Bryophytes from the Azorean native vegetation: their diversity and contribution to ecosystem services

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Não sobrevive a espécie mais forte, mas a que se adapta à mudança.

Charles Darwin

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Summary

Bryophytes are an important component of plant diversity, being found from sea level to mountaintops, and are especially conspicuous on the Azores islands. These plants are relying on environmental water, which they acquire by intercepting rain and dew (liquid water) and using fog (water vapor), and then transporting these externally, by capillary forces, and internally, in different cells (specialized or not). Thus, bryophytes play an important role in water-flow regulation of forests through their unique water holding ability. Nevertheless, these roles and physiological features of bryophytes are not totally understood nor quantified. This work studied diversity and eco-physiological features of bryophytes on Pico and Terceira islands (Azores, Portugal). The major goals of this study are: (i) to investigate the diversity and distribution patterns of bryophyte communities on Pico Island, characterizing their native habitats along an elevational transect (from 10 to 2200 m); (ii) quantify the ability of a selected group of 14 species, common in native vegetation of the Azores, to hold water, both internally and externally; and (iii) analyze *in situ,* for one year, the hydration level of selected species, at three elevations on Terceira Island. A standardized protocol (BRYOLAT) was used to access richness and distribution of bryophytes, with observations in 100 m^2 plots every 200 m a.s.l.. The bryophytes' richness reached 51 % (144) of all species known from Pico Island. Their distribution richness exhibited a hump-shaped pattern along the elevational gradient with a maximum of diversity at 800 m (49 liverworts and 23 mosses). At these elevations the favorable conditions that increase complexity in forest structure are responsible for a higher diversity of suitable habitats for bryophytes. It was also possible to identify new locations for both common and rare species (*Echinodium renauldii, Antitrichia curtipendula*). The ecophysiological characterization study involved six liverworts and eight mosses (from two divisions and four classes) that occur on native vegetation of the Azorean Islands. The absolute water content (AWC) was obtained through measurements of specimens saturated, without free water, and completely dry. Most of the 14 target species showed an ectohydric behavior pattern retaining more than 60 % of water through gametophyte surface. The AWC value ranged from 646 % in *Polytrichum commune* to 5584 % in *Sphagnum subnitens*. The water loss by direct evaporation showed, for most of species, an exponential decay curve along time. The hydration status of the same 14 bryophyte species was assessed through Field Water Content and Relative Water Content measurements on Terceira Island. Five samples per species were collected in the field and measured monthly along the four seasons. FWC increases along the gradient and species generally exhibit higher values in wetter seasons (Winter and Spring), but patterns are not equal for all classes. Understanding how much native bryophytes, acquire, store, and release water into the system contributes to the knowledge of native vegetation resilience in the face of climate change and, especially, potential impacts on the availability and quality of water — a major ecosystem service performed by plants.

Keywords: Azorean Native Vegetation, Bryophytes, Elevation, Forest, Liverworts, Mosses, Water Content.

Resumo

Os briófitos são uma componente importante na diversidade de plantas, ocorrendo desde o litoral ao topo da montanha, e são especialmente conspícuos nas florestas açorianas. Essas plantas dependem muito da água disponível no habitat, a qual interceptam pela chuva, orvalho ou nevoeiro, e transportam externamente (capilaridade) e internamente (estruturas celulares). Neste sentido, os briófitos desempenham um papel importante na regulação dos fluxos de água nas florestas pela sua extraordinária capacidade de retenção de água. Contudo, este papel fundamental dos briófitos nos ecossistemas e as suas características fisiológicas não estão totalmente estudados nem quantificados. Este trabalho focou-se num estudo de diversidade e ecofisiologia de briófitos das ilhas Pico e Terceira (Açores, Portugal). Os principais objetivos são: (i) investigar a diversidade e padrão de distribuição das comunidades de briófitos da ilha do Pico, caracterizando os seus habitats nativos ao longo de um gradiente altitudinal (dos 10 aos 2200 m de altitude); (ii) quantificar a capacidade de 14 espécies, comuns da floresta nativa dos Açores, de reter água (interna- e externamente); e (iii) analisar *in situ,* durante 1 ano, o estado de hidratação das espécies selecionadas em 3 altitudes, na ilha Terceira. Uma metodologia padronizada (BRYOLAT) foi usada para determinar a distribuição de briófitos ao longo de um gradiente altitudinal (a cada 200 m) através de observações em plots de 100 m^2. No total, 51 % (144) da riqueza de briófitos conhecida para a ilha foi alcançada. A distribuição, ao longo do gradiente altitudinal, apresentou um pico de riqueza aos 800 m (49 hepáticas e 23 musgos). Nesta faixa altitudinal são muito favoráveis as condições climáticas aumentando a complexidade da floresta (ótimos habitats para os briófitos). Novos locais foram registados para a ocorrência do musgo endémico raro *Echinodium renauldii* bem como um registo de uma espécie nova para os Açores, o musgo *Antitrichia curtipendula* (1600 m). A caracterização ecofisiológica envolveu seis hepáticas e oito musgos representando taxonomicamnente duas divisões e quatro classes. O conteúdo absoluto de água (AWC) foi determinado em ensaios experimentais através da saturação das amostras (peso saturado) e da sua completa desidratação (peso seco). A maioria das 14 espécies demonstraram preferencialmente um comportamento ectohídrico, mais de 60 % da água retida ocorre pela superfície da planta. A capacidade máxima de retenção de água variou de 646 % no *Polytrichum commune,* a 5584 % no *Sphagnum subnitens.* A perda de água por evaporação directa demonstrou, para a maioria das espécies, um declínio exponencial ao longo do tempo, onde no minuto 1 o máximo de água perdida foi exibido pela classe Bryopsida (espécie *Thuidium tamariscinum:* 12 %) e a taxa máxima de evaporação foi alcançada pela classe Sphagnopsida (0.84 g/min). O nível de hidratação das espécies em campo foi analisado através do FWC (conteúdo de água em campo) e do RWC (conteudo de água relativo à capacidade máxima). Cinco réplicas por espécie foram colhidas no campo e medidas mensalmente ao longo de 4 estações. O FWC, nalgumas classes, aumentou com o gradiente altitudinal e sazonalmente nas estações mais húmidas (inverno e primavera). Perceber quanta água os briófitos nativos adquirem, retêm e libertam para os ecossistemas contribui para um melhor conhecimento da capacidade da vegetação nativa resistir a alterações, por exemplo climáticas, bem como os seus potenciais impactos sobre a disponibilidade e qualidade da água – importante serviço dos ecossistemas realizados pelas plantas.

Palavras-chave: Altitude, Briófitos, Conteúdo de Água, Floresta, Hepáticas, Musgos, Vegetação Nativa Açoreana.

General Introduction

Biodiversity on oceanic islands

Oceanic islands have been used in studies of biogeography, ecology, evolution and conservation as they represent globally replicated, but relatively simplified, real world systems (Whittaker & Fernández-Palacios, 2007; Kueffer & Fernández-Palacios, 2010). For instance, because oceanic islands are isolated from the mainland areas, they efficiently filter out some terrestrial organisms and promote the evolution of others, resulting in unique species and assemblages derived from the exceptional environments and evolutionary opportunities (MacArthur & Wilson, 1967; Gillespie & Roderick, 2002; Whittaker & Fernández-Palacios, 2007).

The formulation of Charles Darwin´s (1859) evolutionary theory, and the theory of island biogeography (MacArthur & Wilson, 1967), were designed to explain patterns of species richness on islands, but with wider applications in conservation biogeography. Both are illustrations of the importance of islands for biological studies (Kueffer & Fernández-Palacios, 2010).

Despite the lower overall species number per unit area (Whittaker & Fernández-Palacios, 2007), oceanic islands usually support a higher proportion of endemic species than mainland areas (Kier et al., 2009), resulting in a disproportionally high fraction of global biodiversity hosted in extremely limited insular zones (Kreft et al., 2008; Kier et al., 2009). Species richness and abundance depend on several factors, with the most fundamental being the availability of suitable habitats; in fact, habitat degradation and fragmentation, and invasive species act negatively to species maintenance (Paulay, 1994; Hanski et al., 2007; Whittaker & Fernández-Palacios, 2007). Most of the past and current losses of island endemic species and native ecosystems resulted from anthropogenic actions such as the introduction of neobiota, selective use or exploitation of species, land-use and habitat destruction (e.g. Schäfer, 2003; Didham et al., 2007; revision in Harter et al., 2015).

Among the world's biodiversity, insular island biota is particularly threatened (Caujapé-Castells et al., 2010). The small populations of the species, with some inherent fragilities (genetically impoverishment, poor dispersal ability) (Carlquist, 1974) and often-restricted distribution range and specialized habitats, put them in the first line to be affected. Since islands offer a generally rich flora with a high level of endemism, meaning, a great number of species which occur only in a restricted area, with a particular set of genes and features, it is imperative to understand how the diversity of ecological communities has evolved and how this diversity influences the ecosystem in order to better preserve them. Undertaking comparative ecological studies globally and regionally is needed to conserve the world´s oceanic island floras (Kueffer & Fernández-Palacios, 2010), that once lost, are lost forever. For instance, Azorean natural vegetation includes endemic and Tertiary relictual taxa (Sjögren, 1973), that prevailed from Pleistocene glaciations mainly due to the highly oceanic conditions (Sunding, 1979), although recent studies show that some Macaronesian endemic and native species appear to have recent radiations (Vitales et al., 2014, Silva et al., 2016). The Azores archipelago, composed by nine oceanic islands, is an important model system for studying biodiversity, due to its remoteness and geological characteristics (Forjaz, 2004) and indeed, many taxonomic groups are relatively well known from the islands (e.g. Borges et al., 2005; 2010; 2011; 2016).

Azores archipelago

The Azores archipelago, in the middle of the North Atlantic Ocean, is formed by nine isolated islands and some islets between coordinates 36º 55´ to 39º 43´ North and 24º 46´ to 31º 16´ West (França et al., 2003). It is located 1570 km from Europe (east) and 3900 km from North America (west) (Monteiro et al., 2008). The archipelago, with all islands inhabited, is geographically divided into three groups: an eastern group, including the islands of Santa Maria and São Miguel; a central group, which is formed by five islands, Terceira, Graciosa, São Jorge, Pico and Faial; and the western group, which is composed by the islands of Flores and Corvo (Forjaz, 2004). The islands are aligned in NW – SE direction. The distance between the islands farthest apart, Flores (extreme W) and Santa Maria (extreme E), is about 600 km. The largest island is São Miguel (747 km^2), while Pico (445 km^2) and Terceira (402 km^2) are respectively the second and third largest islands, and Corvo (17 km^2) is the smallest one (França et al., 2003). The archipelago covers approximately 2332 km^2 of land, where about half of the total area lies below 300 m, almost half (45 %) between 300 – 800 m, and only about 5 % are above 800 m a.s.l. (DREPA, 1988). In fact, although Pico Island holds the highest peak of Portugal, reaching 2351 m a.s.l. (França et al., 2003), the second highest elevation is in São Miguel Island (Pico da Vara, 1105 m a.s.l.), while Terceira reaches 1021 m a.s.l. with a maximum elevation in the Santa Bárbara Volcanic

Complex (Forjaz, 2004). The geologic age of these volcanic islands ranges between 8.12 million years old (Santa Maria) and 0.30 million years old (Pico) (França et al., 2003), although recent authors have different interpretations of geological age (Hildebrand et al., 2014). The archipelago, located across the Mid-Atlantic ridge, where it lies at the confluence of the American, Eurasian and African continental plates (França et al., 2003), frequently experiences volcanic and seismic activities. All Azorean islands consist of an old basaltic base complex, covered with a series of volcanic breccias, conglomerates, younger basalt, and other products of recent volcanic eruptions (França et al., 2003). Marine fossiliferous sediments can be found from sea level up to 130 m a.s.l. on the easternmost island of Santa Maria and the Formigas reef (Agostinho, 1937; Ávila et al., 2008).

The Azores belong to the Macaronesia biogeographical region, which is also comprised of Madeira, Savage, Canaries and Cape Verde archipelagos, and are included in the Mediterranean hotspot described by Myers and colleagues (2000) as one of the richest regions concerning fungi, plant and animal diversity in Europe. Currently there are 8047 species and subspecies known from the Azores, including marine and terrestrial elements (Borges et al., 2010a), but a high proportion is exotic to the archipelago.

The typical native vegetation of pristine Azorean landscapes, as was found in the 15th century by the first Portuguese settlers, was almost entirely formed by dense evergreen shrub and tree species of small to medium stature and closed canopy (Frutuoso, 1998). However, this area was greatly reduced due to human activities (agriculture, forestry, urban development), and currently the native forest bears just a small fraction of its original primary forest habitats (estimated at less than 3 %) and is mostly restricted to high and steep areas above 500 m (Triantis et al., 2010; Gaspar et al., 2011). The smallest islands, Corvo and Graciosa, no longer preserve native forests (Gaspar et al., 2008) and few endemic species (*cf.* Borges et al., 2010a). Nevertheless, about a fifth (21 %) of the Azores' territory is currently under some level of protection (PNA [cited 2016]), there is a natural park on each island and the archipelago has a marine natural park (Calado et al., 2009). However, native forest communities are restricted to much smaller fragments, more consentaneous with the areas categorized as natural reserves (8 %), where the islands of Terceira, Pico and Flores are the largest contributors to that percentage (PNA [cited 2016]).

The general conditions of the Azorean climate are determined by the archipelago's geographic location, in the mid-Atlantic, far from the direct influence of any continental mass (Agostinho, 1938; Azevedo, 1996). The Azorean islands are characterized by a mild and agreeable climate, with small fluctuations in temperature, large amounts of precipitation and high air humidity and strong wind regimes, most likely to come from the SE and NW sectors (Azevedo et al., 2004). In Winter/Summer months the mean average temperature ranges from 14 ºC to 22 ºC at sea level, from 12 ºC to 20 ºC at 350 m, from 10 ºC to 18 ºC at 650 m and from 8 ºC to 16 ºC at 1000 m, so the climate varies from a temperate humid on lower altitudes to cold oceanic at upper parts (Azevedo et al., 2004). Humidity is high, ranging from 82 % at 350 m a.s.l. to 99 % at 1000 m a.s.l., with only relatively small fluctuations (± 1 %) between seasons (Agostinho, 1938; Azevedo et al., 2004). Precipitation increases with elevation in a more or less regular way (Azevedo et al., 2004). Annual precipitation varies between values less than 1000 mm at low elevations and 4000 mm at upper elevations in Winter months (Azevedo et al., 2004). Dissimilarly to other climate variables, precipitation shows an increase from east to west of the archipelago (Agostinho, 1942; Azevedo et al., 2004) showing São Miguel Island values from 600 – 800 mm/year and Flores Island from 1400 – 1600 mm/year) (Azevedo et al., 2004).

The Azores began to attract naturalists in the 18^{th} century, including geologists, botanists and zoologists (review in Arruda, 1998, 2015). In 1838, Guthnick and Hochstetter performed a scientific exploration of the archipelago, which resulted in a published flora (Seubert & Hochstetter, 1843; Seubert, 1844). Academics such as Morelet and Drouet (1857), Watson (1843, 1844, 1870), Trelease (1897), Druce (1911), Guppy (1914, 1917), Tutin and Warburg (1932), Allorge and Allorge (1937), and Cedercreutz (1941) also published notes and catalogues about the Azorean islands' flora (Palhinha, 1966). Between 1934 and 1938, the Portuguese Ruy Telles Palhinha from "Instituto Botânico, Faculdade de Ciências de Lisboa" investigated the Azorean plants, and his studies were later edited by A. R. Pinto da Silva and published as the *Catálogo das Plantas Vasculares dos Açores* (Palhinha, 1966), an important checklist of what was known up to the first half of the 20^{th} century.

After, and especially in the last three decades, many research groups from the University of the Azores have contributed importantly to the knowledge of the evolutionary history and biodiversity of the Azores (Jorge et al., 2011). Most of these data are available on the list of the terrestrial and marine biota from the Azores (Borges et al., 2010a) and on the Azorean Biodiversity Portal (http://azoresbioportal.uac.pt/pt/) dedicated to Azorean biodiversity and its distribution across the islands.

Elevational gradients

Elevational gradients are an important concept in ecology and biogeography to study the distribution of biodiversity. Since these gradients are known to mimic latitudinal gradients but in shorter distances, they have been increasingly used as a model template for large-scale gradient studies (Rahbek, 1995). In fact, elevational gradients are easier to study since they exhibit many ecotones within a limited geographical area (Gabriel et al., 2014). Studies of elevational gradients have used vascular plants (e.g., Odland, 2010), invertebrates (e.g., Hodkinson, 2005) and vertebrates (Rahbek, 1997; 2005) and have helped scientists understand ecosystem dynamics through the presentation of numerous and various environmental and biological shifts (Kitching et al., 2011).

The authors McCain & Grytnes (2010) reported four general main patterns in elevational species richness: (i) a monotonic decline; (ii) a low-elevation plateau; (iii) a low-elevation plateau with a mid-elevation peak; and (iv) a unimodal pattern with a mid-elevational peak (hump shaped). Moreover, studies with bryophytes have revealed additional patterns, such as (v) an increase of diversity with increasing elevation (Bruun et al., 2006; Ah-Peng et al., 2007; Chantanaorrapint & Frahm, 2011) and (vi) a double peak of diversity along the studied transect (Sun et al., 2013). Most of these results depend on the proportion of the complete elevational gradient sampled. Hump-shaped patterns were most commonly found when an entire gradient was studied, while monotonic patterns were found when gradients were shortened (Nogués-Bravo et al., 2008). These findings indicate that it is most useful to take full ecological gradients, at best native vegetation, from sea level to timberline or to mountain tops (Kessler et al., 2011). In addition, elevational gradients may be improved by repeating standardized transects in several comparable regions, at different latitudes, with different areas, and different distances from the continents (e.g., Odland, 2010). For ferns and bryophytes, such studies are being done in the Azores and other archipelagos around the world (*cf.* MOVECLIM project; Gabriel et al., 2014).

From 2012 to 2016, the knowledge of the Azorean flora along elevational gradients was enhanced by the MOVECLIM project (Montane Vegetation as Listening Posts for Climate Change), led by Claudine Ah-Peng from the University of La

Réunion. This European project (EraNet Biome) promoted the study of plant diversity and distribution in native areas along elevational gradients on oceanic islands in three different oceans (Atlantic, Indian and Pacific). It originally aimed to characterize the bryophytes and ferns of several tropical and subtropical islands such as La Réunion, La Palma, Guadeloupe, Tahiti, including also Pico Island. In the Azores besides Pico Island, the protocol was also implemented on the islands of Terceira (2012), Flores (2013), São Miguel (2013), São Jorge (2014) (Gabriel et al., 2014) and Faial (2015).

Bryophytes along elevational gradients

Bryophytes have recently been used as model organisms, allowing to better understand the distribution of the diversity along latitudinal and altitudinal gradients (Rhode, 1996; Ah-Peng et al., 2012). Bryophytes exist at broad latitudinal and elevational ranges and are thus an ideal group elevational studies, as they are found from the sea level to mountain tops, tolerating a wide range of environmental conditions (Andrew & Rodgerson, 2003). Bryophytes are an important part of the Azorean vegetation with a striking and luxuriant presence. The known bryoflora, *c.* twice the number of indigenous vascular species is comprised of 480 species and subspecies: five hornworts, 164 liverworts and 311 mosses (Gabriel et al., 2010). Of all these *taxa*, seven (1.46 %) are endemic from Azores (END) and 14 (2.92 %) are endemic from Macaronesia (MAC); and four (0.83 %) were introduced (i) into the archipelago (Borges et al., 2010a; Gabriel et al., 2010). Both the total richness and the proportion of endemic bryophytes in the Azores is of the same order of magnitude than other archipelagos of Macaronesia, such as Madeira (11/512) (Manuela Sim-Sim, pers. com.) and Canary Islands (6/503) (Arechavaleta et al., 2010); moreover, the endemicity is considered relatively high if compared with the Iberian region (7/1083) (Sérgio et al., 2014). Only a few bryophytes are considered invasive in Europe (Hill et al., 2006; Ros et al. 2007, 2013) which is an important feature when studying diversity.

In the Azores, the first elevational studies with bryophytes used a phytosociological approach where aggregates of organisms were described, providing a simplified scheme for the discussion of the plant cover (Dias, 1989). The presence, coverage (%) and fertility of each plant was recorded, and the set of studied plots showed the amplitude of the ideal community (Gabriel, 2000). The first studies on Azorean bryophytes communities along elevational transects were performed by the couple Pierre and Valentine Allorge, based on their fieldwork of 1937 (Allorge &

Allorge, 1938, 1946). In 1946, they proposed an altitudinal division of the bryoflora in five levels, from sea level to the summit of Pico Island in relation with the different species of phanerogams and cryptogams. A number of ecological studies followed, using mostly Terceira Island and Pico Island as models (e.g., Gabriel, 2000; Homem, 2005; Borges et al., 2009; Aranda et al., 2010; Henriques et al., 2017). The most recent study was conducted by Henriques (2016), under the MOVECLIM project, where the author investigated the influence of climate and space on elevational distribution patterns of mosses and liverworts on Terceira Island.

Other studies, but without using a complete elevational gradient, were performed by many investigators. Purvis et al. (1994), studied lichen elevational distribution, describing the flora of the upper slopes of Pico Island between 1200 m and 2351 m altitude. Gabriel and Bates (2005) studied the bryophyte community composition and habitat specificity in the natural forests of Terceira Island, between 400 m and 950 m. Homem (2005) considered the bryophytes biodiversity, conservation and management in different spatial scales on Pico and Terceira Islands. Aranda et al. (2010) assessed the completeness of bryophytes inventories from Terceira Island.

Bryophyte biology and diversity

Bryophytes, predominantly terrestrial plants, were the first colonizers of land and are the second largest group of plants worldwide (Goffinet & Shaw, 2009). These small sized (few millimeters to half a meter) green organisms, are characterized by a life cycle featuring alternating a dominant haploid and an ephemerous diploid generation (Vanderpoorten & Goffinet, 2009).

Taxonomically, bryophytes are classified in three divisions: as hornworts (division Anthocerotophyta), liverworts (division Marchantiophyta) or mosses (division Bryophyta) (Vanderpoorten & Goffinet, 2009). These three major lineages show differences in the morphology and anatomy of the gametophyte and the sporophyte (Vanderpoorten & Goffinet, 2009). They include approximately 150 hornworts (Renzaglia et al., 2009), 7,486 liverworts (Söderström et al., 2016) and 13,000 mosses (Goffinet & Shaw, 2009). Of these, 4 % of hornworts, 8 % of liverworts and 16 % of mosses may be found in Europe (Hill et al., 2006; Söderström et al., 2007).

Traditionally bryophytes are less studied than vascular plants, but a few bryologists have been improving knowledge about this group, trying to establish complete checklists for several countries and regions (e.g., Hodgetts, 2015, for Europe) and also red-lists (e.g. Garilleti & Albertos, 2012; Sérgio et al., 2013; Sim-Sim et al., 2014). The bryoflora for Europe is well known in comparison with the rest of the world, both for mosses (Hill et al., 2006; Ros et al., 2013) and liverworts (Ros et al., 2007; Söderström et al., 2016). For Macaronesia the updated list of species was achieved in the last decade (Gabriel et al., 2005, 2010; González-Mancebo et al., 2008; Sérgio et al., 2008).

Hornworts' gametophytes are always thalloid, more or less flattened, not differentiated into a stem and leaves, and their cells have just one large chloroplast (Renzaglia et al., 2009). Liverworts' gametophytes mostly display bilateral symmetry (Crandall-Stotler et al., 2009), are thalloid, either simple (order Metzgeriales) or complex (order Marchantiales), or composed by a leafy stem, with orbicular leaves arranged in two or three parallel rows (order Jungermanniales). Mosses' gametophytes bear lanceolate leaves, typically arranged in spiral rows showing a radial symmetry (Goffinet & Shaw, 2009). Further morphological details may be found on chapter 2.

According to the latest check-list (Gabriel et al., 2010), the Azorean bryoflora is comprised of 480 species: five hornworts, 164 liverworts and 311 mosses. In the Azores, hornworts are represented by class Anthocerotopsida subdivided into three orders and three families. The classes Jungermanniopsida and Marchantiopsida represent the division of liverworts: the first one encompasses circa 82 % of all liverwort species of the archipelago, while the second one includes 29 thallose species (Gabriel et al., 2010). Four classes of mosses are referred to within the Archipelago of the Azores: class Bryopsida, with "true mosses", encompasses circa 90 % of all moss species present in the Azores; class Andraeopsida, is represented by a single species, while class Polytrichopsida and class Sphagnopsida have respectively 11 and 16 species referred to within the region (Gabriel et al., 2010). Further details on the biology of the species may also be found on chapter 2.

Bryophytes have a simpler structure than vascular plants. They do not produce flowers, seeds or fruits, and they have no real roots but they do have root-like structures (rhizoids) mainly for anchoring and water absorption (Hallingbäck & Hodgetts, 2000). These plants have unique physiologies that allow them to survive and prosper in extreme conditions of cold and dryness, which are unparalleled by any other major group of plants (Nakatsubo, 1997). They are also able to reflect environmental changes faster than other plants. Physiologically, many species are poikilohydric, which means that their hydration status depends on their habitat conditions; if conditions are not satisfactory enough to realize photosynthesis (e.g., water absence, extreme temperature, or insufficient light) these plants can suspend their metabolism therefore keeping themselves in the system for long periods (Tuba et al., 2011). Because of this physiological ability, they are able to occupy extreme and stressed environments such as iron stoves, darkened caves, exposed mountain summits, geothermal vents and meltwaters (from snow and ice), toxic environments (e.g., soil rich in heavy metals) and cold deserts (Nakatsubo, 1997; Hallingback & Hodgetts, 2000; Glime, 2017a).

Bryophytes play several vital roles in terrestrial ecosystems contributing to primary productivity: as humus formation, either on the ground or on tree branches (Nakatsubo, 1997); carbon and nutrient accumulation and cycling, through their effective uptake and slow release (Waite & Sack, 2010); and cloud and rain water interception and retention (Hallingback & Hodgetts, 2000). The latter is probably the ecosystem service most well-recognized and studied. Indeed, bryophytes are able to absorb water quickly and release it slowly (Ah-Peng et al., 2017), thus maintaining high levels of humidity in the canopy and understory of forests, even when atmospheric water inputs are reduced or absent (Veneklaas et al., 1990). Bryophyte species contribute to the regulation of water flows and help prevent flash floods, erosion, and downstream landslides, by slowly releasingly water into watercourses (Hallingback & Hodgetts, 2000). They also seem useful in regard to interaction with other species by providing habitats and camouflage for various invertebrates (During & Van Tooren, 1990), nesting material for animals, namely birds (Rydin, 2009), but mostly promoting seed germination and the establishment of other plants (During & Van Tooren, 1990). In addition, they are important first colonizers of hard and abiotic substrata allowing soil stabilization and avoiding erosion (Nakatsubo, 1997; Hallingback & Hodgetts, 2000). As economic value, traditionally bryophytes have long been used for many purposes such as in gardening, horticulture, medicine, decoration and as an energy source (e.g., fuel, peat bricks) (Longton, 1992; Hallingbäck & Hodgetts, 2000).

Since the 20th century, cryptogams as lichens and bryophytes were used as environmental bioindicators, depicting the quality of the environment on the basis of changes in species composition, morphology, physiology, and as biomonitors, providing both qualitative and quantitative information on changes in the systems. For instance, they are often used as bioindicators of either atmospheric or aquatic systems, since their richness decreases in polluted environments (Frahm, 2003; Ah-Peng & Rausch De Traubenberg, 2004; Dymytrova, 2009), but also a change in species composition can be observed, with a disapearance of sensitive species and more resilient species colonizing polluted systems. Since they do not possess roots, they are directly exposed to pollutants (Homem & Gabriel, 2008) and are thus often used as true biomonitors of pollution or change (e.g., Maciel, 2008; Govindapyari et al., 2010). For instance, mosses are among the most efficient organic adsorbents for heavy metals, and *Sphagnum* sp. was recently considered the most inert and efficient metal and proton adsorbent (González & Pokrovsky, 2014).

Water relations and ecosystem services

The concept of water relations of bryophytes began in the 18^{th} century. Several studies have since shown efficient water uptake by bryophyte leaves (see revision in Rundel, 1982). In 1947, the studies of absorption and conduction of water performed by Buch (1947) indicated that bryophytes are divided in two major physiological groups, the endohydric and the ectohydric (Proctor, 2000a).

The endohydric species have a well-developed conducting strand and basal rhizoidal system, so they mostly absorb the water from the substrate and internally conduct it up to the actively photosynthesizing leaves at the tip (Hébant 1977; Proctor, 1979b, 1982; see revision in Proctor, 2000a). Most of these endohydric species present a water-repellent surface and a tuft growth form (Proctor, 1982). Such bryophytes (e.g., Polytrichaceae, Mniaceae, Marchantiaceae) usually grow on moist, porous and often nutrient-rich substrata as well as in base-rich woods, fens and weedy habitats on bare soil (Proctor, 1982).

The ectohydric species do not have a well-developed conducting strand and consequently it is not as important that they are connected to the ground to uptake water (Proctor, 1982). These species, all leafy liverworts and the majority of mosses (e.g., Grimmiaceae, Orthotrichaceae and many Hypnaceae), readily absorb and also lose water through their entire surface (thallus or shoot) (Proctor, 1982). Accordingly, they generally do not have strong connections to soil but instead live on rock, bark, or other impermeable substrata (Proctor, 1982). For these species, rain, dew and high air relative humitidy are very important sources of water to activate the photosynthesis (Proctor, 2000b).

However, some bryophytes combine many of these characteristics, such as a wettable surface with predominantly internal conduction; they are called myxohydric bryophytes (Proctor, 1982).

The movement of water in a bryophyte gametophyte could occur through three different pathways. Externally, water conduction occurs in an interconnecting network of capillary spaces amongst the leaves, in stem tomentum of rhizoids and/or paraphyllia, and in papilla systems on leaf surfaces (Longton, 1988; Proctor, 2009). The apoplast way, water moves in cell-wall capillary spaces and by matric forces; or the symplast way, in which water moves within the cytoplasm by osmosis (Dilks & Proctor, 1979; Proctor et al., 1998). Symplast movement predominates in endohydric species (see revision in Proctor, 2000a). According to Proctor (2000a), the water conduction in most mosses and leafy liverworts occurs mostly externally, and this fraction is responsible for the variation in total water content. Externally and internally, several morphological adaptations and water-related traits contribute to the higher or lower ability of bryophytes to acquire and hold water for longer time (Vitt et al., 2014). The external capillary water conduction and reduction of direct water evaporation may be strongly influenced by the pattern of branching and leaf arrangement of mosses and leafy liverworts (Rundel, 1982) as well as the height and density of the patches, and leaf characteristics (e.g., length, sheathing base, concavity, divergence/spacing from stem, margin rolling, orientation/disposition, nerve extension; papilla and mamilla) (Proctor, 1982; Guerra et al., 1992; Elumeeva et al., 2011). Internally, for some species, water movement within the shoots occurs in tissues by simple diffusion between cells, and for another species by specialized water-conducting cells, the hydroids, which are dead and hollow cells at maturity, forming large central strands of bryophyte stems (Rundel, 1982). Other ones are the stereids, living support cells adjacent to the hydroids (Trachtenberg & Zamski, 1979).

Summarizing, bryophytes retain water in their cells both through external (ectohydric) capillary movement and internal (endohydric) transport (Glime, 2017c). When fully hydrated, they metabolize but when dry they became inactives and can survive months to many years (Glime, 2017c). The architecture of the plant as well most of all the structures associated (e.g., branch and leaf arrangements, rhizoidal tomentum, central strand, hydroids, paraphyllia) facilitate the water retention and hinders the water loss (Glime, 2017c). Water storage is thus an important ecological role bryophytes perform, especially in native vegetation, where their biomass may be considerably (e.g. Frahm, 1990; 2003; Veneklaas et al., 1990).

Thesis aims and outline

The present investigation was undertaken on the Azorean native vegetation with a focus on Pico and Terceira Islands. Despite their ecological importance, and prevalence in native vegetation, knowledge of Azorean bryophyte diversity and physiology are still insuficcient, and need further analysis. Thus, the major goals of this study are to describe the diversity and distribution of bryophytes along a complete elevational gradient in Azorean native ecosystems and to quantify the water holding ability of characteristic species, laying the foundations for a complete quantification of one of the most important roles bryophytes play in ecosystems.

The specific aims of this work are:

To identify and characterize the Azorean vegetation regarding bryophytes along an elevational gradient on Pico Island;

To characterize and quantify the Absolute Water Content of 14 bryophyte' species, commonly found on Azorean native vegetation;

To assess the *in situ* hydration status (Field Water Content and Relative Water Content) of common bryophyte species in three native vegetation types on Terceira Island during one year.

The first pages of thesis present the subject and introduce the basis for the rest of the study. The thesis is divided into four chapters. The first chapter describes the vegetation of Pico Island regarding bryophytes flora. An investigation of bryophyte community structure was done along the elevational gradient of the island. Bryophyte' communities growing on rock, soil, humus, dead wood and trees (bark and leaves) were sampled and subjected to multivariate analysis. The second, descriptive, chapter provides information about the bryophyte species selected for the eco-physiological studies presented in Chapters 3 and 4. Six species from division Marchantiophyta (class Jungermanniopsida) and eight from division Bryophyta (Classes Sphagnopsida, Polytrichopsida and Bryopsida) were selected to represent the most common and abundant bryophytes of native Azorean vegetation, not only to achieve a good representation of the bryophytes of the system, but also ensuring that the populations were able to sustain the collecting pressure. A brief information about morphology, reproduction strategy, colonization and conservation status, ecological data, distribution in the Azores and detailed photographies are presented in this chapter. Chapters 3 and 4 showcase experimental studies, with the above mentioned 14 bryophyte species; these studies were performed on Terceira Island (2014 – 2016). Chapter 3 characterizes and quantifies the ability of selected bryophytes to retain water through different pathways (external and internal) and presents the maximum ability of each species to hold water (Absolute Water Content). Chapter 4 investigates a year-long *in situ* variation of the hydration level of selected bryophytes, from three native vegetation stands. Finally, a general discussion integrates the new ideas proposed along the chapters and draws some conclusions. Supplementary information for chapters 1, 3 and 4 is given in Appendixes. Two Annexes, based on material published during the elaboration of this work are also included in this document. Annex 1, portrays the description of the vascular plant communities found on Pico MOVECLIM transect while Annex 2, includes the description of a new moss record found in Pico Island for the Azores during this work.