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Integrating a phylogenetic framework for mapping biodiversity patterns to set conservation priorities for an oceanic island flora

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Abstract

Effective biodiversity conservation requires accurate assessments to inform management decisions, particularly in biodiversity-rich regions. The Gran Canaria Biosphere Reserve (GCBR) is located in one of the Canary Islands, an oceanic archipelago that belongs to the Mediterranean biodiversity hotspot and lies <100 km from NW Africa. We aim to help improve conservation in this territory by complementing traditional biodiversity metrics with phylogenetic analyses, using the two official plant DNA barcode sequences (matK and rbcL), and distribution data for 202 endemic angiosperm taxa within the GCBR, which encompasses about 42% of Gran Canaria's territory. We compare the geographical patterns of Phylogenetic Diversity (PD) and Phylogenetic Endemism (PE) with traditional diversity metrics such as Species Richness (SR) and Weighted Endemism (WE), and we use categorical analyses of neo-and paleoendemism. Our results highlight significant centres of PD and PE that do not entirely overlap with those detected for SR and WE. Notably, the northern region of the GCBR includes important conservation areas, representing either accumulations of ancestral diversity or spots of incipient speciation. Moreover, evolutionarily significant areas displaying high values of neo- and paleophylogenetic endemism were identified in the east and southeast of the GCBR beyond the current core zones and protected areas. These results highlight the enhanced resolution provided by PD and related metrics, and offer a more nuanced understanding of plant biodiversity compared to SR alone. This study underscores the need to establish a new core zone to preserve all key plant evolutionary sites within the GCBR and to ensure comprehensive protection of

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the endemic flora, which will require coordination among conservation biologists and decision-makers. The methodology used showcases the value of integrating taxonomic and phylogenetic diversity metrics for guiding the design of protected areas and improving territorial management in the Canaries and other oceanic archipelagos.

K E Y W O R D S

biosphere reserve, Canary Islands, endemism hotspots, evolutionary history, Gran Canaria, management, phylogenetic diversity, spatial and temporal patterns

1 | INTRODUCTION

Biodiversity is experiencing unprecedented and rapid threats that impose an urgent need to develop highresolution analyses and science-based strategies for its management and conservation. This need is particularly urgent in biodiversity hotspots (Joppa et al., 2011; Myers et al., 2000). Such urgency is reflected in both local policies and international treaties such as the IPBES Global Assessment Report (2023) and the UN Biodiversity Agreement, where over 190 parties at COP 15 set a global target to protect at least 30% of the world's lands by 2030 (CBD, 2022). Mapping and correlating different biodiversity facets can provide valuable information for the delineation of protected natural areas (Xu et al., 2019), especially in the face of rapid landscape transformation and the ongoing global climate crisis (Newbold et al., 2015; Pimm et al., 2014). The progressive improvement and cheapening of molecular techniques make it possible to implement phylogenetic approaches to help prioritize the protection of species and/or habitats with high conservation value (Mardis, 2011).

Until the early Holocene, most biodiversity hotspots were areas where the environmental risk of extinction was considered low, which largely explains their current status as reservoirs of global biodiversity and rare species (Enquist et al., 2019; Whittaker & Fernández Palacios, 2007). One example is provided by the Canary Islands (Figure 1), an oceanic archipelago in the Atlantic Ocean near the coast of northwestern Africa, which was presumably buffered against Pleistocene glaciations (e.g., Patiño et al., 2015; Rodríguez-Sánchez et al., 2009),

Gran Canaria Protected Natural Areas C01_INR Inagua C06 SNR Los Marteles CO8_SNR Guguy C09_Tamadaba NP C10_Pilancones NP C11 Nublo RP Iberian Peninsula C17_Tauro NM C20_Riscos Tirajana NM C21 Roque Nublo NM C25_Las Cumbres PL C27_Fataga PL C-09 C-01 Africa The Canary Islands 10 Kilometers

FIGURE 1 Left: Geographical setting of the Canarian archipelago, with Gran Canaria filled in black. Right: Map of Gran Canaria with the Protected Natural Areas currently included within the GCBR, highlighted in different colors (numbers correspond to the administrative codes of these areas used by the Cabildo de Gran Canaria, see legend).

and still harbors a high number of endemic species. Many of these taxa are closely related to those that went extinct in mainland Africa and Europe due to those climatic events (Caujapé-Castells et al., 2022; Francisco-Ortega et al., 1999; Quézel, 1978). Yet, the manyfold impacts of the recent and rapid increase in human activities on the Canarian biodiversity (reviewed in Caujapé-Castells et al., 2010; Fernández-Palacios et al., 2011) add to the potential natural threats posed by the geographical isolation, topographical complexity and very limited habitat occupancy that characterize this oceanic archipelago and its terrestrial biota.

Because biodiversity occurs in given regions and ecosystems, conservation actions should ideally be informed by indicators that relate to the species composition and the evolutionary history of the territories (Davies et al., 2011). The conservation of species and ecosystems, along with the underlying evolutionary processes, has been recognized as one of the highest priorities for preserving biodiversity, especially in response to the threats posed by current global changes (Mace et al., 2003). Thus, in order to protect biodiversity in the long term, we need to characterize and measure key indicators of conservation status (Faith, 2013). The use of phylogenetic metrics in conservation biology arises from the acceptance by the scientific community that accumulated evolutionary differences may help explain or predict evolutionary and ecological processes (Tucker et al., 2017).

Specifically, there are two cases of wide applicability for many endemic species in the Canaries where phylogenetic metrics can contribute to conservation decisions: when prioritizations have to be made for a larger number of rare species, and when information on the threat status of species is missing (Winter et al., 2013). By highlighting evolutionary history and distinctiveness, phylogenetic metrics enable conservationists to prioritize species that represent the most unique evolutionary lineages, complementing rarity assessments based on abundance or geographical distribution. Additionally, phylogenetic metrics help focus on species that, despite lacking comprehensive threat assessments, represent singular phylogenetic lineages. This ensures that conservation decisions are guided not only by present data referred to taxa, but also by their long-term evolutionary significance. The phylogenetic diversity (PD henceforth) index developed by Faith (1992a, 1992b) is the most widely applied, and was defined as the minimum total length of the branches required to cover a specified set of taxa on a phylogeny. Subsequently, Rosauer et al. (2009) proposed another measure of the spatial restriction of phylogenetic diversity: the phylogenetic endemism (PE). PE combines Faith's PD definition with weighted endemism (WE) for taxa in a phylogeny (Laffan &

Crisp, 2003) to identify areas where substantial components of phylogenetic diversity are spatially restricted. All these phylogeny-based measures of biodiversity mirror the evolutionary history of species (Faith, 2013; Swenson & Enquist, 2007) and their feature diversity, which refers to the variety of traits that species have developed over time within a region (Carstensen et al., 2013; Faith, 2013). Therefore, a practical approach to characterize and preserve functional diversity (i.e., the adaptations of plants in response to diverse threats such as climate change or habitat fragmentation, Fletcher et al., 2019; Yachi & Loreau, 1999) is to maximize the preservation of PD (Davies & Buckley, 2011) and related metrics.

The Macaronesian region comprises five oceanic archipelagos (Azores, Madeira, Salvages, Canary Islands and Cape Verde, Fernández-Palacios et al., 2024) and is included in the so-called "Mediterranean Basin hotspot" (Myers et al., 2000). Notably, some authors (e.g., Joppa et al., 2011) argue that hotspot regions harbor most of the flowering plant species that remain undiscovered and undescribed, thus reinforcing the idea that conservation efforts should focus on these areas. The Canary Islands host a rich and very unique flora, being the European area with the highest levels of plant endemicity (25.9%, Aedo et al., 2013). In addition, the Canaries encompass zones with particularly high levels of biodiversity which are of key conservation importance at the regional scale. For instance, the island of Gran Canaria, despite its relatively small area (1560 km²), contains about 260 species of endemic spermatophytes, 103 of which are exclusive to this island (Caujapé-Castells et al., 2022). About 42% of the terrestrial part of Gran Canaria was declared a Biosphere Reserve (GCBR henceforth) by UNESCO in 2005, and 85% of the land in the GCBR (and 50% of Gran Canaria) has some degree of protection to date.

Due to both the high density of endangered and rare plants in the GCBR and to its great environmental complexity (https://www.unesco.org/en/mab/gran-canaria), this part of the island sets forth important challenges for the design of science-based biodiversity conservation strategies and territorial management. Although the human population density within the GCBR (Data S1) is relatively low compared to the eastern and northern fringes of Gran Canaria (http://www.gobiernodecanarias. org/istac/, ISTAC, 2020), the substantial influx of visitors (both locals and tourists) together with unregulated activities and infrastructure development, have significant impacts on the native biodiversity of this reserve. Therefore, substantial effort is still needed to ensure the present and future preservation of biodiversity in the GCBR.

Herein, we use the distribution data of the Canarian flora provided by the Biodiversity Data Bank of the



FIGURE 2 Spatial distribution of the diversity parameters assessed for the Canarian endemic flora within the Gran Canaria Biosphere Reserve: (a) taxon richness (SR), (b) phylogenetic diversity (PD), (c) weighted endemism (WE), (d) phylogenetic endemism (PE), (e) corrected weighted endemism (CWE), and (f) corrected phylogenetic endemism (CPE). Grids with the highest values are shown in red, while those with the lowest values are shown in blue (see scale bars). The boundaries of core, buffer, and transition zones, as well as the overall Biosphere Reserve delimitation, are depicted in Figure S1.

Canary Islands (BIOTA, henceforth) and the DNA sequences of the two plastid markers officially accepted as barcode regions for land plants (matK and rbcL; CBOL Plant Working Group, 2009, CBOL PWG henceforth) to provide quantitative indicators that help ensure the effective conservation of regions with the highest floristic conservation interest within the GCBR. To achieve this goal we: (a) estimate the PD of the endemic angiosperm Canarian Flora known in the GCBR, (b) compare the patterns obtained for PD and PE with other related taxonomic diversity metrics (SR and WE), (c) assess the existence of potential neo- biodiversity floristic hotspots (areas with an accumulation of species resulting from recent speciation processes) and paleo- biodiversity hotspots (which concentrate more ancient or relict taxa) (following Mishler et al., 2014), and (d) quantify to what extent the existing protected areas within the GCBR represent the inferred centres of plant phylogenetic diversity and endemism within this territory.

MATERIALS AND METHODS 2

2.1 Study area

2.1.1 | The Gran Canaria biosphere reserve

The Canary Islands are an oceanic hotspot of seven main islands, some of which are of considerable geological antiquity (e.g., Fuerteventura with 21 Ma), while others are much younger and still volcanically active (e.g., La Palma and El Hierro) (Carracedo et al., 2002). Gran Canaria is characterized by a great diversity of ecological and climatic zones represented in different vegetation types distributed along an altitudinal gradient: coastal shrublands, palm groves, thermophilous woodlands, laurel forest and pine forest (del Arco Aguilar et al., 2010). Coastal halophytic, sand dune or rocky habitats can also be found on this island. The area of Gran Canaria declared as Biosphere Reserve encompasses ca. 655 km², a broad variety of natural and anthropogenic landscapes, and also 11 Protected Natural Areas (PNAs) that cover 80.55% of its land surface (the map in Figure 1 and Data S1 offer a detailed description of the current GCBR zoning and its biodiversity composition). A high number of endemic plant taxa (202 Canarian endemics, 95 of them endemic to Gran Canaria) are present in the GCBR, which contains the most rugged and oldest areas of the island (ca. 15.5 Ma; van den Bogaard 2013). Therefore, this is a unique area to study some of the evolutionary processes which have generated high levels of endemic plant biodiversity. For this study, the terrestrial area of the GCBR was divided into 2,869 cells of 500 m^2 (Figure 2).

Sampling and datasets 2.2

A complete list of the Canarian endemic plants distributed across the GCBR was compiled using the Biodiversity DataBank of the Canary Islands (widely known as BIOTA. https://www.biodiversidadcanarias.es/biota/). This frequently updated, georeferenced database provides high quality taxonomic and distributional information based on published documents and reports, validated by over a hundred international, national, and local experts. According to Steinbauer et al. (2016), the quality of the BIOTA database is particularly good for endemic species because of the large mean number of occupied grid cells per species, and their number of occurrence records is roughly twice as high as those available for non-endemic native species. Thus, although there could be in some cases a potential for error in non-detection when a species is present, we believe that the records in the BIOTA database accurately reflect the occurrence patterns of the endemic taxa (see also Caujapé-Castells et al., 2022). To further ensure accuracy and reliability in establishing the presence or absence of each species distributed within each of the 2,869 GCBR's 500 m² cells, we followed the criteria of de la Cruz (2012), by including only records with maximum geographical accuracy (levels 1 and 2). The data compiled from BIOTA were cross-referenced and complemented using the databases of the Canarian Botanic Garden 'Viera y Clavijo'-UA CSIC (henceforth JBCVCSIC), and additional considerations were made based on the geographical distribution of each species. Thus, the final list of the 202 Canarian endemic plant taxa from 28 families distributed across the GCBR that were included in the present study is an extended and refined version of the dataset used in earlier analyses (Caujapé-Castells et al., 2013, 2016; Jaén-Molina et al. 2015). Every cell in the grid includes a presence or absence value for each of the 202 Canarian endemic taxa occurring in the GCBR, with the number of occurrences per taxon and cell ranging from a minimum of 1 to a maximum of 109. A total of 68,794 occurrence records were used for the analyses (see Data S6). In all cases, sampling of the 202 taxa was conducted

by biologists from the JBCVCSIC with high expertise in the taxonomic identification of the Canarian endemic flora, who collected leaf material for the molecular analyses, and voucher specimens. A total of 227 samples (silica-dried leaves from several individuals and populations representing these taxa) were deposited in the DNA Bank of the Canarian flora at the JBCVCSIC. Vouchers made from freshly collected samples were further verified by taxonomic experts and deposited in the herbarium LPA at the JBCVCSIC (see Data S3).

2.3 | DNA isolation, amplification and sequencing

DNA extractions were performed from silica-gel dried material (at least one specimen of each taxon), using the CTAB protocol (Doyle & Doyle, 1987; Palmer et al., 1988) with some modifications. The method described in Dellaporta et al. (1983) was used for the 67 samples for which the CTAB protocol failed to provide DNA extractions of sufficient quality. DNA extracts were electrophoresed on 1% agarose gels, and their concentrations measured with the spectrophotometer ND-1000 (NanoDrop). Approximately 100 μ L of each total DNA sample was purified using UltraClean PCR Clean-up kit (MoBio Laboratories Carlsbad, California, USA). High quality aliquots with a concentration of about 50 ng/ μ l were stored at the DNA Bank of the Canarian flora at the JBCVCSIC.

PCRs were performed following the protocol described in Jaén-Molina et al. (2015). The PCR products were sent to Macrogen Inc. in Korea for bidirectional sequencing on an ABI 3730XL (Applied Biosystems, Foster City, CA, USA). The primers used for amplification and sequencing reactions are listed in Table S1. All DNA sequences are deposited in GenBank; accession codes for sequences newly generated for this study are provided in Data S3.

2.4 | Phylogenetic reconstruction

We used the DNA sequences of the two plastid barcoding markers (*rbcL* and *matK*) to build a Bayesian supertree for the 202 Canarian endemic angiosperm taxa known in the GCBR. The final concatenated matrix, with a total of 1,146 bp (480 bp corresponding to *rbcL* and 666 bp to *matK*) was aligned with MAFFT v.7.304b (Katoh & Standley, 2013) under default settings, and refined in GENEIOUS v5.4 (Drummond et al., 2012). Gblocks v.0.91b (Castresana, 2000) was used to eliminate unreliable alignment regions. *Amborella trichopoda* Baill. (Amborellaceae) and *Ginkgo biloba* L. (Ginkgoaceae) were chosen as outgroups.

We used a phylogenetic framework for our biodiversity measures, based on a time-calibrated species-level supertree covering all the taxa present in the GCBR. We ran dating analyses using BEAST v.1.8.4 (Drummond et al., 2012). Prior to these analyses, we used Partition-Finder 2 (Lanfear et al., 2017) to select the best substitution model, using the greedy algorithm with linked branch lengths under the Bayesian information criterion. Based on these analyses, the two plastid regions were included into a single partition and analyzed under the HKY substitution model. We then ran BEAST for two independent analyses of 100 million generations each, sampling every 100 generations. The single plastid partition was assigned to an uncorrelated lognormal relaxed clock model, considering a mean rate of 5.0×10^{-4} substitutions/site/Myr with a standard deviation of 1.0×10^{-4} , sampled from a normal distribution (Palmer, 1991). Bayesian reconstructions were conducted under two different tree priors, including speciation models defined by Yule and birth-death Process priors. Convergence of the MCMC analyses was assessed by checking that all parameters had an effective sample size (ESS) >200, using Tracer v.1.7 (Rambaut et al., 2018); 20% of trees were discarded as burn-in. Finally, we compared the posterior distributions of each combination of clock and tree priors using the marginal likelihood estimate (MLE) of each model, estimated from steppingstone sampling and path sampling. We obtained the MLEs with 150 path steps, each with a chain length of one million iterations, and the other parameters were set by default. We directly calculated the log-Bayes factors (BF) from MLEs and used BF to compare the support of all the models tested. We considered that BF values above two indicated that one model was significantly favored over another. Based on BF, the uncorrelated lognormal relaxed clock model was selected under a birth-death tree model. The resulting maximum clade credibility (MCC) tree was employed in the subsequent analyses.

The resulting topology was consistent with the relationships observed between genera and species according to current taxonomic knowledge, and also with the current classification of families of angiosperms (i.e, APG IV Chase et al., 2016).

2.5 | Data analyses

2.5.1 | Phylogenetic diversity and other biodiversity estimates

Six standard biodiversity indices were calculated in the package BIODIVERSE v0.6 (Laffan et al., 2010) for each of the 2,869 cells of 500 m² in which the GCBR is circumscribed: Taxon richness (SR), weighted endemism (WE), phylogenetic diversity (PD), phylogenetic endemism (PE), and the corrected version of weighted and phylogenetic endemism (CWE and CPE) (see Mishler et al., 2014). Based on the Bayesian tree obtained, the different diversity metrics were calculated and mapped to identify how they vary across the different grid cells, in order to detect specific patterns of spatial biodiversity distribution (e.g., PD or SR hotspots) in the GCBR landscape. We also calculated two additional diversity indices that provide complementary information on how PD and

PE can be influenced by contrasting branch lengths: relative phylogenetic diversity (RPD), and relative phylogenetic endemism (RPE) (González-Orozco et al., 2015; Mishler et al., 2014). These indices are ratios that compare the original values of PD and PE with their values based on an alternative phylogenetic tree with the same topology but with all branches of equal length (Mishler et al., 2014). Both RPD and RPE provide a more refined perspective on biodiversity by incorporating relative measures (i.e., relative abundance of each lineage or relative distribution of endangered endemism), which allows for a more comprehensive assessment of phylogenetic relationships, and highlights areas of particular conservation importance.

2.5.2 | Statistical analysis

We used a Spearman's correlation coefficient test to explore the relationship among the six biodiversity indices (SR, PD, WE, PE, and their corrected version CWE and CPE) for the Canarian endemic flora, both within and outside the protected natural areas of the GCBR. To handle non-normal data distribution (results not shown), we used a non-parametric Kruskal-Wallis test followed by Nemenyi pairwise tests for multiple comparisons involving all six biodiversity indices (with Bonferroni correction, see Data S5 with Rho and p values) using the function kwAllPairsNemenyiTest. These analyses aimed to identify significant differences (p < 0.05) in the spatial distribution of the biodiversity parameters between the different zones within the GCBR. The statistical analyses were performed in the R packages "corrplot" (Wei & Simko, 2021) and "PMCMRPlus" (Pohlert, 2023).

2.5.3 | Phylogenetic diversity and endemism analyses

We performed categorical analysis of neo- and paleoendemism with CANAPE (Mishler et al., 2014). This method consists of a two-step procedure, which tests the relative contribution of all short and long branches to phylogenetic endemism (PE) based on randomization analysis. Accordingly, grid cells were categorized into five independent, non-overlapping groupings as described in Thornhill et al. (2016): neo-endemism (i.e., grid cells with low RPE indicating a concentration of rare short branches on the original tree), paleo-endemism (grid cells with high RPE indicating a concentration of rare long branches of the original tree), mixed-endemism (a mixture of both rare long and rare short branches), super-endemism (extremely high levels of both neo- and paleo-endemism), and nonsignificant. Thus, CANAPE allowed us to identify grid cells with significant concentrations of neo- or paleoendemism, as well as mixtures of the two.

3 | RESULTS

3.1 | Phylogenetic diversity and other biodiversity estimates

Our results reveal heterogeneity in the values of the calculated biodiversity indices throughout the GCBR. Only the northern area of the GCBR (red cells indicating the highest PD values in Figure 2a–f, see color legend) stands out for showing high values in both taxonomic (SR, WE, CWE) and phylogenetic metrics (PD, PE and CPE). Meanwhile, in the eastern and southeastern areas of the GCBR (highlighted in red and blue cells in Figure 2b–d, see legend), PD provided greater discrimination among the grid cells compared to SR. This allowed us to identify the cells in the grid with significant evolutionary richness which could not be detected through taxonomic richness alone.

In the context of the administrative GCBR zonation (Data S1), many cells in the buffer and transition zones showed higher PD and PE values than the cells with the highest values of these parameters within the two core zones (Figure 2). Although one of these core zones (Guguy SNR) is indeed the area with the highest average PD and PE, the other core zone (Inagua INR) had only a few grids with moderately high values of either PD, PE, or other diversity metrics (Figure 2a–f). Other areas in the east and in the southeast, which also emerged as evolutionarily important for the endemic flora were found in the buffer and transition zones adjacent to the current limits of the GCBR (Figure 2b–d).

3.2 | Diversity metrics inside and outside the GCBR's protected natural areas

When comparing the biodiversity metrics obtained inside and outside the 11 Protected Natural Areas (PNAs) within the GCBR, we observed two main results: (1) all differences detected within the GCBR's total area and administrative zones (core area, buffer zone, transition area, see Figure 3a) were significant, except for CWE (Kruskal–Wallis non-parametric test, p > 0.05); and (2) in the comparisons within the GCBR's transition zone, we detected higher levels of SR and PD in the PNAs, but the values of CWE and CPE were significantly higher in the grids of non-PNAs in the north (see "NOT INCLUDED N", boxplot in light blue, Figure 3b).

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FIGURE 3 Legend on next page.

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FIGURE 4 Map illustrating the distribution of significant phylogenetic endemism (PE) identified through the categorical analysis of neo- and paleo-endemism (CANAPE) for the 202 Canarian endemic plant taxa across the 2,869 cells of 500 m² in which the GCBR was compartmentalized. The different categories of endemism represented are described in the legend (see text for definitions).

3.3 | Phylogenetic diversity and endemism analyses

The CANAPE analyses highlighted the north (Tamadaba NP) and centre of the GCBR (Inagua INR and Roque Nublo RP) as the areas with the highest concentration of phylogenetic paleo-endemism (blue grids in Figure 4) and neo-endemism (red grids in Figure 4). Additionally in the NW, NE and east of the GCBR, the analysis showed a substantial number of cells with mixed phylogenetic endemism (vellow areas in Figure 4). Notably, although some of the regions with mixed values of PE were circumscribed within protected areas (Guguy SNR, "Paisaje Protegido de Las Cumbres" or "Monumento Natural Roque Nublo"), many others fell outside any PNA.

4 | DISCUSSION

Phylogenetic information offers a powerful tool for identifying areas of conservation significance by pinpointing biodiversity hotspots within a region. Phylogenetic diversity (PD) estimates and related metrics enhance the information available for conservation decisions, offering insights that species richness (SR) alone cannot provide. By focusing on evolutionary relationships rather than species counts alone, we gain a deeper understanding of the biological uniqueness and potential ecological value of specific areas, thus better identifying conservation priorities. In this context, our findings are particularly striking because they show that PD and related metrics produce more detailed patterns of biodiversity than traditional measures such as SR and related metrics.

FIGURE 3 Box plots of the distribution of biodiversity parameters (PD and SR) comparing territories inside and outside the Natural Protected Areas (respectively, 1,861 and 1,007 grid cells of $500m \times 500m$); (a) across the entire GCBR's zonation, and (b) only between grids in the Gran Canaria Biosphere Reserve's transition zone. "NOT INCLUDEDN" refers to areas outside protected natural areas in the north (205 grid cells), while "NOT INCLUDEDS" refers to areas outside protected natural areas in the south (834 grid cells). The Horizontal bars represent the mean values. Grids within the core zones are not shown, as they are located within protected natural areas. Different letters indicate groups with significant differences according to Kruskal-Wallis tests.

It is important to note that all species are considered equal under the SR index, meaning that grids with the same number of species will have the same value regardless of their genetic or taxonomic differences. By contrast, the PD index offers higher discrimination because it estimates the evolutionarily distinctness of each taxon within a grid ('feature diversity' sensu Faith, 1992b). Consequently, regions containing more species with high or unique feature diversity will also show higher PD values. Overall, areas with higher feature diversity are considered to maximize the chance of an effective response to environmental threats in the long term, making them solid candidates for conservation prioritization (e.g., Forest et al., 2007). This emphasizes the need to integrate SR values with a multi-dimensional phylogenetic framework (PD and PE) for effective biodiversity protection and management decisions (Cadotte & Tucker, 2018).

Our results underscore the significance of the northern region of the GCBR in terms of taxonomic and phylogenetic diversity. Particularly, the PD estimates provide a higher detail than SR, also allowing us to highlight areas of significant evolutionary value in the east and southeast of the GCBR which could not be detected only with SR (Figure 2). Furthermore, significant differences in biodiversity metrics exist inside and outside the GCBR's protected natural areas. All these findings contribute to our understanding of the GCBR's biodiversity patterns and can inform future conservation initiatives and management strategies (Morlon et al., 2011).

The spatial resolution of our data $(0.5 \text{ km}^2 \text{ cells})$ is much higher than that used in similar investigations conducted in other regions, for example, South Africa (Forest et al., 2007), Wales (de Vere et al., 2012), or the Canaries (Reyes-Betancort et al., 2008, only with taxonomic diversity). This increased level of detail enables a more precise and thorough mapping of biodiversity patterns within the GCBR, allowing us to detect finer-scale variations and to identify more accurately areas of high floristic diversity. Consequently, this study positions the Gran Canaria Biosphere Reserve as one of the bestknown floristically rich areas globally. Unlike phylogenetic diversity approaches in other hotspots that used data only for plant genera, (Forest et al., 2007), our study employs species-level data, enabling us to address critical questions with more taxonomic detail, such as the impact of biodiversity disturbances on overall PD values, and whether areas with the highest PD also have the highest genetic diversity per taxon. This enhanced taxonomic and spatial detail is crucial for facilitating targeted actions to protect the most critical areas and unique ecosystems, and increasing biodiversity knowledge to be incorporated into effective conservation planning and management strategies.

4.1 | The relationship between phylogenetic diversity and species richness

The different indices applied show relevant differences in the makeup of Canarian endemic plant diversity across the GCBR, which do not correspond with the current administrative zonation of this territory, nor with the distribution of protected areas within it (Figures 1 and 2).

Considering our results, special conservation protection should be given to the northern area of the GCBR, which encompasses a large area of Tamadaba Natural Park and the cliffs of the 'Andén Verde' (Data S1). These regions feature the highest values of PD and PE and may represent 'evolutionary sanctuaries' based on their accumulation of ancestral diversity. Conversely, other areas within the GCBR show comparatively much higher SR values than PD values, which suggests the ongoing generation of new genetic diversity by admixture between closely related lineages. This may provide evolutionary advantages for adapting to environmental changes (Abbott et al., 2013; Caujapé-Castells et al., 2017; Rieseberg et al., 2003), or for colonizing new habitats (Gomulkiewicz & Holt, 1995). Such areas can be considered as evolutionary cradles associated with potential non-anthropogenic hybridization.

Finally, high values of PD and PE and of other biodiversity metrics are found in the eastern and southeastern regions of the GCBR, suggesting that they harbor key areas for biodiversity conservation not only in terms of individual taxa, but also from a phylogenetic point of view, which extends the "hotspots within hotspots" concept (Cañadas et al., 2014). Protecting such phylogenetic and taxonomic richness is a crucial step to mitigate the impacts of climate change and other future threats related to biodiversity loss (e.g., Davies & Buckley, 2011).

4.2 | Phylogenetic endemism hotspots beyond protected areas in the GCBR

The GCBR features high biogeographical and ecological complexities (Data S1), encompassing a representation of all the main vegetation belts/plant communities of Gran Canaria (i.e., *Euphorbia* shrublands; thermo-sclerophyllous woodlands, humid and dry pine forests, and patches of laurel forest and summit scrub). Over 50% of the GCBR's plant endemic taxa are listed as threatened, with 20 of them facing extinction in addition to those previously mentioned, for example, *Argyranthemum lidii* Humphries, *Digitalis isabelliana* (Webb & Berthel.) Linding, *Globularia ascanii* Bramwell & G. Kunkel, or *Solanum lidii* Sunding. Some of these species have only a few populations and/or <100 individuals remaining in the wild, for example, *Globularia*



FIGURE 5 Proposed alternative zonation of the GCBR, which would add a new core zone (highlighted in blue, see Section 4) to the two existing ones.

sarcophylla Svent., Helianthemum inaguae Marrero Rodr., Gonz.-Mart. & Gonz.-Art., Pericallis hadrosoma (Svent.) B. Nord. or Gonospermum oshanahanii (Marrero Rodr., Febles & C. Suárez) Febles (see Data S2 for detailed information).

A high number of both neo-endemics and paleoendemics co-occur in the NW, NE and East of the GCBR. Also, CANAPE analyses pinpoint critical zones with mixed values of PE outside of protected areas (Figure 4 and Data S2). This suggests that a more comprehensive and inclusive conservation approach should be implemented to consider both protected areas and those territories beyond their limits which have the highest values of PD and PE. The loss of key species in an ecosystem can lead to the cascading extinction of other species that depend on them, as well as the disappearance of key evolutionary processes for maintaining populations (Caujapé-Castells et al., 2010 and references therein). Hence, any environmental changes in the regions where threatened taxa with limited distribution ranges occur may entail the loss of some plants exclusive to Gran Canaria, as is the case of *Ruta museocanariensis* Marrero Rodr., Vidal Matutano, Delgado Darias & Jaén Molina, recently reported as possibly extinct in the wild (Marrero-Rodríguez et al., 2023; Data S2).

4.3 | Territorial, conservation and management implications of the PD estimates

All diversity metrics highlight the north of the Gran Canaria Biosphere Reserve as an important area for

endemicity and evolution. Quite unexpectedly, the core zones established in the current administrative zonation of the GCBR (Figure 1) do not correspond to the areas with the highest floristic PD and PE values. Indeed, both Guguy SNR and Inagua INR hold important natural values, which led to their inclusion as core zones (see Data S1), but they do not stand out in terms of either SR or PD values associated with floristic diversity. Notably, the PD values of the Inagua core zone are among the lowest in the GCBR. Rather, some northwestern (Tamadaba NP and Andén Verde), eastern (Artenara and Tejeda), and southeastern (Mogán and San Bartolomé de Tirajana) regions concentrate the highest values of PD and PE. All these regions lie within the transition zone, where anthropogenic disturbances are higher and thus can lead to the loss or fragmentation of populations of endangered local endemics. Such is the case of Bencomia brachystachya Svent., Crambe tamadabensis A. Prina & Marrero Rodr. or Dracaena tamaranae Marrero Rodr., Almeida-Pérez & Gonz-Mart (del Arco et al., 2002).

The detection of high PD, PE, and WE indices in regions not yet included in protected areas or core zones highlights the need to redefine the current administrative zonation of the GCBR to effectively preserve the areas with the highest floristic conservation values (Figure 5). In agreement with Caujapé-Castells et al. (2016), we propose to create a third core zone covering all the cells with the highest PD, PE and SR values in the perimeter of the Tamadaba Natural Park (Tamadaba's pine forest and Andén Verde), and also adjacent areas (Figure 5). Even though these neighboring grids do not have such high diversity values, they are key to possible migration processes from close areas within the buffer and transition zones where human activities are allowed, and they may serve to foster connectivity between the populations of several endangered species (Data S2). This is especially relevant from a conservation standpoint, given that evolutionary richness (PD and PE) and connectivity may increase ecological resilience to climate change (Oliveira et al., 2022). This proposal is extremely challenging for managers, as it entails the expansion of the current buffer zone and the creation of a new core zone encompassing areas with heterogeneous land uses, both private and public. The establishment of permanent co-governance groups involving landowners and stakeholders may contribute to the implementation of this and other biodiversity management measures within the GCBR.

While the GCBR is already compliant with the Convention on Biological Diversity (CBD, 2010), this study provides new data to refine the number and boundaries of its protected areas. By ensuring protection of areas with previously overlooked phylogenetic value of the endemic spermatophyte flora, we could preserve the

continuity of ecological and evolutionary processes in this area (Faith, 1992b; Forest et al., 2007). In parallel, it is crucial to raise awareness of the rich but fragile biodiversity that the GCBR harbors and to acknowledge the invaluable ecosystem services provided by the protected areas worldwide (Roman et al., 2010). Urgent measures should be taken to mitigate the impacts of overexploitation, invasive species or anthropic pressures, such as investing resources in the early detection of potentially invasive species and reducing the number of visitors to the protected areas such as biosphere reserves around the world (Spenceley et al., 2021).

CONCLUSIONS 5

The identification of the areas of greatest biodiversity at the regional and global scales using the most up-to-date scientific knowledge is critical to lay the groundwork for conservation policies and management guidelines, both locally and internationally. While most current conservation efforts aim at preserving diversity in the short term by halting biodiversity loss and reducing extinction rates, it is equally important to safeguard the processes that drive diversification, thus maintaining the adaptive potential of the species and ecosystems (Faith, 2013).

The phylogenetic framework used in this study has allowed us to highlight areas within the GCBR that should be considered high priority conservation targets or require additional protection, for example, through expanding the limits of some existing protected areas and the implementation of a new core zone within the northwestern region of the current administrative zonation. Also, we propose governance measures aimed at improving biodiversity management and regulating current land uses, while encouraging and compensating private owners. Finally, the phylogenetic diversity indicators associated with the endemic angiosperm flora within the GCBR emphasize the need for a comprehensive conservation approach that takes into account both protected and non- protected areas. We believe that the implementation of the new spatial planning proposed can significantly contribute to a better biodiversity conservation and management of the GCBR, and provide inspiration to other biosphere reserves or similar territories. It is crucial to ensure the long-term persistence of the biodiversity they host and their ability to adapt to climate change challenges (e.g., Kueffer et al., 2014). This approach can be particularly relevant for other ecologically significant enclaves across the Canarian archipelago and for other oceanic islands that face present and future threats due to global climate crisis (Fernández-Palacios et al., 2021).

AUTHOR CONTRIBUTIONS

Juli Caujapé-Castells, Ruth Jaén Molina and Jairo Patiño conceived the ideas; Magui Olangua-Corral, Águedo Marrero, Juli Caujapé-Castells, Ruth Jaén Molina and Carlos García-Verdugo did field work; Ruth Jaén Molina, conducted laboratory work; Águedo Marrero and Magui Olangua-Corral organized and reviewed the data and taxonomic determination related to the herbarium sheets: Ruth Jaén Molina, Jairo Patiño and Salvador de la Cruz analyzed the data; Juli Caujapé-Castells, Ruth Jaén Molina and Jairo Patiño led the writing. All authors discussed the manuscript and reviewed the final version.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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