

Origin and fate of the single-island endemic moss *Orthotrichum handiense*

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ABSTRACT

Aim Our aims were: to determine the evolutionary origin of the single-island endemic moss *Orthotrichum handiense*; to assess whether its endemism results from a recent origin or founder event, a loss of dispersal ability, specific habitat requirements, or contraction of a formerly wider range; and to make predictions about its ability to face ongoing climate change.

Location Fuerteventura, Canary Islands.

Methods The evolutionary origin of *O. handiense* was determined by phylogenetic analysis and molecular dating. The spatial genetic structure and demographic history of 48 individuals of *O. handiense* were analysed with inter-simple sequence repeat (ISSR) markers through analyses of molecular variance, Mantel tests, mismatch distributions and bottleneck analyses. The macroclimatic envelope of the species was modelled using an ensemble approach of eight species distribution models, and its suitable areas predicted for extant, past (21 ka) and future (2050, 2080) conditions.

Results *Orthotrichum handiense* was resolved as sister to the Californian *O. underwoodii* and their most recent common ancestor was dated to early Miocene–Pliocene. ISSR analyses revealed extremely low levels of genetic diversity and provided evidence for a recent bottleneck and for isolation-by-distance at the local scale. The different models investigated all pointed to the mismatch between the limited extant distribution and the extent of macroclimatically suitable areas. All models predicted climatic unsuitability on Fuerteventura and Lanzarote at 21 ka, but were conflicting in other areas. A dramatic reduction and loss of suitable areas were predicted for 2050 and 2080, respectively.

Main conclusions The phylogenetic position of *O. handiense* points to a long-distance dispersal event from a western North American ancestor and emphasizes the differences in the origin of Macaronesian endemic bryophytes and angiosperms. The predicted absence of suitable macroclimatic conditions in Fuerteventura at 21 ka supports the hypothesis of a palaeoendemic origin and a recent founder event in Fuerteventura, consistent with the low levels of genetic diversity and with evidence for a recent bottleneck. While the biogeographical history of the species hence involves major dispersal events over periods of tens of thousands of years, its ability to respond quickly to predicted climate change during the next few decades is questioned.

Keywords

Climate change, Fuerteventura, isolation by distance, long-distance dispersal, moss, *Orthotrichum handiense*, palaeoendemic, single-island endemic, species distribution models, taxon cycle.

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INTRODUCTION

Single-island endemics (SIEs) are those species that are restricted to a single island (Whittaker & Fernández-Palacios, 2007). In angiosperms, SIEs dominate the endemic floras of many oceanic islands, and the distribution patterns of such an endemic element within an archipelago are typically left-skewed, with very few endemic taxa widespread across the whole archipelago (Carine & Schaefer, 2010, and references therein). In the Canary Islands, for instance, angiosperm SIEs represent 70% (567 species) of the endemic flora of the archipelago (Archavaleta *et al.*, 2010). Analyses of patterns of endemism in the Canarian angiosperm flora further highlighted the highly localized concentration of endemic species, facilitating the recognition of intra-island areas of endemism (Carine *et al.*, 2009). In bryophytes, distribution patterns in the endemic flora across archipelagos are inverted, with more multiple-island endemics (MIEs) than SIEs (Fig. 1). In the Canaries for instance, *Orthotrichum handiense* is the only species of bryophyte endemic to a single island (Losada-Lima *et al.*, 2010).

Because bryophytes exhibit globally higher dispersal capacities than seed plants (Medina *et al.*, 2011), differences in dispersal ability among taxonomic groups offer a straightforward interpretation of the differences in their distribution patterns. In agreement with the 'progression rule' hypothesis (i.e. the displacement from older to younger islands within an archipelago; Funk & Wagner, 1995), Vanderpoorten *et al.*

(2011) proposed that SIE bryophytes are of recent origin, and that their number reflects the comparatively short period of time between the speciation event and the time for new species to disperse towards other islands.

The Madeiran endemic moss *Hedenasiastrum percurrans*, which has never been observed with sporophytes or specialized gemmae, was, however, shown to have originated 40 million years ago (Ma) and to be of palaeoendemic origin (Aigoïn *et al.*, 2009). Its failure to colonize other islands or archipelagos could hence be interpreted in terms of real dispersal limitations. Indeed, the limited dispersal ability of SIEs fits perfectly with the traditional view that island species quickly lose their dispersal ability (Whittaker & Fernández-Palacios, 2007). This hypothesis has, however, been recently challenged in spore-producing plants (Hutsemékers *et al.*, 2011). Alternatively, although the importance of competition in shaping communities remains an area of controversy (e.g. Saunders & Gibson, 2005), the failure of SIEs to occupy other areas could be interpreted in terms of competition, as encapsulated in either the niche pre-emption hypothesis (Silvertown *et al.*, 2005) or the taxon cycle hypothesis (Wilson, 1961; Ricklefs & Bermingham, 2002).

Orthotrichum handiense is restricted to Fuerteventura (González-Mancebo *et al.*, 2011; Medina *et al.*, 2011), the oldest of the emerged islands in the Canaries (20–21 Ma; Carracedo, 2011), and more precisely, to the Jandía Peninsula (143.2 km²; Lara *et al.*, 1999). This is the highest extant part of an island (807 m a.s.l.), which once peaked at

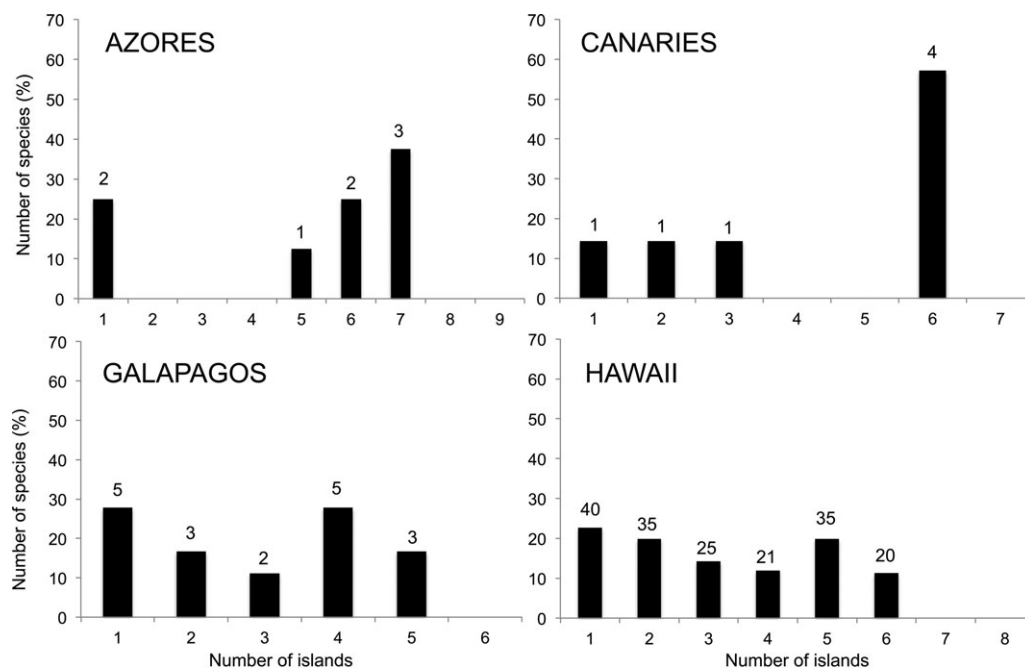


Figure 1 Endemic bryophyte distribution for oceanic archipelagos illustrating, in each case, the number of endemic species in percentage (numbers of species indicated on the bars) having a distribution spanning a given number of islands. The volcanic archipelagos considered are the Azores (number of islands = 9; Gabriel *et al.*, 2010), Canaries (7; Losada-Lima *et al.*, 2010), Hawaii (7; Staples *et al.*, 2004; Staples & Imada, 2006) and Galápagos (6; Gradstein & Weber, 1982). Other complementary sources of information were considered (J. Patiño *et al.*, in prep.). The x-axis represents the number of islands where the species have been recorded, although it should be noted that archipelagos have differing numbers of islands.

2500 m (Carracedo *et al.*, 2005). Owing to its relatively high elevation and situation with respect to the sea, Jandía is one of the few areas on Fuerteventura that is directly influenced by the cloud banks of the trade-wind inversion layer. Jandía has therefore been identified as a refugium for Tethyan Tertiary palaeoendemic lineages (Santos-Guerra, 1990; González-Mancebo *et al.*, 2009).

Using a combined approach of species-level phylogenetics, molecular dating, population genetics and species distribution modelling, we address the question of whether the SIE status of *O. handiense* is the result of a recent evolutionary origin, a recent colonization of the archipelago after dispersal from a continental area, failure of establishment in other potential areas due to a loss of dispersal ability, specificity to unique habitat conditions, or the contraction of a formerly wider range driven by competitive displacement as, for instance, specified within the taxon cycle hypothesis (Wilson, 1961; Ricklefs & Bermingham, 2002). In addition, we project its potential distribution in the future under different climate change scenarios.

MATERIALS AND METHODS

Study area, study species and sampling design

Orthotrichum handiense was described in 1999 as a new endemic moss from the Jandía Peninsula in Fuerteventura (Lara *et al.*, 1999). The possibility that the species can be discovered elsewhere cannot be completely ruled out, but its extremely distinctive morphological features make it unlikely to be confused with any other species in the genus and its endemic status has subsequently been confirmed by intensive fieldwork in Macaronesia and the Mediterranean (Lara *et al.*, 2003; González-Mancebo *et al.*, 2009, 2011) and taxonomic revisions of the genus in the Western Palearctic (Lara *et al.*, 2009). *Orthotrichum handiense* (bryophyte nomenclature follows Losada-Lima *et al.*, 2010; Medina *et al.*, 2012) is mainly epiphytic on the only common shrub species in Jandía – *Asteriscus sericeus* (vascular plant nomenclature follows Arechavaleta *et al.*, 2010), which is also endemic to Fuerteventura (but is now found in cultivation on most of the islands in the archipelago). *Orthotrichum handiense* also occurs occasionally on *Kleinia neriifolia* and basaltic rocks at elevations ranging from 650 m to c. 800 m, occupying a range estimated at 45 ha (González-Mancebo *et al.*, 2009).

Within *Orthotrichum*, molecular work confirmed the main division into phaneroporous and cryptoporous taxa (Goffinet *et al.*, 2004), but subgeneric division within the latter has been questioned (Sawicki *et al.*, 2012). Our phylogenetic sampling therefore included all of the Northern Hemisphere cryptoporous species that share with *O. handiense* a similar morphology in terms of position of the stomata, peristomial arrangement and leaf morphology. Our ingroup sampling thus included 24 species, including four new taxa whose descriptions will be published elsewhere (*Orthotrichum* species 1 to 4; see Appendix S1 in Supporting Information). Two phaneroporous species,

O. acuminatum and *O. affine*, as well as *Ulota crispa* and *Nyholmiella obtusifolia*, were used as outgroups. Wherever possible, each species was represented by several accessions from different geographical regions. Within Jandía, *O. handiense* was collected in the peaks of La Palma, Zarza, Ingenieros and the most north-easterly peak of Jandía. The distances separating these peaks ranged from 323 m to 638 m. In total, 48 cushions separated by at least 5 m were sampled (Appendix S2).

Molecular protocols

DNA was extracted following the protocol described by Goffinet *et al.* (1998), although DNA of some specimens was extracted with the DNeasy Plant Mini commercial kit (Qiagen, Valencia, CA). Four chloroplast loci were targeted for the phylogenetic analyses, namely the *atpB-rbcL* intergenic spacer, part of the *rps4* gene, the *trnG* gene (exons 1 and 2 and the intervening intron), and the *trnL-F* spacer region. These loci were amplified and sequenced in both forward and reverse directions (for more details, see Appendix S1). The polymerase chain reaction (PCR) mix included 0.2 µL *Taq* polymerase, 2.5 µL Mg²⁺ buffer, 1 µL of 10 µM dNTP mix, 1 µL of each primer (10 µM) and DNA extracts diluted in water for a total volume of 25 µL. The PCR included an initial denaturation step of 5 min at 94 °C, 30 cycles of 30 s denaturation at 95 °C, 1 min annealing (48 °C for *trnG* and 52 °C for the other loci) and a 30 s extension at 68 °C, followed by a final extension step of 7 min. PCR products were purified using the Nucleospin Extraction Kit (Macherey-Nagel, Düren, Germany) and sequenced on an ABI Prism 3100 Genetic Analyser. Sequence contigs were assembled using SEQUENCHER 3.1.1 (Gene Codes, Ann Arbor, MI).

The 48 cushions of *O. handiense* were analysed with inter-simple sequence repeat (ISSR) markers. Nine primers (A4, ISSR4, OW1, OW3, OW4, OW5, OW12, UBC 825 and UBC 888; MWG-Biotech, Ebersberg, Germany) were employed. PCR reaction mix included 0.8 units *Taq* polymerase, 2 mM MgCl₂, 200 mM of each dNTP, 400 mM of primer, 10 mM of buffer, 2% of BLOTTO (10% skimmed milk powder and 0.2% NaNO₃) and DNA diluted in water for a total volume of 20 µL. The PCR included 3 min at 94 °C followed by 30 cycles of 15 s at 94 °C, 30 s at 45 °C and 1 min at 72 °C, followed by a final extension step of 7 min at 72 °C. A 5-µL aliquot of each amplification reaction was separated on a 6% polyacrylamide gel. The DNA bands were visualized by silver staining. Presence/absence of polymorphic ISSR marker bands was manually scored using SIGMAGEL 1.0 (Jandel Scientific, San Rafael, CA). The entire procedure, starting from the PCR, was repeated twice for 24 randomly selected specimens to ensure the reproducibility of the scoring.

Phylogenetic and dating analyses

The cpDNA matrix was aligned with CLUSTAL W (Larkin *et al.*, 2007) and subjected to a heterogeneous Bayesian inference as implemented in MRBAYES 3.2.1 (Ronquist &

Huelsenbeck, 2003). For each locus, the best substitution model was selected according to the Akaike information criterion using jMODELTEST 0.1.1 (Posada, 2008). Four Metropolis-coupled Monte Carlo Markov chains were run twice independently and sampled every 1000 of 3,000,000 generations. The convergence of two independent cold chains was estimated in two ways. First, the standard deviation of split frequencies was < 0.01 after 3,000,000 generations. Second, visual inspection of the plot of the log-likelihood score at each sampling point suggested that the four chains reached stationarity. The trees of the 'burn-in' for each run were excluded from the tree set, and the remaining trees from each run were combined to form the full sample of trees assumed to be representative of the posterior probability distribution.

A 50% majority-rule consensus of the trees sampled from the posterior probability distribution was used to fix the topology in a molecular dating analysis using an uncorrelated lognormal relaxed clock as implemented in BEAST 1.6.1 (Drummond & Rambaut, 2007). In the absence of fossil evidence in *Orthotrichum*, a prior distribution on the overall rate of molecular evolution was incorporated to the ucl-mean parameter in BEAST. We used a normal distribution with a mean and standard deviation of 5.0×10^{-4} and 1.0×10^{-4} substitutions per site per million years, respectively (Huttunen *et al.*, 2008; Aigoin *et al.*, 2009), which corresponds to the average absolute substitution rates of cpDNA across a wide range of algae and land plants (Palmer, 1991; Schnabel & Wendel, 1998). A Yule prior on branching rates was employed and four independent chains of 100,000,000 generations were sampled every 10,000 generations. Convergence and acceptable mixing of the sampled parameters were checked using TRACER 1.5 (Rambaut & Drummond, 2009). After discarding the burn-in steps, the runs were combined to obtain an estimate of the posterior probability distributions of the dates of divergence.

Genetic diversity and population differentiation

Genetic diversity metrics corrected for sample size – including average gene diversity over loci, Shannon index's of genetic diversity, percentage of polymorphic loci (% PL), and unbiased expected heterozygosity – were calculated using GENALEX 6 (Peakall & Smouse, 2006) and ARLEQUIN 3.5 (Excoffier & Lischer, 2010). Analysis of molecular variance (AMOVA) as implemented by ARLEQUIN was used to partition genetic variance within and among populations. Significance of the differentiation among localities was assessed after 10,000 random permutations of individuals among localities.

Spatial autocorrelation analyses were implemented to investigate patterns of genetic variation along gradients of geographical distance. Pairwise kinship coefficients (F_{ij}) between individuals were computed with SPAGED1 1.3 (Hardy & Vekemans, 2002) using J. Nason's estimator. The significance of the slope of the regression of F_{ij} on the logarithm of the spatial dis-

tance between individuals was tested by 999 random permutations of population locations (Mantel test).

The past demography of the populations was explored using Luikart & Cornuet's (1998) sign test as implemented in BOTTLENECK 1.2.02 (Piry *et al.*, 1999) using both the infinite-allele model (IAM) and the stepwise mutation model (SMM). The bottleneck test was complemented with two additional analyses performed in ARLEQUIN. First, Tajima's D was used to determine whether the observed patterns of genetic variation departed from expectations of neutral evolution in a theoretical population of constant size through time. Second, we compared the observed frequency distribution of pairwise differences among individuals (mismatch distribution; Rogers & Harpending, 1992) with expected distributions from a population expansion. Populations at demographic equilibrium or in decline should exhibit a multimodal distribution of pairwise differences, whereas populations that have experienced a sudden demographic expansion should display a unimodal distribution (Rogers & Harpending, 1992). Expected distributions under a model of sudden demographic expansion were calculated with ARLEQUIN from 1000 parametric bootstrap replicates. The raggedness index of the observed mismatch distribution was also computed. Low raggedness values are typical of an expanding population, whereas high values are observed among stationary or bottlenecked populations (Harpending, 1994).

Species distribution modelling

The occurrence of *O. handiense* in only five pixels of *c.* 1 km (0.0083° grid size) renders any attempt at modelling the distribution of the species challenging (e.g. Guisan & Zimmermann, 2000). Models for species with a narrow environmental range variation might, however, prove stable and reliable, even when generated with few presences (Pearson *et al.*, 2007; Mateo *et al.*, 2010). We ran a set of analyses with a range of settings to take uncertainty in the models into account and produce an ensemble of model outputs (Araújo & New, 2007; Mateo *et al.*, 2012) to seek areas in Macaronesia, north-western Africa and the Iberian Peninsula (Fig. 2a) that would exhibit similar climatic conditions to those in which *O. handiense* is currently recorded. Modelling methods that incorporate interactions between predictor variables and complex response shapes (e.g. GBM, MARS and BRUTO) have been shown to outperform most methods when data sets with large sample sizes are available (Elith *et al.*, 2006; Guisan *et al.*, 2007). The use of these techniques on small data sets has, however, been questioned (Wisz *et al.*, 2008; Mateo *et al.*, 2010). To describe the extant climate envelope of *O. handiense* and determine if such conditions can be found in other areas under present, past and future climate conditions, we employed BIOCLIM, DOMAIN and MAXENT, which have been recommended in the case of small data sets (Hernandez *et al.*, 2006; Papeş & Gaubert, 2007; Pearson *et al.*, 2007).

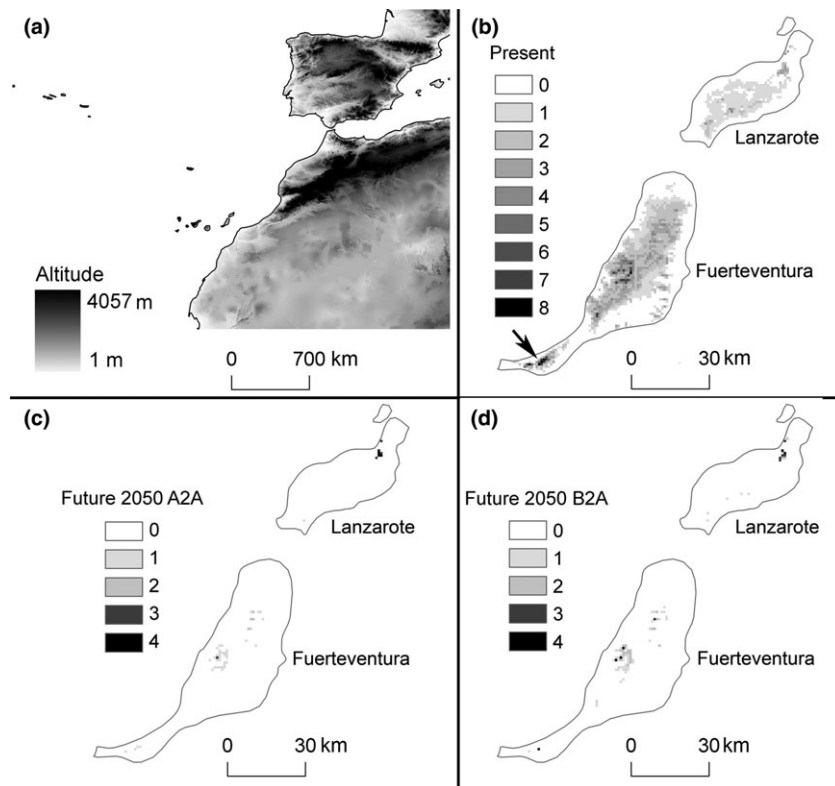


Figure 2 The study area and ensemble models of the predicted climate suitability for the Fuerteventura endemic moss *Orthotrichum handiense* at two time points. (a) Study area; (b)–(d) close-ups of Fuerteventura and Lanzarote, where panel (b) shows present conditions, with the arrow indicating actual area of occupancy of *O. handiense* (complete figures for each model are provided in Appendix S3), panel (c) shows future scenario A2A for 2050, and panel (d) shows future scenario B2A for 2050. The models are based on contemporary climate envelope models using MAXENT (two options), DOMAIN (75, 85 and 95 threshold), and BIOCLIM (1.5%, 2.5% and 5% threshold). The grey scale refers to the numbers of models predicting the occurrence of the species.

We ran the DOMAIN and BIOCLIM models in DIVA-GIS 7.5 (Hijmans *et al.*, 2004; <http://www.diva-gis.org/>). DOMAIN is a climate envelope technique that measures, through Gower's distance index, the climatic similarity between pixels where the target species is present and those where it is not. The index ranges between 0 and 100, high values corresponding to high climatic similarity among pixels. The gradient of climatic similarities among pixels was converted into a binary presence/absence maps to determine whether two pixels exhibited similar climatic conditions using a threshold approach. A range of values from 70 to 95 (the threshold value recommended by Carpenter *et al.*, 1993) was employed to determine whether different model settings affected the interpretation of the results. BIOCLIM (Busby, 1991) is another climate envelope technique that seeks the climatic range of the points for each climatic variable and then uses the concept of a bounding box to enclose the data points formed from a number of climate variables, within statistically defined limits. Different envelopes were constructed from the ranges of climate variables that enclosed 90–99% of the data points. MAXENT 3.3.3.k (Phillips *et al.*, 2006) was run with the following parameter selection: maximum training sensitivity plus specificity threshold, five replicates (bootstrap), regularization value $\beta = 2$. In

MAXENT, the environmental layers are used to produce 'features', which constrain the species' probability distribution. We contrasted two 'feature' options ('linear, quadratic and product features' versus 'autofeatures') that affect the complexity of the model produced.

Nineteen bioclimatic variables from WorldClim (Hijmans *et al.*, 2005) were employed as environmental predictors. Guisan & Zimmermann (2000) recommended that at least 10 data points should be used to obtain a meaningful estimate of the response of the target species per fitted environmental variable. Following Pearson *et al.* (2007), who included 20 variables to model the distribution of species with up to five presence records, we decided to use several variables in the model to describe a global climate setting rather than focusing on one or a few variables, but decreased the number of variables to be included by eliminating one of the variables in each pair with a Pearson correlation value > 0.8 . As background, we randomly selected 5000 points over the Canary Islands. The variables included in the model were: BIO1 (annual mean temperature), BIO9 (mean temperature of the driest quarter), BIO10 (mean temperature of the warmest quarter), BIO12 (annual precipitation) and BIO17 (precipitation of the driest quarter).

An ensemble model was generated using eight different single binary models for present climatic conditions: MAXENT (two 'feature' options), DOMAIN (75, 85 and 95 threshold), and BIOCLIM (5%, 2.5% and 1.5% threshold). We then used this ensemble model to determine whether similar climatic conditions to those where *O. handiense* currently occurs were found at 21 ka, and will be present in the future. Palaeoclimatic data were obtained from the Palaeoclimate Modelling Intercomparison Project Phase II (PMIP2 for 21 ka) employing both the Model for Interdisciplinary Research on Climate (MIROC) and the Community Climate System Model (CCSM) projections. Future projections (2050 and 2080) were derived by using climate model outputs according to three scenarios (A1, A2A and B2A) proposed by the Intergovernmental Panel on Climate Change Data Distribution Centre (IPCC, 2007).

RESULTS

The 50% majority-rule consensus of the trees sampled from the posterior probability distribution generated by the MRBAYES analysis is presented in Fig. 3. The three specimens of *O. handiense* form a clade with a posterior probability (PP) of 1.00. *Orthotrichum handiense* is embedded within a clade with a PP of 1.00, mainly composed of Californian endemics. Within that clade, *O. handiense* is resolved as sister to *O. underwoodii* and their sister relationship has a PP of 1.00. The most recent common ancestor of *O. handiense* and *O. underwoodii* dates back to the early Miocene–Pliocene (10.4 Ma; 95% highest posterior density interval (HPD): 4.36–18.21 Ma).

The nine primers screened produced 95 reliable ISSR bands in the 48 colonies of the four localities studied. The average number of loci per primer was $9.46 (\pm 1.91)$. Of these loci, 18 (18.95%) were polymorphic (Table 1), ranging from 11 to 13 per site. The average multilocus gene diversity was 0.051 ± 0.007 and ranged from 0.025 to 0.061 per site (Table 1). The Shannon index ranged from 0.044 to 0.086 per site, with an average of 0.073 ± 0.010 . Total multilocus expected heterozygosity was 0.455 and ranged between 0.250 and 0.501 per site (Table 1).

The AMOVA demonstrated a significant geographical partitioning of genetic variation ($F_{ST} = 0.53$, $P < 0.001$) among localities. A significant pattern of isolation by distance was found, as shown by the significance of the slope of the regression analysis between pairwise F_{ij} and geographical distances (Fig. 4).

A significant signature of a genetic bottleneck was detected, with a number of loci exhibiting significant heterozygote excess of 1 and 21 ($P < 0.001$) under both the IAM and SMM models, respectively. Tajima's D was significantly negative ($D = -1.847$; $P < 0.01$). The mismatch distribution was multimodal, with a raggedness index of 0.262.

The ensemble model of the three SDM techniques employed with a range of settings to take uncertainty in the response into account is presented in Fig. 2, and the results

of each model for the present are shown in Appendix S3. With DOMAIN and a 95 threshold value, climatic suitability was restricted to a few areas in Fuerteventura. The potential distribution area was enlarged to cover both Fuerteventura and Lanzarote at lower threshold values up to 70. Similar results were obtained with BIOCLIM with a range of threshold values between 1.5 and 5%, although the potential distribution area was more restricted than with DOMAIN. In MAXENT, the potential distribution area similarly encompassed scattered areas in Fuerteventura, Lanzarote and north-western Africa using the 'linear, quadratic and product features' option (Appendix S3). With the 'autofeature' option, scattered areas from all of the Canary Islands and north-western Africa were predicted as climatically suitable (Appendix S3). The different models investigated all pointed to the climatic unsuitability of Fuerteventura and Lanzarote at 21 ka, but returned an ambiguous picture in other areas. While both DOMAIN and BIOCLIM projections pointed to complete climate unsuitability across the Canary Islands and the nearby continents, areas identified as potentially suitable for *O. handiense* were resolved in some of the other Canary Islands and/or north-western Africa with MAXENT (Fig. 5). For 2050, all the models pointed to a substantial reduction in climatic suitability (Figs 2c & d) and none of the models predicted survival in any area in 2080.

DISCUSSION

Orthotrichum handiense was resolved, in agreement with previous morphological investigations (Garilletti *et al.*, 2001), as sister to *O. underwoodii*, and their most recent common ancestor was dated to the early Miocene to early Pliocene (95% HPD, 4.36–18.21 Ma; average, 10.4 Ma). Because *O. handiense* is embedded within a clade otherwise solely composed of Californian endemics, and because its origin largely post-dates the opening of the North Atlantic, about 40 Ma, its distribution must be interpreted in terms of a long-distance dispersal event of North American origin. While the prevalence of long-distance dispersal (LDD) over vicariance has been questioned in angiosperms (Kadereit & Baldwin, 2012), LDD remains to date the only documented mechanism accounting for the large suite of trans-Atlantic disjunctions observed in bryophytes (Huttunen *et al.*, 2008; Devos & Vanderpoorten, 2009), emphasizing differences in dispersal ability between the two groups.

The western North American origin of *O. handiense* adds to the growing evidence for the trans-Atlantic origin of a large suite of Macaronesian endemic bryophytes (for reviews see Vanderpoorten *et al.*, 2007; Devos & Vanderpoorten, 2009) and fully supports the hypothesis (Vanderpoorten *et al.*, 2011) that Macaronesian endemic angiosperms and bryophytes exhibit completely different evolutionary origins owing to their different dispersal capacities. Indeed, while the vast majority of Macaronesian endemic angiosperms originated from ancestors distributed in southern Europe or northern Africa (Carine *et al.*, 2004), the data presented here

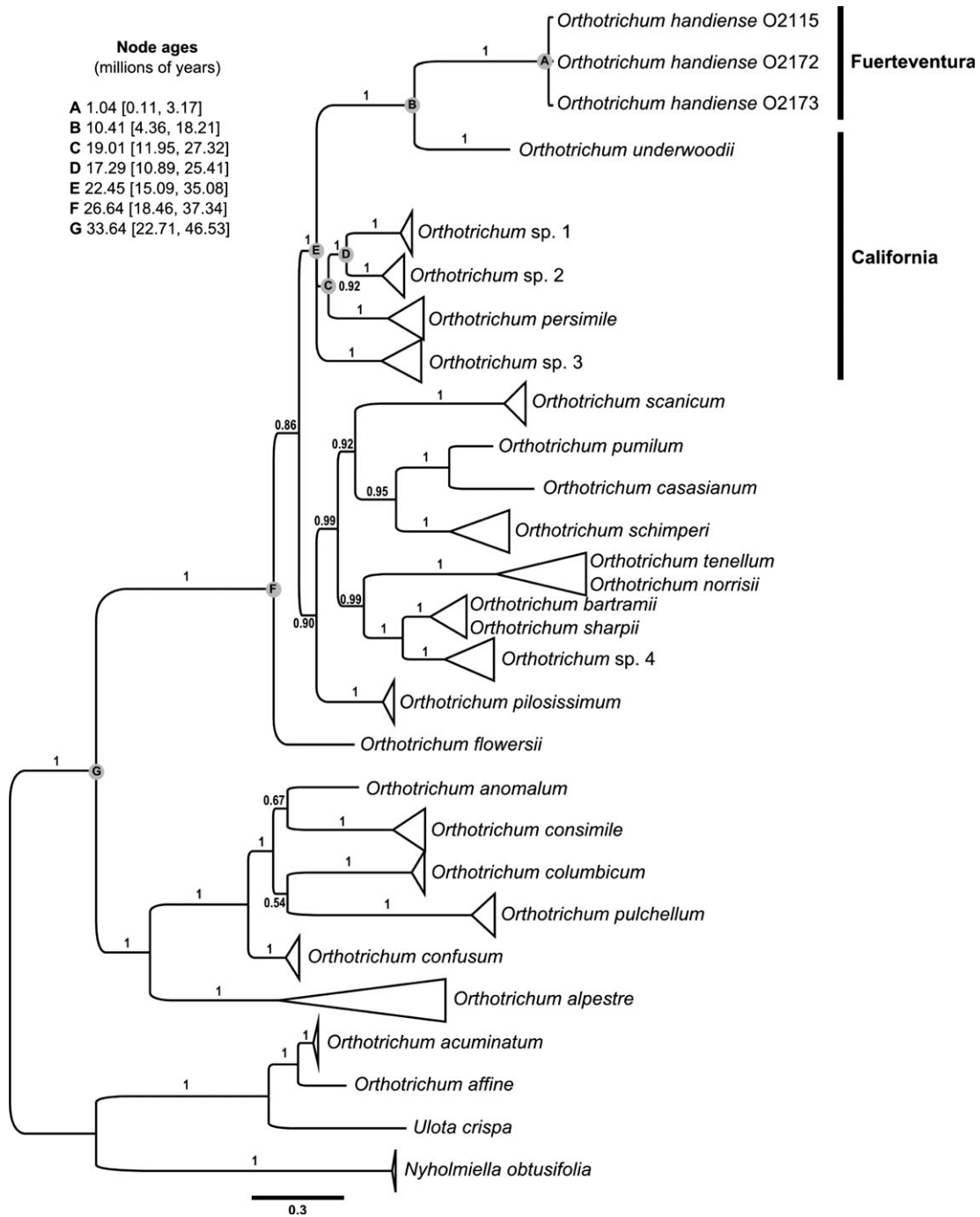


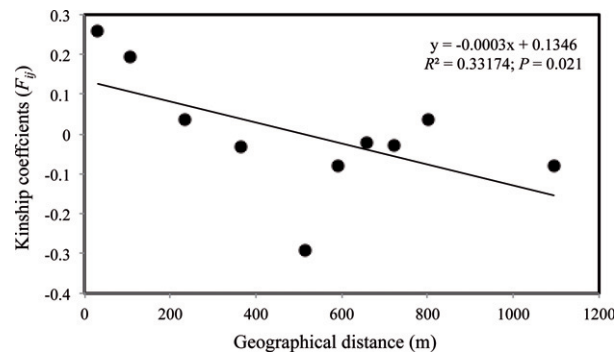
Figure 3 Fifty per cent majority-rule consensus of the trees sampled from the posterior probability distribution generated by a Bayesian analysis of combined sets *atpB-rbcL*, *rps4*, *trnG*, *trnL-F* sequence data in *Orthotrichum handiense* and its closest species. Numbers on branches correspond to their posterior probabilities and the bar indicates the number of substitutions per site. Mean posterior divergence times (and 95% highest posterior density intervals) are presented for selected nodes in millions of years. *Orthotrichum* species 1–4 are unpublished taxa resulting from ongoing research (R. Medina *et al.*, in prep.), all of them consistently diagnosable by both morphology and molecular methods.

fully support the notion that Macaronesian endemic bryophytes tend to evolve from geographically remote source populations to hamper gene flow with nearby continental populations and enhance the chances of speciation (Vanderpoorten *et al.*, 2011).

Despite its ancient origin, which readily rules out the hypothesis that the restricted range of the species results from a recent speciation event, *O. handiense* exhibits extremely low levels of genetic diversity. The Shannon index of 0.044–0.086 reported here for *O. handiense* pales by

Table 1 Standard diversity indices for the sampled specimens of *Orthotrichum handiense* from four localities on Fuerteventura (Canary Islands), using nine ISSR markers.

Site	La Palma	Zarza	Ingenieros	North-eastern	Total
No. of colonies	10	18	12	8	48
No. of bands	91	91	92	87	95
No. of private bands	0	0	3	0	3
No. of polymorphic sites	12 (12.63%)	13 (13.68%)	12 (12.63%)	11 (11.58%)	18 (18.95%)
Average gene diversity over loci	0.062 ± 0.036	0.063 ± 0.035	0.0630.036	0.028 ± 0.019	0.053 ± 0.041
Shannon's index	0.081 ± 0.022	0.086 ± 0.023	0.0820.022	0.044 ± 0.012	0.073 ± 0.010
Expected heterozygosity	0.492 ± 0.086	0.465 ± 0.116	0.5010.071	0.250 ± 0.001	0.455 ± 0.093

**Figure 4** Mean pairwise kinship coefficients (F_{ij}) resulting from comparisons of the inter-simple sequence repeat patterns between pairs of individuals (48) of the moss *Orthotrichum handiense* in relation to the geographical distance separating them.

comparison with similar studies employing ISSR markers in mosses (0.119 and 0.174 in Canarian populations of *Isoetecium myosuroides*; Patiño *et al.*, 2010; 0.238 and 0.316 in Italian populations of *Pleurochaete squarrosa*; Spagnuolo *et al.*, 2007). The low levels of genetic diversity in *O. handiense* are consistent with the significant signal of a recent bottleneck found in patterns of extant genetic variation. It is also consistent with the mismatch observed between the limited extant distribution and the extent of macroclimatically suitable areas, which points to either a recent founder event or a severe range contraction caused by the emergence of more competitive species during the taxon cycle typically found on oceanic islands (Ricklefs & Bermingham, 2002).

These two hypotheses are not necessarily mutually exclusive and indeed, reconstructions of the extent of climatically suitable areas 21 ka suggest that both apply. The climatic range to which *O. handiense* is currently restricted might not reflect its complete climatic range, so that the projection of the climate envelope fitted to present locations and climate into the past might result in an underestimation of the actual past range of the species. All of the investigated models predicted the absence of *O. handiense* in Fuerteventura and Lanzarote 21 ka. Only MAXENT projections pointed to the existence of suitable climate conditions in other Canary Islands and/or the North African coast (Fig. 5). Substantial uncertainty thus remains regarding the actual area of diversification of *O. handiense* following its LDD from western North America. These predictions are, however, fully congruent with the minimum age of the diversification of the spe-

cies, 100 ka, and with its palaeoendemic origin and comparatively recent arrival to Fuerteventura.

This dynamic scenario is fully consistent with the idea that the extremely restricted current range of *O. handiense* is not due to severe dispersal limitations. A significant partitioning of genetic variation was found among populations that are several hundreds of metres apart, and a significant correlation between genetic similarity and geographical distance between pairs of specimens was observed. This observation clearly indicates that isolation by distance (IBD) operates at the local scale in *O. handiense*. A moss capsule typically contains, however, hundreds of thousands of spores. Even though the deposition of spores follows a relatively fat-tailed deposition model (Sundberg, 2005; Pohjamo *et al.*, 2006) resulting in the observed IBD patterns, every capsule has the potential to contribute to regional or transcontinental dispersal, so that local IBD and instances of rare long-distance dispersal events are not mutually exclusive. The spatial genetic structure observed in *O. handiense* is, in fact, very similar to that reported for widespread species in a continental setting (Snäll *et al.*, 2004; Hutsemékers *et al.*, 2010; Korpelainen *et al.*, 2011), further supporting the idea that island bryophytes do not lose their dispersal power (Hutsemékers *et al.*, 2011). *Orthotrichum handiense* is monoicous and produces sporophytes in abundance (*c.* 60% shoots are fertile; González-Mancebo *et al.*, 2009) and during most of the year, further weakening the hypothesis that its SIE status is due to its limited dispersal ability.

The interpretation of *O. handiense* as an ancient species, whose recent occurrence in Fuerteventura was made possible

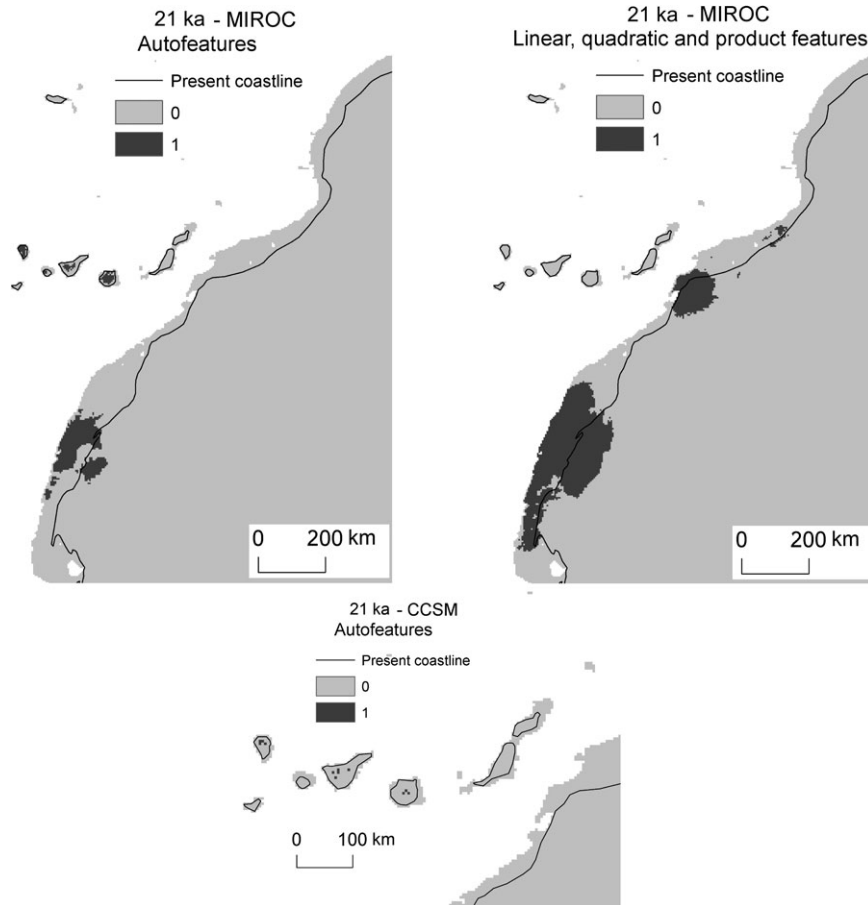


Figure 5 Model of the predicted climate suitability for the Fuerteventura endemic moss *Orthotrichum handiense* at 21 ka using MAXENT (option 1: autofeatures; option 2: linear, quadratic, and product features). Palaeoclimatic data were obtained from the Paleoclimate Modeling Intercomparison Project Phase II (PMIP2) employing both MIROC and CCSM projections.

thanks to the presence of specific macroclimatic conditions, reinforces the role of oceanic archipelagos, and in particular of Macaronesia, as refugia for palaeoendemics that have gone extinct (or appear to have done) in their primary continental regions (Aigoïn *et al.*, 2009; Bell & Hyvönen, 2010). This status is, however, seriously threatened in the context of climate change. All of the investigated models pointed to the severe decrease of climatically suitable conditions for *O. handiense* across the Canary Islands by 2050 and to their complete absence by 2080. These results, coupled with the rarity of LDD events in the biogeographic history of *O. handiense* and evidence for local isolation-by-distance patterns, further cast doubts about the ability of this and other moss species (Désamoré *et al.*, 2012) that have been traditionally perceived as efficient dispersers to avoid extinction due to predicted climate change by migrating towards suitable areas within such a short timeframe.

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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 accession numbers for the specimens of the genus *Orthotrichum*, *Ulota* and *Nyholmiella* sampled for the phylogenetic and molecular dating analyses.

Appendix S2 Voucher information for the 48 individuals of *Orthotrichum handiense* sampled for the spatial genetic structure and demographic history analyses.

Appendix S3 Predicted climate suitability for the Fuerteventura endemic moss *Orthotrichum handiense* under present climate conditions according to the climate envelope fitted to present locations and climate, using MAXENT (two options), DOMAIN (75, 85 and 95 threshold), and BIOCLIM (1.5%, 2.5% and 5% threshold).

BIOSKETCH

Jairo Patiño is a postdoctoral researcher of the Belgian Funds for Scientific Research at the University of Liège, Belgium. His scientific interests include island biogeography, ecology and evolution of spore-dispersed plants on oceanic islands and the conservation of the Macaronesian laurel forest.

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