Structure and applications of BRYOTRAIT-AZO, a trait database for Azorean bryophytes

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Abstract – Trait databases are invaluable sources of information in ecological studies exploring the links between species traits and their surrounding environment. While digital vascular plant trait databases are already numerous, sets of bryophyte trait data are not equally available online. To help fill in this gap, we present the BRYOTRAIT-AZO database, a trait dataset for the Azorean bryoflora which aims to gather and facilitate access to all the published morphological information for the archipelago's bryophytes. As an example of its applications we examined the variation of moss leaf size, orientation and nerve extension along Terceira Island's elevational gradient, testing hypothesis related with trait presence and function. We identified a shift from mosses with twisted and shorter but longly costate leaves at lower elevation to mosses with longer untwisted leaves, with short or absent nerves at higher ground. These changes reflect the transition from sunnier, warmer and drier conditions at low elevation to shadier, cooler and damper settings at the island summit, in accordance with the hypothesis that smaller, twisted and longly costate leaves are better adapted to more xeric environments. As exemplified, this database can be a valuable tool for future studies at a regional or even a global scale, coupling functional data with bryophyte distribution information to identify trait roles on ecosystem functioning, but also general diversity and species co-occurrence patterns and community assembly rules.

Elevational gradient / functional traits / hornworts / liverworts / mosses / Macaronesia

INTRODUCTION

Botany, much like other biological sciences, is becoming a data-rich field (Marx, 2013). As a result, there's an increasing need for ways of storing, accessing and analyzing vast amounts of plant data (Howe *et al.*, 2008). For this purpose, digital databases seem to be the answer, as they store data in a computer-readable form, allowing it to be easily accessed, shared and updated, as well as directly used in computer-based analysis (Zou *et al.*, 2015).

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Digital standardized databases primarily arose to accommodate biomedical data (such as the Protein Data Bank in 1971, containing information on protein structures) (Attwood *et al.*, 2011), and nowadays are mainly used in research areas such as phylogenetics and the so-called "omics" sciences (genomics, proteomics and metabolomics) (Tariq & Niaz, 2011; Zou *et al.*, 2015) allowing for significant scientific progress in these fields.

Among plant datasets, trait databases are numerous (see, for example, Ollivier *et al.*, 2007; Kleyer *et al.*, 2008; Kattge *et al.*, 2011a) and most are built from primary data (collected firsthand), be it observational or experimental. Kattge *et al.* (2011b) proposed a general structure for such datasets, with trait value entries being accompanied by additional geographical and environmental information (covariates) to facilitate interpretation and standardization. However, databases compiled from secondary (bibliographic) data sources (see Hill *et al.*, 2004, 2007) seldom have the option of including covariate data, unless it was originally documented and is provided in the literature being consulted. This is a limitation but not necessarily a drawback, since the requirements of a database depend on its purpose (Kattge *et al.*, 2011b). If the aim is mainly to characterize the species–trait matrix for a given region, the dataset does not need to describe intraspecific variability, focusing instead on interspecific differences using the species' mean state per trait.

As environmental changes result in variation on the ecological forces acting locally as filters, species are positively or negatively selected by having or lacking certain adaptive characteristics (Bresson *et al.*, 2011), also known as functional traits. These functional traits, as defined by Pérez-Harguindeguy *et al.* (2013: 169), are "any morphological, physiological or phenological feature, measurable for individual plants, at the cell to the whole-organism level, which potentially affect its fitness or its environment".

Several botanical studies have pointed out key plant traits that appear to be strongly related with performance, such as plant size (Dubuis *et al.*, 2013; Pescador *et al.*, 2015), leaf traits (Sim-Sim *et al.*, 2004; Dubuis *et al.*, 2013; Read *et al.*, 2013), seed mass (Dubuis *et al.*, 2013) or plant life-form (McIntyre & Lavorel, 2001). Many of these are based on trait data collected along elevational gradients, as these provide ample and gradual variation on several abiotic factors along relatively short distances (Grytnes & McCain, 2007).

Bryophytes (Divisions Anthocerotophyta, Marchantiophyta and Bryophyta), being mainly ectohydric plants, tend to rely on water and nutrient transport along the plant's external surface, thus having high moisture requirements (Tuba *et al.*, 2011), exacerbated by their dependence on water for fertilization (Vanderpoorten & Goffinet, 2009). As a result, most features linked with bryophyte fitness have to do with desiccation tolerance, as is patent in the works of Watson (1914a, 1914b), where approximately 40 traits (such as life form, leaf shape and arrangement on stem or presence of non-chlorophyllous cells) are associated with survival under conditions of water deficit. Aside from adaptation to xerophytic conditions, studies have also linked bryophyte trait variation with other environmental factors. Soil pH and grazing pressure proved to influence bryophyte adaptive strategies (life strategy and growth form) and reproduction-related traits (such as sexual condition, spore size and asexual reproduction) in alpine environments in southern Norway (Austrheim *et al.*, 2005). Differences in microhabitat irradiance showed correlation with variation in leaf and cell morphological traits (such as cell size, cell wall thickness and costa size) for Hawaiian bryophytes (Waite & Sack, 2010). However, despite the publication of some compilations of distribution data and/or species ecological preferences for European taxa (Düll, 1984, 1992; Dierssen, 2001), these findings are not translating

in the emergence of online digital bryophyte trait datasets, with the exception of BRYOATT (Hill *et al.*, 2007), a compilation of attributes of the British and Irish bryoflora taxa, largely derived from literature.

In this context we intend to 1) present the BRYOTRAIT-AZO database (available online at http://islandlab.uac.pt/software/ver.php?id=26), a comprehensive trait dataset for the Azorean bryoflora that, in a first phase, aims to gather all the published morphological information for the archipelago's bryophyte taxa and 2) to exemplify possible applications of the dataset, examine the variation of moss leaf morphology with respect to its size, orientation and nerve extension along Terceira Island's elevational and climatic gradient, testing hypothesis related with the presence of the traits in the moss community and their functions for the plants.

METHODOLOGY

The BRYOTRAIT-AZO database

Geographical range: the Azorean archipelago

The Azorean archipelago, composed by nine main islands and some inhabited islets of volcanic origin, is situated in the North Atlantic Ocean between the latitudes 36°55′ and 39°43′ N and the longitudes 24°46′ and 31°16′ W, approximately 1600 km west of mainland Portugal (França *et al.*, 2003). The islands, with a total land surface of 2325 km^2, are aligned according to a W/NW-E/SE axis and clustered in three groups: (1) the western group, composed by Flores and Corvo; (2) the central group, with Faial, Pico, São Jorge, Graciosa and Terceira and (3) the eastern group, comprising São Miguel and Santa Maria islands. Maximum elevation ranges from 402 m in Graciosa to 2351 m in Pico island, with several islands reaching more than 1000 m a.s.l. (Forjaz, 2004).

The climate in the archipelago is temperate oceanic, with small average thermal amplitudes (13-14°C in February and 23-24°C in August), high humidity values and abundant rainfall, increasing from east to west as solar radiation decreases (Azevedo *et al.*, 2004). These longitudinal gradients in rainfall and irradiance are mirrored along each island's elevational gradient, and both are known to influence the distribution of vascular plants and bryophytes between and within the islands (Sjögren, 2003). Additionally, the archipelago's native vegetation has been considerably affected by human activities during the last 600 years, leading to its gradual replacement with pastureland and exotic forest (Gaspar *et al.*, 2008; Triantis *et al.*, 2010).

Bryophyte data sources

Data was compiled from more than 50 sources, ranging from books to journal articles and electronic floras (all discriminated in a datasheet of the database file), with particular emphasis on works such as "The liverwort flora of the British Isles" (Paton, 1999), "The Moss Flora of Britain and Ireland" (Smith, 2004), the "Identification Keys to the Liverworts and Hornworts of Europe and Macaronesia" (Schumacker & Váňa, 2005) and the illustrated handbooks of mosses, liverworts and hornworts of the Iberian Peninsula and the Balearic Islands (Casas *et al.*, 2006, 2009).

The primary source of taxonomic and regional distribution information was the ATLANTIS 3.1 database, a compilation of all published and unpublished (e.g. herbaria) data on the distribution of terrestrial and marine biodiversity on a small scale grid (500 m × 500 m UTM cells) for the Azorean archipelago (Borges *et al.*, 2010a) (accessible online at http://www.atlantis.angra.uac.pt/atlantis).

The BRYOATT database (Hill *et al.*, 2007) was also an invaluable source of data, since many species are common among the Azores and Britain. Five trait fields shared between the two databases (gametophyte length, life form, vegetative propagules, sexual condition and spore size) were filled with BRYOATT data; nonetheless, when in possession of different trait values from Iberian-Macaronesian or Azorean literature, such as Casas *et al.* (2006, 2009) or Gabriel *et al.* (2011), these were preferred to the former in order to account for possible regional adaptations.

A case study: climatic variation and moss leaf morphology in Terceira Island

Terceira's climate with elevation

In Terceira, an increase in elevation is accompanied by a linear decrease both in solar radiation, due to an increase in cloud cover as a result of orography (Magarreiro, 2011), and in temperature, while resulting in a linear increase in relative humidity and a more or less regular increase in rainfall (Azevedo *et al.*, 2004). These gradual shifts in climatic variables from a sunnier, warmer and drier environment at low elevation to a shadier, cooler and damper setting at the island summit are accompanied by shifts in the vascular species (Dias *et al.*, 2005; Coelho *et al.*, 2016) and in the bryoflora, with certain species restricted to lower or higher grounds (Gabriel *et al.*, 2011).

Taxa and traits

As mosses are the most speciose phyla of bryophytes in the island, with 207 species, from which 134 are acrocarps, 60 are pleurocarps and 13 are cladocarps, we look at these three moss groups and assess the elevational variation of some aspects of their leaf morphology, namely their leaf length, the extension of their leaf nerve or costa and the twisted or untwisted orientation of their leaves. Leaf size has proven to vary along spatial and climatic gradients in order to optimize water-use efficiency, with larger leaves being favored by shade and low temperature, both for vascular plants (e.g. Parkhurst & Loucks, 1972; Hamann, 1979; Ackerly *et al.*, 2002; Peppe *et al.*, 2011; Guerin *et al.*, 2012) and for bryophytes (Waite & Sack, 2010). In costate mosses, measures of leaf length and nerve length appear to correlate positively, with longer leaves accommodating longer costae (Waite & Sack, 2010); however, considering not the actual length of the nerve (an absolute value) but a qualitative assessment of its extension across the length of the leaf (a relative value, e.g. spreading for ¼ or ¾ of the leaf length), the pattern might be different. Excurrent nerves, extending beyond the tip of the leaf into structures like hyaline hairpoints, are characteristic of xerophytic environments (Watson, 1914a; Ah-Peng *et al.*, 2014) that favor taxa with shorter leaves. So, relatively speaking, shorter leaves tend to have extended nerves while longer leaves tend to have short nerves. Lastly, the spirally twisted orientation of dried acrocarpic moss leaves forms efficient capillaries and exposes almost exclusively their distal part, which is usually equipped with xerophytic adaptations such as hairpoints, curved margins, bistratosity or greater density of papillae (Watson, 1914a; Guerra *et al.*, 1992). Weighing this information together with the climatic elevational data, we hypothesize that, for Terceira Island,

an increase in elevation should result in a shift from mosses with twisted and shorter leaves with extended nerves at lower elevation to mosses with longer untwisted leaves, with short or even absent nerves at higher elevation.

Data analysis

In order to delimit Terceira's elevational gradient, the island's 1021 m elevation was divided into 20 equal horizontal bands of 51 m ([0-51] m, [51-102] m, [102-153] m, etc.), hereafter named b01 to b20. To allocate the assemblage of Terceira's 207 mosses along that same gradient, a total of 4099 distribution records were gathered from the ATLANTIS 3.1 database (Borges *et al.*, 2010b), after excluding all dubious entries (without sampling date or collected in undefined locations) and all record duplicates (further details in Henriques *et al.* 2016, in press).

Using the trait data available on the BRYOTRAIT-AZO database we examined trait variation with elevation for three leaf traits, representing the three types of variables present in the dataset: continuous (maximum leaf length; expressed in mm), categorical (leaf nerve) and binary (leaf orientation). For leaf nerve extension we considered three different values: absent for nerveless leaves, short when the nerve extends for less than half leaf length and long when it extends for half or more than half of the leaf length (including in this category percurrent and excurrent nerves). Leaf orientation is considered twisted if the dried leaves are contorted and curled in on themselves and untwisted if they are not. For the continuous variable, trait value per band was considered as the average of maximum leaf length for all acrocarpic mosses present in that band. For the binary and categorical traits, we calculated the frequency of each trait value as the percentage of mosses per band exhibiting said value, thus creating a measurement independent of richness.

Following a generalized trend in ecological studies (e.g. Lomolino, 2001; Kessler *et al.*, 2011), we employed Terceira island's elevational gradient as a surrogate of some climatic components, such as temperature and precipitation. We then checked for correlations between trait value frequency and elevation using least squares linear regressions, with the coefficient of determination (R^2) indicating how well the linear model fits the variability of the response data around its mean (0 - no fit at all; 1 - perfect fit) and p-values indicating if the fit is statistically significant (significance level = 0.05).

RESULTS

The BRYOTRAIT-AZO database

Database structure

The database is named after "Bryophytes" and "Traits" and includes the three first letters of the archipelago it pertains to (in this case, the Azores). It includes information for the five hornworts (Division Anthocerotophyta), the 165 liverworts (Division Marchantiophyta) and the 318 mosses (Division Bryophyta) currently referred to the Azores (Gabriel *et al.*, 2010) and is divided into five main sections: 1. Taxonomy and nomenclature; 2. Distribution and native status; 3. Rarity; 4. Adaptive strategies and 5. Morphology. They are briefly presented in the following subsections.

Taxonomy and nomenclature

The taxonomic classification and nomenclature of all taxa from Division to subspecies follows Söderström *et al.* (2016) for liverworts and hornworts and Gabriel *et al.* (2010) for mosses, updating it with information for six species newly recorded for the archipelago since the book's publication, namely the liverwort *Cololejeunea schaeferi* Grolle (Ellis *et al.*, 2015a) and the mosses *Antitrichia curtipendula* (Hedw.) Brid. (Ellis *et al.*, 2015b), *Bryum gemmiferum* R. Wilczek & Demaret, Didymodon cordatus Jur. (both in Ellis *et al.*, 2013a), *Didymodon umbrosus* (Müll. Hal.) R.H. Zander (Ellis *et al.*, 2013b) and *Rhynchostegiella litorea* (De Not.) Limpr. (Ellis *et al.*, 2011).

Distribution & native status

The taxa's European distribution is presented according to the categories defined in the BRYOATT database (Hill *et al.*, 2007), adapted from Hill & Preston (1998). Each taxon is assigned to a latitudinal biome category, corresponding to the major biome in which it is found, and an eastern limit longitudinal one, corresponding to the maximum of the taxa's eastern distribution in Europe.

Regionally, both the distribution in the archipelago and the native status follow Gabriel *et al.* (2010). Occurrence in each of the nine Azorean islands is given, from the western to the central group, using the following symbols: COR - Corvo; FLO - Flores; FAI - Faial; PIC - Pico; GRA - Graciosa; SJG – São Jorge; TER - Terceira; SMG - São Miguel; SMR - Santa Maria. Native status can take the following values: AZ endemic, if the taxon is endemic of the Azores, meaning that it occurs only in the Azores, as a result of either speciation events (neo-endemics) or extinction of the mainland populations (palaeo-endemics); MAC endemic, if the taxon is endemic of Macaronesia, meaning that its distribution is restricted to the Azores, Madeira, the Canary Islands and/or Cape Verde archipelagos; EUR endemic, if the taxon is endemic of Europe, with its distribution restricted to continental Europe and Macaronesia and INT for introduced taxa, thought to occur in the archipelago as a result of human activities.

Rarity

The IUCN conservation status of the Azorean species is presented according to the assessment of the European Committee for Conservation of Bryophytes (ECCB, 1995; Dierssen, 2001). An updated evaluation of species distributions and threat assessment is in progress (Hodgetts, 2015), using new Red Data List categories not considered in the previous work. Keeping to these new categories and referring to the older ones between brackets when direct correspondence is not available, species appear labeled as: DD when data deficient; EN when endangered; VU when vulnerable and LR when lower risk, adding in this last category an (R) for species previously known as rare, (RT) for regionally threatened and (T) for threatened.

Adaptive strategies

Resorting to the use of Glime's (2013a, 2013b) terminology, in this section we grouped information on life strategies, life forms and growth forms.

During (1979) defined six life strategy categories: fugitives, colonists, perennial stayers, short-lived shuttles, annual shuttles and long-lived shuttles, which he later updated to seven with the addition of "dominants", also adding sub-categories to the colonist (pioneer and ephemeral colonist) and perennial stayers (competitive and stress tolerant perennial) strategies (During, 1992), thus resulting in a total of 11 categories and sub-categories that we considered for our database. Following Glime (2013a), we grouped these strategies into R (fugitives, colonists, annual shuttles and short-lived shuttles) and K strategies (long-lived shuttles, perennials and dominants).

According to Mägdefrau (1982), life form refers to the shape of shoot assemblages taken together with their branching pattern and direction of growth, which can be modified by the characteristics of the plant's surrounding environment (e.g. cushion, mat, dendroid) while growth form refers to the structure of a plant's individual shoot, which is determined genetically (e.g., thalloid, acrocarpous, pleurocarpous).

Morphology

The morphological units characterized in the database can be spores or belong either to the gametophyte or sporophyte generation and are categorized accordingly (Fig. 1). For the gametophyte generation, two development stages are considered, namely protonema and gametophore, each subject to characterization, as well as seven different structures of the gametophore stage. For the sporophyte generation, three structures are characterized: the foot, the setae and the capsule.
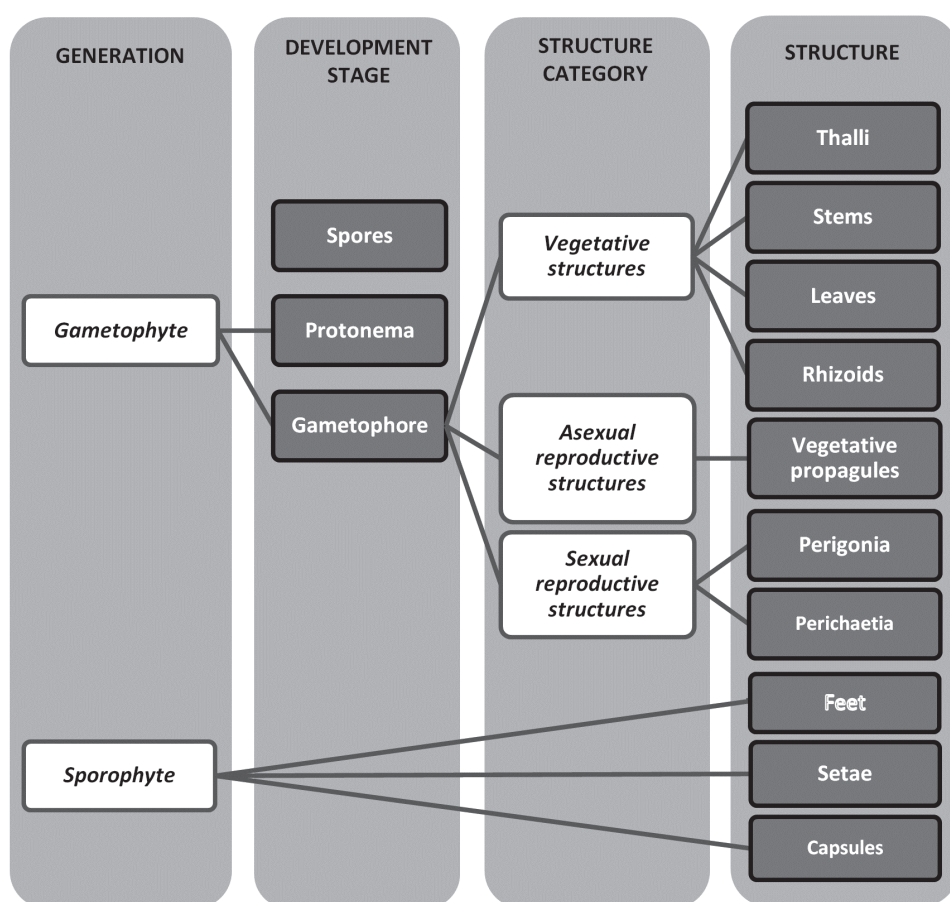

Fig. 1. Categorization of the morphological units considered in the database. Only the development stages and structures in dark grey boxes are described.

Not all taxa display all possible structures (e.g. thalloid taxa have no leaves and foliose taxa have no thallus), so not all database fields are filled. Leaves are the only structures sub-divided into different types, namely stem leaves, branch leaves and underleaves. Furthermore, some structures are not only characterized as a whole but additionally divided into sub-structures, such as the leaf lobules, the stem paraphyllias or the capsule operculum, all individually described as well.

Relevant morphological units are characterized by means of a set of 40 possible variables related with their presence, position, numbers, persistence, colour, size and structure (all described thoroughly and exemplified in a datasheet of the database file). Once again, not all variables apply to all morphological units, and some apply solely to a single unit, as is the case of spore polarity or leaf divergence.

Terceira's case study

Overall, all three traits vary along Terceira's gradient according to our initial premise. Leaf length increases almost linearly with elevation, not only for all mosses taken together ($R^2 = 0.82$; $p < 0.001$) but also for acrocarps ($R^2 = 0.89$, $p < 0.001$) and pleurocarps ($R^2 = 0.77$, $p < 0.001$) alone. For cladocarps, the increase is not statistically significant. Of the two main groups, acrocarps show the steepest increase in leaf length, ranging from 3.1 mm at low elevation to 7.6 mm at the island's summit (Fig. 2).
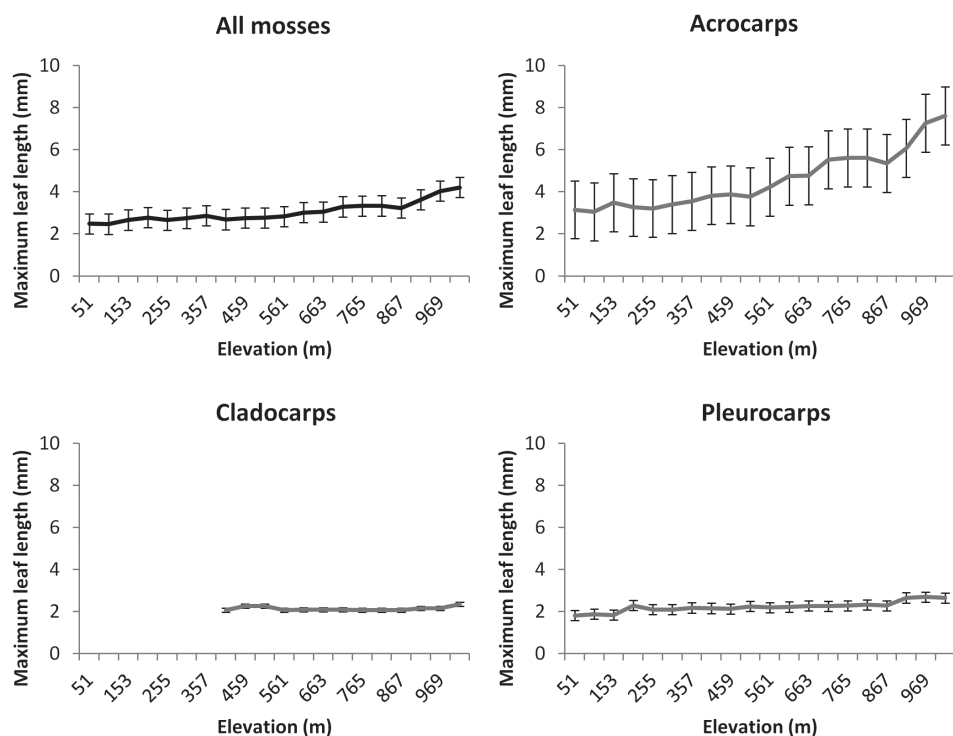

Fig. 2. Variation of maximum leaf length (mm) per 51 m wide band for all mosses and for each moss group (acrocarps, cladocarps and pleurocarps) along Terceira's elevational gradient, with vertical bars representing the standard deviation.

All mosses

All mosses

Acrocarps
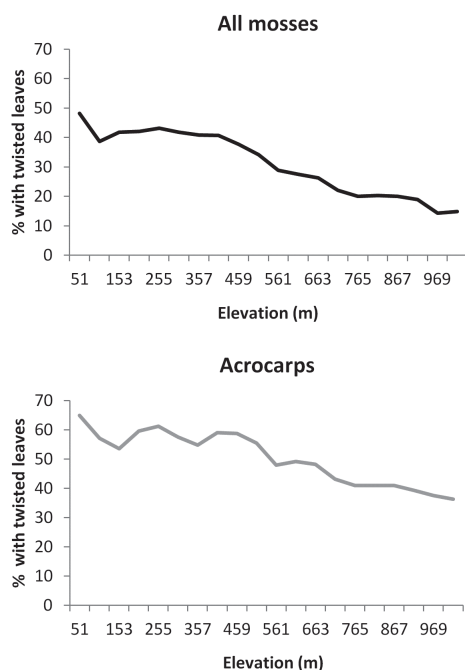

Pleurocarps

■ absent ■ short ■ long

Fig. 3. Percentage of taxa per 51 m wide band exhibiting twisted leaves along Terceira's elevational gradient both for all mosses and acrocarps alone.
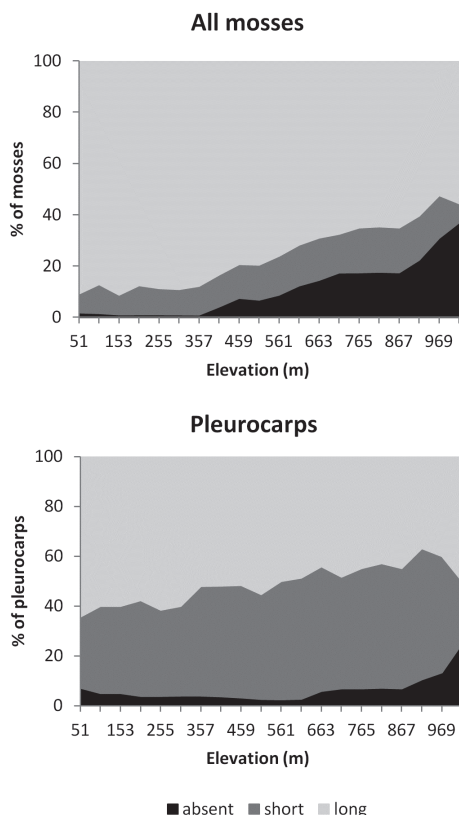
Fig. 4. Percentage of mosses and pleurocarps per 51 m wide band according to leaf nerve extension.

As for leaf orientation, the percentage of mosses with twisted leaves decreases with elevation ($R^2 = 0.93$, $p < 0.001$), from around 50% in the lowlands to 15% at the top of the island. This adaptation is exclusive to acrocarps ($R^2 = 0.87$, $p < 0.001$) (Fig. 3).

Lastly, leaf nerve extension decreases along the gradient, with almost half the taxa of the two upper bands having short nerved or nerveless leaves, while in the lowlands species with leaf nerves extending for more than half leaf length comprise around 90% of the moss bryoflora (Fig. 4). All cladocarps have nerveless leaves, and all acrocarps have long nerved leaves. The frequency of mosses with nerveless or short-nerved leaves increases significantly along the gradient ($R^2 = 0.86$; $p < 0.001$ and $R^2 = 0.43$; $p < 0.01$, respectively) the same applying for pleurocarps alone ($R^2 = 0.36$; $p < 0.01$ and $R^2 = 0.24$; $p < 0.05$, respectively). On the contrary, the frequency of taxa with long leaf nerves decreases significantly with elevation both when all mosses ($R^2 = 0.94$; $p < 0.001$) and only pleurocarps ($R^2 = 0.80$; $p < 0.001$) are examined.

DISCUSSION

Using both the BRYOTRAIT-AZO and ATLANTIS databases, along with information about climatic variation along Terceira's elevational gradient, we examined the applicability of our data in testing hypothesis for leaf trait function using the Island's moss flora. All of the three leaf traits we investigated for the island's moss flora showed patterns of variation with elevation that coincided with our initial hypothesis of a shift from lowland communities where the majority of mosses present xerophytic adaptations to high elevation communities (maximum elevation 1021 m) where most taxa lack these same adaptations.

This shift can be explained by the island's climatic gradients. Leaf length increases and nerve extension decreases with elevation, reflecting the presence of taxa with shorter leaves with long nerves in the sunnier, warmer and drier lowlands and taxa with longer leaves with short or absent nerves in the shaded, cooler and moister mountainous areas. Smaller leaves have less available surface for water loss during desiccation periods, a limiting factor in the lowlands, while upland taxa need longer and broader leaves to be able to thrive in more shaded environments with less available solar radiation (Glime, 2007; Waite & Sack, 2010). As for leaf nerves, these function as avenues for water transport (Crandall-Stotler & Bartholomew-Began, 2007) and also stiffen the leaves, providing them mechanical support during desiccation (Guerra *et al.*, 1992; Waite & Sack, 2010) thus constituting an advantage in drier conditions, which can explain why 80% of lowland taxa have leaf nerves that extend for more than half of the leaf length.

Our results further show that the longer leaves of higher elevation mosses tend to be untwisted, not curling their blades, while the shorter leaves of the lowland taxa are, for almost half of them (48%), curled when dry which may help to limit the available surface area for water loss. The twisted orientation of leaves implies that these are contorted and curled in such a way that they form more efficient capillaries and expose, almost exclusively, their upper parts, where there are adaptations such as hairpoints, that reduce desiccation and sunlight damage (Guerra *et al.*, 1992).

As expected, we found some marked morphological differences between the three moss groups considered, linking them to specific climatic niches. Cladocarps, all belonging to the genus *Sphagnum*, show almost no variation in leaf length along their elevational distribution range, as well as lacking twisted or nerved leaves. These *Sphagnum* species thrive in relatively cold areas with humid climates (Gignac, 2001) and are presently found in Terceira only above 400 m. On the contrary, acrocarps showed signs of adaptation to more xeric conditions, with all taxa presenting leaves with long nerves and more than half of the taxa per band presenting twisted leaves, up to the middle of the gradient. These results are consistent with the fact that acrocarpic mosses, the earliest mosses to evolve (Tuba *et al.*, 2011), are considered to be more drought-resistant than pleurocarps or cladocarps (Fletcher, 1991) and are known to gradually replace pleurocarps in regional species pools as the climate becomes drier and warmer (Varo *et al.*, 1992).

While linking trait expression with taxonomy it is important to mention that, for certain traits, despite a genetic predisposition to fall within a certain range of values, habitat seems to play a role in limiting or favoring their development (Glime, 2015). This environmental induced plasticity means that the value of certain traits can vary intraspecifically, according to the species surroundings. As an example, when studying bryophytes and lichens with an Arctic-Alpine distribution,

Watson (1925) discovered that there were preponderantly xerophytic acrocarpic mosses common to the lowlands showing variations in structure when living in moister conditions on the mountain tops. Their hyaline leaf tips, considered to be structural adaptations to xeric environments, were well developed on their characteristic lowland habitats but were less prominent or even absent at high elevation. We can reason that the same intraspecific variation can occur for the traits we examined and that a more detailed study based on locally collected data could yield sturdier results. In cases such as these, it is necessary to consider the tradeoffs between using available data and collecting it. Obtaining an accurate idea of the local elevational variation of traits with intraspecific plasticity, such as hairpoint or leaf nerve length, requires *in loco* data collection throughout the gradient, instead of relying solely on qualitative or presence/absence data provided by floras. Still, as data collection through direct observation can often be logistically and/or financially demanding, many studies (such as ours) can benefit from the availability of previously existent data, depending on their intended scale and purpose.

CONCLUSIONS

The BRYOTRAIT-AZO database is a compilation of taxonomical, distributional and morphological information for the Azorean bryoflora intended to facilitate access to scattered species data, laying the foundation for future applications like the creation of interactive online species identification keys or trait-based ecological studies exploring the links between the occurrence of traits and environmental conditions in the archipelago. Being available online in a digital format, this dataset can be easily accessed, shared, updated and directly used in computer-based analysis, such as the case study we presented.

As an example of a trait-based distributional analysis, we tested the correlation between Terceira's climatic variations along an elevational transect and three aspects of moss leaf morphology. As a result, we were able to identify an environmentally driven transition in the island from moss taxa with shorter and twisted leaves with extended nerves in the warmer and drier areas to taxa with longer, untwisted leaves with short or absent nerves in the cooler and moister areas. This shift testifies in favor of the trait function hypotheses that establish small leaves, lengthy nerves and the twisted leaf orientation typical of acrocarps as xerophytic adaptations and suggests that the taxa exhibiting these traits may be better equipped to adapt to future global warming trends. Nonetheless, intraspecific trait plasticity needs also to be taken into account if we want to accurately determine the full range of species answers to local environmental variation.

While lacking in this particular facet, the BRYOTRAIT-AZO database can still be a valuable tool for future studies with a regional (archipelago or island-level) scope of analysis, in which *in loco* data collection can prove to be financially demanding and forbiddingly time-consuming. Moreover, bryophyte data collected during previous studies, such as those conducted in several Azorean islands as part of the international MOVECLIM project (Gabriel *et al.*, 2014) can now be coupled with this dataset in order to characterize the current functional composition of the Azorean bryoflora. At a global scale, this database structure can be adapted to incorporate bryophyte trait information for other regions, such as the archipelagos of the MOVECLIM network, namely the Mascarenes, Antilles, Canaries and French

Polynesia. A set of standardized databases such as these could be very useful in studies aiming to identify general patterns of global diversity of mosses, liverworts and hornworts, shed some light on species co-occurrence patterns, community assembly rules and the role of different bryophyte traits on ecosystem functioning.

REFERENCES

ACKERLY D.D., KNIGHT C.A., WEISS S.B., BARTON K. & STARMER K.P., 2002 — Leaf size, specific leaf area and microhabitat distribution of chaparral woody plants: Contrasting patterns in species level and community level analyses. *Oecologia* 130: 449-457.

AH-PENG C., FLORES O., WILDING N., BARDAT J., MARLINE L., HEDDERSON T.A.J. & STRASBERG D., 2014 — Functional Diversity of Subalpine Bryophyte Communities in an Oceanic Island (La Réunion). *Arctic, antarctic and alpine research* 46(4): 841-851.

ATTWOOD T.K., GISEL A., ERIKSSON N.-E. & BONGCAM-RUDLOFF E., 2011 — Concepts, Historical Milestones and the Central Place of Bioinformatics in Modern Biology: A European Perspective. *In*: Mahdavi M.A. (ed.), *Bioinformatics - trends and methodologies*. Rijecka, InTech, pp. 3-39.

AUSTRHEIM G., HASSEL K. & MYSTERUD A., 2005 — The role of life history traits for bryophyte community patterns in two contrasting alpine regions. *The bryologist* 108: 259-271.

AZEVEDO E.B., RODRIGUES M.C. & FERNANDES J.F., 2004 — O Clima dos Açores. Climatologia *In*: Forjaz V.H. (ed.), *Atlas básico dos Açores*. Ponta Delgada, Observatório Vulcanológico e Geotérmico dos Açores, pp. 25-48.

BORGES P.A.V., COSTA A., CUNHA R.T., GABRIEL R., GONÇALVES V., MARTINS A.M.F., MELO I., PARENTE M., RAPOSEIRO P., RODRIGUES P., SANTOS R.S., SILVA L., VIEIRA P. & VIEIRA V., 2010a — *Listagem dos organismos terrestres e marinhos dos Açores*. Cascais, Princípia Editora.

BORGES P.A.V., GABRIEL R., ARROZ A.M., COSTA A., CUNHA R.T., SILVA L., MENDONÇA E., MARTINS A.M.F., REIS F. & CARDOSO P., 2010b — The Azorean Biodiversity Portal: An internet database for regional biodiversity outreach. *Systematics and biodiversity* 8: 423-434.

BRESSON C.C., VITASSE Y., KREMER A. & DELZON S., 2011 — To what extent is altitudinal variation of functional traits driven by genetic adaptation in European oak and beech?. *Tree physiology* 31: 1164-1174.

CASAS C., BRUGUÉS M., CROS R.M. & SÉRGIO C., 2006 — *Handbook of mosses of the Iberian Peninsula and the Balearic Islands*. Barcelona, Institut d'Estudis Catalans.

CASAS C., BRUGUÉS M., CROS R.M., SÉRGIO C. & INFANTE M., 2009 — *Handbook of liverworts and hornworts of the Iberian Peninsula and the Balearic Islands*. Barcelona, Institut d'Estudis Catalans.

COELHO M.C.M., ELIAS R.B., KLUGE J., PEREIRA F., HENRIQUES D.S.G., ARANDA S.C., BORGES P.A.V., AH–PENG C. & GABRIEL R., 2016 — Long–term monitoring across elevational gradients (II): vascular plants on Pico Island (Azores) transect. *Arquipelago. Life and marine sciences* 33 (in press).

CRANDALL-STOTLER B.J. & BARTHOLOMEW-BEGAN S.E., 2007 — Morphology of Mosses (Phylum Bryophyta). *In*: Flora of North America Editorial Committee (ed.). *Flora of North America - North of Mexico*, *Volume 27*, *Bryophytes*, *Part 1*. New York, Oxford, Oxford University Press, pp. 3-13.

DIAS E., MENDES C., MELO C., PEREIRA D. & ELIAS R.B., 2005 — Azores central islands vegetation and flora field guide. *Quercetea* 7: 123-173.

DIERSSEN K., 2001 — Distribution, ecological amplitude and phytosociological characterization of European bryophytes. *Bryophytorum bibliotheca* 56: 1-289.

DUBUIS A., ROSSIER L., POTTIER J., PELLISSIER L., VITTOZ P. & GUISAN A., 2013 — Predicting current and future spatial community patterns of plant functional traits. *Ecography* 36: 1158-1168.

DÜLL R., 1984 — Distribution of the European mosses. *Bryologische Beiträge* 5: 1-232.

DÜLL R., 1992 — Indicator values of mosses and liverworts. *Scripta geobotanica* 18: 175-214.

DURING H.J., 1979 — Life Strategies of Bryophytes: A Preliminary Review. *Lindbergia* 5: 2-18.

DURING H.J., 1992 — Ecological classifications of bryophytes and lichens. *In*: Bates J.W. & Farmer A.M. (eds.), *Bryophytes and Lichens in a Changing Environment.* Oxford, Clarendon Press, pp. 1-31.

ECCB, 1995 — *Red Data Book of European Bryophytes*. Trondheim, ECCB.

ELLIS L.T., BEDNAREK-OCHYRA H., OCHYRA R., ARANDA S.C., COLOTTI M.T., SCHIAVONE M.M., DULIN M. V, ERZBERGER P., EZER T., KARA R., GABRIEL R., HEDENÄS L., HOLYOAK D.T., ÓDOR P., PAPP B., SABOVLJEVIĆ M.S., SEPPELT R.D., SMITH V.R., SOTIAUX A., SZURDOKI E., VANDERPOORTEN A., ROOY J. V & ZARNOWIEC J., 2011 — New national and regional bryophyte records, 26. *Journal of bryology* 33: 66-92.

ELLIS L.T., ARANDA S.C., ASTHANA A.K., BANSAL P., NATH V., SAHU V., BAYLISS J., ASTHANA G., SRIVASTAVA S., YADAV S., BRUGUÉS M., CANO M.J., DULIN M. V, FUDALI E., FUERTES E., GABRIEL R., PEREIRA F., SILVA J.A.F., GRADSTEIN S.R., HÁJKOVÁ P., HÁJEK M., HERAS P., INFANTE M., LEBOUVIER M., MARKA J., NEWSHAM K.K., OCHYRA R., PANTOVIC J., SABOVLJEVIĆ M.S., PHEPHU N., ROOY J. VAN, PHILIPPOV D.A., PORLEY R.D., PUCHE F., SCHÄFER-VERWIMP A., SEGARRA-MORAGUES J.G., SÉRGIO C., SMITH V.R., STEFANUT S., VÁŇA J. & WIGGINTON M.J., 2013a — New national and regional bryophyte records, 37. *Journal of bryology* 35: 290-305.

ELLIS L.T., ASTHANA A.K., GUPTA R., NATH V., SAHU V., BEDNAREK-OCHYRA H., OCHYRA R., CYKOWSKA B., ARANDA S.C., FISCHER E., GABRIEL R., GÓRSKI P., GREMMEN N., HESPANHOL H., KURBATOVA L.E., SMITH R.I.L., LONG D.G., BELL D., MOGRO F., SÉRGIO C., GARCIA C.A., STOW S., MARTINS A., SMITH V.R., VÁŇA J., & VANDERPOORTEN A. 2013b — New national and regional bryophyte records, 34. *Journal of bryology* 35: 62-70.

ELLIS L.T., ALEFFI M., BAKALIN V.A., BEDNAREK-OCHYRA H., BERGAMINI A., BEVERIDGE P., CHOI S.S., FEDOSOV V.E., GABRIEL R., GALLEGO M.T., GRDOVIC S., GUPTA R., NATH V., ASTHANA A.K., JENNINGS L., KÜRSCHNER H., LEBOUVIER M., NAIR M.C., MANJULA K.M., RAJESH K.P., NOBIS M., NOWAK A., PARK S.J., SUN B.-Y., PLÁŠEK V., ČÍHAL L., POPONESSI S., MARIOTTI M.G., SABOVLJEVIĆ A.D., SABOVLJEVIĆ M.S., SAWICKI J., SCHNYDER N., SCHUMACKER R., SIM-SIM M., SINGH D.K., SINGH D., MAJUMDAR S., SINGH DEO S., ŞTEFĂNUŢ S., SULEIMAN M., SENG C.M., CHUA M.S., VÁŇA J., VENANZONI R., BRICCHI E. & WIGGINTON M.J., 2015a — New national and regional bryophyte records, 42. *Journal of bryology* 37(1): 68-85.

ELLIS L.T., AH-PENG C., ARANDA S.C., BEDNAREK-OCHYRA H., BOROVICHEV E.A., CYKOWSKA-MARZENCKA B., DUARTE M.C., ENROTH J., ERZBERGER P., FEDOSOV V., FOJCIK B., GABRIEL R., COELHO M.M.C., HENRIQUES D.S.G., ILINA O. V, GIL-NOVOA J.E., MORALES-PUENTES M.E., GRADSTEIN S.R., GUPTA R., NATH V., ASTHANA A.K., KOCZUR A., LEBOUVIER M., MESTERHÁZY A., MOGRO F., MEŽAKA A., NÉMETH C., ORGAZ J.D., SAKAMOTO Y., PAIVA J., SALES F., PANDE N., SABOVLJEVIĆ M.S., PANTIVIĆ J., SABOVLJEVIĆ A.D., PÉREZ-HAASE A., COSTA D.P. DA, PLÁŠEK V., SAWICKI J., SZCZECIŃSKA J., CHMIELEWSKI J., POTEMKIN A., SCHÄFER-VERWIMP A., SCHOFIELD W.B., SÉRGIO C., SIM-SIM M., SJÖGREN S., SPITALE D., STEBEL A., ŞTEFĂNUŢ S., SUÁREZ G.M., FLORES J.R., THOUVENOT L., VÁŇA J., YOON Y.-J., KIM J.H. & ZUBEL R., 2015b — New national and regional bryophyte records, 45. *Journal of bryology* 37(4): 308-329.

FLETCHER M., 1991 — *Moss Grower's Handbook*. Berkshire, Seventy Press.

FORJAZ V.H., 2004 — *Atlas básico dos Açores*. Ponta Delgada, Observatório Vulcanológico e Geotérmico dos Açores.

FRANÇA Z., CRUZ J. V, NUNES J.C. & FORJAZ V.H., 2003 — Geologia Dos Açores: Uma Perspectiva Actual. *Açoreana* 10: 11-140.

GABRIEL R., SJÖGREN E., SCHUMACKER R., SÉRGIO C., ARANDA S.C., CLARO D., HOMEM N. & MARTINS B., 2010 — List of Bryophytes (Anthocerotophyta, Marchantiophyta, Bryophyta). *In*: Borges, P.A.V., Costa, A., Cunha, R., Gabriel, R., Gonçalves, V., Martins, A.F., Melo, I., Parente, M., Raposeiro, P., Santos, R.S., Silva, L., Vieira, P. & Vieira, V. (eds), *A list of the terrestrial and marine biota of the Azores*. Cascais, Principia, pp. 99-115.

GABRIEL R., HOMEM N., COUTO A.B., ARANDA S.C. & BORGES P.A.V., 2011 — Azorean bryophytes: a preliminary review of rarity patterns. *Açoreana* 144: 149-206.

GABRIEL R., COELHO M.M.C., HENRIQUES D.S.G., BORGES P.A.V., ELIAS R.B., KLUGE J. & AH-PENG C., 2014 — Long-term monitoring across elevational gradients to assess ecological hypothesis: a description of standardized sampling methods in oceanic islands and first results. *Arquipélago. Life and marine sciences* 31: 45-67.

GASPAR C., BORGES P.A.V. & GASTON K.J., 2008 — Diversity and distribution of arthropods in native forests of the Azores archipelago. *Arquipélago. Life and marine sciences* 25: 1-30.

GIGNAC L., 2001 — Bryophytes as indicators of climate change. *The bryologist* 104: 410-420.

GLIME J.M., 2007 — Light: Adaptations for shade. *In*: Glime J.M., *Bryophyte Ecology. Volume 1. Physiological Ecology*, Ebook sponsored by Michigan Technological University and the International Association of Bryologists. Available at www.bryoecol.mtu.edu. Accessed on 10/05/2016.

GLIME J.M., 2013a — Adaptive Strategies: Life Cycles. *In*: Glime J.M., *Bryophyte Ecology. Volume 1. Physiological Ecology*, Ebook sponsored by Michigan Technological University and the International Association of Bryologists. Available at www.bryoecol.mtu.edu. Accessed on 03/02/2016.

GLIME J.M., 2013b — Adaptive Strategies: Growth and Life Forms. *In*: Glime, J. M., *Bryophyte Ecology. Volume 1. Physiological Ecology*, Ebook sponsored by Michigan Technological University and the International Association of Bryologists. Available at www.bryoecol.mtu. edu. Accessed on 15/03/2016.

GLIME J.M., 2015 — Water relations: Leaf strategies – structural. *In*: Glime, J. M., *Bryophyte Ecology. Volume 1. Physiological Ecology*, Ebook sponsored by Michigan Technological University and the International Association of Bryologists. Available at www.bryoecol.mtu.edu. Accessed on 21/01/2016.

GRYTNES J.-A. & MCCAIN C.M., 2007 — Elevational Trends in Biodiversity. *In*: Levin S.A. (ed.), *Encyclopedia of Biodiversity*. New York, Elsevier, pp. 1-8.

GUERIN G.R., WEN H. & LOWE A.J., 2012 — Leaf morphology shift linked to climate change. *Biology letters* 8: 882-886.

GUERRA J., MARTÍNEZ-SÁNCHEZ J. & ROS R.M., 1992 — On the degree of adaptation of the moss flora and vegetation in gypsiferous zones of the south-east Iberian Peninsula. *Journal of bryology* 17: 133-142.

HAMANN O., 1979 — On Climatic Conditions, Vegetation Types, and Leaf Size in the Galapagos Islands. *Biotropica* 11: 101-122.

HENRIQUES D.S.G., BORGES P.A.V., AH-PENG C. & GABRIEL R., 2016 — Mosses and Liverworts show contrasting elevational distribution patterns in an oceanic island (Terceira, Azores): The influence of climate and space. *Journal of bryology* (in press).

HILL M.O. & PRESTON C.D., 1998 — The geographical relationships of British and Irish bryophytes. *Journal of bryology* 20: 127-226.

HILL M.O., PRESTON C.D. & ROY D.B., 2004 — PLANTATT: Attributes of British and Irish Plants - Status, Size, Life history, Geography and Habitats. Cambridgeshire, Centre for Ecology & Hydrology. Available at http://nora.nerc.ac.uk/9535/1/PLANTATT.pdf. Accessed on 21/02/2014.

HILL M.O., PRESTON C.D., BOSANQUET S.D.S. & ROY D.B., 2007 — BRYOATT: Attributes of British and Irish Bryophytes. Cambridgeshire, Centre for Ecology and Hydrology. Available at http://nora.nerc.ac.uk/1131/1/BRYOATT.pdf. Accessed on 21/02/2014.

HODGETTS N.G., 2015 — *Checklist and country status of European bryophytes – towards a new Red List for Europe*. Irish Wildlife Manuals 84, National Parks and Wildlife Service, Department of Arts, Heritage and the Gaeltacht, Ireland. Available at https://www.npws.ie/sites/default/files/publications/pdf/IWM84.pdf. Accessed on 03/04/2016.

HOWE D., COSTANZO M., FEY P., GOJOBORI T., HANNICK L., HIDE W., HILL D.P., KANIA R., SCHAEFFER M., ST PIERRE S., TWIGGER S., WHITE O., & RHEE S.Y., 2008 — Big data: the future of biocuration. *Nature* 455: 47-50.

KATTGE J., DÍAZ S., LAVOREL S., PRENTICE I.C., LEADLEY P., BÖNISCH G., GARNIER E., WESTOBY M., REICH P.B., WRIGHT I.J., CORNELISSEN J.H.C., VIOLLE C., HARRISON S.P., VAN BODEGOM P.M., REICHSTEIN M., ENQUIST B.J., SOUDZILOVSKAIA N.A., ACKERLY D.D., ANAND M., ATKIN O., BAHN M., BAKER T.R., BALDOCCHI D., BEKKER R.M., BLANCO C.C., BLONDER B., BOND W.J., BRADSTOCK R., BUNKER D.E., CASANOVES F., CAVENDER-BARES J., CHAMBERS J.Q., CHAPIN F.S., CHAVE J., COOMES D.A., CORNWELL W.K., CRAINE J.M., DOBRIN B.H., DUARTE L.D.S., DURKA W., ELSER J., ESSER G.,

ESTIARTE M., FAGAN W.F., FANG J., FERNÁNDEZ-MÉNDEZ F., FIDELIS A., FINEGAN B., FLORES O., FORD H., FRANK D., FRESCHET G.T., FYLLAS N.M., GALLAGHER R. V., GREEN W.A., GUTIERREZ A.G., HICKLER T., HIGGINS S.I., HODGSON J.G., JALILI A., JANSEN S., JOLY C.A., KERKHOFF A.J., KIRKUP D., KITAJIMA K., KLEYER M., KLOTZ S., KNOPS J.M.H., KRAMER K., KÜHN I., KUROKAWA H., LAUGHLIN D., LEE T.D., LEISHMAN M., LENS F., LENZ T., LEWIS S.L., LLOYD J., LLUSIÀ J., LOUAULT F., MA S., MAHECHA M.D., MANNING P., MASSAD T., MEDLYN B.E., MESSIER J., MOLES A.T., MÜLLER S.C., NADROWSKI K., NAEEM S., NIINEMETS Ü., NÖLLERT S., NÜSKE A., OGAYA R., OLEKSYN J., ONIPCHENKO V.G., ONODA Y., ORDOÑEZ J., OVERBECK G., OZINGA W.A., PATIÑO S., PAULA S., PAUSAS J.G., PEÑUELAS J., PHILLIPS O.L., PILLAR V.D., POORTER H., POORTER L., POSCHLOD P., PRINZING A., PROULX R., RAMMIG A., REINSCH S., REU B., SACK L., SALGADO-NEGRET B., SARDANS J., SHIODERA S., SHIPLEY B., SIEFERT A., SOSINSKI E., SOUSSANA J.-F.F., SWAINE E., SWENSON N., THOMPSON K., THORNTON P., WALDRAM M., WEIHER E., WHITE M., WHITE S., WRIGHT S.J., YGUEL B., ZAEHLE S., ZANNE A.E. & WIRTH C., 2011a — TRY - a global database of plant traits. *Global change biology* 17: 2905-2935.

KATTGE J., OGLE K., BÖNISCH G., DÍAZ S., LAVOREL S., MADIN J., NADROWSKI K., NÖLLERT S., SARTOR K. & WIRTH C., 2011b — A generic structure for plant trait databases. *Methods in ecology and evolution* 2: 202-213.

KESSLER M., KLUGE J., HEMP A. & OHLEMÜLLER R., 2011 — A global comparative analysis of elevational species richness patterns of ferns. *Global ecology and biogeography* 20: 868-880.

KLEYER M., BEKKER R.M., KNEVEL I.C., BAKKER J.P., THOMPSON K., SONNENSCHEIN M., POSCHLOD P., VAN GROENENDAEL J.M., KLIMEŠ L., KLIMEŠOVÁ J., KLOTZ S., RUSCH G.M., HERMY M., ADRIAENS D., BOEDELTJE G., BOSSUYT B., DANNEMANN A., ENDELS P., GÖTZENBERGER L., HODGSON J.G., JACKEL A.-K., KÜHN I., KUNZMANN D., OZINGA W.A., RÖMERMANN C., STADLER M., SCHLEGELMILCH J., STEENDAM H.J., TACKENBERG O., WILMANN B., CORNELISSEN J.H.C., ERIKSSON O., GARNIER E. & PECO B., 2008 — The LEDA Traitbase: a database of life-history traits of the Northwest European flora. *Journal of ecology* 96: 1266-1274.

LOMOLINO M. V., 2001 — Elevation gradients of species-density: Historical and prospective views. *Global ecology and biogeography* 10: 3-13.

MAGARREIRO C. DE L.C., 2011 — *Contribuição para o Atlas Solar dos Açores*. Master of Science Thesis. Lisbon, University of Lisbon.

MÄGDEFRAU K., 1982 — Life-forms of bryophytes. *In*: Smith A.J.E. (ed.), *Bryophyte Ecology*. London, Chapman and Hall, pp. 45-58.

MARX V., 2013 — The big challenges of big data. *Nature* 498: 255-260.

MCINTYRE S. & LAVOREL S., 2001 — Livestock grazing in subtropical pastures: steps in the analysis of attribute response and plant functional types. *Journal of ecology* 89: 209-226.

OLLIVIER M., BARALOTO C. & MARCON E., 2007 — A trait database for Guianan rain forest trees permits intra- and inter-specific contrasts. *Annals of forest science* 64: 781-786.

PARKHURST D.F. & LOUCKS O.L., 1972 — Optimal Leaf Size in Relation to Environment. *Journal of ecology* 60: 505-537.

PATON J.A., 1999 — *The liverwort flora of the British Isles*. Colchester, Harley Books.

PEPPE D.J., ROYER D.L., CARIGLINO B., OLIVER S.Y., NEWMAN S., LEIGHT E., ENIKOLOPOV G., FERNANDEZ-BURGOS M., HERRERA F., ADAMS J.M., CORREA E., CURRANO E.D., ERICKSON J.M., HINOJOSA L.F., HOGANSON J.W., IGLESIAS A., JARAMILLO C.A., JOHNSON K.R., JORDAN G.J., KRAFT N.J.B., LOVELOCK E.C., LUSK C.H., NIINEMETS Ü., PEÑUELAS J., RAPSON G., WING S.L. & WRIGHT I.J., 2011 — Sensitivity of leaf size and shape to climate: Global patterns and paleoclimatic applications. *New phytologist* 190: 724-739.

PÉREZ-HARGUINDEGUY N., DÍAZ S., GARNIER E., LAVOREL S., POORTER H., JAUREGUIBERRY P., BRET-HARTE M.S., CORNWELL W.K., CRAINE J.M., GURVICH D.E., URCELAY C., VENEKLAAS E.J., REICH P.B., POORTER L., WRIGHT I.J., RAY P., ENRICO L., PAUSAS J.G., VOS A.C., BUCHMANN N., FUNES G., QUÉTIER F., HODGSON J.G., THOMPSON K., MORGAN H.D., STEEGE H., HEIJDEN M.G.A., SACK L., BLONDER B., POSCHLOD P., VAIERETT M.V., CONTI G., STAVER A.C., AQUINO S. & CORNELISSEN J.H.C., 2013 — New handbook for standardised measurement of plant functional traits worldwide. *Australian journal of botany* 61: 167-234.

PESCADOR D.S., DE BELLO F., VALLADARES F. & ESCUDERO A., 2015 — Plant Trait Variation along an Altitudinal Gradient in Mediterranean High Mountain Grasslands: Controlling the Species Turnover Effect. *Plos One* 10: e0118876.

READ Q.D., MOORHEAD L.C., SWENSON N.G., BAILEY J.K. & SANDERS N.J., 2013 — Convergent effects of elevation on functional leaf traits within and among species. *Functional ecology* 28: 37-45.

SCHUMACKER R. & VÁŇA J., 2005 — *Identification Keys to the Liverworts and Hornworts of Europe and Macaronesia (Distribution and Status)*. Poznań, Poland, SORUS Publishing & Printing House.

SIM-SIM M., CARVALHO S. & FONTINHA S., 2004 — Diversity of Bryophytes – Useful indicators of Madeira Laurel forest conservation. *In*: Marchetti M. (ed.), *Monitoring and Indicators of Forest Biodiversity in Europe - From Ideas to Operationality*. Joensuu, Finland, European Forest Institute, pp. 247-255.

SJÖGREN E., 2003 — Azorean bryophyte communities - a revision of differential species. *Arquipélago. Life and marine sciences* 20: 1-29.

SMITH A.J.E., 2004 — *The Moss Flora of Britain and Ireland*. Cambridge, Cambridge University Press.

SÖDERSTRÖM L., HAGBORG A., VON KONRAT M., BARTHOLOMEW-BEGAN S., BELL D., BRISCOE L., BROWN E., CARGILL D.C., DA COSTA D.P., CRANDALL-STOTLER B.J., COOPER E., DAUPHIN G., ENGEL J., FELDBERG K., GLENNY D., GRADSTEIN S.R., HE X., HENTSCHEL J., ILKIU-BORGES A.L., KATAGIRI T., KONSTANTINOVA N.A., LARRAÍN J., LONG D., NEBEL M., PÓCS T., PUCHE F., REINER-DREHWALD E., RENNER M., SASS-GYARMATI A., SCHÄFER-VERWIMP A., SEGARRA-MORAGUES J., STOTLER R.E., SUKKHARAK P., THIERS B., URIBE J., VÁŇA J., WIGGINTON M., ZHANG L. & ZHU R.-L., 2016 — World checklist of hornworts and liverworts. *PhytoKeys* 59: 1-828.

TARIQ H. & NIAZ T., 2011 — Orgene: An organ based categorized human genome database. *Journal of biochemical technology* 3: 266-269.

TRIANTIS K.A., BORGES P.A.V., LADLE R.J., HORTAL J., CARDOSO P., GASPAR C., DINIS F., MENDONÇA E., SILVEIRA L.M.A., GABRIEL R., MELO C., SANTOS A.M.C., AMORIM I.R., RIBEIRO S.P., SERRANO A.R.M., QUARTAU J.A. & WHITTAKER R.J., 2010 — Extinction debt on oceanic Islands. *Ecography* 33: 285-294.

TUBA Z., SLACK N.G. & STARK L.R., 2011 — *Bryophyte ecology and climate change*. Cambridge UK, Cambridge University Press.

VANDERPOORTEN A. & GOFFINET B., 2009 — *Introduction to bryophytes*. Cambridge UK Cambridge University Press.

VARO J., GUERRA J., ZAFRA M.L. & ROS R.M., 1992 — Regression and invasion of bryophytes in the south and southeast of the Iberian Peninsula. *Biological conservation* 59: 129-131.

WAITE M. & SACK L., 2010 — How does moss photosynthesis relate to leaf and canopy structure? Trait relationships for 10 Hawaiian species of contrasting light habitats. *New phytologist* 185: 156-172.

WATSON W., 1914a — Xerophytic adaptations of bryophytes in relation to habitat. *New phytologist* 13: 149-169.

WATSON W., 1914b — Xerophytic adaptations of bryophytes in relation to habitat (continued). *New phytologist* 13: 181-190.

WATSON W., 1925 — The bryophytes and lichens of Arctic-Alpine vegetation. *Journal of ecology* 13: 1-26.

ZOU D., MA L., YU J. & ZHANG Z., 2015 — Biological databases for human research. *Genomics, proteomics & bioinformatics* 13: 55-63.