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How do temperate bryophytes face the challenge of a changing environment? Lessons from the past and predictions for the future

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Abstract

Bryophytes are a group of early land plants, whose specific ecophysiological and biological features, including poikilohydry, sensitivity to moderately high temperature and high dispersal ability, make them ideal candidates for investigating the impact of climate changes. Employing a combined approach of species distribution modelling (SDM) and molecular phylogeography in the temperate moss *Homalothecium sericeum*, we explore the significance of the Mediterranean refugia, contrasting the southern and northern refugia hypotheses, determine the extent to which recolonization of previously glaciated areas has been facilitated by the high dispersal ability of the species and make predictions on the extent to which it will be impacted by ongoing climate change. The Mediterranean areas exhibit the highest nucleotidic diversities and host a mixture of ancestral, endemic and more recently derived haplotypes. Extra-Mediterranean areas exhibit low genetic diversities and Euro-Siberian populations display a significant signal of expansion that is identified to be of Euro-Siberian origin, pointing to the northern refugia hypothesis. The SDMs predict a global net increase in range size owing to ongoing climate change, but substantial range reductions in southern areas. Presence of a significant phylogeographical signal at different spatial scales suggests, however, that dispersal limitations might constitute, as opposed to the traditional view of spore-producing plants as efficient dispersers, a constraint for migration. This casts doubts about the ability of the species to face the massive extinctions predicted in the southern areas, threatening their status of reservoir of genetic diversity.

Keywords: bryophyte, climate change, dispersal, molecular phylogeography, refugium, species distribution modelling

Received 16 February 2012; revised version received 21 April 2012 and accepted 8 May 2012

Introduction

The Mediterranean region appears as a climatic change hotspot (Giorgi, 2006), wherein the increases in both temperature and water stress under the influence of current global climatic change appear to be without any historical precedent in the Quaternary (Petit *et al.*, 2005). As a result, Species Distribution Models (SDMs) predict in the region a local turnover of 60–80% of tree species between the 1990s and 2050 that is about two or three times higher than that predicted for more northern areas (Bakkenes *et al.*, 2002; Thuiller *et al.*, 2005).

The SDMs have, however, several limitations (Keenan *et al.*, 2011). The projection of species distributions in the past or in the future relies on the assumption that species conserve identical niche preferences and migrate to locations that remain suitable. Although evidence for a significant degree of niche conservatism supports in most cases the application of SDMs (Araújo & Peterson, 2012; Petitpierre *et al.*, 2012), species can, however, locally adapt to novel environmental conditions (Jezkova *et al.*, 2011). Extant distributions also represent a complex mix of ecological factors and dispersal limitations that are likely to blur the macroclimatic signal in species distributions (see Normand *et al.*, 2011, for review).

Therefore, evaluating the predictions of SDMs for the past using independent observations from pollen records (Svenning *et al.*, 2011) or molecular phylogeographies (Eckert, 2011; Rodríguez-Sánchez & Arroyo, 2011; Svenning *et al.*, 2011) remains the only way to assess the predictive power of those models for the

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future (see Rodríguez-Sánchez & Arroyo, 2011; for review). In Europe, Italy, the Balkans and the Iberian Peninsula have typically been identified as major glacial refugia, as genetic data suggest population size has been very stable over time (southern refugia hypothesis (SRH), Hewitt, 1999, 2000, 2004; Médail & Diadema, 2009). The substantial levels of differentiation among Mediterranean populations and between Mediterranean and extra-Mediterranean populations of temperate tree species suggest, however, that the Mediterranean areas may not have been the source of postglacial colonization in many instances (Petit *et al.*, 2003, 2005). Rather, evidence from fossils (Svenning *et al.*, 2011), SDM (Svenning *et al.*, 2008) and molecular phylogeography (Petit *et al.*, 2003, 2005; Magri *et al.*, 2006) suggest that trees were scattered in moist microhabitats across Europe during the Last Glacial Maximum (LGM) (northern refugia hypothesis (NRH); see Bhagwat & Willis, 2008; for review). According to the NRH, rapid expansion and diversification triggered by new geographical and/or ecological niche opportunities resulted in low genetic diversity north of 45°N (Petit *et al.*, 2005).

Bryophytes are a group of early land plants, whose specific ecophysiological and biological features make them ideal candidates for investigating the impact of climate change (Tuba *et al.*, 2011). Particularly relevant features include poikilohydry and the reliance on atmospheric precipitation for water and nutrient uptake; extreme sensitivity to moderately warm temperatures in the temperate flora (Furness & Grime, 1982); and efficient dispersal ability (see Hutsemékers *et al.*, 2011; for review). As a result, bryophyte distributions are expected to quickly vary depending on climate change, as confirmed by previous studies of range dynamics (Frahm & Klaus, 2001; Zechmeister *et al.*, 2007) and stratigraphic analyses of macroremains preserved in peat (Jonsgard & Birks, 1995; Ellis & Tallis, 2000).

In this article, we investigate the impact of past and present climates on the distribution and genetic diversity and structure of temperate bryophytes and explore the role of the Mediterranean in their recent evolutionary history. Using the moss *Homalothecium sericeum* as a model and building on the preliminary phylogeography of Hedderson & Nowell (2006), we employ a combined approach of SDMs and molecular phylogeography to address the following issues:

- Did the Mediterranean act as glacial refugium, from which extra-Mediterranean areas were subsequently recolonized (SRH), or do the patterns of spatial genetic structure and diversity conform to a scenario of high divergence and isolation of Mediterranean

areas and recolonization of temperate areas from microrefugia located at >45°N (NRH)?
- To what extent has recolonization of previously glaciated areas been facilitated by the high dispersal ability of *H. sericeum*? Did intense dispersal erase any phylogeographical signal in extant patterns of genetic variation?
- What will be the impact of ongoing climate change for the future distribution of *H. sericeum*?

Material and methods

### Specimen sampling and molecular protocols

Homalothecium sericeum was selected as a typical element of the wide-temperate moss flora of Europe. A total of 130 specimens collected across the entire European range of *H. sericeum* were sampled (Fig. 1, Appendix S1). Three cpDNA loci (*atp*B-*rbc*L, *rpl*16 and *trn*G) were amplified and sequenced in both directions following the protocols described in Laenen *et al.* (2011). Contigs were constructed and aligned using Sequencher 3.1 (Gene Codes Corporation, Ann Arbor, MI). Gaps were inserted where necessary to preserve positional homology in the alignment and indels were scored as binary characters, regardless of their length.

Population genetics analyses

Individuals exhibiting identical multi-locus sequences were grouped within the same haplotype using DnaSP (Librado & Rozas, 2009). Molecular variation was geographically partitioned into five regions, namely Macaronesia, West Mediterranean, East Mediterranean, Euro-Siberian and Atlantic according to Blondel *et al.* (2010) (Fig. 1). Each region was characterized by its haplotypic (He) and nucleotidic (pi) diversity corrected for sample size using Arlequin 3.11 (Excoffier *et al.*, 2005).

Genetic differentiation among geographical regions and presence of phylogeographical signal in the data were assessed by means of comparative analyses employing fixation index (F_{st}) and N_{st}. N_{st} is a measure of genetic differentiation among populations; it is analogous to F_{st}, but takes the genetic distances among haplotypes (here, the Tamura and Nei distance) into account (Pons & Petit, 1996). When $N_{st} > F_{st}$, it means that mutation rates are higher than dispersal rates, generating a phylogeographical pattern. The significance of F_{st} and N_{st} was tested by constructing the distribution of the null hypothesis by means of 999 random permutations of individuals among populations, as implemented by Spagedi 1.3 (Hardy & Vekemans, 2002). The existence of a phylogeographical signal was tested by assessing the significance of the observed difference between N_{st} and F_{st} values by means of 999 random permutations of the allele distance matrix.

We further investigated patterns of genetic differentiation at the scale of individuals within geographical regions along gradients of geographical distance. We estimated pairwise
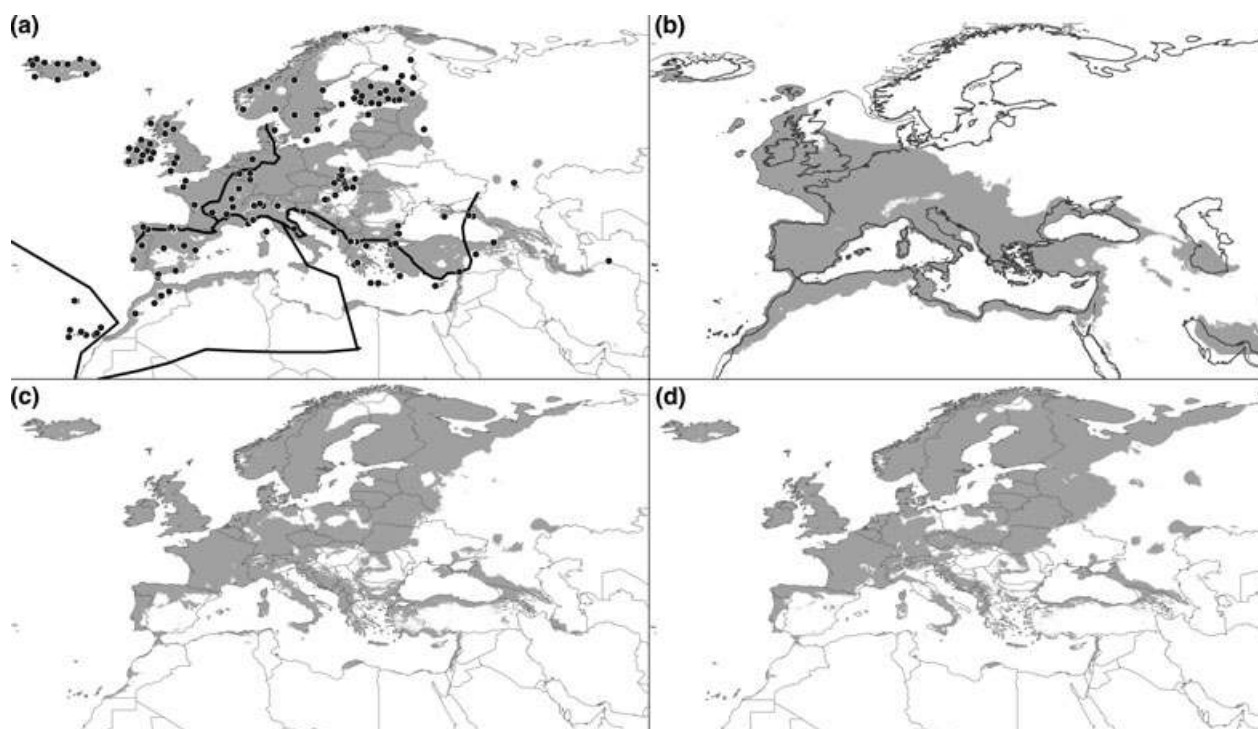
Fig. 1 Predicted binary environmental suitability for *Homalothecium sericeum* across time stages in five biogeographical regions (Macaronesia, West Mediterranean, East Mediterranean, Euro-Siberian and Atlantic), according to the niche model fitted to present locations and climate: (a) present, (b) Last Glacial Maximum/MIROC model, (c) Future projection for 2050 under the A1b scenario, and (d) Future projection for 2080 under the A1b scenario. Dots represent specimens used for extrapolating the niche of *Homalothecium sericeum.*

kinship coefficients between individuals, F_{ij}, using J. Nason's estimator, as well as N_{ij}, a F_{ij} analogue that takes phylogenetic relationships among haplotypes into account. F_{ij} and N_{ij} were computed from global haplotype frequencies within each geographical region. To test for isolation by distance (IBD), the significance of the slope of the regression of F_{ij} or N_{ij} on the logarithm of spatial distance between individuals, $\ln(d_{ij})$, was tested by means of 999 random permutations of population locations (Mantel test) with Spagedi. The mean F_{ij} or N_{ij} values were also computed over i, j pairs separated by geographical distance intervals, d, giving $F_{(d)}$ and $N_{(d)}$. Threshold distance separating intervals were calculated to keep the number of pairwise comparison homogenous between intervals. The difference between $N_{(d)}$ and $F_{(d)}$ was tested by means of 999 random permutations of the genetic distance matrix to test the presence of a phylogeographical signal at different spatial scales.

We sought to detect the signature of past demographic events in present patterns of genetic variation using Fu's Fs statistic. A significantly negative Fs statistics characterizes an excess of low-frequency polymorphisms, indicating population expansion (Fu, 1997). The F_S statistic was calculated using frequency distribution of haplotypes for each biogeographical region separately using Arlequin.

Phylogenetic relationships among the 130 haplotypes and two other *Homalothecium* species used as outgroups, *H. lutescens* and *H. philippeanum*, were inferred by Bayesian analysis using MrBayes 3.1 (Ronquist & Huelsenbeck, 2003). A HKY

substitution model was selected based on the Akaike information criterion as implemented by jModeltest 0.1.1 (Posada, 2008). Indel evolution was described using a model employing identical forward and backward transition rates. Four Metropolis-coupled Markov chain Monte Carlo simulations were run for 10 000 000 generations using MrBayes. Trees and model parameters were sampled every 10 000 generations.

The trees sampled from the posterior probability distribution were used to reconstruct ancestral distribution areas. Each haplotype was assigned to the biogeographical regions where it was sampled. The probabilities of dispersal from one region to another were calculated by estimating the instantaneous rates of dispersal among all possible pairs of regions. We used the 'global' approach, wherein model parameters are first fixed and then used to derive the set of most likely ancestral character states (Pagel, 1999). We examined the impact of the choice of a range of model parameters within and among trees by using the Markov chain model implemented by BayesTraits 1.0 (Pagel *et al.*, 2004) to estimate the posterior probability distributions of ancestral states and rate coefficients. The latter were sampled from flat, uniform prior distributions ranging between 0 and 100. The rate at which parameters are changed ('ratedev') was set at the beginning of each run so that the acceptance rate of the proposed changes globally ranges between 20% and 40%. The chain was run for 10 000 000 generations, and rate parameters and probabilities of ancestral distribution areas were sampled every 1000 generations.

Species distribution models

The presence points of the 130 specimens used in the molecular analyses were completed with an additional 65 observations from herbarium specimens at the Liège (LG) and Madrid (MA) herbaria to cover the entire distribution range of *H. sericeum* in Europe, northern Africa and Macaronesia. Altogether, these data are representative of the entire macroclimatic niche of the species, which is further distributed in a few localities of eastern Canada, southwest Asia, eastward to Iran and additional records from Kashmir and China (Hedderson & Nowell, 2006).

Nineteen bioclimatic variables from Worldclim (Hijmans *et al.*, 2005) were employed as environmental predictors in Maxent 3.3.3k (Phillips *et al.*, 2006). As background, we randomly selected 10 000 points over the entire distribution area of the species. To avoid multicollinearity, 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 ran different models using Maxent to find the optimal variable combination for this data set and used different options for these parameters: regularization multiplayer, selection of background, percentage of test sample, number of replicates. The best model was subsequently identified by means of the AUC statistic value. The parameters selected were: regularization multiplayer = 3, percentage of test sample = 20%, number of replicates = 30 (k-fold cross-validation procedure), background at random in the entire study area. We then used the model to project the potential distribution of *H. sericeum* in the past and in the future. For this purpose, we used data modelled by the Paleoclimate Modelling Intercomparison Project Phase II (PMIP2 for 21 000 years BP) employing both MIROC and CCSM projections (21 ky BP). Future projections (2050 and 2080) were derived by using climate model outputs according to three 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 & Reisinger, 2007). The averaged models were then edited in ArcInfo 9.3 (ESRI, California, USA). The predicted presence values were converted from the logistic gradient to binary presence/absence data using a threshold approach to minimize the commission error (Fielding & Bell, 1997). Because presence-only data were available, a maximum commission error of 0.10 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 to assess changes in range size.

Results

Population genetics and molecular phylogeography

The cpDNA data matrix included 24 variable positions, allowing the identification of 19 haplotypes. Haplotypic and nucleotidic diversities ranged from 0.88 (West Mediterranean) to 0.59 (Euro-Siberian) and 0.001466 (East Mediterranean) to 0.000331 (Euro-Siberian) respectively (Table 1). The Fu's F_S statistic was significantly negative in the Euro-Siberian region ($F_S = -2.99$, $p < 0.05$).

A significant genetic differentiation was found among biogeographical regions ($F_{ST} = 0.181$, $p < 0.0001$). The global N_{ST} (0.469, $p < 0.0001$) was significantly higher than F_{ST} ($p < 0.01$), indicating the presence of a significant phylogeographical signal in the data. Pairwise F_{ST} values among biogeographical regions ranged between 0.051 ($p > 0.05$) between the Atlantic and Euro-Siberian regions to 0.22–0.35 ($p < 0.05$) between Macaronesia and the other biogeographical regions (Table 2). A significant phylogeographical signal, as demonstrated by $N_{ST} > F_{ST}$ at $p < 0.05$, was further found between Macaronesia and the four other biogeographical regions, and between the East Mediterranean and the Euro-Siberian and Atlantic regions (Table 2).

Evidence for IBD was found among specimens within each of the biogeographical regions except Macaronesia and the Atlantic, as evidenced by the significant slope of the regression analyses between pairwise N_{ij} values along a distance gradient (Table 3). Average pairwise N_{ij} values were significantly higher than average F_{ij} values for distance classes < 500km in the eastern Mediterranean and Atlantic region, demonstrating the presence of phylogeographical signal at that scale.

A total of 990 trees were sampled from the posterior probability distribution generated by the Bayesian analysis of the cpDNA matrix. Their 50% majority-rule consensus is presented in Fig. 2. Four haplotypes that are mainly East Mediterranean in distribution but with a few occurrences in the West Mediterranean and one in Macaronesia formed a basal polytomy. Their most recent common ancestor was reconstructed to be of East Mediterranean origin with a posterior probability (p.p.) of 0.92. This polytomy of Mediterranean haplotypes

Table 1 Haplotypic (He ± S.D.) and nucleotidic (pi ± S.D.) diversities, sample size (N), number of haplotypes (*n*) and Fu *Fs* statistics and associated *p*-value in each of the five European biogeographical regions in the moss *Homalothecium sericeum*

	Macaronesia	West Mediterranean	East Mediterranean	Euro-Siberian	Atlantic
He ± S.D.	0.73 ± 0.04	0.88 ± 0.06	0.78 ± 0.06	0.59 ± 0.08	0.67 ± 0.10
pi ± S.D.	0.000454 ± 0.000365	0.000987 ± 0.000653	0.001466 ± 0.000899	0.000331 ± 0.00029	0.000586 ± 0.000444
Fs (*p* value)	1.95 (0.85)	−0.59 (0.41)	0.86 (0.72)	−2.99 (0.035)	24.89 (1.00)
n (N)	4 (27)	7 (20)	6 (20)	8 (45)	5 (18)

Table 2 Genetic divergence (Pairwise F_{ST} (below diagonal) and N_{ST} (above)) at three cpDNA loci in the moss *Homalothecium sericeum* among the four European biogeographical regions. The *p*-value (in parentheses) associated to the F_{ST} and N_{ST} are associated to the null hypotheses that $F_{ST} = 0$ and that $F_{ST} = N_{ST}$ respectively.

	Euro-Siberian	Atlantic	East Mediterranean	West Mediterranean	Macaronesia
Euro-Siberian	–	0.008 (0.810)	0.318 (0.001[*])	0.150 (0.058)	0.818 (0.002[*])
Atlantic	0.051 (0.049)	–	0.288 (0.021)	0.073 (0.690)	0.759 (0.001[*])
East Mediterranean	0.074 (0.028)	0.067 (0.049)	–	0.138 (0.070)	0.483 (0.017[*])
West Mediterranean	0.087 (0.013[*])	0.121 (0.014[*])	0.053 (0.060)	–	0.635 (0.004[*])
Macaronesia	0.350 (0.001[*])	0.302 (0.001)[*]	0.231 (0.001[*])	0.225 (0.001[*])	–

[*]indicates that the test remains significant after the correction of Benjamini & Yekutieli (2001) for multiple tests at the 0.05 significance level

Table 3 Slope (and *p*-value) of the regression analyses between pairwise N_{ij} values along a distance gradient and phylogeographical signal ($N_{ij} > F_{ij}$ test) at different spatial scales in the moss *Homalothecium sericeum* in the five European biogeographical regions

| Region	Slope	*p*-value of $N_{ij} > F_{ij}$
West Mediterranean	$-2.190 \ 10^{-4}$ (0.038)	>0.05 at any distance interval
East Mediterranean	$-2.978 \ 10^{-4}$ (0.015)	0.041 for distances < 500km
Euro-Siberian	$-2.704 \ 10^{-4}$ (0.007)	>0.05 at any distance interval
Atlantic	$-5.343 \ 10^{-5}$ (0.32)	0.009 for distances < 500km
Macaronesia	$-2.903 \ 10^{-4}$ (0.18)	>0.05 at any distance interval

was basal to a dichotomic branch supported with a p.p. of 0.95 leading to a strictly Macaronesian clade comprised of three haplotypes and supported with a p.p. of 1.00, and to a branch supported with a p.p. of 1.00 leading to a second large polytomy of haplotypes from the Mediterranean, Atlantic and Euro-Siberian regions. The most recent common ancestor of this large polytomy was reconstructed to be of Euro-Siberian origin with a p.p. of 0.82. Two clades were further resolved within this large polytomy. Reconstructions of ancestral distribution areas for the first clade (p.p. 0.99) were ambiguous. The clade included haplotype 18, which is comprised of Atlantic and Euro-Siberian accessions, and haplotypes 6 and 9, which included accessions from the West Mediterranean and the Atlantic and formed a clade with a p.p. of 1.00. This West Mediterranean/Atlantic clade was reconstructed to be of West Mediterranean origin with a p.p. of 0.96. The second main clade that was resolved within the large polytomy of Euro-Siberian origin had a p.p. of 0.98. It included haplotype 3, with 50 accessions from both Mediterranean regions, the Atlantic and the Euro-Siberian regions and two haplotypes with one accession, which were both sampled from the Euro-Siberian region. Ancestral distribution areas pointed to an Euro-Siberian origin of the clade with a p.p. of 0.95.

Species distribution models and projections for the LGM and the future

The selected model had a mean AUC value of 0.88 ± 0.05 over the 30 replicates. The variables that most contributed to the model were: annual range temperature (45.95%), precipitation of the coldest quarter (13.57%) and maximum temperature of warmest month (12.45%). The extant potential distribution included a large area across Macaronesia, western North Africa and Europe, from the southernmost Mediterranean areas northwards to Iceland and northwestern Scandinavia and from the westernmost areas to Caucasus.

MIROC (Fig. 1) and CCSM (Appendix S2) projections returned similar results for the LGM distribution in the southern part of Europe, but a wider northern range was predicted with MIROC. *Homalothecium sericeum* showed a broader distribution than at present across the Mediterranean basin and the Atlantic coast (Fig. 1). In northern Europe, the extant conditions seemed to be more suitable for *H. sericeum* compared to the LGM, where no suitable areas were predicted north of Germany. The binary model predicted that the LGM distribution area represented only 58.64% of the extant distribution area (Table 4). The prediction for the species range for 2050 showed that the distribution area will increase (Fig. 1), with gains from 15.6% to 32.8% as compared to present time depending on the climate scenarios, especially towards northeastern areas (Table 4). A relative loss of 15.8–18.8% was predicted to occur mainly in the southern part of the current range. Large portions of the distribution across the central and western range (80.5–82.5%) will remain unaffected. In 2080, the trend will continue, with a further severe decrease in the Mediterranean (19.6–31%%) and an almost complete extinction in northern Africa, while
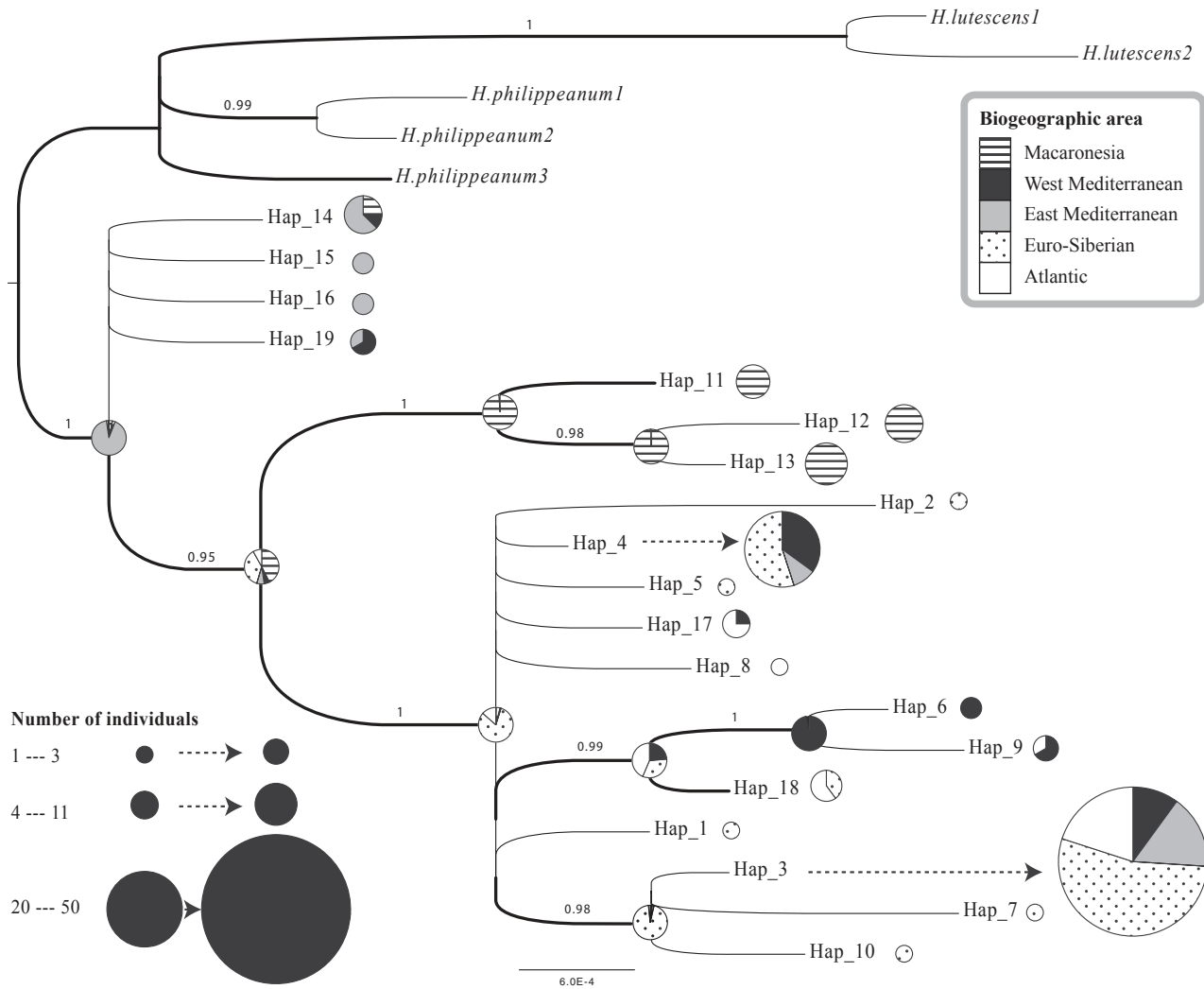
Fig. 2 50% majority-rule consensus of 990 trees sampled from the posterior probability distribution generated using the bayesian analysis of cpDNA sequences of 130 accessions of the moss *Homalothecium sericeum* across its European range. Pie diagrams at terminal nodes represent the proportion of the biogeographical areas occupied by the accessions belonging to each haplotype. Pie diagrams at internal nodes represent the posterior probability of ancestral areas (see Material and Methods for further details about ancestral area reconstructions).

Table 4 Percentage of area maintained, gained and lost as compared to the present distribution area in the moss *Homalothecium sericeum* in Europe according to past (21 000 ky BP using the MIROC projection) and future (2050 and 2080; A1b, A2a and B2a scenarios) modelled distribution ranges

	Stable presence	Loss	Gain
Present vs. 21000 Ky MIROC	58.4	41.6	17.8
Present vs. 2050 (A1b)	81.3	18.6	32.8
Present vs. 2050 (A2a)	80.5	17.8	26.4
Present vs. 2050 (B2a)	82.5	15.8	15.6
Present vs. 2080 (A1b)	72.4	27.6	42.0
Present vs. 2080 (A2a)	67.2	31.0	40.9
Present vs. 2080 (B2a)	78.7	19.6	24.8

the range increase will continue to affect northern Europe for a total relative increase of 24.8–42.0% as compared to present time (Table 4).

Discussion

Response of the temperate moss Homalothecium sericeum to past climate change

The SDM predicted substantial differences in extant and LGM areas for *H. sericeum* across its European range, with a loss of 41.36% in the central and north-eastern range as compared to its extant distribution. As this prediction is based on a niche model built under present-day conditions, its validity depends on whether

the species indeed maintained its ecological niche. This assumption is, at first sight, weakened by the fact that bryophytes may develop tolerance in response to changes in climatic conditions, as suggested by the seasonal variation of their cold tolerance (Rutten & Santarius, 1993) and cold-hardening experiments (Minami *et al.*, 2006). In support to the SDM predictions, however, analyses of extant patterns of genetic variation in *H. sericeum* demonstrated a significant signal of population expansion in the Euro-Siberian region. In fact, although most bryophyte species are preadapted to cold and survive temperatures ranging from −10 to −27 °C (Glime, 2007), their poikilohydric condition prevents them to achieve a positive net photosynthesis during an extended frost period. Therefore, changes in bryophyte communities depending on major climatic shifts during the Quaternary era are evident from the succession of macroremains preserved in peat (Jonsgard & Birks, 1995). Although the indicator status of *H. sericeum* for old-growth forests characterized by steno-ecological conditions in the Mediterranean (Brunialti *et al.*, 2010) is not suggestive of a wide plasticity, these observations do not necessarily rule out the hypothesis of a shift in ecological niche. They suggest, however, that the extent of climate change during the LGM has been sufficient to force the species to migrate to face past climate changes in a much similar way as did temperate tree species (Svenning *et al.*, 2008).

As documented for other temperate mosses (Cronberg, 2000; Stech *et al.*, 2011), ferns (Vogel *et al.*, 1999; Trewick *et al.*, 2002) and angiosperms (see Petit *et al.*, 2005; for review), *H. sericeum* exhibits its highest nucleotidic diversity in the Mediterranean. This pattern points to the long-term accumulation of mutations within a relatively stable environment. Ancestral area reconstructions further identified the East Mediterranean as the area of origin of the species whose ancient presence in the region is testified by the presence of macrofossils in the Kimmeridgian and Chaudinian floras (Miller, 1984). These observations are fully consistent with previous studies that underlined the importance of the East Mediterranean as a reservoir for plant evolution (Mansion *et al.*, 2008, 2009). The presence of Macaronesian, West and East Mediterranean haplotypes in basal position of the *H. sericeum* phylogeography and the existence of an endemic basal Macaronesian clade dated at about 2.5 myrs (Huttunen *et al.*, 2008), point to several westwards colonization waves in the early evolutionary history of the species. This westward colonization pattern corresponds to the most common situation of postglacial recolonization scenarios in higher plants (Petit *et al.*, 2005), further emphasizing the similarity in postglacial

recolonization patterns between temperate moss and tree species.

Despite the fact that the Mediterranean exhibits the highest levels of genetic diversity, ancestral area reconstructions identify the Euro-Siberian region as the origin of the radiation of the extra-Mediterranean haplotypes. This suggests that the NRH, previously evidenced in boreo-nemoral mosses such as *Sphagnum squarrosum* (Szövényi *et al.*, 2006), also holds for wide-temperate species like *H. sericeum*. Recolonization from several scattered microrefugia resulted in a rapid expansion and diversification, as demonstrated by the significantly negative Fu's F_S statistics and the large polytomy of the phylogeography at that level, potentially triggered, as suggested for temperate tree species (Petit *et al.*, 2005), by new geographical and/or ecological niche opportunities. This would explain the differences in shape of the phylogeography in the Mediterranean (including Macaronesian) vs. temperate clades, i.e., long branches bearing witness of long-term accumulation of mutations within a historically stable environment, as further demonstrated by the LGM reconstructions, vs. presence of a large polytomy suggesting radiation within a new environment respectively. Long accumulation of mutations within a comparatively stable environment would further explain why Macaronesian populations of *H. sericeum* are not genetically depauperate, as opposed to the general perception that endemic island plant species and populations have reduced genetic diversity compared with more common and widespread ones (Frankham, 1997; but see Désamoré *et al.*, 2012 for review).

Dispersal limitations in the recolonization of glaciated areas

While a clear signal of population expansion in *H. sericeum* is present within the Euro-Siberian region, the significance of the regression between pairwise individual kinship coefficients and geographical distance within most geographical regions points to the presence of an isolation-by-distance pattern. Dispersal limitations are further emphasized by the global significant phylogeographical signal in the data at different spatial scales, evidencing that the mutation rate exceeds the migration rate. Exactly as in the case of the moss *Pleurochaete squarrosa* (Grundmann *et al.*, 2007), the comparatively long branches from the large polytomy in the phylogeography of *H. sericeum* suggest that differentiation among populations within the same biogeographical region has been fairly high, pointing to a recent rapid expansion followed by strong isolation of the populations as a result of the limited dispersal abilities of this species. Similar limitations to routine dispersal at the

landscape scale were recently reported in mosses (Snäll et al., 2004; Hutsemékers et al., 2010). Thus, dispersal limitations might constitute, as increasingly reported in seed plants (Normand et al., 2011), a migration constraint, even in organisms such as spore-producing plants, which are primarily thought to disperse in a very effective way.

Dispersal limitations in dioecious, and hence, rarely fruiting species such as H. sericeum, Fissidens serrulatus and Kindbergia praelonga are further evidenced by the endemicity of their respective Macaronesian clades (Werner et al., 2009; Hedenäs, 2010). Thus, while suitable habitat conditions were reconstructed for H. sericeum in Macaronesia during the LGM, populations of that region were not involved in the postglacial recolonization of Europe, as has been reported in other moss species (Hutsemékers et al., 2011; Laenen et al., 2011). Rather, the close relationships of the Macaronesian clade with the Eastern Mediterranean clade is reminiscent of the Macaronesian-East Mediterranean disjunction observed in other mosses such as Homalia webbiana, whose isolated phylogenetic position (Olsson et al., 2011) points to a relictual origin and numerous extinctions. These patterns are fully consistent with the relictual series hypothesis (see Carine, 2005, for review), according to which Macaronesian island taxa are the relicts of the fragmentation and reduction of a formerly wider range owing to climate change in Europe and northern Africa.

Predicting the response of H. sericeum to ongoing climate change

Benefits from the predicted increase in the total distribution range of H. sericeum under the impact of ongoing climate change will be similar to those predicted for the temperate tree flora and be largely restricted to the northern regions (Thuiller et al., 2006). In contrast, populations of the Mediterranean face a high risk of extinction over much larger areas than temperate trees such as Fagus sylvatica (Kramer et al., 2010). Given the relative dispersal limitations and the accumulation of genetic diversity in southern areas for H. sericeum and other temperate moss species (Cronberg, 2000; Stech et al., 2011), the comparatively reduced loss of range in southern areas is likely to lead to a substantial decrease of genetic diversity in Europe. Although bryophytes potentially take advantage of dewfall as a source of water (Bates et al., 2005), their poikilohydric condition involves that they become dormant upon desiccation. A positive net photosynthesis is hence difficult or impossible to achieve in areas where moss patches are hydrated for insufficient periods of time, explaining the relative

rarity of mosses in xeric environments. In addition, all of the temperate and boreal species investigated by Furness & Grime (1982) died at 35 °C and most shoots died eventually at >30 °C. Typical temperate forest mosses such as Thuidium tamariscinum died after about 20 days at 29 °C. In bryophytes, acclimatization of water-saturated shoots by short exposure to temperatures above 30 °C for a few hours results in a small, albeit significant increase in the thermal stability of the photosynthetic apparatus (Meyer & Santarius, 1998). This suggests that short-term thermal hardening of hydrated tissues may take place in a similar fashion in bryophytes and flowering plants through the production of heat-shock proteins. However, the short-term heat-hardening capacity of turgid bryophytes is extremely low and, as opposed to that of angiosperms, may not be ecologically relevant (Meyer & Santarius, 1998). Substantial changes are therefore to be expected in the composition of the temperate moss flora of southern Europe. Given the locally important contribution of large carpets of terrestrial pleurocarpous moss species to the biomass of temperate forests, these changes will potentially have severe functional consequences in terms of water storage, nutrient cycling and availability of microhabitats for other organisms (see Tuba et al., 2011, for review).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Voucher information and GenBank accessions numbers.
Appendix S2. Predicted binary environmental suitability for *Homalothecium sericeum* at the Last Glacial Maximum (CCSM projection).

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