galapagos finches' endemicity until after his return to England – the priolo, however, had he seen it, might well have revealed it to him whilst on the voyage.

Of the 107 species of Açorean terrestrial snails, some 50% (49) are endemic (Borges & Gabriel, 2009). Island endemicity is related to age, size, elevation, climate, niche availability and the degree of isolation, that is, the distance from a mainland and its biota. In the case of the Açores, some 1,200 kilometres from mainland Europe, combined with the relative youth of the islands, the low level of endemicity is hardly surprising. Further, even though they are volcanic, oceanic islands are typically unproductive. This is because such young, steep, islands cannot hold water nor retain nutrients and this helps us understand why the carrying capacity of islands is low. That is, they cannot sustain the energy-expensive lives of large animals, either herbivorous or carnivorous. Similarly, there are few endemic species of marine plants and animals on such young islands (Morton & Britton, 2000a, b). Some algae, a couple of fishes, a chiton, an ophiuroid, a few sponges, barnacles and, possibly, some of the 20 rissoid gastropods recorded from the Açores, including *Alvania mediolittoralis* (Ávila *et al.*, 2008), are considered to be endemic. As more research is undertaken, however, so either conspecifics or very closely related species are found nearby, such as in the Mediterranean, the Canaries or, even, on seamounts elsewhere.

Frias Martins (1995) recognized the Açorean rocky shore elobiid snail *Ovatella vulcani* as endemic, but as this is a pulmonate, like its endemic terrestrial leptaxine relatives, this may well be true. The intertidal limpet *Patella candei gomesii* is considered to be an Açorean endemic subspecies (Cúrdia *et al.*, 2005).

With such a wide variety of degrees of exposure to wave action in the Açorean littoral, there is a propensity for great morphological variation as has been demonstrated for the only common intertidal littorine, *Littorina striata* (Backeljau *et al.*, 1995). Without care, such ecophenotypic variation may lead to the unwarranted description of endemicity.

## MARINE CONSERVATION IN THE AÇORES

The only places where terrestrially derived nutrients are retained on steep, typically recently formed, volcanic, offshore islands are lagoons and this makes such habitats extremely important. By their very nature, the young Açorean islands arise near vertically from the seabed and two lagoons occur on the steep (precipitous) northern shore of the island of São Jorge. The sea grass *Ruppia maritima* is known only from Fajã dos Cubres (Morton *et al.*, 1995) whilst within the sediments of Fajã de Santo Cristo, also on São Jorge, occurs the only known, probably introduced, population of *Venerupis decussata* in the Macaronesian islands (Morton & Tristão da Cunha, 1993). Both of these lagoons have been described in general terms by Morton & Tristão da Cunha (1993) and Morton *et al*. (1995, 1998), and there is a marsh at Lajes on the island of Pico and which has been described, also in general terms, by Morton *et al*. (1996). All these isolated miniature lagoonal wetlands are threatened and are in urgent need of greater study. For example, it has been shown by Jordaens *et al.* (2000) that there has been a loss of genetic variation in the strongly isolated population of *Tapes* (=*Venerupis*) *decussata* in the Fajã de Santo Cristo such that it is highly vulnerable to extirpation.

In some locations on the Açores we can demonstrate that marine colonization has been not just fast, but dramatic, occurring within just a few years. On the island of Terceira, there was a

FIGURE 13. A, The quarry at Cabo da Praia on Terceira in 1995 and B, in 2006. (Photo's courtesy of J.A. Paulus Bruno).

marsh at Paul, Praia da Vitória (Morton *et al.*, 1997). This, however, has now been drained. There was, however, a coastal quarry at Cabo da Praia, also on Terceira, and which when studied for the book '*Coastal Ecology of the Açores*' (Morton *et al.*, 1998) was found to contain tidally inundated pools (Figure 13A). It was also shown to be home to numerous species of coastal plants, two species of *Assiminea* (Gastropoda), the amphipod *Orchestia mediterranea* and, a near-unique (for the Açores) collection of migrating coastal birds including some American vagrants, for instance, the Hudsonian godwit (*Limosa haemastica*). Since first described by Morton *et al*. (1997), growing numbers of bird species have been recorded from the quarry at Cabo da Praia (Table 2) with, now, 26 species identified. It is today considered to be the most significant coastal wader site in the archipelago. The question is, however, since, the quarry was only constructed in ~1983, how did such a collection of species come to colonize it?

FIGURE 14. The floor of the quarry at Cabo da Praia on Terceira in March 2010 after a cleanup by the Environmental Division of Bensaúde, one of the companies that has a concession for the fuel storage facilities at Pedreira do Cabo da Praia, adjacent to the wetland. (Photo: Marco Lopes, Bensaúde).

TABLE 2. Birds recorded from the quarry at Cabo da Praia, Terceira.

| **Species** | **July 1997 (Morton *et al.*, 1998)** | **October 1997 (Morton *et al.*, 1998)** | **February 2006 (S. Rodebrand)** | **March 2006 (B. Carlsson)** | **July/August 2007 (B. Carlsson)** |
|---|---|---|---|---|---|
| *Charadrius hiaticula* (Ringed plover) | | | 3 | 1 | |
| *Charadrius dubius* (Little-ringed plover) | Pairs | 20-30 | | | |
| *Charadrius alexandrinus* (Kentish plover) | 30 (Resident) | 30 | 39 | 30 | (96-126, x = >112 in May and June) |
| *Charadrius semipalmatus* (Semipalmated plover) | | | 1 | - | |
| *Pluvialis squatarola* (Grey plover) | 1 (First summer) | 6 (Winter plumage) | | | |
| *Calidris canutus* (Red knot) | | 7 | 3 | 3 | |
| *Calidris alba* (Sanderling) | 1 | >100 | 41 | 60 | |
| *Calidris minuta* (Little stint) | | | 3 | 3 | |
| *Calidris minutilla* (Least sandpiper) | | | 1 | - | |
| *Calidris fuscicollis* (White-rumped sandpiper) | | | 1 | - | |
| *Calidris ferruginea* (Curlew sandpiper) | | | 2 | 2 | |
| *Calidris alpina* (Dunlin) | | 5 (Winter plumage) | 4 | | |
| *Tringa ochropus* (Green sandpiper) | 1 | | | | |
| *Limosa limosa* (Black-tailed godwit) | 3 (breeding plumage) | | 1 | 1 | |
| *Limosa lapponica* (Bar-tailed godwit) | | 8 | | 1 | |
| *Limosa haemastica* (Hudsonian godwit) | | | | | 1 |
| *Numenius phaeopus* (Whimbrel) | 2 | 1 | 6 | 4 | |
| *Arenaria interpres* (Turnstone) | 12 (Adults + first summer) | 20 | 29 | 50 | (29-68, x = 54) |
| *Philomachus pugnax* (Ruff) | | | 1 | | |
| *Sterna hirundo* (Common tern) | Present | 40 | | | |
| *Sterna dougallii* (Roseate tern | Present | 2 | | | |
| *Larus cachinnans* (Yellow-legged gull) | | Present | | | |
| *Larus ridibundus* (Black-headed gull) | | 3 (Winter plumage) | | | |
| *Ardea cinerea* (Grey heron) | 3 | 4 | | | |
| *Egretta garzetta* (Little egret) | 1 | 2 | | | |
| *Anas platyrhynchos* (Mallard) | | 2 females | | | |

Charles Darwin also pondered such a question and in the *The Origins of Species by means of Natural Selection*, he considered that birds might be responsible for such rapid colonizations. He reported that:

*'..the leg of a red-legged partridge (*Caccabis rufa*) had a ball of hard earth adhering to it. … the earth had been kept for three years, but when broken, watered and placed under a bell glass, no less than 82 plants sprung from it…'* and *'can we doubt that the many birds which are annually blown by gales across great spaces of ocean and which annually migrate….must*

*occasionally transport a few seeds embedded in dirt adhering to their feet or beaks'* (Darwin, 1878).

Regrettably, along with the destruction of the marsh at Paul, the entrance to the unique, man-created, quarry habitat at Cabo da Praia, has been largely developed (Figure 13B). But what a wonderful project it would have constituted to test Darwin's theories of how coastal plants and maybe animals could have colonized Açorean shores – both by transport across the sea with ocean currents and by birds.

A postscript to this development, however, is that one of the companies which has a concession for the fuel storage facilities at Pedreira do Cabo da Praia on Terceira, adjacent to the quarry, has, in March 2010, undertaken a cleanup of the floor of Cabo da Praia (Figure 14), perhaps signaling a change in environmental awareness in relation to this highly important Açorean wetland.

Many great men both taught and influenced Charles Darwin, as a young, 22 year-old, adventurer on H.M.S. *Beagle*. These included a number of distinguished 19th century scholars upon whose shoulders Darwin stood. John Stevens Henslow was Darwin's early botanical mentor. The botanist Joseph Dalton Hooker inspired Darwin to study biogeography and how plants are transported across the oceans. Darwin's greatest mentor, the geologist Charles Lyell, inspired him to think first about geology (on Cape Verde) and then to marry his thoughts on this subject with his others on biology to come up with the great unifying theory of the evolution of life on Earth, but also the evolution of the Earth itself. And, eventually, to discover how island floras and faunas are obtained and, themselves, evolve in wonderful isolation. Robert FitzRoy, Captain of H.M.S.

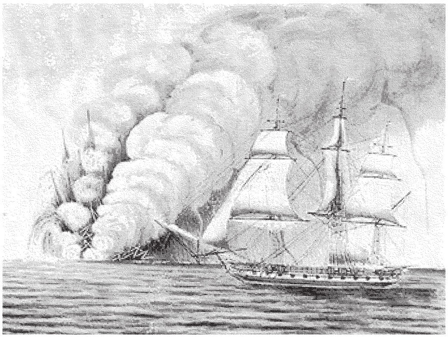

FIGURE 15. The eruption of Sabrina Island on 19 June 1811, as drawn by Lieutenant John William Miles of H.M.S. *Sabrina*. (After Tillard, 1812).

*Beagle,* became the foil against whom, as his companion naturalist, Darwin debated the ideas that were slowly fomenting in his mind. FitzRoy eventually became a Vice-Admiral, famous in his own right for creating the modern science of weather forecasting. As a devoted Christian, however, he would eventually divorce himself from Darwin's heresy and, as he saw it, unjustly awarded fame, and committed suicide by cutting his own throat on 30 April 1865.

Interestingly, an eminent Açorean, Colonel José Agostinho (1888-1978), became chief scientist with the Portuguese National Weather Service and, for providing the British with meteorological and sea-state data during the Second World War, was made an Honorary Commander in the Order of the British Empire by King George VI. This act and its recognition is in remarkable recognition of the Anglo-Portuguese Alliance of 1373. This came about when John I (1358-1433), the tenth King of Portugal and the Algarve, now famously, married, in 1387, Philippa of Lancaster, daughter of John of Gaunt (1340-1399) of England. Prince Henry the Navigator (1394-1460) was their third son so that, in many ways, the cultural and, especially, the maritime histories of Portugal and England are inextricably linked, even today. I had the privilege of meeting Colonel Agostinho in 1965 in Angra do Heroísmo.

Although the Açorean islands were of little interest to Darwin when he visited them in 1836, his views changed subsequently. Firstly, his attention was drawn to the islet of Sabrina that arose from the sea during June and July 1811 (Tillard, 1812) just opposite Ponta da Ferraria on São Miguel (Figure 15). Coincidentally, H.M.S. *Sabrina* was in the vicinity and onto the shores of the newly formed islet stepped Captain James Tillard to claim it for Great Britain. This caused a diplomatic rift until the islet disappeared back into the sea from which it had arisen in August 1811. Nevertheless, for Darwin, this was incontrovertible proof that volcanic islands do arise and may sink over the course of their lifetimes, albeit with great differences in rates. A similar event occurred in the 20th century when the Capelinhos volcano erupted on the west coast of Faial in 1957. This eruption was studied by the Açorean vulcanologist Frederico de Menezes Avelino Machado (1918-2000) and which when I visited it in 1965 was still volcanically active. Machado was assisted in this research by Victor Hugo Lecoq de Lacerda Forjaz (born 1940), who became Professor of Vulcanology at the University of the Açores and is today Director of the Observatório Vulcanológico e Geotérmico dos Açores.

Secondly, and more importantly, however, Darwin entered into correspondence with Francisco d'Arruda Furtado (1854-1887), a native Açorean, much interested in natural history, a devotee of Darwin, and a believer in evolution through natural selection. Darwin was perplexed as to how the lizard (*Lacerta dugesi*), earthworms and snails had arrived in the Açores. He asked Furtado specifically to determine if the lizard's eggs could survive in seawater. The truth is probably much more prosaic, however: all could have arrived, except for the endemic leptaxine snails (van Riel *et al.*, 2005) *via* human interventions. Indeed, Chaves (1949), provides an introduction date of 1860 for the Macaronesian lizard although this seems highly improbable. However, more interestingly, in response to a request from Furtado for research advice, in a reply letter dated 3 July 1881, Darwin suggested to him that: (1), If possible, the most distant outlying islands and their plants and animals should be compared with those of the other islands; (2), all the plants and animals from the highest mountain summits on all the islands ought to be collected; (3), searches made for glacial deposits and for the presence of fossil remains, in such stones and (4), any light-houses should be inspected for any land-birds that might have flown into the glass and killed. In such cases, their feet and beaks should be examined not only for earth, but the whole contents of their alimentary canals dried out and placed on damp pure sand under a small bell-glass to see if any seeds are present which would germinate. If so, grow any plants and name them.

Thirdly, as described above, Darwin knew that seeds from the New World occurred regularly on Açorean beaches and he used this fact as the *raison d'etre* for his experiments on the survival of seeds and other plant pieces in seawater. Thus, when asking his friend Joseph Hooker for seeds to be collected from Hitcham in Suffolk, England, he specifically requested that they include those from plants also known to grow in the Açores.

Hence, although Darwin's visit to the Açores was not initially inspiring, the islands subsequently became so for him. Similarly, he laid down the initial basis for our understanding of how the Açorean flora and fauna was obtained. Finally, however, and although the word conservation was not in Darwin's vocabulary (in the natural history sense), his researches upon and understanding of the forces that created the archipelago and how they became colonized show us what is important with regard to marine conservation in the Açores.

The predominant rocky shores, washed by oceanic currents are probably going to provide us with only a few, if any, examples of endemic species. There may similarly be few endemic species making up the communities of other intertidal habitats. In one or two places in the Açores, however, there are intertidal, lagoonal, wetlands. In particular, Fajã dos Cubres and Fajã de

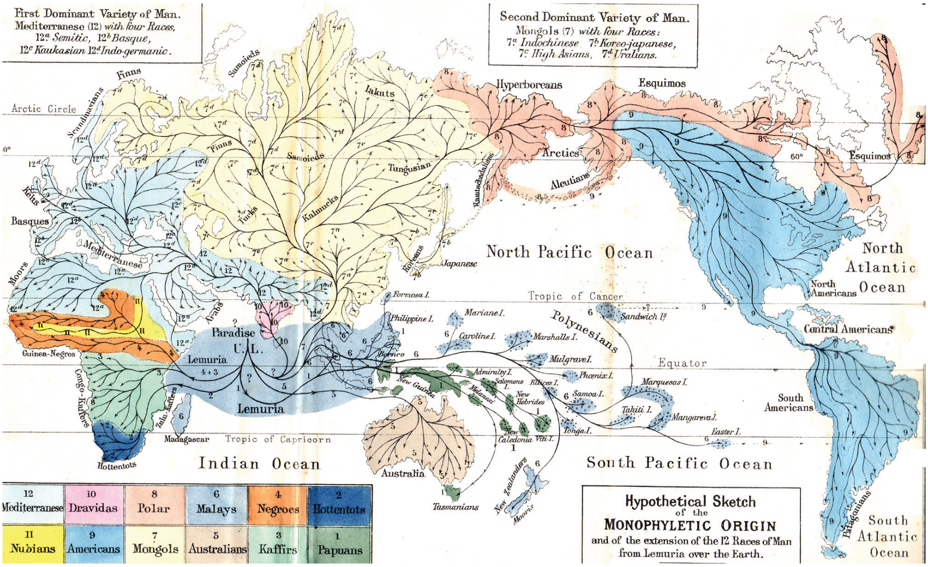

FIGURE 16. An illustration showing the origins of mankind from Paradise – Lemuria – located in the Western Indian Ocean. The frontispiece to Ernst Haeckel's *History of Creation* (1876).

Santo Cristo, both on São Jorge, the marsh at Lajes on the island of Pico and, especially, the quarry at Cabo da Praia on Terceira, have much to reveal about how such isolated communities have become established – a question that Darwin was deeply concerned with, but who never saw these little habitats in the Açores. In particular, the modern quarry at Cabo da Praia, on Terceira, because it is isolated from sea, except *via* the surrounding basaltic rock wall filter could tell us much about the origins of the Açorean biota and, more interestingly, how its representatives have obtained purchase on the islands.

In his understanding of the evolution of life, Darwin also discovered important facts concerned with the evolution of the Earth, thereby achieving the marrying of biology and geology, that is, the unification of the history of life on Earth and, finally, the rejection of the biblical account of creation. It is interesting though, that despite meeting, believing in evolution through natural selection and supporting Darwin, Ernst Haeckel (1834-1919), the great German anatomist, embryologist and illustrator, continued to argue that human evolution consisted of exactly 22 phases, the 21st (back in time), being the 'missing link' and representing a halfway step between apes and humans. But, that our origins were still in Paradise (Figure 16). Clearly, even this enlightened contemporary of Darwin, still felt the need to acknowledge the Christian orthodox view of Genesis. But the illustration represents more, because its image of human evolution still resonates today in the minds of some, generations later, and highlights the continuing struggle between science and faith for the soul of humanity and haunts the progress of humankind towards a more tolerant world.

In the context of island evolution, however, and especially in the comparatively new geological context of the Açores, the researches of Charles Darwin remain unchallenged and are critical to our understanding of island biogeography. And it is his seminal discoveries that have, in turn, led to a better understanding of the need for conservation not only on land, but also on the riparian edge of the sea, especially on island archipelagos where new found life clings precariously.

## ACKNOWLEDGEMENTS

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# *The dynamics of Colonization*

AÇOREANA, 2011, Suplemento 7: 75-91

# SPECIATION AND THE EVOLUTION OF DARWIN'S FINCHES

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## ABSTRACT

Speciation is a process of divergence of two lineages formed from one, which eventually leads to a cessation of gene exchange. Darwin's finches in the Galápagos archipelago exemplify the three-step process envisioned by Charles Darwin: initial colonization of a new area; divergence in separate locations, chiefly through natural selection; and finally the development of a barrier to interbreeding between the divergent lineages. In this article we summarize findings from our long-term study of finch populations that was designed to throw light on this important part of evolutionary biology. Finch species differ mainly in beak size and shape, two traits that are heritable. Two genes that affect development of beaks differently in the species of ground finches have been discovered. Evolution by natural selection of beak size has been inferred from indirect evidence. The evidence includes a successful prediction of beak sizes on several islands according to island-specific distributions of seed sizes. There is direct evidence on Daphne Major Island where the medium ground finch population (*Geospiza fortis*) has several times experienced natural selection during droughts. This can be considered as a model of divergent evolution that takes place in allopatry. In 1983 Daphne was colonized by the large ground finch (*G. magnirostris*). Many years later *G. fortis* diverged from it during a severe drought, becoming smaller on average as a result of a competitive interaction and natural selection. It is an example of character displacement, and a model of divergent evolution at the secondary sympatric phase of speciation.

A pre-mating barrier to interbreeding arises in allopatry as a result of divergence in beak morphology and song. Paternal song and the appearance of both parents are learned early in life, and later they are used when mates are chosen. The sexual imprinting results in a pre-mating reproductive isolation from coexisting species that differ in song and morphology. The barrier to interbreeding occasionally leaks through hybridization, and the resulting hybrids backcross to one species or the other depending on the song of their fathers. No intrinsic post-zygotic isolating factors have been identified. When feeding conditions that are suitable for hybrid survival persist for many years, species converge as a result of introgression; speciation then goes into reverse. Over the long course of finch history there have probably been numerous oscillations in climatic and feeding conditions, causing finch populations to alternate between fission and fusion tendencies. Eventually the species diverge so much that they no longer interbreed; at this point gene exchange ceases and fission becomes permanent.

## RESUMO

A especiação é um processo de divergência de duas linhagens formadas a partir de uma, que eventualmente leva a uma cessação de troca genética. Os tentilhões de Darwin no arquipélago das Galápagos exemplificam o processo em três etapas previsto por Charles Darwin: colonização inicial de uma nova área; divergência em sítios separados, principalmente através de selecção natural; e finalmente o desenvolvimento de uma barreira ao cruzamento entre as linhagens divergentes. Neste artigo sumarizamos as descobertas do nosso estudo de longo termo sobre populações de tentilhões, o qual foi desenhado para lançar luz sobre esta parte importante da biologia evolutiva. As espécies de tentilhões diferem sobretudo no tamanho e forma do bico, duas características que são hereditárias. Foram descobertos dois genes que afectam de maneira diferente o desenvolvimento dos bicos nas espécies de tentilhões do solo. A evolução do tamanho do bico por selecção natural tem sido inferida por evidência indirecta. A evidência inclui a predição bem sucedida dos tamanhos dos bicos em várias ilhas de acordo com as distribuições específicas para cada ilha dos tamanhos das sementes. Há evidência directa na Ilha de Daphne Major onde a população do tentilhão-de-solo-médio (*Geospiza fortis*) tem por várias vezes experimentado selecção natural durante secas. Tal pode ser considerado um modelo de evolução divergente que acontece em alopatria. Em 1983 Daphne foi colonizada pelo tentilhão-de-solo-grande (*G. magnirostris*). Muitos anos mais tarde *G. fortis* divergiu deste durante uma seca severa, tornando-se em média mais pequeno como resultado de interacção competitiva e selecção natural. É um exemplo de

deslocamento de caracteres, e um modelo de evolução divergente na fase simpátrica secundária da especiação.

Uma barreira pré-acasalamento ao entrecruzamento aparece em alopatria como resultado de divergência na morfologia do bico e no canto. O canto paterno e o aspecto de ambos os progenitores aprendem-se cedo na vida, e são usados mais tarde quando se escolhem os parceiros. A impressão sexual resulta num isolamento reprodutor pré-acasalamento de espécies que co-existem e que diferem em canto e morfologia. A barreira ao entrecruzamento falha ocasionalmente através da hibridização, e os híbridos resultantes cruzam-se de novo com uma ou outra espécie dependendo do canto dos seus pais. Não foram identificados factores de isolamento pós-zigóticos. Quando persistem por muitos anos condições favoráveis à sobrevivência dos híbridos, as espécies convergem como resultado da introgressão; a especiação então faz marcha atrás. Durante o longo curso da história dos tentilhões devem ter acontecido numerosas oscilações nas condições climáticas e de alimentação, causando nas populações de tentilhões alternância entre tendências para fissão e fusão. Eventualmente as espécies divergem de tal modo que deixam de se entrecruzar; nessa altura deixa de existir troca de genes e a fissão torna-se permanente.

## INTRODUCTION

One hundred and fifty years ago Charles Darwin established the scientific basis for understanding how evolution occurs by natural selection. He developed the principle of natural selection and applied it to the question of how new species form. Speciation is the process by which one species splits into two (Figure 1). Darwin was much clearer on how speciation began than how it finished. In his view geographical separation of populations was a vital factor. To one of his many correspondents he wrote:

> *"… those cases in which a species splits into two or three or more new species … I should think near perfect separation would greatly aid in their "specification" to coin a new word"* (Darwin 1878).

Fortunately "specification" did not catch on and we now use the term speciation.

To understand how the process is completed we have to move forward well into the era of Mendelian genetics to find a clear, minimally sufficient, statement from a population geneticist. Hermann Muller (1940) wrote

> *"Thus a long period of non-mixing of two groups is inevitably attended by the origination of ac-tual immiscibility, i.e. genetic isolation".*

Genetic drift would be enough, though natural selection would help.

The theme of this article is that many interesting evolutionary events evolutionarily can occur between the beginning of speciation and the end. We have learned this by following in Darwin's footsteps in the Galápagos, studying in detail the finches that were named after him by Lowe (1936) in recognition of how they helped him develop his theory of evolution by natural selection.

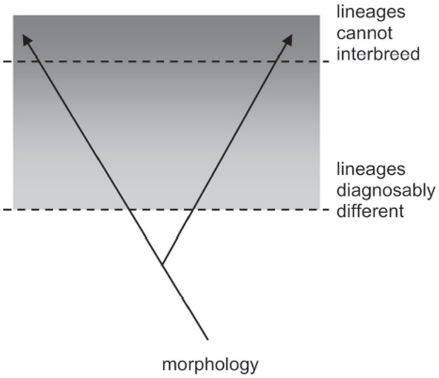

FIGURE 1. The evolution of two species from one. From Grant & Grant (2008).

## DARWIN'S FINCHES

Darwin envisaged a three-step process in the formation of a new species: colonization of a new area; divergence in separate locations, when populations become adapted to novel environmental conditions through natural selection; and finally, the formation of a barrier to interbreeding between divergent lineages. He showed characteristic insight by suggesting that investigations of what we now call, "young adaptive radiations" could provide windows through which we might view the processes involved. Darwin's finches are ideal in many ways for doing this. They constitute a young adaptive radiation that is present and intact in the environment in which the species evolved over the last two to three million years. Thirteen species occur in the Galápagos archipelago, and a fourteenth occurs to the north on Cocos Island. On several of the islands the natural vegetation has been scarcely affected by humans, if at all, therefore whatever we can discover about the relationship between finches and their environment can be directly extrapolated backwards in time to the conditions under which the finches evolved without having to make any qualifications. Unfortunately this cannot be said about other classical adaptive radiations elsewhere, such as the cichlid fish in the Great Lakes of Africa or the honeycreeper finches of the Hawaiian archipelago.

## SPECIATION

The geographical essence of Darwin's concept of speciation is captured in Figure 2: first an allopatric phase with divergence, then a sympatric phase with or without interaction. Evolutionary biologists have argued about the relative importance of various factors in these two phases. Genetic drift, for example, may or may not play an important role in divergence whereas natural selection almost certainly does. Divergence in allopatry may be pronounced enough to allow coexistence in sympatry without any interaction (Stresemann, 1936). David Lack (1945, 1947) argued this was unlikely, given the extreme similarity of some of the species. He suggested instead that the species would probably interact in sympatry, competing for food, an ecological interaction, and interbreeding to a small extent, a reproductive interaction. If the morphologically most similar individuals of the two populations suffered the most, because they were the most likely to compete for food and interbreed with a loss of fitness, further divergence of the sympatric populations would occur under natural selection, minimizing competition and the chances of interbreeding. The net result would be coexistence of ecologically differentiated and reproductively isolated species.

## ADAPTATION IN ALLOPATRY

Populations of the same species on different islands differ in both morphology and ecology. For example the sharp-beaked ground finch (*Geospiza difficilis*) is small and has a small beak on Genovesa, an island where the dry season food supply is dominated by small seeds, nectar, and pollen. On other islands, such as Pinta, Santiago and Fernandina, with larger and harder seeds, fruits, and arthropods, the beaks of this species are large and more robust. Evolutionary biologists often infer adaptive evolution by natural selection in

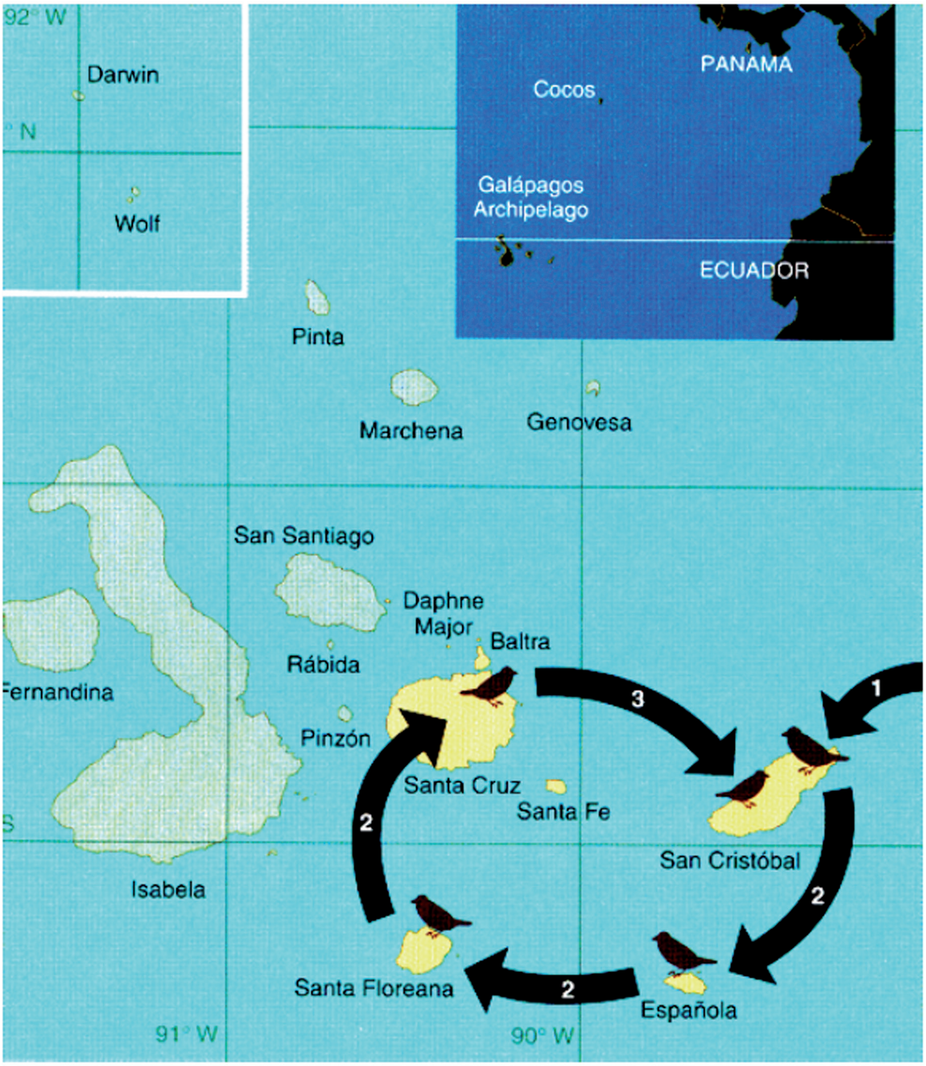

FIGURE 2. A representation of the three-step process of allopatric speciation. From Grant & Grant (2008).

the past from associations like these between organisms and their environment (Bowman, 1961).

The adaptive argument has been strengthened by a successful prediction of beak sizes of finches on an island from a measure of their food supply (Schluter & Grant, 1984). The distribution of sizes of seeds on an island gives a quantitative profile of the ecological opportunity available to the granivorous *Geospiza* species. This is sometimes referred to as an adaptive landscape. We estimated the adaptive landscapes on 16 islands by randomly sampling the seed supply on each. The estimation procedure involved establishing two relationships across all species and all islands, and integrating them: between seed size and beak size, and between finch population biomass and seed bio mass. Each of the landscapes has one to three peaks in expected population density in relation to beak size. Then, we compared the beak sizes of finches on an island, one at a time, with those beak sizes predicted from the expected maxima in density (Figure 3), with four results. First, observed beak sizes of the four granivorous species of finches closely matched the predicted beak sizes. Second, no two species occupied the same position on the beak size axis in relation to a peak in density. Third, all of the peaks were occupied by a finch species. Fourth, the identity of the finch species beneath a peak changed from one island to another in some cases, nevertheless the alignment with the peak was always maintained.

Notwithstanding support from inferential evidence, the adaptive argument could be im-

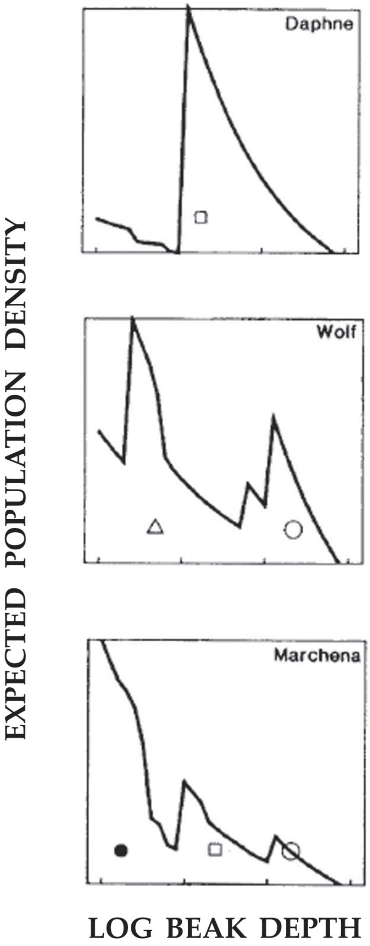

FIGURE 3. Alignment of *Geospiza* species with peaks in an adaptive landscape. Symbols: square, *G. fortis*; triangle, *G. difficilis*; open circle, *G. magnirostris*; closed circle, *G. fuliginosa*. Adapted from Schluter & Grant (1984).

proved. It would be helped if natural selection could be demonstrated as an observed process instead of just being inferred. We have been able to demonstrate the process on the small island of Daphne Major in the center of the archipelago. The island is about 120 m high, 0.75 km long, 0.5 km wide and has never been settled by humans.

## NATURAL SELECTION

We began a detailed study of the medium ground finch (*G. fortis*) and the cactus finch (*G. scandens*) in 1973. By capturing a large number of finches in mistnets, banding them with a unique combination of color and metal bands, measuring and weighing them, and then releasing them, we were able to quantify the feeding of finches of known measurements (Boag & Grant 1984). We soon found that large-beaked members of the *G. fortis* population were able to crack open large and hard seeds, whereas smaller members of the population either were unsuccessful or did not even attempt to do so. As mentioned above, food size is positively correlated with beak size; finches with large beaks can crack open large and hard seeds whereas finches with small beaks cannot, for mechanical reasons (Bowman, 1961; Herrel *et al.*, 2005). Importantly, we then determined that beak size was a highly heritable trait from a regression of measurements of offspring on the measurements of their parents. The heritability of beak depth was approximately 0.75, on a scale of 0 to 1. This is unusually high.

We were lucky to be present in 1977 when a severe drought affected the archipelago. This was not so fortunate for the finches, for 85 percent of the *G. fortis* population died. Survival was size-selective: large birds survived better than small ones (Figure 4). The reason lay in their ability to crack or tear open the large woody fruits of *Tribulus cistoides* that were relatively common after the majority of small and soft seeds had been consumed.

Natural selection in 1977 was followed in 1978 by an evolutionary response in the population when the survivors bred and produced the next generation (Figure 4). The offspring were large like their parents, and distinctly larger than the population average before selection began in 1976. In fact the average size of the offspring measured when they had reached full adult size was predicted with remarkable accuracy by the breeder's equation, where *r*, the evolutionary response to selection, is given by the product of the heritability of the trait ($h^2$) and a measure of the strength of selection (*s*).

This was not a unique event. During the next 25 years we documented other episodes of selection, smaller in magnitude, associated with droughts (Figure 5), and oscillating in direction according to the particular food supply at the beginning of each drought (Grant & Grant, 2002).

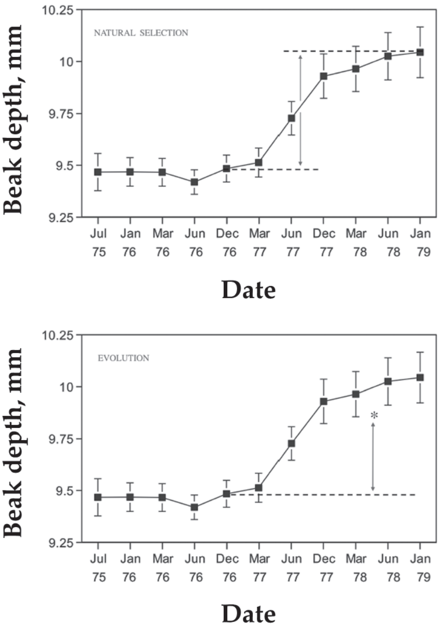

FIGURE 4. Natural selection in 1977 (above). The magnitude of the evolutionary response in the next generation (below) was determined by the strength of selection and the heritability of beak depth.

## CHARACTER DISPLACEMENT IN SYMPATRY

The preceding example of natural selection involved no interaction between populations of finches. It can be considered a model of how adaptive evolution occurs in allopatry, driven by a change in the environment. Whether or not the population of *G. fortis* on the neighboring island of Santa Cruz had changed at the same time is not known, as it was logistically beyond our capacity to study populations in both places at the same time. Almost 30 years after our first documentation of natural selection another episode of selection

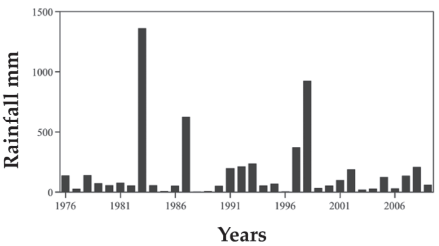

FIGURE 5. Annual variation in the rainfall on Daphne Major Island.

took place, and this time interactions between species did occur (Grant & Grant 2006). This episode can be considered a model of how adaptive evolution occurs in sympatry, driven not only be a change in the environment but also by competition for a limited supply of food.

In 2003 and 2004 the island experienced another drought, and when it ended with rain falling in February of 2005 90 percent of the *G. fortis* population had died. This was not a repetition of the 1977 drought, but instead a selective shift towards small beak size occurred (Figure 6). The reason lay in interactions with another species, *G. magnirostris*, the large ground finch (Figure 7). *Geospiza magnirostris* established a breeding population on the island in 1983 at the beginning of an extraordinarily long and intense El Niño event that brought more than a meter of rain to the island. The population gradually increased in size, so when the drought began in 2003 there were more than 200 alive on the island. Being superior competitors for *Tribulus* fruits, *G. magnirostris* caused a decline in the larger members of the *G. fortis* population that previously, in 1977, had survived relatively well on those fruits. As a result the average beak size of the *G. fortis* population declined to an unprecedented low size (Figure 6). The offspring generation also had small beaks, as expected from the high heritability of beak size. Evolution by natural selection had occurred once again, leading to a divergence of the interacting populations. In other words, it was an example of character displacement (Grant & Grant, 2006).

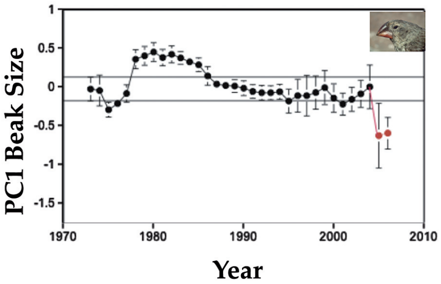

FIGURE 6. Natural selection on *G. fortis* in 2004-05 caused by competition with *G. magnirostris.* From Grant & Grant (2006, 2008).

## REPRODUCTIVE ISOLATION

For coexistence in sympatry to be sustained it is not enough that different, they should be reproductively isolated from each other. How does reproductive

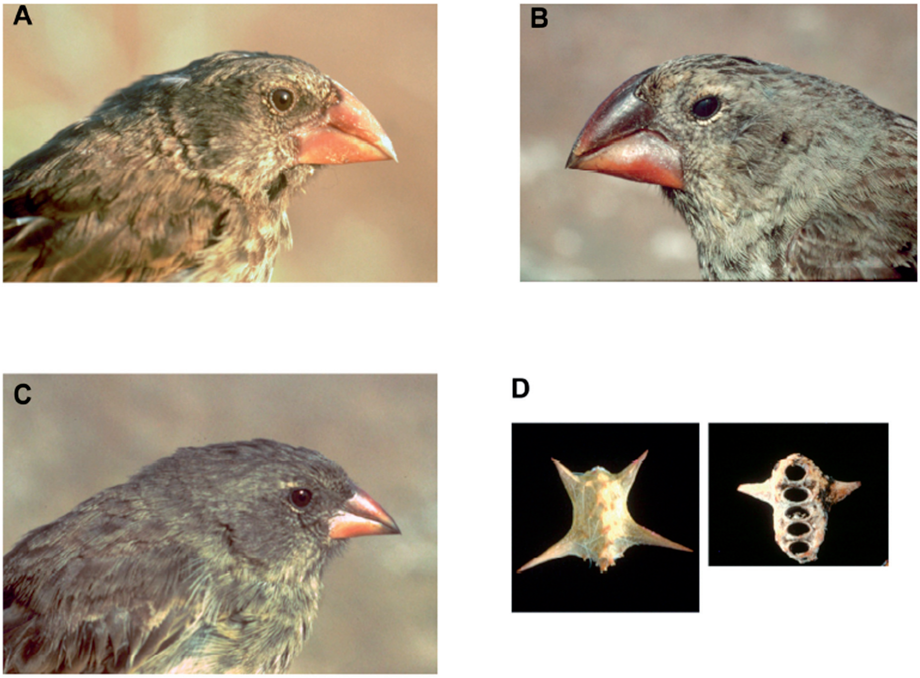

FIGURE 7. During a drought large *G. fortis* (A) compete with *G. magnirostris* (B) for the seeds of *Tribulus cistoides* (D) and die at a higher rate than the small *G. fortis* (C), which can only feed on small seeds. The result is natural selection (Figure 6) and character displacement of *G. fortis*, an enhanced difference between the two species. From Grant & Grant (2006).

isolation arise between coexisting species and what constitutes the barrier to interbreeding? For many species of birds differences in plumage color and pattern, and differences in courtship behavior, constitute the barrier. These factors are not applicable the Darwin's ground finches. Instead the species differ in song and morphology, especially in the size and shape of their beaks. The role of each of factor in species discrimination and mate choice has been tested experimentally. A set of experiments on several islands with pairs of stuffed museum specimens showed that ground finches discriminate populations between their own and another species by using visual cues in the absence of song (Ratcliffe & Grant, 1983). Another set of experiments with playback of tape-recorded song demonstrated that species are capable of discriminating on the basis of acoustic cues alone, in the absence of visual cues (Ratcliffe & Grant, 1985). These two sets of cues function in tandem. Research by Robert Bowman (1983) with captive finches gives clues as to how this happens. Using birds raised in sound-proof chambers he demonstrated that song is learned early in life in an imprinting-like process. The sensitive period for learning appears to be short, from approximately day 10 to day 40 of age, when the offspring are dependent on their parents for food. They frequently see both parents at this time. Thus paternal song and the appearance of both parents are learned early in life, and later they are used when mates are chosen (Grant & Grant, 1998). This process is sexual imprinting, and it typically constrains the choice of mates to a member of the same species.

## A BARRIER THAT LEAKS

Species-specific song and morphology are the two elements of the barrier, a pre-mating barrier, to interbreeding. Occasionally the barrier leaks when species interbreed, which gives us the opportunity to determine if a post-mating barrier between species also exists. Interbreeding occurs when the imprinting process is perturbed, for example by the death of the father while the offspring are in the nest. If another species is nesting nearby, the offspring may learn the song sung by the male of that species. We have also known a pair of *G. scandens* that usurped the nest of a pair of *G. fortis*, resulting in one *G. fortis* egg hatching and being raised by the pair of *G. scandens*. The *G. fortis* male, cross-fostered by *G. scandens*, sang a *G. scandens* song.

In the first ten years of our study hybrids did not survive long enough to breed. We thought they might have suffered from some intrinsic weakness due to their genetic composition. However, as an alternative possibility, they might have died of starvation because at that time there was a lack of seeds in the dry season suitable for birds of their intermediate size; this was a time when *Tribulus* fruits dominated the composition of the food supply in the dry season. This second possibility turned out to be correct because from 1983 onwards hybrids survived well and bred. The 1983, 1987 and 1991 cohorts of hybrids and backcrosses combined survived as well as if not slightly better than the species that gave rise to them (Figure 8). They attracted mates, displaying the same imprinting in doing so as the two parental species, that is they chose mates according to the song sung by their fathers. They laid eggs and fledged offspring with as much success as the species. Thus hybrids and backcrosses do not seem to be at a fitness disadvantage, for reasons of either viability or fertility. Therefore these species are reproductively isolated from each other by a premating barrier that leaks, rarely, and there is no post-mating barrier.

## SPECIATION IN REVERSE

Genetically compatible species that interbreed converge morphologically, reversing the process of divergence that gave rise to the two species in the first place. *G. fortis* and *G. scandens* are currently experiencing convergence on Daphne (Figure 9). If the exchange of genes and resulting convergence continues without being checked it will eventually lead to the fusion of the species into a single panmictic population. If this happens, speciation will have collapsed. However convergence may stop if environmental conditions

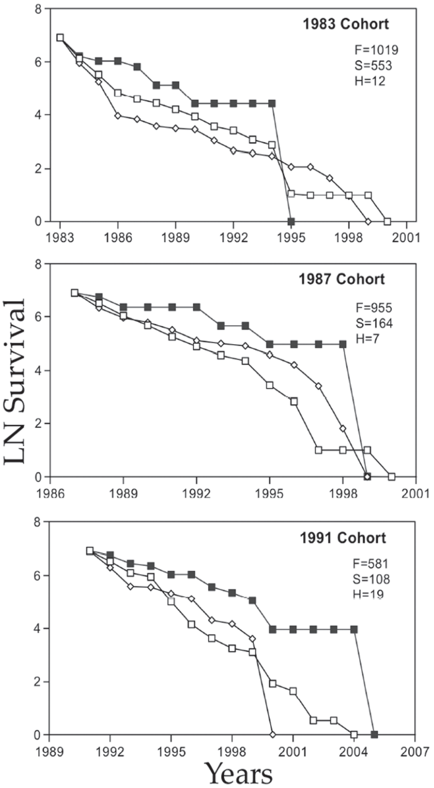

FIGURE 8. Survival of hybrids (including backcrosses) (H) in relation to the two parental species, *G. fortis* (F) and *G. scandens* (S). Symbols: Diamonds, *G. fortis*; open squares, *G. scandens*; filled squares, hybrids. From Grant & Grant (2008).

change. If the environment reverts to a state similar to that in the 1970's when hybrids did not survive long enough to breed they will diverge again. We consider it likely that climatic and botanical conditions have oscillated repeatedly over the long course of finch history, causing finch populations to alternate between fission and fusion. Eventually fission becomes permanent. How does this happen?

Again, the Daphne study provides some valuable insight. The barrier to interbreeding becomes watertight, and hence interbreeding ceases altogether, when the species differ in morphology to a pronounced degree. On Daphne Major *G. magnirostris* has never hybridized with the two resident and distinctly smaller species *G. fortis* (Figure 9) and *G. scandens*, despite some occasional misimprinting. At least nine male *G. fortis* have misimprinted on *G. magnirostris* song over a period of 25 years. If song was the only cue used in the choice of a mate, *G. fortis* should have bred with *G. magnirostris*, as they have done with *G. scandens*, but this has never happened. Instead, those misimprinted *G. fortis* that have nested near a pair of *G. magnirostris* have been repeatedly harassed by the male. The only misimprinted *G. fortis* male to have successfully bred almost gave up singing, and then obtained a conspecific mate. In this case morphology was clearly the sole basis of mate choice. Consistent with this, *G. fortis* do occasionally pair and apparently breed with *G. magnirostris* on Santa Cruz where the difference between the species is smaller. Therefore interbreeding diminishes as the species continue to diverge and eventually fission becomes permanent.

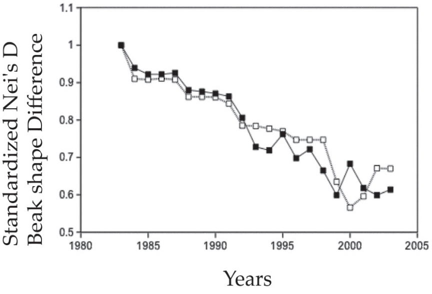

FIGURE 9. Convergence of *G. fortis* and *G. scandens* in microsatellite profiles (closed symbols) and beak shape (open symbols) as a result of introgressive hybridization. From Grant & Grant (2008).

## EVOLUTIONARY POTENTIAL OF HYBRIDIZATION

Introgressive hybridization was once thought to be rare and mainly a phenomenon of plants, but is now known to occur in a wide variety of taxa, from micro-organisms to macro-organisms (Schwenk *et al.*, 2008). It could cause a collapse of two species. We have speculated that it does more than this. Under favorable ecological conditions it might allow one or both of the hybridizing species to evolve faster, or even along a new trajectory, than would otherwise be possible (Grant & Grant, 2008). This idea follows from the increase in additive genetic variance underlying continuously varying, ecologically meaningful, traits like beak size that occurs with introgressive hybridization. Introgression of genes has another effect, it weakens the genetic correlation between traits if the hybridizing species differ in their allometries. The enhanced genetic variation and altered genetic covariation relaxes constraints on further evolution and enhances the potential for change. Thus introgressive hybridization could be an important factor in the early stages of speciation.

## GENETIC FACTORS INVOLVED IN THE DEVELOPMENT OF BEAKS

An investigation has recently begun into the genetic basis of observed variation at the level of individual genes. Arhat Abzhanov and colleagues have discovered two genes that are expressed differently in the development of beaks of the six ground finch species. Bone morphogenetic protein (Bmp4) affects beak development in depth and width planes (Abzhanov *et al.*, 2004) and Calmodulin (CaM) influences length development (Abzhanov, 2006). The two genes influence beak growth at roughly the same time (about day 5) in embryonic development, but independently. Therefore a change in beak shape follows from a change in expression of just one of them. These findings raise many questions about gene regulation and interaction with other genes that current research is attempting to answer. Eventually it may be possible to identify the exact genetic basis of beak variation within a population, and to understand how variation within a population is converted to variation (differences) between or among species. When that happens we will then have a much better comprehension of how one species becomes two: the origin of species, to use Darwin's language.

## EPILOGUE

We end with a conservation message. Galápagos has taught us that neither species nor environments are static entities, but dynamic, and constantly changing. Therefore to conserve species and their environments, we must keep them both capable of further change.

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# PATTERNS OF COLONIZATION AND SPECIES DISTRIBUTION FOR AZOREAN ARTHROPODS: EVOLUTION, DIVERSITY, RARITY AND EXTINCTION

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## ABSTRACT

Here we address a list of questions based on long-term ecological and biogeographical studies performed in the Azores, a remote volcanic oceanic archipelago composed by nine islands. The target group are the arthropods, and the main habitat the *Laurisilva*, the Azorean native forest. Diversification of Azorean arthropod species is affected by island age, area and isolation. However, results obtained for over a decade show that distinct groups are differently affected by these factors, which has lead to the extreme diverse distribution patterns currently observed. Spatial distribution of arthropods in each island may be interpreted as caused by a typical “mass effect”, with many species following a “source-sink” dynamics. Truly regionally rare species are those that are habitat specialists, many of them being threatened endemic species. Although various endemics persist as sink populations in human-made habitats (*e.g.*, exotic forests), more than half of the original endemic forest arthropods may already have vanished or may eventually be driven to extinction in the future. Those species which have evolved in and are mainly found in native forests, have been dramatically affected by hitherto unrecognized levels of extinction debt, as a result of extensive destruction of native forest. We argue that immediate action to restore and expand native forest habitat is required to avoid a future of disastrous extinctions of a biologically unique fauna with an unique evolutionary history.

## RESUMO

Com base em estudos ecológicos e biogeográficos realizados nos Açores (um arquipélago remoto composto por nove ilhas vulcânicas) durante muitos anos de uma forma continuada, apresentamos um conjunto de questões. O grupo alvo são os artrópodes e o principal habitat é a Laurissilva, a floresta nativa dos Açores. A diversificação das espécies de artrópodes dos Açores é afectada pela idade das ilhas, área das ilhas e seu isolamento. No entanto, os estudos que decorreram durante os últimos dez anos mostram que os vários tipos de grupos taxonómicos e ecológicos são afectados de forma diferente por estes factores, tendo como consequência padrões de distribuição espacial únicos. A distribuição espacial dos artrópodes em cada ilha é causada for “efeitos de massa”, muitas espécies possuindo dinâmicas “fonte-sumidouro”. As espécies verdadeiramente raras à escala regional são aquelas que são especialistas de um particular habitat, muitas delas sendo espécies endémicas ameaçadas. Embora várias espécies endémicas persistam com populações sumidouro em habitats criados pelo Homem (e.g. florestas exóticas), mais de metade das espécies especialistas da floresta nativa já estão extintas ou poderão extinguir-se no futuro. De facto, aquelas espécies que evoluíram e apenas são encontradas nas florestas nativas, foram afectadas de forma dramática como resultado da destruição alargada das florestas nativas dos Açores. Defendemos que a única forma de evitar a extinção de uma fauna única das florestas nativas dos Açores será através de medidas de restauro desta floresta.

## INTRODUCTION

Charles Darwin and Alfred R. Wallace were both fascinated by islands and the foundations of their evolutionary theory were mostly based on evidences obtained from isolated oceanic islands like the Galápagos, Hawaii and Madeira. Their initial observations and conclusions were seminal for the formulation of comprehensive theorems and hypotheses on evolutionary mechanisms responsible for the maintenance and increase of biodiversity following island colonization. Since then, islands have been regarded as natural laboratories for the study of evolutionary, ecological and ecosystems processes (Vitousek *et al.*, 1995; Wagner & Funk, 1995; Clarke & Grant, 1996; Thornton, 1996; Whittaker & Fernández-Palacios, 2007), due to their isolated character and their depauperated and disharmonic faunas and floras (Carlquist, 1974; Williamson, 1981; Whittaker & Fernández-Palacios, 2007). Changes in traits related to defences and flight, species radiation and endemism, as well as occupation of vacant niches, are just some examples of important fundamental concepts in Evolutionary Ecology developed as the result of data obtained from island biology studies (Whittaker & Fernández-Palacios, 2007). Not surprisingly, one of the most popular models in ecological literature is the "Theory of Island Biogeography" (MacArthur & Wilson, 1963, 1967), designed to explain patterns of species richness on islands, but with wider applications, namely in biodiversity, conservation and management (Rosenzweig, 2004).

Studies of island species and their natural histories have become fundamental to the understanding of the evolution, biology and ecology of animals and plants. Good examples are the now classic works of Carlquist (1974) and Williamson (1981). Some important works were published about island archipelagos, like the Atlantic Islands (Berry, 1992; Hounsome, 1993; Biscoito, 1995; Ashmole & Ashmole, 2000; Fernández-Palacios & Martin Esquivel, 2002; Fernández-Palacios & Morici, 2004; Serrano *et al.*, 2010), Hawaii (Wagner & Funk, 1995), Krakatau (Thornton & Rosengren, 1988; Thornton, 1996), Pacific Islands (Keast & Miller, 1996) and Pitcairn Islands (Benton & Spencer, 1995). Special publications on evolution on islands (Clarke & Grant, 1996; Emerson, 2002; Gillespie & Roderick, 2002) and one unique on ecological function (Biological Diversity and Ecosystem Function on islands - Vitousek *et al.*, 1995) have been published recently. More than describing unusual body adaptations, such as wingless birds and giant, arborescent herbs, recent studies emphasise how unique and distinct oceanic island ecosystems are. Special attention is given to how fragile these ecosystems are and the need of urgent conservation measures.

Here we describe the results of a long-term ecological study on arthropods carried out in the Laurisilva, the native forest of the Azores, a remote volcanic oceanic archipelago. We address a list of questions arising from the results obtained from a number of studies performed in the last ten years.

## AZOREAN NATURAL HISTORY AND BIODIVERSITY

Charles Darwin visited the Azores during the expedition of the *Beagle* (September 1836) (Keynes, 1988). Despite a discussion on the mechanisms of dispersal, making reference to the neighbouring archipelago of Madeira, and some mention to arborescence of *Erica azorica* (only studied recently by Ribeiro *et al*., 2003), he made no significant comments about the arthropods of the Azores. Although the Azores is an isolated archipelago with a diverse geological history and a wide range of elevations, the relatively low endemic richness and the lack of remarkable adaptive radiation compared with other archipelagos (*e.g.*, Canary Islands) resulted in it receiving less attention (but see Wallace, 1876).

Crotch (1867) comments on the almost complete indifference of naturalists towards the Azores, noting, as an example, that while the English entomologist T.V. Wollaston intensively sampled in archipelagoes of Madeira, the Canaries and Cape Verde, he did little in the Azores. The historical lack of interest on Azorean arthropods can, in part, be explained by the lack of knowledge of the faunistic composition of many Azorean taxa until recently (but see Borges *et al*., 2005a, 2010a), but this trend is changing. Recently there has been an increasingly interest in the Azorean biota that is reflected in the raising number of publications on the biogeography, ecology, applied entomology, biospeleology and systematics of its arthropods (see details below). The present work shows the importance of evidence obtained from the Azores for the understanding of general island processes.

The current estimate of terrestrial species and/or subspecies in the Azores is 6,164 (about 6,112 species), of which 452 (411 species) are endemic (Borges *et al.*, 2010a) (see Table 1). Arthropods are the most diverse taxon with about 2,298 species and subspecies, 266 of which are endemic (Table 1; see also Borges *et al.*, 2010a).

## AZOREAN ARTHROPOD BIODIVERSITY: THE MAIN QUESTIONS

Invertebrates are generally relegated to a secondary place in biodiversity conservation programs and there are sociological, educational and scientific reasons for this (Cardoso *et al.*, 2011a, b). One significant factor is the lack of communication between scientists and stakeholders and overcoming this problem is essential for all ongoing arthropod research projects. Conservation of the Azorean natural biodiversity requires the elaboration of a global and integrated strategy based on the knowledge of current species distributions and how of current land-use will impact future distributions (see *e.g.*, Borges *et al.*, 2008; Cardoso *et al.*, 2009b; Meijer *et al.*, 2011). Consequently it is crucial to understand how land overexploitation, increased tourist activities, displacement of native species by exotic ones and climate change, may affect Azorean biodiversity and ecosystem functioning. In the last ten years we have invested considerable effort to raise awareness about the importance of Azorean arthropod biodiversity relative to the total biodiversity of the Azores and of the Atlantic Biogeographic Region (see *e.g.*, Borges *et al.*, 2005a, 2008a, 2010a). Our ultimate goal is to ensure that the highly diverse endemic arthropods island biodiversity conservation areas are protected, in the hopes that this will halt, and hopefully reverse, the general trend of biodiversity decline in the Azores (see Triantis *et al.*, 2010a).

The BALA project (2000-2010; **B**iodiversity of **A**rthropods from the **L**aurisilva of the **A**zores) (see Borges *et al.*, 2000, 2005b; Gaspar *et al.*, 2008), that surveyed arthropods distribution in Azorean native forests, was an important step towards the inclusion of arthropod groups in biodiversity conservation planning in the Azores. The systematically collected data allowed inferences to be made about the biology, ecology, rarity and conservation status of the different arthropod species. Transects

TABLE 1. Total and endemic terrestrial diversity (species and subspecies) of the main groups of the Kingdoms Fungi, Chromista, Protoctista, Plantae and Animalia in the Azores (more details in Borges *et al.*, 2010a).

| **Kingdom and Phylum/ Division** | **Common name** | **Total** | **Endemic** |
|---|---|---|---|
| **FUNGI** | | **1328** | **34** |
| Zygomycota (Fungi) | Zygomycete fungi | 2 | 0 |
| Ascomycota (Fungi) | Sac fungi, Cup fungi | 231 | 20 |
| Ascomycota (Lichen) | Lichen | 775 | 10 |
| Basidiomycota (Fungi) | Basidiomycete fungi | 307 | 4 |
| Basidiomycota (Lichen) | Lichen | 6 | 0 |
| Lichen (Fungi Imperfecti) | Lichen | 7 | 0 |
| **CHROMISTA** | | **4** | **0** |
| Oomycota | Water molds | 4 | 0 |
| **PROTOCTISTA** | | **575** | **7** |
| Bacillariophyta | Diatoms | 536 | 7 |
| Amoebozoa | Amoebae | 39 | 0 |
| **PLANTAE** | | **1590** | **80** |
| **Bryophyta** | **Bryophytes** | ***480*** | ***7*** |
| Anthocerotophyta | Hornworts | 5 | 0 |
| Marchantiophyta | Liverworts | 164 | 1 |
| Bryophyta | Mosses | 311 | 6 |
| **Tracheobionta** | **Vascular Plants** | ***1110*** | ***73*** |
| Lycopodiophyta | Quillworts | 7 | 1 |
| Pterydophyta | Ferns | 69 | 6 |
| Pinophyta | Gymnosperms | 4 | 1 |
| Magnoliophyta | Dicots and monocots | 1030 | 65 |
| **ANIMALIA** | | **2667** | **331** |
| Platyhelminthes | Flatworms | 31 | 0 |
| Nematoda | Roundworms | 131 | 2 |
| Annelida | Earthworms | 22 | 0 |
| Mollusca | Slugs and snails | 114 | 49 |
| Arthropoda | Arthropods | 2298 | 266 |
| Chordata (Vertebrata) | Vertebrates | 71 | 14 |
| **TOTAL** | | **6164** | **452** |

(150 m x 5 m) were randomly placed within fragments of protected native forest. The number of transects per forest fragment was set up using a logarithmic scale, assuming a species-area relationship (SAR) with a slope ($z$) of 0.35 in a log-log scale (*i.e.*, a 10 fold area increase implies a duplication of the number of species): 2 transects were set up for 10 ha forest fragments, 4 transects for 100 ha fragments and 8 transects for 1,000 ha fragments. Consequently, higher sampling effort was applied to larger protected native forest areas (*i.e.* "proportional sampling"), making it possible to capture not only "area *per se* effects" but also unveil patterns that could be prevalent in larger areas, such as, spatial beta diversity.

In this paper we compile and synthesize the results of recent research on the biodiversity and ecology of Azorean arthropods, which were at least partly based on data obtained from long term projects (*e.g.*, BALA, "Biodiversity of cave invertebrates"), and many others of shorter duration (*e.g.*, Interfruta). During the last ten years several general questions were raised and several specific goals (noted below) were pursued:

*Inventory of Azorean arthropods and diversity hotspots*

- list all arthropod taxa from the Azores (see Borges *et al.*, 2005c, 2010b);
- describe new taxa (Blas & Borges, 1999; Ribes & Borges, 2001; Platia & Borges, 2002; Quartau & Borges, 2003; Borges *et al.*, 2004, 2007; Borges & Wunderlich, 2008);
- examine the shape and characteristics of discovery curves in order to obtain a provisional picture of the taxonomic completeness of current inventories and an estimation of the amount of work still needed to attain taxonomic completeness (Lobo & Borges, 2010).
- identify hotspots of species diversity in the Azores (*e.g.* Borges *et al.*, 2005b; Borges & Gabriel, 2009).

*Ecological patterns of species distribution and abundance (i.e. rarity)*

- test if the He & Gaston (2003) abundance–variance–occupancy model accurately predicts species distribution across different spatial scales

and whether endemic, native (non-endemic) and introduced species occupy different parts of the abundance–variance–occupancy space (Gaston *et al*., 2006);
- assess patterns of distribution and species richness of canopy phytophagous insect among islands and host plants (see Ribeiro *et al*., 2005; Santos *et al*., 2005);
- describe patterns of rarity in one well-sampled island, i.e., Terceira, identifying types of local pseudo-rare species (Borges *et al*., 2008);
- explore patterns of diversity, abundance and distribution of different taxonomic, colonization and trophic groups of arthropods in Azorean native forests at different strata and sites (Gaspar *et al*., 2008);
- test the "resource concentration hypothesis", that predicts there is a positive relationship between the density of phytophagous insects or predator arthropods and the spatial distribution/abundance of host plants (Ribeiro & Borges, 2010);
- test if more abundant and widespread plant species are those that support populations of the rarest regional arthropod species (Ribeiro & Borges, 2010);

*Evaluate the role of environmental variables*
- examine how a variety of biotic, abiotic and anthropogenic factors influence endemic and introduced arthropod richness on an oceanic island (Terceira) (Santos *et al*., 2005; Borges *et al*., 2006);
- evaluate the degree to which environmental suitability assessed with presence/absence models account for abundance estimates (Jimenez-Valverde *et al*., 2009);

*Effects of scale and sampling on species richness, beta diversity and density*
- analyze the effect of variation in the size of sampling units on species richness estimations, and evaluate the accuracy of the predictions obtained with various estimators presently available when different strategies are used to group the same dataset into different sized samples (Hortal *et al*., 2006);
- assess how differently beta diversity measures for incidence data and pairwise comparisons behave with re-

gard to varying degrees of sampling effort, and recommend diversity measures that are relatively robust to undersampling (Cardoso *et al.*, 2009a);
- test the hypothesis that "host-habitat area" affects the following insect density estimates: mean number per tree canopy or reserve transects (Ribeiro & Borges, 2010).

*Effect of disturbance in ecological communities*
- understand how several taxonomic and ecological attributes of arthropod communities vary with respect to different levels of disturbance as well as assessing to what extent potential disturbance factors are influencing site integrity (Santos *et al.*, 2005; Cardoso *et al.*, 2007);

*Biogeography of Azorean arthropods*
- investigate some biodiversity patterns relating to spider distribution between islands, habitats, colonization status and biogeographical origin (Borges & Wunderlich, 2008);
- study the factors promoting diversification of several Azorean arthropod groups (Borges & Hortal 2009) and extending this to the rest of Macaronesia (Cardoso *et al.*, 2010a; Triantis *et al.*, 2010b);
- identify the biogeographical factors underlying spider species richness in the Macaronesian region and assessing the importance of species extinctions in shaping current diversity (Cardoso *et al.*, 2010a);
- investigate whether there is a significant gain in information if one uses non-parametric richness estimators to build SAR models with standardized surveys data, rather than using the observed number of species ($S_{obs}$) (Borges *et al.*, 2009);
- investigate if species-area relationships from entire archipelagos are congruent with those of their constituent islands (Santos *et al.*, 2010).

*Surrogacy patterns in arthropods*
- evaluate the effectiveness of arthropods as predictors of diversity for a wide range of taxonomic and non-taxonomic groups, for multiple measures of biodiversity and for different spatial scales (Gaspar *et al.*, 2010);
- evaluate the effectiveness of cave-adapted arthropods as

predictors of diversity of rare bryophytes in cave entrances and the diversity of bacteria in cave mats.

*Conservation of Azorean arthropods*

- examine the relative value of 19 forest fragments in seven of the Azorean islands to improve the conservation of Azorean soil epigean arthropod biodiversity (Borges *et al.*, 2005b; Gaspar *et al.*, 2011);
- investigate the relationships between endemic and introduced arthropod richness, to assess whether areas with high levels of endemic species richness deter invasions (Borges *et al.*, 2006);
- investigate the relevance of current human-made habitats (*e.g.* exotic forest; agroecosystems) for the protection of rare species (see Cardoso *et al.*, 2009b, 2010b; Meijer *et al.*, 2011);
- test nestedness patterns of endemic, native and introduced species (Cardoso *et al.*, 2010b);
- quantify the magnitude and taxonomic distribution of extinction debt in the Azores as an important step for effective conservation planning (Triantis *et al.*, 2010a);
- list the 100 highest management priority taxa in Macaronesia and in the Azores, the so-called Top 100 (Cardoso *et al.*, 2008; Martín *et al.*, 2010).
- genetic characterization of populations of endemic species to investigate their uniqueness and examine how this information could help in the prioritization of conservation efforts.

## WHAT HAVE WE LEARNED SO FAR?

### *Inventory of Azorean arthropods and diversity hotspots*

The knowledge base of Azorean arthropod biodiversity is not uniform, and many groups have not been adequately sampled. Furthermore, many groups have not received appropriate taxonomic revision, due to little traditional taxonomic research being carried out in the last decade, and the lack of taxonomists familiar with the Azorean fauna (Amorim, 2005; Borges *et al.*, 2005a; Lobo & Borges, 2010). As with any other biome, solving this problem is not simple since, for example, traditional taxonomic work has been neglected in the last decades in Europe (see Boero, 2010). The most relevant effort to rectify the lack of taxonomic expertise preventing advance in biodiversity research was the establishment of the "Azorean Biodiversity Group" (http://cita.angra.uac.pt/biodiversidade/), that, among other things, is supporting research on classical (as well as molecular) taxonomy and ecology of arthropods of the Azores. Moreover, the web site "Azorean Biodiversity Portal" (http://www.azoresbioportal.angra.uac.pt/) (see Borges *et al.*, 2010c) allows everyone to access updated information on Azorean biodiversity. As a direct outcome of this online database many national and international taxonomists have shown a growing interest in Azorean biodiversity and many new collaborations have been established, including taxonomic revisions (see Borges *et al.*, 2010b) and additional field work to collect specimens.

The results obtained during the BALA project (see above) showed that some forest reserves are clearly more diverse than others, both in terms of alpha and gamma diversities. The effect of forest fragmentation has not been studied in detail (see future work below), but the data obtained suggests that small fragments play a much more important role than previously thought (see Borges *et al.*, 2005b; Borges & Gabriel, 2009). For instance, based both on the presence of unique species and high species richness, the Pico Alto region in the archipelago´s oldest island, Santa Maria, is a hotspot of biodiversity (Borges *et al.*, 2005b; Borges & Gabriel, 2009). Over 57 endemic arthropod species are known from Pico Alto (Santa Maria Isl.), *i.e.* 21% of the Azorean endemic arthropods occurring in an area representing <0.25% of Azorean native forests. Other relevant areas occur on the islands of São Miguel (Pico da Vara), Terceira (Terra Brava, Caldeira da Serra de Santa Bárbara), São Jorge (Topo), Pico (Caveiro, Mistério da Prainha) and Flores (Morro Alto and Pico da Sé) (see Borges & Gabriel, 2009; online at http://www.azoresbioportal.angra.uac.pt/files/publicacoes_Brochura BIODIVERSIDADE AORES vFINAL.pdf).

Results obtained from other studies, such as the survey of subterranean invertebrates (1999-2005) revealed the poor stage of knowledge on the Azorean cave invertebrates. For instance, the number of cave

*Trechus* listed for the islands increased from 4 to 7, plus an epigean species in the same genus (Borges *et al.*, 2004; Amorim, 2005; Borges *et al.*, 2007).

### *Ecological patterns of species distribution and abundance (i.e. rarity)*

The data for diverse species assemblages at different spatial scales, regardless of species status, can be well described by an abundance-variance-occupancy model (Gaston *et al.*, 2006). Most importantly, we observed that outliers include restricted specialized forest endemic species (*e.g. Trechus terrabravensis* and *Cedrorum azoricus azoricus*) that only occupy pristine native forest sites where they are quite abundant (Gaston *et al.*, 2006).

We have found that free-living herbivores insect in the canopies of Azorean native forests are mainly generalists, as expected for a relatively young and isolated volcanic archipelago (Ribeiro *et al.*, 2005). Interestingly, the proportion of rare species is higher for herbivores insects than for predatory arthropods (Borges *et al.*, 2008). Ribeiro & Borges (2010) also showed that there is a clear dominance of generalist species in canopies of Azorean trees and shrubs, which holds also true for the overall spider and chewing insect communities in Terceira island (Borges *et al.*, 2008). The observation of a widespread distribution of spiders on tree canopies in the native forest could be explained by their high dispersal ability and generalist feeding habits (Borges & Wunderlich, 2008). Consequently, the abundance of herbivorous insects seems to be strongly affected by the occurrence and population densities of spider species. One particular plant species, *Erica azorica*, has greater than expected herbivore densities per crown, possibly as it represents enemy free/predictable space (Ribeiro & Borges, 2010). In the case of agricultural habitats, we found that both abundance and species richness of predatory groups inhabiting the canopy of different fruit trees (apple, orange, and peach trees) are negatively correlated with canopy volume, and positively correlated with tree density. On the other hand, herbivore species, especially sucking insect species, show the opposite trend (Santos *et al.*, 2005).

In terms of rarity, four important types were detected in the Azores (see Borges *et al*., 2008; Ribeiro & Borges, 2010): 1) dense and intermediately dense species; 2) truly rare species, which are rare on any host species and with very low population densities regionally; 3) pseudo-rare species found in small numbers on a specific host tree, which are dense on neighbouring tree species, *i.e.* host-tourists; 4) pseudo-rare species found in small numbers on any tree species that are common in other habitats on the island, i.e., habitat-tourists.

Truly rare and specialist species should also be favoured by the presence of large quantities of resources, and although large tree species have similar numbers of rare species, most of these species are truly rare on *Juniperus brevifolia*, *Laurus azorica* and *Erica azorica* (see Ribeiro & Borges, 2010). Therefore, the high frequency of *E. azorica* and *J. brevifolia* populations throughout the Azorean native forest fragments creates the opportunity for the survival of rare insect and spider species populations on these hosts (Ribeiro & Borges, 2010).

Other surveys focused on arthropods from very specific habitats typical of volcanic islands such as the Azores - lava tubes and volcanic pits - revealed that cave adapted species rarity vary as a function of cave abundance and the number that have actually been sampled (see Amorim, 2005). For the most studied Azorean cave beetle species, (in the genus *Trechus*) some are found at high densities at many sites (*e.g*., *T. picoensis* from Pico Isl. occurs in 9 caves and 134 specimens have been collected so far from the Torres lava tube), while others are only found at one site and despite the amount of sampling efforts involved only a few specimens have been collected (*e.g*., only 2 individuals of *T. jorgensis* are known from Bocas do Fogo pit in São Jorge Isl.).

### *Evaluate the role of environmental variables*

We have shown for the soil arthropod fauna of native forest in Terceira Island that abiotic (climatic and geomorphological) variables provided a better explanation for the variation in endemic species richness than anthropogenic ones, whereas the inverse was observed with respect to introduced species richness (see Borges *et al*., 2006). Concerning the abundance of species, Jimenez-Valverde *et al*., (2009) observed that Azorean arthropod species are highly influenced by land-use variables, in such a way that the climate factors lose relevance and the climatic suitability may be diluted in predicting local abundance of species. However, in their analysis of the arthropod communities associated with fruit orchards, Santos *et al*., (2005) found a strong influence of both climatic and anthropogenic variables on the abundance and diversity of different functional guilds.

### *Effects of scale and sampling in species richness, beta diversity and density*

Arthropod data from BALA´s standardized sampling protocol was used to evaluate the effects of scale (across sites, forest fragments and islands) and sampling in species richness, beta diversity and density (see Hortal *et al*., 2006; Cardoso *et al*., 2009a; Ribeiro & Borges, 2010). Several estimators (ACE, Chao1, Jackknife1 and 2 and Bootstrap) provided consistent estimations of species richness, regardless of sample grain size. In addition several nonparametric estimators presented certain insensitivity to how samples are aggregated (Hortal *et al*., 2006).

Cardoso *et al*., (2009a) demonstrated that beta diversity values are close to the real values, when communities being compared approach sampling completeness. However, the $\beta_{-2}$ index from Harrison *et al*., (1992) should be used as the most consistent measure in cases in which the sampling completeness degree of a dataset is unknown.

In general, the three structurally most complex and abundant plant "host islands", *i.e.*, *E. azorica*, *J. brevifolia* and *L. azorica*, accumulated the highest proportion of regionally rare arthropod species, corroborating the "host as an island hypothesis" (Ribeiro & Borges, 2010).

### *Effect of disturbance in ecological communities*

In broad terms current fragments of Azorean native forest are not uniform in their conservation status. In fact, Cardoso *et al*. (2007) clearly demonstrated that when using an Index of Biotic Integrity (IBI) adapted to the epigean arthropods of the Azorean native forests, many fragments of native forest would be considered highly disturbed. More importantly, these authors showed that most species thrived in highly disturbed sites are of limited importance for conservation efforts, and that the percentage of endemic species is significantly higher in pristine than in degraded sites.

*Biogeography of Azorean arthropods*

Borges & Brown (1999) showed that island geological age was an important variable explaining Azorean endemic arthropods species richness. Recently, there has been increased interest in the determining the importance of geological age and other geographical variables to explain patterns of island diversity in Macaronesia (*e.g.* Whittaker *et al.*, 2008, 2009; Borges & Hortal, 2009; Borges *et al.*, 2009; Cardoso *et al.*, 2010a; Triantis *et al.*, 2010b).

In most of these studies the main observation was that a combination of islands' area and geological age are enough to provide a basic explanation for the diversity of endemic arthropods in the Azores, in spite of some differences between taxonomic or ecological groups and the additional role of island relative isolation (Borges & Hortal, 2009; but see Cardoso *et al.*, 2010a). The main conclusion was that due to the recent age of the archipelago (see Borges & Hortal, 2009; Triantis *et al.*, 2010b) a simple area-age model (AT) is adequate for the Azorean fauna, and not the more complex area-age-age$^2$ (ATT$^2$) firstly proposed by Whittaker *et al.* (2008, 2009) within the context of The General Dynamic Model of Oceanic Island Biogeography (GDM). In fact, when testing the GDM, Borges & Hortal (2009) showed that: i) cave species appear to have evolved quite quickly, producing a number of species during the initial stages of island development, when cave systems formed by lava tubes and volcanic pits were abundant and pristine prior to natural collapsing of structures; ii) taxa with low dispersal ability, particularly beetles, showed strong negative relationships with the distance to Santa Maria, the oldest island and reservoir of lineages either coming from the mainland or remaining from the older archipelago composed of Santa Maria and the Northeast part of São Miguel; iii) the diversity of evolutionary responses in different organisms is so varied that no general model, like the one proposed by Whittaker and colleagues (Whittaker *et al*., 2008, 2009) is able to predict the patterns and processes of diversification.

Spiders apparently follow a different pattern from the one observed for most arthropod groups. Analyzing the biogeographical factors underlying spider species richness in the Macaronesian region Cardoso *et al*. (2010a) showed that for the Azores, island area and the proportion of remaining natural forest were the best predictors of species richness. The effect of island age on species richness, if important in diversification processes, has nowadays been masked by the effect of native habitat destruction. Triantis *et al*. (2010b) found that the AT model was the most parsimonious for explaining diversity patterns of indigenous, endemic, single island endemic and proportion of single island endemic beetles and arthropods in the Azores, corroborating the results of Borges & Hortal (2009).

Santos *et al*. (2010) observed that archipelagos follow the same island species–area relationships (ISAR) as their constituent islands, which means that the Macaronesian archipelagos could be studied as four data points when testing the relationship between species richness and area. Borges *et al*. (2009) found that if data comes from standardized surveys (as is the case of BALA data), the slope and goodness of fit for species area relationships obtained with estimated values (using non-parametric estimators; see also Hortal *et al*., 2006) were not significantly different from those obtained from observed species richness.

Molecular data generated for a few Azorean endemic arthropods groups (the beetles *Trechus* and *Tarphius*, and the butterfly *Hipparchia*) and their neighboring insular and continental congeneric species reveal that the Azorean taxa form monophyletic clades (Fujaco *et al*., 2003; Amorim, 2005). This supports single colonization events of the Azores, as expected for such remote oceanic island. If true, then the diversification currently observed within these groups would be the result of intra archipelago speciation from single ancestors, as opposed of multiple arrivals of distinct lineages (Amorim *et al*., subm.). Nevertheless, the possibility that multiple colonization events occurred but have gone extinct cannot be completely dismissed.

### *Surrogacy patterns in arthropods*

Gaspar *et al*. (2010) evaluated the effectiveness of taxonomic, colonization and trophic groups of arthropods from native forests of the Azores archipelago as surrogates of the diversity of other arthropod groups. The results indicated that spiders (Araneae) and true bugs (Hemiptera) may be more promising surrogates of arthropod diversity for the Azorean native forests at the transect, fragment and island scales (Gaspar *et al*., 2010). As spiders are easy to identify, abundant in both terrestrially and within tree canopies (Borges & Wunderlich, 2008; Borges *et al*., 2008; Gaspar *et al*., 2008) and probably good indicators of futures trends for other taxa (Cardoso *et al*., 2010a), we suggest the use of this group for future rapid monitoring studies in Azorean forests.

### *Conservation of Azorean arthropods*

Human activities and invasive species are among the most important factors impacting Azorean arthropod communities (Godman, 1870; Borges *et al*., 2006, 2008). The number of described species known from the Azores is continuously rising (Borges *et al*., 2010a), but a great proportion are recently introduced ones, that tend to exhibit lower densities, less spatial density variance, and occupy fewer sites than native and endemic species (Gaston *et al*., 2006). On Terceira island, non-indigenous species are mainly limited to those sites under anthropogenic influence located mainly on low to medium altitude areas or, when in high-altitude forests, in marginal areas of the few forest remnants (Borges *et al*., 2006). For example, the protection of forest specialists, like the ground-beetles *Trechus terrabravensis* and *Cedrorum azoricus azoricus* (see Gaston *et al*., 2006) requires the management of invasive species, to avoid them entering the pristine native forest sites, such as those found in Serra de Santa Bárbara (see also Borges *et al*., 2006; Cardoso *et al*., 2007).

The impacts of land use changes are severe (Borges *et al*., 2008; Cardoso *et al*., 2009) and many Azorean endemic forest dependent species are on the edge of extinction (Triantis *et al*., 2010a). Despite the fact that unmanaged exotic forests are providing alternative habitat suitable for some endemic species (forest specialist arthropods, particularly saproxylic beetles from S. Maria Island; Meijer *et al.*, 2011), most endemic forest specialist arthropods are restricted to native forests and only have sink populations in semi-natural grasslands or exotic forests (Borges *et al.*, 2008; Cardoso *et al.*, 2009; Triantis *et al.*, 2010a).

Endemic and introduced species were all found to be highly nested in habitats of Terceira Island. Indeed, native forests and intensively managed pastures seem to be the main drivers of species composition at any site, having mostly endemic and introduced species, respectively (Cardoso *et al.*, 2010b). This result implies that there is a predictable pattern of species loss and gain from natural forests to exotic forests, semi-natural pastures and finally intensively managed pastures, as suggested by the nestedness analysis (Cardoso *et al.*, 2009b; 2010b). The roles of selective extinction (see also Triantis *et al.*, 2010a), as is exemplified by a gradient of disturbance (Cardoso *et al.*, 2007), and habitat change could explain the nested pattern for endemics.

Interestingly, hardly any exotic insect or spider were able to colonize the native forest canopy habitat (Borges *et al.*, 2008; Borges & Wunderlich, 2008), so are not widespread in all the Azorean habitats. For instance, the Azorean *Laurisilva* seems that has not yet been colonized by any of the invasive ant species found adjacently to human constructions. Spiders are the most abundant terrestrial predators in the Azores (Borges & Wunderlich, 2008; see also Gaspar *et al.*, 2008), particularly in forests, and may serve as early indicators for future disappearance patterns of other insular taxa (Cardoso *et al.*, 2010a).

The most disturbed study sites in the Azores were found on the islands of Faial (Cabeço do Fogo), Flores (Caldeiras Funda, Rasa), Pico (Lagoa do Caiado), São Jorge (Pico Pinheiro), São Miguel (Atalhada, Graminhais, Pico da Vara), Santa Maria (Pico Alto) and Terceira (Algar do Carvão, Matela, Pico do Galhardo), while the pristine areas were on Terceira (Terra Brava, Biscoito da Ferraria, Caldeira da Serra de Santa Bárbara), Pico (Caveiro, Mistério da Prainha) and Flores

(Morro Alto, Pico da Sé) islands (Cardoso *et al.*, 2007; Gaspar *et al.*, 2011).

Invasive plant species are the most important drivers in terms of ecological and ecosystem change in the Azores (Borges *et al.*, 2010d) and the spread of species like *Hedychium gardneranum, Hydrangea macrophylla, Rubus ulmifolius, Pittosporum undulatum, Clethra arborea* (see Silva & Smith, 2006; Hortal *et al.*, 2010) is of great concern. Areas of high conservation value due to the presence of single island endemics, such as Pico Alto on Santa Maria and Pico da Vara on São Miguel, are now heavily disturbed by invasive plants. Human driven ecosystem disturbances have to be minimized and special measures by the Azorean Government are already being applied for the control of invasive plants in several islands. The ongoing projects in Pico da Vara (S. Miguel) to manage areas of special importance for birds are good examples of active conservation in the Azores (*e.g.* Ceia *et al.*, 2009; Heleno *et al.*, 2009).

A list of Azorean threatened taxa, based on both protection priority and management feasibility, has been drawn up (Cardoso *et al.*, 2008; Martín *et al.*, 2010). Arthropods represent 17 species of the 100 most important Macaronesian taxa (Martín *et al.*, 2010) and 24 of the 100 most important in the Azores (Cardoso *et al.*, 2008). This list will be used to determine those new species to be included in the revision of the NATURA 2000 list of Azorean priority species for conservation (Paulino Costa, pers. comm.). This will be an important step towards the inclusion of arthropods in conservation initiatives for the Azorean archipelago, including several new areas based on the occurrence of unique arthropod species (e.g. Atalhada in São Miguel; Pico Alto in Santa Maria; Fontinhas in Terceira) (see Gaspar *et al.*, 2011).

### *Future work in the conservation of Azorean biodiversity*

The study of arthropod ecology in the Azores has proven to be a valuable tool for designing biodiversity conservation plans in the archipelago. However, any hope for a successful management and conservation program of endemic fauna and flora must meet local economic interests. Local people, with direct interest in the use of land for agriculture have a higher impact on the sustainability of the Azorean habitats than policy makers, managers and conservationists altogether. Several initiatives, resulting from outcomes of the BALA project, have been undertaken through organized seminars and meetings as well as brochures and books (Borges & Gabriel, 2009; Cardoso *et al*., 2009c) in recent years increasing public understanding of why value arthropod biodiversity and thus to protect their habitats. The information on arthropod diversity and distribution provided by the BALA project and parallel studies is being used by the regional government to define and give legal status to the designated areas for protection. The next steps would be to establish management plans for the areas, including the establishment of periodic diversity monitoring plans for these zones to determine the effectiveness of the conservation strategies adopted to date. The management and monitoring plans should include: i) the identification of specific threats to the protected areas, ii) the definition of practical measures to minimize these threats, and iii) the selection of specific groups of organisms and sampling methods that can be used to periodically monitor the overall diversity of the areas.

## FUTURE RESEARCH AND CONCLUDING REMARKS

The islands of the Azores have undergone dramatic changes in land-use and their biodiversity is now under serious threat (see Borges *et al*., 2008). With the current knowledge on Azorean arthropod biodiversity it is now possible to address more complex issues, such as being able to:

1) predict species extinctions using the available information of species abundance on Azorean islands (see also Triantis *et al*., 2010a) and compare data obtained in 1999-2000 with new data that was collected in 2010 (FCT Project PTDC/BIA-BEC/100182/2008 – “Predicting extinctions on islands: a multi-scale assessment);
2) evaluate the extent and the mechanisms through which fragmentation of natural habitats affects species communities. To do this, we will build a relevant framework to evaluate and compare habitat size effects on the species richness of native versus ex-

otic free-living herbivore insects and predatory spiders. We anticipate that these results will advance in species–area relationship modelling techniques, that are crucial for both theoretical and conservation applications in the Azores (see a recent application in Guilhaumon *et al.*, 2008);

3) the study of species-environment relationships, as islands are especially good places to address these questions;
4) identify evolutionary significant units for conservation by generating mitochondrial and nuclear molecular datasets of several arthropod endemic species (e.g., FCT - PTDC/BIA-BEC/104571/2008 project – "What can the Macaronesian islands teach us about speciation? A case study of *Tarphius* beetles and *Hipparchia* butterflies").

Further studies, using different sampling techniques, should be carried out to improve our knowledge of the diversity and distribution of less known groups of arthropods, such as Hymenoptera, Diptera, Collembola and Acari, these less known groups of arthropods are diverse and abundant and should play important functional roles in native communities.

Time scale, whether it is hours, days, months or years, has seldom been explored in the previous projects, despite the fact it will also influence the way diversity and distribution of arthropods is perceived, and hence, may provide additional information that is important for conservation planning. A study is currently exploring spider diversity in a native forest fragment at different hours of the day (Cardoso, unpublished data). Furthermore, a comparison of data from 2000 with those from 2010 (FCT Project PTDC/BIA-BEC/100182/2008 – "Predicting extinctions on islands: a multi-scale assessment; Triantis *et al.*, 2010a) will also offer valuable insights on the effect of time scale on the diversity and distribution of arthropods in the Azores.

The patterns and causes of arthropod rarity in Azorean native forests should continue to be explored in detail to distinguish between arthropod species that are truly rare from those that are rare at a given time, as this has major implications for the definition of the most effective conservation strategies.

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# STUDYING THE COST OF MIGRATION: A COMPARISON OF *PSEUDALETIA UNIPUNCTA* POPULATIONS FROM CANADA AND THE AZORES

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## ABSTRACT

In North America, the armyworm, *Pseudaletia unipuncta* is considered a seasonal migrant, with immigrants from the southern United States moving into more northerly, temporarily available habitats each spring. However, as this species cannot survive the prevailing winter conditions in the north, their offspring emigrate southward in the fall. Migration is initiated by sexually immature individuals, with the rate of sexual maturation being modulated by juvenile hormone titers that vary depending on temperature and photoperiodic cues. In contrast, in the Azores, armyworm populations persist all year round and are not believed to be regular seasonal migrants.

The entomological studies addressing the possible costs of flight on future reproduction, or the evolution of traits that could minimize these potential costs, have compared winged and wingless (e.g. aphids) or short and long winged (e.g true bugs) morphs. However, the presence of migrant and non-migrant populations of the armyworm offered an excellent opportunity to address these questions in a species where all adult individuals have a well-developed capacity for flight. I will present morphological, behavioural and physiological data from migrant and non-migrant populations of *P. unipuncta* and discuss the results within the framework of tradeoffs between migration and reproduction.

## RESUMO

Na América do Norte, a lagarta-das-pastagens, *Pseudaletia unipuncta* é considerada como migrante sasonal, com imigrantes do sul dos Estados Unidos deslocando-se cada primavera para habitats temporariamente disponíveis mais a norte. Todavia, como esta espécie não pode sobreviver as condições de inverno prevalecentes no norte, a sua prole migra para o sul no Outono. A migração é iniciada por indivíduos sexualmente imaturos, com a taxa de maturação sexual sendo modulada por concentrações titradas de hormona juvenil que variam conforme sinais de temperatura e fotoperíodo. Em contraste, nos Açores, as populações de lagarta-das-pastagens persistem durante todo o ano e crê-se que não sejam migrantes sasonais regulares.

Os estudos entomológicos que abordam os custos possíveis do voo na reprodução futura, ou a evolução de características que possam minimizar tais custos, têm comparado morfos com asas e sem asas (e.g. afídeos) ou de asa curta e asa comprida (hemípteros). Todavia, a presença na lagarta-das-pastagens de populações migrantes e não migrantes oferece uma oportunidade excelente para se abordar tais questões numa espécie onde todos os adultos possuem capacidade de voo bem desenvolvida. Apresentarei dados morfológicos, comportamentais e fisiológicos de populações migrantes e não migrantes de *P. unipuncta* e discutirei os resultados num enquadramento de negociação entre migração e reprodução.

## INTRODUCTION

Insects have evolved two general strategies to cope with habitat deterioration (Southwood, 1977; Solbreck, 1978), both of which are accompanied by marked physiological and behavioral changes induced by environmental cues (Tauber, *et al*. 1986). Individuals enter a state of arrested development at a specific stage in the life cycle and remain in diapause/ aestivation until local conditions once again become suitable for reproduction, and this has been termed the "here-later" strategy. The alternative is for individuals to emigrate from the current site in search of habitats suitable for immediate reproduction elsewhere, referred to as the "there-now" strategy. At the onset of migration adults are usually sexually immature adults which led Johnson (1969) to propose the "oogenesis-flight syndrome", a model in which migratory flight and reproduction are seen as ecological/physiological alternatives, but where both processes are regulated by the Juvenile Hormone (JH) (Rankin, 1989). While this model has served as a good point of departure for studies on insect migration it is now evident that the two processes are not as mutually exclusive (Rankin *et al*., 1986; Sappington & Showers, 1992). Adaptations to facilitate migratory behaviour (such as larger body size) may also incur associated costs with respect to reproduction, with migrants generally being older at the onset of reproduction and having a lower total fecundity than conspecific non-migrants (Roff & Fairbairn, 1991). However, different physiological mechanisms have evolved to reduce these potential reproductive costs in migrants (Rankin & Burchsted, 1992). Thus, it is now clear that migration is a syndrome of traits and that there are variations on the “here-later”, “there-now” strategies. Clearly, we need a much better understanding of the basic physiological and genetic mechanisms controlling these traits to fully comprehend the overall phenomenon of insect migration (Gatehouse, 1997). In addition, as many pests in both agriculture and forestry are migrants the information obtained from this research would also be important for the development of rational pest management practices.

## THE ARMYWORM AS A MODEL

I initially started working on the true armyworm, *Pseudaletia unipuncta*, to look at pheromone mediated mating and the potential of using the sex pheromone as a suitable monitoring tool. Our early studies on calling behaviour (the emission of sex pheromone by a receptive female) found that even under summer conditions, females did not reach sexual maturity for several days following emergence (Turgeon & McNeil, 1982), a different pattern than observed for resident species, which start calling and mate very soon after emergence. We also found that the precalling period differed significantly as a function of both temperature and daylength (Delisle & McNeil, 1987; Table 1), leading to the suggestions that the precalling period may be a trait that could be used to identify migrant moth species (McNeil, 1986). During the same period we were running field trials studying the seasonal patterns of moth activity using light and pheromone trap

TABLE 1. The effect of temperature and photoperiod on the age at which virgin *Pseudaletia unipuncta* females from North America initiate calling for the first time (after Deslisle & McNeil, 1987).

| **Temperature** | **Photoperiod** | **Age (days ± SEM** |
|---|---|---|
| 25 ºC | 16L:8D | 5.8 ± 0.4 |
| | 12L:12D | 9.0 ± 0.9 |
| 10 ºC | 16L:8D | 17.4 ± 0.6 |
| | 12L:12D | 21.1 ± 1.1 |

catches. We found that while males were captured in light traps during both summer and fall, very few males were captured in pheromone traps on the fall (McNeil, 1987). In addition, while >95% of females captured in light traps during the summer flight period were mated the vast majority of those caught in the fall were sexually immature, and had extensive lipid reserves (McNeil, 1987). Furthermore, Fields & McNeil (1986) found that none of stages in the armyworm life cycle were able to survive the winter conditions in Quebec. Based on these findings the scope of the programme was expanded to use the armyworm as a model species to study different facets of insect migration in response to predictable, seasonal changes in habitat quality.

The initial emphasis was placed on understanding the underlying physiology processes associated with sexual maturation, as well as the female calling behaviour and male responsiveness to sex pheromones, under different ecological conditions. We were able to demonstrate that ovarian development, calling behaviour and pheromone synthesis in virgin females are closely synchronized and modulated by JH (Cusson & McNeil, 1989; Figure 1). Furthermore, it was clear that when insects were reared at cool temperatures and short daylength (10 °C, 12L:12D), their JH production was low, resulting in delayed sexual maturation of both sexes (McNeil *et al.*, 1994), in a manner similar the model proposed by Rankin & Riddiford (1978). Thus, the findings supported the idea that the summer appearance of species outside the area where they successfully overwinter is the result of sea-

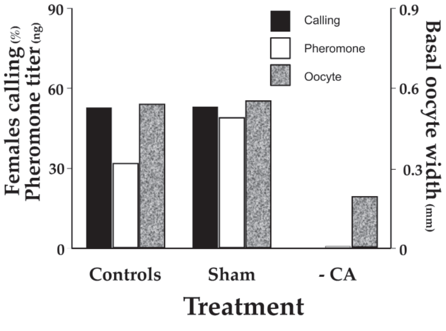

FIGURE 1. The effect of ablating the corpora allata from newly emerged *Pseudaletia unipuncta* females on state of ovarian development, pheromone production and the expression of calling behaviour after five days at 25 °C, 16L:8D and 65% R.H (modified from Cusson & McNeil, 1989).

sonal migration, as proposed by Walker (1979), rather than the result of a unidirectional expansion into zones where resources are temporarily available due to current agricultural practices, as postulated in the "Pied Piper" hypothesis (Rabb & Stinner, 1978).

The delay in maturation under conditions that serve as reliable cues of impending habitat deterioration would allow adults to locate resources and increase lipid deposits necessary for migration, wait for the appropriate weather conditions for long distance flight, and/or provide an extended time window to location a more suitable habitat. Consequently, the working hypothesis for the seasonal biology of *P. unipuncta* in North America is that both the spring northward and southward fall migratory flights were initiated in response to the short daylength, cool temperatures cues. In this manner armyworm would avoid the high summer temperatures in the southern United States that negatively affect survival and fecundity and the lethal freezing winter temperatures in northern habitats (McNeil, 1987).

## THE ARMYWORM FROM THE AZORES AS A MODEL

*Pseudaletia unipuncta* is also found in the Azores where it is a sporadic pest of pasture grasses. Given that the Azores is a volcanic archipelago these populations were probably founded by migrants from either Europe or North America that were blown off track, although the possibility of accidental introductions by man cannot be completely discarded. However, unlike populations in Canada, different life stages are found throughout the year in the Azores (Tavares, 1989) suggesting that the populations may be non-migrants. A great deal of the research examining the potential costs of flight on reproduction, and the evolution of adaptations to reduce such costs, has used species where there are distinct morphs with different capacities for flight, such as apterous and alate aphids or macropterous and brachypterous hemipterans (e.g. MacKay & Wellington, 1975; Denno *et al*, 1989). Thus, having migratory and non migratory populations of an insect where adults in all populations use flight to locate food, mates and, in the case of females, suitable oviposition sites would provide a unique opportunity to address these questions.

Consequently we expanded the scope of the project, to compare certain life history traits of armyworm from North America and the Azores colonies, established using eggs collected from females caught in light traps on the island of São Miguel and Normandin, Quebec, were reared for one generation at 25 ºC, 16L:8D to reduce potential maternal effects (Rossiter, 1991) before comparative studies were carried out. Using only females (sexed as pupae, using the characteristics reported by Breeland (1958) we compared the developmental time from the emergence of the 1st instar larvae to adult emergence, the mass and wing surface are of newly emerged females, the age to first calling, as well as the reproductive period and live time fecundity of once mated females. As seen in Table 2, while Azorean females took significantly less time to develop and had a lower body mass with smaller wings, they became sexually mature at a much younger age and produced significantly more eggs. These results support the idea that the larger body mass and larger wing surface area to facilitate long distance migration has a cost with respect to reproduction.

TABLE 2. Life history traits of *Pseudaletia unipuncta* females from migratory and non-migratory populations

| **Trait** | **North America** | **Azores** |
|---|---|---|
| Development (days) | 36.4 ± 0.2 | 33.8 ± 0.2** |
| Mass at emergence (mg) | 231 ± 5 | 209 ± 5** |
| Wing surface area ($cm^2$) | 5.5 ± 0.1 | 4.9 ± 0.1** |
| Age at first calling (days) | 10.2 ± 0.7 | 3.1 ± 0.1** |
| Reproductive period (days) | 7.3 ± 0. | 11.2 = 0.5* |
| Life time fecundity | 1359 ± 131 | 1608 ± 75* |

Subsequent studies comparing the underlying physiology of pheromone production showed that the differences observed in the age of sexual maturation between the non-migratory and migratory populations was more complex than just the earlier onset of JH production following emergence (McNeil *et al*, 1996, 2000, 2005). It was clear from the age related patterns of JH titers in the haemolymph that both the timing of production and the levels of the hormone detected in virgin females are significantly different (Figure 2). This same was observed pattern in the two geographic strains (Figure 3) when we compared the activity of control corpora allata (the source of JH biosynthesis) with

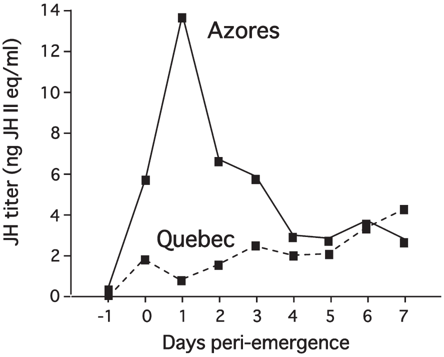

FIGURE 2. A comparison of the temporal patterns of in vitro Juvenile Hormone titers in the haemolymph of virgin *Pseudaletia unipuncta* females from North America and the Azores (modified after McNeil *et al*., 2000).

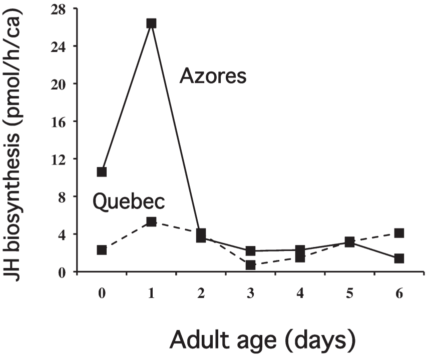

FIGURE 3. A comparison of the temporal patterns of in vitro Juvenile Hormone biosynthesis by the corpora allata of virgin *Pseudaletia unipuncta* females from North America and the Azores (modified after McNeil *et al*., 2005).

those incubated in allatotropin, a neuropeptide implicated in the control of JH (Kataoka *et al*., 1989). These finding strongly support the hypothesis that the selective pressures acting on the control of reproduction in migrant populations is markedly different, probably due to the fact that while JH modulates sexual maturation it is also necessary for sustained flight. In fact, McNeil & Tobe (2001) proposed a model whereby the neuropeptides allotropin and allostatin play differing roles within the same species, depending on the ecological conditions under which the insects were reared.

We are continuing to use comparisons between Azorean and North American populations of the armyworm to determine how migrants initiate and finish migratory flights, as well as investigating the possibility that migrants have evolved specific traits to reduce the cost of migration on future reproduction.

## INTERPRETING THE DIFFERENCES

Little is known concerning the cues that actually initiate migratory flight, although insects probably have some ability to select suitable weather conditions to facilitate migration in the appropriate direction (Taylor & Reling, 1986). We have noted that even when armyworm moths are tested on flight mills under controlled laboratory conditions there is considerable between night variability in both flight speed and distance flown. We are currently testing the hypothesis that the initiation of flight is related to changes in atmospheric pressure. Our prediction is that populations from North America Québec will exhibit increase flight activity when weather conditions favor long distance movement while those from the Azores will have reduced flight activity, as movement under such conditions in nature would result in them being blown out to sea.

In *Drosophila melanogaster* two larval behaviors, roving and sitting, were associated with allelic polymorphism of the *foraging* gene (*for*) (Osborne *et al.*, 1997), and this polymorphism also affects the olfactory response of adults to food odors (Shaver *et al.*, 1998). Subsequently, it was shown that differential expression of a *foraging* gene homolog (*Amfor)*, which also encodes a guanosine 3′,5′-monophosphate (cGMP)-dependent protein kinase (PKG), was associated with changes in the age related polyethism of switching from within hive activities to active foraging for nectar and pollen by worker honey bees (Ben-Shahar *et al.*, 2002). The sitting and roving behavior of fly larvae is similar to the nurse and foraging behavior of bees in the sense that they describe the tendency for individuals to remain sessile versus becoming mobile. The involvement of the *fo*r gene in both instances suggests a possible general role for this gene mediating "stay-or-move" like behaviors in a wide range of insects. As we have already demonstrated that armyworm moths switch from a reproductive (sessile) to a migratory (mobile) phase in response to decreases daylength and temperature conditions and, that under fall conditions, males do not respond to the female sex pheromones (McNeil *et al.*, 1995) we are testing the hypothesis that, in the armyworm, a *foraging* gene homolog will be differentially expressed in response to cues associated with good and poor habitat quality. Furthermore, it is believed that age-related polymorphism in honeybee workers is regulated by changes in juvenile hormone (JH) titers (Robinson, 1987), suggesting the involvement of a pleiotropic network of genes. We have shown that under fall conditions, at the time of southward migration, both sexes of the armyworm have significantly lower rates of JH biosynthesis and sexual maturation than their counterparts under summer conditions (Cusson, *et al.*, 1994). Therefore, we postulate that a *for* gene will be up-regulated in armyworm moths about to migrate, at a time when JH titers are low, and be down-regulated when JH titers are high, as insects will be reproducing and not undertaking long distance movement. We will continue comparing moths from North America and the Azores in this project, for if there is a *foraging* gene homolog associated with migration, expression should differ between migrant and non migrant populations, especially with respect to the levels of PKG activity (Ben-Shalar *et al.*, 2002) in flight muscle.

We will also examine the flight muscle looking at myofibrils and sarcoplasm, as well as mitochondrial and tracheol density/volume (Guderley *et al.*, 2006). In addition we will measure the activity of the oxidative enzymes citrate synthase (CS) and hydroxyacylcoA dehydrogenase HOAD in the different generations of both migrant and non migrant populations to obtain additional insight about muscle performance (O'Brien & Suarez, 2001). The prediction is that adults from the migrant North American population will have larger muscle mass, greater mitochondria volume/density, larger/more tracheoles to facilitate oxygen flow and higher activities of CS and HOAD than those from the Azores, when reared under identical conditions. Furthermore, similar differences are expected, especially in the migratory population, when one compares individuals reared under summer and fall conditions.

As noted earlier, North American moths captured in light traps in the fall have substantial lipid reserves, and these would serve as fuel for extensive migratory flight. Benoit & McNeil, (unpublished) have shown that while adults have some lipid stores upon emergence they accumulate more through nectar feeding. However, the essential fatty acids can only be obtained from larval food sources and we have preliminary data suggesting that armyworm adults in the migratory phase used less essential fatty acids during extended flight than their summer counterparts (Anthonypillai, 2007). We have postulated that this could be an adaptation to reduce the fitness tradeoff between migratory flight and future reproduction. We are currently testing the hypothesis that migrants differentially conserve essentially fatty acids that can only be obtained from plants during larval feeding and that cannot be obtained from adult feeding. Again we are comparing individuals from the same geographic population when reared under different temperature and photoperiodic regimes, as well as comparing populations from the Azores and North America.

The presence of non-migratory populations of *P. unipuncta* in the Azores has provided a wonderful opportunity to study the costs of migration in Lepidoptera, and we hope that some of the broader findings will also hold for other migratory insects. Thus, while some may have felt that this island archipelago offers little from a biological perspective, I would have to respectfully disagree.

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# PRELIMINARY DATA ABOUT THE BREEDING CYCLE AND DIURNAL ACTIVITY OF THE AZOREAN BAT (*NYCTALUS AZOREUM*)

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## ABSTRACT

The main aim of this study is to get information about the breeding habits of the Azorean bat that can be crucial for its conservation.

Of the 22 roosts detected, 17 were located on trees, 3 on houses and 2 on rocks. Most of the adult females (103) were captured at maternity colonies. By contrast only one adult male was captured. As expected, the males of the Azorean bat seem to be solitary. The maternity colonies are formed from April until September/October. Before that period the individuals appear to be alone or in small groups as it is established for the closest related species, *Nyctalus leisleri*. Most of the juveniles are born from mid June to July, as with *N. leisleri*. The annual cycle of *N. azoreum* probably is monoesteric with delayed fertilization as it is usual for the bats of temperate zones. The emergence from the roosts occurs before sunset, although the other species of this genus tend to emerge later. This seems to be a peculiarity of this endemic species, probably related to the scarcity of diurnal predators in the Azores allowing this species to forage during the insect abundance peak period.

## RESUMO

O objectivo principal deste estudo foi obter informação acerca dos hábitos de nidificação do morcego açoriano, os quais podem ser cruciais para a sua conservação.

Dos 22 dormitórios detectados, 17 encontravam-se em árvores, 3 em casas e 2 em rochas. A maioria das fêmeas adultas (103) foi capturada em colónias de maternidade. Pelo contrário apenas foi capturado um macho. Assim, tal como esperado, os machos do morcego açoriano parecem ser solitários. As colónias de maternidade formam-se de Abril a Setembro/Outubro. Antes deste período os indivíduos parecem estar sozinhos ou em pequenos grupos tal como está estabelecido para a espécie mais próxima, *Nyctalus leisleri*. A maioria dos juvenis nasce de meados de Junho a meados de Julho, como acontece com *N. leisleri*. O ciclo anual de *N. azoreum* provavelmente é monoestérico com fertilização retardada tal como é comum nos morcegos das zonas temperadas. A saída dos dormitórios ocorre antes do pôr-do-sol, embora as espécies deste género apresentem tendência para sair mais tarde. Esta parece ser uma particularidade desta espécie endémica, provavelmente relacionada com a escassez de predadores diurnos nos Açores, o que permite que esta espécie procure alimento durante o pico de abundância de insectos.

## INTRODUCTION

From the ten species of mammals that occur regularly in the Azores, the Azorean bat, *Nyctalu*s *azoreum* (Thomas, 1901), is the only endemic species. First considered an introduced species by some authors (Morelet, 1860; Drouët, 1861), it was described as a valid species by Oldfield Thomas in 1901; however, most authors have classed it as a subspecies of the larger Leisler's bat, *Nyctalus leisleri* (Kuhl, 1817). It is currently recognized a distinct species and it is separated from the Leisler's bat on morphological, genetic and behavior grounds (Palmeirim, 1991; Rainho e*t al*, 2002; Salgueiro e*t al*, 2004; Salgueiro e*t al*, 2007; Speakman & Webb, 1993). It is thought to have originated from the Leisler's bat that colonized the Azores relatively recently (Salgueiro e*t al*, 2007).

It is resident on the Oriental and Central Groups of the Azores archipelago. Despite being abundant on some islands it is rare on others, namely on Santa Maria island. This is one reason why it is regarded as vulnerable in the red list of IUCN (Hutson *et al.*,2001; IUCN, 2007) and critically endangered in the Red Data Book of Vertebrates (Cabral *et al*., 2006).

Previous studies of the Azorean bat were based on Museum specimens (Palmeirim, 1991; Speakman & Webb, 1993), on field observations or collection of samples for short periods of time (Moore, 1975; Rainho e*t al*, 2002) thus overlooking one of the most striking features of the Azorean bat: its tendency to be more diurnal than other insectivorous bats (Moore, 1975; Speakman & Webb, 1993; Irwin & Speakman, 2003). Generally echolocating bats have evolved in order to avoid predation by diurnal birds of prey and normally forage after sunset when the number of small insects is reduced (Avery, 1986; Speakman, 1990; Speakman, 1991; Jones & Rydell, 1994; Speakman, 1995).

Bats show a wide range of social and roosting behaviors during the year. Roosts are used by bats for a variety of purposes (mating, maternity and hibernacula, for example) at different times of the year. As the closest related species, *N. leisleri*, hibernates from late September to early April, as the females of this species give birth from mid June (Schober & Grimmberger, 1993) and as there is lack of data about the breeding cycle of the Azorean bat this study was done from March to August.

Speakman & Webb (1993) recorded the Azores bats from 30 minutes prior to sunset to 30 minutes after dawn as they assumed that they were not continuously active throughout the day. A more detailed study of the diurnal activity of the endemic bat should be carried out for an extended period of time.

The main aims of this study were, then, to obtain information about breeding habitats and the diurnal activity of *Nyctalus azoreum*, both of which could be crucial for the conservation of the only Azorean endemic mammal.

## METHODS

The search for the roosts was conducted from March to August, 1998 throughout São Miguel Island. Inquiries were initially done to find roosts but the majority was detected in Caloura, Capelas, Furnas and Ponta Delgada (São José and São Pedro), following the bats flying, after an occasional observation of bats entering or leaving a roost or after hearing their sounds. The number of individuals in each roost was recorded, looking directly into the roost (roosts with small number of individuals) or counting the bats leaving a roost in the evening (roosts with high number of individuals). The counts were made more than one time and, as often as possible, mainly at the larger colonies where counting innacuracy is more probable.

The individuals were captured using mist-nets and traps especially made for the different sizes of the holes.

The bats were classed by their ability to fly: adults (powered flight) – more than one year old; juveniles (erratic flight) – between one year and one month old; newborns (unable to fly) – less than one month old.

The reproductive status of adult females, throughout the breeding season, was assessed following Kunz (1990): Pregnant - visible distention of the lower abdomen; not pregnant – without visible distention of the lower abdomen.

The emergence of the bats from the roosts was recorded on 14 roosts. The individuals were counted from one hour before sunset until 45 minutes after sunset. In one of these roosts counts were made during a 24 hour period, divided by 4 consecutive days. All the recordings were done by two observers: one counting and the other writing down.

## RESULTS AND DISCUSSION

One hundred and seventeen bats were captured, of which 103 adult females, 1 adult male, 2 juvenile females, 5 juvenile males, 2 new born females and 4 new born males.

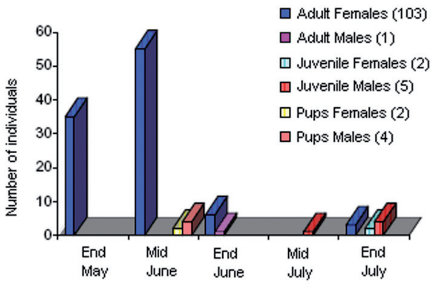

FIGURE 1. Number of individuals captured during the breeding season

The mean weight (g) was: adults, 10.1 (±0.81), n=50; juveniles, 9.6 (±1.02), n=7; pups, 3.3 (±1.29), n=6. As expected, juveniles seem to grow very fast. Growth rates are usually fast in bats as their wings must achieve near adult dimensions before they fly (Altringham, 1996). This endemic bat shows a smaller weight than that of the closest species (*N. leisleri* 11-20 g, Schober & Grimmberger, 1993). According to Salgueiro *et al*, (2007) the weight of the Azorean bat ranges from 6 to 15 g, although the sample size, ages or reproductive state of females are not mentioned.

From the 22 roosts detected the majority was located on trees (17 = 77%) and the remaining on houses (3 = 14%) and on rocks (2 = 9%). The closest species, *N. leisleri* and *N. noctula* (Schreber, 1774), show similar habits (Glaisler & Dungel, 1979; Schober & Grimmberger, 1993). The number of roosts found in Caloura, Capelas, Furnas, São José and São Pedro were, respectively: one, two, twelve, six and one. Ten roosts were maternity colonies and harbored 684 individuals [2 roosts were located on houses; mean number of individuals 117 (± 1); 8 roosts were located on trees, median number of individuals 30, maximum 219, minimum 15, interquartile range 29], 4 roosts had less than 10 individuals and more than one [total number of individuals - 19; mean number of individuals – 5 (± 3)], and 8 roosts had 1 individual. Males and females of *N. leisleri* occupy summer roosts. Whereas males use roosts alone or in small groups, females gather in maternity roosts of 20 to 50 females (in trees) and several hundreds (in buildings) (Schober & Grimmberger, 1993). The high number of individuals on roosts located on houses and the large variation of numbers on roosts located on trees, as shown in the present study, are crucial in terms of conservation of this insular species, for it strongly indicates that the potential loss of important roosts could be a real threat to the Azorean bat.

The site fidelity to the roosts was low especially to the ones with reduced number of individuals. There are plenty of available roosts and the Azorean bat may moves from one to another, possibly due to disturbance, a situation to be taken into account in terms of conservation of this species. There is, then, urgent need to have more detailed knowledge about the distribution and fidelity of to roosts throughout the geographical range of the Azorean bat, either in the islands were the endemic bat is more common, but more so where this species is rare.

The high number of adult females captured is explained by the fact that most captures were done at nursery colonies. By contrast only one adult male was captured. Males of some species of European bats, namely *N leisleri* and *N. noctula,* live alone or in small groups. Each male guards a harem of females and often keeps its mating territory for several years whereas females may move to other male territories. *Nyctalus leisleri* mates in late August or September and again in spring (Altringham, 1996; Schober & Grimmberger, 1993). As expected, the males of the Azorean bat may be solitary during the breeding season. As the nursery colonies are more conspicuous and noisy they were more easily detected than the male roosts.

The number of individuals in a roost seems to be influenced by the available space (generally at the houses the colonies were larger than at the trees and the trees with larger cavities harbored higher number of females and juveniles). The same result has been found for *N. leisleri* (Schober & Grimmberger, 1993) although maternity colonies of the Azorean bat seem to be larger than the ones of the the Leisler's bat (Kanuch & Celuch 2007; Schober & Grensmberger, 1993) but this can be influenced by the available mature trees with large holes.

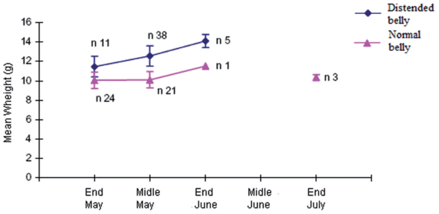

FIGURE 2. Variation of the mean weight of adult females during the breeding season.

The adult females with distended lower abdomen (54) weighed more than the adult females without distended lower abdomen (46) (Figure 2) throughout the breeding season ($H_{gl(6)}$ =68,2; p<0.05). There were significant statistical differences between the females with distended lower abdomen during the breeding season ($H_{gl(2)}$=14.7; p<0.05). These differences are related with the different stages of reproductive state of females and it seems that by mid June the majority of females are pregnant (64%). As the first pregnant females were detected by the end of May and births began to occur by mid June the length of gestation appears to be longer than 45 days at least for these females. Fetal growth in bats is amongst the slowest in mammals and the period of gestation in bats is very variable among species. The range of variation of the gestation period within species in the wild populations of bats could reach ten days and is largely due to environmental factors affecting food supply (Altringham, 1996). For this reason, the relation of the length of gestation and availability of preys of the Azorean bat needs to be studied at different sites throughout its geographical range.

The maternity colonies are formed from April to September/October (Figure 3). Before that period the individuals seem to be alone or in small groups. Probably mating roosts are established during autumn as it is known for the Leisler's bat (Schober & Grimmberger, 1993).

Most juveniles are born during the last two weeks of June and the first week of July. This high synchronization of births is similar to the closest species (Jones & Rydell, 1994). The annual cycle of the Azorean bat seems to be monoesteric with delayed fertilization as it is usual for the bats of temperate zones.

The emergence of *N. azoreum* from the roosts occurs one hour before sunset (Figures 4 and 5).

The different species of this genus tend to emerge later (Schober & Grimmberger, 1993) and this is what we would expect in an animal that relies on echolocation rather than vision. Other insectivorous bats also do not show consistent daylight active behavior, although it was detected recently in a population of Soprano pipistrelles (*Pipistrellus pygmeus)* from Italy, under very special conditions (Walker, 2010). Early emergence is, then, an unusual behavior for an insectivorous bat and seems to be a peculiarity of this endemic species. This is probably related to the scarcity of diurnal predators in the Azores allowing the Azorean bat to forage during the insect abundance peak period. In fact the buzzard (*Buteo buteo*) is the only diurnal bird of prey in the Azores and it occasionally feeds on bats.

As it is an insectivorous animal, to know its foraging hab-

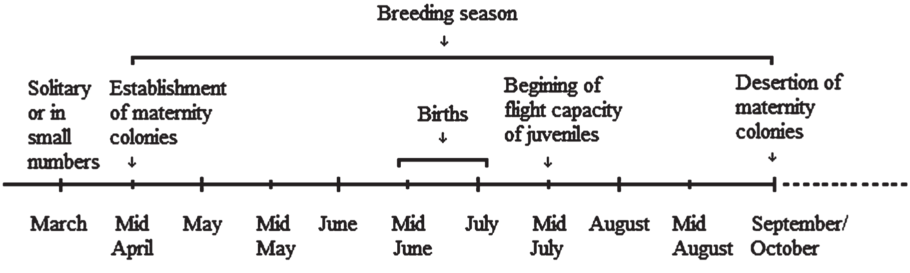

FIGURE 3. Social organization of the Azorean bat.

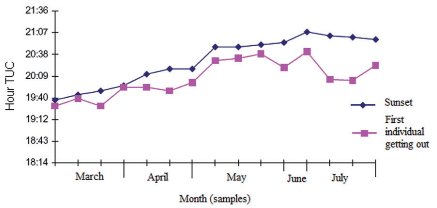

FIGURE 4. Emergence of the Azorean bat from different roosts (n=14) during the breeding season.

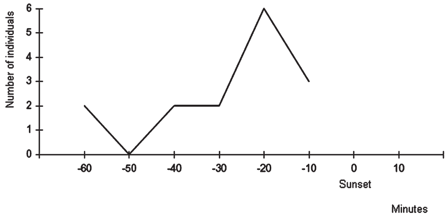

FIGURE 5. Emergence of the first individual from 14 roosts during the breeding season.

its would be a priority. An integrated ongoing improvement of the landscape throughout the archipelago should take place including policies to refrain deforestation, to enhance restoration of the native vegetation and to change agricultural and cattle raising practices. These policies should be based upon restrictions in the use of pesticides and other pollutants and will prove to be very valuable to an appropriate management and effective protection of this isolated species. Simultaneously, they will benefit the remaining biodiversity and will contribute to a sustainable, higher quality of life in the Azores islands.

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# AZOREAN BRYOPHYTES: A PRELIMINARY REVIEW OF RARITY PATTERNS

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## ABSTRACT

Bryophytes are not exempt of rarity and threat, although their small size, mute colours and difficult field identification may mask their true conservation status. Actually, it is known that a quarter of all European bryophytes are under actual or potential threat. The first Red Data Book for European Bryophytes was produced in 1995, largely based on national red lists and on the work of a vast team of bryologists who assessed the conservation status of each European species. The red listing of bryophytes has undoubtedly contributed to increase the awareness of planners to this group of organisms, and several efforts have been made, through Europe, to preserve sites based on their bryological interest. Accordingly, a specific Red List for the Azorean Bryophytes may help regional managers to identify particularly endangered species, thus allowing for the creation of measures to improve their preservation. In this paper we have used an adaptation of the works of Deborah Rabinowitz (1981), who created a typology to access different forms of rarity, using three variables: Geographical Distribution, Abundance and Habitat Specificity. All the 480 species and subspecies known to occur in the Azores were surveyed; of these, 215 species lacked sufficient data to be analyzed (data deficient), 121 were not considered rare and 144 (1 hornworts, 56 liverworts and 87 mosses) were considered rare, at least in one of the three parameters considered. The benefits and limitations of the methodology are briefly discussed. Several practical suggestions are proposed in order to enhance the conservation of selected bryophyte species.

## RESUMO

Os briófitos podem ser tão raros e estar tão ameaçados como os demais organismos do planeta, apesar de o seu pequeno tamanho, cores discretas e difícil identificação no campo poderem mascarar o seu verdadeiro estatuto de conservação. De facto, é reconhecido que cerca de um quarto de todos os briófitos da Europa estão efectiva ou potencialmente ameaçados. O primeiro "Livro Vermelho dos Briófitos da Europa" foi produzido em 1995, amplamente baseado em listas vermelhas nacionais e no trabalho de uma vasta equipa de briólogos que avaliaram o estatuto de conservação para as espécies Europeias. A classificação de briófitos em listas vermelhas tem contribuído para aumentar a sensibilidade dos gestores para este grupo de organismos e alguns esforços têm sido desenvolvidos na Europa, para preservar locais tendo como característica o seu interesse briológico. Consequentemente, uma lista vermelha para os briófitos dos Açores pode auxiliar os gestores regionais a identificar espécies particularmente ameaçadas, tornando-se o primeiro passo para assegurar a sua protecção. Neste artigo usamos uma adaptação dos trabalhos de Deborah Rabinowitz (1981), que criou uma tipologia para desocultar e avaliar várias formas de raridade, utilizando três variáveis: Distribuição Geográfica, Abundância e Especificidade do Habitat. Todas as 480 espécies e subespécies dos Açores foram investigadas: 215 *taxa* não tinham informação suficiente para ser analisados (deficientes em dados), 121 não foram consideradas raros e 144 briófitos (1 antocerota, 56 hepáticas e 87 musgos) foram considerados raros pelo menos num dos parâmetros considerados. Os benefícios e limitações desta metodologia são brevemente discutidos. São propostas algumas sugestões práticas para melhorar a estratégia de conservação dos briófitos seleccionados.

## INTRODUCTION

One of the most interesting characteristics of the Azores is their extraordinary wealth of bryophytes (480 species and subspecies, Gabriel *et al.*, 2010), comparable to the diversity present in other Macaronesian archipelagos (González-Mancebo *et al.*, 2008; Sérgio *et al.*, 2008), a feature unparalleled in other groups of Azorean organisms (Izquierdo *et al.*, 2004; Borges *et al.*, 2008, 2010a). In addition, Azorean islands host a high proportion of European bryophyte species (Homem & Gabriel,

2008) and also many endemic species of vascular plants, molluscs and arthropods (Borges *et al.*, 2010b), many of which are in danger as a consequence of historical human occupation and land-use changes (Borges *et al.*, 2000, 2009; Cardoso *et al.*, 2010; Martín *et al.*, 2010; Triantis *et al.*, 2010). In fact, the conservation of island biota was always considered a true priority since most of the recorded extinctions have occurred in islands (Sax & Gaines, 2008).

In spite of more than four centuries of Human occupation, the Azores and other Macaronesian archipelagos, still possess natural habitats (Borges *et al.*, 2009; Gaspar *et al.*, 2011), and these islands are some of the very few places in Europe where the 'biodiversity crisis' is particularly critical and a proper conservation strategy may effectively contribute to preserve unique pristine communities. Presently, about a fifth of the Azorean islands area is under some legal protection status (Monteiro & Furtado, 2010), and a few remnants of native forests have persisted since the Portuguese occupation in the early 15th century, although grasslands and exotic plantation forests dominate the islands these days (Borges *et al.*, 2009).

Most ecological studies in islands, and in particular in the Azores, are limited in their time span and a detailed understanding of the long-term responses of island bryophyte communities to global change drivers is not known. Bryophytes have long been considered indicator groups for habitat change, as their lack of roots makes them totally dependent on the atmospheric (or aquatic) inputs of nutrients (eg. Frego, 2007; Gignac, 2010). Besides, bryophytes are a characteristic part of the Azorean native forests, covering all kinds of substrata, including leaves of vascular species, with luxuriant communities (Homem & Gabriel, 2008), and are generally considered remnants of the subtropical flora that endured the Quaternary glaciations (but see Aigoin *et al.*, 2009, who recently questioned the relictual origin of Macaronesian bryophytes). Thus, assessing the conservation status for bryophytes may couple with policies for native habitats protection.

A red list ranks *taxa* according to their threat level and extinction risk, and assessments for the red list compile current knowledge of conservation status and threats to individual species (ex. Knapp & Monterrosa Salomón, 2010). Few vascular plants and even fewer bryophytes (only 101 of the ca. 18000 species!) have been formally assessed using the IUCN system (IUCN, 2010). However, one of the targets of the Global Strategy for Plant Conservation is "a preliminary assessment of the conservation status of all known plant species, at national, regional and international levels" (UNEP, 2002). There are various approaches to achieve this goal, including the use of expert's opinions (ex. Sérgio *et al.*, 1992; Schumacker, 2001; Sjögren, 1995), the use of herbarium labels information (ex. Krupnick *et al.*, 2008), the creation of specific software to create red lists accommodating the IUCN criteria (ex. RAMAS, 2007), but lately it has been advised that a thorough use of all available information, including georeferenced herbarium specimens and other parameters such as population size and local abundance, would be a good way forward to stimulate conservation (ex. Brummitt *et al.*, 2008). In practice, not many species have been studied in any of these ways and the information necessary to do so is impressive. Nevertheless, the need to better understand the rarity of species is pressing and simple methods of ranking should at least be essayed for all groups of organisms.

The pioneer work of Deborah Rabinowitz (1981, 1986) has enlightened the rarity concept, acknowledging that

> *"There are many ways in which a species can become rare and this path has profound evolutionary and ecological consequences"* (Rabinowitz, 1981: 205).

To define rarity, she used a three dimensional system including distribution, abundance and habitat specificity. Each one of these dimensions was further subdivided into two qualitative categories (wide or narrow, large or small, generalist or specialist, respectively), resulting in an eight cells table, from which, only one cell includes common species, those with wide distributions, large populations and generalist. All other combinations suffer from at least one form of rarity. Knowing the rarity status of species is critical to evaluate both their extinction proneness and their roles in the ecosystems (Gaston, 1994, 2010).

One of the most useful resources to study biodiversity in the Azores is the regional species database, ATLANTIS, where grid-based spatial incidence information, allied to temporal data, has been gathered for several groups of organisms (lichens, bryophytes, vascular plants, marine invertebrates, terrestrial molluscs, arthropods and vertebrates) (Borges *et al.*, 2010c; Martín *et al.*, 2010). Parallel to this work, the biological and ecological features of bryophytes have also been noted by RG and co-workers. The information thus gathered may therefore serve as a starting point for an assessment of the rarity of bryophytes, using Rabinowitz' approach (considering range, abundance and distribution). Such a characterization has been applied to vascular plant species (ex. Rabinowitz *et al.*, 1986; McIntyre, 1992), vertebrates (ex. Kattan, 1992; Goerck, 1997), insects (ex. Fattorini, 2011) and was essayed for European liverworts (Weibull & Söderström, 1995).

In this study we used all the information available to Azorean bryophytes, as inserted in ATLANTIS database, supplemented with literature and herbaria ecological features, to analyze the rarity patterns of the species and provide a preliminary conservation assessment, at the regional level, of this important indicator group. It is expected that it may be the basis of an Azorean Red List for Azorean bryophytes.

## METHODS

### *Study Area*

The nine islands composing the archipelago of the Azores, are situated in the North Atlantic Ocean, extending along a west-northwest to east-southeast orientation (between 36° 30′ - 40° North latitudes and 24° 30′ - 31° 30′ West longitudes). The joined area of the islands is 2,323 km$^2$ (larger island, São Miguel, 745 km$^2$; smaller island, Corvo, 17 km$^2$) (Forjaz, 2004). The archipelago's highest altitude is reached in Pico Island, at 2,350 m, but the second highest island (São Miguel) is just 1,105 m altitude. The Azores were uninhabited when Portuguese navigators arrived in the early 15th century, and the earlier descriptions of the islands portray them as intensely forested (Frutuoso, 1963). Nowadays the Azorean population includes about 241,800 people, at a density of 104 inhabitants per square kilometre (Forjaz, 2004). It is estimated that laurel forests occupied about 85% of the present area of Azores; unfortunately, most of this natural habitat has been disturbed, remaining only around 6,000 ha (Fernández-Palacios *et al.*, 2011; Gaspar *et al.*, 2011).

*Data Sources*

A tentative categorization of rarity was essayed for all the 480 bryophyte species and subspecies included in the most recent check-list of the Azorean Islands (Gabriel *et al.*, 2010). The analyzed data came from literature and herbarium records. The first step included a thorough analysis and interpretation of the available literature, dating back to the 19th century (167 sources; see Appendix 1); this list includes books, chapters and papers as well as some grey literature such as academic thesis, letters and fieldwork reports (see Borges *et al.*, 2010c for details). Secondly, the collection of bryophytes deposited at the University of the Azores was also examined. All information was fed to the ATLANTIS database (Borges, 2005). This database includes 29,323 species citations coming from literature (most of them, ca. 80%, with recognizable locations and indication of date of collection) and 11,237 citations coming from herbarium records (most of them placed at the bryophyte collection of the University of the Azores). One of the authors (RG) has further compiled information on fruiting, ecology and substrate preferences for each bryophyte record; in some occasions the habitat type was inferred from other published sources or direct knowledge of local experts. Although gaps of information are inevitable, and have indeed been demonstrated (see Aranda *et al.*, 2010), this database is deemed to be as complete as possible and a good starting point to analyze rarity issues. A webpage, the Azorean Biodiversity Portal (http://www.azoresbioportal.angra.uac.pt/), with data on the taxonomy, detailed distribution of the species on the Azorean Islands (grid of 500 m x 500 m), European conservation status and some pictures and common names (whenever possible) has been available to the general public since 2008 (Borges *et al*., 2010c).

*Rarity dimensions*

*Geographical distribution*

Due to the high dispersal ability characteristic of the group (see revision in Rydin, 2008), bryophytes occurring in the Azores were considered to have a narrow geographical distribution when their presence was known only from the Macaronesian Islands (i.e. Macaronesian endemic species and subspecies) and a wide distribution, whenever they also occurred elsewhere. This data was obtained from the recent checklist for Azorean bryophytes (Gabriel *et al*., 2010).

*Abundance*

Abundance was the most difficult parameter to quantify, as it refers to the size of the populations, which is not immediate in bryophyte studies (Hallingbäck *et al*., 1998; Hallingbäck, 2007). Different authors have used different approaches to estimate abundance, such as the examination of museum specimens (see Fattorini, 2011 for arthropods), and others have not considered this parameter for bryophytes (ex. Söderström & Séneca, 2008; Vanderpoorten & Hallingback, 2008). In order to reach an estimation of abundance for bryophytes, we have taken advantage of a recurrent pattern in ecological communities, i.e. the positive intraspecific or interspecifc relationship between mean local abundance and regional distribution (Gaston, 1994, 1996), which assumes that

> "*Within a taxonomic assemblage, locally abundant species tend to be widespread and locally rare species tend to be restricted in their distribution.*" (Gaston, 1996: 211).

The key issue here is the use of the small-scale distribution as a proxy of abundance. The importance of scaling, rarity and risk, has been highlighted by Hartley & Kunin (2003), working with two plant species (*Dianthus armeria* L. and *Silene otites* (L.) Wibel) at a distribution resolution of 1-km in Great Britain. Bearing this in mind, and using the ATLANTIS database, we have calculated for each species the number of geographical cells (500 m x 500 m) allocated with the highest precision values (precision 1 – very precise locations, usually point UTM data; 2 – localities never exceeding 25 km$^2$) in all Azorean Islands (see Borges *et al*., 2010c), and subsequently divided that value by the total number of 500 $m^2$ cells of the archipelago (10044 cells), thus reaching an estimate of the area of occupancy (AOO) for each bryophyte. This ratio of relative area of occupancy was then considered a predictor of the local abundance for each species. All the species were ranked by this index, and those which fell below the median value were considered of low abundance while the others were considered as abundant.

*Ecological tolerance*

Habitat specificity was used as a proxy of ecological tolerance. RG's species database on ecological traits was categorized in 12 different habitat types (Coastal habitats, Mesic areas, Native forests, Semi-natural grasslands, Mountainous areas, Aquatic habitats, Peat bogs, Urban habitats, Parks and Gardens, Intensive pastures, Exotic forest plantations and Cave entrances). Table 1 includes a summary description of each of the habitats considered.

The islands survey is not equitable (Table 2); for example, if the number of records per $km^2$ is considered, Corvo, Terceira and Graciosa are the best inspected of the Azorean Islands while São Miguel is the worst. Likewise, the percentage of records to which it was not possible to assign a habitat varied according to the islands (highest in Faial and São Jorge and lowest in Terceira and Corvo) but, in average it did not reach one tenth (9.7%) of the 34976 records considered.

To appreciate the ecological range of a species, all the records where this was possible, were allocated to one of the 12 habitat types. Then, the number of records present in one habitat was divided by the total number of locations of that habitat (normalizing the records per habitat). Finally, for those species that had 12 or more described occurrences, the Lloyds Index of Patchiness (L) was applied: $L = S_x^2 - x / x^2 + 1$ (Basset, 1999), where $S_x^2$ and x are respectively the variance and mean of the samples in the 12 different habitat types. A specialist species in the present context is a species that showed preference for a particular habitat, the value of the index increasing for more specialized species. According to the interpretation of different authors (eg. Basset, 1999; Gabriel & Bates, 2005) those species with an L value larger or equal to three, were considered

TABLE 1. Brief description of the habitats considered in this paper and an indication of the number of independent locations where bryophytes were collected in the Azores.

| **Habitat types** | **Description** | **Number of locations** |
|---|---|---|
| Coastal habitats | Coastal habitats are situated at the lowest altitudes, near the sea, mostly up to an altitude of 50 m, which may be higher, depending on the Island. | 124 |
| Mesic areas | Mesic areas occur above the coastal habitats and receive intermediate amounts of precipitation. These areas are presently dominated by fields (mostly corn fields), intensive pastures and exotic plantations. | 204 |
| Native forests | Native forests are the remnants of the former dominant ecosystem types, found by the first settlers. They include evergreen tree species such as *Laurus azorica, Erica azorica, Ilex perado* subsp. *azorica* and *Juniperus brevifolia.* | 522 |
| Semi-natural grasslands | These are open areas, mostly located among native forest fragments, including several herbaceous plant species. | 42 |
| Mountainous areas | This habitat (high mountain) is restricted to Pico Island, above 1200 m altitude. | 57 |
| Aquatic habitats | This habitat includes lagoon margins, temporary and permanent rivulets, cascades and other interior waters habitats. | 212 |
| Peat bogs | Large, open areas dominated by *Sphagnum* spp. | 115 |
| Urban habitats | Habitats that may be found in cities and villages, including buildings and other human constructions. | 70 |
| Parks and Gardens | Areas covered with exotic species, organized to appreciate nature. | 48 |
| Intensive pastures | Areas dominated by *Holcus*, *Bromus* or *Lolium* species, used by grazing cattle. | 129 |
| Exotic plantation forests | Areas dominated by *Eucalyptus* spp., *Cryptomeria japonica* or *Pittosporum undulatum.* | 163 |
| Cave entrances | Specific habitat, including all the rocky walls of caves (lava tubes) and volcano entrances (pits and pit caves), where light penetrates. | 81 |

with restricted habitat requirements. Before proceeding to the calculus of L, the number of occurrences in a given habitat was normalized for the number of total occurrences in that habitat. For instance, while there were 522 locations inside native for-

TABLE 2. General characteristics of the Azorean Islands, including the total number of bryophyte' records made in the archipelago and the absolute and relative frequencies of records to which no habitat could be attributed. ([1]. Forjaz, 2004).

| **Azorean Island** | **Area**[1] | **Highest point**[1] | **Inhabitants**[1] | **Number of records** | **Records without habitat information** | |
|---|---|---|---|---|---|---|
| | ($km^2$) | (m) | (Censos 2001) | ($N_T$) | ($N_H$) | (%) |
| Santa Maria | 97 | 587 | 5578 | 942 | 98 | 10,4 |
| São Miguel | 745 | 1105 | 131609 | 3897 | 224 | 5,7 |
| Terceira | 400 | 1021 | 55833 | 13104 | 433 | 3,3 |
| Graciosa | 61 | 405 | 4780 | 1576 | 32 | 2,0 |
| São Jorge | 244 | 1053 | 9674 | 4054 | 744 | 18,4 |
| Pico | 445 | 2350 | 14806 | 6501 | 780 | 12,0 |
| Faial | 173 | 1043 | 15063 | 2076 | 404 | 19,5 |
| Flores | 141 | 911 | 3995 | 1551 | 126 | 8,1 |
| Corvo | 17 | 720 | 425 | 1275 | 103 | 8,1 |

ests, there were only 163 locations placed in exotic plantation forests.

*Vulnerability index*

Species considered rare on distribution, abundance and ecological tolerance, tend to be the most prone to extinction (Kattan, 1992; Manne & Pimm, 2001). The consequent application of the three criteria, with their binomial measurements: Distribution (large/small), Abundance (common/rare) and Ecological tolerance (wide/narrow), led to the following categorization: 1. Species that are not rare; 2. Scarce species (rare in abundance); 3. Species with narrow ecological tolerance; 4. Restricted species (species rare by geographical range); 5. Scarce species with narrow ecological tolerance; 6. Scarce and restricted species; 7. Restricted species with narrow ecological range and 8. Restricted and scarce species with narrow ecological range. Similar categories may be appreciated for other groups such as vertebrates (ex. Kattan,

1992) and arthropods (Fattorini, 2011) and also for bryophytes Söderström (1995).

## RESULTS

Of the 480 species referred to the Azores, only 265 (55.2%) could be analyzed following the combination of criteria used (Appendix 2). From the evaluated species, about half (121; 45.7%) were not considered rare (1. Species that are not rare) but six of the seven types of rarity proposed by Rabinowitz (1981) were found within the Azorean bryophytes' dataset (absolute and relative frequencies of the eight categories may be seen in Figure 1). If one considers single categories of rarity by themselves, less than half (112; 42.3%) of the evaluated species presented narrow ecological tolerance, more than one fifth (56; 21.1%) were considered scarce and only 17 evaluated species (6.8%) had restricted distributions.

The results of the Chi-square test show that the hypothesis of overall independence of the three factors may be rejected ($X^2=47.36$; df=2; $p < 0.05$), indicating that these factors are not independent. Separate analysis of the 2 x 2 tables also indicated that all measures were not independent ($p<0.05$).

Twenty four species, nine liverworts and 15 mosses, previously classified in the European Red List of Bryophytes (ECCB, 1995; Dierssen, 2001), four of which (*Acanthocoleus aberrans, Jamesoniella rubricaulis, Fissidens azoricus* and *Neckera cephalonica*) also suggested by Sjögren (1995) to become protected species in the Azores, could not be evaluated in this analysis. All of these 24 species are scarce (rare by abundance) and none had the necessary number of collections to allow a full assessment of their ecological tolerance. Among them there are five restricted species, two Azorean endemics (*Fissidens azoricus* and *Trematodon perssoniorum*) and three Macaronesian endemics (*Leucodon canariensis, Neckera cephalonica* and *Tortula bogosica*). *Trematodon perssoniorum* which, so far, was only found in São Miguel Island seems to prefer aquatic habitats, and was collected mostly around Lagoa das Furnas and Ribeira Quente (seven records at different times), while *Riccia ligula* was only recorded in intensive pastures (six records) and *Jamesoniella rubricaulis* was only collected above 1000 m (five records).

## DISCUSSION

Only about half (265) of all Azorean bryophytes species and subspecies (480) could be classified using the three rarity categories proposed by Rabinowitz (1981). In itself, this exposes a serious lack of information, regarding mostly abundance and ecological tolerance, which thwarts the design of a comprehensive conservation policy for bryophytes. Without appropriate knowledge of the biology of the species, it is not possible to understand why a bryophyte is rare or threatened and it is very difficult to propose measures that would induce its recovery.

The data presented in Figure 1 and Appendix 2, shows that most of the analyzed bryophytes that may be considered rare have wide range distributions (247 species), which is not surprising, considering that bryophytes successfully disperse by spores. Actually some authors such as Medina, Draper & Lara (2011), have argued that due to their high dispersal ability, bryophytes would tend to ubiquity. The hypothesis "*Everything is everywhere, but the environment selects*" (EiE) has generally been accepted by microbiologists (ex. O'Malley, 2007) and is being considered for larger organisms with microscopic dispersing stages (e.g. spores), such as ferns or bryophytes (ex. Fontaneto, 2011). An indirect evidence of this wide distribution ability is the low endemism value found among Azorean bryophytes (n=7; 1,5%), much lower those found among native vascular species or arthropods (Borges *et al.*, 2010b). Moreover, according to the study of Söderström & Séneca (2008), the liverwort flora of Europe and Macaronesia consists of mainly widespread species, and, unlike what happens with vascular species, the rarest species occur in oceanic areas (and not in the Mediterranean region).

Eight of the 17 Macaronesian and Azorean endemic bryophytes evaluated, exhibited restricted distributions (Appendix 2, "vulnerability index 4"), while not appearing to be scarce or restricted in their habitat requirements. Interestingly enough, all of these eight species have been reported to the three geographical groups of islands and are presently known of six (*Breutelia azorica*) or more, of the nine Azorean islands (other seven species). Although the

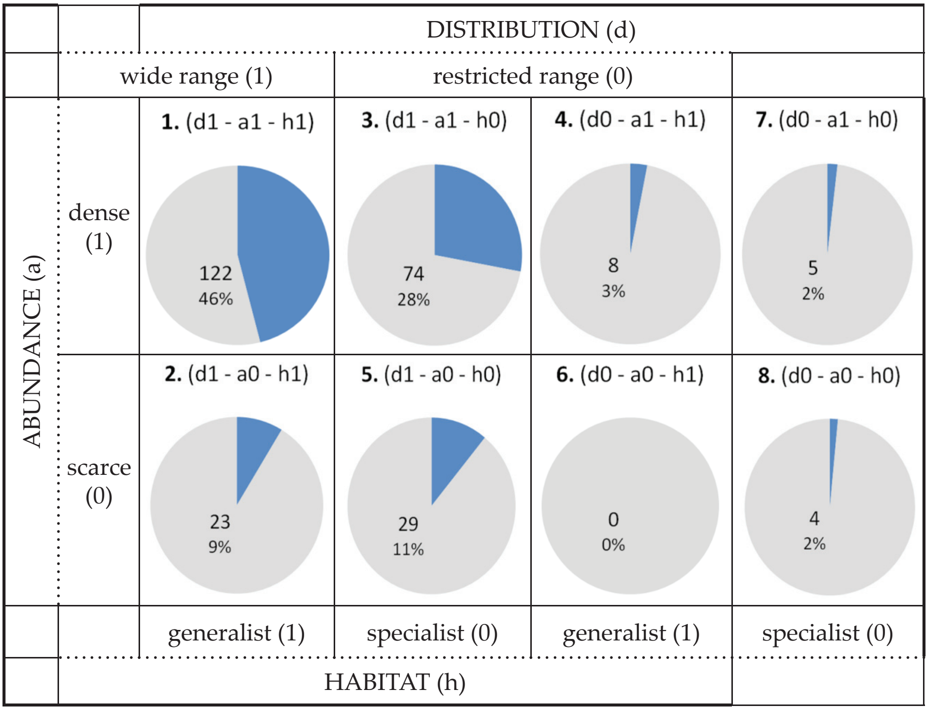

FIGURE 1. Distribution of rarity types within the evaluated bryophyte species (n=265) in the Azores. Numbers indicate number of species per category; dark areas of pie charts indicate the percent of the dataset each rarity type represents. 1, Species that are not rare; 2, Scarce species (rare by abundance); 3, Species with narrow ecological tolerance; 4, Restricted species (rare by range); 5, Scarce species with narrow ecological tolerance; 6, Restricted and scarce species; 7, Restricted species with narrow ecological range; 8, Restricted and scarce species with narrow ecological tolerance.

Chi-square tests indicated a significant association among distribution, rarity and abundance, endemism is not always associated with narrow ecological tolerance or with scarcity; species such as *Andoa berthelotiana* and *Leucodon treleasei* have been abundantly collected in different types of habitats and all islands of the Azores (eg. González-Mancebo *et al.*, 2009). If these species evolved in Macaronesia (neoendemics), or survived only in Macaronesia (paleoendemics), they should indeed be well adapted to the Azorean ecosystems. Notwithstanding, *Echinodium renauldii*, which was recently confirmed as a true endemic species (Stech *et al*., 2008), is considered vulnerable by the IUCN (BSG, 2010), on account of its decreasing population trend and occurrence in less than ten localities in five islands of the Azores; this view is shared by Sjögren (1995). Fortunately, the number of places where this species has been collected is now known to be higher (more than 40 locations) and its presence was confirmed in two more islands (Corvo and Terceira) since 1995.

Almost half (n=112; 42,3%) of all the analyzed bryophytes were considered specialists in their habitat requirements, as referred by their high Lloyd index values, achieved when a high proportion of the total number of collections are grouped into one, or mostly two, habitats. Man-made habitats, such as exotic forests, grasslands or urban habitats do not seem to harbour specialist bryophyte species. This in itself has sobering implications for conservation, because of the historical decrease and fragmentation of native habitats (Triantis *et al*., 2010; Gaspar *et al*., 2011).

Forty liverworts and 24 mosses, more than half (!) of the specialist bryophyte species evaluated in this study (n=112) and about a quarter of all evaluated species show preference for natural forests (n=64; 24.2%). This is not surprising in view of what we know about the original plant cover of the islands – a dense forest ecosystem (ex. Frutuoso, 1963) that is lavishly covered with bryophytes in all occurring substrata. In spite of its obvious decrease in area (Silveira, 2007), the diversity and luxuriance of the communities that may be observed in the remaining native forest fragments (ex. Gabriel & Bates, 2005; Homem, 2005) is still staggering; thus, it is understandable, that this is the single most important habitat for bryophyte conservation in the Azores. Recently it was also demonstrated that Azorean native forests are a unique habitat for the conservation of most endemic arthropods (Triantis *et al*., 2010), and a high proportion of those species are now under threat of extinction due to its reduction. Bryophytes depending on native fragments are probably under the same pressures and would greatly benefit from an increase in the areas devoted to natural forests and from a careful control of the quality of remaining fragments, such as the removal of invasive species.

Peat bogs are structurally very different from forests, in their openness and permanent access to water and eleven species were considered specialists from this habitat, taking advantage of these special conditions. Obviously, *Sphagnum* and *Polytrichum* species (the green and brown makers of peatlands) are prone to be found in these habitats, but the persistent presence of the rare *Isopterygium tenerum* in Furnas do Enxofre (Terceira Island), should also be noted.

Surprisingly, or not (see Gabriel *et al.*, 2006; Jennings, 2009), caves (lava tube and pit caves entrances) are an equally interesting habitat for the specialist group of bryophytes. Beyond *Asterella africana*, that has been collected specifically in such habitats, two other liverworts and eight mosses find refuge in these harsh environments, where competition from vascular species is certainly lower. Besides the 11 species that have mostly been collected at cave entrances, some species such as *Plagiochila longispina*, *Cyclodictyon laete-virens*, *Plagiothecium nemorale*, *Tetrastichium virens* and others, may be found both in native forest and cave entrances. This ability to colonize cave rocks is likely to expand their altitudinal range, as many of the lowest altitude records were from cave entrances. It is clear that caves are acting as refugia for some of these species. Due to the particular way abundance was inferred from the data, this is the least independent rarity dimension studied. The main issue is the lack of standardized data from where to take sound information (but see Gabriel & Bates, 2005 and Homem, 2005). However as showed by Couto (2010), standardized data on abundance obtained for several sites, was well correlated with distribution at the scale of Terceira Island. Bearing this in mind, additional efforts to get standardized information for different habitats and islands should be made. A relatively high number of the evaluated species (n=56; 21.1%), showed low abundance values, and were thus considered scarse. Scarse species include representatives from the three taxonomic groups (hornworts, liverworts and mosses); some examples include species that have been collected in a few places and were considered specialists such as *Asterella africana* (cave entrances), *Leptoscyphus azoricus* (native forests) or *Isopterygium tenerum* (peat bogs) but also species such as *Cephalozia lunulifolia, Fissidens coacervatus* or *Campylopus brevipilus*.

It is important to recognize that among the species that could not be evaluated are Azorean rare bryophytes seem to be found mostly in three important habitats: native forests, peat bogs and cave entrances. While a commendatory effort has been made in order to create natural parks in all islands including most native forests fragments, no such effort has been made to encompass lava tubes (Pereira *et al*., 2011), which are largely under private land and require adequate legislation to protect them, and peat bogs are presently very disturbed habitats.

About a third (n=43, 26 liverworts and 17 mosses; 30.1%) of all conservation dependent bryophytes (n=143) exist in five or more Island Parks. These Parks (one for each Island) have recently been created in the Azores and incorporate areas using different levels of protection, generally following IUCN criteria for protected areas (ex. Dudley, 2008). Nevertheless, there is a quarter of all conservation concern species (n=35 species, 22 liverworts and 13 mosses; 24.5%), including *Acrobolbus wilsonii, Adelanthus decipiens, Aphanolejeunea madeirensis, Leptoscyphus azoricus, Pallavicinia lyellii, Campylopus shawii* or *Cyclodictyon laetevirens* that exist in less than five Island Parks. While some of these species have a restricted range in the archipelago, occurring also in few islands (ex. *Kurzia pauciflora, Cheilolejeunea cedercreutzii*), others, such as *Plagiochila punctata* (7 Islands – 3 Island Parks), *Calypogeia azorica* (6 – 3), *Cyclodictyon laetevirens* (6 – 3), *Pallavicinia lyellii* (6 – 2) or *Trichocolea tomentella* (4 – 1) are not adequately protected by the current design of the Island Parks.

This work illustrates that even among relatively well studied groups of organisms – bryophytes, in a very confined region – the Azores, where a continuing collection, identification and reporting effort has been made through time, it was not possible to have a clear picture of the general rarity patterns of all species, and only about half of the reported taxa (n=265; 55.2%)

could be assessed using a simple method of categorization. This hinders conservation efforts, as only a fraction of knowledge is available to managers and decision makers, while enlightening the way forward. It is clear that better floristic knowledge and expertise on bryophytes is necessary in the Azores, if we are to preserve the wealth of species and the natural communities where they occur. As Knapp & Monterrosa Salomón have stated: *"[this] method is not a substitute for a quantitative conservation assessment…"* (2010: 527), however it is a way of setting priorities for further study or monitoring. Some suggestions follow:

1. The 143 species selected at least by one of Rabinowitz's dimension of rarity should be followed and all efforts should be made to adequately conserve their habitats.
2. The 24 species previously selected by IUCN criteria (ECCB, 1995; Dierssen, 2001), that could not be evaluated in this study for lack of collection records, should be very carefully prospected in the field and their evolution monitored, especially the four species that were also mentioned by the experts Erik Sjögren (1995) and / or René Schumacker (2001): *Acanthocoleus aberrans*, *Jamesoniella rubricaulis*, *Fissidens azoricus* and *Neckera cephalonica*.
3. One liverwort (*Aphanolejeunea madeirensis*) and three mosses (*Fissidens coacervatus*, *Sphagnum nitidulum*, *Thamnobryum rudolphianum*) have come out as restricted, scarce and with a narrow ecological tolerance, which means they were considered rare in the three dimensions considered. While it is obvious that their conservation in the Azores should be carefully planned, the taxonomic status of *S. nitidulum* and *F. coacervatus*, should be clarified.
4. Island Parks are acting as "safe areas" for a number of bryophyte species however, other conservation concern species would benefit from a reshape, sometimes quite straightforward, of those protected areas.
5. Some species that are not routinely included in red lists have nonetheless come up as rare in one or two

dimensions, an aspect already discussed for mosses by Sjögren (2006). This enlightens the scale problem of conservation: it is important to acknowledge that regional, as well as global, conservation plans should be enforced.

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APPENDIX 2. Data on Azorean bryophyte species and subspecies as classified in the Rabinowitz (1981) rarity criteria used in this work. (Mean altitude includes all the records; dd, data deficient; na, not applicable; es, SJÖGREN, 1995; rs, Schumacker, 2001; Old IUCN Criteria: based on ECCB, 1995 and Dierssen, 2001).

| Species | Endemic grouping | Groups of Islands | Number of Islands | Presence in Island Parks | Number of 500 x 500 m cells | Lloyd index (>11 records) | Habitat with highest number of records | Minimum altitude (m) | Mean altitude (m) | Maximum altitude (m) | Records <1976 | Records >1975 | Old IUCN criteria | Experts' opinion | Vulnerability Index |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **HORNWORTS** | | | | | | | | | | | | | | | |
| ***Anthoceros caucasicus* Steph.** | | 3 | 9 | 6 | 146 | 1,8 | ExFor (18) | 200 | 520,5 | 825 | 14 | 45 | r | | 1. Species that are not rare |
| ***Anthoceros punctatus* L.** | | 3 | 9 | 7 | 447 | 1,3 | NaFor (24) | 100 | 372,3 | 700 | 49 | 51 | | | 1. Species that are not rare |
| ***Phaeoceros carolinianus* (Michx.) Prosk.** | | 1 | 4 | 1 | 3 | dd | na (1) | 350 | 350,0 | 350 | 0 | 4 | | | |
| ***Phaeoceros laevis* (L.) Prosk.** | | 3 | 8 | 5 | 70 | 0,6 | NaFor (6) | 175 | 440,0 | 700 | 3 | 12 | | | 2. Scarce species (rare by abundance) |
| ***Phymatoceros bulbiculosus* (Brot.) Stotler, W. T. Doyle *et* Crand.-Stotl.** | | 3 | 4 | 1 | 67 | dd | na (2) | dd | dd | dd | 4 | 3 | | | |
| **LIVERWORTS** | | | | | | | | | | | | | | | |
| ***Acanthocoleus aberrans* (Lindenb. *et* Gottsche) Kruijt** | | 1 | 3 | 2 | 20 | dd | NaFor (4) | 500 | 690,0 | 750 | 4 | 1 | r | es; rs | |
| ***Acrobolbus wilsonii* Nees** | | 2 | 4 | 3 | 117 | 6,1 | NaFor (47) | 500 | 864,3 | 1050 | 20 | 32 | v | es; rs | 3. Species with narrow ecological tolerance |
| ***Adelanthus decipiens* (Hook.) Mitt.** | | 3 | 6 | 4 | 179 | 6,4 | NaFor (92) | 500 | 856,8 | 1500 | 34 | 65 | | es | 3. Species with narrow ecological tolerance |
| ***Anastrophyllum minutum* (Schreb.) R. M. Schust.** | | 3 | 8 | 5 | 137 | 1,6 | NaFor (26) | 250 | 692,7 | 2300 | 15 | 33 | | | 1. Species that are not rare |
| ***Aneura pinguis* (L.) Dumort.** | | 3 | 5 | 4 | 92 | dd | NaFor (5) | 500 | 616,7 | 850 | 6 | 5 | | | |
| ***Aphanolejeunea azorica* (V. Allorge *et* Ast) Pócs et Bernecker** | | 3 | 9 | 7 | 198 | 2,0 | NaFor (76) | 150 | 592,9 | 1050 | 75 | 65 | v | | 1. Species that are not rare |
| ***Aphanolejeunea madeirensis* (Schiffn.) Grolle** | MAC | 2 | 5 | 4 | 83 | 4,6 | NaFor (36) | 250 | 658,8 | 925 | 36 | 6 | r | rs | 8. Restricted and scarce species with narrow ecological tolerance |
| ***Aphanolejeunea microscopica* (Taylor) A. Evans** | | 3 | 8 | 6 | 624 | 4,2 | NaFor (570) | 50 | 701,8 | 1100 | 468 | 185 | | | 3. Species with narrow ecological tolerance |
| ***Aphanolejeunea sintenisii* Steph.** | | 3 | 9 | 8 | 390 | 2,4 | NaFor (180) | 150 | 549,8 | 975 | 85 | 195 | v | | 1. Species that are not rare |
| ***Asterella africana* (Mont.) A. Evans** | | 3 | 7 | 5 | 79 | 7,9 | Caves (21) | 10 | 387,8 | 875 | 13 | 25 | v | rs | 5. Scarce species with narrow ecological tolerance |

| **Species** | **Endemic grouping** | **Groups of Islands** | **Number of Islands** | **Presence in Island Parks** | **Number of 500 x 500 m cells** | **Lloyd index (>11 records)** | **Habitat with highest number of records** | **Minimum altitude (m)** | **Mean altitude (m)** | **Maximum altitude (m)** | **Records <1976** | **Records >1975** | **Old IUCN criteria** | **Experts' opinion** | **Vulnerability Index** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Barbilophozia attenuata*** **(Mart.) Loeske** | | 2 | 6 | 5 | 195 | 2,8 | NaFor (42) | 400 | 656,1 | 1000 | 19 | 33 | | | 1. Species that are not rare |
| ***Bazzania azorica*** **H. Buch** ***et*** **H. Perss.** | AZ | 3 | 6 | 6 | 376 | 7,8 | NaFor (320) | 350 | 766,4 | 1050 | 112 | 232 | r | rs | 7. Restricted species with narrow ecological range |
| ***Blepharostoma trichophyllum*** **(L.) Dumort.** | | 3 | 9 | 5 | 167 | 2,0 | NaFor (35) | 150 | 700,0 | 1050 | 12 | 40 | | | 1. Species that are not rare |
| ***Calypogeia arguta*** **Nees** ***et*** **Mont.** | | 3 | 9 | 8 | 245 | 2,8 | NaFor (57) | 100 | 501,3 | 975 | 35 | 102 | | | 1. Species that are not rare |
| ***Calypogeia azorica*** **Bischl.** | MAC | 3 | 6 | 3 | 116 | 3,3 | NaFor (21) | 150 | 555,2 | 750 | 8 | 26 | r | es; rs | 7. Restricted species with narrow ecological range |
| ***Calypogeia fissa*** **(L.) Raddi** | | 3 | 9 | 9 | 455 | 3,3 | NaFor (181) | 200 | 601,8 | 1050 | 65 | 279 | | | 3. Species with narrow ecological tolerance |
| ***Calypogeia integristipula*** **Steph.** | | 3 | 4 | 4 | 16 | dd | NaFor (8) | 800 | 808,3 | 825 | 11 | 1 | | | |
| ***Calypogeia muelleriana*** **(Schiffn.) Müll. Frib.** | | 3 | 8 | 7 | 468 | 3,1 | NaFor (242) | 150 | 667,5 | 1050 | 105 | 228 | | | 3. Species with narrow ecological tolerance |
| ***Calypogeia neesiana*** **(C. Massal.** ***et*** **Carestia) Müll. Frib.** | | 3 | 5 | 3 | 64 | 3,9 | NaFor (22) | 500 | 636,5 | 825 | 15 | 13 | | | 5. Scarce species with narrow ecological tolerance |
| ***Calypogeia sphagnicola*** **(Arnell** ***et*** **J. Perss.) Warnst. et Loeske** | | 3 | 6 | 2 | 15 | 3,0 | NaFor (13) | 650 | 750,0 | 925 | 12 | 4 | | rs | 5. Scarce species with narrow ecological tolerance |
| ***Calypogeia suecica*** **(Arnell** ***et*** **J. Perss.) Müll. Frib.** | | 3 | 4 | 3 | 58 | 1,7 | ExFor (6) | 350 | 425,0 | 550 | 7 | 9 | | | 2. Scarce species (rare by abundance) |
| ***Cephalozia bicuspidata*** **(L.) Dumort.** | | 3 | 8 | 8 | 334 | 1,9 | NaFor (87) | 225 | 637,0 | 1075 | 49 | 91 | | | 1. Species that are not rare |
| ***Cephalozia connivens*** **(Dicks.) Lindb.** | | 2 | 3 | 2 | 50 | dd | NaFor (4) | 800 | 893,8 | 925 | 2 | 4 | | | |
| ***Cephalozia crassifolia*** **(Lindenb.** ***et*** **Gottsche) Fulford** | | 3 | 6 | 6 | 333 | 5,5 | NaFor (211) | 250 | 693,8 | 1000 | 73 | 178 | v | | 3. Species with narrow ecological tolerance |
| ***Cephalozia lunulifolia*** **(Dumort.) Dumort.** | | 2 | 5 | 4 | 65 | 5,2 | NaFor (8) | 625 | 805,0 | 1025 | 9 | 3 | | | 5. Scarce species with narrow ecological tolerance |
| ***Cephaloziella baumgartneri*** **Schiffn.** | | 1 | 2 | | 10 | dd | Mesic (3) | dd | dd | dd | 3 | 2 | | | |
| ***Cephaloziella calyculata*** **(Durieu et Mont.) Müll. Frib.** | | 1 | 1 | 1 | 3 | dd | na (1) | dd | dd | dd | 0 | 1 | r | | |
| ***Cephaloziella dentata*** **(Raddi) Steph.** | | 2 | 2 | 1 | 9 | dd | NaFor (3) | 500 | 539,3 | 650 | 0 | 7 | | | |
| ***Cephaloziella divaricata*** **(Sm.) Schiffn.** | | 3 | 3 | 3 | 76 | dd | Mesic (6) | 225 | 475,0 | 600 | 6 | 4 | | | |
| ***Cephaloziella hampeana*** **(Nees) Schiffn.** | | 1 | 2 | 1 | 3 | dd | na (2) | 550 | 575,0 | 600 | 0 | 3 | | | |

| Species | Endemic grouping | Groups of Islands | Number of Islands | Presence in Island Parks | Number of 500 x 500 m cells | Lloyd index (>11 records) | Habitat with highest number of records | Minimum altitude (m) | Mean altitude (m) | Maximum altitude (m) | Records <1976 | Records >1975 | Old IUCN criteria | Experts' opinion | Vulnerability Index |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Cephaloziella rubella* **(Nees) Warnst.** | | 1 | 1 | 1 | 4 | dd | na (2) | 550 | 550,0 | 550 | 0 | 2 | | | |
| *Cephaloziella turneri* **(Hook.) Müll. Frib.** | | 1 | 2 | 1 | 6 | dd | na (2) | dd | dd | dd | 2 | 0 | | | |
| *Cheilolejeunea cedercreutzii* **(H. Buch** ***et*** **H. Perss.) Grolle** | MAC | 2 | 4 | 4 | 105 | 3,0 | NaFor (31) | 250 | 786,0 | 1050 | 19 | 17 | v | es; rs | 7. Restricted species with narrow ecological range |
| *Chiloscyphus coadunatus* **(Sw.) J. J. Engel** ***et*** **R. M. Schust.** | | 3 | 9 | 5 | 255 | 2,3 | NaFor (30) | 100 | 452,7 | 900 | 17 | 46 | | | 1. Species that are not rare |
| *Chiloscyphus fragrans* **(Moris** ***et*** **De Not.) J. J. Engel** ***et*** **R. M. Schust.** | | 3 | 8 | 7 | 546 | 2,0 | NaFor (132) | 25 | 594,2 | 1000 | 120 | 81 | | | 1. Species that are not rare |
| *Chiloscyphus minor* **(Nees) J. J. Engel** ***et*** **R. M. Schust.** | | 2 | 3 | | 1 | dd | na (2) | 175 | 418,8 | 700 | 8 | 0 | | | |
| *Chiloscyphus pallescens* **(Ehrh. ex Hoffm.) Dumort.** | | 3 | 5 | | dd | dd | NaFor (4) | 350 | 633,3 | 850 | 4 | 3 | | | |
| *Chiloscyphus polyanthos* **(L.) Corda** | | 3 | 7 | 5 | 274 | 2,6 | NaFor (14) | 200 | 622,2 | 925 | 24 | 7 | | | 1. Species that are not rare |
| *Chiloscyphus profundus* **(Nees) J. J. Engel** ***et*** **R. M. Schust.** | | 3 | 8 | 5 | 102 | 2,9 | NaFor (18) | 10 | 485,6 | 875 | 27 | 17 | | | 1. Species that are not rare |
| *Cladopodiella francisci* **(Hook.) Jörg.** | | 2 | 2 | 2 | 19 | dd | na (2) | 400 | 508,3 | 575 | 2 | 3 | | rs | |
| *Cololejeunea minutissima* **(Sm.) Schiffn.** | | 3 | 9 | 9 | 586 | 2,0 | NaFor (368) | 10 | 566,6 | 1050 | 358 | 262 | | | 1. Species that are not rare |
| *Colura calyptrifolia* **(Hook.) Dumort.** | | 3 | 8 | 6 | 473 | 2,8 | NaFor (221) | 300 | 724,8 | 1100 | 165 | 115 | rt | | 1. Species that are not rare |
| *Conocephalum conicum* **(L.) Dumort.** | | 3 | 9 | 9 | 426 | 6,2 | Caves (130) | 50 | 530,4 | 1400 | 91 | 210 | | | 3. Species with narrow ecological tolerance |
| *Conocephalum salebrosum* **Szweykowski, Buczkowska** ***et*** **Odrzykoski** | | 1 | 1 | | dd | dd | na (1) | dd | dd | dd | 1 | 2 | | | |
| *Corsinia coriandrina* **(Spreng.) Lindb.** | | 3 | 7 | 4 | 212 | 2,7 | Mesic (16) | 10 | 63,3 | 250 | 25 | 10 | | | 1. Species that are not rare |
| *Diplophyllum albicans* **(L.) Dumort.** | | 3 | 8 | 8 | 338 | 2,3 | NaFor (106) | 250 | 682,7 | 2300 | 64 | 107 | | | 1. Species that are not rare |
| *Drepanolejeunea hamatifolia* **(Hook.) Schiffn.** | | 3 | 8 | 8 | 524 | 4,0 | NaFor (562) | 10 | 706,9 | 1300 | 484 | 344 | | | 3. Species with narrow ecological tolerance |
| *Dumortiera hirsuta* **(Sw.) Nees subsp.** *hirsuta* | | 3 | 8 | 8 | 534 | 4,4 | Caves (78) | 10 | 522,0 | 1025 | 80 | 147 | r | | 3. Species with narrow ecological tolerance |
| *Exormotheca pustulosa* **Mitt.** | | 3 | 5 | | 124 | 2,7 | Mesic (6) | 25 | 100,0 | 175 | 9 | 5 | r | rs | 1. Species that are not rare |

| **Species** | **Endemic grouping** | **Groups of Islands** | **Number of Islands** | **Presence in Island Parks** | **Number of 500 x 500 m cells** | **Lloyd index (>11 records)** | **Habitat with highest number of records** | **Minimum altitude (m)** | **Mean altitude (m)** | **Maximum altitude (m)** | **Records <1976** | **Records >1975** | **Old IUCN criteria** | **Experts' opinion** | **Vulnerability Index** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Fossombronia angulosa*** **(Dicks.) Raddi** | | 3 | 9 | 8 | 235 | 1,2 | NaFor (12) | 150 | 376,4 | 700 | 29 | 27 | | | 1. Species that are not rare |
| ***Fossombronia caespitiformis*** **De Not.** ***ex*** **Rabenh. subsp.** ***caespitiformis*** | | 2 | 4 | 3 | 82 | 1,8 | Mesic; NaFor (4) | 200 | 385,0 | 650 | 10 | 5 | | | 2. Scarce species (rare by abundance) |
| ***Fossombronia caespitiformis*** **De Not. ex Rabenh. subsp.** ***multispira*** **(Schiffn.) J. R. Bray et D. C. Cargill** | | 2 | 6 | 3 | dd | dd | Mesic; Urban (3) | 100 | 100,0 | 100 | 4 | 7 | | | |
| ***Fossombronia echinata*** **Macvicar** | | 1 | 1 | | 2 | dd | na (1) | 150 | 150,0 | 150 | 0 | 1 | k | | |
| ***Fossombronia pusilla*** **(L.) Nees** | | 2 | 4 | 2 | 20 | dd | na (2) | 400 | 400,0 | 400 | 2 | 2 | | | |
| ***Frullania azorica*** **Sim-Sim** ***et al.*** | IB-MAC | 3 | 9 | 9 | 688 | 2,1 | Coast (60) | 10 | 154,4 | 800 | 59 | 164 | | | 1. Species that are not rare |
| ***Frullania fragilifolia*** **(Taylor) Gottsche** ***et al.*** | | 1 | 3 | | dd | dd | NaFor (4) | dd | dd | dd | 0 | 8 | | | |
| ***Frullania microphylla*** **(Gottsche) Pearson** | EUR | 3 | 9 | 9 | 777 | 1,8 | NaFor (227) | 10 | 493,4 | 1100 | 381 | 307 | | | 1. Species that are not rare |
| ***Frullania tamarisci*** **(L.) Dumort.** | | 3 | 9 | 9 | 1016 | 2,1 | NaFor (606) | 10 | 588,2 | 1225 | 366 | 729 | | | 1. Species that are not rare |
| ***Frullania teneriffae*** **(F. Weber) Nees** | | 3 | 9 | 7 | 509 | 1,7 | NaFor (243) | 10 | 670,8 | 1350 | 283 | 228 | | | 1. Species that are not rare |
| ***Geocalyx graveolens*** **(Schrad.) Nees** | | 3 | 7 | 6 | 188 | 4,9 | NaFor (77) | 475 | 675,0 | 1000 | 19 | 68 | | | 3. Species with narrow ecological tolerance |
| ***Gongylanthus ericetorum*** **(Raddi) Nees** | | 3 | 7 | 5 | 199 | 3,2 | Mesic (22) | 25 | 350,0 | 700 | 28 | 12 | | | 3. Species with narrow ecological tolerance |
| ***Gymnocolea inflata*** **(Huds.) Dumort.** | | 2 | 2 | 2 | 43 | 1,8 | NaFor (8) | 300 | 837,5 | 950 | 0 | 13 | | rs | 2. Scarce species (rare by abundance) |
| ***Harpalejeunea molleri*** **(Steph.) Grolle** | | 3 | 9 | 9 | 638 | 1,5 | NaFor (114) | 10 | 474,2 | 1075 | 94 | 143 | | | 1. Species that are not rare |
| ***Herbertus dicranus*** **(Taylor** ***ex*** **Gottsche** ***et al.*****) Trevis.** | | 1 | 1 | 1 | 79 | dd | na (1) | 1925 | 1925,0 | 1925 | 1 | 0 | | | |
| ***Herbertus sendtneri*** **(Nees) Lindb.** | | 3 | 7 | 7 | 271 | 3,7 | NaFor (94) | 425 | 826,8 | 1500 | 39 | 76 | r | | 3. Species with narrow ecological tolerance |
| ***Heteroscyphus denticulatus*** **(Mitt.) Schiffn.** | MAC | 3 | 8 | 7 | 369 | 2,6 | NaFor (21) | 75 | 384,4 | 900 | 13 | 34 | r | rs | 4. Restricted species (rare by range) |
| ***Hygrobiella laxifolia*** **(Hook.) Spruce** | | 1 | 3 | | dd | dd | na (1) | 525 | 525,0 | 525 | 0 | 1 | | | |

| Species | Endemic grouping | Groups of Islands | Number of Islands | Presence in Island Parks | Number of 500 x 500 m cells | Lloyd index (>11 records) | Habitat with highest number of records | Minimum altitude (m) | Mean altitude (m) | Maximum altitude (m) | Records <1976 | Records >1975 | Old IUCN criteria | Experts' opinion | Vulnerability Index |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Jamesoniella rubricaulis* (Nees) Grolle** |  | 2 | 2 | 1 | 52 | dd | Mount (5) | 1000 | 1133,3 | 1200 | 2 | 4 | k | es |  |
| ***Jubula hutchinsiae* (Hook.) Dumort. subsp. *hutchinsiae*** |  | 3 | 7 | 7 | 594 | 4,2 | NaFor (184) | 75 | 604,7 | 1925 | 90 | 228 |  |  | 3. Species with narrow ecological tolerance |
| ***Jungermannia atrovirens* Dumort.** |  | 3 | 7 | 4 | 82 | dd | NaFor (3) | 50 | 410,0 | 650 | 4 | 6 |  |  |  |
| ***Jungermannia callithrix* Lindenb. *et* Gottsche** |  | 3 | 8 | 8 | 437 | 2,0 | NaFor (30) | 175 | 528,1 | 950 | 17 | 55 |  |  | 1. Species that are not rare |
| ***Jungermannia gracillima* Sm.** |  | 3 | 8 | 5 | 73 | 1,6 | Aquat (12) | 350 | 615,4 | 975 | 12 | 21 |  |  | 2. Scarce species (rare by abundance) |
| ***Jungermannia hyalina* Lyell** |  | 3 | 8 | 2 | 18 | 1,4 | NaFor (17) | 300 | 500,0 | 700 | 22 | 17 |  |  | 2. Scarce species (rare by abundance) |
| ***Jungermannia pumila* With.** |  | 2 | 4 | 2 | 122 | 1,3 | NaFor (5) | dd | dd | dd | 5 | 9 |  |  | 1. Species that are not rare |
| ***Kurzia pauciflora* (Dicks.) Grolle** |  | 3 | 4 | 4 | 106 | 7,1 | NaFor (17) | 550 | 690,0 | 925 | 11 | 17 |  |  | 3. Species with narrow ecological tolerance |
| ***Lejeunea eckloniana* Lindenb.** |  | 3 | 9 | 8 | 321 | 2,3 | NaFor (37) | 25 | 386,6 | 925 | 30 | 77 |  | es | 1. Species that are not rare |
| ***Lejeunea flava* (Sw.) Nees subsp. *moorei* (Lindb.) R. M. Schust.** |  | 3 | 8 | 7 | 269 | 1,8 | NaFor (99) | 50 | 511,4 | 950 | 57 | 123 | (r) |  | 1. Species that are not rare |
| ***Lejeunea hibernica* Bischl. *et al. ex* Grolle** | EUR | 3 | 4 | 4 | 181 | 2,4 | NaFor (11) | 75 | 586,1 | 800 | 6 | 9 | r | es | 1. Species that are not rare |
| ***Lejeunea lamacerina* (Steph.) Schiffn.** |  | 3 | 9 | 9 | 847 | 1,9 | NaFor (547) | 10 | 535,3 | 1050 | 481 | 721 |  |  | 1. Species that are not rare |
| ***Lejeunea patens* Lindb.** |  | 3 | 9 | 7 | 565 | 2,2 | NaFor (156) | 150 | 785,6 | 1500 | 113 | 95 |  |  | 1. Species that are not rare |
| ***Lepidozia cupressina* (Sw.) Lindenb. subsp. *pinnata* (Hook.) Pócs** |  | 3 | 6 | 6 | 375 | 5,7 | NaFor (227) | 525 | 756,1 | 1100 | 91 | 161 |  |  | 3. Species with narrow ecological tolerance |
| ***Lepidozia pearsonii* Spruce** |  | 1 | 1 | 1 | 2 | dd | na (2) | 975 | 975,0 | 975 | 0 | 2 |  |  |  |
| ***Lepidozia reptans* (L.) Dumort.** |  | 3 | 7 | 7 | 428 | 3,7 | NaFor (130) | 400 | 690,0 | 1050 | 60 | 94 |  |  | 3. Species with narrow ecological tolerance |
| ***Lepidozia stuhlmannii* Steph.** |  | 1 | 3 | 1 | 34 | dd | NaFor (8) | 650 | 812,5 | 1000 | 0 | 10 |  |  |  |
| ***Leptoscyphus azoricus* (H. Buch *et* H. Perss.) Grolle** | EUR | 3 | 5 | 4 | 80 | 6,2 | NaFor (56) | 550 | 797,6 | 1050 | 20 | 39 | v | es; rs | 5. Scarce species with narrow ecological tolerance |
| ***Leptoscyphus cuneifolius* (Hook.) Mitt.** |  | 1 | 3 | 3 | 20 | dd | NaFor (5) | 400 | 662,5 | 1000 | 4 | 8 |  | es |  |
| ***Lophozia bicrenata* (Schmidel *ex* Hoffm.) Dumort.** |  | 2 | 5 | 2 | 31 | dd | na (2) | 150 | 843,8 | 2000 | 3 | 2 |  |  |  |

| **Species** | **Endemic grouping** | **Groups of Islands** | **Number of Islands** | **Presence in Island Parks** | **Number of 500 x 500 m cells** | **Lloyd index (>11 records)** | **Habitat with highest number of records** | **Minimum altitude (m)** | **Mean altitude (m)** | **Maximum altitude (m)** | **Records <1976** | **Records >1975** | **Old IUCN criteria** | **Experts' opinion** | **Vulnerability Index** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Lophozia incisa*** **(Schrad.) Dumort. subsp.** ***incisa*** | | 3 | 7 | 5 | 97 | 3,1 | NaFor (8) | 550 | 685,7 | 800 | 11 | 3 | | | 3. Species with narrow ecological tolerance |
| ***Lophozia longiflora*** **(Nees) Schiffn.** | | 2 | 5 | 2 | 7 | dd | NaFor (4) | 550 | 656,3 | 850 | 0 | 5 | | | |
| ***Lophozia ventricosa*** **(Dicks.) Dumort. aggr.** | | 2 | 5 | 5 | 90 | 1,9 | NaFor (20) | 350 | 702,1 | 1050 | 25 | 4 | | | 1. Species that are not rare |
| ***Lunularia cruciata*** **(L.) Lindb.** | | 3 | 9 | 5 | 137 | 1,7 | Mesic (11) | 100 | 347,7 | 950 | 20 | 24 | | | 1. Species that are not rare |
| ***Mannia androgyna*** **(L.) A. Evans** | | 3 | 6 | 4 | 231 | 3,5 | Urban (8) | 25 | 62,5 | 100 | 18 | 6 | | | 3. Species with narrow ecological tolerance |
| ***Marchantia paleacea*** **Bertol.** | | 3 | 8 | 7 | 249 | 1,4 | NaFor (15) | 75 | 458,3 | 875 | 43 | 16 | k | | 1. Species that are not rare |
| ***Marchantia polymorpha*** **L.** | | 2 | 3 | | | dd | na (2) | 650 | 650,0 | 650 | 5 | 0 | | | |
| ***Marchantia polymorpha*** **L. subsp.** ***montivagans*** **Bischl.** ***et*** **Boisselier** | | 1 | 1 | 1 | 47 | dd | na (2) | dd | dd | dd | 0 | 5 | | | |
| ***Marchantia polymorpha*** **L. subsp.** ***ruderalis*** **Bischl.** ***et*** **Boisselier** | | 2 | 4 | | dd | dd | na (2) | dd | dd | dd | 1 | 1 | | | |
| ***Marchesinia mackaii*** **(Hook.) Gray** | | 3 | 9 | 9 | 812 | 1,8 | NaFor (93) | 10 | 386,3 | 825 | 147 | 173 | | | 1. Species that are not rare |
| ***Marsupella adusta*** **(Nees emend. Limpr.) Spruce** | | 2 | 3 | 2 | 10 | dd | Mount (3) | 625 | 1906,3 | 2350 | 6 | 0 | k | | |
| ***Marsupella emarginata*** **(Ehrh.) Dumort.** | | 3 | 8 | 7 | 179 | 1,8 | NaFor (19) | 50 | 601,9 | 1600 | 20 | 28 | | | 1. Species that are not rare |
| ***Marsupella funckii*** **(F. Weber** ***et*** **D. Mohr) Dumort.** | | 3 | 7 | 4 | 55 | 0,5 | NaFor (9) | 500 | 612,5 | 675 | 6 | 9 | | | 2. Scarce species (rare by abundance) |
| ***Marsupella profunda*** **Lindb.** | | 1 | 1 | 1 | 4 | dd | na (1) | dd | dd | dd | 0 | 1 | v | | |
| ***Marsupella sparsifolia*** **(Lindb.) Dumort.** | | 1 | 3 | 2 | 6 | dd | NaFor (3) | 825 | 862,5 | 900 | 1 | 2 | | | |
| ***Marsupella sphacelata*** **(Gieseke** ***ex*** **Lindenb.) Dumort.** | | 2 | 3 | 3 | 10 | dd | NaFor (5) | 700 | 775,0 | 850 | 7 | 1 | | | |
| ***Metzgeria furcata*** **(L.) Dumort.** | | 3 | 8 | 7 | 527 | 2,4 | NaFor (163) | 225 | 623,6 | 1050 | 225 | 83 | | | 1. Species that are not rare |
| ***Metzgeria leptoneura*** **Spruce** | | 3 | 6 | 6 | 309 | 3,6 | NaFor (99) | 450 | 732,4 | 1000 | 74 | 41 | | | 3. Species with narrow ecological tolerance |
| ***Microlejeunea ulicina*** **(Taylor) A. Evans** | | 3 | 7 | 7 | 206 | 1,4 | NaFor (13) | 100 | 342,0 | 950 | 19 | 25 | | | 1. Species that are not rare |
| ***Mnioloma fuscum*** **(Lehm.) R. M. Schust.** | | 3 | 6 | 5 | 198 | 8,7 | NaFor (124) | 475 | 801,1 | 1075 | 47 | 86 | r | es | 3. Species with narrow ecological tolerance |

| Species | Endemic grouping | Groups of Islands | Number of Islands | Presence in Island Parks | Number of 500 x 500 m cells | Lloyd index (>11 records) | Habitat with highest number of records | Minimum altitude (m) | Mean altitude (m) | Maximum altitude (m) | Records <1976 | Records >1975 | Old IUCN criteria | Experts' opinion | Vulnerability Index |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Mylia taylorii*** **(Hook.) Gray** | | 2 | 2 | 1 | 4 | dd | na (1) | 775 | 775,0 | 775 | 1 | 1 | | | |
| ***Nardia geoscyphus*** **(De Not.) Lindb.** | | 3 | 7 | 4 | 68 | 1,7 | NaFor (7) | 325 | 614,3 | 925 | 5 | 13 | | | 2. Scarce species (rare by abundance) |
| ***Nardia scalaris*** **Gray** | | 3 | 9 | 9 | 415 | 1,7 | NaFor (67) | 150 | 563,2 | 1000 | 49 | 138 | | | 1. Species that are not rare |
| ***Nowellia curvifolia*** **(Dicks.) Mitt.** | | 3 | 6 | 5 | 318 | 4,5 | NaFor (145) | 250 | 721,7 | 1075 | 81 | 84 | | | 3. Species with narrow ecological tolerance |
| ***Odontoschisma denudatum*** **(Mart.) Dumort.** | | 3 | 6 | 4 | 154 | 3,3 | NaFor (28) | 300 | 659,2 | 1000 | 19 | 17 | | | 3. Species with narrow ecological tolerance |
| ***Odontoschisma prostratum*** **(Sw.) Trevis.** | | 3 | 8 | 8 | 485 | 3,0 | NaFor (154) | 225 | 608,9 | 1025 | 88 | 175 | | | 3. Species with narrow ecological tolerance |
| ***Pallavicinia lyellii*** **(Hook.) Carruth.** | | 3 | 6 | 2 | 197 | 6,6 | NaFor (46) | 450 | 733,0 | 1100 | 8 | 41 | v | es | 3. Species with narrow ecological tolerance |
| ***Pellia epiphylla*** **(L.) Corda s.l.** | | 3 | 7 | 5 | 218 | 4,6 | NaFor (125) | 50 | 650,8 | 1000 | 52 | 193 | | | 3. Species with narrow ecological tolerance |
| ***Plagiochasma rupestre*** **(J. R. Forst. *et* G. Forst.) Steph.** | | 2 | 4 | 1 | 2 | dd | na (2) | dd | dd | dd | 5 | 1 | | | |
| ***Plagiochila bifaria*** **(Sw.) Lindenb.** | | 3 | 9 | 9 | 729 | 4,2 | NaFor (569) | 100 | 676,2 | 1500 | 179 | 586 | | | 3. Species with narrow ecological tolerance |
| ***Plagiochila exigua*** **(Taylor) Taylor** | | 3 | 9 | 7 | 351 | 3,5 | NaFor (185) | 225 | 739,5 | 1100 | 100 | 117 | | | 3. Species with narrow ecological tolerance |
| ***Plagiochila longispina*** **Lindenb. *et* Gottsche** | | 3 | 9 | 7 | 114 | 4,0 | NaFor (20) | 300 | 635,5 | 975 | 17 | 24 | v | es | 3. Species with narrow ecological tolerance |
| ***Plagiochila papillifolia*** **Steph.** | | 1 | 1 | | dd | dd | na (2) | 800 | 800,0 | 800 | 0 | 2 | | | |
| ***Plagiochila punctata*** **(Taylor) Taylor** | | 3 | 7 | 3 | 122 | 6,9 | NaFor (7) | 525 | 847,5 | 1050 | 7 | 5 | | | 3. Species with narrow ecological tolerance |
| ***Plagiochila retrorsa*** **Gottsche** | | 1 | 2 | 1 | 1 | dd | na (1) | 650 | 650,0 | 650 | 0 | 3 | | | |
| ***Porella canariensis*** **(F. Weber) Bryhn** | | 3 | 9 | 9 | 456 | 1,2 | NaFor (53) | 10 | 406,2 | 950 | 57 | 100 | t | | 1. Species that are not rare |
| ***Porella obtusata*** **(Taylor) Trevis.** | | 3 | 8 | 5 | 130 | 2,6 | NaFor (60) | 25 | 501,5 | 1000 | 7 | 101 | | | 1. Species that are not rare |
| ***Radula aquilegia*** **(Hook. F. *et* Taylor) Gottsche *et al.*** | | 3 | 7 | 7 | 537 | 2,7 | NaFor (263) | 150 | 692,8 | 1075 | 134 | 203 | | | 1. Species that are not rare |
| ***Radula carringtonii*** **J. B. Jack** | | 3 | 9 | 9 | 673 | 1,4 | NaFor (170) | 25 | 499,5 | 1500 | 104 | 264 | r | | 1. Species that are not rare |

| Species | Endemic grouping | Groups of Islands | Number of Islands | Presence in Island Parks | Number of 500 x 500 m cells | Lloyd index (>11 records) | Habitat with highest number of records | Minimum altitude (m) | Mean altitude (m) | Maximum altitude (m) | Records <1976 | Records >1975 | Old IUCN criteria | Experts' opinion | Vulnerability Index |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Radula complanata* (L.) Dumort.** | | 3 | 6 | 3 | 110 | 1,8 | Mesic (6) | 25 | 450,0 | 825 | 29 | 4 | | | 1. Species that are not rare |
| ***Radula holtii* Spruce** | EUR | 3 | 8 | 7 | 190 | 1,7 | NaFor (52) | 75 | 558,4 | 1050 | 56 | 31 | r | es | 1. Species that are not rare |
| ***Radula lindenbergiana* Gottsche *ex* C. Hartman** | | 3 | 8 | 7 | 413 | 2,5 | Parks (16) | 25 | 303,1 | 925 | 57 | 41 | | | 1. Species that are not rare |
| ***Radula nudicaulis* Steph.** | | 2 | 5 | 3 | 79 | 3,9 | NaFor (25) | 550 | 795,6 | 1500 | 10 | 18 | r | es | 5. Scarce species with narrow ecological tolerance |
| ***Radula wichurae* Steph.** | MAC | 3 | 9 | 9 | 282 | 1,8 | NaFor (42) | 10 | 267,4 | 950 | 38 | 154 | v | rs | 4. Restricted species (rare by range) |
| ***Reboulia hemisphaerica* (L.) Raddi *s.l.*** | | 3 | 9 | 7 | 295 | 1,7 | Mesic (24) | 50 | 370,8 | 925 | 33 | 41 | | | 1. Species that are not rare |
| ***Riccardia chamedryfolia* (With.) Grolle** | | 3 | 8 | 8 | 443 | 4,2 | NaFor (76) | 150 | 606,3 | 1000 | 61 | 109 | | | 3. Species with narrow ecological tolerance |
| ***Riccardia latifrons* (Lindb.) Lindb.** | | 3 | 9 | 7 | 274 | 2,1 | NaFor (28) | 100 | 478,2 | 900 | 29 | 26 | | | 1. Species that are not rare |
| ***Riccardia multifida* (L.) Gray** | | 3 | 8 | 8 | 338 | 1,9 | NaFor (51) | 175 | 615,3 | 1000 | 38 | 58 | | | 1. Species that are not rare |
| ***Riccardia palmata* (Hedw.) Carruth.** | | 3 | 6 | 5 | 73 | 3,3 | NaFor (15) | 450 | 727,5 | 950 | 11 | 9 | | | 5. Scarce species with narrow ecological tolerance |
| ***Riccia beyrichiana* Hampe *ex* Lehm. *et* Lindenb.** | | 1 | 1 | 1 | 44 | dd | na (1) | dd | dd | dd | 0 | 2 | | | |
| ***Riccia bifurca* Hoffm.** | | 2 | 2 | 2 | 48 | dd | na (1) | 525 | 525,0 | 525 | 1 | 4 | | | |
| ***Riccia crozalsii* Levier** | | 3 | 6 | 4 | 167 | 1,8 | Mesic (6) | 25 | 178,6 | 475 | 4 | 12 | | | 1. Species that are not rare |
| ***Riccia crystallina* L. emend. Raddi** | | 2 | 2 | | 24 | dd | na (2) | dd | dd | dd | 2 | 0 | | | |
| ***Riccia glauca* L.** | | 2 | 3 | 2 | 57 | dd | Mesic (3) | dd | dd | dd | 2 | 5 | | | |
| ***Riccia huebeneriana* Lindenb.** | | 1 | 1 | 1 | 2 | dd | Aquat (3) | 550 | 550,0 | 550 | 0 | 3 | r | | |
| ***Riccia ligula* Steph.** | | 1 | 1 | | 1 | dd | InPas (6) | 325 | 325,0 | 325 | 0 | 6 | r | | |
| ***Riccia nigrella* DC.** | | 3 | 6 | 4 | 224 | 2,9 | Mesic (7) | 475 | 500,0 | 550 | 12 | 8 | | | 1. Species that are not rare |
| ***Riccia sorocarpa* Bischl.** | | 2 | 5 | 1 | 37 | dd | Mesic (4) | 325 | 375,0 | 475 | 3 | 8 | | | |
| ***Riccia subbifurca* Warnst. *ex* Croz.** | | 1 | 1 | 1 | 1 | dd | na (2) | 525 | 525,0 | 525 | 0 | 2 | | | |
| ***Riccia trabutiana* Steph.** | | 1 | 1 | | dd | dd | na (1) | dd | dd | dd | 0 | 1 | r | | |
| ***Riccia warnstorfii* Limpr. *ex* Warnst.** | | 2 | 2 | 1 | 29 | dd | na (1) | dd | dd | dd | 2 | 1 | | | |

| Species | Endemic grouping | Groups of Islands | Number of Islands | Presence in Island Parks | Number of 500 x 500 m cells | Lloyd index (>11 records) | Habitat with highest number of records | Minimum altitude (m) | Mean altitude (m) | Maximum altitude (m) | Records <1976 | Records >1975 | Old IUCN criteria | Experts' opinion | Vulnerability Index |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Saccogyna viticulosa*** **(L.) Dumort.** | EUR | 3 | 9 | 9 | 778 | 2,0 | NaFor (317) | 10 | 598,6 | 1050 | 142 | 364 | | | 1. Species that are not rare |
| ***Scapania compacta*** **(A. Roth.) Dumort.** | | 2 | 4 | 3 | 15 | 2,1 | NaFor (3) | 200 | 697,2 | 975 | 5 | 9 | | | 2. Scarce species (rare by abundance) |
| ***Scapania curta*** **(Mart.) Dumort.** | | 2 | 6 | 4 | 41 | 2,5 | NaFor (14) | 475 | 769,0 | 1075 | 19 | 4 | | | 2. Scarce species (rare by abundance) |
| ***Scapania gracilis*** **Lindb.** | | 3 | 8 | 8 | 555 | 3,5 | NaFor (290) | 125 | 739,0 | 1500 | 110 | 244 | | | 3. Species with narrow ecological tolerance |
| ***Scapania nemorea*** **(L.) Grolle** | | 3 | 6 | 3 | 166 | 1,9 | NaFor (31) | 400 | 653,8 | 1000 | 19 | 39 | | | 1. Species that are not rare |
| ***Scapania paludosa*** **(Müll. Frib.) Müll. Frib.** | | 1 | 1 | | dd | dd | na (2) | dd | dd | dd | 2 | 0 | | | |
| ***Scapania scandica*** **(Arnell et H. Buch) Macvicar** | | 1 | 1 | 1 | 1 | dd | na (1) | 2350 | 2350,0 | 2350 | 1 | 0 | | | |
| ***Scapania undulata*** **(L.) Dumort.** | | 3 | 8 | 7 | 336 | 2,6 | NaFor (69) | 250 | 696,4 | 1100 | 63 | 47 | | | 1. Species that are not rare |
| ***Southbya tophacea*** **(Spruce) Spruce** | | 2 | 2 | | dd | dd | na (1) | 500 | 500,0 | 500 | 0 | 1 | | | |
| ***Sphaerocarpos texanus*** **Austin** | | 1 | 1 | | 1 | dd | na (1) | dd | dd | dd | 0 | 1 | | | |
| ***Targionia hypophylla*** **L.** | | 3 | 9 | 6 | 236 | 2,3 | Mesic (19) | 50 | 318,8 | 950 | 29 | 14 | | | 1. Species that are not rare |
| ***Targionia lorbeeriana*** **Müll. Frib.** | | 1 | 1 | | dd | dd | na (1) | dd | dd | dd | 0 | 1 | | | |
| ***Telaranea azorica*** **(H. Buch *et* H. Perss.) Pócs *ex* Schumacker *et* Váña** | MAC | 3 | 6 | 5 | 265 | 6,9 | NaFor (105) | 250 | 784,1 | 1075 | 69 | 46 | v | es; rs | 7. Restricted species with narrow ecological range |
| ***Telaranea europaea*** **Engel *et* Merr.** | | 3 | 9 | 9 | 404 | 3,0 | NaFor (271) | 150 | 645,9 | 1025 | 101 | 265 | r | | 3. Species with narrow ecological tolerance |
| ***Trichocolea tomentella*** **(Ehrh.) Dumort.** | | 2 | 4 | 1 | 133 | 3,8 | NaFor (17) | 550 | 712,5 | 1000 | 18 | 6 | | | 3. Species with narrow ecological tolerance |
| ***Tylimanthus laxus*** **(Lehm. *et* Lindenb.) Spruce** | | 3 | 6 | 6 | 245 | 1,9 | NaFor (48) | 10 | 706,6 | 1500 | 31 | 55 | v | es; rs | 1. Species that are not rare |
| **MOSSES** | | | | | | | | | | | | | | | |
| ***Aloina ambigua*** **(Bruch *et* Schimp.) Limpr.** | | 1 | 2 | | 21 | dd | Mesic (6) | dd | dd | dd | 7 | 1 | | | |
| ***Aloina rigida*** **(Hedw.) Limpr.** | | 1 | 1 | | 12 | dd | na (1) | dd | dd | dd | 0 | 1 | | | |
| ***Alophosia azorica*** **(Renauld *et* Cardot) Cardot** | MAC | 3 | 7 | 5 | 363 | 1,3 | NaFor (60) | 100 | 576,2 | 1000 | 31 | 93 | r | | 4. Restricted species (rare by range) |

| Species | Endemic grouping | Groups of Islands | Number of Islands | Presence in Island Parks | Number of 500 x 500 m cells | Lloyd index (>11 records) | Habitat with highest number of records | Minimum altitude (m) | Mean altitude (m) | Maximum altitude (m) | Records <1976 | Records >1975 | Old IUCN criteria | Experts' opinion | Vulnerability Index |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Amblystegium confervoides* (Brid.) Schimp.** |  | 2 | 2 |  | dd | dd | Caves (3) | 50 | 150,0 | 250 | 0 | 3 |  |  |  |
| ***Amblystegium serpens* (Hedw.) Schimp.** |  | 3 | 3 | 1 | 38 | dd | na (1) | 50 | 75,0 | 125 | 5 | 1 |  |  |  |
| ***Amphidium mougeotii* (Bruch *et* Schimp.) Schimp.** |  | 2 | 5 | 3 | 41 | dd | NaFor (5) | 250 | 942,9 | 2350 | 5 | 4 |  |  |  |
| ***Andoa berthelotiana* (Mont.) Ochyra** | MAC | 3 | 9 | 9 | 1068 | 1,6 | NaFor (233) | 10 | 498,6 | 1550 | 203 | 461 | r |  | 4. Restricted species (rare by range) |
| ***Andreaea rupestris* Hedw.** |  | 1 | 2 | 1 | 39 | dd | Mount (5) | 1500 | 1612,5 | 1750 | 5 | 0 |  |  |  |
| ***Anoectangium aestivum* (Hedw.) Mitt.** |  | 1 | 1 | 1 | 44 | dd | na (1) | dd | dd | dd | 2 | 0 |  |  |  |
| ***Anomobryum julaceum* (P. Gaerth., B. Mey. et Scherb.) Schimp.** |  | 3 | 8 | 8 | 291 | 1,3 | NaFor (19) | 10 | 447,9 | 950 | 25 | 42 |  |  | 1. Species that are not rare |
| ***Archidium alternifolium* (Hedw.) Schimp.** |  | 3 | 4 | 1 | 107 | dd | na (2) | 300 | 450,0 | 600 | 5 | 3 |  |  |  |
| ***Atrichum angustatum* (Brid.) Bruch *et* Schimp.** |  | 3 | 8 | 6 | 236 | 1,1 | Mesic (11) | 150 | 468,3 | 900 | 18 | 30 |  |  | 1. Species that are not rare |
| ***Atrichum tenellum* (Röhl.) Bruch *et* Schimp.** |  | 1 | 1 | 1 | 1 | dd | Aquat (3) | 550 | 550,0 | 550 | 0 | 3 |  |  |  |
| ***Atrichum undulatum* (Hedw.) P. Beauv.** |  | 3 | 8 | 4 | 176 | 1,3 | NaFor (31) | 300 | 556,8 | 800 | 26 | 45 |  |  | 1. Species that are not rare |
| ***Aulacomnium palustre* (Hedw.) Schwägr.** |  | 2 | 3 | 1 | 16 | dd | NaFor (5) | 700 | 850,0 | 950 | 6 | 2 |  | es |  |
| ***Barbula convoluta* Hedw.** |  | 2 | 3 | 2 | 26 | dd | na (1) | 50 | 50,0 | 50 | 1 | 1 |  |  |  |
| ***Barbula unguiculata* Hedw.** |  | 3 | 9 | 6 | 189 | 1,9 | Mesic (7) | 50 | 267,5 | 575 | 7 | 16 |  |  | 1. Species that are not rare |
| ***Bartramia pomiformis* Hedw.** |  | 1 | 1 | 1 | 4 | dd | na (2) | dd | dd | dd | 1 | 0 |  |  |  |
| ***Bartramia stricta* Brid.** |  | 3 | 6 | 3 | 117 | 3,1 | Coast (7) | 25 | 240,6 | 800 | 12 | 4 |  |  | 3. Species with narrow ecological tolerance |
| ***Blindia acuta* (Hedw.) Bruch et Schimp.** |  | 3 | 5 | 5 | 92 | 1,6 | NaFor (15) | 450 | 725,0 | 950 | 14 | 7 |  |  | 1. Species that are not rare |
| ***Brachymenium notarisii* (Mitt.) A. J. Shaw** |  | 3 | 4 | 3 | 27 | dd | na (2) | 150 | 325,0 | 500 | 4 | 2 | r |  |  |
| ***Brachytheciastrum velutinum* (Hedw.) Ignatov *et* Huttunen** |  | 3 | 8 | 4 | 49 | 2,5 | ExFor (10) | 25 | 450,0 | 1500 | 10 | 17 |  |  | 2. Scarce species (rare by abundance) |
| ***Brachythecium albicans* (Hedw.) Schimp.** |  | 2 | 3 | 1 | 2 | dd | na (2) | 200 | 416,7 | 525 | 1 | 2 |  |  |  |
| ***Brachythecium mildeanum* (Schimp.) Milde** |  | 2 | 3 | 2 | 32 | dd | NaFor (4) | 50 | 528,1 | 875 | 10 | 0 |  |  |  |

| **Species** | **Endemic grouping** | **Groups of Islands** | **Number of Islands** | **Presence in Island Parks** | **Number of 500 x 500 m cells** | **Lloyd index (>11 records)** | **Habitat with highest number of records** | **Minimum altitude (m)** | **Mean altitude (m)** | **Maximum altitude (m)** | **Records <1976** | **Records >1975** | **Old IUCN criteria** | **Experts' opinion** | **Vulnerability Index** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Brachythecium rivulare*** **Schimp.** | | 3 | 8 | 5 | 102 | 2,3 | NaFor (7) | 275 | 430,6 | 650 | 8 | 11 | | | 1. Species that are not rare |
| ***Brachythecium rutabulum*** **(Hedw.) Schimp.** | | 3 | 8 | 5 | 125 | 2,0 | InPas (14) | 125 | 419,2 | 975 | 9 | 39 | | | 1. Species that are not rare |
| ***Brachythecium salebrosum*** **(Hoffm. *ex* F. Weber *et* D. Mohr) Schimp.** | | 3 | 9 | 6 | 202 | 1,7 | ExFor (5) | 100 | 209,4 | 350 | 10 | 6 | | | 1. Species that are not rare |
| ***Breutelia azorica*** **(Mitt.) Cardot** | AZ | 3 | 6 | 5 | 220 | 1,7 | NaFor (54) | 250 | 719,1 | 1200 | 62 | 30 | r | | 4. Restricted species (rare by range) |
| ***Bryoerythrophyllum inaequalifolium*** **(Taylor) R. H. Zander** | | 1 | 2 | 1 | 40 | dd | na (2) | dd | dd | dd | 0 | 2 | r | | |
| ***Bryoxiphium norvegicum*** **(Brid.) Mitt.** | | 1 | 1 | 1 | 1 | dd | na (1) | 325 | 325,0 | 325 | 0 | 1 | | | |
| ***Bryum argenteum*** **Hedw.** | | 3 | 8 | 3 | 153 | 2,9 | Mesic (9) | 50 | 215,0 | 525 | 18 | 14 | | | 1. Species that are not rare |
| ***Bryum canariense*** **Brid.** | | 3 | 8 | 7 | 251 | 1,9 | Mesic (15) | 10 | 161,4 | 575 | 21 | 20 | | | 1. Species that are not rare |
| ***Bryum creberrimum*** **Taylor** | | 3 | 4 | | dd | dd | na (0) | dd | dd | dd | 0 | 0 | | | |
| ***Bryum gemmiparum*** **De Not.** | | 2 | 3 | 1 | 5 | dd | na (1) | dd | dd | dd | 2 | 0 | | | |
| ***Bryum kunzei*** **Hornsch.** | | 1 | 1 | | dd | dd | na (2) | dd | dd | dd | 2 | 0 | | | |
| ***Bryum mildeanum*** **Jur.** | | 3 | 4 | 3 | 68 | dd | Aquat (4) | 150 | 150,0 | 150 | 5 | 1 | | | |
| ***Bryum radiculosum*** **Brid.** | | 2 | 3 | 1 | 8 | dd | na (2) | dd | dd | dd | 2 | 2 | | | |
| ***Bryum ruderale*** **Crundw. *et* Nyholm** | | 2 | 3 | 2 | 103 | dd | na (2) | dd | dd | dd | 0 | 4 | | | |
| ***Bryum sauteri*** **Bruch *et* Schimp.** | | 1 | 2 | 1 | 15 | dd | na (1) | dd | dd | dd | 0 | 2 | | | |
| ***Bryum subapiculatum*** **Hampe** | | 2 | 2 | 2 | 10 | dd | na (1) | 200 | 200,0 | 200 | 1 | 2 | | | |
| ***Bryum tenuisetum*** **Limpr.** | | 2 | 2 | | 22 | dd | na (1) | 10 | 10,0 | 10 | 0 | 2 | k | | |
| ***Bryum torquescens*** **Bruch *et* Schimp.** | | 3 | 7 | 5 | 75 | 1,9 | Mesic (10) | 10 | 268,6 | 600 | 8 | 18 | | | 2. Scarce species (rare by abundance) |
| ***Calliergonella cuspidata*** **(Hedw.) Loeske** | | 3 | 6 | 3 | 239 | 3,4 | InPas (24) | 225 | 536,3 | 800 | 24 | 32 | | | 3. Species with narrow ecological tolerance |
| ***Campylopus atrovirens*** **De Not.** | | 2 | 3 | | dd | dd | na (1) | dd | dd | dd | 0 | 1 | | | |
| ***Campylopus brevipilus*** **Bruch *et* Schimp.** | | 3 | 8 | 6 | 59 | 4,8 | PeBog (9) | 250 | 511,8 | 900 | 4 | 23 | | | 5. Scarce species with narrow ecological tolerance |

| Species | Endemic grouping | Groups of Islands | Number of Islands | Presence in Island Parks | Number of 500 x 500 m cells | Lloyd index (>11 records) | Habitat with highest number of records | Minimum altitude (m) | Mean altitude (m) | Maximum altitude (m) | Records <1976 | Records >1975 | Old IUCN criteria | Experts' opinion | Vulnerability Index |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Campylopus cygneus*** **(Hedw.) Brid.** | | 3 | 8 | 8 | 430 | 2,3 | NaFor (90) | 200 | 682,7 | 1200 | 63 | 117 | k | | 1. Species that are not rare |
| ***Campylopus flaccidus*** **Renauld *et* Cardot** | | 2 | 2 | 1 | 1 | dd | na () | | | | | | k | | |
| ***Campylopus flexuosus*** **(Hedw.) Brid.** | | 3 | 9 | 8 | 277 | 1,6 | NaFor (47) | 250 | 615,4 | 1000 | 57 | 64 | | | 1. Species that are not rare |
| ***Campylopus fragilis*** **(Brid.) Bruch *et* Schimp.** | | 3 | 9 | 8 | 344 | 1,5 | NaFor (19) | 150 | 573,8 | 900 | 24 | 34 | | | 1. Species that are not rare |
| ***Campylopus incrassatus*** **Müll. Hal.** | | 3 | 6 | 2 | 25 | dd | PeBog (4) | 550 | 771,4 | 1200 | 0 | 8 | | | |
| ***Campylopus introflexus*** **(Hedw.) Brid.** | | 3 | 9 | 1 | 40 | dd | na (2) | 325 | 400,0 | 475 | 1 | 7 | | | |
| ***Campylopus pilifer*** **Brid.** | i | 3 | 9 | 9 | 1112 | 1,3 | Mesic (51) | 10 | 411,2 | 1500 | 144 | 148 | | | 1. Species that are not rare |
| ***Campylopus pyriformis*** **(Schultz) Brid.** | | 3 | 8 | 7 | 148 | 2,4 | NaFor (37) | 10 | 578,4 | 1025 | 12 | 96 | | | 1. Species that are not rare |
| ***Campylopus shawii*** **Wilson** | | 3 | 6 | 4 | 133 | 3,9 | NaFor (33) | 525 | 788,0 | 1500 | 15 | 40 | r | | 3. Species with narrow ecological tolerance |
| ***Campylopus subulatus*** **Schimp. *ex* J. Milde** | | 1 | 1 | 1 | 1 | dd | na (1) | 775 | 775,0 | 775 | 0 | 1 | | | |
| ***Ceratodon purpureus*** **(Hedw.) Brid. subsp. *purpureus*** | | 3 | 9 | 6 | 249 | 1,2 | ExFor (11) | 10 | 484,7 | 1450 | 27 | 30 | | | 1. Species that are not rare |
| ***Ceratodon purpureus*** **(Hedw.) Brid. subsp. *stenocarpus* (Bruch. *et* Schimp. *ex* Müll. Hal.) Dixon** | | 1 | 1 | 1 | 1 | dd | na (1) | 875 | 875,0 | 875 | 0 | 1 | | | |
| ***Cheilothela chloropus*** **(Brid.) Lindb.** | | 1 | 1 | 1 | 7 | dd | na (1) | dd | dd | dd | 2 | 0 | | | |
| ***Cirriphyllum piliferum*** **(Hedw.) Grout.** | | 3 | 9 | 2 | 12 | dd | na (2) | 625 | 680,0 | 800 | 1 | 5 | | | |
| ***Cryphaea heteromalla*** **(Hedw.) D. Mohr** | | 1 | 1 | 1 | 1 | dd | na (1) | dd | dd | dd | 1 | 0 | | es | |
| ***Ctenidium molluscum*** **(Hedw.) Warnst.** | | 2 | 2 | 1 | 49 | dd | Aquat (4) | 200 | 237,5 | 325 | 6 | 1 | | | |
| ***Cyclodictyon laetevirens*** **(Hook. *et* Taylor) Mitt.** | | 2 | 6 | 3 | 205 | 6,5 | NaFor (85) | 350 | 636,8 | 1000 | 25 | 114 | r | es | 3. Species with narrow ecological tolerance |
| ***Cynodontium bruntonii*** **(Sm.) Bruch *et* Schimp.** | | 1 | 1 | | dd | dd | na (0) | dd | dd | dd | 0 | 0 | | | |
| ***Daltonia stenophylla*** **Mitt.** | | 2 | 5 | 5 | 166 | 3,0 | NaFor (42) | 550 | 804,5 | 1000 | 25 | 27 | v | es | 3. Species with narrow ecological tolerance |
| ***Dialytrichia mucronata*** **(Brid.) Broth.** | | 2 | 2 | | 11 | dd | na (1) | dd | dd | dd | 1 | 0 | | | |
| ***Dicranella heteromalla*** **(Hedw.) Schimp.** | | 3 | 7 | 4 | 94 | 2,3 | ExFor (10) | 150 | 513,6 | 900 | 15 | 12 | | | 1. Species that are not rare |

| Species | Endemic grouping | Groups of Islands | Number of Islands | Presence in Island Parks | Number of 500 x 500 m cells | Lloyd index (>11 records) | Habitat with highest number of records | Minimum altitude (m) | Mean altitude (m) | Maximum altitude (m) | Records <1976 | Records >1975 | Old IUCN criteria | Experts' opinion | Vulnerability Index |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Dicranella howei* Renauld *et* Cardot** | | 2 | 2 | 1 | 1 | dd | na (2) | 550 | 550,0 | 550 | 0 | 3 | | | |
| ***Dicranella schreberiana* (Hedw.) Dixon** | | 1 | 2 | 1 | 10 | dd | na (1) | 400 | 475,0 | 550 | 0 | 2 | | | |
| ***Dicranella subulata* (Hedw.) Schimp.** | | 1 | 1 | | dd | dd | na (0) | dd | dd | dd | 1 | 0 | | | |
| ***Dicranella varia* (Hedw.) Schimp.** | | 3 | 4 | 2 | 110 | dd | na (2) | 700 | 787,5 | 875 | 11 | 0 | | | |
| ***Dicranoweisia cirrata* (Hedw.) Lindb. *ex* Milde** | | 1 | 2 | 1 | 7 | dd | na (1) | 175 | 175,0 | 175 | 1 | 1 | | | |
| ***Dicranoweisia crispula* (Hedw.) Lindb. ex Milde** | | 2 | 3 | 1 | 5 | dd | Mount (4) | 200 | 920,0 | 2350 | 4 | 7 | | | |
| ***Dicranum bonjeanii* De Not.** | | 2 | 3 | 3 | 42 | dd | NaFor (6) | 550 | 740,0 | 900 | 5 | 2 | | | |
| ***Dicranum canariense* Hampe *ex* Müll. Hal.** | | 2 | 3 | 3 | 66 | 3,9 | NaFor (15) | 525 | 662,5 | 925 | 1 | 20 | | | 5. Scarce species with narrow ecological tolerance |
| ***Dicranum flagellare* Hedw.** | | 1 | 3 | 2 | 28 | dd | NaFor (3) | 575 | 650,0 | 800 | 1 | 3 | | | |
| ***Dicranum majus* Sm.** | | 1 | 1 | 1 | 15 | dd | NaFor (4) | 675 | 687,5 | 700 | 0 | 4 | | | |
| ***Dicranum scoparium* Hedw.** | | 3 | 6 | 4 | 83 | 5,6 | NaFor (12) | 500 | 860,7 | 1450 | 11 | 7 | | | 5. Scarce species with narrow ecological tolerance |
| ***Dicranum scottianum* Turn.** | | 3 | 8 | 8 | 436 | 4,4 | NaFor (256) | 175 | 703,1 | 1925 | 119 | 173 | | | 3. Species with narrow ecological tolerance |
| ***Didymodon acutus* (Brid.) Saito** | | 2 | 2 | 1 | 2 | dd | na (1) | 900 | 900,0 | 900 | 0 | 1 | | | |
| ***Didymodon insulanus* (De Not.) Hill** | | 3 | 4 | 2 | 51 | dd | Mesic (3) | 200 | 212,5 | 225 | 7 | 2 | | | |
| ***Didymodon luridus* Hornsch.** | | 2 | 6 | 1 | 92 | dd | Mesic (4) | 50 | 268,8 | 575 | 2 | 9 | | | |
| ***Didymodon rigidulus* Hedw.** | | 1 | 1 | | 1 | dd | na (1) | 500 | 500,0 | 500 | 0 | 1 | | | |
| ***Didymodon tophaceus* (Brid.) Lisa** | | 3 | 6 | 5 | 192 | 3,6 | Urban (6) | 150 | 225,0 | 375 | 12 | 5 | | | 3. Species with narrow ecological tolerance |
| ***Didymodon vinealis* (Brid.) R. H. Zander** | | 2 | 5 | 4 | 127 | 2,3 | Mesic (6) | 75 | 433,3 | 875 | 12 | 3 | | | 1. Species that are not rare |
| ***Diphyscium foliosum* (Hedw.) D. Mohr** | | 3 | 9 | 8 | 257 | 1,3 | NaFor (35) | 300 | 617,6 | 1500 | 37 | 50 | | | 1. Species that are not rare |
| ***Ditrichum pallidum* (Hedw.) Hampe** | | 2 | 3 | 2 | 35 | dd | na (1) | dd | dd | dd | 1 | 3 | | | |
| ***Ditrichum punctulatum* Mitt.** | | 1 | 1 | 1 | 2 | dd | na (1) | 1200 | 1200,0 | 1200 | 0 | 1 | | | |

| Species | Endemic grouping | Groups of Islands | Number of Islands | Presence in Island Parks | Number of 500 x 500 m cells | Lloyd index (>11 records) | Habitat with highest number of records | Minimum altitude (m) | Mean altitude (m) | Maximum altitude (m) | Records <1976 | Records >1975 | Old IUCN criteria | Experts' opinion | Vulnerability Index |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Ditrichum subulatum* Hampe | | 2 | 3 | 2 | 3 | dd | na (2) | 900 | 900,0 | 900 | 2 | 1 | | | |
| *Echinodium renauldii* (Cardot) Broth. | AZ | 3 | 7 | 6 | 168 | 2,3 | NaFor (15) | 75 | 426,3 | 1250 | 18 | 32 | v | es | 4. Restricted species (rare by range) |
| *Entosthodon attenuatus* (Dicks.) Bryhn | | 3 | 8 | 7 | 419 | 1,3 | NaFor (27) | 150 | 570,0 | 950 | 45 | 38 | | | 1. Species that are not rare |
| *Entosthodon muhlenbergii* (Turner) Fife | | 1 | 2 | 1 | 7 | dd | na (2) | dd | dd | dd | 2 | 0 | | | |
| *Entosthodon obtusus* (Hedw.) Lindb. | | 3 | 7 | 6 | 172 | 1,0 | NaFor (11) | 275 | 675,0 | 950 | 17 | 8 | | | 1. Species that are not rare |
| *Entosthodon pulchellus* (H.Philib.) Brugués | | 2 | 2 | 1 | 56 | dd | Urban (3) | dd | dd | dd | 3 | 0 | | | |
| *Ephemerum cohaerens* (Hedw.) Hampe | | 1 | 1 | 1 | 1 | dd | na (1) | dd | dd | dd | 0 | 1 | e | | |
| *Epipterygium tozeri* (Grev.) Lindb. | | 3 | 9 | 7 | 466 | 3,2 | Caves (32) | 25 | 336,9 | 1000 | 22 | 88 | | | 3. Species with narrow ecological tolerance |
| *Eucladium verticillatum* (Brid.) Bruch et Schimp. | | 3 | 4 | 4 | 122 | 2,7 | Aquat (6) | 375 | 487,5 | 650 | 12 | 3 | | | 1. Species that are not rare |
| *Eurhynchium striatum* (Hedw.) Schimp. | | 1 | 2 | 1 | 105 | 2,8 | Aquat; ExFor (4) | 300 | 341,7 | 400 | 10 | 6 | | | 1. Species that are not rare |
| *Fissidens adianthoides* Hedw. | | 1 | 2 | 1 | 13 | dd | NaFor (6) | 250 | 491,7 | 675 | 2 | 7 | | | |
| *Fissidens asplenioides* Hedw. | | 3 | 9 | 9 | 613 | 1,6 | NaFor (91) | 10 | 492,4 | 1000 | 115 | 225 | r | | 1. Species that are not rare |
| *Fissidens azoricus* (P. de la Varde) Bizot | AZ | 1 | 1 | | 4 | dd | na (2) | 325 | 375,0 | 400 | 1 | 2 | k | es | |
| *Fissidens bryoides* Hedw. *s.l.* | | 3 | 9 | 6 | 382 | 2,3 | Aquat (16) | 25 | 407,9 | 950 | 28 | 54 | | | 1. Species that are not rare |
| *Fissidens coacervatus* Brugg.-Nann. | MAC | 2 | 5 | 2 | 23 | 3,1 | ExFor (11) | 25 | 234,6 | 575 | 0 | 34 | t | | 8. Restricted and scarce species with narrow ecological tolerance |
| *Fissidens crassipes* Wilson *ex* Bruch et Schimp. subsp. *crassipes* | | 3 | 6 | 1 | 45 | dd | na (2) | 275 | 275,0 | 275 | 0 | 2 | | | |
| *Fissidens crassipes* Wilson *ex* Bruch et Schimp. subsp. *warnstorfii* (M.Fleisch.) Brugg.-Nann. | | 3 | 4 | 3 | 103 | 5,2 | Aquat (11) | 250 | 316,7 | 400 | 12 | 2 | | | 3. Species with narrow ecological tolerance |
| *Fissidens crispus* Mont. | | 3 | 4 | 2 | 44 | dd | na (1) | dd | dd | dd | 1 | 2 | | | |
| *Fissidens curvatus* Hornsch. | | 1 | 1 | 1 | 7 | dd | na (1) | dd | dd | dd | 1 | 0 | k | | |
| *Fissidens dubius* P. Beauv. | | 3 | 6 | 3 | 92 | dd | NaFor (5) | 400 | 537,5 | 675 | 4 | 4 | | | |

| Species | Endemic grouping | Groups of Islands | Number of Islands | Presence in Island Parks | Number of 500 x 500 m cells | Lloyd index (>11 records) | Habitat with highest number of records | Minimum altitude (m) | Mean altitude (m) | Maximum altitude (m) | Records <1976 | Records >1975 | Old IUCN criteria | Experts' opinion | Vulnerability Index |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **_Fissidens monguillonii_ Thér.** | | 1 | 1 | | dd | dd | na (1) | dd | dd | dd | 1 | 0 | r | | |
| **_Fissidens pusillus_ (Wilson) Milde** | | 2 | 2 | | 1 | dd | na (1) | 100 | 100,0 | 100 | 0 | 2 | | | |
| **_Fissidens rivularis_ Bruch _et_ Schimp.** | | 3 | 7 | 1 | 94 | 3,9 | Aquat (6) | 500 | 685,7 | 800 | 9 | 11 | | | 3. Species with narrow ecological tolerance |
| **_Fissidens serratus_ Müll. Hal.** | | 2 | 4 | 3 | 28 | dd | na (2) | 650 | 650,0 | 650 | 4 | 1 | | | |
| **_Fissidens serrulatus_ Brid.** | | 3 | 9 | 9 | 566 | 4,5 | NaFor (153) | 75 | 557,5 | 1000 | 122 | 262 | | | 3. Species with narrow ecological tolerance |
| **_Fissidens sublinaefolius_ (P. de la Varde) Brugg.-Nann.** | MAC | 3 | 6 | 4 | 163 | 4,9 | Aquat (24) | 800 | 800,0 | 800 | 37 | 1 | r | | 7. Restricted species with narrow ecological range |
| **_Fissidens taxifolius_ Hedw. subsp. _pallidicaulis_ (Mitt.) Mönk.** | | 3 | 9 | 3 | 537 | 1,2 | NaFor (23) | 25 | 391,7 | 950 | 66 | 58 | | | 1. Species that are not rare |
| **_Fissidens taxifolius_ Hedw. subsp. _taxifolius_** | | 3 | 8 | 6 | 84 | 4,6 | Caves (48) | 50 | 297,5 | 1000 | 6 | 119 | | | 3. Species with narrow ecological tolerance |
| **_Fissidens viridulus_ (Sw. _ex_ anon.) Wahlenb.** | | 3 | 8 | 5 | 122 | 4,6 | Caves (20) | 25 | 318,5 | 600 | 12 | 32 | | | 3. Species with narrow ecological tolerance |
| **_Fontinalis antipyretica_ Hedw.** | | 3 | 3 | 1 | 27 | dd | Aquat (9) | 550 | 550,0 | 550 | 8 | 3 | | | |
| **_Funaria hygrometrica_ Hedw.** | | 2 | 2 | 2 | 107 | 1,6 | Mesic (6) | 325 | 360,0 | 500 | 10 | 6 | | | 1. Species that are not rare |
| **_Glyphomitrium daviesii_ (Dicks.) Brid.** | | 2 | 2 | 1 | 10 | dd | na (2) | 200 | 200,0 | 200 | 3 | 0 | r | | |
| **_Grimmia elongata_ Kaulf.** | | 1 | 1 | 1 | 40 | dd | na (1) | 1500 | 1500,0 | 1500 | 1 | 0 | | | |
| **_Grimmia hartmanii_ Schimp.** | | 1 | 1 | | dd | dd | na (1) | dd | dd | dd | 0 | 1 | | | |
| **_Grimmia incurva_ Schwägr.** | | 1 | 1 | 1 | 15 | dd | na (1) | 2000 | 2000,0 | 2000 | 1 | 0 | | | |
| **_Grimmia laevigata_ (Brid.) Brid.** | | 1 | 2 | | 9 | dd | na (2) | 50 | 87,5 | 125 | 0 | 3 | | | |
| **_Grimmia lisae_ De Not.** | | 3 | 9 | 7 | 570 | 1,8 | Mesic (61) | 10 | 249,5 | 800 | 61 | 95 | | | 1. Species that are not rare |
| **_Grimmia montana_ Bruch et Schimp.** | | 1 | 1 | | 1 | dd | na () | | | | | 1 | | | |
| **_Grimmia pulvinata_ (Hedw.) Sm.** | | 3 | 4 | | 13 | dd | na (2) | 25 | 25,0 | 25 | 2 | 2 | | | |
| **_Gymnostomum calcareum_ Nees _et_ Hornsch.** | | 3 | 6 | 5 | 177 | 7,1 | Urban (6) | 675 | 675,0 | 675 | 8 | 5 | | | 3. Species with narrow ecological tolerance |
| **_Gymnostomum viridulum_ Brid.** | | 1 | 1 | 1 | 25 | dd | na (1) | dd | dd | dd | 0 | 2 | | | |

| **Species** | **Endemic grouping** | **Groups of Islands** | **Number of Islands** | **Presence in Island Parks** | **Number of 500 x 500 m cells** | **Lloyd index (>11 records)** | **Habitat with highest number of records** | **Minimum altitude (m)** | **Mean altitude (m)** | **Maximum altitude (m)** | **Records <1976** | **Records >1975** | **Old IUCN criteria** | **Experts' opinion** | **Vulnerability Index** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Gyroweisia tenuis*** **(Hedw.) Schimp.** | | 1 | 1 | | 16 | dd | na (1) | 300 | 300,0 | 300 | 0 | 1 | | | |
| ***Herzogiella striatella*** **(Brid.) Iwats.** | | 1 | 2 | | 2 | dd | na (1) | 150 | 175,0 | 200 | 0 | 2 | | | |
| ***Heterocladium flaccidum*** **(Schimp.) A.J.E. Sm.** | | 2 | 2 | 1 | 11 | 12,2 | Caves (24) | 275 | 435,4 | 600 | 1 | 24 | | | 5. Scarce species with narrow ecological tolerance |
| ***Heterocladium heteropterum*** **(Brid.) Schimp.** | | 3 | 9 | 9 | 437 | 3,6 | NaFor (61) | 100 | 564,0 | 1450 | 65 | 152 | | | 3. Species with narrow ecological tolerance |
| ***Heterocladium wulfsbergii*** **I. Hagen** | | 3 | 7 | 6 | 142 | 3,7 | NaFor (21) | 100 | 618,1 | 1925 | 8 | 40 | | | 3. Species with narrow ecological tolerance |
| ***Homalia lusitanica*** **Schimp.** | | 1 | 1 | 1 | 35 | dd | Aquat (5) | 100 | 166,7 | 300 | 4 | 3 | | es | |
| ***Homalia webbiana*** **(Mont.) Düll** | | 3 | 5 | 3 | 31 | 3,4 | Aquat (12) | 50 | 207,8 | 300 | 6 | 17 | r | es | 5. Scarce species with narrow ecological tolerance |
| ***Homalothecium sericeum*** **(Hedw.) Schimp.** | | 2 | 3 | 1 | 31 | dd | na (1) | 100 | 150,0 | 200 | 3 | 0 | | | |
| ***Hookeria lucens*** **(Hedw.) Sm.** | | 3 | 4 | 2 | 32 | dd | NaFor (7) | 625 | 793,8 | 975 | 3 | 4 | | | |
| ***Hygroamblystegium fluviatile*** **(Hedw.) Loeske** | | 1 | 1 | | dd | dd | na (1) | 50 | 50,0 | 50 | 0 | 1 | | | |
| ***Hygroamblystegium humile*** **(P. Beauv.) Vanderp., Goffinet *et* Hedenäs** | | 1 | 1 | 1 | 11 | dd | na (1) | 650 | 650,0 | 650 | 2 | 1 | | | |
| ***Hygroamblystegium tenax*** **(Hedw.) Jenn.** | | 2 | 2 | | 1 | dd | na (2) | 600 | 750,0 | 900 | 4 | 0 | | | |
| ***Hygroamblystegium varium*** **(Hedw.) Mönk.** | | 3 | 4 | 3 | 68 | dd | NaFor (5) | 125 | 491,7 | 600 | 3 | 6 | | | |
| ***Hygrohypnum luridum*** **(Hedw.) Jenn.** | | 2 | 2 | 1 | 32 | dd | na (1) | dd | dd | dd | 0 | 3 | | | |
| ***Hylocomium splendens*** **(Hedw.) Schimp.** | | 3 | 5 | 3 | 218 | 2,2 | NaFor (19) | 75 | 831,3 | 1500 | 30 | 9 | | | 1. Species that are not rare |
| ***Hyocomium armoricum*** **(Brid.) Wijk *et* Marg.** | | 1 | 4 | 2 | 52 | 2,4 | NaFor (22) | 200 | 640,4 | 700 | 30 | 15 | | es | 2. Scarce species (rare by abundance) |
| ***Hypnum andoi*** **Smith** | | 2 | 4 | 1 | 54 | dd | na (2) | 225 | 593,8 | 875 | 1 | 4 | | | |
| ***Hypnum cupressiforme*** **Hedw.** | | 3 | 9 | 8 | 382 | 1,3 | Mesic (61) | 10 | 363,6 | 950 | 104 | 189 | | | 1. Species that are not rare |
| ***Hypnum imponens*** **Hedw.** | | 3 | 4 | 4 | 50 | dd | na (2) | 550 | 730,0 | 1025 | 7 | 2 | | | |
| ***Hypnum jutlandicum*** **Holmen *et* E. Warncke** | | 3 | 9 | 5 | 145 | 1,7 | NaFor (9) | 150 | 475,0 | 850 | 12 | 20 | | | 1. Species that are not rare |

| **Species** | **Endemic grouping** | **Groups of Islands** | **Number of Islands** | **Presence in Island Parks** | **Number of 500 x 500 m cells** | **Lloyd index (>11 records)** | **Habitat with highest number of records** | **Minimum altitude (m)** | **Mean altitude (m)** | **Maximum altitude (m)** | **Records <1976** | **Records >1975** | **Old IUCN criteria** | **Experts' opinion** | **Vulnerability Index** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **_Hypnum uncinulatum_ Jur.** | EUR | 3 | 9 | 9 | 696 | 2,0 | NaFor (452) | 10 | 624,7 | 1500 | 326 | 487 | rt | | 1. Species that are not rare |
| **_Imbribryum alpinum_ (Huds. _ex_ With.) N. Pedersen** | | 3 | 8 | 5 | 47 | 0,7 | NaFor (7) | 450 | 771,9 | 1550 | 6 | 8 | | | 2. Scarce species (rare by abundance) |
| **_Isopterygium tenerum_ (Sw.) Mitt.** | | 2 | 4 | 4 | 64 | 7,1 | PeBog (12) | 300 | 583,9 | 675 | 3 | 14 | e | | 5. Scarce species with narrow ecological tolerance |
| **_Isothecium alopecuroides_ (Dubois) Isov.** | | 2 | 2 | 1 | 1 | dd | na (1) | dd | dd | dd | 1 | 0 | | | |
| **_Isothecium myosuroides_ Brid.** | | 3 | 7 | 4 | 137 | 4,1 | NaFor (7) | 275 | 810,4 | 1500 | 11 | 7 | | | 3. Species with narrow ecological tolerance |
| **_Isothecium prolixum_ (Mitt.) Stech, Sim-Sim, Tangney _et_ D.Quandt** | MAC | 3 | 9 | 8 | 612 | 2,6 | NaFor (265) | 200 | 681,7 | 1925 | 134 | 225 | r | | 4. Restricted species (rare by range) |
| **_Kiaeria blyttii_ (Bruch _et_ Schimp.) Broth.** | | 1 | 1 | 1 | 15 | dd | na (1) | 2000 | 2000,0 | 2000 | 1 | 0 | | | |
| **_Kindbergia praelonga_ (Hedw.) Ochyra** | | 3 | 9 | 9 | 581 | 2,6 | InPas (107) | 10 | 455,0 | 1050 | 160 | 340 | | | 1. Species that are not rare |
| **_Leptobarbula berica_ (De Not.) Schimp.** | | 2 | 3 | 2 | 122 | dd | Urban (4) | 475 | 475,0 | 475 | 2 | 4 | | | |
| **_Leptobryum pyriforme_ (Hedw.) Wilson** | | 1 | 1 | 1 | 39 | dd | PeBog (3) | dd | dd | dd | 5 | 0 | | | |
| **_Leptodictyum riparium_ (Hedw.) Warnst.** | | 2 | 2 | 2 | 65 | dd | Aquat; Parks (3) | dd | dd | dd | 6 | 2 | | | |
| **_Leptophascum leptophyllum_ (Müll. Hal.) J. Guerra _et_ J. M. Cano** | i | 3 | 6 | 2 | 140 | dd | Mesic (4) | dd | dd | dd | 0 | 7 | | | |
| **_Leucobryum albidum_ (P. Beauv.) Lindb.** | | 3 | 7 | 6 | 217 | 1,3 | NaFor (18) | 175 | 615,4 | 1025 | 35 | 7 | | | 1. Species that are not rare |
| **_Leucobryum glaucum_ (Hedw.) Angstr.** | | 3 | 7 | 6 | 220 | 5,2 | PeBog (62) | 250 | 612,6 | 950 | 46 | 77 | | | 3. Species with narrow ecological tolerance |
| **_Leucobryum juniperoideum_ (Brid.) Müll. Hal.** | | 3 | 9 | 9 | 357 | 2,4 | NaFor (201) | 100 | 578,4 | 1000 | 27 | 298 | | | 1. Species that are not rare |
| **_Leucodon canariensis_ (Brid.) Schwägr.** | MAC | 2 | 3 | 1 | 76 | dd | na (1) | 50 | 141,7 | 275 | 1 | 4 | r | | |
| **_Leucodon sciuroides_ (Hedw.) Schwägr.** | | 2 | 4 | 2 | 30 | dd | InPas (6) | 50 | 100,0 | 150 | 0 | 8 | | | |
| **_Leucodon treleasei_ (Cardot) Paris** | MAC | 3 | 9 | 5 | 311 | 2,3 | Mesic (7) | 25 | 178,1 | 275 | 13 | 9 | k | | 4. Restricted species (rare by range) |
| **_Loeskeobryum brevirostre_ (Brid.) M.Fleisch.** | | 2 | 4 | 4 | 56 | 1,4 | NaFor (10) | 225 | 637,5 | 850 | 10 | 7 | | | 2. Scarce species (rare by abundance) |
| **_Microcampylopus laevigatus_ (Thér.) Giese _et_ Frahm** | | 3 | 8 | 7 | 293 | 1,7 | NaFor (19) | 275 | 564,3 | 925 | 28 | 48 | r | es | 1. Species that are not rare |

| **Species** | **Endemic grouping** | **Groups of Islands** | **Number of Islands** | **Presence in Island Parks** | **Number of 500 x 500 m cells** | **Lloyd index (>11 records)** | **Habitat with highest number of records** | **Minimum altitude (m)** | **Mean altitude (m)** | **Maximum altitude (m)** | **Records <1976** | **Records >1975** | **Old IUCN criteria** | **Experts' opinion** | **Vulnerability Index** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Mnium hornum*** **Hedw.** | | 3 | 6 | 4 | 145 | 1,4 | NaFor (10) | 375 | 638,0 | 1550 | 23 | 16 | | | 1. Species that are not rare |
| ***Myurium hochstetteri*** **(Schimp.) Kindb.** | | 3 | 9 | 9 | 977 | 1,6 | NaFor (321) | 10 | 610,5 | 1925 | 164 | 382 | | | 1. Species that are not rare |
| ***Neckera cephalonica*** **Jur.** ***et*** **Unger** | MAC | 1 | 1 | 1 | 4 | dd | na (1) | 1500 | 1500,0 | 1500 | 1 | 0 | k | es | |
| ***Neckera complanata*** **(Hedw.) Huebener** | | 1 | 1 | | dd | dd | na (0) | dd | dd | dd | 0 | 1 | | | |
| ***Neckera crispa*** **Hedw.** | | 3 | 4 | 2 | 8 | dd | na (2) | 625 | 625,0 | 625 | 2 | 0 | | | |
| ***Neckera intermedia*** **Brid.** | IB-MAC | 3 | 9 | 8 | 399 | 1,7 | NaFor (31) | 50 | 565,7 | 1925 | 60 | 52 | rt | es | 1. Species that are not rare |
| ***Neckera pumila*** **Hedw.** | | 1 | 1 | 1 | dd | dd | Mount (3) | 1000 | 1166,7 | 1500 | 3 | 0 | | | |
| ***Orthotrichum diaphanum*** **Schrad.** ***ex*** **Brid.** | | 3 | 5 | 2 | 54 | 5,7 | Urban (8) | 100 | 100,0 | 100 | 12 | 2 | | | 5. Scarce species with narrow ecological tolerance |
| ***Orthotrichum tenellum*** **Bruch** ***ex*** **Brid.** | | 1 | 1 | 1 | 25 | dd | na (1) | dd | dd | dd | 2 | 0 | | | |
| ***Oxyrrhynchium hians*** **(Hedw.) Loeske** | | 3 | 9 | 7 | 181 | 1,2 | NaFor (9) | 100 | 352,7 | 800 | 17 | 26 | | | 1. Species that are not rare |
| ***Oxyrrhynchium pumilum*** **(Wilson) Loeske** | | 3 | 9 | 5 | 231 | 2,0 | Caves (9) | 75 | 310,7 | 675 | 27 | 18 | | | 1. Species that are not rare |
| ***Oxyrrhynchium speciosum*** **(Brid.) Warnst.** | | 2 | 5 | | 48 | 9,2 | Caves (20) | 150 | 477,1 | 700 | 10 | 24 | | | 5. Scarce species with narrow ecological tolerance |
| ***Philonotis arnellii*** **Husn.** | | 1 | 2 | 1 | 3 | dd | Aquat (3) | 525 | 543,8 | 550 | 0 | 5 | | | |
| ***Philonotis caespitosa*** **Jur.** | | 3 | 3 | 3 | 54 | dd | na (2) | 50 | 366,7 | 525 | 5 | 3 | | | |
| ***Philonotis calcarea*** **(Bruch** ***et*** **Schimp.) Schimp.** | | 3 | 3 | 2 | 49 | dd | na (2) | dd | dd | dd | 3 | 0 | | | |
| ***Philonotis fontana*** **(Hedw.) Brid.** | | 3 | 5 | 3 | 104 | 8,5 | NaFor (8) | 575 | 822,7 | 950 | 9 | 8 | | | 3. Species with narrow ecological tolerance |
| ***Philonotis hastata*** **(Duby) Wijk** ***et*** **Margad.** | | 3 | 6 | 4 | 142 | 1,6 | Aquat (11) | 50 | 497,2 | 1000 | 19 | 8 | k | | 1. Species that are not rare |
| ***Philonotis marchica*** **(Hedw.) Brid.** | | 2 | 3 | 1 | 24 | 4,0 | Aquat (10) | 300 | 300,0 | 300 | 14 | 2 | | | 5. Scarce species with narrow ecological tolerance |
| ***Philonotis rigida*** **Brid.** | | 3 | 9 | 9 | 643 | 1,1 | NaFor (43) | 10 | 486,9 | 1050 | 74 | 86 | | | 1. Species that are not rare |
| ***Philonotis tomentella*** **Molendo** | | 1 | 1 | | dd | dd | na (1) | dd | dd | dd | 0 | 1 | | | |
| ***Philonotis uncinata*** **(Schwägr.) Brid.** | | 3 | 8 | | dd | dd | na (0) | dd | dd | dd | 0 | 2 | | | |

| Species | Endemic grouping | Groups of Islands | Number of Islands | Presence in Island Parks | Number of 500 x 500 m cells | Lloyd index (>11 records) | Habitat with highest number of records | Minimum altitude (m) | Mean altitude (m) | Maximum altitude (m) | Records <1976 | Records >1975 | Old IUCN criteria | Experts' opinion | Vulnerability Index |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **_Physcomitrium pyriforme_ (Hedw.) Brid.** | | 1 | 2 | 1 | 19 | dd | na (1) | dd | dd | dd | 2 | 0 | | | |
| **_Plagiomnium rostratum_ (Schrad.) T. J. Kop.** | | 2 | 3 | 1 | 2 | dd | na (2) | 450 | 450,0 | 450 | 2 | 1 | | | |
| **_Plagiomnium undulatum_ (Hedw.) T. J. Kop.** | | 3 | 8 | 7 | 266 | 3,7 | NaFor (50) | 175 | 579,7 | 1000 | 39 | 81 | | | 3. Species with narrow ecological tolerance |
| **_Plagiothecium nemorale_ (Mitt.) A. Jaeger** | | 3 | 8 | 8 | 352 | 6,0 | NaFor (61) | 100 | 543,1 | 1200 | 45 | 97 | | | 3. Species with narrow ecological tolerance |
| **_Plagiothecium succulentum_ (Wilson) Lindb.** | | 2 | 4 | 3 | 6 | dd | Aquat (6) | 150 | 590,6 | 875 | 1 | 8 | | | |
| **_Plasteurhynchium meridionale_ (Schimp.) M.Fleisch.** | | 3 | 7 | 4 | 32 | 3,5 | Parks (4) | 175 | 325,0 | 550 | 6 | 7 | | | 5. Scarce species with narrow ecological tolerance |
| **_Platyhypnidium riparioides_ (Hedw.) Dixon** | | 3 | 9 | 7 | 268 | 5,0 | Aquat (40) | 50 | 423,4 | 900 | 43 | 30 | | | 3. Species with narrow ecological tolerance |
| **_Pleuridium acuminatum_ Lindb.** | | 3 | 5 | 2 | 75 | dd | na (2) | dd | dd | dd | 0 | 2 | | | |
| **_Pleuridium subulatum_ (Hedw.) Rabenh.** | | 3 | 4 | | dd | dd | Mesic (3) | dd | dd | dd | 5 | 0 | | | |
| **_Pleurozium schreberi_ (Brid.) Mitt.** | | 3 | 6 | 5 | 63 | 2,1 | NaFor (16) | 425 | 786,9 | 1300 | 14 | 9 | | | 2. Scarce species (rare by abundance) |
| **_Pogonatum aloides_ (Hedw.) P. Beauv.** | | 3 | 8 | 8 | 322 | 1,3 | NaFor (36) | 150 | 545,8 | 900 | 45 | 41 | | | 1. Species that are not rare |
| **_Pogonatum nanum_ (Hedw.) P. Beauv.** | | 1 | 2 | 2 | 23 | dd | NaFor (5) | 750 | 775,0 | 800 | 8 | 0 | | | |
| **_Pogonatum urnigerum_ (Hedw.) P. Beauv.** | | 2 | 2 | 1 | 64 | 3,4 | NaFor (14) | 350 | 703,6 | 800 | 17 | 2 | | | 5. Scarce species with narrow ecological tolerance |
| **_Pohlia andalusica_ (Höhn.) Broth.** | | 1 | 1 | | dd | dd | na (1) | dd | dd | dd | 1 | 0 | | | |
| **_Pohlia annotina_ (Hedw.) Lindb.** | | 3 | 7 | 6 | 76 | 0,9 | NaFor (8) | 800 | 885,0 | 1000 | 11 | 4 | | | 2. Scarce species (rare by abundance) |
| **_Pohlia bulbifera_ (Warnst.) Warnst.** | | 2 | 2 | 2 | 76 | dd | Aquat (3) | 550 | 600,0 | 650 | 4 | 2 | | | |
| **_Pohlia cruda_ (Hedw.) Lindb.** | | 1 | 1 | 1 | 32 | dd | Mount (3) | 1225 | 1312,5 | 1400 | 3 | 0 | | | |
| **_Pohlia melanodon_ (Brid.) A. J. Shaw** | | 1 | 1 | 1 | 14 | dd | na (1) | dd | dd | dd | 2 | 0 | | | |
| **_Pohlia nutans_ (Hedw.) Lindb.** | | 1 | 1 | 1 | 1 | dd | na (2) | 1500 | 1500,0 | 1500 | 2 | 0 | | | |
| **_Pohlia proligera_ (Kindb.) Broth.** | | 3 | 5 | 4 | 31 | 3,1 | InPas (6) | 550 | 550,0 | 550 | 5 | 13 | | | 5. Scarce species with narrow ecological tolerance |