# Title

Allopatric and sympatric drivers on the diversification dynamics of *Aeonium* (Crassulaceae) from the Canary Islands

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# Abstract

Although species radiations on island archipelagos are broadly studied, the geographic and ecological modes of speciation that underlie diversification are often not fully understood. Both allopatry and sympatry play a role during radiations, particularly on islands with profound habitat diversity. Here, we use the most diverse Canary Island plant radiation, *Aeonium* (Crassulaceae), to phylogenetically test two hypotheses: (1) allopatric speciation, which predicts that closely related taxa are ecologically similar but do not co-occur, and (2) sympatric speciation, whereby closely related taxa co-occur geographically but are ecologically distinct. We fitted niche and spatial distribution models based on extensive field surveys to quantify geographic and ecological divergence among taxa integrated in a phylogenetic context. While allopatry seems to be the main driver in speciation among islands, within-island speciation occurs in sympatry. Contrary to our expectation, phylogenetically closely related species tend to occupy similar ecological niches, suggesting that ecological niche divergence among species accumulates slowly, even in sympatry. This suggests that evolutionary young taxa, may be partially reproductively isolated due to subtle phenotypic differences, such as reproductive morphology and phenology rather than by ecology and may putatively exacerbate divergence among populations. Thus, allopatry and sympatry are complementary speciation mechanisms on oceanic islands, jointly spurring this enigmatic radiation.

# Keywords: Adaptive radiation, niche evolution, species distribution modeling, ecological niche, phylogenetic methods

# Introduction

Adaptive radiation, i.e., the proliferation of a single ancestral lineage into a variety of species adapted to different ecological niches, is an important evolutionary process often resulting in rapid bursts of biodiversity (Schluter, 1996, 2000; Wagner et al., 2012). Adaptive radiations often occur on islands or in island-like habitats such as freshwater lakes (Wagner et al., 2012; Feiner et al., 2021; Ronco et al., 2021; Barreto et al., 2023) or mountain ranges (Hughes and Atchison, 2015; Donoghue et al., 2022), where colonizing species encounter vacant niches to which they adapt. Diversification in such systems often occurs in close geographic proximity or sympatry, such as in postglacial radiation of freshwater fish (Seehausen and Wagner, 2014) or *Howea* palms and *Metrosideros* mountain roses on Lord Howe Island (Barluenga et al., 2006; Savolainen et al., 2006; Osborne et al., 2019, 2020). Archipelagos comprising multiple islands can add complexity because a lineage may diversify repeatedly and independently on different islands, even into similar ecological niches, potentially with gene flow among islands (Palmer and Kronforst, 2015). Species differentiation among islands evolves primarily through allopatry, resulting in ecologically similar species among different islands, such as the Galapagos finches (Grant, 1981) or the *Anolis* lizards of the Greater Antilles (Feiner et al., 2021). Species radiations on archipelagos, therefore, offer the opportunity to disentangle the role of geographic isolation and ecological differentiation during species diversification, which has rarely been done, especially for plant radiations (Cerca et al., 2023).

A central mechanism of speciation is reproductive isolation, which can arise in allopatry or sympatry, with contrasting predictions on the relation between phylogenetic, ecological, and geographic divergence among taxa within a radiation (Westram et al., 2022; Fig. 1). Allopatric speciation can occur when geographic isolation suffices for reproductive isolation to emerge, e.g., by accumulating over time (Givnish, 2010). If isolation is primarily geographic (Fig. 1a-b), phylogenetically closely related taxa might be initially ecologically close (i.e., the distance between the ecological optima of two species is small), and ecological divergence may increase gradually over time (Fig. 1b; Crisp and Cook, 2012; Egan et al., 2022). In a contrasting scenario, where geographic distance among phylogenetically closely related taxa is high, species may later co-occur if genetic divergence has been acquired (Fig. 1a). Allopatric speciation through geographic isolation seems overall very common (Coyne, 2007). However, if speciation is predominantly sympatric, reproductive isolation may arise through different mechanisms, including niche differentiation, sexual selection, behavioral or mechanic isolation (Higashi et al., 1999; Schluter, 2000; Haller et al., 2014; Zuppinger-Dingley et al., 2014). Here, we test the ecologic isolation scenario (Fig. 1c-d), where geographic distance does not play a part and is independent of phylogenetic distance (Fig. 1c). At the same time, when ecological divergence is a primary reproductive barrier, ecological distance is expected to be high even when species are phylogenetically closely related (McGee et al., 2020). With increasing phylogenetic distance, the ecologic distance between taxa-pairs is expected to become randomized, occupying more divergent niches (Fig. 1d). While there is evidence for both mechanisms in various adaptive radiations, it remains unclear which scenario better explains the accumulation of ecological disparity among species during adaptive island radiations, especially in plants (Steinbauer et al., 2017; McGee et al., 2020; Cerca et al., 2023).

We test this two-scenario hypothesis in the iconic adaptive radiation of *Aeonium* (Crassulaceae), a genus of succulent plants that diversified on the Canary Islands across a multitude of ecologically distinct habitats over the last ~8 million years (Jorgensen and Olesen, 2001; Kim et al., 2008; Schenk, 2021; dos Santos et al., 2022; Messerschmid et al., 2023). The seven main islands of the archipelago are ecologically highly heterogeneous (e.g., contrasting elevation from sea level up to 3715 m high, and consequently a diversity of slope and surface aspects), home to more than 2000 plant species, of which 25% are endemic, spurring centuries of research into plant diversification, including the *Sonchus* alliance (Asteraceae), *Echium* (Boraginaceae), *Crambe* (Brassicaceae) or *Sideritis* (Lamiaceae; Izquierdo et al., 2001; Kim et al., 2008; Kunkel, 2012; Barajas Barbosa et al., 2023). *Aeonium* is the most speciose Canarian plant genus and is largely endemic to the archipelago (Liu, 1986; Izquierdo et al., 2001; Bañares-Baudet, 2015; Messerschmid et al., 2023). While most endemics are restricted to a single island, several taxa occur on multiple islands (Table 1), and despite former research on this system (e.g., Jorgensen and Olesen, 2001; Messerschmid et al., 2023), the role of allopatric and sympatric diversification in relation to ecological differentiation has not been studied.

We extensively sampled all 38 Canarian endemic *Aeonium* taxa (i.e., species and subspecies, Table 1) to test for the relation of geographic and ecological divergence during phylogenetic diversification. Specifically, we quantified (1) phylogenetic divergence for all taxa-pairs using a recent, dated, nearly complete phylogeny (Messerschmid et al., 2023); (2) ecological optima, the potential distribution of all taxa, and pairwise ecological distances using spatial distribution models (SDM) based on thousands of novel field observations on all Canarian *Aeonium* taxa; (3) pairwise geographic separation based on actual distribution areas; (4) reproductive traits potentially involved in reproductive isolation between taxa-pairs that occur and originated on the same island. Using these data, we tested for the ecologically- and geographically-driven divergence scenarios depicted in Fig. 1. We asked the following questions: (1) Are taxa distributed across all islands with potentially suitable ecological niches? (2) Are ecological and (3) geographic isolation between taxa established early or late during phylogenetic diversification? And finally, (4) does character displacement of reproductive traits have a likely role in reproductive isolation in cases of sympatric speciation? Jointly, answers will allow us to discern the relative importance of geographic and ecological isolating mechanisms during the adaptive radiation of an enigmatic Canary Island plant clade.

# Materials and methods

## Study area and fieldwork

The Canary Islands is the largest archipelago of Macaronesia. It comprises seven main volcanic islands across 400 km and is located in the North Atlantic Ocean, about 100 km off the coast of the Sahara Desert, at ca. 28°N. The archipelago is characterized by significant microclimatic heterogeneity, and the islands are generally subdivided into six major habitats: sub-tropical laurel forest, pine forest, Macaronesian heathland (*fayal-brezal*), thermophile shrubland, xerophytic scrubland (*cardonal-tabaibal*), and alpine (Fernández-Palacios et al., 2008; Bañares-Baudet, 2015). The easternmost islands are the more arid and the most eroded due to the influence of the desert’s dry winds and their geologic age (23–15 Ma; Van Den Bogaard, 2013). The westernmost islands are younger (15–1.1 Ma) and characterized by higher topographical complexity, thus exhibiting extreme climatic differences, particularly between the northern (humid) and southern (dry) ranges of the islands (Van Den Bogaard, 2013). These local climatic characteristics are especially evident on high-elevational islands through the formation of a “sea of clouds” (Herrera et al., 2001), a scenic sight often observed from high-elevation areas, where it is possible to observe clouds forming in the low-land.

We surveyed the archipelago, covering all 38 *Aeonium* species and subspecies (see Table 1) following Bañares-Baudet (2015). Surveys were performed between February and September in 2018–2020 and aimed at capturing the ecological breadth of the islands through high-resolution presence/absence observation points. To guarantee a dense and stratified sampling, we divided each sampled island into climatic quarters based on the average of the mean annual temperature (bio01) and annual precipitation (bio12): 1) dry and hot; 2) dry and cold; 3) wet and hot; 4) wet and cold. The quarters of each island were sampled through extensive driving and hiking. A total of 10’180 data points were collected using a Global Positioning System receiver (GPS 72H, Garmin, Taiwan) with a positional accuracy of ~ 5 m, including 9’719 presences (including data points with multi-taxa occurrences) and 2’450 absences (Fig. 2). Points were registered at c. 50 – 200 m intervals, noting all occurring *Aeonium* species. For each island, we managed to observe all *Aeonium* taxa known to occur. Fuerteventura was not visited because its only species was scored from Lanzarote. These data were complemented with 365 observations from online datasets (GBIF.org and BIENdata.org, both accessed on 01/11/2018), thoroughly cleaned for accuracy by removing all observations that did not coincide with a species’ natural range, all observations from private, public, and botanic gardens, and observations with coarse resolution.

## Environmental data

We compiled a total of 35 environmental variables considering basic plant survival needs: light, precipitation, temperature, geology, and habitat. Macroclimatic variables (32 variables, including 19 bioclim variables and 13 monthly and annual total surface radiation) were extracted from CHELSA V.1.2 (Karger et al., 2017). CHELSA V.1.2 provides bioclimatic variables at a resolution of 30 arcsec (~ 1 km at the equator). The resolution was further downscaled locally to a resolution of ~ 5 m for the Canarian archipelago (Patiño et al., 2023). From these 32 continuous variables, we pre-selected a set of non-correlated continuous variables to explain the genus’ macro-climatic preferences within the archipelago. We tested the variables against our occurrences based on the severity of the effect of multicollinearity using the variance inflation factor *vif* function from the *usdm* package in R (Naimi et al., 2014). The variable pre-selection allows a comparison among species’ niches within the same spectrum of variables. The selected variables are proxies for light (total surface solar radiation of December), precipitation (precipitation of the driest quarter and precipitation seasonality), and temperature (temperature seasonality), defining a representation of the limitations of survival of the genus in general. Specifically, precipitation limitations are caused by seasonality and summer drought; temperature is limiting due to the extreme summers; sunlight limitation in the winter distinguishes species that preferably face North or South sectors of the islands. For seven rare taxa with less than 50 observations (Table 1), we included mean annual temperature, annual precipitation, and annual surface solar radiation by default. Including the bioclimatic variables that best represent the overall macroclimate, we expect to reduce the bias that the low observation number could potentially cause.

We extracted geologic and vegetation layers for all islands from GRAFCAN (del Arco et al., 2006; IGME, 2008). The vegetation layer was reclassified into seven habitats: the six main habitat types present on the Canary Islands already described above (see above) and a classification of *other*, which includes all habitats that do not fit in the above classification, as well as urban zones (Supplementary Table 1). The geology was first divided into two layers, one representing the chemical composition and the second representing the rock texture or grain size. Both layers were reclassified into mafic, intermediate, or felsic for the chemical composition, mostly reflecting the amount of silica or rock acidity, and into aphanitic, pyroclastic, and phaneritic for the geologic texture, mostly affecting the type of weathering (Supplementary Table 1). After reclassification, all categorical variables were resampled using the CHELSA grid. All variables were converted to a resolution of 100 m.

## Species distribution modeling

For the SDMs, we used a presence-absence dataset per species and environmental data (Supplementary Table 2). The presence-absence binomial dataset (0 = absence, 1 = presence) was built by combining presence observations (field-collected and online resources) with randomly generated pseudo-absence points over the whole Canary archipelago environment. The number of pseudo-absences (*npa*) was 10’000 times the number of presences (*np*) (Barbet-Massin et al., 2012). In addition, we applied an inverse weighting by assigning a weight of 1 to all presences and 1 divided by the sum of all presences to all pseudo-absences. The weight of field-collected absences (W*a*) was calculated with a higher rate than the weight of pseudo-absences (W*pa*): ; . For the environmental data, we allowed a maximum of 1 variable per 10 observations (two variables were exceptionally considered for *A. aizoon*, with only 17 presences recorded; Supplementary Table 2).

We applied three SDM algorithms: two regression methods (generalized linear models, GLM (Nelder and Wedderburn, 1972), and generalized additive models, GAM (Hastie and Tibshirani, 1986)), and one classification algorithm (random forest, RF; Breiman, 2001). The predictive performance of each model was estimated using a random cross-validation (70%) of the original data, while the remaining subset was used to estimate each model’s performance. To predict presence-absence, we calculated a threshold based on the evaluation of each model. The predictive power of each model was estimated with the area under the curve (AUC) of a receiver operating characteristic (ROC) curve, true skill statistic (TSS), and Cohen’s kappa coefficient (K). Final ensemble projections were computed with the binary predictions of the three models (Supplementary Fig. 1 – 38). Multi-model ensembles were preferred to single best models due to their improved robustness and lower generalization error of the prediction than its constituent models (Trolle et al., 2014). More details about the SDM procedure according to the ODMAP standardized protocol (Zurell et al., 2020) are found in Supplementary Table 3.

## Distance matrices

We compared all taxa-pairs (species and subspecies) on ecologic, geographic and phylogenetic levels. Ecological niche distances were calculated to the detriment of ecological niche overlap as many taxa-pairs have no niche overlap, while ecological optima may still be close or distant. We performed Huisman-Olff-Fresco (HOF) curves of the bio01, bio04, bio12, bio17, and srad12 variables to calculate ecological niche distances. We selected these variables because they are the most informative, reflecting means and seasonality of temperature and precipitation, allowing for a more distinct differentiation among taxa (see Results). We extracted 100 random presence points from the SDM predictions for each taxon to calculate the HOF curves. To allow for a high probability of occurrence, we limited predictions with a minimum of two out of the three models. Random points outside the SDM predictions delimitations were also extracted for each species to feed absence information. HOF curves for each variable were calculated with the R package *eHOF* (Jansen and Oksanen, 2013)using a binomial distribution with a logit link function. After establishing no support for multimodal curves and flat responses (Supplementary Table 4), we selected the optimum under the best-supported unimodal model (models IV and V, optimum without and with skew, respectively), based on AICc (Burnham and Anderson, 2004). Then, for each taxa-pair, we calculated the Euclidean distance between both optima for each considered climatic variable. For more accurate taxa comparisons, we used bio01 as a proxy for ecological distance, as it is the only variable considered for all taxa for the SDMs (Supplementary Table 5). The same analyses were performed for all the selected variables (see Supplementary Fig. 40 – 42).

For geographic distances, we created a categorical and a continuous scale. The categorical scale was assembled based on the distribution of the taxa-pairs per island (whether species co-occur on the same island). Based on our field observations, the continuous scale was assembled by calculating the shortest Euclidean distance in km between the presences of two taxa.

Finally, the phylogenetic distance for each taxa-pair was based on the estimated age of their most recent common ancestor based on the most recent dated phylogeny of the genus (Messerschmid et al., 2023). Here, we computed a maximum clade credibility summary with median node heights based on a posterior distribution from the BEAST analysis of Messerschmid et al. 2023, pruned to include the species of the current study. Euclidean pairwise distances were computed using the R package *ape* (Paradis and Schliep, 2019).

## Correlates of sympatric speciation

To understand how sympatric speciation may act *in situ*, we identified likely empirical examples of sympatric speciation. We selected taxa-pairs that were (1) single island endemics on the same island and (2) had diverged on that island according to a recent biogeographic reconstruction (Messerschmid et al., 2023). Among these, for each island, we chose the phylogenetically most closely related taxa-pair (but see Supplementary Table 5 for all taxa-pairs); no such pairs could be identified for Lanzarote and El Hierro. Sympatric speciation is unlikely driven by simple switches between specialist pollinators because all species have generalist hymenopteran/dipteran morphologies (open, radial, bowl-shaped), and at least some closely occurring species share pollinators (Esfeld et al., 2009). Therefore, we attempted to identify other causes of sympatric speciation by compiling data for each pair on observed hybrid formation, flowering phenology, and flower color (Bañares-Baudet 2015).

## Statistical analyses

To answer whether taxa are actually distributed across all islands with potentially suitable climatic niches, we scored all the islands for which multiple grid cells support the species’ occurrence based on all three SDMs and compared these to the known distribution based on Bañares-Baudet (2015), which is congruent with our personal observations. To answer whether ecological and geographic isolation between taxa is established early or late during phylogenetic diversification, we tested the relation of either isolating variable with phylogenetic divergence. Conventional regression-correlation analyses are inappropriate when the variance of the response variable changes with values of the controlling factors (Scharf et al., 1998; Koenker and Hallock, 2001), as we expect for the scenarios depicted in Fig 1a, 1b, and 1d. Instead, we can employ quantile regression, where we model quantiles, rather than the mean, as a response. Specifically, we first computed the slope of the bivariate relation across a series of quantile regression fits (with tau ranging from 0.1 to 0.9 in steps of 0.05), taking phylogenetic distance as the predictor. We then fitted a simple linear model with tau as predictor and slope as response. A significantly positive relation indicates evidence for limiting ecological factors (*sensu* Scharf et al. 1998; Fig. 1b), while we expect a significantly negative relation for scenarios 1a and 1d, indicating geographic and/or ecological distinctness is required for speciation. Should no relation be significant, then we fit a simple bivariate linear model with phylogenetic distance as the predictor. We performed these analyses for geographic distance and all ecological distances using three sets of species pairs: all taxa-pairs, those co-occurring on the same island, and those not co-occurring on the same island.

Finally, to reveal reproductive traits that may have a role in reproductive isolation in sympatric speciation, we establish differences in a range of variables between the selected sympatric taxa-pairs.

# Results

### Geographic distance

The distribution of points between geographic and phylogenetic distances (Fig. 3a-c) reveals no triangular pattern, as hypothesized in Fig. 1a. Instead, the pattern observed in our results tends to be random, more in line with the sympatric isolation scenario (Fig. 1c). This scenario is particularly stronger among all taxa-pairs and different islands (Fig. 3a-b). The pattern observed in within-island pairs (Fig. 3c) shows less randomness, with most points accumulating on very low geographic distances, and just a few reflecting higher distances (> 30 km). Our results show that most taxa-pairs that co-occur on the same islands (Fig. 3c) are frequently in geographically close proximity (maximum of 59.78 km). We found a statistically significant relationship between phylogenetic and geographic distances among all taxa-pairs (*p* < 0.001; Fig. 3a). We did the same analysis for taxa-pairs that occur on different islands (Fig. 3b) and on the same islands (island co-occurrence; Fig. 3c), and no statistically significant correlation was found (*p* = 0.068; *p* = 0.683, respectively). These results suggest that geographic isolation occurs among islands. However, within islands, reproductive isolation is not caused by geographic distance. In accordance with our expectation (Fig. 1c), our model reveals a random pattern for all taxa-pairs and among islands taxa-pairs (Fig. 3a-b). Results also show an increasing geographical distancing during early speciation (short phylogenetic distances) until reaching a peak of maximum geographic distance, which is attained when the phylogenetic distance is between 1.770 and 3.566 Ma, after which tends to slightly decrease with increasing phylogenetic distance (Fig. 3b). The pattern within islands is different, as the geographic distance is independent of the phylogenetic distance, suggesting randomness (Fig. 3c). Furthermore, most points show geographic overlap (geographic distance close to 0; Fig. 3c) among most taxa-pairs that co-occur on the same islands. The randomness observed in Fig. 3a-c is further corroborated by the analysis of the slopes of the quantile regressions (Supplementary Fig. 39). This result does not clearly discriminate between scenarios, but suggests that within-island speciation is not allopatric and, thus, more likely sympatric (see Fig. 1a, 1c).

Strikingly, approximately all taxa also have putatively suitable ecological niche space on islands where they do not occur (Table 1; Supplementary Figs. 1 – 38). This suggests that taxa are often dispersal limited and rarely jump among islands, which provides effective reproductive isolation, while most speciation occurs within islands. Furthermore, this also implies that among islands, allopatry is a crucial isolation mechanism.

### Ecologic distance

According to our premise (Fig. 1), if the geographic distance is independent of phylogenetic distance, we would expect that niche distance is high when phylogenetic distance is low (Fig. 1d). However, our analyses show the opposite pattern, with the ecological niche distance significantly increasing with phylogenetic distance in all scenarios (Fig. 3d-f). The strongest correlation found was within-island taxa-pairs only (Pearson’s correlation index (*ρ*) = 0.427, *p* < 0.001; Fig. 3f, but see also Supplementary Fig. 42), while the taxa-pairs across the whole archipelago and taxa-pairs different islands showed identical correlations (*ρ* = 0.334, *p* < 0.001; Fig. 3d-e; but see also Supplementary Fig. 40 – 41). This suggests that, in general, closely related species tend to share relatively similar ecological niches, becoming increasingly different with phylogenetic distance. Among different islands, the pattern is not so easily observable, probably due to the different habitats that characterize each island. Furthermore, among different islands, the ecological distance among taxa-pairs is less important for speciation, as speciation in that scenario is expected to be allopatric, granted the geographical distance. This demonstrates that speciation does not require ecological divergence, even in sympatry, as divergence is acquired with the accumulation of genetic differentiation.

### Ecologic distance within islands

All islands showed a similar positive correlation pattern between ecological and phylogenetic distances (Fig. 4). Positive significant correlations were found on La Palma (*ρ* = 0.509, *p* = 0.015; n = 22; Fig.4c), La Gomera (*ρ* = 0.396, *p* = 0.014; n = 48; Fig. 4d), and Tenerife (*ρ* = 0.309, *p* < 0.001; n = 132; Fig. 4a). The islands of Gran Canaria and El Hierro, showed similar tendencies, though not statistically significant (*ρ* = 0.302, *p* = 0.196; n = 20; Fig.4b; and *ρ* = 0.570, *p* = 0.109; n = 9; Fig. 4e, respectively). The island of Lanzarote was not tested for this analysis, having only one taxa-pair (BAL-LAN; see Results but also Table 1 and Supplementary Table 5). Throughout the analyses of all islands, it seems that closely related species generally do not occupy strikingly different habitats, suggesting that speciation occurred in close geographic proximity and within similar ecological niches. In fact, the second quadrant (representing low phylogenetic distances and high ecological distances) is mostly empty (a pattern similar to Fig. 3f), demonstrating a clear triangular shape, similar to what is expected in the allopatric speciation scenario (Fig. 1b). The highest ecological distances are observed in pairs relatively distantly related phylogenetically, reaching 13.04 oC in Tenerife (Fig. 4a; Supplementary Table 5) and 11.46 oC in La Gomera (Fig. 4d; Supplementary Table 5). At the same time, phylogenetically distantly related taxa-pairs tend to evenly occupy both similar and distant ecological niches, as observed in the primary analysis (Fig. 3d-f) and as expected according to the allopatric speciation scenario (Fig. 1b).

### Correlates of sympatric speciation

Among our selected taxa-pairs that constitute the result of putative sympatric speciation, we overall found that phylogenetically closely related taxa are also ecologically similar, so we compared reproductive traits that could explain reproductive isolation in those cases. Specifically, we compared the phylogenetically closest related taxa-pairs on each island for the following reproductive traits: the presence of wild hybrids, phenology, and petal color (Table 2). The Canarian *Aeonium* largely overlap in their phenology, and hybrids are common among some taxa-pairs (Supplementary Table 5). About 82.5% of all the taxa bloom during spring (March to May), at least for part of their blooming season.

The phylogenetically closest taxa-pair is the Gomeran endemics *A. castello-paivae* and *A. decorum*. Both species can be found within close geographic proximity, and even though they overlap in flowering season (May), sightings of natural hybrids are rare (Table 2). Furthermore, the species produce flowers with different petal colors (greenish-white and pinkish-white, respectively), suggesting different (or diverging) pollination syndromes and the potential importance of sexual selection (pollinator-driven selection) in this particular study system. Another example of sympatric speciation is the Tenerifean pair, *A. ciliatum* and *A. volkerii*. Both species are endemic to the subtropic Laurel forests, with *A. ciliatum* occupying the core of the Laurel forests and *A. volkerii* occupying the south-facing drier slopes of those forests (see Supplementary Figs. 9 and 38). Though hybrids between these two species have never been recorded, they are very closely related, occupying similar niches within the same geographic space. Furthermore, they both overlap their flowering seasons, showing differences in flower color, like in the previous example (Table 2). In Gran Canaria, although relatively closely related, *A. arboreum and A. undulatum* form no hybrids. This is justified based on the highly divergent phenology (with *A. arboreum* blooming between September and November, and *A. undulatum* between April and May) and relatively distant geographic distribution (Table 2). Finally, in La Palma, though with a higher phylogenetic distance, *A. davidbramwellii* and *A. nobile* may form wild hybrids. The flowering season of *A. davidbramwellii* overlaps with the flowering season of *A. nobile* only in April, and though both species have very distinct petal colors (greenish white and dark red, respectively), gene flow sporadically occurs.

# Discussion

Our results corroborate the importance of both allopatric and sympatric speciation in the diversification of *Aeonium*, where allopatric speciation seems to be the primary speciation mechanism among islands (Fig. 3b), while sympatric speciation drives diversification within islands. The allopatric speciation among islands hypothesis is further corroborated by the comparison between the actual and potential distribution of species on islands (Table 1). Though most species are single-island endemics, they rarely reach their potential niche on other islands. Thus, contrary to the Darwin’s finches example, where gene flow among islands results in introgressive hybridization (Grant and Grant, 2010), in *Aeonium,* the pattern is similar to what is observed with the *Anolis* lizards: low migration among islands contributing to allopatric speciation (Glor et al., 2005). On the other hand, when a species of *Aeonium* migrates to a new island, the process of speciation is repeated within the new island. Sympatric speciation seems to be the primary speciation mechanism in such cases and is more common than expected by other studies (Losos and Glor, 2003). Although we expected to find sympatric speciation related to clear ecological differentiation, all within-island speciation events seem to have occurred in relatively approximate sympatry, with phylogenetically closely related pairs being in relatively close geographic and ecological proximity (Fig. 3c, f; Fig. 4). This highlights that ecological differentiation, when measured from modeled niches, is not a primary driver during the early stages of speciation but increases with time as genetic differences accumulate among species (Fig. 3f).

### Niche conservatism and niche divergence

Our study reveals relatively low ecological distances between phylogenetically closely related taxa, including within-island taxa (Fig. 3; Fig. 4). This is consistent with niche conservatism, the maintenance of the ancestral ecological niche within a lineage, which only later in time starts diverging (Wiens, 2004; Donoghue and Edwards, 2014). Nevertheless, it also indicates a steadily though slowly evolving niche rather than a purely static feature. Paradoxically, niche conservatism has been demonstrated to promote speciation, particularly in fragmented landscapes with pockets of very heterogeneous habitats (Gutiérrez-Ortega et al., 2020; Kelt et al., 2023; Klečková et al., 2023). Dramatic local climatic changes trigger similar scenarios, confining populations in patches of suitable habitats isolated by patches of unsuitable habitats (Gutiérrez-Ortega et al., 2020). Finally, landscape changes caused by geological activity also create similar isolation scenarios that can quickly result in genetic divergence among populations (Harter et al., 2015). Niche conservatism is thus consistent with allopatric speciation through the minimization or elimination of gene flow for at least a period of time. Phylogenetic niche conservatism has been shown to share similar patterns among different biological groups, from mammals to fishes, from mollusks to plants (Särkinen et al., 2012; Maltseva et al., 2021; Egan et al., 2022; Kelt et al., 2023). Patchy habitats contributing to increased diversification through increased ecological opportunity and competition avoidance may also be common (Stroud and Losos, 2016; Fernández-Palacios et al., 2021). Like other oceanic islands, the Canary Islands accommodate contrasting landscapes, heterogeneous habitats, great geological activity, and high orographic complexity, contributing to reproductive isolation within islands (Harter et al., 2015; Hanz et al., 2022).

Higher ecological distances that reveal divergence are only found with increased phylogenetic distances in our study (Fig. 3d-f; Fig. 4). As the lineage diversifies, the ecological niche of a taxon becomes increasingly divergent from that of a sister taxon. Though big ecological jumps seem to be rare, subtle but continuous niche differences accompanied by niche-related adaptation could explain the divergence in niche preferences among taxa (Crisp and Cook, 2012). Thus, most niche divergence accumulates after speciation (or at least not before its final stages) rather than it being the cause of speciation.

### Selection and reinforcement

We evaluated the potential reproductive isolation barriers in taxa-pairs, most likely resulting from sympatric speciation, by looking at the overlapping phenology (flowering time) and petal color (highly associated with selective pollinator attraction). The most significant divergence in flower traits is the petal color, suggesting selective pollinator attraction (e.g., *A. ciliatum* and *A. volkerii*, *A. castello-paivae* and *A. decorum*; Table 2). Such interspecific differentiation in flower traits could be an example of past reinforcement, i.e., the evolutionary process by which reproductive isolation increases in response to costly hybridization, leading to the build-up of prezygotic reproductive barriers in sympatry (Hopkins and Rausher, 2012; Hopkins, 2013). By reducing gene flow between species through selective pollination, the flowering season is expected to diverge further, which could, for example, explain the deviation of *A. castello-paivae* to a late spring/early summer flowering season, contrasting with a mid-spring flowering season of *A. decorum* (Table 2). Divergence in breeding or flowering time can generally generate strong reproductive isolation (Taylor and Friesen, 2017; Osborne et al., 2020). The parallel Tenerifean example (*A. ciliatum* and *A. volkerii*) shows similar petal color divergence, though remarkably, hybrids between these two species have never been described (Table 2). Again, this suggests specific sexual selection through selective pollination (Lankinen and Green, 2015). Although reinforcement was not the target of this study, nor easy to test in the wild, former experiments on *Phlox* (Polemoniaceae) provide support to this hypothesis (Hopkins and Rausher, 2012). When two closely related species co-occur, reproductive trait divergence is more accentuated by selection against unfit, intermediate phenotypes (Hopkins, 2013). On the other hand, if the same species occur in separate locations, the level of divergence is lower. Under reinforcement, we would expect the slight differences among species to be exacerbated when they co-occur. For example, in a location where both *A. castello-paivae* and *A. decorum* coexist, the first species may flower later in June, while the latter will flower earlier in April, avoiding co-flowering in May (Table 2). By doing so, they are likely to avoid hybridization by avoiding pollinator competition (Beans, 2014; Baack et al., 2015). Shifts in flowering time have also been found to be effective prezygotic isolation mechanism in other plants that sympatrically co-occur on islands (Osborne et al., 2020). Unfortunately, to our knowledge, there is no phenologic field data of sympatric and allopatric populations of *Aeonium* to support or disprove this hypothesis. Another strategy is selective pollination attraction by enhancing the differences between both flowers (strongly greenish vs. strongly pinkish when both species co-occur). This reinforcement mechanism has been shown to reduce hybridization, thus being part of the reproductive isolation mechanism in sympatric plants and also explaining why closely related taxa rarely form hybrids (Table 2; Hopkins and Rausher, 2012; Baack et al., 2015).

# Conclusions

This study focused on the importance of allopatric and sympatric speciation of a plant group in an archipelago. Our results demonstrate that in our study case, both allopatry and sympatry are responsible for the diversification of *Aeonium*. While allopatry contributes strongly to diversification through repeated speciation among islands, within islands, speciation frequently happens in close geographic proximity, including sister species occurring empirically and potentially in the same areas. Within-islands, we show that phylogenetically closely related taxa tend to occupy similar ecological niches, speciating in great geographic and ecological proximity. Furthermore, we also found that ecological divergence in early speciation is a rare phenomenon unless if already geographically isolated. Thus, we demonstrate that most speciation events within islands occur in sympatry.

The drivers of allopatric speciation are mostly physical barriers, particularly islands. However, within islands, this is explained by contrasting landscapes, heterogeneous habitats, great geological activity, and high orographic complexity characteristic of the Canary Islands. However, in sympatry, prezygotic barriers are often more important (Higashi et al., 1999; McGee et al., 2020). Without physical barriers to reproduction, gene flow can be minimized through sexual selection, an underlying driver that remains understudied in plants. We suggest that further studies on sympatric evolution in plants focus on reproductive morphology and pollination syndromes to comprehensively investigate sexual selection and reinforcement in plants as drivers of sympatric speciation in plants.

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# Data Availability Statement

The data that support the findings of this study will be archived at the Dryad Digital Repository and is temporarily available for revision purposes only at <https://datadryad.org/stash/share/oYJk6ETcC047o7W1aKc8Pq4mBf8f8fjwGG-hDQXpauk>

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**Table 1.** Sampled taxa, actual distribution, potential distribution, and number of observations. Insular actual and potential distribution of taxa indicated with the following letter code: Fv: Fuerteventura, Gc: Gran Canaria, Gm: La Gomera, Hr: El Hierro, Lz: Lanzarote, Pa: La Palma, Tf: Tenerife. Actual distributions based on Bañares-Baudet (2015) and Messerschmid et al (2023); potential distributions correspond to the distribution of ensemble projections of our model when the three models agree (see Materials and Methods and Supplementary Fig. 1 – 38); Fuerteventura only considered for actual distributions (see Materials and Methods).

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Code | Taxa | Actual distribution | Potential distribution | Occurrences |
| AIZ | *A. aizoon* (Bolle) T.H.M.Mes | Tf | Pa, Tf | 17 |
| APP | *A. appendiculatum* Bañares | Gm | Hr, Pa, Gm, Tf, Gc | 66 |
| ARB | *A. arboreum* (L.) Webb & Berthel. | Gc | Hr, Pa, Gm, Tf, Gc | 231 |
| AUR | *A. aureum* (C.Sm. ex Hornem.) T.H.M.Mes | Tf, Gc | Pa, Gm, Tf, Gc | 231 |
| BAL | *A. balsamiferum* Webb & Berthel. | Fv, Lz | Hr, Gc, Lz | 26 |
| CAN | *A. canariense* (L.) Webb & Berthel. | Tf | Tf | 411 |
| CAS | *A. castello-paivae* Bolle | Gm | Pa, Gm, Gc | 251 |
| CHR | *A. canariense* subsp. *christii* (Burchard) Bañares | Hr, Pa | Hr, Pa, Tf, Lz | 639 |
| CIL | *A. ciliatum* (Willd.) Webb & Berthel. | Tf | Tf | 395 |
| CUN | *A. cuneatum* Webb & Berthel. | Tf | Tf | 121 |
| DAV | *A. davidbramwellii* H.Y.Liu | Pa | Pa, Gm, Tf, Gc | 878 |
| DEC | *A. decorum* Webb ex Bolle | Gm | Hr, Pa, Gm, Tf, Gc | 384 |
| DIP | *A. diplocyclum* (Webb ex Bolle) T.H.M.Mes | Hr, Pa, Gm | Hr, Pa, Gm, Tf, Gc | 498 |
| DOD | *A. dodrantale* (Willd.) T.H.M.Mes | Tf | Hr, Pa, Gm, Tf, Gc | 33 |
| GOM | *A. gomerense* (Praeger) Praeger | Gm | Hr, Pa, Gm, Tf, Gc | 28 |
| GOO | *A. goochiae* Webb & Berthel. | Pa | Pa, Tf | 152 |
| HAW | *A. haworthii* Webb & Berthel. | Tf | Pa, Tf | 145 |
| HIE | *A. hierrense* (R.P.Murray) Pit. & Proust | Hr | Hr, Pa, Gm, Gc | 376 |
| HOL | *A. arboreum* subsp. *holochrysum* (H.Y.Liu) Bañares | Hr, Pa, Gm, Tf | Hr, Pa, Gm, Tf, Gc | 1515 |
| LAN | *A. lancerottense* (Praeger) Praeger | Lz | Gc, Lz | 310 |
| LAT | *A. canariense* subsp. *latifolium* (Burchard) Bañares | Gm | Hr, Pa, Gm, Gc | 293 |
| LIN | *A. lindleyi* subsp. *lindleyi* Webb & Berthel. | Tf | Pa, Gm, Tf | 240 |
| MER | *A. urbicum* subsp. *meridionale* (Bañares) Bañares | Tf | Pa, Gm, Tf, Gc | 173 |
| NOB | *A. nobile* (Praeger) Praeger | Pa | Pa, Gm, Tf, Gc | 76 |
| PER | *A. percarneum* (R.P.Murray) Pit. & Proust | Gc | Hr, Pa, Gm, Gc | 654 |
| PSE | *A. pseudourbicum* Bañares | Tf | Pa, Gm, Tf | 112 |
| SAU | *A. saundersii* Bolle | Gm | Hr, Pa, Gm, Tf | 38 |
| SED | *A. sedifolium* (Webb ex Bolle) Pit. & Proust | Pa, Tf | Pa, Gm, Tf, Gc | 70 |
| SIM | *A. simsii* (Sweet) Stearn | Gc | Hr, Pa, Gm, Gc | 259 |
| SMI | *A. smithii* (Sims) Webb & Berthel. | Tf | Pa, Gm, Tf, Gc | 43 |
| SPA | *A. spathulatum* (Hornem.) Praeger | Hr, Pa, Gm, Tf, Gc | Hr, Pa, Gm, Tf, Gc | 359 |
| TAB | *A. tabuliforme* (Haw.) Webb & Berthel. | Tf | Pa, Tf | 196 |
| UND | *A. undulatum* Webb & Berthel. | Gc | Pa, Gm, Tf, Gc | 273 |
| URB | *A. urbicum* (C.Sm. ex Hornem.) Webb & Berthel. | Tf | Pa, Tf | 477 |
| VAL | *A. valverdense* (Praeger) Praeger | Hr | Hr, Gc | 280 |
| VIR | *A. canariense* subsp. *virgineum* (Webb ex Christ) Bañares | Gc | Pa, Gm, Gc | 79 |
| VIS | *A. lindleyi* subsp. *viscatum* (Bolle) Bañares | Gm | Hr, Pa, Gm, Gc | 83 |
| VOL | *A. volkerii* Hernández & Bañares | Tf | Hr, Pa, Gm, Tf, Gc | 38 |

**Table 2. Comparison of the taxa-pairs with the highest phylogenetic proximity per island**. Information on hybrids, phenology and flower colour was collected from Bañares-Baudet (2015). Distances (ecological, phylogenetic and geographic) were calculated as described in the Materials and Methods section. Ecological distances represented in oC, phylogenetic distances in Ma, geographic distances in km. Taxa-pairs are ordered in the table according to their phylogenetic distance. Taxa-pairs from El Hierro and Lanzarote were excluded for not meeting the requirements (see Materials and Methods).

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Taxa pairs | Island co-occurrence | Hybrids | Distance | | | Phenology | Flower colour |
| Ecological | Phylogenetic | Geographic |
| CAS | La Gomera | yes (rare) | 0.779 | 0.523 | 0.016 | May – Jun | Greenish-white |
| DEC |  |  |  |  |  | Apr – May | Pinkish-white |
| CIL | Tenerife | no | 0.512 | 0.718 | 0 | Jun – Jul | Greenish-white |
| VOL |  |  |  |  |  | Apr – Jul | Pinkish-white |
| ARB | Gran Canaria | no | 0.924 | 1.002 | 2.075 | Sep – Nov | Yellow |
| UND |  |  |  |  |  | Apr – May | Yellow |
| DAV | La Palma | yes | 0.584 | 2.393 | 0 | Mar – Apr | Greenish-white |
| NOB |  |  |  |  |  | Apr – Jun | Dark red |

**Figure captions**

**Figure 1.** The expectation of the geographic and ecologic distribution of taxa-pairs along with phylogenetic distance in a two-scenario hypothesis: the geographic and ecologic isolation scenarios. **(a)** in the geographic isolation scenario, the geographic distance among taxa-pairs is expected to be highest with low phylogenetic distances; **(b)** in the geographic isolation scenario, taxa-pairs are expected to become ecologically more distant with increasing phylogenetic distance increases; **(c)** in the ecologic isolation scenario, geographic distance is expected to be not a contributor to speciation, and thus random; **(d)** in the ecologic isolation scenario, the ecologic distance among taxa-pairs is expected to be highest with low phylogenetic distances. Each dot represents a hypothetical taxa-pair.

**Figure 2.** Field survey for spatial data on the Canary Islands. **(a)** Location of the Canary Islands on the west coast of Africa; **(b)** archipelago and elevation (Basemap Layer Credits: Esri, GEBCO, NOAA, National Geographic, Garmin, HERE, NGDC, Geonames.org, and other contributors; elevation extracted from Sandwell et al., 2014). Sampling points on the islands of **(c)** La Palma, **(d)** El Hierro, **(e)** La Gomera, **(f)** Tenerife, **(g)** Gran Canaria, and **(h)** Lanzarote. Fuerteventura was not sampled, having only one naturalized species from Lanzarote (*A. balsamiferum*). Green dots indicate the presence of at least one species; red crosses indicate absences.

**Figure 3.** Hypotheses testing by comparing geographic and ecological distances against phylogenetic distance. **(a)** Geographic distance against phylogenetic distance among all taxa-pairs **(b)** Geographic distance against phylogenetic distance among taxa-pairs that do not coexist on the same islands; **(c)** Geographic distance against phylogenetic distance among taxa-pairs that co-occur on the same islands; **(d)** Ecological distance against phylogenetic distance among all taxa-pairs **(e)** Ecological distance against phylogenetic distance among taxa-pairs that do not coexist on the same islands; **(f)** Ecological distance against phylogenetic distance among taxa-pairs that co-occur on the same islands. Red solid lines in (a), (b) and (c) and red dotted lines in (d), (e) and (f) represent the best-fit regression lines; Blue lines in (d), (e) and (f) indicate the 50% quantile; Gray lines in (d), (e) and (f) indicate the estimated regression quantiles (5%, 10%, 25%, 75%, 90%, 95%). Each dot indicates one taxa-pair.

**Figure 4.** Ecological distance against phylogenetic distance on each island: **(a)** Tenerife; **(b)** Gran Canaria; **(c)** La Palma; **(d)** La Gomera; **(e)** El Hierro. Red dotted lines represent the best-fit regression lines; blue lines indicate the 50% quantile; gray lines indicate the estimated regression quantiles (5%, 10%, 25%, 75%, 90%, 95%). Each dot indicates one taxa-pair.