

## Approximate Bayesian Computation Reveals the Crucial Role of Oceanic Islands for the Assembly of Continental Biodiversity

JAIRO PATIÑO<sup>1,2,3,\*</sup>, MARK CARINE<sup>4</sup>, PATRICK MARDULYN<sup>5</sup>, NICOLAS DEVOS<sup>6</sup>, RUBÉN G. MATEO<sup>1,7</sup>,  
JUANA M. GONZÁLEZ-MANCEBO<sup>2</sup>, A. JONATHAN SHAW<sup>6</sup>, AND ALAIN VANDERPOORTEN<sup>1,3</sup>

<sup>1</sup>Department of Biology, Ecology and Evolution, University of Liège, Bât. B22, Boulevard du Rectorat 27, 4000, Liège, Belgium; <sup>2</sup>Department of Plant Biology, University of La Laguna, c/ Astrofísico Francisco Sánchez, s/n, 28071, Tenerife, Spain; <sup>3</sup>Azorean Biodiversity Group (GBA, CE3C – Center for Ecology, Evolution and Environmental Changes) and Platform for Enhancing Ecological Research & Sustainability (PEERS), Universidade dos Açores, Rua Capitão João d'Ávila, Pico da Urze, 9700-042 Angra do Heroísmo, Terceira, Açores, Portugal; <sup>4</sup>Plants Division, Department of Life Sciences, The Natural History Museum, Cromwell Road, London, SW7 5BD, UK; <sup>5</sup>Evolutionary Biology and Ecology, Université Libre de Bruxelles (ULB), CP 160/12, av FD Roosevelt 50, 1050, Brussels, Belgium; <sup>6</sup>Department of Biology, Duke University, Box 90338, Durham, NC 27708, USA; and <sup>7</sup>Department of Ecology and Evolution, University of Lausanne, Lausanne, CH-1015, Switzerland

\*Correspondence to be sent to: Department of Biology, Ecology and Evolution, Liege University, Bât. B22, Boulevard du Rectorat 27, 4000, Liège, Belgium; E-mail: jpatino.llorente@gmail.com

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**Abstract.**—The perceived low levels of genetic diversity, poor interspecific competitive and defensive ability, and loss of dispersal capacities of insular lineages have driven the view that oceanic islands are evolutionary dead ends. Focusing on the Atlantic bryophyte flora distributed across the archipelagos of the Azores, Madeira, the Canary Islands, Western Europe, and northwestern Africa, we used an integrative approach with species distribution modeling and population genetic analyses based on approximate Bayesian computation to determine whether this view applies to organisms with inherent high dispersal capacities. Genetic diversity was found to be higher in island than in continental populations, contributing to mounting evidence that, contrary to theoretical expectations, island populations are not necessarily genetically depauperate. Patterns of genetic variation among island and continental populations consistently fitted those simulated under a scenario of *de novo* foundation of continental populations from insular ancestors better than those expected if islands would represent a sink or a refugium of continental biodiversity. We suggest that the northeastern Atlantic archipelagos have played a key role as a stepping stone for transoceanic migrants. Our results challenge the traditional notion that oceanic islands are the end of the colonization road and illustrate the significant role of oceanic islands as reservoirs of novel biodiversity for the assembly of continental floras. [Approximate Bayesian computation; bryophytes; colonization; long-distance dispersal; island biogeography; last glacial maximum.]

Oceanic islands have long been viewed as natural laboratories where some of the most fundamental theories in ecology and evolutionary biology have been elaborated (Losos and Ricklefs 2009). Given the strength of a founder event from one or a few successful migrants, theory suggests that oceanic island lineages should be genetically depauperate (Barrett et al. 1996; Frankham 1997). The geographic isolation and topographical complexity of oceanic islands, however, have promoted both allopatric speciation and adaptive radiations, resulting in unique biotas characterized by high levels of endemism, and a suite of specific life history traits, known as island syndromes (Carlquist 1974; Whittaker and Fernández-Palacios 2007). In particular, the loss of dispersal capacities following island colonization, first discussed by Charles Darwin (Darwin 1859), has been documented in a phylogenetically diverse range of lineages including insects, birds, and angiosperms (Carlquist 1974; Cody and Overton 1996; Whittaker and Fernández-Palacios 2007).

Low levels of genetic diversity, limited dispersal capacities, and the loss of defensive capacities (owing to the relaxed pressure of interspecific competition and predation on islands), have driven the view that oceanic islands are “the end of the colonization road,” with insular biotas typically lacking the capacity to disperse and establish in continental areas. Oceanic islands have, therefore, traditionally been considered

as evolutionary “sinks” of biodiversity (Wilson 1961; Carlquist 1974). Experimental (Cody and Overton 1996; Talavera et al. 2012; Patiño et al. 2013) and genetic (Fernández-Mazuecos and Vargas 2011; Hutsemékers et al. 2011) support for island syndromes, such as the loss of dispersal power and low-genetic diversity, are, however, conflicting. A growing body of phylogenetic evidence points to discrete episodes of continental back-colonization at the level of individual lineages, suggesting that oceanic islands might play a role as refugia (the “boomerang effect”; Caujapé-Castells 2011; Fernández-Mazuecos and Vargas 2011; Hutsemékers et al. 2011). Such an interpretation is consistent with several features of oceanic islands during the glacial periods of the Pleistocene including buffered climate conditions as compared to continents (Weiss and Ferrand 2007; Weigelt et al. 2013), a larger size (Rijsdijk et al. 2015) and, due to the emergence of seamounts that are currently submerged, a higher connectivity with continents than today (Fernández-Palacios et al. 2011). Striking examples of *de novo* continental colonization following an insular, stepping-stone model of colonization (e.g., Filardi and Moyle 2005) have further challenged the traditional perception of oceanic islands as sinks of biodiversity. Altogether, this has revolutionized the discipline of island biology, suggesting that islands are not always necessarily the end of the “colonization road” (Heaney 2007; Bellemain

and Ricklefs 2008). Nevertheless, evidence for the colonization of continents from islands is equivocal in many instances, and the intensity of migrations, the associated changes in effective population sizes, and the timing of those events, remain largely unknown.

Bryophytes (mosses, liverworts, and hornworts) exhibit a suite of biological traits that make them particularly interesting to determine whether oceanic islands may indeed represent sources of biodiversity for continental floras. Bryophytes are dispersed by spores and asexual diaspores that may be transported by air currents across large distances (Muñoz et al. 2004). Mounting phylogeographic evidence points to the high capacities of bryophytes for transoceanic dispersal (see Lewis et al. 2014 for review), and macroecological patterns suggest that island bryophyte communities are much more at equilibrium in terms of species richness with continental ones due to recurrent migrations than are angiosperm communities (Patiño et al. 2014). In agreement with plant groups such as angiosperms (Caujapé-Castells 2011), a few case studies in bryophytes have shown that oceanic islands appear as potential refugia that have played a key role for the postglacial recolonization of continental floras during the Late Pleistocene (Hutsemékers et al. 2011; Laenen et al. 2011). Furthermore, the much lower levels of competition in bryophyte communities than in angiosperms (Rydin 2009) implies that the niche preemption hypothesis, a likely barrier to island–continent migration due to saturated continental communities (see Whittaker and Fernández-Palacios 2007 for review), may not apply to the former.

Here, we utilize an integrative approach with species distribution modeling and population genetic analyses based on approximate Bayesian computation (ABC) (Bertorelle et al. 2010; Csilléry et al. 2010) to investigate oceanic island–continental relationships at the scale of an entire biogeographic region. As compared to phylogenetic approaches previously employed to reconstruct the biogeographic history of sister–species relationships (e.g., Losos and Ricklefs 2009; Caujapé-Castells 2011), ABC approaches offer a promising tool in biogeography to infer the intensity and timing of changes in demographic parameters (e.g., effective population size) over recent time periods (Fagundes et al. 2007), associated, for instance, with the climatic fluctuations during the Late Pleistocene analyzed in the present study.

The bryophyte flora of the northeastern Atlantic (NEA) was employed as a model because it represents an exceptional case wherein a substantial portion of the flora is restricted or largely restricted to the Macaronesian oceanic archipelagos of the Azores, Madeira, and the Canary Islands together with the western fringes of continental Europe and northwest Africa (Supplementary Fig. S1 available on Dryad at <http://dx.doi.org/10.5061/dryad.7cj77>). Based on earlier studies that have challenged the view of oceanic islands as the end of the “colonization road” (Carine et al. 2004; Bellemain and Ricklefs 2008) and have in

particular pointed out the role of the NEA islands as dynamic refugia (Fernández-Mazuecos and Vargas 2011; Hutsemékers et al. 2011; Laenen et al. 2011), we initially contrasted two competing historical scenarios for the NEA bryophyte flora (Fig. 1), in which the islands are: 1) dead ends for lineages of continental origin; or 2) glacial refugia for the postglacial recolonization of continental regions. Preliminary population genetic analyses and species distribution models returned, however, conflicting results that could not be fully explained by these two traditional scenarios, and we therefore tested a new competing hypothesis (3), according to which islands are sources of *de novo* colonization for continental biodiversity.

## MATERIALS AND METHODS

### *Model Organisms and Geographic Framework*

The NEA bryophyte flora was selected as a model because it exhibits many species that are disjunct between the western fringe of Europe and Macaronesia (Preston and Hill 1999; Supplementary Fig. S1, available on Dryad at <http://dx.doi.org/10.5061/dryad.7cj77>), a biogeographic region including the Azores, Madeira, and the Canary Islands (Fernández-Palacios et al. 2011). The NEA bryophyte flora typically exhibits affinities for wet, mild climates. According to Preston and Hill (1999) biogeographic classification of European bryophytes, 19 mosses and 32 liverworts of the NEA bryophyte flora are qualified as hyperoceanic (restricted to the extreme western fringe of the continent), and another 90 and 38 species, respectively, as oceanic (restricted to Western Europe). Because of their biogeographic affinities, (hyper) oceanic species are mainly restricted to the subtropical evergreen forest in Macaronesia and to the wettest areas along the European and western Mediterranean fringes.

Eleven species were selected (Supplementary Data S1 available on Dryad at <http://dx.doi.org/10.5061/dryad.7cj77>), representing approximately 20% and 9% of the hyperoceanic and oceanic species of the NEA flora, respectively. The species included 10 mosses (*Dicranum scottianum* Turner ex Robt. Scott, *Fissidens serrulatus* Brid., *Homalia lusitanica* Schimp., *Myurium hochstetteri* (Schimp.) Kindb., *Ptychomitrium nigrescens* (Kunze) Wijk & Margad., *P. polyphyllum* (Sw.) Bruch & Schimp., *Sematophyllum substrumulosum* (Hampe) E. Britton, *Tetrastichium fontanum* (Mitt.) Cardot, *T. virens* (Cardot) S.P. Churchill, and *Ullota calvescens* Wilson), and one liverwort (*Saccogyna viticulosa* (L.) Dumort.). Only one liverwort species was included in our data set because many NEA liverwort species are also present in tropical areas, and particularly in the Neotropics (Preston and Hill 1999). We focused on species that are either entirely restricted to the NEA region or, if they are more widespread, are otherwise restricted to areas of the western Mediterranean with a similar mesoclimate. Between 40 and 90 specimens were sampled across the entire range of each species in

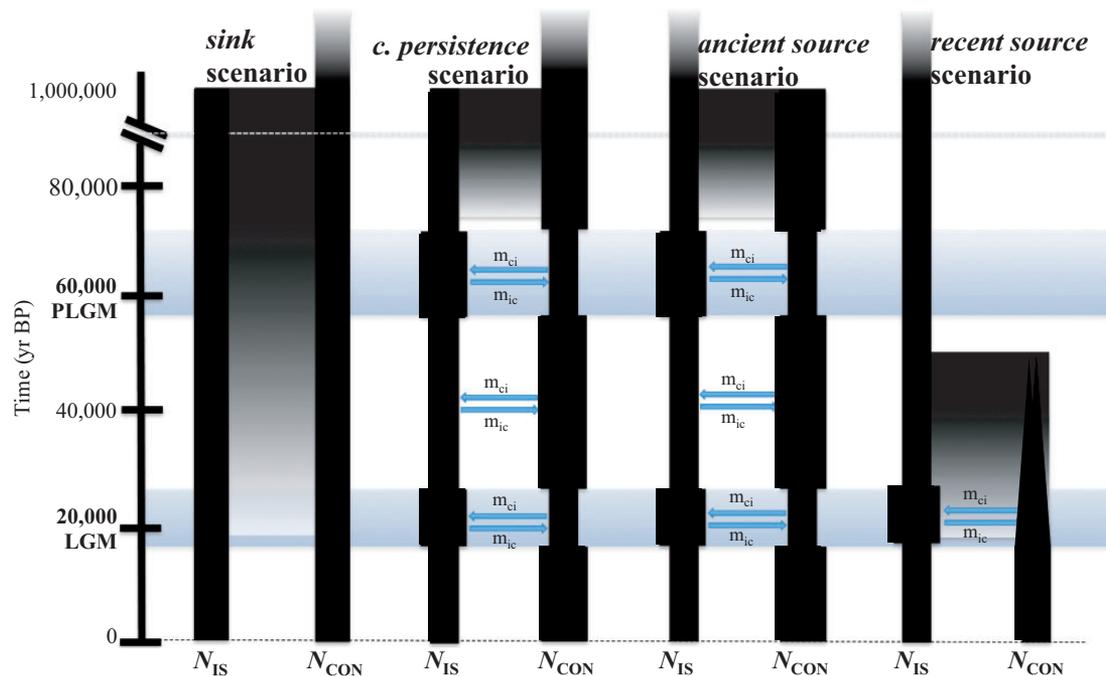


FIGURE 1. Competing hypothetical scenarios for the origin and relationships between island and continental populations. *Sink scenario*: island populations originate from continental ancestor(s) and never back-colonized the continent. *Continental persistence (c. persistence) scenario*: island populations originate from continental ancestor(s), but subsequent migrations are unconstrained. Effective population size varies with climatic conditions. *Source scenario*: continental populations originate from island ancestor(s), and expand since an initial founder event that took place before the PLGM (*ancient source*), or between the LGM and PLGM (*recent source*). LGM = Last Glacial Maximum (from 26,000 to 19,000 years BP); PLGM = Penultimate Last Glacial Maximum (also called the first major ice advance, from 74,000 to 59,000 years BP). A semi-transparent band highlights the two glacial periods, LGM and PLGM.  $N_{IS}$  and  $N_{CON}$  = the effective population size in the island and continental regions, respectively. The gray gradient area indicates the temporal period where the founding event of the derived population could take place under each demographic scenario.

Europe (and parts of northwestern Africa in the case of *S. substrumulosum*) and Macaronesia (Supplementary Fig. S1 and S2, and Data S1 available on Dryad at <http://dx.doi.org/10.5061/dryad.7cj77>). For each species, we aimed to sample balanced numbers of specimens from islands and continents. In some species, which exhibit a narrow distribution on the continent (e.g., *Ptychomitrium nigrescens*, *Tetrastichium fontanum*, and *T. virens*), however, sampling size was larger on the islands, reflecting the distribution of the species.

#### Species Distribution Modeling

Species distribution models (SDMs) were generated for each species to produce estimates of past and present population size depending on different historical scenarios, which were used as prior distributions in the ABC analyses (see further). The macroclimatic conditions that prevail under present conditions at each of the sampling points with a resolution of 5 km<sup>2</sup> were employed as predictors. To avoid sampling bias and the nonindependence among observations, only points that were separated by at least 0.04 decimal degrees (~5 km) from each other were retained. Geographic coordinates for specimens used in this study are provided in Appendix S1 available on Dryad at <http://dx.doi.org/10.5061/dryad.7cj77>. Nineteen bioclimatic

variables from Worldclim database ([www.worldclim.com](http://www.worldclim.com)) were employed as environmental predictors. As background, we randomly selected 10,000 points in the area circumscribed in Supplementary Fig. S1a available on Dryad at <http://dx.doi.org/10.5061/dryad.7cj77>. This area was defined beyond the current species ranges, including the Macaronesian archipelagos, the western fringe of Europe, and the western Mediterranean, to a larger area including large portions of North Africa and the western half of Europe, as the geographic background should not only reflect the extant, but also the potentially occupied range in the past (Acevedo et al. 2012). 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 ( $R$ ) > 0.8. The final set of variables used to run the models for all the species were: maximum temperature of warmest month, minimum temperature of coldest month, precipitation of wettest month, precipitation of driest month, and precipitation of warmest quarter.

Models were generated using an ensemble of four different techniques, including Generalized Linear Models, MaxEnt (Maximum Entropy), Gradient Boosting Machine, and Random Forests, as implemented by BIOMOD 2.0 (Thuiller et al. 2009 and references therein). For MaxEnt, the regularization multiplayer

was changed to two to avoid overprediction (Mateo et al. 2013). Models were calibrated with 70% of the data and then evaluated with the remaining 30% using the area under the curve (AUC) and the maximum true skill statistic (TSS). For each technique, presences and pseudo-absences used to calibrate the model were weighted such as to ensure neutral (0.5) prevalence. The procedure was replicated 10 times, resulting in a total of 40 models (10 replicates  $\times$  4 techniques). The models with an AUC  $>0.8$  and a TSS  $>0.7$  were selected to generate the final ensemble model, and their contribution to the latter was proportional to their goodness-of-fit statistics.

The ensemble models generated for each species were then projected onto palaeoclimatic layers of the last glacial maximum (LGM) using general circulation model simulations from two climate models by the Paleoclimate Modeling Intercomparison Project Phase II (PMIP2 for 21,000 years BP): The Community Climate System Model (CCSM, version 3; Collins et al. 2006) and the Model for Interdisciplinary Research on Climate (MIROC, version 3.2; Sakamoto et al. 2012).

Binary maps of the potential presence of each species were generated to visually represent the extent of potentially suitable areas. For that purpose, the continuous suitability index was transformed into a binary presence/absence variable from a given threshold. To take the influence of the criterion employed to define the threshold into account, we generated three binary models: one minimizing the commission error, one maximizing the AUC, and one maximizing the TSS score of the binary model. For each species, a consensus model of the three different binary models was finally generated.

#### DNA Extraction, Amplification, and Sequencing

Total genomic DNA was isolated from each specimen listed in Supplementary Data S1 (available on Dryad at <http://dx.doi.org/10.5061/dryad.7cj77>) using a Cetyltrimethylammonium Bromide (CTAB) extraction protocol without RNase treatment (Doyle and Doyle 1987) and purified using the GeneClean III Kit (MP Biomedicals, OH, USA). For a range of chloroplast DNA and nuclear DNA, loci were screened for amplification success and nucleotide variation for each species. The nuclear loci employed in the present study were characterized by McDaniel et al. (2013), who specifically targeted unicopy genes that, in the haploid moss gametophyte, are not expected to include paralogous copies. In fact, direct sequencing of PCR products did not reveal competing peaks at single positions, which would be indicative of the presence of several copies as shown, for instance, in multicopy ribosomal regions such as the 18S-26S internal transcribed spacer (ITS; Košnar et al. 2012). The list of selected loci for each species, along with information on primer sequences, annealing temperatures, and sequence assembling is provided in Supplementary Table S1 (available on Dryad at <http://dx.doi.org/10.5061/dryad.7cj77>).

Molecular data sets comprised a total of between one and six chloroplast and nuclear loci depending on the species (Supplementary Table S1, available on Dryad at <http://dx.doi.org/10.5061/dryad.7cj77>).

For the nuclear loci BI894288–188, AW086779–195 and AW086783–208, touchdown polymerase chain reactions (PCRs) were performed to enhance specificity, sensitivity, and yield. The first cycling phase started with an annealing temperature equal to the melting temperature of the primers plus 10°C (McDaniel et al. 2013). PCR products were purified before sequencing using the Exonuclease Enzymatic Reaction (New England Biolabs, Ipswich, MA, USA).

Forward and reverse sequencing of the purified amplicons was conducted using the BigDye Terminator v. 3.1 cycle sequencing kit (Applied Biosystems, Foster City, CA, USA). Forward and reverse sequences were assembled and edited using Sequencher 4.01 (Gene Codes, Ann Arbor, MI, USA). Contigs were aligned using Clustal W (Larkin et al. 2007) and GUIDANCE (Penn et al. 2010), and the alignments obtained were manually refined using PhyDE (Müller et al. 2006). Regions of incomplete data at the 3' and 5' ends of the target loci were excluded from subsequent analyses.

A total of 1925 cpDNA and 465 nDNA sequences were produced for the 649 specimens analyzed. In addition, 70 DNA sequences of *F. serrulatus* were downloaded from GenBank. In the genetic analyses described in the subsequent sections, the nDNA loci were treated as unlinked regions ranging from 391 to 704 bp, whereas the cpDNA loci were treated as a single (linked) locus, ranging from 364 to 794 bp. All GenBank accession numbers are available from <http://www.sysbio.oxfordjournals.org/>, and DataDryad repository at <http://dx.doi.org/10.5061/dryad.7cj77> (Supplementary Data S1, available on Dryad at <http://dx.doi.org/10.5061/dryad.7cj77>).

#### Model Setting

We compared the observed patterns of genetic diversity and structure with those expected under three demographic scenarios in an ABC framework (Csilléry et al. 2010; Wegmann and Excoffier 2010). The *sink* scenario fits with the theory according to which islands are the “end of the colonization road” because they accumulate biodiversity of continental origin (see Bellemain and Ricklefs 2008 for review). In the *sink* scenario, migrations were accordingly strictly asymmetric from continental sources to oceanic islands (Fig. 1). In the *continental persistence* scenario, island populations were derived, but not disconnected from continental ones (i.e., migration rates from or towards the islands were not constrained). In the *source* scenario, continental populations were founded *de novo* by migrants of insular origin. To determine the timing of continental colonization (Fig. 1), the source scenario was further split into *recent* and *ancient source* scenarios, according to which the founding event of the continental populations took place either between the LGM and the

first major ice advance during the Late Pleistocene (here called the penultimate last glacial maximum [PLGM]; Van Andel and Tzedakis 1996) (*recent source*) or before the PLGM (*ancient source*). The time of the continental founding event ( $T_{\text{MERGE}}$ ), therefore, distinguished the two variants of the *source* scenario. The glaciations had a similar impact on effective population sizes in the *continental persistence* and the *ancient source* scenarios. However, the two differ in that the island populations display a role as sinks or sources, respectively, in the *continental persistence* and the *ancient source* scenarios.

#### Estimation and Prior Distributions of Demographic Parameters and the ABC Approach

The prior distributions of the parameters employed in the ABC analyses are listed in Supplementary Tables S2 and S3 (available on Dryad at <http://dx.doi.org/10.5061/dryad.7cj77>). Absolute nucleotide substitution rates were sampled from a log-uniform distribution according to the results of relaxed-clock analyses across the Moss and Liverwort Tree of Life (Laenen et al. 2014), with an upper bound of  $4 \times 10^{-4}$  and  $5 \times 10^{-4}$  substitutions/site/myr in mosses and liverworts, respectively, and a lower bound conservatively set at  $1 \times 10^{-7}$  substitutions/site/myr in both lineages. The age of first sexual reproduction was employed as a proxy for generation time (Lorenzen et al. 2011). All the investigated species are, according to During's (1992) classification of life strategies, perennials, forming long-lasting carpets in relatively stable habitats such as rocks or forest ground, or long-lived shuttles, colonizing relatively long-lived habitats such as tree trunks and branches. Such species are sexually mature around the age of 5 years (Longton 1997). In the complete absence of information on migration rates, the latter were sampled from a log-uniform distribution ranging from a 0 to 1 proportion of migrants from population  $i$  to  $j$  per generation (Supplementary Table S2, available on Dryad at <http://dx.doi.org/10.5061/dryad.7cj77>) (Fagundes et al. 2007; Csilléry et al. 2010; Wegmann and Excoffier 2010; Lorenzen et al. 2011).

In a review on the theoretical effective population size in bryophytes, Bengtsson and Cronberg (2009) concluded that “the effective size is rarely much smaller than the scored number of haploid gametophytic individuals.” Bryophyte populations are, however, highly clonal (Cronberg et al. 2006; Hutsemékers et al. 2010, 2013; Karlin et al. 2011), so that the actual number of individuals in a population is extremely difficult to assess (Patiño et al. 2013). Thus, information on effective population size in bryophytes is extremely scarce (e.g., Hutsemékers et al. 2011; Shaw et al. 2014). Here, effective population sizes at the present time and at the LGM for the oceanic archipelagos ( $N_{\text{MAC}}$ ) and the continental regions ( $N_{\text{CONTINENT}}$ ) were derived from the final consensus species distribution models (see above). For each species, the number of macroclimatically suitable

pixels of  $5 \text{ km}^2$  was summed up in Macaronesia and in the continental region, respectively (circumscribed in Supplementary Fig. S1, available on Dryad at <http://dx.doi.org/10.5061/dryad.7cj77>). From a review of the literature documenting small-scale patterns of genetic variation in bryophytes (Shaw 2009 and references therein), we found that the number of different genotypes reported in populations on hundreds of square meters to a few square kilometers, ranges between 1 and 25. We considered that this represents the minimal number of actual distinct individuals in such populations. We, therefore, set the upper bound of the uniform distribution, from which effective population size per pixel of  $5 \text{ km}^2$  was sampled, to a conservative value of 50.

The summation of this potential  $N_e$  across suitable pixels defined a range that was used as a proxy for the carrying capacity of each region (Supplementary Table S3 available on Dryad at <http://dx.doi.org/10.5061/dryad.7cj77>). Although the time lag between habitat availability and colonization is low in vagile organisms like bryophytes, making it possible to use maps of ecological suitability as proxies for actual distributions (Mateo et al. 2013), species do not necessarily occupy their entire potential range due to dispersal and/or other limitations. The procedure described above, therefore, leads to a maximum theoretical estimation of the carrying capacity of each region. We then extrapolated the potential carrying capacities obtained for the LGM to the PLGM, and for the present time to the last interglacial (26,000–56,000 years BP). The fact that, for all the species and time slices considered, the mode of the posterior probability distribution of  $N_e$  (Results section) was centered within the range of the prior distribution (Supplementary Table S3, available on Dryad at <http://dx.doi.org/10.5061/dryad.7cj77>), and that the 95% upper limit of the posterior distribution lied within the range of the prior, confirms that the prior that we employed is realistic.

To simulate founder effects during the continental colonizations in the *recent source* scenario, we forced the size of the continental population to be small and sampled its value from a uniform prior ranging between 2 and 100 individuals (Supplementary Table S3, available on Dryad at <http://dx.doi.org/10.5061/dryad.7cj77>). For the other models, including the *sink*, *continental persistence*, and *ancient source* scenarios, priors for continental population size during the founding event were drawn from the SDM approach described above. In all models, the ancestral population size was sampled from a uniform prior distribution ranging between 10 and 20,000 individuals to allow for the coalescence of the most ancestral alleles.

#### ABC Analyses and Model Selection

The fit of the observed data to the four biogeographic scenarios (*sink*, *continental persistence*, *ancient source*,

and *recent source*; Fig. 1) was investigated using a standard rejection procedure proposed by Pritchard et al. (1999). The program SIMCOAL v. 2.0 was employed to perform coalescent simulations (Laval and Excoffier 2004). For each species and scenario,  $10^6$  serial-coalescent simulations were conducted. At each simulation, parameter values were randomly sampled from the prior distributions described in Supplementary Tables S2 and S3 (available on Dryad at <http://dx.doi.org/10.5061/dryad.7cj77>). The procedure resulted in the simulation of  $10^6$  sequence matrices of the same size (i.e., number of sequences, alignment length) as those of the observed data. We tested a total of four scenarios, resulting in four million serial-coalescent simulations per species (a total of 44 million simulations were performed in the present study).

We then used the program Arlsumstat (Excoffier and Lischer 2010) to compute, for each species and geographic region (i.e., Macaronesia and Western Europe plus northwestern Africa), the following summary statistics of genetic diversity and differentiation: 1) mean multilocus heterozygosity within each region; 2) mean multilocus number of pairwise differences within each region; and 3) global multilocus  $F_{ST}$  between Macaronesia and continental Western Europe and northwestern Africa. These summary statistics were computed for both the observed data ( $S_{obs}$ ; Supplementary Table S4, available on Dryad at <http://dx.doi.org/10.5061/dryad.7cj77>) and simulated data ( $S_{sim}$ ). Following Beaumont et al. (2002), an Euclidean distance (Equation 1) was calculated between the observed and simulated summary statistics (which were previously normalized, see further).

$$\delta = \|S_{sim} - S_{obs}\| \quad (1)$$

For each scenario and species, we retained the best 5000 simulations (i.e., those with the smallest Euclidean distance between the simulated and observed summary statistics) resulting in 20,000 simulations for the four scenarios for each species. The Euclidean distances from those 20,000 retained simulations per species were recomputed from standardized summary statistics with common mean and standard deviation (option “standardize-Stats” in ABCtoolbox), and the simulations were sorted by ascending Euclidean distances. The posterior probability of each model was then taken as the proportion of the first 1000 simulations performed under a given model included in the set of 1000 smallest distances (Estoup et al. 2004).

Once the best model had been selected, we estimated demographic parameters under this scenario using a general linear model (ABC-GLM) postsampling regression adjustment for the 1000 retained simulations (Wegmann et al. 2010). We report the mode, median, and 95% confidence interval for each model parameter estimate.

Since model choice under an ABC framework can be biased by the use of insufficient summary statistics (Robert et al. 2011), we empirically attempted to

evaluate the performances of the specific ABC analyses implemented here. For this purpose, we estimated the rate at which our favored demographic model (the *source* scenario, see Results) was chosen when the data were generated under the two other alternative hypotheses, the *sink* and the *continental persistence* scenarios. This was performed by simulating 100 new data sets under the *sink* and the *continental persistence* scenarios, and by analyzing each resulting 100 pseudo-observed data sets in exactly the same way as the original observed data (Wegmann and Excoffier 2010; Wegmann et al. 2010).

## RESULTS

Species distribution modeling, employing macroclimatic variables as predictors and projected onto palaeoclimatic layers for the LGM (Fig. 2) revealed that the extent of climatically suitable areas on islands remained stable or increased at the LGM (Supplementary Figs. S2 and S3, available on Dryad at <http://dx.doi.org/10.5061/dryad.7cj77>). Conversely, on the continental regions the extent of climatically suitable areas at the LGM was substantially reduced in comparison to the present (Supplementary Figs. S2 and S3, available on Dryad at <http://dx.doi.org/10.5061/dryad.7cj77>), except for *T. fontanum* and *T. virens* (Supplementary Fig. S3, available on Dryad at <http://dx.doi.org/10.5061/dryad.7cj77>). The extent of climatically suitable areas on the continental regions at the LGM, however, remained much larger than that on the oceanic islands (Fig. 2c).

Genetic diversity was substantially higher in island than in continental populations across 9 of the 11 species analyzed (Supplementary Table S4, available on Dryad at <http://dx.doi.org/10.5061/dryad.7cj77>). Genetic variation was slightly higher in continental populations only in *F. serrulatus* and *S. viticulosa* (Supplementary Table S4, available on Dryad at <http://dx.doi.org/10.5061/dryad.7cj77>).

The relative posterior probabilities calculated for each model provided strong statistical support for the two variants of the *source* scenario (Fig. 3), suggesting that the continental European populations of all species are derived from Macaronesian migrants. For six species (*H. lusitanica*, *P. nigrescens*, *S. viticulosa*, *T. fontanum*, *T. virens*, and *U. calvoescens*), we obtained estimates indicating that the continental populations were founded from insular ancestors 28,500–41,500 years BP (95% highest posterior density interval [HPD] for the upper bounds ranging from 20,000–49,000) (Supplementary Table S5, available on Dryad at <http://dx.doi.org/10.5061/dryad.7cj77>). Both the *ancient* and the *recent source* scenarios efficiently described the demographic history of another four species (*D. scottianum*, *M. hochstetteri*, *P. polyphyllum*, and *S. substrumulosum*) for which the continental populations were founded from insular ancestors 29,500–530,000 years BP (95% HPD for the upper bounds ranging from 446,000 to 869,000) (Supplementary Table S5, available on Dryad at <http://dx.doi.org/10.5061/dryad.7cj77>).

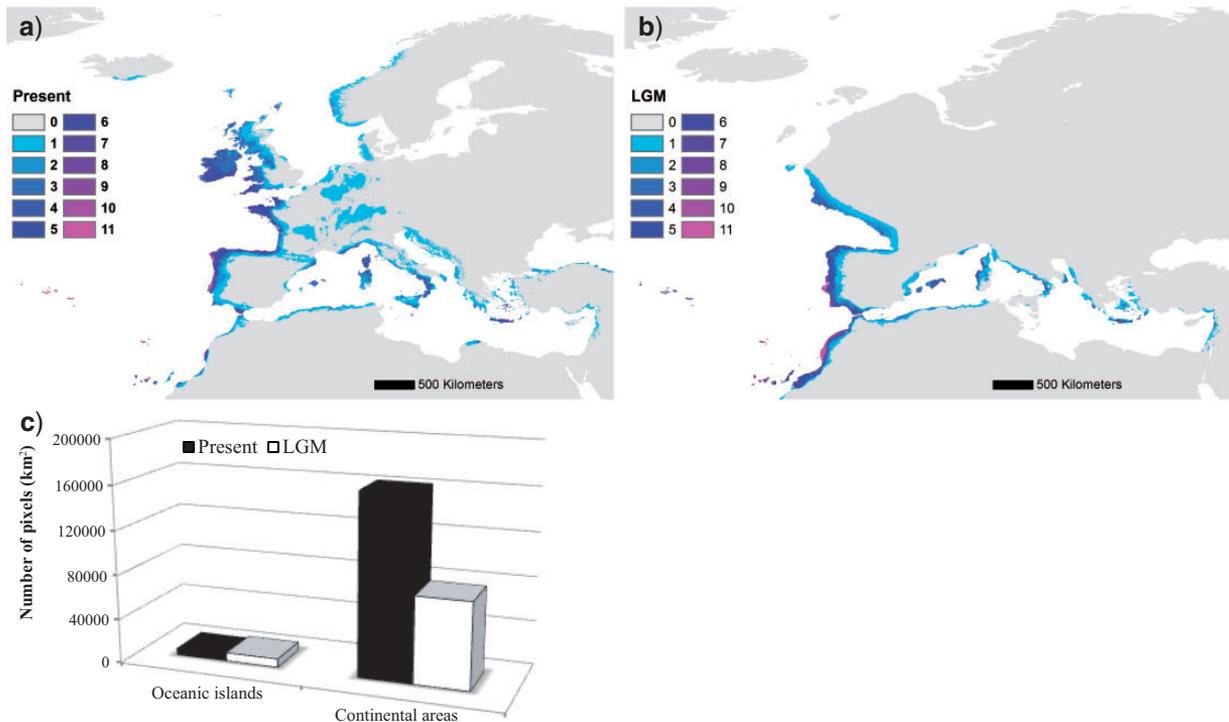


FIGURE 2. Modeled potential ranges of 11 bryophyte species distributed across Macaronesia, including the Azores, Madeira, and the Canary Islands, and the NEA coasts at present (a) and the LGM (b). The color scale represents the number of species for which macroclimatic conditions are defined as suitable. Bar diagram (c) shows the total number of 5 km<sup>2</sup> pixels across the continental and insular regions at present and LGM for the 11 species together.

The single exception was *F. serrulatus*, where the summary statistics of genetic structure and diversity observed were consistently closer to those derived from simulated data that fit with the *ancient source* scenario (Fig. 3); the continental populations were founded *ca.* 260,000 years BP (Supplementary Table S5, available on Dryad at <http://dx.doi.org/10.5061/dryad.7cj77>).

The standard rejection procedure was validated by the analyses of pseudo-observed data sets generated under the *sink* and *continental persistence* scenarios. The analyses of the pseudo-observed data sets generated under the *sink* scenario marginally favored the *recent source* scenario in a range of 3–12 cases out of 100 with an associated estimated probability ranging from 0.027 to 0.445 (Supplementary Table S6, available on Dryad at <http://dx.doi.org/10.5061/dryad.7cj77>). The analyses of the pseudo-observed data sets generated under the *continental persistence* scenario favored the *recent source scenario* in 1–21 cases of 100, depending on the species with an estimated probability ranging from 0.062 to 0.434 (Supplementary Table S6, available on Dryad at <http://dx.doi.org/10.5061/dryad.7cj77>). With both types of pseudo-observed data sets, the *source* scenario was significantly rejected (probability of this scenario <0.05) in 90% of the cases, showing the potential of this ABC procedure to discriminate the *source* scenarios from the *sink* and the *continental persistence* scenarios.

## DISCUSSION

This study supports the hypothesis that the Macaronesian archipelagos were the point of departure for the establishment of a significant component of the NEA bryophyte flora during glacial–interglacial cycles from the mid to the Late Pleistocene. Accordingly, genetic diversity in Atlantic bryophytes was substantially higher in island than in continental populations (Supplementary Table S4, available on Dryad at <http://dx.doi.org/10.5061/dryad.7cj77>), contributing to mounting evidence that, contrary to theoretical expectations (Barrett et al. 1996; Frankham 1997), island populations are not necessarily genetically depauperate (Fernández-Mazuecos and Vargas 2011; Laenen et al. 2011; Désamoré et al. 2012; García-Verdugo et al. 2015). The extremely low-continental genetic diversity contrasts markedly with the extent of suitable areas at the LGM as defined by the SDMs (Fig. 2b). This finding suggests either that continental populations went through a much more severe bottleneck than SDM analyses indicate, or that continental populations were established from relatively recent founding events.

The standard rejection procedure showed the potential of the ABC procedure to discriminate the *source* scenarios from the *sink* and the *continental persistence* scenarios. The summary statistics of genetic structure and diversity across a set of independent lineages were

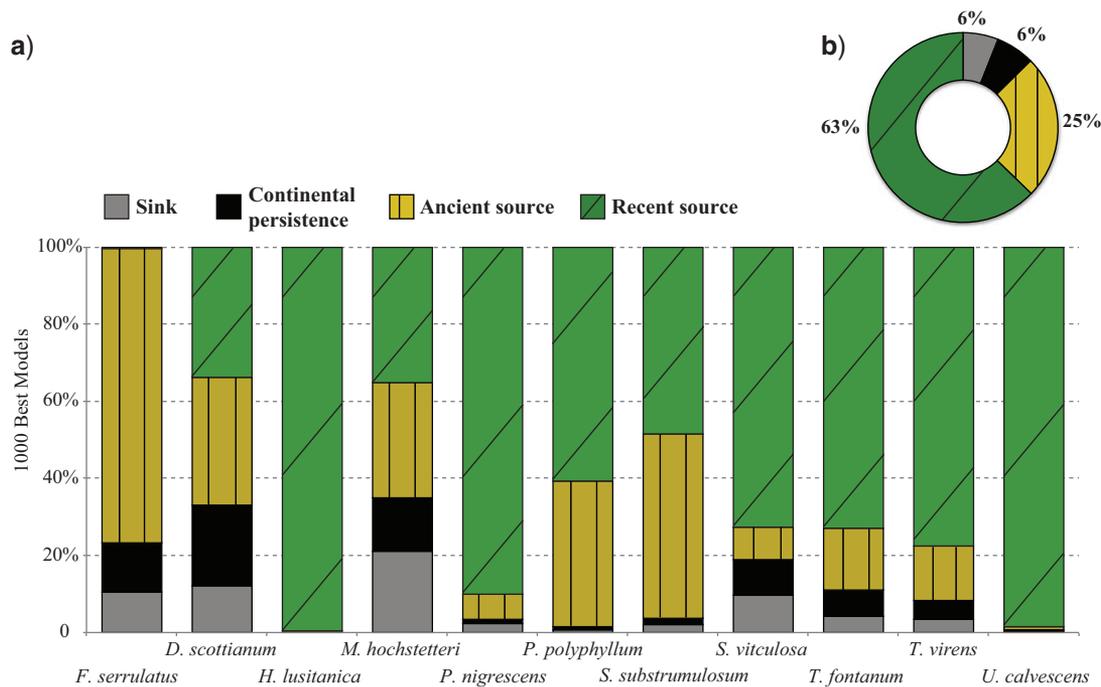


FIGURE 3. Support for demographic models inferred by ABC model selection. a) The four competing historical scenarios are represented by dark green (*recent source scenario*), light green (*ancient source scenario*), blue (*continental persistence scenario*), and brown (*sink scenario*). The y-axis reflects the number of the 1000 best simulations for each inferred scenario. Pie diagram (b) represents the average of best-supported simulations for the four competing scenarios across the 11 bryophyte species analyzed.

consistently closer to those derived from simulated data that fit the *source* scenarios than from simulated data fitting the *sink* or *continental persistence* scenarios. The explicit, model-based framework used allowed us to estimate the intensity of migrations, changes in effective population sizes, and the timing of those events (Fig. 3; Supplementary Table S5, available on Dryad at <http://dx.doi.org/10.5061/dryad.7cj77>). Under the *source* scenarios, the effective population sizes on islands ( $N_{\text{ISLAND}}$ ) exhibited slight expansions during the LGM or remained essentially stable through time, whereas continental populations were founded *de novo* from migrants of insular origin. These demographic reconstructions are fully congruent with reconstructions of the Late Pleistocene island environment, according to which Macaronesian islands experienced buffered climate conditions and were, due to eustatic sea level changes, larger than today and better connected to Europe and North Africa owing to the presence of presently submerged seamounts (Fernández-Palacios et al. 2011; Rijdsdijk et al. 2015).

Reconstructing the biogeographic origin of insular ancestors is complicated by the increasing uncertainties associated with dispersal and extinction events moving back in time. Both floristic (Preston and Hill 1999; Vanderpoorten et al. 2007) and phylogenetic (Devos and Vanderpoorten 2009; Heinrichs et al. 2013) evidence, however, point to a Neotropical origin for much of the NEA bryophyte flora. In line with this pattern, for eight out of the nine genera investigated here, ~90% of their species are not found in the Holarctic realm

(including Europe and Asia), and none of the 11 species has ever been reported in the rich fossil bryophyte flora preserved in European amber (Frahm 2004; Grolle and Meister 2004). These observations suggest that the Macaronesian archipelagos have likely played a key role as a stepping stone for trans-continental migrants before they continue with their 'colonization road' to a new continental environment. However our results would also be compatible with a scenario of complete extirpation from NEA continental regions before the Pleistocene followed by recolonization.

The time frame for the continental colonization events encompasses the Late Pleistocene, except in one lineage. Thus, for six species, the patterns of genetic variation observed fitted the *recent source* scenario (Fig. 3) with the mode of the posterior probability distribution ranging from 28,500 to 41,500 years (Supplementary Table S5, available on Dryad at <http://dx.doi.org/10.5061/dryad.7cj77>), and for a further four species, the variation was compatible with both the *ancient* and *recent source* scenarios; the mode of the posterior probability distribution ranging between 29,500 and 530,000 years BP. The observed data fitted the *ancient source* scenario in only one species (*F. serrulatus*). The dominant signal of a recent origin of the continental Atlantic fringe flora, but over different time periods, points to a very high-floristic turnover, probably resulting from both continental extinctions during the glacial periods and extensive migrations during interglacials. This underpins the notion that bryophytes may colonize new suitable habitats as soon as they

become available (Hutsemékers et al. 2008) making them prime indicators of climate change (Tuba et al. 2011).

In this respect, the 5% of mosses and 8% of liverworts of the Macaronesian bryophyte flora that are endemic to the islands, as well as the 4% of mosses and 8% of liverworts that are disjunct between Macaronesian and tropical areas, appear as candidates for migration to Western Europe in the future. Beyond the classical perception of oceanic islands as hot spots of endemic biodiversity (Whittaker and Fernández-Palacios 2007), the present study points to the role of such systems as reservoirs of novel biodiversity for the recent assembly of continental floras at the scale of a biogeographic region in spore-dispersed plants. Given the uncertainties linked to the increasing rate of climate change during the Anthropocene in continental areas (Diffenbaugh and Field 2013), not least in temperate broadleaf and Mediterranean biomes (Loarie et al. 2009), this study offers a new perspective on the conservation value of oceanic islands; these small and isolated landmasses could serve as key climatic refugia in the face of future climate change.

#### SUPPLEMENTARY MATERIAL

Data available from the Dryad data Repository: <http://dx.doi.org/10.5061/dryad.7cj77>.

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