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RESEARCH ARTICLE

Global insular leaf size shifts follow the island rule, independently of insect herbivory and macroclimate

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Abstract

1. The island rule, originally formulated for animals, predicts that small-bodied mainland species evolve larger body sizes on islands (gigantism), but that this effect weakens with increasing mainland body size, ultimately reversing and leading to dwarfism for the largest species. This dynamic is expected to produce a positive, saturating relationship between island and mainland body size, with insular size increases at small sizes and reductions at large sizes. Despite extensive support in animals, this prediction has rarely been tested in plants. Consequently, it remains unclear whether the island rule applies to plants, whether it operates consistently across evolutionary scales, and how biotic and abiotic drivers jointly shape insular size shifts.
2. We tested the island rule in plants by examining leaf size variation—an organ-level analogue of body size—across 48 island species from six oceanic systems and their mainland counterparts. We conducted both conspecific comparisons (same species on islands and the mainland; $n=19$ pairs) and congeneric comparisons (island endemics paired with closely related mainland species; $n=29$ pairs) to assess patterns across evolutionary scales. We also measured insect herbivory and recorded climatic variables to explore ecological correlates of island–mainland variation in leaf size.
3. Although mean leaf size did not differ significantly between island and mainland populations for either conspecific or congeneric comparisons, we detected a non-linear, positive saturating relationship between mainland and island leaf sizes, consistent with an island rule-like pattern. Small-leaved mainland species tended to evolve larger leaves on islands, whereas this effect diminished for larger leaved

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species, a pattern observed in both conspecific and congeneric comparisons. Insect herbivory and climate did not explain these relationships.

4. *Synthesis*: These findings demonstrate that plants follow the island rule for leaf size and suggest that mainland-to-island shifts at opposite ends of the mainland leaf size spectrum offset one another, possibly explaining no overall difference in leaf size between island and mainland populations.

KEYWORDS
climatic conditions, functional island biogeography, herbivore pressure, leaf dwarfism, leaf gigantism, oceanic islands

1 | INTRODUCTION

Oceanic islands have long fascinated ecologists and evolutionary biologists, who view them as natural laboratories where distinctive biodiversity patterns and species traits emerge under isolation (Borregaard et al., 2017; Losos & Ricklefs, 2009; Schrader et al., 2024; Whittaker et al., 2017). In plants, island-related patterns often involve the evolution of suites of traits (i.e. so-called syndromes) thought to result from unique selective pressures common to many island systems—such reduced as herbivory, limited availability of pollinators and seed dispersers, lower interspecific competition (Baeckens & Van Damme, 2020; Biddick, Hendriks, & Burns, 2019) and variable climatic regimes (Weigelt et al., 2013). Hallmark traits reflecting adaptation to these conditions include shifts in plant size—manifesting as either gigantism or dwarfism—secondary woodiness in formerly herbaceous lineages, reduced dispersal structures, simplified reproductive strategies favouring self- or wind-pollination, and decreased defensive investment in the absence of large herbivores (reviewed by Burns, 2019). Collectively, these convergent patterns highlight the repeated influence of similar selective forces shaping plant evolutionary shifts on islands.

A recurring theme in island-associated plant evolution are striking changes in plant size, or by extension, in organ dimensions such as leaves, seeds or fruits (Burns, 2016; Kavanagh, 2015). In particular, island plants often differ markedly from their mainland relatives in leaf size, though the direction and magnitude of these differences may vary. For example, studies in island-rich regions such as Zealandia and Macaronesia have documented leaf and seed gigantism in island (relative to mainland) populations (e.g. Burns et al., 2012; Ciarle & Burns, 2024; Cox & Burns, 2017; García-Verdugo et al., 2010; Kavanagh, 2015). However, studies in other insular systems have instead found reductions—or no detectable differences—in leaf size for island plants as compared to their mainland counterparts (e.g. Burns, 2016; Ciarle et al., 2025; Kokubugata et al., 2010; Zhang et al., 2025). These mixed results can nonetheless be explained under the so-called 'island rule' framework, originally proposed by Foster (1964) and well supported in animals, particularly vertebrates (Benítez-López et al., 2021). This theory posits that small-bodied mainland species tend to evolve larger sizes (i.e. gigantism) on islands, but that this relationship weakens as mainland body size increases—likely due to allometric or metabolic constraints (Biddick, Hendriks, & Burns, 2019; Burns, 2016)—ultimately giving way to an inverse pattern with increasing mainland body size, that is, the largest-bodied mainland species evolving smaller sizes (i.e. dwarfism) on islands (Foster, 1964; Van Valen, 1973). Several explanations have been put forward to explain this pattern. For example, gigantism may evolve due to weaker biotic pressures on islands—such as reduced competition and the absence of predators—allowing organisms to allocate fewer resources to defence and more to growth (Meiri et al., 2007). Dwarfism, on the other hand, has been attributed to energetic and resource constraints typical of insular environments, where limited food availability, reduced habitat area and high population densities favour smaller body sizes with lower metabolic demands (Foster, 1964; Lomolino et al., 2013). In plants, however, tests of the island rule are far less common (Burns, 2019), and a handful of studies conducted to date have reported mixed patterns (e.g. Burns, 2022; Zhang et al., 2025) and therefore leave its validity uncertain outside the animal realm. For instance, different types of plant size-related traits may exhibit contrasting mainland-to-island shifts because they play different roles or respond differently to changes in biotic or abiotic forces acting on islands (Biddick, Hendriks, & Burns, 2019; Ottaviani et al., 2020). Placing these responses within a framework of functional island biogeography could shed insight into variable trait shifts across island systems.

One key challenge in island-associated shifts in body or organ size is disentangling the role of biotic and abiotic factors potentially responsible for evolutionary shifts in plant size-related traits between islands and the mainland. Variation in climate-related factors such as temperature and precipitation are an obvious candidate, given their strong influence on plant form and function (Díaz et al., 2016; Wright et al., 2017). For instance, smaller leaves are favoured in drier environments to minimize water loss through transpiration (Luo et al., 2021; McDonald et al., 2003; Yates et al., 2010), whereas larger leaves provide advantages for light capture in shaded or humid habitats (Lusk et al., 2019). Islands often differ climatically relative to nearby continents, including cooler, wetter and less seasonal environments, or unique wind and fog regimes (Weigelt et al., 2013), conditions which may drive leaf morphological and functional divergence between island

and mainland plants (e.g. increasing resource availability favouring growth-related traits, including size of vegetative organs). Likewise, biotic interactions such as herbivory impose strong selective forces locally and often differ in strength across these contexts (Brown et al., 1991; Moreira & Abdala-Roberts, 2024). On islands, where herbivores are typically less abundant or diverse leading to lower herbivory rates, plants may relax investment in defences (e.g. against vertebrate herbivores; Burns, 2019; Moreira & Abdala-Roberts, 2022), leading to resource reallocation away from defences to growth and organ development (e.g. leaves). However, few studies have formally assessed the relative role of these abiotic and biotic factors in driving island-to-mainland variation in leaf size (e.g. per the island rule), leaving a critical gap in our understanding of the mechanisms driving shifts in plant morphology and function.

Another key challenge in studying island-associated shifts in plant organ size is linking variation within and across species to understand evolutionary responses at different temporal scales (Agrawal, 2020; Biddick & Burns, 2021). Intraspecific comparisons, which examine populations of the same species across islands and mainland sites, provide valuable insight into microevolutionary processes, including local adaptation, phenotypic plasticity and short-term responses to environmental pressures. At this scale, researchers can test how populations evolve under novel island conditions and the extent to which trait variation is shaped by immediate ecological factors. On the other hand, interspecific (e.g. congeneric) comparisons capture broader scale macroevolutionary dynamics, including long-term trait divergence, lineage-specific responses, and speciation following colonization events (Moreira, Abdala-Roberts, Cubas, et al., 2025; Rolland et al., 2023; Veron et al., 2019). Studies that concurrently test and compare patterns across scales can offer unique complementary views on evolutionary processes that together yield a more comprehensive understanding of how island environments shape size-related traits linked to function.

In this study, we examined variation in leaf size across 48 species from six oceanic island systems and conducted cross-scale analyses of island-associated shifts in this trait. We performed an intraspecific (conspecific) analysis by comparing populations of the same species on islands and the mainland ($n=19$ conspecific pairs), as well as a congeneric analysis by comparing island endemic species with their closest mainland relatives ($n=29$ congeneric pairs). In addition to leaf size, we quantified insect herbivory and recorded climatic variables to test for potential drivers of trait variation between insular and continental environments. Specifically, we addressed the following questions: (1) Do island plants differ in leaf size compared with their mainland counterparts, and are these patterns consistent with the island rule? We expected mainland species with small leaves to evolve larger leaves on islands (gigantism), with this effect weakening in lineages with larger mainland leaves and ultimately leading to dwarfism in species with the largest mainland leaves. (2) Is island–mainland variation in leaf size associated with climatic factors and herbivory? Here, we predicted that reduced abiotic stress (e.g. more humid and cooler climates) and lower enemy pressure (reduced herbivory) on islands would be associated with larger leaves. By jointly testing these predictions using both conspecific and congeneric comparisons across geographically distant systems, and by exploring ecological correlates of island-associated trait shifts, our study provides one of the most robust and comprehensive tests to date of divergence in plant functional traits on islands.

2 | MATERIALS AND METHODS

2.1 | Study systems and sampling

We selected six oceanic island systems—Galápagos, Canary Islands, Azores, Lord Howe Island, Mauritius and the California Channel Islands (Figure 1)—which differ widely in size (14.5–2040 km^2), isolation from the mainland (31–1529 km), climatic conditions (annual precipitation: 261–1752 mm; mean annual temperature: 15.3–23.0°C) and herbivory rates (0.65%–4.96% of leaf area damaged by chewing insects; data from this study). Within each island–mainland system, we selected 5–10 native plant species (mean = 8), totalling 19 species present on both islands and the mainland (i.e. conspecific comparisons), as well as 29 insular endemic species paired with a mainland relative (i.e. congeneric comparisons; 58 species total); there were no species shared between these two levels of comparison (see Table S1). The selected species were identified and verified by regional experts to ensure both taxonomic accuracy and confirmed origin. Specifically, the dataset was filtered to exclude any taxa classified as non-native or whose presence in the insular systems studied was, directly or indirectly, the result of human-mediated introduction. For congeneric comparisons, we generally selected the closest mainland relative of each insular species (e.g. van Huysduynen et al., 2021; Vargas, 2014). When the closest relative was not available, we used the second or third closest relative. We also adjusted species pairing criteria in other exceptional cases such as *Azorina vidalii* (Azores), the sole member of its genus, which was compared with a species from the same family (*Jasione montana*) (Table S1). In addition, *Eugenia kanakana* (Mauritius) was paired with the mainland *Syzygium bernieri* (Myrtaceae) because no closely related continental congeners were available and both species share comparable growth forms, ecological niches and close phylogenetic affinity within the Myrtaceae. Similarly, *Euphorbia balsamifera* (Canary Islands), which is absent from the selected mainland sites, was substituted with the closely related congener *Euphorbia regis-jubae* (Table S1). As a whole, the selected island species comprised 8 herbaceous species, 24 shrubs and 16 trees, while the mainland assemblage included 10 herbaceous species, 23 shrubs and 15 trees (Table S1). For woody species, we sampled only non-reproductive saplings (juvenile plants) to avoid confounding effects of ontogeny and reproductive phenology on leaf trait variation. To reduce habitat-related variation, island and mainland populations were matched within the same habitat type (e.g. grasslands, forests, coastal dunes). For conspecific comparisons,

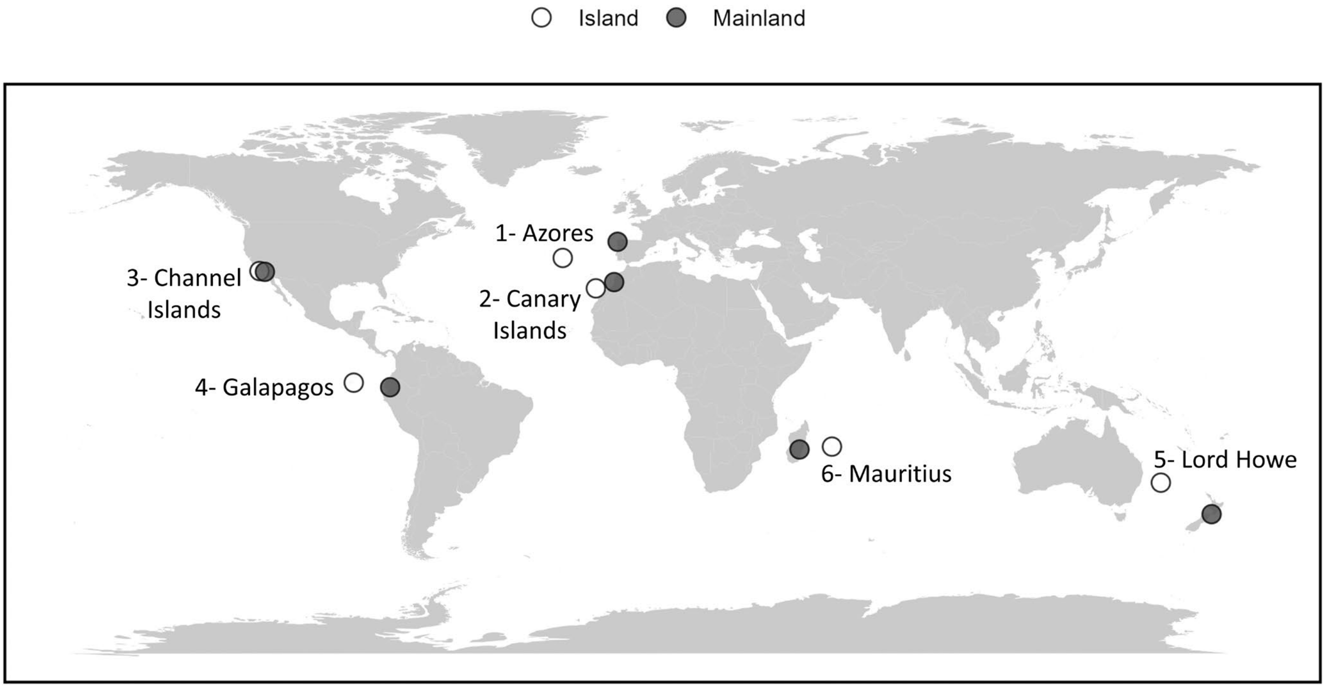

FIGURE 1 Map showing the six island–mainland systems included in this study, with white points indicating island sampling sites and grey points indicating mainland sites. The systems are as follows: (1) Azores Islands versus mainland Spain, (2) Canary Islands versus mainland Morocco, (3) Channel Islands versus mainland California, (4) Galápagos Islands versus mainland Ecuador, (5) Lord Howe Island versus mainland New Zealand, and (6) Mauritius Island versus mainland Madagascar. Although New Zealand and Madagascar can be considered islands, they were treated as mainland regions in this study due to their large size and because they represent the most likely source regions for the flora of Lord Howe and Mauritius, respectively.

we sampled three island and three mainland populations per species; for congeneric comparisons, we sampled three populations of the island endemic and three populations of its mainland relative. Populations were spaced at least 1 km apart. Within each population, we selected 4–5 individuals growing under similar abiotic conditions (e.g. slope, light availability) to minimize microclimatic variation. In total, the sampling design yielded 1291 plants, resulting from: 6 island systems × 5–10 species pairs × 6 populations (three island + three mainland) × 4–5 individuals per population.

2.2 | Fieldwork permits

The fieldwork was conducted under the following permits: 2022-00180 (Canary Islands), LHIB 02/23 (Lord Howe Island), MU/NPPO/202501544 (Mauritius), MAAE-DNB-CM-2021-0198 and MAAE-DNB-CM-2021-0198-M-00011 (Galapagos Islands), 31/2022/DRCT (Azores) and 53/22/MEDD/SG/DGGE/DAPRNE/SCBE.Re (Madagascar).

2.3 | Leaf area and herbivory measurements

We sampled plants at the end of the growing season at each site to obtain a measure of cumulative herbivory. For each plant, we recorded height and randomly collected 10 fully expanded leaves, ensuring similar age by using leaf position along the branch, coloration and texture as sampling criteria. All leaves were photographed using a Nikon COOLPIX P100 digital camera with a reference scale. Leaf area was estimated for three undamaged leaves (out of the 10 collected) using ImageJ software, and values were averaged to obtain mean leaf area per plant. Most observed damage (>98%) was caused by chewing insects. The percentage of leaf area consumed ('insect herbivory' hereafter) was quantified for all 10 leaves per plant using BioLeaf – Foliar Analysis™ (Brandoli Machado et al., 2016). For statistical analyses, we used the average herbivory value across the 10 leaves per plant.

2.4 | Climatic conditions

We characterized temperature- and precipitation-related conditions for each population using a subset of eight bioclimatic variables obtained at a 2.5-min spatial resolution from the WorldClim database version 2.1 (Fick & Hijmans, 2017), that provides historical climate data from 1970 to 2000. The selected variables capture key aspects of temperature and precipitation regimes, namely BIO1 (annual mean temperature, °C), BIO4 (temperature seasonality, calculated as the standard deviation of monthly temperature × 100), BIO5 (maximum temperature of the warmest month, °C), BIO6 (minimum temperature of the coldest month, °C), BIO12 (annual precipitation, mm), BIO13 (precipitation of the wettest month, mm), BIO14 (precipitation of the driest month, mm), and BIO15 (precipitation seasonality, measured as the standard deviation of monthly precipitation).

2.5 | Statistical analyses

2.5.1 | Leaf size variation between island and mainland plants

First, we assessed whether there was an overall difference in leaf size between island and mainland plants by fitting a general linear mixed model with mean leaf size as the dependent variable, and insularity (two levels: island vs mainland), comparison type (two levels: congeneric vs conspecific), and their interaction as fixed effects. Island–mainland system and island species identity were included as random effects to account for shared evolutionary history and environmental variation within each system, as well as for the paired island–mainland design, respectively. In addition, plant height was included as a covariate in all models to account for organism size-related variation affecting leaf size associated with environmental conditions or plant age. We acknowledge that plant height represents an imperfect proxy for organism size, as it does not capture variation in architecture, biomass allocation or growth form across species and environments, and may be difficult to disentangle from passive allometric effects affecting leaf size independently of adaptive responses (Gao et al., 2024). However, given the logistical constraints of sampling across multiple global systems and taxa, height provided a standardized and comparable metric of plant size that could be consistently measured across species and at least partially account for allometric and environmental effects in testing for variation in leaf size. Leaf size was log-transformed to ensure normality of residuals.

Second, we tested whether leaf size variation followed the island rule by fitting a general linear mixed model with mean island leaf size as the dependent variable, predicted by mean mainland leaf size, including both its linear and quadratic terms (to test for a non-linear association, per the island rule), comparison type, and their two-way interactions. Island–mainland system was included as a random effect. Island and mainland leaf sizes were log-transformed to ensure normality of residuals. Evidence for the island rule would be indicated by a non-linear positive relationship, as reflected by a significant quadratic term, for which the rate of leaf size increase from mainland to island is steepest for small-leaved mainland plants and declines with increasing mainland leaf size, eventually saturating or decreasing (dwarfism) at the largest mainland leaf sizes.

2.5.2 | Correlates of mainland-to-island shifts in leaf size

To investigate candidate factors associated with (and potentially underlying) any such island rule-like relationship between mainland and island leaf size, we fitted a general linear mixed model with the leaf size log-ratio (lsLR), calculated as the natural logarithm of the ratio between mean island leaf size and mean mainland leaf size for each island–mainland pair (at both conspecific and congeneric levels), as the dependent variable, and the logarithm of the ratios of island to mainland climatic variables (temperature and precipitation) and herbivory as predictors. Previously, climatic variation across populations was summarized with a Principal Component Analysis, which indicated that annual precipitation and mean annual temperature were the strongest correlates of the first two principal components, respectively (Table S2, Figure S1). These variables were included as climatic predictors in the model.

All models were conducted at the species level. Models were implemented using the *lmer* function from the *lmerTest* package (Kuznetsova et al., 2017) in R version 4.3.3 (R Core Team, 2024). It is important to note that island isolation, island size, and latitude were initially included as covariates in all models, but none had a significant effect and were subsequently removed. Plant growth form was not considered in the analyses because there was no replication within the comparison types.

3 | RESULTS

3.1 | Leaf size variation between island and mainland plants

Leaf size did not differ significantly, on average, between island and mainland plants, nor between congeneric and conspecific comparisons, and there was no significant interaction between insularity and comparison type (Table 1, Figure 2). However, a follow-up model examining the relationship between island and mainland leaf size revealed a significant positive non-linear association, consistent with the island rule at both the congeneric and conspecific level. Specifically, the quadratic term for the logarithm of mainland leaf size significantly predicted the logarithm of island leaf size at both levels ($\hat{\beta}=0.143\pm0.036$, $t=3.95$, $p<0.001$ for congeneric comparisons; $\hat{\beta}=0.312\pm0.039$, $t=8.00$, $p<0.001$ for conspecific comparisons) (Table 2). This indicates a non-linear relationship in which island leaf size increases steeply with

TABLE 1 Effects of insularity (two levels: Island vs. mainland), comparison type (two levels: Congeneric vs. conspecific), and their interaction on leaf size across six island–mainland systems.

	F	$DF_{num,den}$	*p*
Insularity	0.67	1, 44.5	0.416
Comparison type	3.61	1, 44.6	0.064
Insularity × comparison type	2.57	1, 44.0	0.116
Plant height	2.49	1, 56.1	0.120

Note: The island–mainland system and the island species identity were included as random effects, and plant height was included as a covariate to account for differences in overall plant stature. Leaf size was log-transformed to ensure normality of residuals, and analyses were conducted using species-mean values in island versus mainland ($n=96$). *F*-values, numerator and denominator degrees of freedom, and associated *p*-values are shown.

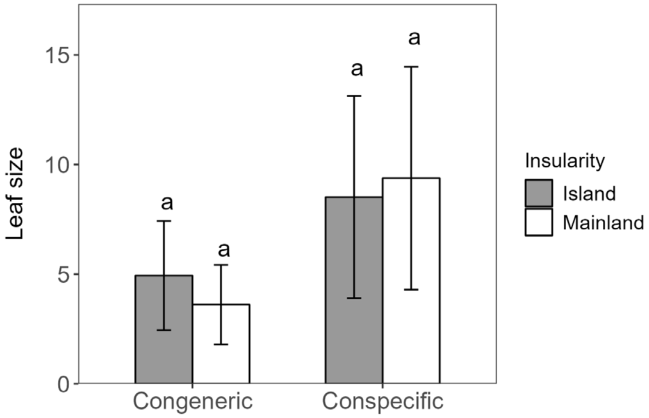

FIGURE 2 Leaf size (cm^2) for island plants (grey bars) and their mainland counterparts (white bars) based on congeneric comparisons ($n = 29$ species pairs) and conspecific comparisons ($n = 19$ species pairs) across six island–mainland systems. Bars represent least square means ± standard error. Letters above the bars indicate non-significant differences ($p > 0.05$) between island and mainland plants. Statistical results are provided in Table 1.

TABLE 2 Effects of mainland leaf size (linear and quadratic terms), comparison type (two levels: Conspecific and congeneric), and their interactions on island leaf size across six island–mainland systems.

	F	$DF_{num,den}$	*p*
Mainland leaf size	49.57	1, 41.6	**<0.001**
Mainland leaf size^2	5.60	1, 41.5	**0.023**
Comparison type	8.51	1, 41.1	**0.006**
Mainland leaf size × comparison type	3.40	1, 41.3	0.073
Mainland leaf size^2 × comparison type	0.03	1, 40.3	0.875

Note: Island–mainland system was included as a random effect. Island and mainland leaf sizes were log-transformed, and analyses were conducted using species-mean values ($n = 48$). F-values, numerator and denominator degrees of freedom, and associated *p*-values are shown. Statistically significant effects ($p < 0.05$) are indicated in bold.

mainland leaf size at small mainland values, followed by a slower rate of increase at mid to larger mainland leaf sizes, eventually saturating (Figure 3). This pattern did not differ significantly between comparison types, as indicated by the non-significant interactions between the linear and quadratic terms of mainland leaf size and comparison type (Table 2, Figure 3).

3.2 | Correlates of mainland-to-island shifts in leaf size

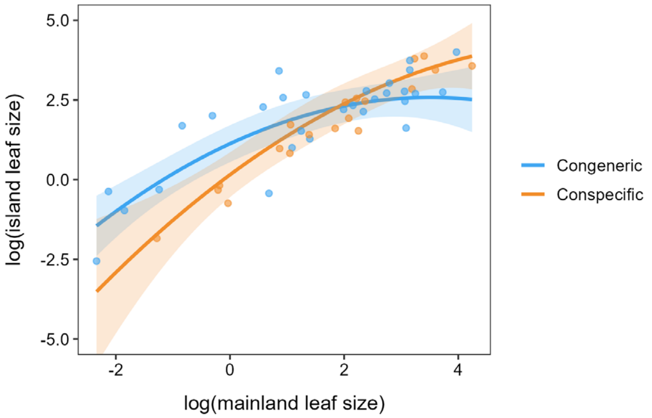

FIGURE 3 Associations between the logarithm of mainland leaf size and the logarithm of island leaf size for congeneric comparisons (blue dots, $n = 29$ species pairs) and conspecific comparisons (orange dots, $n = 19$ species pairs) across six island–mainland systems. Evidence for the island rule is given by a convex relationship between island and mainland leaf size, where the slope is steepest for species with the smallest mainland leaves and gradually decreases for species with larger mainland leaves. Statistical results are shown in Table 2.

TABLE 3 Effects of the logarithm of the ratios of island to mainland insect leaf herbivory, mean annual temperature, and annual precipitation on the leaf size log-ratio (lsLR)—calculated as the natural logarithm of the ratio between mean island and mainland leaf size—for congeneric and conspecific pairs across six island–mainland systems.

	t	DF	*p*
Congeneric comparisons			
Herbivory	−0.77	22.7	0.452
Temperature	0.78	8.9	0.457
Precipitation	1.16	8.0	0.278
Conspecific comparisons			
Herbivory	−0.81	5.7	0.447
Temperature	0.82	0.9	0.567
Precipitation	2.36	2.3	0.124

Note: Island–mainland system was included as a random effect, and analyses were conducted using species-mean values ($n = 48$). *t*-values, associated degrees of freedom and corresponding *p*-values are reported.

Island-to-mainland ratios in leaf herbivory and climatic factors—namely annual mean temperature and annual precipitation—did not significantly correlate with island-to-mainland (log) ratios of leaf size, and this pattern was consistent across comparison types (Table 3, Figure 4).

4 | DISCUSSION

4.1 | Leaf size shifts align with the island rule

We found no overall difference in leaf size between island and mainland plants, and this was consistent across evolutionary scales of analysis (i.e. within and across species). This lack of divergence aligns

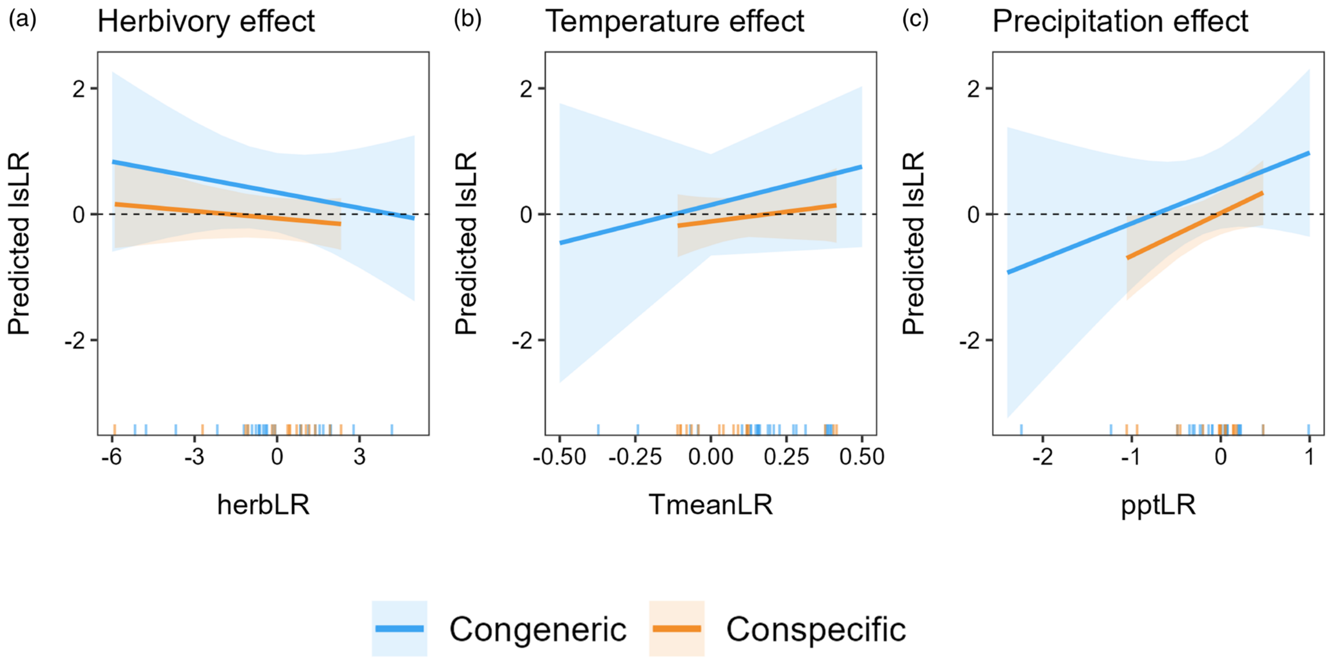

FIGURE 4 Associations between the predicted values of the leaf size log-ratio (lsLR)—calculated as the natural logarithm of the ratio between mean island and mainland leaf size—and the logarithm of the ratios of island to mainland (a) insect leaf herbivory (herbLR), (b) mean annual temperature (TmeanLR), and (c) annual precipitation (pptLR) for congeneric comparisons (blue lines) and conspecific comparisons (orange lines) across six island–mainland systems. None of the associations were statistically significant. Full model results are provided in Table 3.

with previous findings from island–mainland comparisons in the Southwest Pacific (e.g. Burns, 2016; Ciarle et al., 2025). That said, leaf size did vary substantially between islands and mainland, ranging from 0.48-fold to 1.94-fold differences for conspecific comparisons (19 species pairs) and 0.23-fold to 12.85-fold for congeneric comparisons (29 species pairs). In turn, a targeted follow-up test of the island rule evaluating the relationship between island and mainland leaf size was consistent with predictions. At both scales, we observed a positive saturating (decelerating) relationship: island leaf size increased steeply relative to mainland leaf size for species or populations with small leaves on mainland, but the rate of increase became progressively weaker and eventually plateaued for populations or species with the largest leaves on mainland. These findings extend the island rule—originally formulated for animal body size (Foster, 1964; Van Valen, 1973)—to a key plant morphological trait and suggest that saturating relationships, such as those observed, contribute to weaken the overall (mean) difference in leaf size between islands and the mainland. This pattern may also help explain variability and inconsistencies across systems reported previously (reviewed by Burns, 2019). The slope (strength of positive association) and shape (e.g. degree of saturation) of the island-to-mainland relationship might be indicative of and correlate with the presence or degree of island-to mainland trait divergence. In our case, the observed (saturating) relationship may be strong enough such that gigantism and dwarfism on islands at small to large mainland leaf sizes (respectively) cancel each other, leading to no overall difference in leaf size between islands and mainland. However, one could envision alternative scenarios. For example, steeper and less saturating relationships might make it more plausible to find significant island versus mainland differences, namely gigantism on islands versus mainland predominates over dwarfism. Overall, these findings highlight the importance of explicitly testing the island rule and the shape of island–mainland relationships for mechanistic insight, rather than relying solely on island versus mainland mean comparisons.

4.2 | No detectable effects of insect herbivory or macroclimate on leaf size shifts in island plants

There were no significant effects of insect leaf herbivory or climatic factors on island–mainland differences in leaf size, suggesting that other unmeasured factors may drive these associations. One possibility is that shifts in leaf size reflect intrinsic allometric or developmental constraints rather than direct responses to biotic or abiotic conditions. Because leaf size is tightly integrated with plant hydraulic architecture and energy balance, physiological limits may restrict the extent to which this trait can diverge, regardless of external pressures (Preston & Ackerly, 2004; Strelin & Diggle, 2022). Consistent with this, the observed saturating relationship between mainland and island leaf size aligns with an island rule-like scaling process that could arise from endogenous processes rather than external drivers (Biddick, Hendriks, & Burns, 2019; Ciarle et al., 2025). That said, selective pressures known to shape leaf size variation cannot be ruled out (Wright et al., 2004; Wright et al., 2017), and may have gone undetected. For example, climatic variables such as mean annual temperature and precipitation—derived from WorldClim at

2.5-min spatial resolution (Hijmans et al., 2005)—may be too coarse to capture the fine-scale variation experienced by plants, particularly within heterogeneous island habitats, despite our efforts to control for habitat-related variation. Islands often exhibit steep environmental gradients and pronounced local heterogeneity, such that other abiotic predictors acting at finer scales—such as soil moisture, wind exposure or solar radiation (Steinbauer et al., 2012; Weigelt et al., 2013; Westerband et al., 2025)—may better capture environmentally driven variation in leaf size and contribute to island-to-mainland differences. On the other hand, it is possible that leaf size is not strongly responsive to some biotic pressures. In our case, while insect herbivory is an important selective force on plants (Agrawal et al., 2012; Marquis, 1992), its impact on leaf morphology is less clear than that of vertebrate herbivores (Hanley et al., 2007). Many islands historically lacked large browsers, and the weak or absent pressure from these herbivores could have influenced leaf size evolution relative to mainland sites where they are present (Burns, 2019; Moreira & Abdala-Roberts, 2024). For the islands included in our study—except Mauritius and the Galápagos—the examined plant species are not thought to have historically experienced strong vertebrate herbivory (Burns, 2019), and insect herbivory levels are likely relatively low and not consistently or strongly different between island and mainland populations (Moreira et al., 2021). In addition, plant–herbivore anachronisms linked to plant traits may also be important in some systems—such as those documented in Madagascar (Bond & Silander, 2007)—further complicating interpretations and the elucidation of underlying herbivory-related dynamics. Finally, for interspecific comparisons, evolutionary history and lineage-specific trait syndromes may obscure ecological patterns (Burns, 2019). Even after controlling for phylogenetic effects using congeneric pairs, closely related species may inherit tendencies towards larger or smaller leaves that are not fully explained by present-day herbivory or climate. Relatedly, the time since colonization or divergence (crown age) may influence leaf size evolution, particularly for interspecific comparisons, although it could also affect intraspecific patterns in some cases (Moreira, Abdala-Roberts, Cubas, et al., 2025).

4.3 | Concluding remarks and future directions

Our findings call for future research aimed at refining our understanding of the drivers of leaf size variation on islands by integrating different ecological and evolutionary perspectives (scales of analyses, types of factors). In particular, exploring finer scale variation in abiotic factors that shape microclimatic conditions—such as water availability, temperature, wind exposure and soil properties—would help clarify how local environments influence leaf size and related traits. Likewise, incorporating systems with a known present or historical influence of vertebrate herbivores would further allow tests of the adaptive role of leaf size under contrasting biotic pressures, complementing studies focused on insect herbivory. Equally important is the need for more detailed investigations of endogenous plant mechanisms underlying leaf size variation, including mechanisms for resource reallocation from defence to growth and the limits to divergence imposed by physiological or allometric constraints (Biddick, Hutton, & Burns, 2019). Relatedly, and although plant height is often used as a proxy for organism size to control for environmental or ontogenetic variation affecting leaf size, it can be influenced by passive allometric relationships, highlighting the need for improvements in controlling for these sources when testing for leaf size-related adaptive patterns. In addition, experimental approaches manipulating water availability, shading or nutrient supply on islands would be particularly valuable for testing physiological limits and trade-offs shaping allocation to leaf size and other traits. Similarly, long-term herbivore exclusion or addition experiments—including both insects and vertebrates where feasible—would help clarify the selective role of biotic pressures. Finally, incorporating phylogenetic comparative methods would help account for evolutionary history and lineage-specific trait syndromes, while expanding sampling to additional islands spanning broader differences in size, isolation, and environmental heterogeneity would increase the power of future tests of island–mainland trait divergence and the island rule in plants.

AUTHOR CONTRIBUTIONS

Xoaquín Moreira formulated the idea of the manuscript and designed the experiment. Xoaquín Moreira, Carla Vázquez-González, Luis Abdala-Roberts, Isabel R. Amorim, Cláudia Baider, Kevin C. Burns, Juli Caujapé-Castells, Jonay Cubas, Lydia S. Dean, Paula Domínguez-Lapido, María-José Endara, F.B. Vincent Florens, Andrea Galmán, Juan Ernesto Guevara-Andino, Ian Hutton, Beatriz Lago-Núñez, Kailen A. Mooney, Asier R. Larrinaga, Fernando Pereira, Finaritra Randimbiarison, Onja H. Razafindratsima and Gonzalo Rivas-Torres performed the experiment. Beatriz Lago-Núñez performed leaf trait analysis. Xoaquín Moreira, Carla Vázquez-González and Kailen A. Mooney contributed reagents/materials/analysis tools. Xoaquín Moreira and Carla Vázquez-González analysed the data. Xoaquín Moreira wrote the first draft of the manuscript with input from Luis Abdala-Roberts and Carla Vázquez-González. All authors significantly contributed to revising the manuscript, gave final approval for publication and agreed to be held accountable for the work performed therein.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data used in this study is archived at figshare: https://doi.org/10.6084/m9.figshare.30041818.v1 (Moreira, Abdala-Roberts, Amorim, et al., 2025).

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SUPPORTING INFORMATION

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

Table S1. List of species sampled across the six island–mainland systems, including their growth form (herb, shrub or tree) and the comparison type (conspecific vs congeneric comparisons). System IDs correspond to the numbering shown in Figure 1.

Table S2. Results of a Principal Component Analysis summarizing the information of eight climatic variables. Factor loadings, eigenvalues and % of variance explained of the two main principal components (PC1 and PC2) are shown. Values in bold show factor loadings greater than 0.90.

Figure S1. Ordination of climatic variables showing island populations (white points) and mainland populations (grey points). The first principal component explained 42.87% of the variance and was positively associated with both annual precipitation and precipitation of the driest month. The second component accounted for 35.06% of the variance and was positively associated with mean and minimum temperatures. This analysis was performed using the *PCA* function in the *FactoMineR* package (Lê et al. 2008) in R (R Core Team, 2024).

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