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The moss *Homalothecium mandonii* as a model for assessing bryophyte response to climate change in Macaronesia

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Abstract. Bryophytes exhibit specific ecophysiological and biological features that make them ideal indicators of climate change. Using species distributions models, we address the question of the impact of climate change on the endemic bryophyte flora of Macaronesia, taking the Macaronesian endemic moss *Homalothecium mandonii* as a model. Projections of the extant macroclimatic niche of the species onto climatic scenarios for the Last Glacial Maximum (LGM) suggested that the potential range of the species was about 200% larger than what it is currently. Paleoclimatic projections further identified Northwest African and Iberian areas as potentially suitable at the LGM, raising the possibility that *H. mandonii* is of paleo-endemic origin. Coupled with previous observations, this points to the role of Macaronesia as a refugium for palaeoendemics that went extinct in their primary continental regions. Projections of the macroclimatic niche of the species into the future predicted,

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however, a striking decrease in suitable range area of 29-53% by 2080. Our predictions thus suggest that, while Macaronesia appears to have been a refugium for species that went extinct on continents in the past, its role as a historical sanctuary might be severely threatened in the ongoing context of climate change.

Keywords: species distribution models, moss, refugium, paleoendemism

O musgo *Homalothecium mandonii* como modelo para avaliação da resposta dos briófitos às alterações climáticas na Macaronésia

Sumário. Os briófitos possuem características ecofisiológicas e biológicas únicas que os tornam excelentes indicadores das alterações climáticas. Com o auxílio de modelos de nicho ecológico, analisou-se em que medida as alterações climáticas podem afectar a brioflora endémica da Macaronésia, em particular o musgo *Homalothecium mandonii*. A projecção do nicho actual desta espécie sobre as camadas macroclimáticas da última glaciação máxima, indicam que a área de distribuição da espécie seria superior em cerca de 200% relativamente à área actual. As projecções paleoclimáticas identificam ainda que a região noroeste de África e a Península Ibérica possuem condições climáticas favoráveis ao desenvolvimento desta espécie, sugerindo que se poderá tratar de um paleoendemismo.

Em conformidade com observações prévias, os resultados obtidos sugerem que a Macaronésia representa um refúgio para as espécies actualmente extintas de zonas continentais. No entanto, as projecções do nicho climático da espécie para o futuro, predizem um declínio da área favorável de 29-53% em 2080. Tais predicções sugerem então que o papel de refúgio climático que a Macaronésia tem desempenhado se encontra fortemente ameaçado como resultado das alterações climáticas em curso.

Palavras-chave: modelos de nicho ecológico, musgos, refúgio, paleoendemismo

Homalothecium mandonii (Bryophyta), un modèle pour estimer la réponse des bryophytes au changement climatique en Macaronésie

Résumé. Les bryophytes présentent des caractéristiques écophysiologiques et biologiques uniques qui en font des indicateurs des changements climatiques de premier choix. A l'aide de modèles de niche écologique, nous examinons dans quelle mesure les changements climatiques affectent la bryoflore endémique de Macaronésie en se focalisant sur la mousse *Homalothecium mandonii*. La projection de la niche actuelle de l'espèce sur des couches macroclimatiques du dernier maximum glaciaire indiquent que l'aire de distribution de l'espèce était environ 200% plus important qu'actuellement. Les modèles indiquent également que l'Afrique du Nord Ouest et la Péninsula Ibérique présentaient des caractéristiques climatiques favorables à l'espèce, suggérant que cette dernière puisse être une paléoendémique. En rapport avec d'autres observations similaires, ces résultats suggèrent que la Macaronésie a pu jouer un rôle clé de refuge pour des espèces actuellement éteintes sur le continent. Les projections de la niche climatique de l'espèce dans le futur montrent par contre un déclin de l'aire favorable de 29-53% en 2080. Ces prédictions suggèrent donc que le rôle de refuge que la Macaronésie a historiquement joué est fortement menacé dans le contexte des changements climatiques en cours.

Mots clés: modèles de niche écologique, mousse, refuge, paléoendémisme

Introduction

Climate change is one of the greatest threats to plant biodiversity, and thus a major challenge for conservationists (Botanical Garden Conservation International, *http://www.bgci.org/ourwork/climatechange/*). Projecting late 21st century distributions for 1,350 European plants species under seven climate change scenarios, THUILLER *et al.* (2005) suggested that more than half of the species could be vulnerable or threatened (sensu IUCN) by 2080. The impact of climate change is, however, predicted to affect some areas more than other and indeed, expected species loss and turnover proved to be highly variable across regions in Europe. Atlantic regions, for instance, appear less sensitive than Mediterranean ones, and the range of some Atlantic species is even predicted to expand in the forthcoming decades (THUILLER *et al.*, 2005). Due to their geographic position, the Azores, Madeira and the Canary Islands have in fact experienced buffered climate change in the past decades (CRAWFORD, 2000; MARTIN *et al.*, 2012). These islands are therefore assumed to have served as refugia since the onset of the Cenozoic Era, which has been a period of long-term cooling leading to range contractions in the extensive tropical and boreotropical forests that covered most of the globe (see NYMAN *et al.*, 2012, for review). The survival of a sub-tropical flora that was decimated in continental Europe in the Cenozoic forms the basis of Engler's hypothesis for the paleo-endemic origin of a unique flora defining the Macaronesian biogeographic region (see VARGAS, 2007, for review). More recently, the strikingly higher levels of genetic diversity observed in Macaronesian plant population as compared to continental ones similarly point to buffered climate change in the Macaronesian islands during the last glacial maximum (LGM) (FERNÁNDEZ-MAZUECOS and VARGAS, 2011).

Bryophytes are a group of early land-plants, whose specific ecophysiological and biological features make them ideal candidates for investigating the impact of climate changes, leading SLACK (2011) to describe them as 'canaries in the coal mine'. In fact, their poikilohydric condition means that their water content is directly regulated by ambient humidity. Physiological activity, and hence growth, is restricted to periods of hydration, with the plant entering dormancy upon desiccation. In the absence of roots and a highly efficient internal water transport system, most bryophytes hence depend primarily on atmospheric water to sustain their needs.

Temperature is also a factor of prime importance in bryophyte physiology for regulating a suite of complementary mechanisms regarding growth and reproduction (GLIME, 2007). A common feature among most bryophytes is their ability to grow at low temperature. Experimental investigations revealed that most temperate species exhibit a growth reduction of less than 50% at 5°C compared to growth at their optimal temperature (FURNESS and GRIME, 1982). Most species, including tropical ones, seem to be pre-adapted to cold and survive temperatures ranging from -10 to -27°C (GLIME, 2007). To the reverse, all of the temperate and boreal species investigated by FURNESS and GRIME (1982) died when kept continuously at 35°C and most shoots died eventually at >30°C. Although acclimatization along a temperature gradient has been demonstrated in some instances (CARBALLEIRA *et al.*, 1998), the sensitivity of temperate species to temperature increase strengthens the hypothesis that bryophytes might respond quickly to climate warming. In fact, as opposed to some organisms that developed the strategy to rapidly adapt to novel environmental conditions (JEZKOVA *et al.*, 2011), little evidence for ecotypic differentiation was found in bryophytes (SHAW, 1991; REYNOLDS and MCLETCHIE, 2011; but see HUTSEMÉKERS *et al.*, 2010), suggesting that they have to migrate to face climate change.

Bryophytes are indeed highly efficient dispersers (see VANDERPOORTEN *et al.*, 2010, for review). This suggests that, as opposed to less mobile organisms, they are able to efficiently track areas of suitable climate through time. This is consistent with previous studies reporting rapid climate-driven community shifts from range dynamics analyses (FRAHM and KLAUS, 2001; ZECHMEISTER *et al.*, 2007) and stratigraphic analyses of macro-remains preserved in peat (JONSGARD and BIRKS, 1995; ELLIS and TALLIS, 2000, 2003). The potential of bryophytes for a high efficiency to colonise habitats as soon as they develop and become available suggests that the time-lag between habitat availability and colonization is reduced, thereby decreasing the major uncertainty associated with dispersal limitation when predicting climate change impacts on biodiversity (NORMAND *et al.*, 2011).

Bryophytes lack, however, a cuticle and decay-resistant tissues, so that the fossil record is extremely poor in the group (see VANDERPOORTEN *et al.*, 2010, for review). Paleontological information is especially scarce on oceanic islands, which, like the Canary Islands, lack peat deposits. Macrofossil remains are restricted to lacustrine deposits, from which no detailed bryophyte record is available (NOGUÉ *et al.*, 2013). In this context, Species Distribution Models (SDMs) offer a unique opportunity to make testable predictions of past distributions and their dynamics (SVENNING *et al.*, 2011) and to accordingly predict future shifts in distribution range.

Here, we expore the extent to which climate change has impacted, and will impact the endemic bryophyte flora of Macaronesia, taking the Macaronesian endemic moss *Homalothecium mandonii* (Mitt.) Geh. as a model.

Material and Methods

Although considered as a synonym of *H. sericeum* in the moss checklist of the Mediterranean and Macaronesia (ROS *et al.*, 2013), *Homalothecium mandonii* was 'resurrected' as a Macaronesian endemic species based on molecular and morphological evidence (HUTTUNEN *et al.*, 2008; L. HEDENÄS *et al.*, unpublished results). It was selected for the present study for exhibiting a typically widespread distribution across Macaronesia, which spans the Canary Islands, Madeira, and the Azores. SDMs were constructed based on 205 datapoints sampled throughout this range. To avoid geographical sampling bias (SYFERT *et al.*, 2013), only points that are separated by at least 0.04 decimal degrees from each other were retained, so that 39 points were eventually used to build the model.

As background, we randomly selected 10,000 points over the entire distribution area of the species. Nineteen bioclimatic variables from Worldclim (HIJMANS *et al.*, 2005) were employed as environmental predictors. To avoid multicolinearity, we ran a correlation analysis on the background points and eliminated one of the variables in each pair with a Pearson correlation value>0.8. We used an ensemble forecasting approach (ARAÚJO and NEW, 2007) combining four different modelling techniques to take modelling uncertainty into account: generalized linear models (GLM; MCCULLAGH and NELDER, 1989), MaxEnt (PHILLIPS *et al.*, 2006), gradient boosting machine (GBM; FRIEDMAN, 2001) and Random forests (RF; BREIMAN, 2001). We used the BIOMOD 2.0 package in R (THUILLER *et al.*, 2009, *www.r-forge.r-project.org*) for the modeling with GBM, BRT and GLM with all the default parameters. For MaxEnt, the regularization multiplayer parameter was changed to two to minimize overprediction. Models were calibrated with 70% of the data and then evaluated with the remaining 30% using Area Under the Curve (AUC) and True Skill Statistic (TSS). For each technique, presences and pseudo-absences used to calibrate the model were weighted to ensure neutral species prevalence (0.5). The procedure was replicated 10 times, with random training and evaluation datasets, so that we obtained 40 models (10 replicates x 4 techniques). The ensemble models was generated with those models that had an AUC > 0.8 and a TSS > 0.7. The contribution of each model to the final ensemble model was proportional to their goodness-of-fit statistics.

We then used the models to project the potential distribution of the species in the present, past and future in Macaronesia and neighbouring continental areas, including Northwestern Africa and the Iberian Peninsula. Past climatic conditions were derived from general circulation model simulations generated by the

Paleoclimate Modelling Intercomparison Project Phase II (PMIP2 for 21000 years BP), namely the Community Climate System Model (CCSM 3; COLLINS *et al.*, 2006) and the Model for Interdisciplinary Research on Climate (MIROC 3.2; HASUMI and EMORI, 2004). Future projections (2050 and 2080) were derived from three climate scenarios (A1, A2 and B2) proposed by the Intergovernmental Panel on Climate Change Data Distribution Centre, with cumulative CO_2 emissions reaching 1205.7, 1332.2 and 901.4 Gt for 2080, respectively (PACHAURI and REISINGER, 2007). The predicted models were converted to binary presence/absence data using a threshold approach to minimize the commission error (FIELDING and BELL, 1997). Because presence-only data were available, a maximum commission error of 0.05 was employed. Cells with predicted occurrences were counted for each time period and a percentage of occupied area relative to the present condition was calculated for each projection in order to assess changes in range size.

Results and discussion

Homalothecium mandonii is currently widely distributed across the Canary islands and Madeira and has a limited range in the Azores (Figure 1a). Its area of extent, of about 1355 km^2, is far above the threshhold of 500 km^2 identified for threatened species in the Canary Islands (GONZÁLEZ-MANCEBO *et al.*, 2012). Both the CCSM and MIROC paleoclimatic models suggest that the potential range of the species was larger at the LGM as compared to what it is currently (Table 1). In fact, both projections indicate that 91-100% of the extant distribution were conserved. Due to lower see levels and larger island size (FERNANDEZ-PALACIOS *et al.*, 2011), there was a total striking increase of 197-251% in potential range as compared to the present within Macaronesia. The eastern Canary islands of Fuerteventura and Lanzarote were connected in the past, explaining the wide distribution of the species in continuous habitats with suitable climate along the entire landmass (Figure 1b, c). As a comparison, MIROC projections suggested that the sister species *H. sericeum* experienced a loss of 42% and a gain of 18% of area suitability at the LGM across Europe (DÉSAMORÉ *et al.*, 2012). This indicates that, while temperate species such as *H. sericeum* experienced in Europe substantial range reductions at the LGM, as confirmed by analyses of their spatial patterns of genetic diversity and structure (DÉSAMORÉ *et al.*, 2012), widespread Macaronesian endemics such as *H. mandonii* thrived on islands.

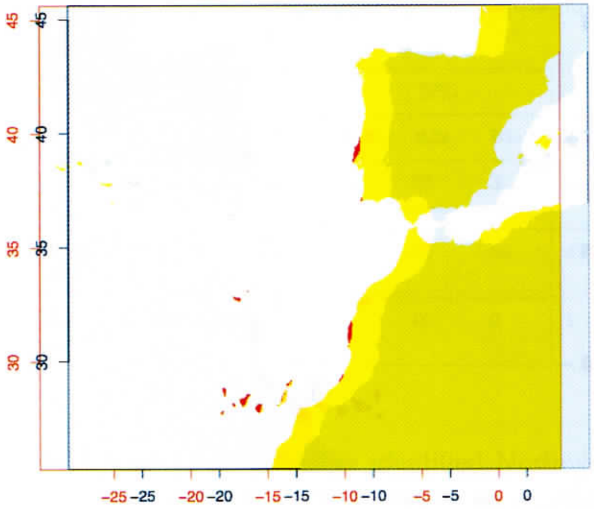

Figure 1a

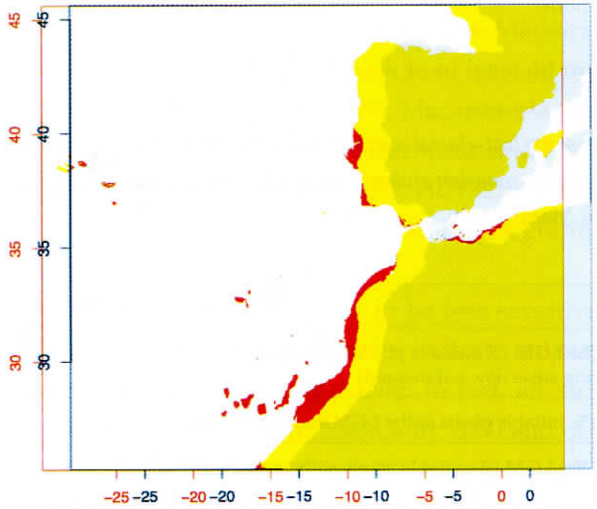

Figure 1b

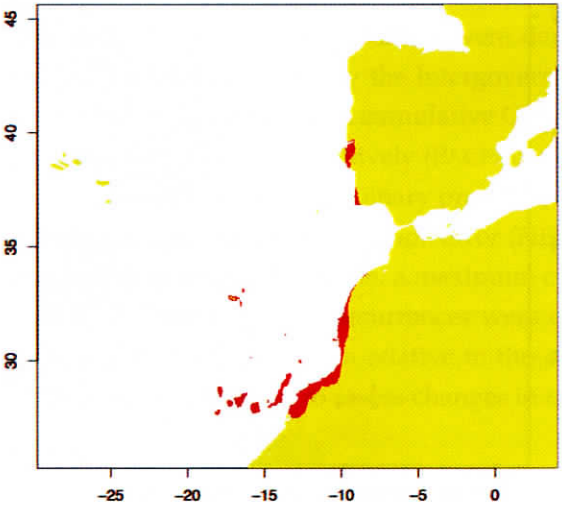

Figure 1c

Figure 1 - *Comparative potential distribution (in red) of the Macaronesian endemic moss Homalothecium mandonii at present time (a) and during the Last Glacial Maximum under MIROC (b) and CCSM (c) projections.*

Table 1 - *Comparison of the last-glacial maximum (LGM) (MIROC and CCSM projections) potential distribution of the Macaronesian endemic moss Homalothecium mandonii as a function of the extant suitable area in Macaronesia.*

	CCSM	**MIROC**
Range expansion at the LGM (% suitable pixels at the LGM but not in the present, including areas now submerged)	197	251
Range conservation (% suitable pixels at the LGM and the present)	91	100
Range contraction at the LGM (% suitable pixels at the present but not at the LGM)	9	0

Table 2 *- Comparison of the extant and future (2050, 2080 under the A1b, A2a, and B2a scenarios proposed by the Intergovernmental Panel on Climate Change Data Distribution Centre) potential distribution of the Macaronesian endemic moss Homalothecium mandonii within Macaronesia.*

	2050			2080		
	A1b	**A2a**	**B2a**	**A1b**	**A2a**	**B2a**
Future range contraction (% suitable pixels in the present but not in the future)	38	25	32	53	43	29
Range conservation (% suitable pixels in the present and the future)	62	75	68	47	57	71
Future range expansion (% suitable pixels in the future but not in the present)	2	0	0	1	0	0

Both CCSM and MIROC projections further identified Northwest African and Iberian areas as potentially suitable at the LGM (Figure 1b, c), raising the possibility that *H. mandonii* is of paleo-endemic origin. Similar conclusions were made for the Canarian endemic *Orthotrichum handiense* (PATIÑO *et al.*, 2013). Other striking examples of paeloendemic moss species in Macaronesia include the monotypic *Alophosia azorica*, whose most recent common ancestor dates back to 253–207 myrs and endemicity to the Azores and Madeira can only be interpreted in terms of relictualism (BELL and HYVÖNEN, 2009). Similarly, the Madeiran endemic and monotypic *Hedenasiastrum percurrens*, dated back to at least 40 myrs, was also interpreted as a paleoendemic (AIGOIN *et al.*, 2009). Macaronesia was further shown to have played a key-role as a refugium for the European and North African bryophyte floras during the LGM (LAENEN *et al.*, 2011; HUTSEMÉKERS *et al.*, 2011). Altogether, these observations point to the substantial biogeographic role of Macaronesia for continental bryophyte floras.

Although Atlantic regions were predicted to be less sensitive than Mediterranean ones (THUILLER *et al.*, 2005), our results indicate substantial and rapid changes in the future distribution of *H. mandonii*. In fact, all models returned a striking decrease in suitable range area of 25-38% by 2050 and of 29-53% by 2080 within Macaronesia depending on the climatic scenarios employed (Table 2). This suggests that, within the next few decades, a common Macaronesian species such as *H. mandonii* will substantially change of conservation status and fit in either the Vulnerable (30% range reduction) or Endangered (50% range reduction) IUCN categories defined for islands (GONZÁLEZ-MANCEBO *et al.*, 2012). In the Fuerteventura endemic *O. handiense*, all of the investigated models pointed to the severe decrease of climatically suitable conditions across the Canary Islands by 2050 and to their complete absence by 2080 (PATIÑO *et al.*, 2013). In *Sideritis* (Lamiaceae, Spermatophyta) similarly, most scenarios predict a decrease in distribution area for most species, and 1-8 of the 23 species present in Macaronesia are predicted to become extinct by 2080 (DIAZGRANADOS *et al.*, 2011). This raises the question of whether the dispersal ability of Macaronesian bryophytes will be sufficient to allow them to migrate in response to climate change within such a short time frame. Altogether, our predictions suggest that, while Macaronesia appears to have been a climatic refugium for species that went extinct on continents in the past, its role as a historical sanctuary might be severely threatened in the ongoing context of climate change.

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