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Repeated asynchronous evolution of single-species endemics of ivies (*Hedera* L.) in Macaronesian archipelagos

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Abstract

Aim: Evolutionary studies of oceanic island endemics are usually focused on lineages that have experienced in situ radiation, while those that speciated once on the island or archipelago but have not further diversified (single-species endemics) remain understudied. The Macaronesian archipelagos, in the Atlantic Ocean, are home to significant numbers of single-species endemics. The genus *Hedera* L. (12 species) includes three single-species endemics from three Macaronesian archipelagos with putatively independent origins. Here, we tested the role of phylogenetic niche conservatism in their evolution. To that end, we (1) reconstructed the spatio-temporal origin of Macaronesian ivies using phylogenomics, and (2) assessed the role of climatic niche during their colonization and speciation.

Location: Azores, Canary Islands, Madeira, western Mediterranean.

Taxon: *Hedera* spp.

Methods: We used 166 samples representing all *Hedera* species to generate genotyping-by-sequencing (GBS) libraries and performed time-calibrated phylogenomic and biogeographic analyses. Climatic preferences and climatic niche evolution were assessed using a geo-referenced database of the western ivy species (2,297 records).

Results: Independent and asynchronous colonization and speciation were estimated for the three Macaronesian ivies, resulting in different degrees of phylogenetic and climatic niche differentiation: *H. canariensis* displayed an early divergence (7.5–12 Ma) and high phylogenetic and niche isolation; *H. azorica* had intermediate phylogenetic isolation and niche divergence from its closest relative *H. helix* (4.4–6.8 Ma) and *H. maderensis* was embedded within the climatically similar *H. iberica* (2.8–4.6 Ma). A strong phylogenetic signal was suggested for climatic niche in the western clade of *Hedera*, where the three Macaronesian ivies are placed.

Main Conclusions: The three Macaronesian ivies represent the evolutionary stages leading to the emergence of single-species island endemics. Climatic niche conservatism appears to be involved in the evolution of single-species endemics, first by facilitating island colonization, and then by limiting in situ diversification.

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KEYWORDS

Araliaceae, Azores, Canary Islands, climatic niche, genotyping-by-sequencing, *Hedera*, island colonization, Macaronesia, Madeira, phylogenomics

1 | INTRODUCTION

Oceanic islands are considered ideal environments to study evolutionary processes due to their isolation and the habitat diversity that they usually exhibit (Emerson, 2002). Macaronesia is a biogeographic region located in the North Atlantic Ocean close to northern Africa and southern Europe, and including five oceanic archipelagos: the Azores, the Canary Islands, Madeira, Savage Islands and Cape Verde (Freitas et al., 2016; Helfgott et al., 2000). The influence of cool humid winds and their wide altitudinal range give these archipelagos atypical climates not found in mainland areas at similar latitudes, and lead to a wide habitat variation within and among archipelagos (Cropper & Hanna, 2014). These archipelagos also exhibit an exceptional variety of colonization, speciation and in situ evolutionary patterns (Patiño et al., 2014) due to their diversity in island size, age, altitudinal range and distance to mainland areas (Fernández-Palacios et al., 2011). Evolutionary patterns range from single to multiple colonization events, with or without back-colonization (Kim et al., 2008), and from spectacular radiations (e.g. *Echium*, García-Maroto et al., 2009; *Cheirolophus*, Vitales et al., 2014; *Argyranthemum*, White et al., 2020; *Helianthemum*, Albaladejo et al., 2021) to lineages that have not speciated on the islands (e.g. *Cistus monspeliensis*, Coello et al., 2021) or that have speciated once but not further diversified (e.g. the endemic monospecific genera *Visnea* and *Vieraea*, Bramwell, 1976; and *Navaea*, Escobar García et al., 2009; the species *Canarina canariensis*, Mairal et al., 2015; *Captoloma canariense*, Culshaw et al., 2021; *Campylanthus salsoioides*, Pokorny et al., 2015; and *Kleinia neriifolia*, García-Verdugo, Caujapé-Castells, Illera, et al., 2019). The combination of climatic and geographical variability and the associated variation in evolutionary patterns make the Macaronesian archipelagos ideal locations to study island colonization, speciation and in situ evolution. While lineages exhibiting radiations in Macaronesian archipelagos have been extensively studied, research focusing on lineages that have speciated once on an archipelago but not further diversified (i.e. 'single-species endemics' sensu Patiño et al., 2014) is limited to the few works mentioned above, despite single-species endemics representing a high proportion of endemism in some archipelagos (e.g. the Azores, Carine & Schaefer, 2009). Single-species endemics tend to dominate certain ecosystems, such as subtropical laurel forests (Fernández-Palacios et al., 2021), which are the habitats with the highest proportion of single-species endemics in Madeira and the Canary Islands (Patiño et al., 2014). Several hypotheses have been proposed to explain this accumulation of single-species endemics in Macaronesian laurel forests (see Fernández-Palacios et al., 2021; Patiño et al., 2014). Some studies suggest that niche conservatism limits diversification of tropical and subtropical plant

lineages in nearby non-tropical habitats (Crisp & Cook, 2012), while others indicate that the long-term stability of tropical and subtropical environments may limit species diversification. Alternatively, ecological hypotheses based on competition, such as niche preemption (Silvertown, 2004), priority effects (Shaw & Gillespie, 2016) and species saturation (Connell, 1971), have also been proposed.

The genus *Hedera* L. (ivies, Araliaceae) includes 12 species, of which three are Macaronesian single-species endemics typical of laurel forests (Fernández-Palacios et al., 2017). Therefore, ivies provide an ideal study system to understand the evolutionary dynamics of single-species endemics. Each of the three Macaronesian ivies is endemic to a different archipelago: *H. azorica* Carrière is endemic to the Azores, *H. canariensis* Wild. to the Canary Islands, and *H. maderensis* K. Koch ex A. Rutherford to Madeira. Although several studies have dealt with the evolutionary history of ivies (Ackerfield & Wen, 2003; Green et al., 2011; Valcárcel et al., 2003, 2017; Valcárcel & Vargas, 2013; Vargas et al., 1999), that of Macaronesian species remains poorly understood. The first phylogenetic study based on the nuclear ITS region (Vargas et al., 1999) already suggested that *Hedera* colonized each Macaronesian archipelago independently. Based on ploidy levels, these authors proposed a polyploid mainland ancestor for the hexaploid Madeiran species, and different diploid ancestors for the diploid Canarian and Azorean species. Subsequent analyses of plastid haplotypes supported a Mediterranean origin of the Canarian species in northern Africa or the southern Iberian Peninsula, and European origins of the Azorean and Madeiran ivies (Valcárcel et al., 2003, 2017). Moreover, the presence of an ancestral haplotype in *H. canariensis* and derived haplotypes in *H. azorica* and *H. maderensis* suggested that colonization of the Canary Islands might have predated that of the other two archipelagos (Valcárcel et al., 2003, 2017). Despite the low phylogenetic resolution of studies based on Sanger sequencing (Green et al., 2011; Valcárcel et al., 2003, 2017; Valcárcel & Vargas, 2013), phylogenetic placement of Macaronesian species in major clades, in combination with ploidy and morphological traits, suggested a close relationship between *H. azorica* and *H. helix* L., between *H. canariensis* and the northern African *H. algeriensis* Hibberd and *H. maroccana* McAll., and between *H. maderensis* and the western European *H. hibernica* (G. Kirchn.) Bean and *H. iberica* (McAll.) Ackerf. & J. Wen (Valcárcel et al., 2017). Nevertheless, hypotheses regarding the evolution of Macaronesian ivy species were not adequately evaluated given the lack of well-supported sister-group relationships.

A recent phylogenomic study using the next-generation sequencing technique genotyping-by-sequencing (GBS) clarified the phylogenetic placement and colonization history of *H. maderensis* (Alonso et al., 2022). This study revealed that the Madeiran ivy is phylogenetically nested within the south-western Iberian endemic *H. iberica*

and described a pattern of budding speciation (Alonso et al., 2022), in which a new species is originated without the extinction of the parental species (Mayr & Bock, 2002). An analysis of the climatic niche of the Madeiran ivy revealed a preference for warm places with high isothermality and humid summers. Interestingly, these climatic preferences largely overlap with those of *H. iberica* (Alonso et al., 2022). This suggested that the climatic niche of *H. maderensis* was first acquired by its mainland ancestor, thus representing an example of pre-adaptation. The climatic niche similarity between *H. maderensis* and *H. iberica* is paralleled by their phenotypic similarity in functional traits (e.g., fruit and seeds dry mass and specific leaf area, Alonso et al., 2022). This pattern of niche conservatism during the evolution of the Madeiran ivy may be related to the lack of island diversification defining single-species endemics. Two other ivy lineages appear to have followed evolutionary paths similar to that of the Madeiran ivy on different Macaronesian archipelagos. A hypothetical pattern of niche conservatism during *Hedera* diversification makes sense given that the genus is considered thermophilous (Andergassen & Bauer, 2002; Parker, 1962) and has been used as an indicator for warm periods in Europe from ancient (late Eocene, Axelrod, 1975) to recent times (late Holocene, Mühller et al., 2005). Indeed, ivies are considered part of the dry subtropical Tertiary flora (Axelrod, 1975; Herrera, 1992; Verdú et al., 2003). However, the latest research suggest that the genus *Hedera* can be climatically characterized as temperate (Coca-de-la-Iglesia et al., 2022). Therefore, the hypothesis of niche conservatism in the Macaronesian ivies still needs to be evaluated.

Here we aimed to analyse colonization and speciation of Macaronesian ivies as an exemplary case of repeated evolution of single-species endemics on islands. We hypothesized that a general pattern of niche conservatism has dominated the evolution of the three Macaronesian ivies. Our specific objectives were (1) to clarify the phylogenetic placement of Macaronesian ivy species by obtaining a well-resolved phylogenetic reconstruction of the genus *Hedera* using the GBS technique; (2) to analyse and compare the climatic niches of Macaronesian ivy species and their Mediterranean relatives based on a database of georeferenced locations and (3) to clarify the spatio-temporal context of the evolutionary history of Macaronesian ivies through phylogenetic dating and biogeographical analyses.

2 | MATERIALS AND METHODS

2.1 | Sampling

A total of 166 samples from 100 locations representing all ivy species were analysed in the phylogenetic study (Figure S1), including 85 new herbarium samples (Data S1) and samples from a previous study (Alonso et al., 2022). We included 62 individuals from 33 populations of Macaronesian ivies: 19 individuals of *H. azorica* (12 populations), 19 individuals of *H. canariensis* (11 populations) and 24 individuals of *H. maderensis* (10 populations). We also included 41 individuals from 18 populations of Mediterranean species that may be closely related to Macaronesian ivies (Valcárcel et al., 2017): *H. algeriensis* (2 individuals,

2 populations), *H. maroccana* (13 individuals, 8 populations) and *H. iberica* (26 individuals, 8 populations). We completed phylogenetic sampling with samples from 32 locations representing the distribution of the widespread European ivies (27 samples from 20 populations of *H. helix* and 19 samples from 12 populations of *H. hibernica*) and 13 locations representing Asian ivies (5 populations of *H. nepalensis*, 4 of *H. pastuchovii* and 2 of *H. colchica* and *H. rhombea*). Four outgroup samples representing closely related genera (*Brassaiopsis*, *Dendropanax*, *Eleutherococcus* and *Kalopanax*; Valcárcel & Wen, 2019) were included.

2.2 | GBS library preparation

DNA extraction was performed using a modified CTAB protocol (Cullings, 1992; Doyle & Doyle, 1987) and DNA concentration was estimated in a Qubit 3.0 Fluorometer. We used 500 ng of DNA per sample to prepare a GBS library. We replicated five samples and included four replicates of samples included in Alonso et al. (2022) to confirm their consistent phylogenetic placement within and between libraries. For library preparation, we followed Fernández-Mazuecos et al. (2018), based on Elshire et al. (2011) with modifications (Escudero et al., 2014; Grabowski et al., 2014). After digestion, ligation and sample pooling, the pool was purified with AMPure XP magnetic beads (Beckman Coulter, USA) with a 1:1 beads: sample ratio. Afterwards, 70 ng of the resulting DNA was amplified for 19 PCR cycles using the NEB Taq 2x Master Mix (New England Biolabs, USA) in an BioRad MyCycler thermocycler (Bio-Rad Laboratories, USA), and the amplified library was purified with a 0.8:1 beads: sample ratio. Quantification and quality control were done in a 2100 Bioanalyzer (Agilent, CA, USA). Paired-end sequencing (Illumina HiSeq X 150 bp; Illumina Inc., USA) was performed by MacroGen Inc. (Seoul, South Korea).

2.3 | GBS data processing and phylogenetic analyses

GBS reads were processed using ipyrad v.0.9.81 (Eaton, 2014; Eaton & Overcast, 2020). Demultiplexing was performed for the library of Alonso et al. (2022) and the new library separately, and the remaining assembly steps were performed with both datasets combined. Data were treated as single-end and de novo assembly was done. We employed the assembly parameters of Fernández-Mazuecos et al. (2020) optimized for *Hedera* in Alonso et al. (2022), with clustering threshold of 0.85 and taxon coverage of 15. Our dataset comprised four ploidy levels (2x, 4x, 6x and 8x; Vargas et al., 1999), two of them found in Macaronesia (2x: *H. azorica* and *H. canariensis*; 6x: *H. maderensis*). Assembling GBS datasets with mixed ploidy levels for phylogenetic analysis presents challenges, and no methodology has been developed to avoid ploidy-related issues. To allow multiple ploidy levels, the maximum number of alleles per locus was set to six. This value provided the highest branch support in the optimization of Alonso et al. (2022), which tested three values (2, 4, 6)

producing similar topologies. To minimize the impact of polyploidy-derived paralogy, parameters for paralogue filtering followed ipyrad documentation. Low recovery of GBS loci is expected for herbarium samples >20 years old, which may increase phylogenetic uncertainty (Fernández-Mazuecos et al., 2018). Therefore, preliminary analyses were run and individuals with uncertain phylogenetic placement and low locus recovery (<500 loci), as well as replicates, were excluded from final analyses.

We ran concatenation-based analyses using Maximum Likelihood (ML) and Bayesian Inference (BI). ML analyses were run in RAxML-HPG 8.2.12 (Stamatakis, 2014) under a GTR+G substitution model, which is the default nucleotide substitution model in RAxML and is commonly used in GBS studies (e.g. Albaladejo et al., 2021; Alonso et al., 2022; Fernández-Mazuecos et al., 2018, 2020). The number of bootstrap replicates was estimated using the bootstopping criterion (Pattengale et al., 2010). BI analyses were run in ExaBayes v.1.4.1 (Aberer et al., 2014) using a parsimony starting tree, and two parallel MCMC runs with two coupled chains for 1.2 million generations under a GTR+G model. Convergence was assessed in Tracer 1.7.2 (Rambaut et al., 2018). The extended majority-rule consensus tree was obtained using a burn-in of 25%. A coalescent-based analysis was run in SVDquartets (Chifman & Kubatko, 2014) implemented in PAUP 4.a168 (Swofford, 2002) with 100 bootstrap replicates summarized in a 50% majority-rule consensus tree. The multispecies coalescent option with exhaustive quartet sampling was used, with one partition per taxon.

2.4 | Climatic niche characterization and phyloecospace

We characterized the range of environmental conditions in which species occur based on their distributions (realized climatic niche; Pearson & Dawson, 2003). A database of occurrences was built (Data S2) representing the distribution of western clade ivies (Figure 1; see below; *H. algeriensis*, *H. azorica*, *H. canariensis*, *H. helix*, *H. hibernica*, *H. iberica*, *H. maderensis* and *H. maroccana*). We focused on macroclimatic variables because of their wide availability and informativeness about broad-scale biogeographic patterns in *Hedera* (Alonso et al., 2022). We downloaded 19 bioclimatic layers at 30-second resolution from WorldClim 2.1 (Fick & Hijmans, 2017) and clipped them to the extent of occurrences using the *raster* package (Hijmans, 2021). We calculated Pearson's pairwise variable correlations and performed a hierarchical cluster analysis ('hclust' function, R Core Team, 2021). For each cluster with $r \geq 0.80$, we retained the most synthetic and biologically relevant variable (Figure S2): bio4 (temperature seasonality), bio8 (mean temperature of the wettest quarter), bio11 (mean temperature of the coldest quarter), bio16 (precipitation of the wettest quarter) and bio18 (precipitation of the warmest quarter). We extracted climatic data for our occurrences using the *raster* package. Climatic data of the selected variables for the background and our occurrences were used as the input for a weighted (weight=0 for occurrences and 1 for background) principal component analysis (PCA) performed with *ecospat* (Broennimann

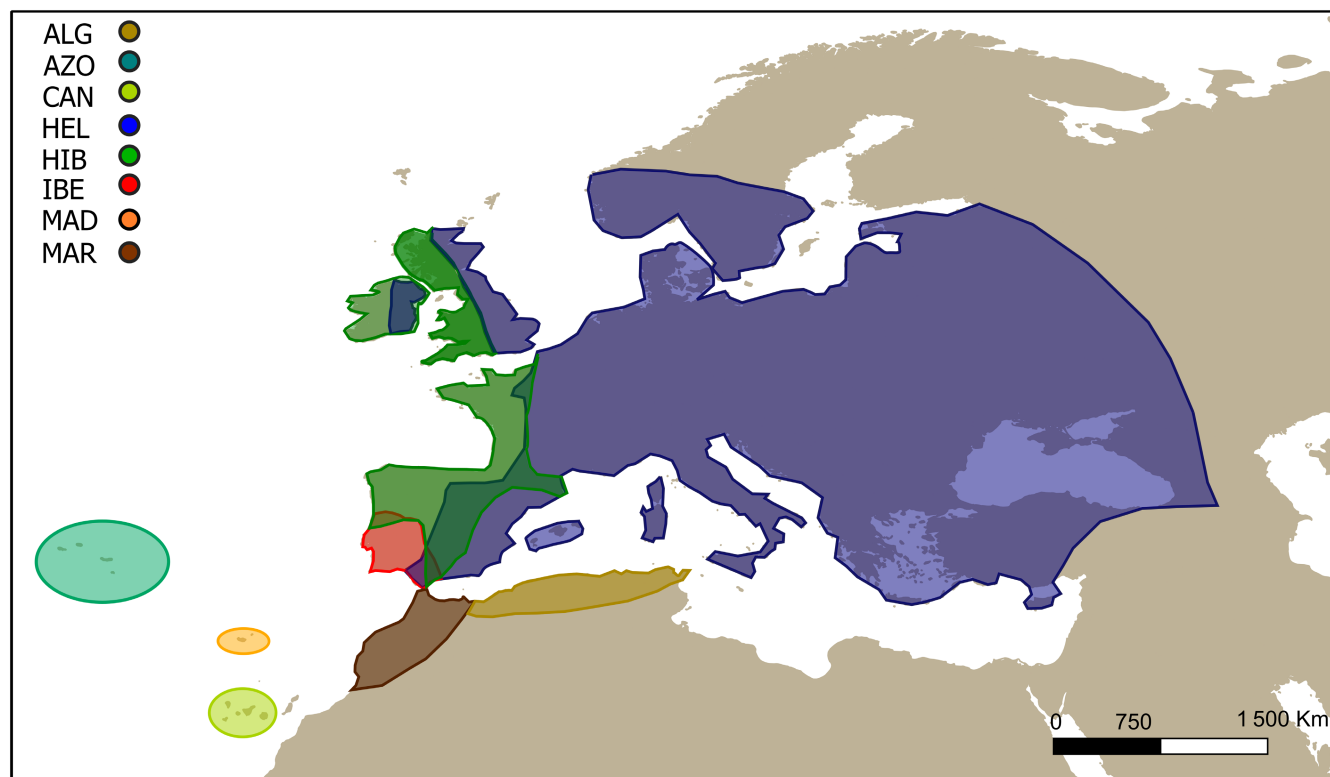


FIGURE 1 Distribution ranges of western ivy species. Only the areas where each species is native are shown. ALG, *H. algeriensis*; AZO, *H. azorica*; CAN, *H. canariensis*; HEL, *H. helix*; HIB, *H. hibernica*; IBE, *H. iberica*; MAD, *H. maderensis*; MAR, *H. maroccana*.

et al., 2022). The PCA results were plotted alongside kernel density estimates of 95% and 100% of the available climatic space calculated with the *ks* package (Duong, 2021). Climatic niche overlap between species was tested calculating Schoener's *D* (Schoener, 1970) and performing niche similarity and equivalency tests implemented in *ecospat* (Broennimann et al., 2012; Warren et al., 2008). Niche similarity tests were used to test niche conservatism, that is, if niche overlap between two species is significantly higher than that obtained if random shifts within the environmental space occurred. Niche equivalency tests were used to test niche divergence, that is, if niche overlap is significantly lower than a null distribution simulated by randomly reallocating the occurrences of both species between their ranges. These tests consider the relative availability of climatic environments in the study area. Therefore, high niche overlap with non-significant similarity can occur in geographically close species, and the opposite can occur for geographically distant species. When a species pair presents significant results in both tests, it can be interpreted that climatic niches of both species are similar but not identical.

To study climatic niche evolution in western ivies, we used a 'phyloecospace' approach (Baldo et al., 2017), which applies the 'phylomorphospace' method (i.e. mapping of morphological diversification; Sidlauskas, 2008) to ecological variables. We pruned the ML tree to include one sample per western taxon, obtained climatic niche positions of species using *ecospat* and projected the phylogenetic tree onto the climatic space using the 'phylomorphospace' tool of *phytools* (Revell, 2012). Pagel's lambda (Pagel, 1999) was calculated in *phytools* for the two components of species position as an additional test of niche conservatism.

2.5 | Divergence time estimation and biogeographic analyses

TreePL (Smith & O'Meara, 2012) was employed to estimate divergence times with the penalized likelihood method using the complete ML tree as input. Fossils of Macaronesian ivies in the literature were considered unreliable or too recent for calibration (Anderson et al., 2009; Góis-Marques et al., 2018, 2019). Additionally, identification of ivy species is based on trichomes that are not well preserved in fossils. Therefore, we used a single calibration at the root of the tree corresponding to the most recent common ancestor of *Hedera* and outgroup species (31.9–51.3 Ma, calibration of Valcárcel & Wen, 2019). After a preliminary analysis to establish the optimal parameter values (gradient-based optimizer $\text{opt}=2$, autodifferentiation based optimizer $\text{optad}=2$ and cross-validation based optimizer $\text{optcvad}=1$), we ran a second analysis with those parameter values and random sampled cross validation with 200,000 iterations for penalized likelihood and 5000 iterations for cross validation. This analysis provided the best value for the smoothing parameter, used in the final analysis (*meanage*, 31.9–51.3 Ma; $\text{smoothing}=1\text{e-}13$). Since TreePL does not provide a measure of uncertainty, we additionally ran

the three steps using only the minimum age (*minage*, 31.9 Ma; $\text{opt}=1$, $\text{optad}=2$, $\text{optcvad}=2$ and $\text{smoothing}=1\text{e-}13$) and only the maximum age (*maxage*, 51.3 Ma; $\text{opt}=4$, $\text{optad}=2$, $\text{optcvad}=2$ and $\text{smoothing}=1\text{e-}9$) as the calibration point, which provided an estimation of maximum and minimum age for nodes. The 'thorough analysis' option was used for all runs.

Biogeographic analyses were performed in BioGeoBEARS (Matzke, 2013) using a pruned version of the *meanage* dated tree with one tip per *Hedera* taxon (the individual that most recently diverged from the sister species). Five biogeographic areas were defined considering the natural distribution ranges of *Hedera* species, previous biogeographic analyses (Valcárcel et al., 2017), and the aim of this study: the Azores, the Canary Islands, Madeira, western continental area (Europe and North Africa) and eastern continental area (Asia). Dispersal-extinction-cladogenesis (DEC) and dispersal-vicariance (DIVALIKE) models were run with and without the +J option, accounting for founder-event speciation (Matzke, 2014, 2022). We considered three periods for time-stratification: the crown node of *Hedera* (20–14.1 Ma), and before (14.1–7.1 Ma) and after (7.1–0 Ma) the emergence of the Azores. We decided not to consider the emergence of the Canary Islands and Madeira, as their palaeoislands most likely emerged before the origin of *Hedera* (68 and 65–67 Ma for the oldest palaeo-island of the Canary Islands and Madeira respectively; Carracedo & Troll, 2021). For each period we constructed 'manual dispersal multipliers' and 'allowed areas' matrices (Data S3) and permitted only continental areas at the crown of *Hedera* (>14.1 Ma) considering that previous biogeographic reconstructions for the Araliaceae family (Valcárcel & Wen, 2019) and *Hedera* (Valcárcel et al., 2017) pointed to a continental origin for the genus. AICc values were used for model comparison. The maximum number of areas per node was restricted to two based on the maximum number of areas currently occupied for the species with the widest range.

3 | RESULTS

3.1 | GBS assembly and phylogenetic analyses

The newly generated library provided 740,539,092 raw reads. Bases with a quality score of Q20 represented 95.4%. In the final dataset, 141 samples were included, and 7,393 loci were retained, with 943,611 bp, 49,885 SNPs, 21,626 parsimony informative positions and 70.97% of missing sites. This percentage of missing data is within the range reported for GBS studies and may be partly related to the phylogenetic distance between the outgroup and the ingroup.

The concatenation-based phylogenetic analyses mostly resolved phylogenetic relationships of *Hedera* at the species level and revealed two supported and geographically structured main clades (Figure 2): an eastern clade (*H. colchica*, *H. nepalensis*, *H. pastuchovii* and *H. rhombea*; bootstrap support BS=100%, Bayesian posterior probability PP=1.0) and a western clade (*H. algeriensis*, *H. azorica*, *H.*

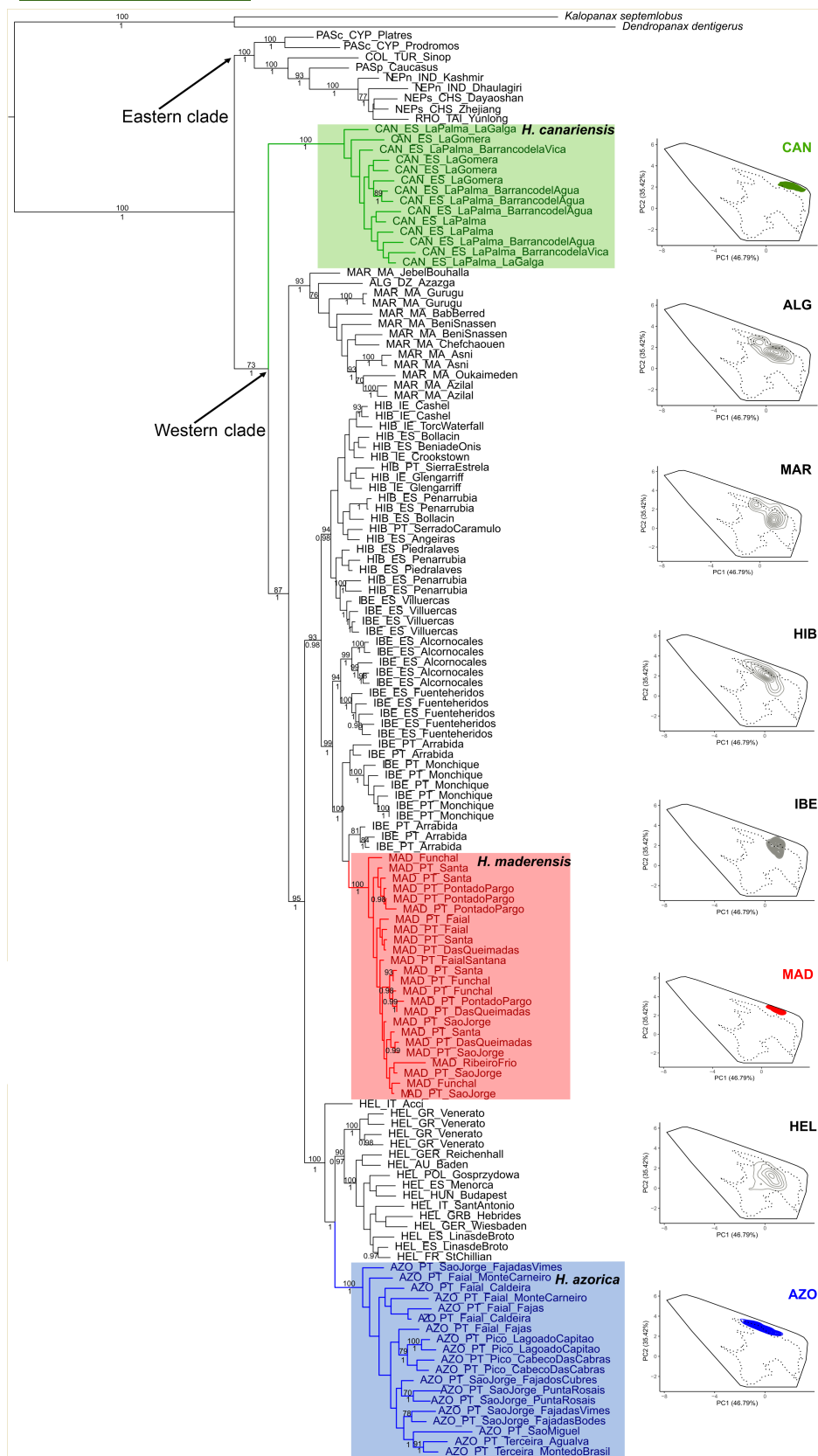


FIGURE 2 Phylogenetic relationships of ivies based on maximum likelihood (ML) analysis of GBS data. Statistical support is provided for strongly supported branches ($BS \geq 80$ and $PP \geq 0.95$). For each of the western species, the density envelopes obtained from the PCA analysis of climatic niches is shown. Contours indicate the limits of the 100% (solid lines) and the 95% (dashed lines) of the available climatic space. ALG, *H. algeriensis*; AZO, *H. azorica*; CAN, *H. canariensis*; HEL, *H. helix*; HIB, *H. hibernica*; IBE, *H. iberica*; MAD, *H. maderensis*; MAR, *H. maroccana*.

canariensis, *H. helix*, *H. hibernica*, *H. iberica*, *H. maderensis* and *H. maroccana*; BS=73%, PP=1.0). Within the western clade, *H. canariensis* exhibited an early divergence as a clade with maximum support sister to a clade including the remaining western species (BS=87%, PP=1.0). Within this clade, the African species *H. algeriensis* and *H. maroccana* formed a well-supported clade (BS=93%, PP=1.0). The remaining species formed a highly supported clade (BS=95%, PP=1.0) including two main clades: a diploid European clade (*H. azorica* and *H. helix*; BS=100%, PP=1.0) and a polyploid European clade (*H. hibernica*, *H. iberica* and *H. maderensis*; BS=93%, PP=0.98). Within the diploid European clade, *H. azorica* (with maximum support) and *H. helix* were reciprocally monophyletic except for an Italian *H. helix* sample that had the earliest-diverging position in the clade according to the BI analysis. *Hedera maderensis* samples formed a monophyletic group with maximum support embedded within *H. iberica*. Phylogenetic resolution within each of the Macaronesian species was very limited. Coalescent-based analysis provided a topology fully congruent with that of the concatenation-based analyses at the species level, and all nodes were supported except for a polytomy in the eastern clade including *H. rhombea* and the two *H. nepalensis* subspecies (Figure S3).

3.2 | Climatic niche characterization and phyloecospace

The first two components of the PCA explained 82.2% of climatic variability (Figure 3a). The first axis (PC1) was determined mostly by variables bio11, bio16 and bio18, and the second axis (PC2) by temperature variables bio4 and bio8. PC1 runs from locations with cold and rainy winters with high summer precipitations to locations with

mild and dry winters and low summer precipitation. PC2 runs from locations with high to low temperature seasonality.

The PCA results (Figures 2 and 3a) show that the Macaronesian species are restricted to the extreme upper region of the available climatic space of western ivies, defined by high values of PC2 (i.e. locations with low temperature seasonality and a warm rainy season in comparison to mainland species). *Hedera canariensis* and *H. maderensis* are restricted to locations with mild and dry winters and the lowest summer precipitation (positive PC1 values) found in the climatic space of western ivies. In contrast, *H. azorica* can also occur in areas with relatively cold and rainy winters and higher summer precipitation (negative PC1 values).

Climatic niche overlap ranged from no overlap for the *H. algeriensis*-*H. maderensis* species pair ($D=0$) to the highest overlap between *H. iberica* and *H. maroccana* ($D=0.475$; Table 1). The climatic niches of the Macaronesian species pairs *H. azorica*-*H. maderensis* and *H. canariensis*-*H. maderensis* were similar but not equivalent, while those of the *H. azorica*-*H. canariensis* pair were neither similar nor equivalent (Table 1). According to niche similarity tests, *H. canariensis* was only similar to two species of its sister clade (*H. maroccana* and *H. maderensis*), *H. azorica* was not similar to its closest relative *H. helix* and *H. maderensis* was similar to its closest relative *H. iberica* (Table 1). According to niche equivalency tests, *H. canariensis* has diverged from all species of its sister clade, *H. azorica* has diverged from its closest relative *H. helix* and *H. maderensis* has not diverged from its closest relative *H. iberica* (Table 1).

Phyloecospace analysis estimated nearby niche positions for the ancestors of the western species (Figure 3b). Besides, niche positions of *H. azorica* and *H. maderensis* are close to those of their sister species along PC1, while the niche position of *H. canariensis* is distant

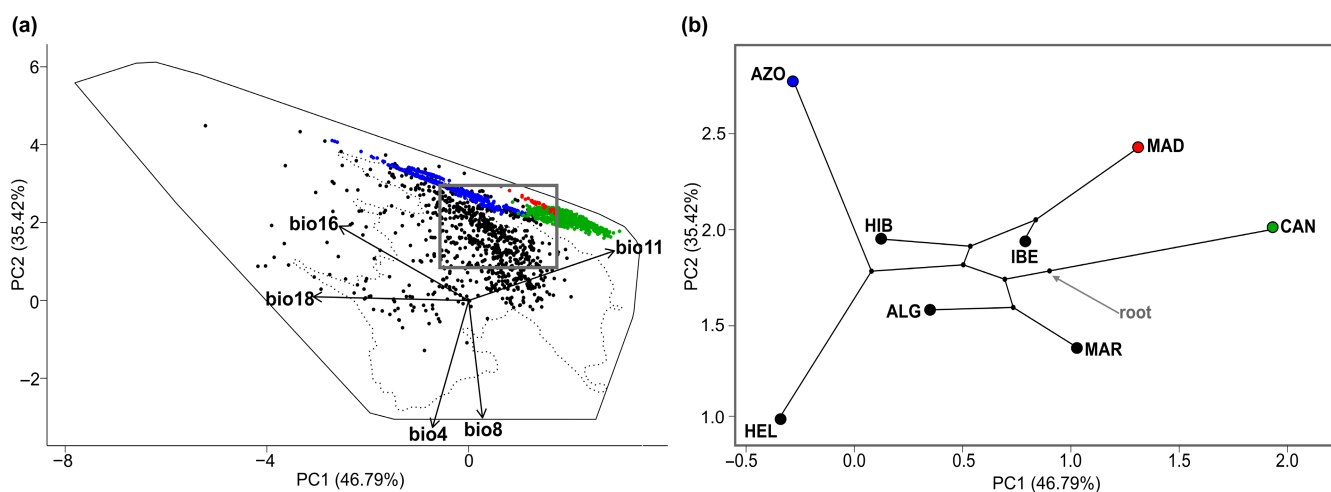


FIGURE 3 Analyses of climatic niches of the western species of ivies, including principal component analysis (PCA) (a) and phyloecospace (b). Macaronesian species are represented in blue (*H. azorica*), green (*H. canariensis*) and red (*H. maderensis*). (a) Coordinates in the climatic space for each of the samples included in the PCA, and contours delimiting the 100% (solid line) and 95% (dashed line) of the available climatic space. Percentage contributions of the original WorldClim variables are provided: bio4 (temperature seasonality), bio8 (mean temperature of the wettest quarter), bio11 (mean temperature of the coldest quarter), bio16 (precipitation of the wettest quarter) and bio18 (precipitation of the warmest quarter). (b) Phyloecospace defined by the ML phylogenetic tree of western ivy species and the principal components of the climatic space. The root of the western clade is indicated. ALG, *H. algeriensis*; AZO, *H. azorica*; CAN, *H. canariensis*; HEL, *H. helix*; HIB, *H. hibernica*; IBE, *H. iberica*; MAD, *H. maderensis*; MAR, *H. maroccana*.

TABLE 1 Climatic niche overlap statistics.

ALG							
AZO	D=0.167 $p_s=0.1181$ $p_e=0.2772$	AZO					
CAN	D=0.007 $p_s=0.2376$ $p_e=0.0099$	D=0.012 $p_s=0.1386$ $p_e=0.0099$	CAN				
HEL	D=0.015 $p_s=0.2574$ $p_e=0.0198$	D=0.019 $p_s=0.2277$ $p_e=0.0099$	D=0.003 $p_s=0.2079$ $p_e=0.0099$	HEL			
HIB	D=0.004 $p_s=0.2772$ $p_e=0.0099$	D=0.023 $p_s=0.1188$ $p_e=0.0099$	D=0.003 $p_s=0.2475$ $p_e=0.0099$	D=0.023 $p_s=0.3762$ $p_e=0.0099$	HIB		
IBE	D=0.207 $p_s=0.0990$ $p_e=0.21782$	D=0.229 $p_s=0.0594$ $p_e=0.28713$	D=0.067 $p_s=0.0693$ $p_e=0.0099$	D=0.014 $p_s=0.2376$ $p_e=0.0099$	D=0.008 $p_s=0.1683$ $p_e=0.0099$	IBE	
MAD	D=0 $p_s=0.2277$ $p_e=0.0099$	D=0.052 $p_s=0.0495$ $p_e=0.0495$	D=0.107 $p_s=0.029$ $p_e=0.0099$	D=0.006 $p_s=0.1287$ $p_e=0.2178$	D=0.017 $p_s=0.0594$ $p_e=0.1584$	D=0.273 $p_s=0.0198$ $p_e=0.3663$	MAD
MAR	D=0.415 $p_s=0.0990$ $p_e=0.1485$	D=0.0336 $p_s=0.0396$ $p_e=0.6336$	D=0.155 $p_s=0.0198$ $p_e=0.0099$	D=0.020 $p_s=0.1782$ $p_e=0.0594$	D=0.007 $p_s=0.1881$ $p_e=0.0198$	D=0.475 $p_s=0.0099$ $p_e=0.7623$	D=0.109 $p_s=0.0198$ $p_e=0.0099$

Note: D, niche overlap metric; p_s , p -value of niche similarity test; p_e , p -value of niche equivalency test. $p_s < 0.05$ indicates that the climatic niche of the tested species is more similar than expected by chance, while $p_e < 0.05$ indicates that the climatic niche of the tested species is less equivalent than expected by chance. Significant p -values are marked in bold.

from those of the rest of the western clade species along this axis. According to PC2, *H. azorica* is clearly differentiated from its sister *H. helix*. Pagel's lambda indicated a strong but non-significant phylogenetic signal for niche position along PC1 ($\lambda=0.999$; $p=0.368$), but very weak for position along PC2 ($\lambda < 0.001$). This suggests that winter temperature and precipitation preferences (PC1) are phylogenetically conserved in this clade, while the tolerance to temperature variation (PC2) is not phylogenetically constrained.

3.3 | Divergence time estimates and biogeographic analyses

A mid-Miocene age was estimated for the crown node of *Hedera* (14.11 [9.56–15.68] Ma; Figure 4). The eastern and western clades started diversification at similar times in the later Miocene (10.70 [7.63–11.52] and 10.24 [7.51–12.00] Ma respectively; Figure 4). *Hedera canariensis* formed the earliest-diverging lineage within the western clade, but the *H. canariensis* crown node had a Pliocene age (3.49 [2.61–4.16] Ma; Figures 4 and S4). The clade encompassing the remaining western species started diversification during the late Miocene (8.03 [6.12–9.62] Ma; Figure 4). The African species (*H. algeriensis* and *H. maroccana*) formed a clade of late Miocene or Pliocene crown age (7.07 [3.92–6.06] Ma) while the remaining western species were part of the more recent polyploid European clade (*H. hibernica*, *H. iberica* and *H. maderensis*; crown age 5.15 [3.46–5.55] Ma) and diploid European clade (*H. helix* and *H. azorica*; crown age 5.94 [4.39–6.84] Ma; Figure 4). The Macaronesian species *H. azorica* and *H. maderensis* diverged from their closest species in the late Miocene to early

Pliocene (5.94 [4.39–6.84] Ma) and the Pliocene (4.40 [2.82–4.57] Ma) respectively. Their crown ages were placed in the Pliocene for *H. azorica* (4.07 [3.33–4.86] Ma) and the Pleistocene for *H. maderensis* at (2.26 [1.37–2.22] Ma; Figures 4 and S4). Therefore, Macaronesian ivy species originated at different times since the Miocene.

The best-fitting biogeographic models were +J models for both DEC (LnL = -7.6, AICc = 43.7) and DIVALIKE (LnL = -16.7, AICc = 41.8; Data S4). The DIVALIKE+J analysis provided the highest resolution (Figure 4). According to this reconstruction, the ancestor of *Hedera* was distributed across western and eastern continental areas (orange in Figure 4, ancestral range probability of $p=0.81$). The most recent common ancestor of the western clade was most likely distributed in the western continental area (yellow in Figure 4; $p=0.85$). The clade including all the western ivies except for *H. canariensis*, and the clade encompassing the polyploid European clade and the diploid European clade had their most recent common ancestors in the western continental area ($p=1.0$ and $p=0.99$ respectively). The most recent common ancestor of *H. helix* and *H. azorica* and the most recent common ancestor of *H. iberica* and *H. maderensis* also had most likely western Mediterranean distribution ($p=0.57$ and $p=0.66$ respectively; Figure 4). Results from the DEC+J model were very similar to those of the DIVALIKE+J model (Figure S5B).

4 | DISCUSSION

We used phylogenomic and climatic niche analyses to disentangle the spatio-temporal origin and evolutionary patterns of three single-species endemics of the same genus (*Hedera*, ivies) from different,

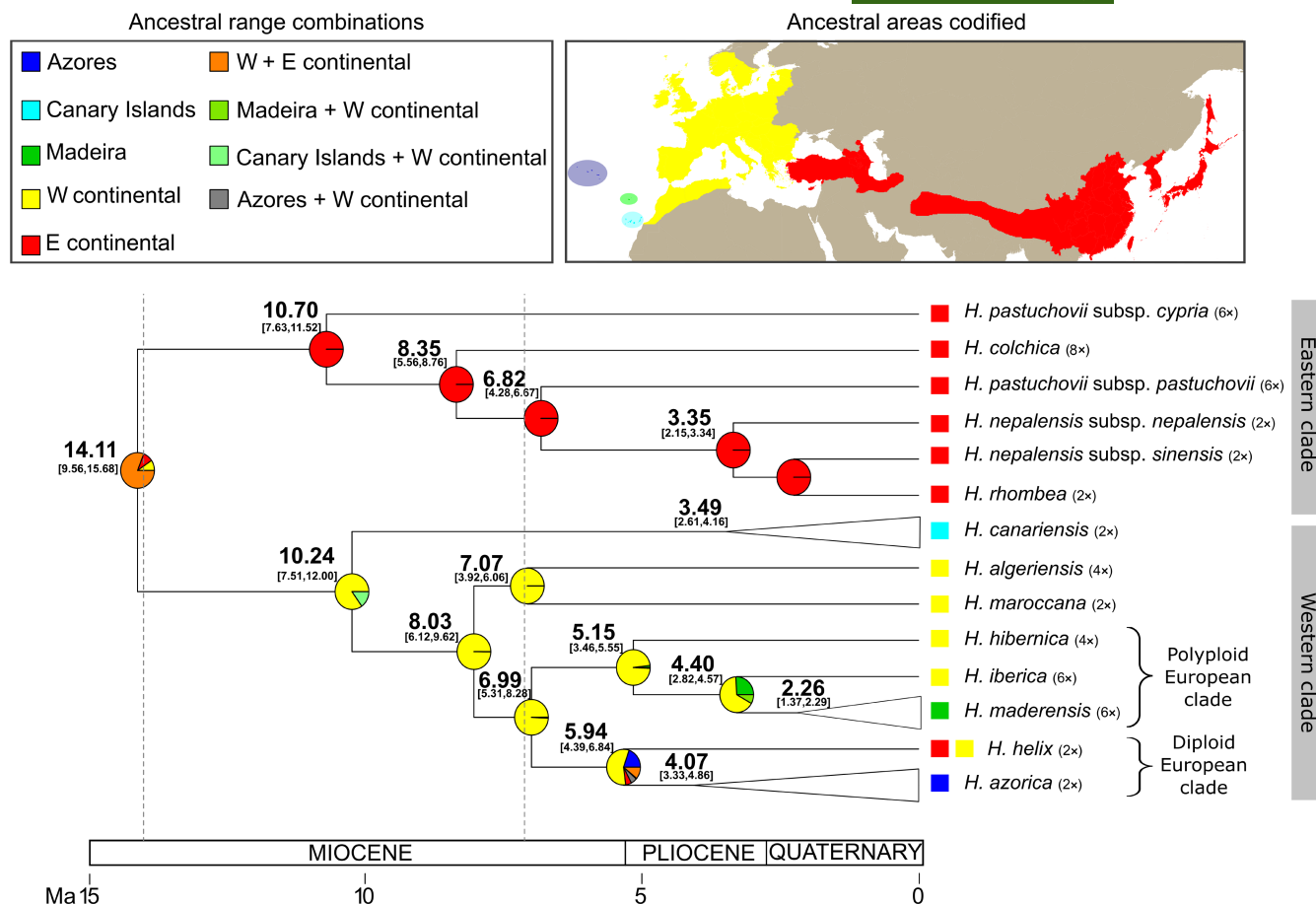


FIGURE 4 Time-calibrated phylogeny of ivies obtained in TreePL and biogeographic reconstruction obtained in BioGeoBEARS using the DIVALIKE+J model. The stem ages of taxa estimated by the TreePL *meanage* analysis (Figure S4) are provided for supported nodes, with ages estimated by the *minage* and *maxage* analyses in brackets. Crown ages are also included for the Macaronesian species and are indicated at the base of triangles. Probabilities of each of the ancestral ranges estimated by BioGeoBEARS (after pruning the tree to include a single terminal per taxon) are shown as pie charts. Each colour represents a certain codified area or combination of areas.

biogeographically related Macaronesian archipelagos. The studied species originated independently and asynchronously since the Miocene, and they thus represent the evolutionary stages during differentiation of single-species island endemics. The three species occur in a peripheral area of the climatic space of European and African ivies, within which their winter temperature and precipitation preferences are phylogenetically conserved. We found an overall pattern of climatic niche conservatism during the evolution of western ivies, which appears to have facilitated colonization of Macaronesian archipelagos, and perhaps limited diversification within them.

4.1 | Asynchronous divergence patterns across Macaronesian archipelagos

While most of the genera with Macaronesian endemic species are restricted to a single archipelago (Fernández-Palacios et al., 2011; Reyes-Betancort et al., 2008), several of them occur in multiple archipelagos. In some of these genera, Macaronesian species from different archipelagos form a monophyletic group as a result of a single colonization event of Macaronesia from the mainland (e.g. *Echium*

and *Sonchus*, in the Canary Islands, Madeira and Cape Verde, Böhle et al., 1996; García-Maroto et al., 2009; Kim et al., 2008, *Sideritis* and *Crambe*, in the Canary Islands and Madeira, Kim et al., 2008). For other genera, presence in multiple Macaronesian archipelagos is the result of multiple colonization events from the mainland. This is the case of *Convolvulus* (in the Canary Islands and Madeira; Carine et al., 2004), *Lotus* and *Scrophularia* (in the five Macaronesian archipelagos; Jaén-Molina et al., 2021; Navarro-Pérez et al., 2015). Multiple colonization events have also occurred in *Hedera* (in the Canary Islands, Madeira and the Azores; Valcárcel et al., 2003). Our GBS phylogenies do not only confirm that each Macaronesian species occurring on a different archipelago originated from an independent colonization event, but also reveal that each colonization occurred at a different moment (Figures 2 and 4). This asynchronous pattern of colonization and divergence across the Macaronesian archipelagos has resulted in differential evolutionary stages for the three species, with a high phylogenetic differentiation for *H. canariensis*, intermediate differentiation for *H. azorica* and limited differentiation for *H. maderensis*, which is phylogenetically nested within *H. iberica* (Figure 2, Alonso et al., 2022).

Our time-calibrated phylogeny indicates that the colonization of Madeira is the most recent among the colonization events of

Macaronesian archipelagos by ivies, and occurred between the late Pliocene and the Pleistocene (1.37–4.57 Ma considering crown and stem ages, see Martín-Hernanz et al., 2023 for a discussion on the relevance of considering both ages; Figure 4). This recent colonization explains the pattern of budding speciation detected (see also Alonso et al., 2022; Figure 2). Although budding speciation was once considered unusual, it is now considered common in plants (Crawford, 2010) and can explain speciation of island endemics as a result of colonization from the mainland (Tseng et al., 2018; Vanderpoorten & Long, 2006). In fact, some examples have been reported for Macaronesian plant species (e.g. the angiosperm *Scrophularia lowei*, Valtueña et al., 2017; and the liverwort *Leptoscyphus azoricus*, Vanderpoorten & Long, 2006).

According to our time-calibrated reconstruction, the colonization of the Azores by *Hedera* occurred during the late Miocene or Pliocene (3.33–6.84 Ma; Figure 4). Our phylogeny indicates that *H. azorica* is closely related to the widespread continental species *H. helix* (Figure 2). Although a pattern of reciprocal monophyly is not fully supported, it is clear that the longer period since the colonization of the Azores in comparison with Madeira has allowed a stronger phylogenetic differentiation from the continental relative. Indeed, a gradual transition from paraphyly to monophyly in the course of species divergence is expected (Cummings et al., 2008; Rosenberg, 2003).

The colonization of the Canary Islands appears to be the most ancient one among Macaronesian ivies (Figure 4) and occurred during the late Miocene or the Pliocene (2.61–12 Ma). The long branch between the stem and crown nodes of *H. canariensis* (approximately 7 Ma) is remarkable. Long branches are frequently observed in cases where the closest relatives of island endemics are mainland species and could be the consequence of extinction of phylogenetically close mainland relatives (García-Verdugo, Caujapé-Castells, Mairal, et al., 2019; García-Verdugo, Caujapé-Castells, & Sanmartín, 2019), leading to phylogenetic isolation of the extant island species. This may be the case of *H. canariensis*, the Macaronesian ivy with the highest phylogenetic differentiation from its mainland relatives, and therefore with the highest uncertainty on colonization time.

None of the Macaronesian ivies exhibits high intraspecific phylogenetic differentiation, regardless of the time frame since colonization (Figures 2 and S4). This is consistent with previous results showing low phylogenetic resolution between populations of the mainland species *H. helix* and *H. hibernica* using GBS (Alonso et al., 2022). This low intra-specific resolution could be a consequence of the high dispersal abilities of ivies, exhibiting fleshy fruits ingested by several bird species that potentially allow endozoochorous dispersal (e.g. *Turdus merula*, *Erithacus rubecula* and *Sylvia atricapilla*; Debussche & Isenmann, 1989; Heleno, 2008).

4.2 | Climatic niche conservatism in single-species endemics

The effect of ecological opportunities as a major speciation force on Macaronesian islands has been largely documented for cases of in situ adaptive radiations associated with niche divergence patterns

(see revision in Florencio et al., 2021). In the case of Macaronesian single-species endemics, the opposite pattern of niche conservatism would be expected (Patiño et al., 2014), but it has been less explored. In a study including six Macaronesian single-species endemics of the Rand Flora, Mairal et al. (2017) identified a major role of niche conservatism in speciation, but additional examples are required for laurel forests, which concentrate the largest proportion of these taxa and are dominated by them (Fernández-Palacios et al., 2021). In our study, we found an overall evolutionary pattern of climatic niche conservatism in western ivies associated with the independent evolution of three single-species endemics inhabiting Macaronesian laurel forests. Climatic niche conservatism is shown by the following: (1) the placement of all western *Hedera* niches in the same general region of climatic space of the European-Mediterranean-Macaronesian regions (Figure 2); (2) the strong (although non-significant) phylogenetic signal of the first axis of climatic niche, summarizing nearly 50% of climatic variation; (3) the stronger niche similarity between close relatives than between distantly related species (Table 1). The latter pattern is exemplified by the three Macaronesian species and their closest relatives (Figure 3b).

The three Macaronesian ivies have converged to narrow (Figure 2) and similar (Table 1) climatic niches in the periphery of the climatic space currently occupied by the genus *Hedera* in Africa and Europe. These peripheral niches display warm winters and low temperature seasonality (Figure 3a), but they can be easily distinguished. Indeed, while the climatic niches of *H. maderensis* and *H. canariensis* are associated with relatively dry and warm environments and exhibit some similarity (Table 1), the niche of *H. azorica* is well differentiated in areas with higher precipitation and has clearly diverged from the niche of *H. canariensis* (Figure 3a, Table 1). This result is congruent with the similarities between the laurel forests of the Canary Islands and Madeira, which are well differentiated from the Azorean laurel forests in terms of climate, species richness and species composition (Fernández-Palacios et al., 2017).

The niche overlap of the *H. iberica*/*H. maderensis* species pair indicates that the climatic characteristics suitable for the establishment of *H. maderensis* can also be found in some mainland areas of the southwestern Iberian Peninsula (Table 1; Alonso et al., 2022). Thus, we interpret their climatic niche similarity as a footprint of pre-adaptation of *H. iberica* populations to the conditions found on Madeira, which facilitated establishment followed by speciation (Alonso et al., 2022). Pre-adaptation is especially relevant to explain the colonization of plant lineages in new environments, and it has been considered crucial for plant invasiveness (Lachmuth et al., 2010; Schlaepfer et al., 2010) and for the establishment of other Macaronesian lineages (*Hypericum canariense*; Dlugosch & Parker, 2007).

In contrast, *H. azorica* exhibits a climatic niche highly differentiated from that of its closest relative *H. helix* (Figure 2, Table 1). In fact, although the broad climatic niche of *H. helix* also includes part of the niche of *H. azorica* (Figures 1 and 3), their overlap is low ($D=0.019$, Table 1). According to our phylogenetic reconstruction, *H. azorica* could have originated through colonization of the Azores

by *H. helix* (Figure 2) followed by genetic and climatic differentiation from this species, leading to a phylogenetic pattern approaching reciprocal monophyly. The high phylogenetic signal of climatic variability captured by PC1 in the western clade of *Hedera* still suggests that niche conservatism predominates in the clade, and phyloecospace analyses show that *H. azorica* and *H. helix* currently exhibit close niche positions for the PC1. However, contrary to the *H. iberica*/*H. maderensis* pair, we do not currently observe a strong footprint of climatic niche pre-adaptation for *H. azorica*/*H. helix* ($p_e = 0.0099$, Table 1). The signal of pre-adaptation may be masked due to the longer time since colonization (compared with *H. iberica*/*H. maderensis*; Figure 4), which has enabled climatic niche differentiation with further adaptation to the Azorean climate, specifically to temperature stability (PC2; Figure 3b). In addition, this longer time since colonization may have enabled the extinction of those *H. helix* populations ancestral to *H. azorica* and hypothetically found in locations with climatic characteristics more similar to those currently found in the Azores. A similar pattern is observed in other Macaronesian lineages (*Carex* sect. *Rhynchocystis*, Sanz-Arnal et al., 2022), where the climatic niche of island taxa is well differentiated from that of the extant mainland relatives.

Finally, the climatic niche of *H. canariensis* is strongly differentiated from those of the remaining extant species of the western clade according to climatic niche equivalency tests (Table 1), particularly along PC1 (Figure 2). This could also be a consequence of the longer time since the colonization of the Canary Islands in comparison to the Azores and Madeira, leading not only to an increased phylogenetic differentiation but also to climatic niche differentiation. Nevertheless, phyloecospace analysis shows that *H. canariensis* has not diverged from its relatives along PC2, and suggests that the ancestor of the western clade of *Hedera* was already present in areas with high temperature stability.

In summary, Macaronesian ivies represent a gradient of evolutionary divergence of single-species island endemics when compared with their mainland relatives. We observed high climatic and phylogenetic isolation in the most ancient species *H. canariensis*, intermediate genetic and climatic differentiation in *H. azorica*, and a budding pattern with climatic niche similarity in the most recent species *H. maderensis*. Our results are consistent with a role of climatic niche conservatism in the evolution of single-species endemics at two stages: first, by facilitating island colonization, followed by differentiation from mainland populations driven by geographical isolation; and second, by limiting in situ diversification, in combination with high dispersal abilities. Our results highlight the importance of analysing ecological niches alongside high-throughput sequencing data to understand evolution and speciation on oceanic islands.

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CONFLICT OF INTEREST STATEMENT

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.


DATA AVAILABILITY STATEMENT

The raw reads (FASTQ files) used in this study are available in the NCBI Sequence Read Archive (SRA) database (Bioproject ID: PRJNA842926).

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BIOSKETCH

Angélica Gallego-Narbón is interested in the evolution and the climatic niche of the plant family Araliaceae. She applies a combination of phylogenomic, biogeographic, climatic and trait reconstruction analyses to study the evolutionary history of the genera of the most diversified clade of Araliaceae at a broad scale ('Asian Palmate group') and the evolution of the species of the genus *Hedera* at a smaller scale.

Author contributions: Mario Fernández-Mazuecos, Virginia Valcárcel and Angélica Gallego-Narbón designed the study. Alejandro Alonso, Angélica Gallego-Narbón and Mario Fernández-Mazuecos performed the laboratory work to prepare GBS libraries. Angélica Gallego-Narbón and Mario Fernández-Mazuecos performed the phylogenetic analyses. Angélica Gallego-Narbón and Alejandro Alonso compiled the database of occurrences and Angélica Gallego-Narbón performed the climatic niche and phyloecospace analyses. Angélica Gallego-Narbón, Virginia Valcárcel



and Mario Fernández-Mazuecos participated in the writing of the manuscript. All the authors contributed to the article and approved the submitted version.

SUPPORTING INFORMATION

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