SEX-SPECIFIC RESPONSES TO CLIMATE CHANGE IN UNISEXUAL BRYOPHYTES

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Communicated by David Hawksworth.

ABSTRACT

Global climate change represents a threat to biodiversity. While we have gained knowledge about impacts on ranges shifts across ecosystems and species, we lack understanding at the infraspecific or population level. Unisexual poikilohydric species may be especially susceptible to global warming as they often exhibit spatial segregation of sexes, driven by physiological and morphological adaptations to specific habitats. Here, we use Ensemble of Small Models (ESMs) to investigate how climate change may differentially affect the distribution range of each sex in four unisexual bryophyte species. We focused on two threatened Macaronesian endemics (*Exsertotheca intermedia*, *Frullania polysticta*) and two, primarily restricted to Macaronesia and western Europe (*Frullania teneriffae*, *Porella canariensis*). All species are predicted to lose over 95% of their climatically suitable areas in the Macaronesia by 2100. However, the Atlantic coastal fringe of Europe and northwestern Africa are predicted to serve as refugia for both male and female Macaronesian endemics. A northward shift in suitable areas is particularly evident for *Frullania teneriffae*, with both sexes expected to expand into areas such as Ireland and the United Kingdom. In contrast, *Porella canariensis* exhibited sex-specific responses on the continent, where female plants showed a clear northward shift into new habitats, while male plants are predicted to face near-extinction in Iberian Peninsula due to reduced environmental tolerance. This study underscores the susceptibility of Macaronesian bryophytes to climate change, emphasizes the necessity of sex-specific strategies in conservation planning, and identifies refugia may facilitate long-term survival, provided Macaronesian bryophytes track climate change in North Atlantic.

KEYWORDS : CONSERVATION · MACARONESIA · ENDEMICS · FEMALE AND MALE PLANTS · ENSEMBLE OF SMALL MODELS

Introduction

Rapid climate change poses a significant threat to sessile organisms like plants, leading to range shifts or increased extinction risks (Hanz et al. 2023; Andrzejak et al. 2025; Zhang et al. 2025). Predicting how plant species will respond to climate change has become a priority for global conservation efforts to guide effective conservation strategies (Thuiller et al. 2008; Mkala et al. 2023). Plants respond to environmental changes through their lifehistory traits, wherein their eco-physiological and reproductive attributes can determine the plant species' fate against historical environmental changes (Becklin et al. 2016). Specifically, sexual systems have been identified as drivers of diversification and distribution in the plant realm (Wang et al. 2020; Ma et al. 2024). Since temperature and precipitation strongly influence plants' geographic spread, evolutionary shifts and extinction rates (Parmesan 2006; Weiskopf et al. 2020), the response of these species to future climate change remains uncertain.

Unisexual (i.e. also known as dioecious, which is defined as separate male and female individuals) plant species may be particularly vulnerable to the effects of climate change, especially in bryophytes, where around 60–70% of species possess unisexual gametophytes (Bisang et al. 2025). This vulnerability arises from their spatial segregation of the sexes, reinforced by sex-specific physiological and morphological adaptations to different environmental conditions (Stark and McLetchie 2006; Bisang et al. 2015). In angiosperms, sex ratio biases have been observed in over 50% of studied unisexual species, with a strong male bias (Barrett et al. 2010; Field et al. 2013). In contrast, bryophytes exhibit an even more pronounced bias of almost 60%, but toward females (Bisang and Hedenäs 2005; Boquete et al. 2023). This imbalance potentially poses a serious threat to bryophytes, where for instance 22.5% of European species are at an elevated risk of extinction (Hodgetts et al. 2019; Zanatta et al. 2020; van Zuijlen et al. 2024). Despite their globally high cold tolerance (Patiño and Vanderpoorten 2018), bryophytes are particularly sensitive to warming, with temperature optima lower than those of angiosperms (He et al. 2016; Perera-Castro et al. 2020). As climate change accelerates, its impact on unisexual bryophyte species might become increasingly critical.

Several ecological hypotheses have been proposed to explain skewed sex ratios towards the female in bryophytes. One key pattern is that female bias increases in warmer, wetter environments, potentially due to the higher resource demands of sporophyte production in females or greater male sensitivity to wet conditions (Bisang et al. 2005; Boquete et al. 2023; Bisang et al. 2025). Such pattern aligns with observations in flowering plants, where females are typically found in moister, more favorable habitats, while drought and resourcepoor conditions favor males (Zhang et al. 2012; Golenberg and West 2013). However, another way to interpret this trend would be in terms of resource allocation and reproductive cost. In a metapopulation study focusing on a dioicous moss, a large number of sporophytic female ramets were observed to die right after reproduction, pointing to the high cost of sporophyte production (Santos et al. 2022).

Climate change may intensify skewed sex ratios in species where climatic and ecological tolerance differs between sexes (Lockley and Eizaguirre 2021). In addition, because skewed sex ratios reduce the effective population size, climate change may result in higher rates of inbreeding and loss of beneficial alleles driven by genetic drift (Hedrick and Kalinowski 2000; Frankham 2005). Key environmental factors, such as temperature and precipitation, have been shown to influence sex ratios in bryophytes (Martins et al. 2025) and flowering plants (Zinn et al. 2010), as well as in other organisms (Edmands 2021). Recently, Martins et al. (2025) demonstrated that in leafy liverworts, female sex expression is more common under conditions of lower temperatures and higher precipitation, whereas male sex expression is favored by higher temperatures and lower precipitation.

Islands often host a high proportion of unisexual taxa, and insularity is known to drive distinct evolutionary and phenotypic changes in island plant populations (Carlquist 1966, 1974; Bawa 1980, 1982; Whittaker et al. 2023). However, the effects of insularity on sex expression in dioecious plants remain largely unexplored. In this context, the niche variation hypothesis suggests that populations occupying broader niches exhibit greater morphological variability than those in more restricted niches (Van Valen 1965). Insular populations are expected to show increased morphological and ecological variability, including expanded niche breadth, as they adapt to reduced competition and unoccupied ecological space (Givnish 1997; Gillespie 2009). Additionally, lower species diversity on islands may intensify intraspecific competition, potentially influencing patterns of sex expression as a counterstrategy (Barrett 1996; Heo et al. 2023). Lastly, Islands have also been recognized as historical refugia against climate change (Hutsemékers et al. 2011; Patiño et al. 2015). Given these factors, we expect stronger climate-driven changes in continental regions compared to islands, particularly for female versus male plants.

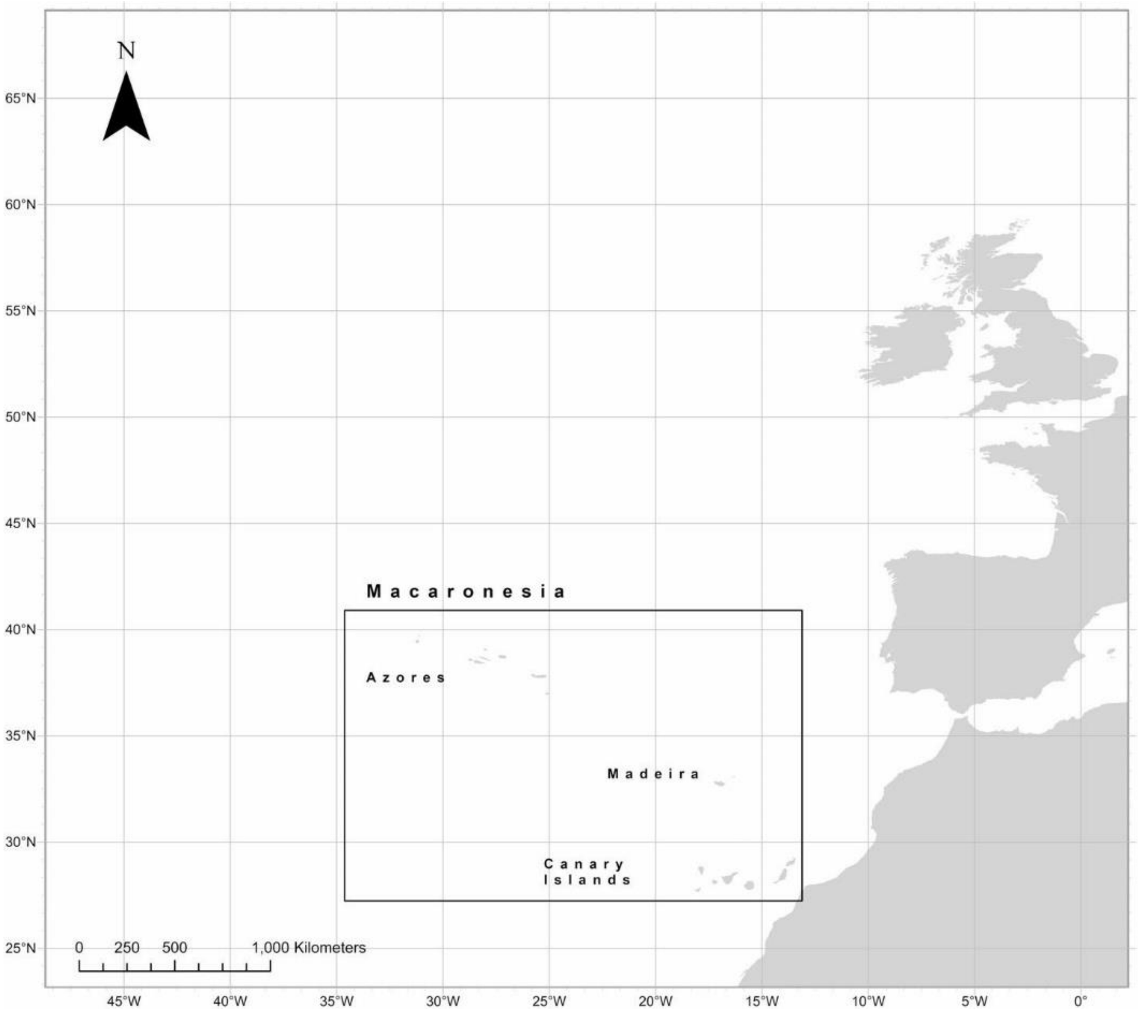
In this study, we aim to investigate whether plant gender influences how bryophyte species respond to climate change, and how such responses may differentially affect the sexes and sex distribution in unisexual bryophyte species across insular and continental regions. This knowledge could inform the development of targeted conservation strategies, particularly for threatened or island endemic species, and enhance biodiversity management in the face of climate change. We focused on two unisexual, threatened species endemic to Macaronesia: a pleurocarpous moss, *Exsertotheca intermedia*, and a leafy liverwort, *Frullania polysticta*. We also examined two unisexual leafy liverworts primarily restricted to Macaronesia and the European Atlantic fringe: *Frullania teneriffae* and *Porella canariensis*. Specifically, our study addresses the following questions: (i) To what extent do species distribution models differ between sexes? and (ii) How do spatial projections vary under current and future climatic conditions?

Methods

STUDY AREA AND SPECIES OCCURRENCE DATA

The study area covered the three northern Macaronesia archipelagos (Canary Islands, Madeira and Azores), western Europe and northwestern Africa (Fig. 1). Macaronesia, comprising the Canary Islands, Madeira, Azores, and Cape Verde (Fernández-Palacios et al. 2024), is part of the 12 biodiversity hotspots which include island ecosystems, as identified by Conservation International in 2005 (Myers et al. 2000). Its flora reflects diverse biogeographical influences through three main components: (1) the Palaeotropical-Tethyan Geoflora, once widespread in Europe and North Africa but now confined to the northern archipelagos (Azores, Madeira, Canary Islands) (Fernández-Palacios et al. 2024); (2) the African Rand Flora, associated with the coastal margins of Africa and Arabia, influencing Madeira, Canary Islands, and Cape Verde (Rodrigues et al. 2020; Fernández-Palacios et al. 2024); and (3) the Macaronesian Neoendemic Flora, derived from Mediterranean ancestors (Price et al. 2018; Fernández-Palacios et al. 2024).

Fig. 1 *Study area: the three northern Macaronesian archipelagos (Canary Islands, Madeira, and Azores), Western Europe, and Northwestern Africa*



To investigate if the species distribution models differ between sexes, we considered four unisexual species: two threatened species endemics to Macaronesia: a pleurocarpous moss (*Exsertotheca intermedia*) and a leafy liverwort (*Frullania polysticta*); and two leafy liverworts primarily restricted to Macaronesia and the European Atlantic fringe (*Frullania teneriffae*, and *Porella canariensis*). Species distributions were obtained from Martins et al. (2025; see Table S1) and are based on specimen records collected from fieldwork and herbarium vouchers. To avoid geographical sampling bias (Syfert et al. 2013; Collart et al. 2021), we retained a single occurrence per 1 km pixel.

In total, 323 occurrences of female plants were obtained from 49, 38, 161 and 75 populations of *E. intermedia*, *F. polysticta*, *F. teneriffae*, and *P. canariensis*, respectively. Additionally, 203 occurrences of male plants were recorded, distributed across 36 populations of *E. intermedia*, 23 of *F. polysticta*, 93 of *F. teneriffae*, and 51 of *P. canariensis* (Table S1).

CLIMATIC VARIABLES

To characterize the climatic conditions associated with the current distribution of sex, data for 19 bioclimatic variables at a 30-arc-second resolution (~ 1 km) were obtained from CHELSA v2.1 (Karger et al. 2017). Since the geographic background should reflect not only the current distribution but also the potentially occupied range in the past (Acevedo et al. 2012) and considering that models for bryophytes built with large geographic backgrounds are recommended (Mateo et al. 2015), we maintained the same geographic background for all species. Additionally, it has been suggested that the distinctive endemic component of the Macaronesian flora is largely a relict of a once widespread subtropical flora that covered southern Europe and northern Africa during the Tertiary period (Sunding 1979).

To avoid multicollinearity, we computed a Pearson's correlation coefficient matrix among climatic variables from 10,000 background points randomly sampled in the study area with the "sp" R package, identifying variables with high correlations (|r| >0.7) (Dormann et al. 2013; Guisan et al. 2017; Zurell et al. 2020). We kept six variables (Table S2), bio 1 (annual mean temperature), bio3 (isothermality), bio 8 (mean temperature of the wettest quarter), bio 9 (mean temperature of driest quarter), bio 13 (precipitation of wettest month) and bio 15 (precipitation seasonality).

MODELLING APPROACH: ENSEMBLE OF SMALL MODELS

A niche similarity test was performed to assess the similarity between female and male plants of the four studied species (*E. intermedia*, *F. polysticta*, *F. teneriffae*, and *P. canariensis*) using Schoener's *D* and a modified Hellinger's *I* metric (Warren et al. 2008). Climatic variation under present and future climatic conditions was summarized via the two first principal components of a Principal Component Analyses (PCA; 85% of the total variance explained for *E. intermedia* and *F. teneriffae*, 82% for *F. polysticta* and 74% for *P. canariensis*). The niche overlap metrics were calculated using the *ecospat.niche.overlap. test* function of the "ecospat" R package (Broennimann et al. 2024), in which plant sex was randomly reassigned across occurrence records 100 times. Collart et al. (2021) suggest that, in the absence of evidence for niche divergence, species distribution models (SDMs) should be based on all available occurrence data at the species level. Conversely, Smith et al. (2019) argue that even when two lineages exhibit greater niche similarity than expected by chance, they may still differ sufficiently in their environmental tolerances, justifying the separate modeling of their niches. In this context, male and female plants can be considered as "two lineages", as they may exhibit distinct environmental tolerances and niche characteristics. Given that the central question of this study is whether species distribution models differ between sexes, we believe it is both logical and appropriate to maintain the data split into male and female categories. This approach ensures a more accurate representation of potential sex-specific differences in environmental tolerances and niche preferences.

As modelling techniques require absence data, we combined occurrences with 10,000 background points (pseudo-absences) randomly selected from the entire study area using the "sp" R package (Pebesma and Bivand 2005; Bivand et al. 2013). The same set of pseudo-absences was used for all datasets.

Considering that 50% of both female and male bryophyte species had fewer than 50 records, we employed an Ensemble of Small Models (ESMs). ESMs are specifically designed for small datasets (Breiner et al. 2018; Erickson and Smith 2023) and have been successfully applied to bryophytes (Collart et al. 2021; Cerrejón et al. 2022; Patiño et al. 2023). The procedure followed to calibrate and evaluate the performance of the ESMs was illustrated in Collart et al. (2021) and was implemented with the "ESM" R package (Collart et al. 2024). ESMs were performed for each species and sex using based on a single modelling technique, gradient boosting machines (GBM; Friedman 2001), as recommended in Breiner et al. 2018; we kept the default model parameters of the package: a Bernoulli distribution, 1000 trees to fit, a tree complexity of 4, a minimum of 5 observations in the terminal nodes of the trees, a learning rate of 0.005, a bag fraction of 0.5, and 3-fold crossvalidation. Models were evaluated using 10 cross-validations, where 70% of the occurrence data were used for model training and the remaining 30% (test set) for evaluation. The bivariate models were then combined by applying a weighted mean based on their Somer's *D* (= 2 * the Area Under the Curve [AUC] – 1; Newson 2002) values and discarding models with a Somer's D ≤ 0, following Breiner et al. (2018). Model accuracy was evaluated by combining the suitability values from the 10 test sets to generate an independent series of suitability values approximately the same size as the original dataset, as recommended by Collart and Guisan (2023). We assessed model accuracy using the Boyce Index, which is specifically designed for presence-only data. Although AUC and MaxTSS require presenceabsence data and can be misleading when applied to presence-only datasets (Leroy et al. 2018), we also calculated these metrics for comparison, as they remain the most used indicators (Guisan et al. 2017).

Following the recommendations of Collart and Guisan (2023), we further evaluated whether our models performed better than random predictions by generating null models. These were created by randomly selecting the same number of background points as occurrence data, repeated 100 times using the *ESM_Null.Models* function of the "ESM" R package (Collart et al. 2024). The null models were then evaluated using their AUC, MaxTSS, and Boyce index, following the procedure described above. The ESMs based on actual occurrence data were considered significant if fewer than 95% of the null models showed higher AUC, MaxTSS, or Boyce index values.

The models were projected under both present (1981–2010) and future (2071–2100) climate conditions. For the future projections, we selected two out of the five models from the CHELSA v2.1 dataset (Karger et al. 2017) from CMIP6, using two Shared Socioeconomic Pathways (SSPs): SSP1-2.6 and SSP5-8.5 (hereafter 2.6 and 8.5). The two SSP scenarios represent the low and high range of future forcing pathways, implementing radiative forcing levels of 2.6 and 8.5 Wm^{-2} in 2100 (O'Neill et al. 2016). The selected global circulations models were UKESM1-0-LL (hereafter UKESM) and MPI-

ESM1-2-HR (hereafter MPI), which correspond to high and low climate sensitivity, respectively (Lange 2019, 2021).

To evaluate the differences in predicted ranges between male and female models, we binarized the continuous suitability index for each model by maximizing the sum of sensitivity and specificity (MaxSSS), as recommended by Liu et al. (2013). Percentages of loss, gain, and range shifts in species, as well as potentially suitable areas for the period 2071– 2100 compared to the present, were calculated using the "biomod2" R package (Thuiller et al. 2024). All analyses were performed in R version 4.4.2 (R Core Team 2024). Maps were created using ArcGIS Pro software by Esri (Environmental Systems Resource Institute, https://www.esri.com/en-us/arcgis/products/arcgis-pro).

Results

Niche overlaps between sexes of the four species ranged from 0.74 to 0.89 for Schoener's D (average 0.81) and from 0.89 to 0.98 for Hellinger's I (average 0.93) under present climate conditions (Table S3). Under future climate scenarios, overlaps remained consistently high, ranging from 0.71 to 0.91 for Schoener's D (average 0.81) and from 0.86 to 0.99 for Hellinger's I (average 0.92) (Table S3).

Female and male models exhibited average AUC, MaxTSS and Boyce index of 0.997 ± 0.002, 0.958 ± 0.021 and 0.921 ± 0.096, respectively (Table S4). These models were significantly better than null models evaluated based on Boyce index, but in only 3 of the 8 models based on AUC and MaxTSS (Table S4).

The potential distribution area of female and male plants of all bryophyte species are predicted to decrease significantly across the Macaronesia region by 2100. This decline is consistent under both climate models (UKESM and MPI) and emission scenarios (SSP2.6 and SSP8.5) (Fig. 2; Figs. S1–S5; Table 1). In 2100, the average potential area in Macaronesia (± SD) for female and male plants is predicted to decrease to 78.9 ± 19.1% and 79.6 ± 18.5%, respectively, of their current potential area under the UKESM model, and to 57.1 ± 35.0% and 62.3 ± 37.8%, respectively, under the MPI model (Table 1). Under the SSP 8.5 scenario, the potential distribution area for both sexes of the two endemics to Macaronesia (*E. intermedia* and *F. polysticta*) is predicted to reach less than 5% of their current suitable area (Table 1), especially according to the MPI model. For non-Macaronesia endemic species, the potential distribution area of female plants of *F. teneriffae* is also predicted to decline to less than 5%, as is the case for female plants of *P. canariensis* under the UKESM model. The reduction is also observed in male plants of *F. teneriffae* and *P. canariensis* under the UKESM and MPI models, respectively (Table 1).

The model projections under current climatic conditions showed that suitable climatic conditions for the occurrence of the endemic Macaronesian bryophyte species are found along a narrow fringe in western Europe and northwestern Africa (Figs. S1–S5). For these continental areas, the average potential area (± SD) for female and male species is predicted to increase to 698.5 ± 1054.9% and 553.3 ± 995.6% of their current potential area under the UKESM model, respectively. In contrast, under the MPI model, the potential area is expected to decrease by 29.4 ± 51.6% and 37.9 ± 54.9% for female and male species, respectively, (Table 1). Under the SSP 8.5 scenario, the potential distribution area for both sexes of the two endemics to Macaronesia *(E. intermedia* and *F. polysticta*) is predicted to exceed 100% of their current suitable area (Table 1) under the UKESM model. In contrast, for the MPI model and the same SSP 8.5 scenario, both female and plants are also predicted to decline to less than 5%. The exception is the male plants of *F. polysticta*, which are predicted to decline to less than 40% (Table 1). For non-Macaronesia endemic species, the potential distribution area for both sexes of *F. teneriffae* is predicted to exceed 95% of their currently suitable area under the UKESM model. In contrast, under the MPI model and the same SSP 8.5 scenario, female and male plants are predicted to decline to less than 50% (Table 1). For *P. canariensis* under the USKEM model and the SSP 8.5 scenario, the potential distribution area for female plants is predicted to exceed 100% of their currently suitable range, whereas male plants are predicted to decline to less than 5%. In contrast, under the MPI model, female plants are predicted to decline to below 60%, while male plants are expected to decrease to less than 5% (Table 1).

Fig. 2 *Examples of the predicted environmentally suitable distribution range in 2100 under the UKESM model and SSP 8.5 scenario for each sex of the studied species in the Madeira Archipelago (see Fig. S5 for MPI model)*

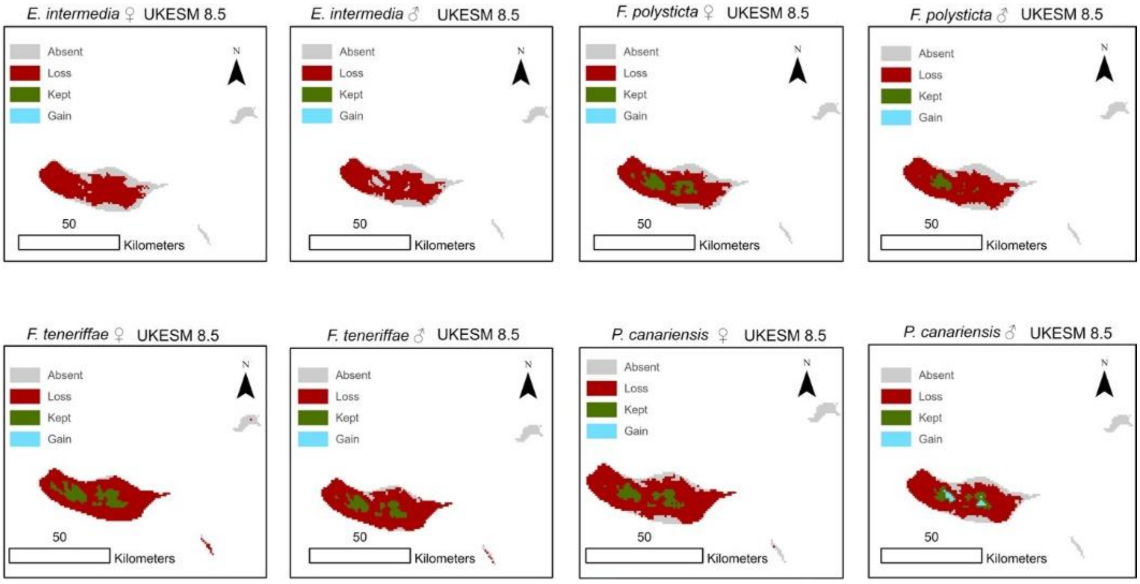


Table 1 Number of 1–km^2 climatically suitable pixels for each sex of the studied species in Macaronesia (nMac), and Western Europe and Northwestern Africa (nCon) under current climate conditions, and in 2100 under two global circulation models (UKESM and MPI) and two shared socioeconomic pathways (SSP 2.6 and 8.5). The percentage of range change (% range change) represents the percentage of climatically suitable areas as compared to the current situation in both Macaronesia (Mac) and continental areas (Con)

		nMac	nCon	% range change Mac	% range change Con
E. intermedia **♀**	Current	1848	529		
	UKESM 2.6	397	1020	−78.5	92.8
	UKESM 8.5	4	16,332	−99.8	2987.3
	MPI 2.6	1489	639	−19.4	20.8
	MPI 8.5	59	1	−96.8	−99.8
E. intermedia **♂**	Current	1344	398		
	UKESM 2.6	462	390	−65.6	−2.0
	UKESM 8.5	2	11,093	−99.9	2687.2
	MPI 2.6	1214	459	−9.7	15.3
	MPI 8.5	66	5	−95.1	−98.7
F. polysticta **♀**	Current	943	967		
	UKESM 2.6	404	884	−57.2	−8.6
	UKESM 8.5	109	13,319	−88.4	1277.4
	MPI 2.6	632	1029	−33.0	6.4
	MPI 8.5	22	48	−97.7	−95.0
F. polysticta **♂**	Current	1200	1231		
	UKESM 2.6	503	1304	−58.1	5.9
	UKESM 8.5	50	18,605	−95.8	1411.4
	MPI 2.6	893	1170	−25.6	−5.0
	MPI 8.5	33	478	−97.3	−61.2
F. teneriffae **♀**	Current	6765	175,743		
	UKESM 2.6	2912	254,690	−57.0	44.9
	UKESM 8.5	276	344,668	−95.9	96.1
	MPI 2.6	5452	235,030	−19.4	33.7
	MPI 8.5	1345	75,375	−80.1	−57.1
F. teneriffae **♂**	Current	6150	45,958		
	UKESM 2.6	2589	105,178	−57.9	128.9
	UKESM 8.5	220	218,337	−96.4	375.1
	MPI 2.6	4929	71,596	−19.9	55.8
	MPI 8.5	1129	20,547	−81.6	−55.3
P. canariensis **♀**	Current	4638	5518		
	UKESM 2.6	1980	7826	−57.3	41.8
	UKESM 8.5	136	63,804	−97.1	1056.3
	MPI 2.6	3306	5332	−28.7	−3.4
	MPI 8.5	853	3279	−81.6	−40.6
P. canariensis **♂**	Current	1730	2012		
	UKESM 2.6	526	369	−69.6	−81.7
	UKESM 8.5	106	26	−93.9	−98.7
	MPI 2.6	510	873	−70.5	−56.6
	MPI 8.5	18	56	−99.0	−97.2

Discussion

The predicted reduction in climatically suitable areas for both female and male plants of all bryophyte species studied in the Macaronesia region is similar. Under the SSP 8.5 scenario, suitable habitat for the two threatened endemics, *E. intermedia* and *F. polysticta*, as well as *F. teneriffae* and *P. canariensis*, is expected to shrink to less than 5% of their current extent. For all species, overlaps between females and males remain high under future scenarios, suggesting that despite severe habitat contraction, spatial co-occurrence and potential for sexual reproduction are largely maintained. Our results align with those obtained in Patiño et al. (2016), who, without distinguishing between sexes, predicted complete extinctions for several Macaronesian bryophytes by 2070 (but see Patiño et al. 2023). Similarly, Hodd et al. (2014) predicted that oceanic bryophyte species in the British Isles would lose suitable climate space as a result of climate change. Ferreira et al. (2016) also demonstrated that bryophytes, vascular plants, and arthropods in the Azores archipelago could lose suitable climatic areas in the near future. A similar trend was predicted for *Sideritis* species in Macaronesia by 2080 (Barber et al. 2013), and *Helianthemum juliae* (Canary Islands endemic) faces high extinction risks in the next 100 years (Marrero-Gómez et al. 2007).

Our study revealed that for the endemic Macaronesian bryophyte species investigated, climatically suitable conditions for the occurrence of both female and male plants are also predicted in a narrow fringe in western Europe and northwestern Africa. By 2100, suitable areas for both female and male plants are predicted to expand under the UKESM model, whereas a decrease in climatically suitable areas is predicted under the MPI model. A narrow range along the western fringe of the Iberian Peninsula was also identified as climatically suitable for Macaronesian endemic bryophytes in Patiño et al. (2016). Moreover, phylogeographic evidence suggests that previously endemic Macaronesian species have repeatedly colonized the western Atlantic fringe of Europe since the last glacial maximum (Patiño et al. 2015). Despite the generally high dispersal capacities of bryophytes (Patiño and Vanderpoorten 2018), there is evidence that dispersal limitation does occur, at least in some species (Zanatta et al. 2020; van Zuijlen et al. 2024), which may further hinder their ability to migrate to macroclimatically suitable areas on the continent in response to the dramatic reduction of suitable habitats on the islands in the coming decades (Patiño et al. 2016).

Aligning with Zanatta et al. (2020), who reported a clear tendency for a northern shift in climatically suitable areas for 40 bryophyte species, representative of Mediterranean, Atlantic, wide-temperate, and Arctic-Alpine biogeographic elements under changing climate conditions until 2050, our results for *F. teneriffae* show similar pattern. The potential distribution area for both sexes of *F. teneriffae* in continental regions is predicted to expand beyond its currently suitable area under the UKESM model. In contrast, the MPI model predicts a reduction of just over 50% in climatically suitable areas for both sexes. Both female and male plants are expected to gain substantial areas in the regions of Ireland and the United Kingdom, while a significant reduction in suitable areas is predicted for the Iberian Peninsula.

The species distribution models revealed variations between sexes exclusively in *P. canariensis.* Notably, under the SSP 8.5 scenario, the UKESM model predicts that the potential distribution area for female plants will expand to over 100% of their current suitable range, while male plants are predicted to decline to less than 5% of their current distribution, particularly in the Iberian Peninsula. Similar to other bryophyte species (Zanatta et al. 2020), female *P. canariensis* plants show a clear tendency for a northern shift in climatically suitable areas. Martins et al. (2025) demonstrated that in leafy liverworts, female plants are more common under conditions of lower temperatures and higher precipitation, which may explain the clear tendency for a northern shift in female plants. Conversely, male plants are more favourably influenced by higher temperatures and lower precipitation (Martins et al. 2025).

The clear difference in climatically suitable areas between sexes in *P. canariensis* highlights the importance of considering sex-specific responses to climate change. Such differences could significantly impact the species' reproductive success and long-term viability, particularly at the infraspecific or population level. The loss of male plants may reduce genetic diversity, limit fertilization opportunities, and increase the risk of local extinctions, especially in small or isolated populations (Hedrick and Kalinowski 2000; Frankham 2005; Aguilar et al. 2006). These findings emphasize the need for incorporating sex-specific models into conservation planning to accurately predict species' responses to future climate scenarios.

Conclusion

Our results highlight the severe impacts of climate change on unisexual bryophyte species in Macaronesia. All studied species, including the Macaronesian endemics (*E. intermedia* and *F. polysticta*), as well as *F. teneriffae* and *P. canariensis*, are predicted to lose more than 95% of their current climatically suitable areas in the Macaronesia region. However, the Atlantic coastal fringe of Europe and northwestern Africa may provide refugia for both sexes, offering hope for their persistence. Furthermore, we show that, despite projected habitat contractions, female–male co-occurrence is expected to remain largely intact for *E. intermedia*, *F. polysticta*, and *F. teneriffae*, suggesting that reproductive potential is preserved under future scenarios. In contrast, *P. canariensis* displays reduced overlap between sexes, reflecting pronounced sex-specific differences in projected distributions and indicating possible reproductive constraints. For this species, currently listed as Least Concern, the apparent persistence of only female plants in continental areas suggests that its conservation status may warrant re-evaluation. A lack of male individuals could increase inbreeding and reduce genetic diversity through drift (Hedrick and Kalinowski 2000; Frankham 2005), undermining long-term viability. These findings emphasize that while some dioecious island species may maintain reproductive resilience under climate change, others face significant risks. Incorporating sex-specific distribution dynamics into conservation assessments and management will be critical to safeguard the persistence of insular plant populations in a rapidly changing world.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10531-025-03157-z.

Acknowledgements AM was funded by FCT (Fundação para a Ciência e a Tecnologia) through the individual research grant 2020.06119.BD, and by FCiências.ID under project services acquisition no. 1057. JP. was funded by the Spanish Ministry of Science and Innovation and Universities (MICINN) through the project PID2023-147122NB-I00 (DecodAdapt) from MICIU/AEI/10.13039/501100011033 and by FEDER, EU, and project PCI2023-145966-2 (BiomonI) funded by MICIU/AEI/10.13039/501100011033 and co-funded by the European Union. We are grateful to the editor and the anonymous reviewer for their valuable comments.

Author contributions AM, MSS and JP conceived the idea for this study. AM analyzed the data with the assistance from FC. AM, MSS and JP led the writing with assistance from FC.

Data availability Data is provided within the manuscript or supplementary information files. High resolution versions of the figures (Figures S1–S4) included in the Supplementary Material are available at https://doi.org/10.6084/m9.figshare.28263464.

DECLARATIONS

Conflict of interest The authors declare that there is no conflict.

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