



# Aridity and coexistence with lichens and vascular plants determine the dynamics of coastal dune bryophyte communities

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## Abstract

Bryophyte communities play a vital functional role in Atlantic coastal dune ecosystems, where they contribute to soil stability, moisture retention, and nutrient cycling. However, these habitats are increasingly affected by climate change and sea level rise, with reported consequences including habitat degradation, shifts in species distributions, and the proliferation of invasive bryophyte species. To assess how bryophyte communities might respond to future climate conditions, 32 coastal dunes were studied along a latitudinal gradient on the western Atlantic coast of the Iberian Peninsula. We investigated (i) how abiotic factors related to aridity influence bryophyte cover and species composition, (ii) whether patterns of co-occurrence with vascular plants (annuals and perennials) and lichens could mitigate climate impacts, and (iii) the role of interactions between the invasive moss *Campylopus introflexus* and native species along the gradient. Our results showed that the moss community is mainly influenced by aridity and annual mean temperature (as defined in the WorldClim database), with biotic interactions playing a minor, yet significant, role. As aridity increases, total moss cover declines noticeably with no consistent patterns of facilitation or competition observed across sites. Based on these findings, we suggest that under future climate scenarios, coastal bryophyte communities are likely to suffer reductions in cover and associated ecosystem functions, with limited buffering potential through plant interactions and a northward shift in species distributions. At the same time, the spread of the exotic moss species *Campylopus introflexus*, associated with lower aridity, could also slow down. Further research is needed to better understand how these changes will affect the ecological integrity of coastal dunes, habitats already recognised as priorities for conservation.

**Keywords** Aridity · Bryophytes · Climate change · Co-occurrence patterns · Invasive species

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## Introduction

Coastal areas, although accounting for less than 15% of the Earth's surface (European Environment Agency, EEA 1999), are home to more than 60% of the worldwide population, including one-third of Europe's population (EEA 1999, 2021). These areas are of great economic and ecological value for many countries as they provide many important ecosystem services for human well-being, such as nutrient cycling, food production, habitat/shelter provision, natural barriers to erosion, water quality control and breeding grounds (Airoldi et al., 2007, Ruiz-Frau et al. 2020). According to the EEA, the extent of dune areas in Western and North-Western Europe has been reduced by 40% over the last century. This reduction is mainly related to urban development, recreational use, and reforestation which took place from the mid-1970 s. Therefore, since 1992, the marine dunes of the Atlantic, North Sea and Baltic have been considered as habitats of Community interest for conservation (Directive 92/43/EEC).

Low water availability, high salinity, nutrient-poor substrates and constant movement characterise Atlantic coastal dunes. They play a critical ecological role in stabilising and protecting coastal areas (European Commission, 2015). However, in addition to these environmental stressors, dune systems are also exposed to anthropogenic disturbances, such as trampling caused by tourism, urban development, and the spread of invasive plant species (Schlacher et al., 2008; Miller et al., 2010; Santoro et al., 2012). These pressures have a direct impact on their fragile biodiversity, which includes highly specialised flora and fauna; and are expected to intensify further under climate change (e.g. sea level rise and increased storms), expanding urban areas, and biological invasions. As a result, coastal dunes will become increasingly threatened, even to the point of disappearing in some areas (Gómez-Pina et al. 2002), leading to severe ecological and economic consequences.

Vegetation plays an important role in the formation, functioning and stability of coastal dunes, as its interaction with wind is a key process for dune development and its dynamics (Ranwell, 1972; Carter, 1995). Among dune vegetation, bryophytes are an important functional group as they can activate nutrient fixation processes, stabilise the dune surface, contribute to soil consolidation and help retain water (Murru et al. 2018). Indeed, the ecological importance of bryophytes in the structure and dynamics of Atlantic coastal dune vegetation has already been highlighted in several studies (e.g. Robbins 1953–1954; Bonnot 1971; Magnusson 1983; Jun & Rozé 2004; Murru et al. 2018). However, as a consequence of climate change and sea level rise, negative effects on dune vegetation have already been reported, such as habitat loss, changes in species distribution, and the presence of invasive bryophyte species such as *Campylopus introflexus* (Rhind et al., 2001, Mendoza-González et al. 2013; Sérgio et al. 2018). The spread of this moss has raised concern due to its ability to form dense carpets that suppress native bryophytes and lichens, altering species composition and reducing biodiversity. In addition, it can modify microhabitat conditions and soil properties, potentially affecting nutrient cycling and water dynamics (Hasse and Daniëls 2006; Sérgio et al. 2018). These impacts highlight the importance of monitoring its expansion and assessing its ecological consequences in dune ecosystems.

In environments with strong abiotic stress, such as low water availability or poor nutrient conditions, facilitative interactions between species may become especially important. Facilitation is a key biotic interaction in shaping patterns of plant diversity at fine scales (Brooker et al. 2008; Forey et al. 2010) that occurs when one plant species enhances the

germination or growth conditions of another (Forey et al. 2009). Some authors have already studied this inter-species facilitation in dune communities (e.g. Shumway 2000; Martínez 2003; Maltez-Mouro et al. 2010; Vaz et al. 2014; Doxford et al. 2013) focusing mainly on the Stress Gradient Hypothesis (SGH; Bertness and Callaway 1994). According to this SGH, facilitation and competition between species are considered important at opposite ends of stress gradients, although some authors have found competition even at high levels of environmental severity (e.g. Armas and Pugnaire 2009; Ariza and Tielborger 2011). Doxford et al. (2013), observed that there can also be extreme spatiotemporal variations in the direction of interactions, and indeed showed that facilitation or competition between bryophytes and annual plants in dunes is correlated with population growth rate: at low growth, facilitation dominates, while at high population growth, competition dominates.

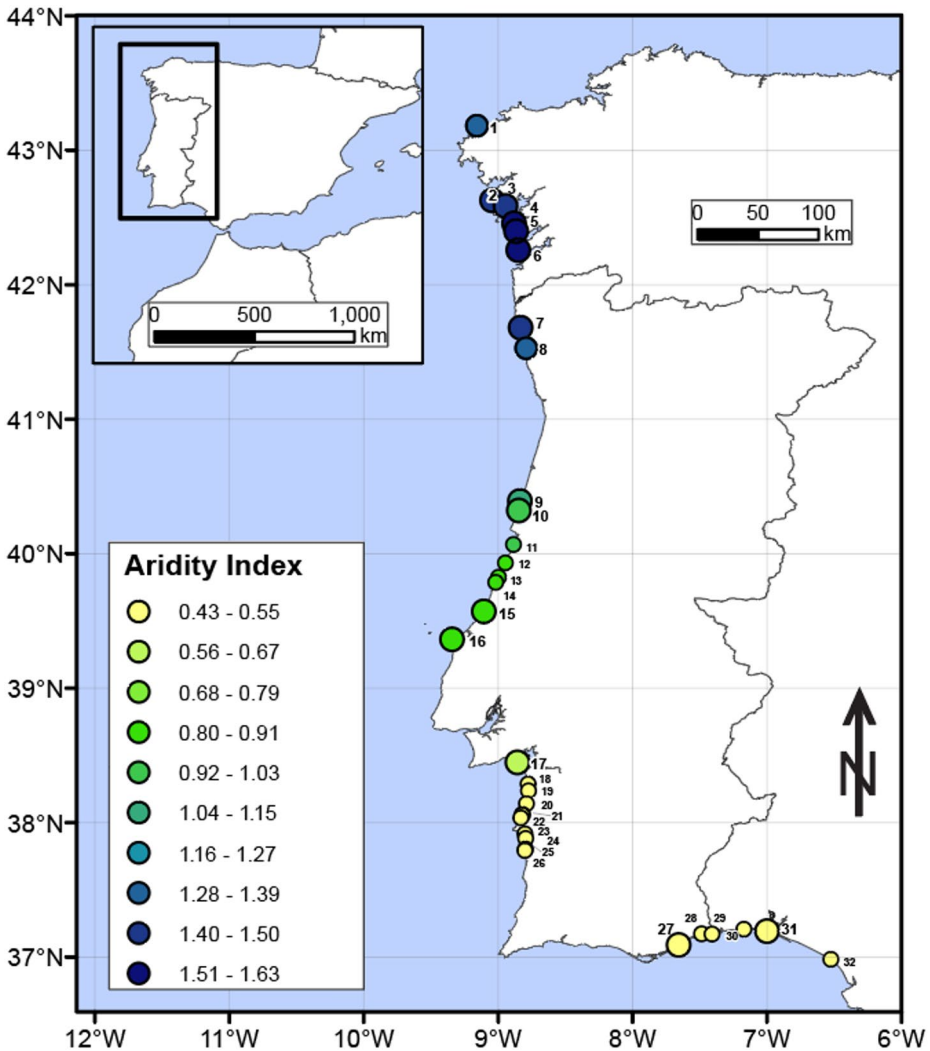
Although derived from a different ecosystem, findings by Monteiro et al. (2024) in post-fire Pyrenean oak forests suggest that bryophyte composition can be influenced by the balance between species' competitive and colonisation abilities and the surrounding vascular plant cover. While these results cannot be directly extrapolated to dune systems, they support the idea that biotic interactions may shape bryophyte communities under certain environmental stress conditions.

The methodology of this study is grounded in a space-for-time substitution to explore the potential responses of vegetation communities in coastal dune ecosystems to future climate change. Specifically, we aim to use this approach to understand how changes in aridity, predicted under various climate change scenarios, may affect these communities. Selecting sampling points along a significant latitudinal gradient on the western coast of the Iberian Peninsula facilitated the inclusion of a range of aridity conditions that we interpret as representative of future climatic scenarios characterized by increased temperatures and reduced precipitation. The validity of this approach is based on the hypothesis that the spatial variability of environmental conditions can offer an approximation of the temporal changes induced by the climate (Blois et al. 2013). Thus, the patterns we identify along this aridity gradient could give us hints about how the coverage, composition, and interactions between bryophyte species and vegetation groups might change in response to current and future climate change. To explore these potential effects of climate change, the study aims to answer the following questions: (i) How do abiotic factors related to aridity affect bryophyte cover and species composition in coastal dune systems, and what does this tell us about how they might respond to climate change in the future?; (ii) Are there consistent patterns of coexistence between bryophytes lichens, and vascular plant groups (annuals and perennials) along the aridity gradient, and could these interactions help to buffer the effects of increased environmental stress?; (iii) How does the invasive moss *Campylopus introflexus* interact with native bryophyte species along the aridity gradient, and how might these interactions shape future moss community dynamics?

## Materials and methods

### Sampling sites and method

We characterised the vegetation of coastal dunes in 32 sampling sites (SS) along the western coast of the Iberian Peninsula (Fig. 1), which covers a marked latitudinal gradient character-



**Fig. 1** Map showing the study area in the Iberian Peninsula and the location of the 32 sampling sites and the corresponding Aridity Index values (from 0.45 = more arid to 1.63 = less arid) for each Sampling Site according to Fick and Hijmans (2017). The 15 sampling sites where moss species were identified have a larger dot size

used by increasing aridity towards the south. Biogeographically, the northernmost sampling sites (SS1-SS8) fall within the Eurosiberian region, whereas the remaining sites (SS9-SS32) belong to the Mediterranean region, which is naturally drier (EEA, 2011). Bryophyte species were identified in 15 sampling sites (out of the 32 SS). The dunes correspond to grey dunes (*habitat 2130*) and, in some cases, transitional areas with sparse woody vegetation characteristic of *habitat 2250*, according to Annex I of the EU Habitats Directive (Directive 92/43/EEC). All surveys were conducted in medium-stabilised dune systems, specifically within interdunal depressions -the intermediate zone between the primary (foredunes) and

secondary dunes-. This zone is typically more protected from direct marine influence and sand movement, and is generally dominated by xerophytic shrubland communities, including species such as *Juniperus spp.* or *Corema album*. Vegetation structure within this zone varied from dense shrub patches to open mosaics with herbaceous cover and bare soil. Sampling sites ranged from 34 to 360 m from the shoreline, depending on the geomorphology of each dune system, but habitat conditions were kept as similar as possible across sites. Sampling was performed during 2017 using the point intercept method (Nunes et al. 2015): at each point, a fine rod was stuck in the ground at a 90° angle and all plant species touching the rod were recorded, by species or by vegetation group (moss, lichen, annual or perennial vascular plant). Cover estimates for individual species or groups were calculated as the proportion of points intercepted per site. In each site, we sampled 4 transects of 50 m parallels to the coastline, every 50 cm ( $n = 404$  points except for SS 7 = 303 and SS 26 = 505. In SS7 and SS26, slight adjustments were made due to the geomorphological characteristics and accessibility of the dunes. At SS26, a larger undisturbed area allowed the extension of transects up to 505 points, while in SS7, the presence of access paths reduced the available transect length to 303 points. We verified that these variations in sampling effort did not significantly affect the vegetation data or introduce bias into the main analyses. Therefore, all available data were retained to maximise site representation. In addition to vegetation, ground cover was also recorded at each point, specifically classifying the presence of bare soil. One composite soil sample was collected from each site by extracting soil from the top 20 cm at the midpoint of each transect and combining these four subsamples.

### Environmental variables

Climate and soil variables were considered to account for the effects of environmental and human disturbances on both moss cover and communities. Data of 19 bioclimatic variables and Aridity Index (AI) were extracted from <http://www.worldclim.org/> database (Fick and Hijmans, 2017) from the global aridity database (<https://cgiaresci.community/2019/01/24/global-aridity-index-and-potential-evapotranspiration-climate-database-v2/>; Trabucco and Zomer, 2009) adopted by the United Nations, respectively. Soil samples were analysed at Faculdade de Ciências da Universidade de Lisboa (Portugal): pH and soil organic matter content (OM) in the laboratory of Ecology, and total nitrogen (N) and total carbon (C) in SIIAF (Stable Isotopes and Instrumental Analysis Facility).

### Soil analysis

Composite soil samples were air-dried and sieved to 2 mm before laboratory analysis at the University of Lisbon. Soil pH was determined both in water (pH H<sub>2</sub>O) and in potassium chloride solution (pH KCl). Organic matter (OM) content was quantified as a percentage of the total sample. Total nitrogen (N) was measured using the Kjeldahl method. Total carbon (C) content was determined by combustion analysis using an elemental analyzer.

### Data analysis

The main gradients of moss composition were described with a NMDS ordination performed on a matrix of sampling sites by species with the function metaMDS of R Package

vegan (Oksanen et al. 2013). Only the 15 SS where moss species were identified were included in the ordination analysis. Data were submitted to Wisconsin double standardization (species are first standardized by maxima and then sites by site totals). The Bray and Curtis method was used to measure the distance/similarity between sites. To select the main factor affecting moss composition, we analysed the relationship between the NMDS ordination and the potential explanatory variables through vector fitting (e.g. Chozas et al. 2015). Then, those potential explanatory variables that were found to be significantly correlated (post-hoc) with the NMDS ordination axes were overlaid (McCune and Grace 2002; Oksanen 2009). For each set of potential explanatory variables studied (climate and soil) multicollinearity was handled by dropping collinear covariates (Graham 2003; Zuur et al. 2010) when correlated at  $|\text{Spearman } r| > 0.8$  (Dormann et al. 2012), remaining Aridity Index, Annual Mean Temperature, Mean Diurnal Range, Isothermality, Temperature Seasonality, Minimum Temperature of the Coldest Month, Mean Temperature Driest Quarter, Precipitation Seasonality, pH, N, C and OM. This approach also allowed us to analyse the role of lichen, perennial, annual and vascular vegetation (e.g. annuals + perennials) covers in determining moss communities. Generalized Additive Models (GAMs) were performed to characterise the relationships of the most important variables conditioning the species composition gradients identified from NMDS analyses with the cover of the mosses using the *mgcv* software package (Wood 2006).

To determine the relationship between biotic (bare soil, lichen, perennial, annual and vascular vegetation (e.g. annuals + perennials) and environmental variables Spearman correlations were performed. In addition, to study vegetation co-occurrence patterns, we used data on the presence/absence at each intercept point of the transects of each plant group total cover (i.e. mosses, lichens, perennials and annuals) for the 32 study sites, and also each moss species cover for the 15 sites where the species were identified. Only species or plant group data with at least 5% coverage per site were considered. Thus, four incidence matrices were obtained for each sampling site, corresponding to the four transects carried out. These four matrices were joined to configure a single incidence matrix per beach. The incidence matrices were constructed using data from each individual point sampled every 50 cm along the transects, rather than aggregated at the transect level. This fine spatial resolution (~ 404 points per site) allowed us to assess co-occurrence at scales where ecological interactions are more likely to occur. To detect non-random patterns of co-occurrence between species and functional groups, we applied the C-score index (Stone and Roberts 1990). The C-score measures the tendency of species pairs to segregate across sites, by quantifying the number of checkerboard units in a presence–absence matrix: high C-scores indicate strong segregation (species rarely co-occur), while low values suggest aggregation (species often co-occur). The degree of spatial aggregation of vegetation types and moss species was assessed through the standardized effect size (SES), calculated following Gotelli and McCabe (2002). SES expresses how much the observed C-score deviates from the mean of randomly simulated matrices, standardised by the standard deviation of simulations. SES values greater than 0 indicate spatial segregation among species and species types, while smaller values indicate spatial aggregation (Maltez-Mouro et al. 2010). Following Gotelli and McCabe (2002), SES values greater than +2 are typically interpreted as significant segregation (suggesting competitive exclusion), while values below -2 indicate significant aggregation (potential facilitation). Values between -2 and +2 are generally not considered different from random expectations. Correlations and their significance were obtained with

the `cor.test` function of the stats package (RStudio Team 2018), and the C-score was performed with the `cooc_null_model` function of the EcoSimR package (Gotelli et al. 2015). All statistical analyses were performed with the statistical program RStudio (RStudio Team 2018).

## Results

### Effects of aridity-related abiotic factors on bryophyte cover and composition

In general, total bryophyte cover showed a positive correlation with climate variables related to precipitation and humidity (i.e., higher cover in wetter conditions) and a negative correlation with variables related to temperature and evapotranspiration (i.e., lower cover in warmer and drier conditions). Regarding the aridity index (AI), which increases as aridity decreases (i.e., higher values indicate wetter conditions), bryophyte cover was positively correlated with AI, meaning that moss cover increased as conditions became less arid.

Correlation analyses were limited to *Campylopus introflexus*, *Hypnum cupressiforme* and *Tortella squarrosa*, as the other moss species identified were too scarce to allow for a meaningful statistical analysis. The coverage of *C. introflexus* showed positive correlations with moisture-related variables and negative correlations with temperature-related variables, similar to the total bryophyte coverage. In the case of *P. squarrosa*, the only abiotic variable that showed a significant correlation was soil nitrogen content, and this association was also positive. As for biotic factors, *P. squarrosa* did not show a clear relationship with any of them. In contrast, total bryophyte cover was associated with litter and lichen cover, and *C. introflexus* with litter, annual plants and perennials. The correlation coefficients ( $r$ ) and their significance levels ( $p$ ) are detailed in Table 1.

The absolute frequencies of mosses, lichens, annual plants, perennial plants, and different species of mosses at each SS are listed in the supplementary table S1. There seems to be a general pattern in which perennial plants predominate in terms of absolute frequency, while annual plants tend to appear less frequently. Mosses were found at 27 of the 32 sampling points, and lichens (all belonging to the genus *Cladonia*) at 18 points. Regarding moss species, a total of 11 bryophyte species were identified at the 15 sampling points where species-level identification was carried out. Only the moss *Tortella squarrosa* (common in unshaded dune habitats) is present at all 15 sampling points, while invasive *Campylopus introflexus* is present at 10 of 15, with a wide variation in frequency for both. The rest of the moss species showed very restricted distributions and low frequencies: 5 of the 11 species were found at a single SS and 2 *spp.* appeared at two SS.

### Patterns of co-occurrence between bryophyte and vascular plant groups

Co-occurrence analysis using presence/absence data for the four main vegetation groups (mosses, lichens, annuals, and perennials) showed that there were few statistically significant interactions ( $p < 0.05$ ) (Fig. 2). Specifically, facilitation between mosses and lichens was observed at 3 of the 27 SS, while patterns suggesting competition between bryophytes and perennial plants were found at 2 sites and with annual plants at 1 site. At the 15 SS where moss species were identified, we also explored species-level co-occurrence between

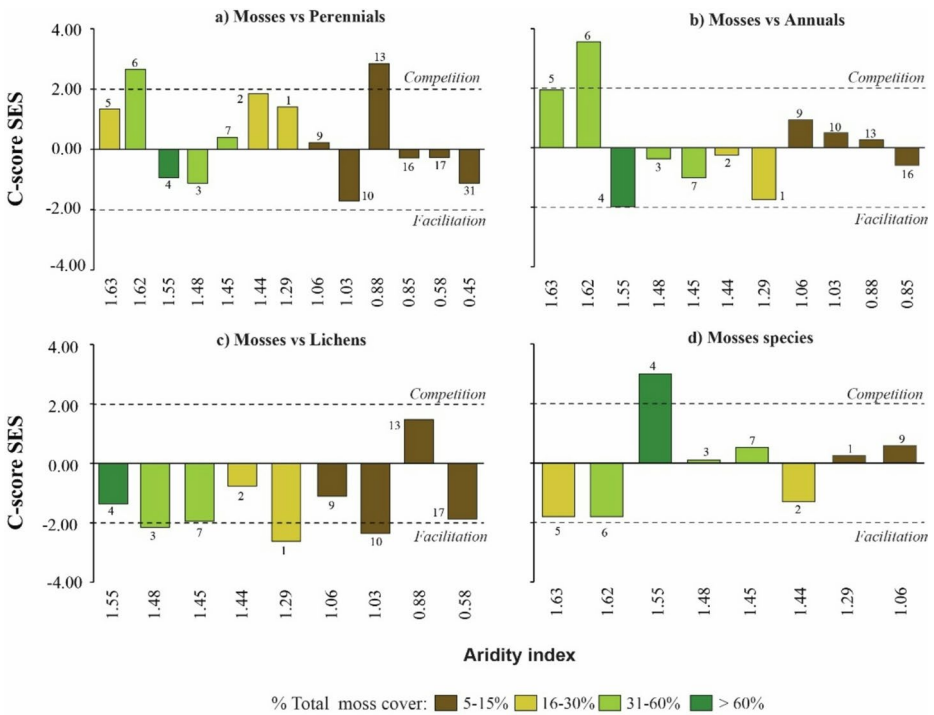
**Table 1** Correlation coefficients (Spearman  $\rho$ ) between total moss cover, species richness, *Campylopus introflexus*, *Hypnum cupressiforme* and *Tortella squarrosa* cover and climate, edaphic and biotic variables. T<sup>a</sup> = temperature and p = precipitation. Vascular vegetation = annuals + perennials. Significances in bold: \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$

Climate variables	32 SS	15 SS			
	Moss cover	Species richness	<i>C. introflexus</i> cover	<i>H. cupressiforme</i> cover	<i>T. squarrosa</i> cover
Aridity Index	<b>0.72***</b>	<b>0.51*</b>	<b>0.92***</b>	0.247	0.18
Annual Mean T <sup>a</sup>	−0.65***	−0.53*	−0.84***	−0.061	−0.14
Mean Diurnal Range	−0.68***	0.10	−0.05	−0.034	−0.39
Isothermality	−0.24	0.38	0.21	−0.356	−0.34
T <sup>a</sup> Seasonality	−0.55**	−0.02	0.04	−0.166	0.04
Max T <sup>a</sup> Warmest Month	−0.75***	−0.17	−0.50	0.024	−0.03
Min T <sup>a</sup> Coldest Month	−0.01	−0.47	−0.49	−0.057	0.22
T Annual Range	−0.73***	0.60	−0.09	−0.101	−0.34
Mean T <sup>a</sup> Wettest Quarter	−0.60***	−0.56*	−0.82***	−0.304	−0.08
Mean T <sup>a</sup> Driest Quarter	−0.67***	−0.39	−0.57*	−0.308	−0.07
Mean T <sup>a</sup> Warmest Quarter	−0.67***	−0.51*	−0.33	−0.288	0.20
Mean T <sup>a</sup> Coldest Quarter	−0.59***	−0.59*	−0.81***	−0.271	−0.06
Annual P	<b>0.67***</b>	<b>0.55*</b>	<b>0.82***</b>	0.312	0.09
P Wettest Month	<b>0.68***</b>	<b>0.55*</b>	<b>0.75***</b>	0.393	0.14
P Driest Month	<b>0.70***</b>	<b>0.51*</b>	<b>0.92***</b>	0.247	0.18
P Seasonality	−0.71***	<b>0.54*</b>	−0.80***	−0.146	−0.34
P Wettest Quarter	<b>0.67***</b>	<b>0.53*</b>	<b>0.80***</b>	0.389	0.12
P Driest Quarter	<b>0.68***</b>	<b>0.52*</b>	<b>0.92***</b>	0.247	0.18
P Warmest Quarter	<b>0.68***</b>	<b>0.51*</b>	<b>0.92***</b>	0.247	0.17
P Coldest Quarter	<b>0.61***</b>	<b>0.51*</b>	<b>0.79***</b>	0.372	0.05
<b>Edaphic variables</b>					
% N in soil	<b>0.47*</b>	−0.18	−0.16	0.09	<b>0.55*</b>
% C in soil	<b>0.49*</b>	0.07	0.34	−0.13	0.40
% Organic matter in soil	0.32	0.30	0.15	0.162	0.26
Soil pH	0.04	0.20	0.16	−0.11	−0.14
<b>Biotic variables</b>					
Bare soil	−0.31	−0.47	−0.42	−0.32	−0.22
Plant Litter	−0.51**	−0.09	−0.65*	0.15	0.12
Lichens	<b>0.48**</b>	0.09	−0.08	0.12	0.12
Vascular vegetation	−0.15	0.28	−0.23	0.08	0.05
Annual Plants	0.15	0.22	<b>0.58*</b>	0.34	0.07
Perennial Plants	−0.14	0.05	−0.54*	−0.14	−0.24

*Campylopus introflexus* and *Pleurochaete squarrosa*. Only one of the 15 sites showed a significant pattern of segregation, suggesting competition.

### NMDS ordination of bryophyte species composition

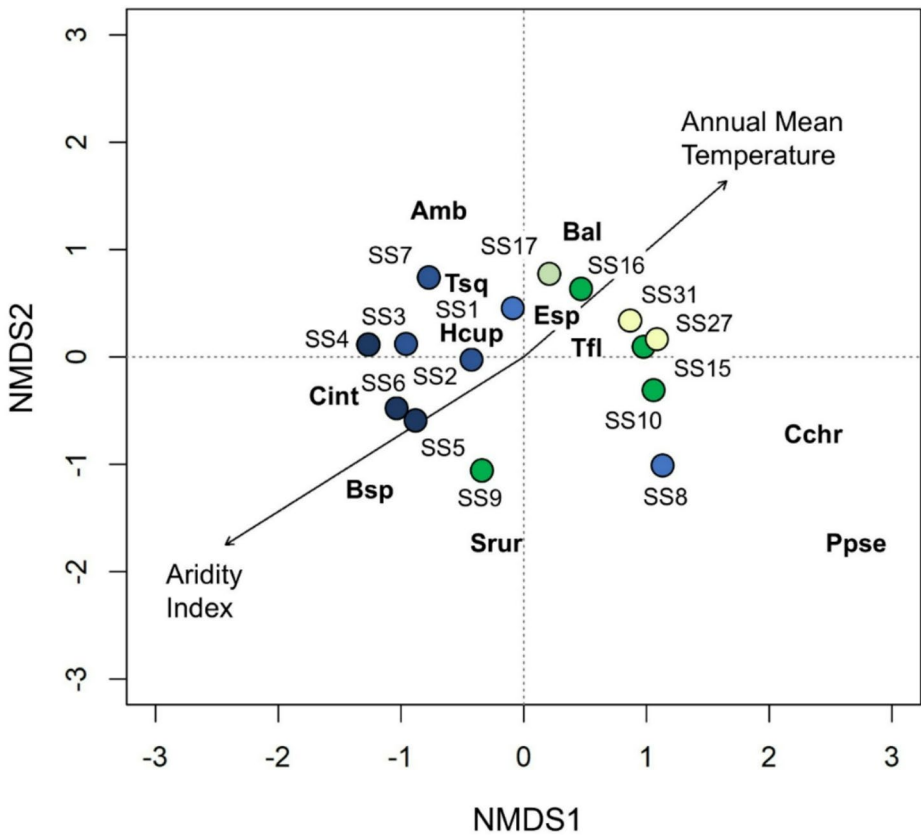
The NMDS analysis (2D, stress = 0.12; Fig. 3) showed that bryophyte species composition was primarily structured along a gradient of aridity and bryophyte cover, with other environmental variables showing no significant influence. Among the tested factors, only aridity and bryophyte cover were significantly associated with NMDS axis 1 (AI,  $r^2 = 0.67$



**Fig. 2** C-score for co-occurrence patterns and standardized effect size (SES) for each vegetation group (i.e., mosses, lichens, perennials, and annuals), and moss species along the aridity gradient with at least 5% cover of each group/species. The aridity index is between 1.63 (less arid) and 0.45 (more arid). The different colours of the columns show the percentage of total moss cover. The dashed lines show the value above which competition between groups/species (> 2) or facilitation (< -2) is considered to exist

$p < 0.0001$ ) albeit together with Annual Mean Temperature (AMT,  $r^2 = 0.40$   $p < 0.05$ ). Other variables such as soil C/N ratio, plant litter, or vascular plant cover did not show significant correlation with the first two axes, despite showing correlations with bryophyte cover in other analyses.

To better understand how aridity influences moss cover in relation to the compositional gradients identified in the NMDS, we applied Generalized Additive Models (GAMs). The GAMs confirmed a significant relationship between the aridity index (AI) and both (i) total moss cover (Deviance explained = 71.8%,  $p < 0.001$ ,  $k = 1.917$ ,  $n = 32$ ) and (ii) the cover of *C. introflexus* (Deviance explained = 60.5%,  $p < 0.01$ ,  $k = 1.805$ ,  $n = 15$ ). No significant relationship was detected between AI and the cover of the other two most abundant species (*Hypnum cupressiforme* and *Tortella squarrosa*). These results are shown in Fig. 4.

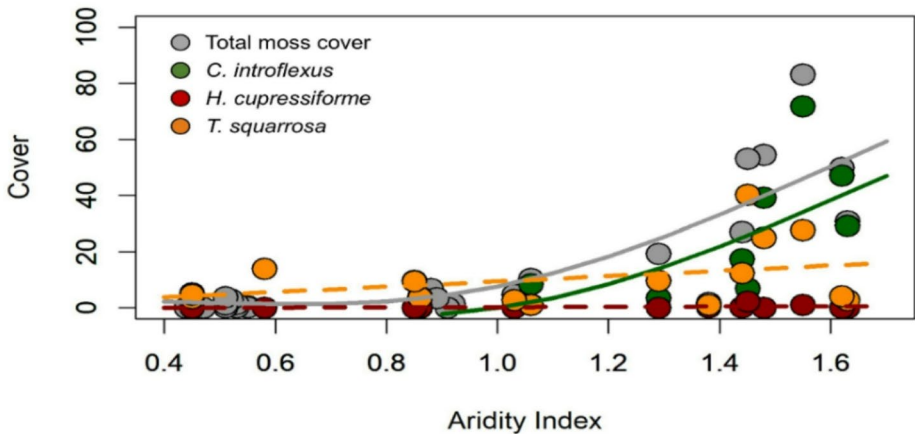


**Fig. 3** Axes 1 and 2 of the 2-dimensional non-metric multidimensional scaling ordination of sampling sites (SS) based on moss cover (NMDS1 and NMDS2). The final stress was 0.12. Blue, green, pale green and yellow circles are study sampling sites according to their Aridity Index (see Fig. 1). Arrows reflect the main gradients identified by the ordination: Aridity Index ( $r^2 = 0.67$   $p < 0.001$ ) and Annual Mean Temperature ( $r^2 = 0.40$   $p < 0.05$ ). Species codes: Amb: *Amblystegiaceae*; Bal: *Brachytecium albicans*; Bsp: *Bryum* sp.; Cchr: *Campyliadelphus chrysophyllus*; Cint: *Campylopus introflexus*; Esp: *Eurhynchium* sp.; Hcup: *Hypnum cupressiforme*; Ppse: *Ptychostomum pseudotriquetrum*; Srur: *Syntrichia ruralis*; fl.: *Tortella flavovirens*; Tsq: *Tortella squarrosa*

## Discussion

### Effects of aridity on bryophyte cover and composition

Our results show that coastal dune moss community dynamics in coastal dunes along the Western Iberian Atlantic Coast are strongly determined by aridity and temperature. Although mosses are present in most of the studied sites, their cover and diversity are low and decline towards the most arid and warm southern areas. Previous studies on Atlantic European coastal dunes (e.g., Jun & Rozé, 2004; Callaghan and Ashton 2007; Provoost et al. 2011) reported a high abundance and species richness of mosses across sites in different countries such as Poland, Denmark, Northern Ireland, the United Kingdom, the Netherlands, Belgium, and France. However, these studies characterised bryophyte communities at local or



**Fig. 4** Relationships between the Aridity Index and (i) the percentage of total cover of mosses along the 32 study sites (in grey), and (ii) the percentage of cover of *C. introflexus* (in dark green), *H. cupressiforme*, (in dark red) and *T. squarrosa* (in orange) in the 15 sampling sites where moss species were identified. Solid lines represent the main trend of a GAM with statistical significance, while dashed lines represent no statistically significant relationships

regional scales, and were mostly conducted within the Eurosiberian biogeographical region, without systematically analysing environmental gradients such as aridity or latitude. Thus, while our findings differ in terms of moss diversity levels, they reflect the influence of a broad biogeographical and climatic gradient, rather than discrepancies within a single climatic zone.

Despite this information, our results are consistent with moss physiology, as their poikilohydric character makes them better adapted to humidity conditions than to drought and heat (Furness and Grime 1982), showing a lower temperature optimum than higher plants (Glime 2007). Biogeographically, only the northernmost sampling sites (first eight SS) fall within the Eurosiberian region, while the rest belong to the Mediterranean region, which is characteristically drier (EEA, 2011). This environment would likely lead to higher evaporation rates, shorter periods of photosynthetic activity and more rapid desiccation, which has already been shown to affect moss growth rates and abundance (He et al. 2016). Therefore, this decrease in species number and frequency towards the south (with the subsequent increase in aridity) is expected. Indeed, moss diversity peaks northwards compared with other plant groups (Mateo et al. 2016; Ronquillo et al. 2023). This biogeographical gradient can act as an environmental filter, limiting not only moss abundance but also excluding less stress-tolerant species from more arid sites, contributing to community simplification.

An alternative explanation for these results could be the uncontrolled urbanisation that has taken place in the coastal areas of southern Europe since the beginning of the century, leading to the loss of vegetation and the disappearance of 70% of the European coastal dune systems (Brown and McLachlan 2010; Gómez-Pina et al. 2002). However, we did not find any relationship between land-use or perturbation and the cover and diversity of mosses in our study area (data not shown). Even so, it is worth noting that the recovery of bryophytes in disturbed dune systems may vary greatly depending on aridity (Kammann et al. 2022; Ladrón de Guevara and Maestre 2022). Moreover, the weak relationship between environ-

mental variables and species composition in the NMDS (Fig. 3), despite strong correlations with total moss cover, suggests that variation in composition could be influenced by unmeasured local factors, stochastic colonisation or historical processes.

### Co-occurrence patterns and plant–bryophyte interactions

These dynamics in the bryophyte community could be even more extreme under climate change conditions (Mendoza-González et al., 2013). Nonetheless, according to the literature, biotic interactions with other plants could help avoid losing bryophyte diversity and abundance in the context of a changing climate and stressful environment (e.g. Ingerpuu et al. 2005; Brooker et al. 2008). The Stress Gradient Hypothesis (SGH) suggests that facilitation occurs under high-stress conditions and competition under low-stress conditions (Bertness and Callaway 1994), while Doxford et al. (2013) found that under these stress conditions, biotic interactions may also depend on population growth rate. However, our data can only partially be explained by SGH (Bertness and Callaway 1994) and based on total cover (not growth rate), competition between mosses and annuals was only found in one of the eleven SS, located at one end of the aridity gradient (SS6, Fig. 4) and with intermediate-high vegetation cover (30–60%).

Competition between mosses and perennials also occurs in this SS6, as well as in SS13, located in the middle of the gradient, with low plant cover (5–15%, Fig. 4). On the other hand, mosses and lichens cover show a positive association, as is often observed due to their role as colonising organisms in the early stages of primary succession in dune systems (e.g. Jun & Rozé, 2004). Therefore, facilitation interactions between them would be expected to be found independently of the aridity gradient. Even so, we only found facilitation between mosses and lichens in 3 of the 9 SS (Fig. 4): in SS1 and SS3, the northernmost study sites, with the rather low aridity values and intermediate-high cover (i.e. 30–60% and >60% respectively); and SS10, with intermediate aridity values and low cover (between 5 and 15%).

The scarcity of significant interactions may also be due to the spatial resolution of our sampling method. With a 50 cm spacing between points, small-scale facilitating or competitive interactions, which are common in bryophyte communities (Ingerpuu et al. 2005), may be missed. In many sites, the low frequency of both mosses and vascular groups may limit the opportunity for coexistence, meaning that the potential for interaction simply does not materialise, rather than being absent. Moreover, co-occurrence models such as the C-score or probabilistic methods (e.g. Veech) require a minimum level of species occurrence to reliably detect patterns. When species or groups are too rare, true ecological interactions may go undetected, not because they don't exist, but because the data are too sparse to reveal them (Griffith et al., 2016).

Beyond these methodological limitations, ecological variability may also contribute to the weak or inconsistent interaction patterns observed. In particular, the irregular distribution and coverage of vascular vegetation at different sites (Table 1) may reduce opportunities for consistent biotic interactions to arise, especially in dune systems with strong spatial heterogeneity. Vaz et al. (2020), already reported the lack of relationship between the diversity patterns of bryophytes, lichens and vascular plants in dunes with contrasting coastal dynamics, regardless of biogeographic context or anthropogenic pressures. Furthermore, the joint effects of regional and local environmental gradients may be buffering or masking

these biotic processes that may be occurring at finer scales as outlined by Brooker et al. (2008) and Vaz et al. (2015). Consequently, in these few interactions found, all the hypotheses proposed by previous studies on the existence of competition/facilitation both at the extremes and at intermediate values of the aridity gradient, as well as those dependent on total vegetation cover, are fulfilled, with no common pattern along the gradient. Given the limited bryophyte-plant vascular interactions, it is unlikely that these interactions will help mitigate potential bryophytes losses caused by climate change events in the future.

### Interactions between *Campylopus introflexus* and native moss species

As regards the increase of alien species aggravated by climate change (Cogoni et al. 2011), the invasive moss *Campylopus introflexus* only appears when the AI increased and was not found in the 5 SS of maximum aridity (Table S1, Fig. 3). This is consistent with its significantly positive correlations with rainfall, and negative correlations with temperature variables (Table 1). These results suggest that *C. introflexus* is likely unable to compete effectively with perennial species, while it can coexist with herbaceous annuals due to a lower competition for light and nutrients (Corbin and D'Antonio 2004). This dynamic is especially pronounced in scenarios where perennial species are present in high densities and annuals in low densities, as found in our study sites (e.g., Coomes et al. 2002).

Overall, these findings confirm that *C. introflexus*, as an invasive species, prefers open areas or habitats associated with disturbance, characterised by sparse vegetation and strong anthropogenic influence (see Sérgio et al. 2018). The spread of *C. introflexus* across European coastal dune systems has been well documented, particularly in disturbed habitats in countries such as the United Kingdom, the Netherlands, and Germany (Hasse and Daniëls 2006), reinforcing its association with human-impacted environments.

Out of the 8 SS where co-occurrence between *T. squarrosa* (very common in coastal dunes) and *C. introflexus* was analysed, only in SS4 was competition between them found (Fig. 4). This SS has the highest cover of the two species and is at the extreme minimum aridity (Table 1; Fig. 3). Based on these results, we confirm that SGH is met but conditional on optimal conditions for both species. In SS where the number of occurrences of one or both species is low, it is likely that the coverage required for competitive interactions is not achieved. As noted above, low co-occurrence frequencies may limit the ability to detect interactions using these models, which could explain the absence of significant segregation in other sites.

### Conclusions

The dynamics of the dune moss community along the western Iberian Atlantic coast are mainly determined by aridity and temperature while biotic interactions with other vegetation groups, such as vascular plants and lichens, play a secondary role. In a scenario of ongoing climate change and increasing drought, these moss communities are likely to reduce their total cover in coastal dunes. The limited role of interactions with other plants groups suggests that they will not be able to buffer this loss. In the future, the areas suitable for most moss species are expected to move northwards, following regions with lower drought intensity and milder climates. As a result, interactions between moss species could

become more important in the more humid Eurosiberian region, while becoming rarer in the drier Mediterranean zone. At the same time, the spread of the invasive moss *Campylopus introflexus* may also change. Although this species is usually associated with perturbed or open habitats, its presence appears to be highly dependent on humidity, and it was not found in the driest sites in our study. This suggests that increased aridity in the future could limit its expansion, at least in the southern part of its potential range. Despite these findings, more research is needed to better understand how projected climate trends will change the structure of bryophyte communities and their ecological functions in these fragile coastal habitats that are of conservation Community concern.

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## Declarations

**Competing interests** The authors declare no competing interests.

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