

Peer Review File

Manuscript Title: Assembly of functional diversity in an oceanic island flora

Reviewer Comments & Author Rebuttals

Reviewer Reports on the Initial Version:

Referees' comments:

Referee #1 (Remarks to the Author):

The manuscript by Barajas-Barbosa et al. entitled “Assembly of functional diversity in an oceanic island flora” [MS number: 2022-02-02651] constitutes a potentially interesting and relevant study for the emerging field of functional island biogeography. While I appreciate the effort made by the authors – especially in relation to the collection of trait data for a high number of Tenerife native angiosperm species – I have spotted a few substantial and critical conceptual and analytical issues. Unfortunately, those concerns reinforced after multiple readings of the paper.

1. Fitting Tenerife native seed plants within the global spectrum of plant form and function. The authors found, along the first PCA axis (plant size functional dimension; Fig. 1), that Tenerife native plants sit right in between the two previously identified “functional hotspots” (Díaz et al. 2016). They correctly acknowledge that this indicates a “shrubby functional hotspot” when discussing their results (e.g. L116-126 and further below). However, they also state that Tenerife plants face similar functional constraints (e.g. L111-116). I do not see how the authors can back this claim. They report that Sørensen similarity coefficient between Tenerife and the global spectrum is 0.69 based on hypervolume overlap for both trait spaces. Yet, one could have expected Tenerife functional space to be completely/mostly included into the global spectrum. This PCA was run and constrained by the same 6 traits as for Díaz et al. (2016), yet along the first axis the distribution between Tenerife and the global dataset (which is composed here of ~2200 species and not ~46000 species as for the original article, and I would have liked to know some more about reasons behind this reduction) is different, as clearly showed by the density distribution (Fig. 1). This functional discrepancy gets even sharper when combined with results reported in Extended Data Fig. 2, wherein the authors added two key leaf traits, namely leaf dry matter content (LDMC) and leaf thickness. From there, it is evident that the first axis related to plant size in the global spectrum of form and function is not working too well on Tenerife, as illustrated by LDMC accounting for the highest loading in the first PCA axis, whereas much less is associated with plant height, seed mass and leaf area. According to the global spectrum of form and function, LDMC – a trait tightly connected to resource economics (namely to water conservation) – should have aligned along the second functional axis, which refers to the leaf economics spectrum (Wright et al. 2004), and should have been strongly related to leaf mass per area (LMA), which is the inverse of specific leaf area (SLA) (de la Riva et al. 2016). To me, this is a clear example showcasing gaps and limitations of the global spectrum of form and function. This global functional spectrum is highly biased towards tree and herb species (and aboveground resource acquisitive functions – see Carmona et al. 2021). Therefore, the shrubby functional hotspot/gap could be “filled” when including shrubs (not a big surprise indeed) and resource conservation strategies – as happening in this case by sampling an area well-known to host many

shrub species, and being a diversification hotspot for them (e.g. Böhle et al. 1996; Kim et al. 1996).

2. Role of functional traits in mediating species persistence and distribution. Related to the first point, I think that discussing implications of the observed functional discrepancy between the trait coordination on Tenerife island vs the global spectrum of form and function for species persistence and distribution would deserve a much higher relevance. Species persistence and distribution may be shaped by different ecological strategies typical of different biogeographic regions. These may coexist on Tenerife, facilitating native species to effectively cope with e.g. aridity in dry habitats, such as thick leaves which may be either succulent (with low LMA and LDMC, more tropical syndrome) or sclerophyllous (with high LMA and LDMC, more Mediterranean syndrome; Cowling et al. 1996). Other persistence-related examples can be discussed, such as the relationships between plant size (seed, leaf, stem) and spatio-temporal isolation. The island rule predicts that larger plants on mainland should become smaller on islands, and smaller plants larger (Burns 2019; Biddick et al. 2019; Biddick & Burns 2021). This implies that intermediate forms should be promoted on islands – which seems to align quite well with results from this study (most species tending to sit in central/intermediate functional positions), with some interesting exceptions (e.g. *Aeonium*, *Polycarpha*; Fig. 5c in Extended Data + L224-232). Additionally, Tenerife is highly habitat-diverse. Based on the tight trait-environment relationship (Lavorel & Garnier 2002), I suggest accounting for the effect of different habitats on trait patterns because it could provide deeper ecological insights – see, for example, Steinbauer et al. (2012) focused on endemic species richness across different habitats and different island-related predictors on Canary Islands. Examining persistence strategies on islands is priority in plant biogeography (Heaney 2007; Ottaviani et al. 2020), and this study could provide key ecological insights relevant also for local extinction risk (Auffret et al. 2017). Finally, in L232-234 I would name traits informing on other functional axes that could be key for insular plant species persistence and distribution (for shrubs in particular, such as resprouting, clonality, longevity).

3. Direct equation between biogeography and evolution. A link between species distribution and evolution, particularly when related to endemism, is undoubted. However, disentangling and estimating the role of specific eco-evolutionary process(es) – including (intra- or inter-island or archipelago) dispersal, (intra- or inter-island or archipelago) speciation, local extinctions – on the distribution of distinct floristic groups (such as species endemic to one island, one archipelago, meta-archipelago, etc.) I am afraid is far more complex than currently presented. It gets even more so when adding trait values and related inferences – a conceptual overstretch/oversimplification in my view. In other words, if the authors wanted to tackle the effect of different eco-evolutionary processes on the diversity of traits, I recommend proceeding with phylogenetic analyses. To this end, I noticed that they have used phylogenetic relatedness to impute ~20% of missing trait data, so I assume they have the species-based phylogenetic information. Whether willing to maintain a strong focus on evolution, they should implement analyses e.g. i) of phylogenetic signal on trait expression (Pagel 1999), ii) to identify hot-node clades (Molina-Venegas et al. 2020), and iii) to decouple phylogeny from functional diversity (de Bello et al. 2017). This integrated analytical framework would allow to better disentangle, for each endemism-based floristic group, whether e.g. deep phylogenetic niche conservatism for specific functions/traits prevails over more recent geographically restricted functional differentiation (Molina-Venegas et al. 2022).

4. Trait analyses. The authors used the terms “functional convergence and divergence” in a few instances. However, these terms require the use of null models to be tested, and I could not find them. The Extended Data Fig. 4 contains interesting results, which could be merged with Fig. 3 by adding two panels related to functional contribution and originality – but I suggest testing for significant differences among the 5 floristic groups rather than against all the other species not belonging to the selected group. I would have liked to inspect the trait-trait hypervolumes (in appendix), not only the kernel density onto the PCAs ran for the different groups (Fig. 2). I also wonder why not working with those 80% of native species for which they have trait data for rather than imputing the missing values for ~20% species based on phylogenetic relatedness.

5. Referencing. Some relevant references are missing, especially from the same archipelago (e.g. Kim et al. 1996; Steinbauer et al. 2012, 2016; Mort et al. 2015; García-Verdugo et al. 2020; Irl et al. 2020; Hanz et al. 2022). Other citations do not necessarily match the message delivered by the original authors, for example Böhle et al. (1996) in L86-87. Böhle and colleagues suggested that for *Echium* species, diversification of insular woody forms in Macaronesia may be largely non-adaptive but associated with a single selective (reproductive) pressure, while the authors cited this reference to back up the role of adaptive radiations on islands. I encourage the authors to check this aspect carefully.

To summarize, I recommend the authors to frame and rebuild their story more tightly using what they have at hand and reach. I suggest focusing more decisively on how traits and trait syndromes related to the selected plant functions can affect the persistence and distribution of the native species on Tenerife (classified by endemism-based floristic groups), while keeping the evolutionary cut for some mild inferences – unless willing to run additional phylogenetic analyses as outline above.

Suggested/additional references

Auffret A et al. (2017) Spatial scale and specialization affect how biogeography and functional traits predict long-term patterns of community turnover. *Funct. Ecol.* 31: 436–443.

Biddick M & Burns KC (2021) A simple null model predicts the island rule. *Ecol. Lett.* 24: 1646–1654.

Carmona CP et al. (2021) Fine-root traits in the global spectrum of plant form and function. *Nature* 597: 683–687.

Cowling RM et al. (1996) Plant diversity in Mediterranean-climate regions. *Trends Ecol. Evol.* 11: 362–366.

de Bello F et al. (2017) Decoupling phylogenetic and functional diversity to reveal hidden signals in community assembly. *Methods Ecol. Evol.* 8: 1200–1211.

de la Riva EG et al. (2016) Leaf Mass per Area (LMA) and its relationship with leaf structure and anatomy in 34 Mediterranean woody species along a water availability gradient. *PLOS ONE* 11: e0148788.

García-Verdugo C et al. (2020) Leaf functional traits and insular colonization: Subtropical islands as a melting pot of trait diversity in a widespread plant lineage. *J. Biogeogr.* 47: 2362–2376.

Hanz DM et al. (2022) High species turnover and low intraspecific trait variation in endemic and non-endemic plant species assemblages on an oceanic island. *J. Veg. Sci.* 33: e13120.

Heaney LR (2007) Is a new paradigm emerging for oceanic island biogeography? *J. Biogeogr.* 34: 753–757.

Irl SDH et al. (2020) Climate controls plant life-form patterns on a high-elevation oceanic island. *J. Biogeogr.* 47: 2261–2273.

Kim SC et al. (1996) A common origin for woody *Sonchus* and five related genera in the Macaronesian islands: Molecular evidence for extensive radiation. *Proc. Natl. Acad. Sci. USA* 93: 7743–7748.

Molina-Venegas R et al. (2020) Phylogenetic patterns of extinction risk in the endemic flora of a Mediterranean hotspot as a guiding tool for preemptive conservation actions. *Front. Ecol. Evol.* 8: 373.

Molina-Venegas R et al. (2022). Biogeographic deconstruction of phylogenetic and functional diversity provides insights into the formation of regional assemblages. *Ecography*: e06140.

Mort ME et al. (2015) Multiplexed-shotgun-genotyping data resolve phylogeny within a very recently derived insular lineage. *Am. J. Bot.* 102: 634–641.

Ottaviani G et al. (2020) Linking plant functional ecology to island biogeography. *Trends Plant Sci.* 25: 329–339.

Pagel M (1999) Inferring the historical patterns of biological evolution. *Nature* 401: 877–884.

Steinbauer MJ et al. (2012). Increase of island endemism with altitude – speciation processes on oceanic islands. *Ecography* 35: 23–32.

Steinbauer MJ et al. (2016). Biogeographic ranges do not support niche theory in radiating Canary Island plant clades. *Glob. Ecol. Biogeogr.* 25: 792–804.

Referee #2 (Remarks to the Author):

Dear Authors,

It is with pleasure that I reviewed your paper entitled Assembly of functional diversity in an oceanic island flora. You will my comments below, organized as suggested by Nature Journal :

A.Summary of the key results

This paper addresses an interesting topic - the role played by biogeographic and evolutionary processes in shaping the distribution and diversity of plant functional traits of an oceanic island, Tenerife. To do so, the authors describe the functional trait space of Tenerife flora and perform a comparative study with global trait space and species groups which have particular biogeographical distributions and diversification histories. They use these observations to infer the effect of isolation, geographic and environmental factors on the functional trait space. They found that (i) Tenerife flora trait space largely overlap global plant trait space, but is concentrated around a functional hotspot dominated by shrubs, (ii) dispersal and speciation processes drive functional divergence and increase richness, (iii) speciation via cladogenesis drive functional convergence (toward shrubs trait syndrome).

B.Originality and significance: if not novel, please include reference

The paper presents a commendable amount of field and analysis work and provides some very useful and interesting insights on how trait space of species assemblages can be shaped by evolutionary, geographic and ecological processes. But this is also the limit of your study, as (in my feeling) your results are providing insights rather than providing a demonstration of the effects of the aforementioned processes. I don't have anything against that, and I value your work. I also

understand and I agree with your methodological approach (which I used myself), but I do think that we should keep in mind that inferring assembly processes from trait space is not trivial (e.g. Münkemüller et al. 2020). There is still serious doubt on our ability to really infer processes from trait composition and diversity patterns, even when relying on statistical comparisons of expected and observed patterns, which is not done here.

For this reason, I did not consider that the paper introduced sufficient that was conceptually novel nor results strong enough to merit its publication in Nature. The work, once presentation and methodological issues are tightened up and clarified, is likely to be sufficiently solid and interesting for publication elsewhere. For example it would probably sit better in a lower impact journal such as Global Ecology and Biogeography.

C.Data & methodology: validity of approach, quality of data, quality of presentation

As said before, I think that the methodological approach used by the authors suggest the imprint of the different mechanisms, but prevent a formal test of the influence processes. There are also some methodological points which should be overcome to increase the quality of the paper (see below).

Trait sampling and measurement.

It is a critical aspect of the paper and a great work that has been done on measuring those traits in the field. Congrats

Trait imputation

L461 : 20% of leaf trait values, 27% of stem density, 26% of seed mass. This means that $\frac{1}{3}$ of Tenerife trait data are not measured. I am not a big fan of trait imputation as whatever the approach used, conceptually trait imputation will only input “expected” values, while distinct traits are generally specific adaptations that are probably not well caught by trait imputation. What could you expect from the results without trait imputation? Given the difference in trait distribution between measured and imputed trait values, I am not expecting a big impact of the imputation on your conclusions. But one important thing could be to check how imputed trait values are distributed among different species groups.

Global trait data.

Why using the data from Diaz et al from 2016 ! It is likely that since 2016 there is way more species coverage, no ? Why not using TRY, BIEN, and data instead see for example <https://www.try-db.org/TryWeb/About.php>

Maybe you could even find some species that you imputed that are now in the latest TRY version (check BIEN database also ?)

D.Appropriate use of statistics and treatment of uncertainties

I am surprised to see that you did not analyze trait space divergence from expected distributions via the use of null models, which would have strengthened the results. I think that using well thought-out null models and providing statistics (e.g standardized effect size) of observed VS expected distribution would be beneficial to your work.

E.Conclusions: robustness, validity, reliability

As said before, I think that the conclusions are a bit oversold given the fact that results are only based on description of trait space.

F.Suggested improvements: experiments, data for possible revision

See section D.

G.References: appropriate credit to previous work?

As far as I know, I think that the references cited in the paper are appropriate

H.Clarity and context: lucidity of abstract/summary, appropriateness of abstract, introduction and conclusions

L38 : “our results reveal that long-distance dispersal, and the interplay between inter-island dispersal and archipelago-level speciation processes drive functional divergence and expand trait space. Conversely, speciation via cladogenesis has overall led to functional convergence, densely packing trait space around shrubbiness.”

I would suggest downgrading your statements in the abstract, as your results “suggest” the imprint of processes rather than “reveal” the effect of different processes.

Other comments on the main text and figures

Note that in the main text you generally interpret the results as patterns that suggest the influence of processes (rather than revealing or proving it), which I appreciate. There is still a few place where some strong statements could be downgraded, though.

Also some minor comments:

L51 : isolation, as well as geographic and environmental factors

Isolation is a geographic factor, no ?

L69-75: “and may help identifying the factors that shape an assemblage [...] Ecological, biogeographical, and evolutionary forces may either expand or constrain trait space, thereby[...] leading to an incomplete and potentially biased understanding of the factors”

I agree with this text section, and you properly put the fingers of the limit of trait based approach. But I do think that such limits also apply to your study, hence precluding a formal test of the effect of eco-evolutionary processes on the Tenerife Flora.

L81: “Biogeographical processes, such as long-distance dispersal, are thus expected to strongly constrain an island trait space, leading to functional convergence, where species share similar trait combinations”

You mean trait related to high dispersal ?

Figure 1. The difference between Tenerife/global trait space is not easy to catch. I would suggest showing and overlay 2D-density for each trait space (as done in Fig.2). You present the trait space resulting from PCA, but the overlap is computed from the hypervolume approach, where each trait is a dimension (right?). I do think that the hypervolume approach is the best way to measure trait space overlap as dimension reduction such as PCA will not consider empty space within the hypervolume, hence overestimating the overlap. My problem here lies in the difference between what is shown (PCA trait based) and what is computed (hypervolume overlap). I would suggest representing hypervolume instead (or both). For example only showing 3 dimensions (following Westoby's LHS scheme ?) or so could be an option.

L114: “Based on hypervolume overlap”. Based on PCA or trait axis ? How many dimensions did you consider ? This is important as the overlap might be largely influenced by these choices, and because on PC1 the two trait spaces seem quite different to me, maybe give a few details ? Also see previous comment.

Pierre Gaüzère

Referee #3 (Remarks to the Author):

A. Summary of the key results

Barajas-Barbosa and colleagues measure a series of morphological traits for a large percentage of species from the flora of Tenerife. They study trait space for the whole seed plant flora of the island and separately for various elements of the flora, in order to examine the contribution of each of these groups to a variety of metrics. They compare the trait space of Tenerife to that obtained from a global dataset. The main result is the comprehensive description of the functional trait space for an insular flora. From this, the authors find that while there is an overlap between the island and the global trait space, the shape and distribution of trait space of Tenerife differs strongly from the global one. Another main finding is how different species categories (defined by endemism, biogeography and evolutionary origin) influence trait space in contrasting ways.

B. Originality and significance: if not novel, please include reference

As far as I am aware, this is the first comprehensive description of functional trait space for a large (diverse) insular flora, making this an original and very significant study. Most previous studies used patchier trait datasets, worked at smaller scales, and/or gathered data from existing trait databases. The authors of this study took a different approach – they measured most of the traits themselves for an impressive percentage of the flora of Tenerife, one of the most diverse oceanic islands in the world. Apart from describing the trait space of the seed plants of Tenerife, the study also presents a series of analyses examining different components of the flora which, when performed at this scale, provide unprecedented insight into how the native flora of an island is assembled. Some of the results are obvious (e.g., Tenerife is dominated by shrubs) and the methods used per se are not particularly novel (measuring plant traits and analyses of trait space), but the way in which they are used and interpreted is very comprehensive, sharp, and effective, and is likely to become a blueprint for how to execute these types of studies.

C. Data & methodology: validity of approach, quality of data, quality of presentation

See my comments under F.

D. Appropriate use of statistics and treatment of uncertainties

I am not an expert on the types of statistical analyses used (trait space metrics), so I prefer not to comment on their appropriateness and validity.

E. Conclusions: robustness, validity, reliability

As far as I can gather, from an island biogeographical perspective the results are rigorous and reliable and the conclusions are robust and have been interpreted with caution, without exaggerations.

F. Suggested improvements: experiments, data for possible revision

- The classification of the flora into five different groups is clear and appropriate, but some of the justifications are a bit odd. a) Why is relictualization singled-out as an important origin of Macaronesian endemics (e.g., why not also mention this for Canary endemics)? b) Why are Tenerife endemics singled-out as representing in-situ speciation (following the same logic as in a), they could be endemic following the extinction on other islands); c) Why is intra-island dispersal singled out for Tenerife endemics? I assume it is equally important for the other groups.
- More detail is needed regarding the group “cladogenetic species”. In order to establish whether species are cladogenetic, well sampled phylogenies are required, to prove that the species result from a single colonization. I guess phylogenies are available for many of these 21 lineages, so perhaps a good idea would be to have a table saying how these decisions of whether species are cladogenetic were made. It is not sufficient to say species are cladogenetic because they are endemic and belong to the same genus. There are multiple examples in which this does not apply. If phylogenies are not available, that’s fine, but it should be noted somewhere that these are “possible cladogenetic” or something like this. Note that it is also possible to have extant non-endemic species that are cladogenetic from the perspective of the islands (and there are some cases of this in the Canaries), if they result from cladogenesis on the Canaries followed by back-colonization of the continent. So the category cladogenetic needs further clarification. The cut-off of three species should also be explained, because clades of two species can also be cladogenetic.
- The statement “most Tenerife endemics emerged via cladogenesis”. I would avoid statements like this, because, without fully sampled phylogenies, we do not know this. In addition, it would be worth clarifying in this statement if by cladogenesis the authors mean within Tenerife, within the Canaries or within Macaronesia, because that matters in this context.
- The main figures are clear and appropriate. However, it would be nice to edit them a bit to make them more memorable. Maybe with some photos of plant species from Tenerife, or a topographical map of the island.
- As a general comment, throughout the manuscript I get the impression that the main point of view supported is that a lot of the traits and adaptations for the endemics evolved in situ on the islands (e.g. “adapted to the arid environments”). Without comparison with mainland ancestors and ancestral state reconstructions this can only be speculated, so I would recommend adding this note of caution.
- Also in general, the main text is a bit plant- and Tenerife-centric, it would be nice to discuss the results in a more global context, perhaps with examples from other islands or even other taxa? There are a few papers on insular trait space in birds and snails, for example.

- L130 - the time of aridification needs a reference.
- L145 - I suggest adding “a general island syndrome for the island Tenerife”, as this is not the case for all islands.
- L194 – promote (unclear whether this applies to species or habitat diversity).
- Trait measurements – for some cases multiple replicates per species were measured, so it would be useful to include the total number of samples measured (only the total number of species is given). I could not find the raw data for the measurements when there are multiple replicates per species. Perhaps this should be provided? It would be interesting to get an idea of how much variation there is within species. Finally, maybe this is mentioned but I missed how the final trait value for each species was computed (mean value across replicates?).
- L459 – L474 – The analyses of trait imputation are not very well explained and I did not fully understand them. The file “Trait_imputed_phylo8.csv” includes traits for all the species, but it is not clear how to identify which species had their traits imputed or which traits were imputed for a given species. Also, more details are needed regarding the analyses – we are told “we constructed the phylogeny using the mega-phylogeny” but it is not clear what “the” phylogeny is. Finally, is this imputation really necessary? It would be useful to know what the results would look like with only the species that were measured vs the dataset with the imputed species. In any case, I got confused as to whether the dataset shown in the main figures (e.g. Fig. 1 and 2) includes also points that are predictions, or just real measurements.
- L494 – what are the traditional approaches?

G. References: appropriate credit to previous work?

Yes.

H. Clarity and context: lucidity of abstract/summary, appropriateness of abstract, introduction and conclusions

The study is very well-written, clear, and easy to follow.

Luis Valente

Author Rebuttals to Initial Comments:

Referees' comments:

Referee #1 (Remarks to the Author):

The manuscript by Barajas-Barbosa et al. entitled “Assembly of functional diversity in an oceanic island flora” [MS number: 2022-02-02651] constitutes a potentially interesting and relevant study for the emerging field of functional island biogeography. While I appreciate the effort made by the authors – especially in relation to the collection of trait data for a high number of Tenerife native angiosperm species – I have spotted a few substantial and critical conceptual and analytical issues. Unfortunately, those concerns reinforced after multiple readings of the paper.

[Response: We thank you for the encouraging feedback and constructive criticism.](#)

1. Fitting Tenerife native seed plants within the global spectrum of plant form and function. The authors found, along the first PCA axis (plant size functional dimension; Fig. 1), that Tenerife native plants sit right in between the two previously identified “functional hotspots” (Díaz et al. 2016). They correctly acknowledge that this indicates a “shrubby functional hotspot” when discussing their results (e.g., L116-126 and further below). However, they also state that Tenerife plants face similar functional constraints (e.g., L111-116). I do not see how the authors can back this claim. They report that Sørensen similarity coefficient between Tenerife and the global spectrum is 0.69 based on hypervolume overlap for both trait spaces. Yet, one could have expected Tenerife functional space to be completely/mostly included into the global spectrum. This PCA was run and constrained by the same 6 traits as for Díaz et al. (2016), yet along the first axis the distribution between Tenerife and the global dataset (which is composed here of ~2200 species and not ~46000 species as for the original article, and I would have liked to know some more about reasons behind this reduction) is different, as clearly showed by the density distribution (Fig. 1). This functional discrepancy gets even sharper when combined with results reported in Extended Data Fig. 2, wherein the authors added two key leaf traits, namely leaf dry matter content (LDMC) and leaf thickness. From there, it is evident that the first axis related to plant size in the global spectrum of form and function is not working too well on Tenerife, as illustrated by LDMC accounting for the highest loading in the first PCA axis, whereas much less is associated with plant height, seed mass and

leaf area. According to the global spectrum of form and function, LDMC – a trait tightly connected to resource economics (namely to water conservation) – should have aligned along the second functional axis, which refers to the leaf economics spectrum (Wright et al. 2004), and should have been strongly related to leaf mass per area (LMA), which is the inverse of specific leaf area (SLA) (de la Riva et al. 2016). To me, this is a clear example showcasing gaps and limitations of the global spectrum of form and function. This global functional spectrum is highly biased towards tree and herb species (and aboveground resource acquisitive functions – see Carmona et al. 2021). Therefore, the shrubby functional hotspot/gap could be “filled” when including shrubs (not a big surprise indeed) and resource conservation strategies – as happening in this case by sampling an area well-known to host many shrub species, and being a diversification hotspot for them (e.g., Böhle et al. 1996; Kim et al. 1996).

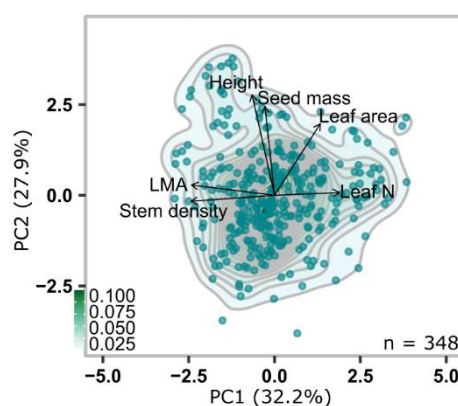
Response: Thank you for these thoughtful comments. We observed a large overall similarity between the flora of Tenerife and the global trait space (74% based on the updated Sørensen index see line: 117; Extended Data Fig. 2c); this left only 26% where both trait spaces do not overlap. Also, the trait variation of the flora of Tenerife clearly mirrors the leaf-height-seed ecology and related trade-offs (e.g., Westoby 1998; Díaz et al. 2016). Please also note that the functional space of Tenerife is completely nested in the global one (see extended Figure 2d). This led us to conclude that species in the Tenerife flora are facing similar biophysical constraints as elsewhere across the globe (see lines: 119-121).

Related to the question of the number of species from Díaz et al. (2016), we would like to highlight that we are using only the species for which Díaz et al. (2016) had complete empirical data for the six traits, which originally had 2214 species (shown in their Figure 2) and now have 2274 species after adding new TRY data. Díaz et al. 2016’s paper also performed the analysis with ca. 46 000 species, for which it was necessary to impute trait values for a large number of species.

Related to the presumed discrepancy between the PCAs in Figure 1 and Figure 2, please note that it is not a fair comparison to compare PCAs using different traits. By adding two additional leaf traits (LDMC and leaf thickness) to the island trait space, differences in the loadings are expected. The most important difference between the two PCAs is that maximum plant height is not driving as much of the trait variation of Tenerife’s trait space (Figure 2). In relation to

the global trait space, this is expected since the majority of Tenerife's plants are of intermediate stature (maximum plant height: mean = 2 m, standard deviation = 3.8 m) and tall trees (> 50 m) are completely absent from the island. Thus, plant height is not the main source of variation for the flora of Tenerife. Rather, we observed that LDMC and LMA contributed considerably to trait variation (see Extended data Fig. 3b).

Our results are consistent with previous studies of regions where plant stature variability is small, and in which the leaf economic spectrum drives the large variability of plants, followed by plant size (e.g., Díaz et al. 2004; Wright et al. 2010). We argue that when analysing a particular flora or region, the dominance of the leaf economic spectrum in the PCA (variance of leaf characteristics) can be due to the fact that variation in size-related traits is constrained by climate. In the case of Tenerife, the arid to semi-arid climate filters species with relatively short stature. These results are consistent even when mapping the Tenerife trait space using only the six traits in Díaz et al. (2016) (see the figure right below), where leaf traits, LMA and Leaf N, and stem density emerge as main drivers of variation:



Gaps and limitations of the global spectrum of form and function. To the best of our knowledge, the global trait space by Díaz et al. 2016 and TRY (where 50% of species are herbs, 30% are trees and 20% are shrubs; see Figure 8 in Kattge et al. 2020) are not biased against shrubs. However, we tested for the potential effects of a 'shrub bias' by using the updated growth form information from the GIFT database (Weigelt et al. 2020; accessed in May 2022) for 188212 species, which is approximately half of all known plant species. Of those, 54% are herbs, 24% are shrubs and 21% are trees. While these proportions are broadly similar to those in Díaz et al. (2016), GIFT currently has a slightly higher percentage of shrubs compared to the reported proportions by TRY in 2020. Whether there would be a third distinct hotspot

composed of the shrubs, or whether they would fill the space between herbs and trees, can only be determined by using empirically measured trait data for those species, which is currently not available. Importantly, a potential underrepresentation in *Díaz et al. (2016)* of shrubs does not negate the fact that Tenerife's trait space is dominated by shrubs. We note that we are not testing the global trait space *per se*, as this has been rigorously tested (e.g., *Díaz et al. 2016; Carmona et al. 2020*), but rather we use it as the best available and most widely accepted backdrop against which to compare the trait space of Tenerife.

Motivated by your comment, we built a null model that also accounts for the potential 'shrub bias' in the global trait space by randomly sampling from the global data the currently known global proportions of herbs, shrubs and trees (see Methods Lines 558-565; Extended Data Fig. 2d). This null model also controls for the difference in species richness between the global and island datasets (see Line 559). The null model results are fully consistent with those of the basic null model (Lines 571-573) that only controls for species richness difference. Thus, both null models support the strong overlap between the global and island trait spaces.

2. Role of functional traits in mediating species persistence and distribution. Related to the first point, I think that discussing implications of the observed functional discrepancy between the trait coordination on Tenerife island vs the global spectrum of form and function for species persistence and distribution would deserve a much higher relevance. Species persistence and distribution may be shaped by different ecological strategies typical of different biogeographic regions. These may coexist on Tenerife, facilitating native species to effectively cope with e.g., aridity in dry habitats, such as thick leaves which may be either succulent (with low LMA and LDMC, more tropical syndrome) or sclerophyllous (with high LMA and LDMC, more Mediterranean syndrome; *Cowling et al. 1996*). Other persistence-related examples can be discussed, such as the relationships between plant size (seed, leaf, stem) and spatio-temporal isolation. The island rule predicts that larger plants on mainland should become smaller on islands, and smaller plants larger (*Burns 2019; Biddick et al. 2019; Biddick & Burns 2021*). This implies that intermediate forms should be promoted on islands – which seems to align quite well with results from this study (most species tending to sit in central/intermediate functional positions), with some interesting exceptions (e.g., *Aeonium, Polycarphaea*; Fig. 5c in Extended Data + L224-232). Additionally, Tenerife is highly habitat-diverse. Based on the tight trait-environment relationship (*Lavorel & Garnier 2002*), I suggest

accounting for the effect of different habitats on trait patterns because it could provide deeper ecological insights – see, for example, Steinbauer et al. (2012) focused on endemic species richness across different habitats and different island-related predictors on Canary Islands. Examining persistence strategies on islands is priority in plant biogeography (Heaney 2007; Ottaviani et al. 2020), and this study could provide key ecological insights relevant also for local extinction risk (Auffret et al. 2017). Finally, in L232-234 I would name traits informing on other functional axes that could be key for insular plant species persistence and distribution (for shrubs in particular, such as resprouting, clonality, longevity).

Response: Thanks for these insightful comments. We fully agree that persistence-related traits could be important for deepening the current understanding of island floras, as persistence could be a key strategy to cope with frequent catastrophic events on islands (e.g., volcanic eruptions) and aridity (Lens et al. 2022). In our revised manuscript, we now expand on the role of functional traits in capturing plant persistence strategies in the environment of Tenerife (Lines: 44, 139-142 and 153-155). However, we are aware of the importance of including persistence related traits, as well as other traits reflecting other life history dimensions, in future studies. We have now added in the revised version of this manuscript text indicating the need to include traits that capture additional dimensions of plant persistence, such as bark thickness, lumen density, resprouting, clonality, and longevity (Lines 25-256).

Island rule. This is a highly interesting topic. However, we do not have the appropriate data to test the island rule. Please note that we have only trait data of the island species and, unfortunately, not for their continental congeners (but see Biddick and Burns 2021). In the revised version of this manuscript, we now address how intermediate plant size (i.e., maximum plant size) is promoted on an island by discussing the dominance of shrubs on Tenerife and relating it to the island's environmental conditions (see Lines: 151-155).

Effect of habitat and environment on trait patterns. This topic has been addressed recently by Hanz et al. (2022), where morphometric trait data sourced from the literature show how the spatial variation of plant functional diversity of the Canary Islands is affected by climatic gradients. We are aware that the environment can limit functional diversity (Cornwell & Ackerly, 2009; Spasojevic et al. 2014), as resource-rich habitats (e.g., productive ecosystems

with high water and nutrient availability) often enable the coexistence of various functional strategies, while resource-limited habitats (i.e., low temperatures) reduce functional diversity and plant strategies. However, we study the functional diversity at the island level, and the biogeographical processes that shape it. Our results clearly show that the dominant environmental conditions at the island level play a role in determining the functional diversity and drive the dominance of shrubs. Motivated by your comment, we investigated the role of the environment and habitat diversity by creating a new map showing the environmental space of Tenerife in relation to all other existing biomes of the world (Extended Data Fig. 7). This map provides ecological insight into the effect of the dominance of dry ecosystems and biomes of Tenerife on the functional diversity of the island.

3. Direct equation between biogeography and evolution. A link between species distribution and evolution, particularly when related to endemism, is undoubted. However, disentangling and estimating the role of specific eco-evolutionary process(es) – including (intra- or inter-island or archipelago) dispersal, (intra- or inter-island or archipelago) speciation, local extinctions – on the distribution of distinct floristic groups (such as species endemic to one island, one archipelago, meta-archipelago, etc.) I am afraid is far more complex than currently presented. It gets even more so when adding trait values and related inferences – a conceptual overstretch/oversimplification in my view. In other words, if the authors wanted to tackle the effect of different eco-evolutionary processes on the diversity of traits, I recommend proceeding with phylogenetic analyses. To this end, I noticed that they have used phylogenetic relatedness to impute ~20% of missing trait data, so I assume they have the species-based phylogenetic information. Whether willing to maintain a strong focus on evolution, they should implement analyses e.g., i) of phylogenetic signal on trait expression (Pagel 1999), ii) to identify hot-node clades (Molina-Venegas et al. 2020), and iii) to decouple phylogeny from functional diversity (de Bello et al. 2017). This integrated analytical framework would allow to better disentangle, for each endemism-based floristic group, whether e.g. deep phylogenetic niche conservatism for specific functions/traits prevails over more recent geographically restricted functional differentiation (Molina-Venegas et al. 2022).

Response: Thank you for these comments, which motivated us to think carefully about our analytical framework. We assessed the effect of different eco-evolutionary processes on the diversity of Tenerife traits by performing the recommended phylogenetic analyses.

First, we calculated the phylogenetic signal for all traits individually to test if the functional trait values of Tenerife were phylogenetically independent (Lines: 518-526 and Extended Data Table 2). We found that the phylogenetic signal in our trait data is consistent with previous studies, showing strong phylogenetic conservatism for maximum plant height, seed mass, stem specific density, and LDMC, and a relatively weaker phylogenetic signal for leaf area (Extended Data Table 2). The missing trait values exhibited a low phylogenetic signal for all traits, indicating that species with measured traits are distributed randomly across the phylogeny. This finding further justifies our decision to utilize imputed trait values based on phylogenetic information as it shows that: i) trait values of closely related species are quite similar and ii) missing values likely occur within clades that include empirical trait data, therefore lowering estimation error.

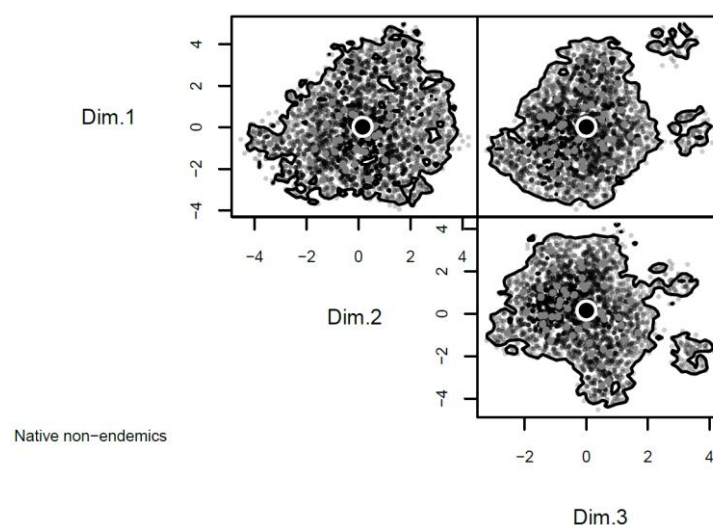
Second, we performed a hot node analysis (*sensu Molina-Venegas et al. 2020* see methods Lines: 618-627), which revealed that only species endemic to Tenerife are more diverse than would be expected by chance (Extended Data Figure 4). This new result supports our initial finding that Tenerife endemics do not add to island-level functional diversity because of niche conservatism, which is potentially due to the abiotic filtering on the island. We updated the main text accordingly (Lines: 210-214).

4. Trait analyses. The authors used the terms “functional convergence and divergence” in a few instances. However, these terms require the use of null models to be tested, and I could not find them. The Extended Data Fig. 4 contains interesting results, which could be merged with Fig. 3 by adding two panels related to functional contribution and originality – but I suggest testing for significant differences among the 5 floristic groups rather than against all the other species not belonging to the selected group. I would have liked to inspect the trait-trait hypervolumes (in appendix), not only the kernel density onto the PCAs ran for the different groups (Fig. 2). I also wonder why not working with those 80% of native species for which they have trait data for rather than imputing the missing values for ~20% species based on phylogenetic relatedness.

Response: In our original submission, we performed rarefaction as a form of null model (Gotelli, 2001) to control for differences in species richness per group (see methods lines: 588-590) and to test the contribution of each group to the whole-island trait space. To avoid

confusion, we changed in the revised manuscript the terminology by using the word ‘null model’ instead of ‘rarefaction’. We also extended our null model analyses to examine functional convergence and divergence by estimating the null expectation of functional diversity metrics (see methods lines: 593-596) by randomly sampling 30 species from the entire species pool. We also added the former Extended Data Figure 4 to what is now Figure 3 in the main text. Following the Reviewer’s suggestion, we also tested for statistical differences across functional diversity metrics, contribution and originality of the five groups (see Figure 3) and added it to Figure 3b.

We interpret your suggestion of inspecting the trait-by-trait hypervolume, as inspecting the hypervolumes of each group. By plotting the hypervolumes *sensu Blonder et al. (2018)* it is possible to do so, but drawing inference from the visualisation of species within groups and across groups is highly limited (see the figure right below; example of the hypervolume for native non-endemics species). We thus opted to visualize the trait spaces using 2D-Density plots Figure 2.



Related to the comment about working with 80% of native seed plant species for which we have empirical trait data, we performed the analyses using only species with complete empirical data for all eight traits (hereafter ‘complete cases’, i.e., 237 out of 436 species, which are all Tenerife native seed plant species). Because we found differences in the results between both datasets, it was not possible to conclude whether our results were ecological or a product of the trait imputation. We further examined this issue by performing all analyses using species with a minimum of 5 empirically-measured traits (hereafter ‘near-complete

cases'), which include 348 species (79.8% of Tenerife's native seed plant flora). These species are missing less than 5% of trait values (see Extended Data Figure 1a), and therefore the emergent patterns of functional diversity are mainly driven by empirical data. We find that the pattern based on near-complete and complete cases are qualitatively similar (ref. Figure 3 and Extended Data Figure 7). Thus, we opted to present the results for near-complete cases in the main text, which allows us to study a large percentage of Tenerife flora (79.81%), as well as to utilize as much as possible the empirical data that we collected.

Lastly, we merged the results of functional diversity metrics with the functional contribution and originality in a single figure in the main text, i.e., Figure 3.

5. Referencing. Some relevant references are missing, especially from the same archipelago (e.g., Kim et al. 1996; Steinbauer et al. 2012, 2016; Mort et al. 2015; García-Verdugo et al. 2020; Irl et al. 2020; Hanz et al. 2022). Other citations do not necessarily match the message delivered by the original authors, for example Böhle et al. (1996) in L86-87. Böhle and colleagues suggested that for *Echium* species, diversification of insular woody forms in Macaronesia may be largely non-adaptive but associated with a single selective (reproductive) pressure, while the authors cited this reference to back up the role of adaptive radiations on islands. I encourage the authors to check this aspect carefully.

Response: Thank you for the suggested references. We carefully checked all references and have removed the citation, as well as the statement related to *Echium* lineage (Line 87). We now also include *Hanz et al. 2020*, *Irl et al. 2020*, *Ottaviani et al 2020* and *Molina-Venegas et al. (2020)*.

To summarize, I recommend the authors to frame and rebuild their story more tightly using what they have at hand and reach. I suggest focusing more decisively on how traits and trait syndromes related to the selected plant functions can affect the persistence and distribution of the native species on Tenerife (classified by endemism-based floristic groups), while keeping the evolutionary cut for some mild inferences – unless willing to run additional phylogenetic analyses as outline above.

Response: Thank you for your thoughtful suggestions. We are confident that the additional analyses improve our manuscript and make our conclusion more robust. Also, we worked hard to find balanced and nuanced wording.

Suggested/additional references

Auffret A et al. (2017) Spatial scale and specialization affect how biogeography and functional traits predict long-term patterns of community turnover. *Funct. Ecol.* 31: 436–443.

Biddick M & Burns KC (2021) A simple null model predicts the island rule. *Ecol. Lett.* 24: 1646–1654.

Carmona CP et al. (2021) Fine-root traits in the global spectrum of plant form and function. *Nature* 597: 683–687.

Cowling RM et al. (1996) Plant diversity in Mediterranean-climate regions. *Trends Ecol. Evol.* 11: 362–366.

de Bello F et al. (2017) Decoupling phylogenetic and functional diversity to reveal hidden signals in community assembly. *Methods Ecol. Evol.* 8: 1200–1211.

de la Riva EG et al. (2016) Leaf Mass per Area (LMA) and its relationship with leaf structure and anatomy in 34 Mediterranean woody species along a water availability gradient. *PLOS ONE* 11: e0148788.

García-Verdugo C et al. (2020) Leaf functional traits and insular colonization: Subtropical islands as a melting pot of trait diversity in a widespread plant lineage. *J. Biogeogr.* 47: 2362–2376.

Hanz DM et al. (2022) High species turnover and low intraspecific trait variation in endemic and non-endemic plant species assemblages on an oceanic island. *J. Veg. Sci.* 33: e13120.

Heaney LR (2007) Is a new paradigm emerging for oceanic island biogeography? *J. Biogeogr.* 34: 753–757.

Irl SDH et al. (2020) Climate controls plant life-form patterns on a high-elevation oceanic island. *J. Biogeogr.* 47: 2261–2273.

Kim SC et al. (1996) A common origin for woody *Sonchus* and five related genera in the Macaronesian islands: Molecular evidence for extensive radiation. *Proc. Natl. Acad. Sci. USA* 93: 7743–7748.

Molina-Venegas R et al. (2020) Phylogenetic patterns of extinction risk in the endemic flora of a Mediterranean hotspot as a guiding tool for preemptive conservation actions. *Front. Ecol. Evol.* 8: 373.

Molina-Venegas R et al. (2022). Biogeographic deconstruction of phylogenetic and functional diversity provides insights into the formation of regional assemblages. *Ecography*: e06140.

Mort ME et al. (2015) Multiplexed-shotgun-genotyping data resolve phylogeny within a very recently derived insular lineage. *Am. J. Bot.* 102: 634–641.

Ottaviani G et al. (2020) Linking plant functional ecology to island biogeography. *Trends Plant Sci.* 25: 329–339.

Pagel M (1999) Inferring the historical patterns of biological evolution. *Nature* 401: 877–884.

Steinbauer MJ et al. (2012). Increase of island endemism with altitude – speciation processes on oceanic islands. *Ecography* 35: 23–32.

Steinbauer MJ et al. (2016). Biogeographic ranges do not support niche theory in radiating Canary Island plant clades. *Glob. Ecol. Biogeogr.* 25: 792–804.

Referee #2 (Remarks to the Author):

Dear Authors,

It is with pleasure that I reviewed your paper entitled Assembly of functional diversity in an oceanic island flora. You will my comments below, organized as suggested by Nature Journal:

[Response: Thank you, we appreciate your thoughtful comments and suggestions.](#)

A.Summary of the key results

This paper addresses an interesting topic - the role played by biogeographic and evolutionary processes in shaping the distribution and diversity of plant functional traits of an oceanic island, Tenerife. To do so, the authors describe the functional trait space of Tenerefi flora and perform a comparative study with global trait space and species groups which have particular biogeographical distributions and diversification histories. They use these observations to infer the effect of isolation, geographic and environmental factors on the functional trait space. They found that (i) tenerife flora trait space largely overlap global plant trait space, but is concentrated around a functional hotspot dominated by shrubs, (ii) dispersal and speciation processes drive functional divergence and increase richness, (iii) speciation via cladogenesis drive functional convergence (toward shrubs trait syndrome).

B.Originality and significance: if not novel, please include reference

The paper presents a commendable amount of field and analysis work and provides some very useful and interesting insights on how trait space of species assemblages can be shaped by evolutionary, geographic and ecological processes. But this is also the limit of your study, as (in my feeling) your results are providing insights rather than providing a demonstration of the effects of the aforementioned processes. I don't have anything against that, and I value your work. I also understand and I agree with your methodological approach (which I used myself), but I do think that we should keep in mind that inferring assembly processes from trait space is not trivial (e.g Münkemüller et al. 2020). There is still serious doubt on our ability to really infer processes from trait composition and diversity patterns, even when relying on statistical comparisons of expected and observed patterns, which is not done here.

Response: We thank you for your appreciation of our extensive field research work. We are fully aware of the challenges of inferring assembly processes from a trait-based approach. In our study, we therefore tested specific pre-defined hypotheses, carefully selected informative functional traits and also carefully selected the different diversity functional metrics guided by our study objectives. Also, we chose an ecologically meaningful species pool (i.e., island flora) and performed appropriate randomizations. To this end, we followed closely the recent proposal by *Münkemüller et al. (2020)* to strengthen inference on underlying assembly mechanisms. Besides this, we are aware that because our study is not a controlled experiment, we can only provide insights into biogeographical and evolutionary processes and cannot test mechanisms. We apologize if this was not clear in the original submission. In our revision, we extensively worked to find a nuanced and balanced discussion of our results and have toned down statements where appropriate to better reflect these limitations (see Lines in abstract 37-38, in main results and discussion line 192 and 221; and in our conclusion line 265).

Lastly, we performed extensive additional statistical null model comparisons between randomly expected results and estimated patterns per each group (see lines: 588-590 and 593-596), as we show now in Figure 3a. As we mentioned in the response to Referee 1, in our first submission, we used rarefaction, which is a type of null model (Gotelli, 2001). To avoid confusion, we changed the term rarefaction for null models throughout.

For this reason, I did not consider that the paper introduced sufficient that was conceptually novel nor results strong enough to merit its publication in Nature. The work, once presentation and methodological issues are tightened up and clarified, is likely to be sufficiently solid and interesting for publication elsewhere. For example it would probably sit better in a lower impact journal such as Global Ecology and Biogeography.

Response: Functional diversity research on oceanic island floras has so far been limited by the lack of empirical trait data. The hugely successful approach of big synthetic studies based on trait databases, such as TRY, at present cannot be extended to islands as coverage for even the most commonly measured traits, like leaf area, leaf nitrogen content or SLA is extremely poor. For instance, our latest search in TRY for species revealed that only twelve native species of Tenerife are included (i.e., *Ilex canariensis*, *Ilex perado*, *Juniperus cedrus*, *Myrica faya*,

Osyris lanceolate, *Persea indica*, *Pinus canariensis*, *Pistacia lentiscus*, *Prunus lusitanica*, *Rhamnus glandulosa*, *Sambucus nigra* and *Pleiomeris canariensis*). The main novelty of our study is that we provide a first comprehensive quantitative description of an almost completely sampled functional trait space for one of the most iconic and diverse oceanic island floras. While we are aware of and discuss the limitations of our study (e.g., Lines: 236-238 and 254-256), our data and improved analysis allow insights that have not been presented before and that advance our understanding of the evolutionary and ecological dynamics of functional diversity of island systems. Our approach can serve as a seminal blueprint to study other islands and archipelagos. These merits of our study have also been pointed out by Referee 3.

C.Data & methodology: validity of approach, quality of data, quality of presentation

As said before, I think that the methodological approach used by the authors suggest the imprint of the different mechanisms, but prevent a formal test of the influence processes. There are also some methodological points which should be overcome to increase the quality of the paper (see below).

Trait sampling and measurement.

It is a critical aspect of the paper and a great work that has been done on measuring those traits in the field. Congrats

Response: Thank you for this comment. It was indeed a big effort.

Trait imputation

L461 : 20% of leaf trait values, 27% of stem density, 26% of seed mass. This means that $\frac{1}{3}$ of Tenerife trait data are not measured. I am not a big fan of trait imputation as whatever the approach used, conceptually trait imputation will only input “expected” values, while distinct traits are generally specific adaptations that are probably not well caught by trait imputation. What could you expect from the results without trait imputation? Given the difference in trait distribution between measured and imputed trait values, I am not expecting a big impact of the imputation on your conclusions. But one important thing could be to check how imputed trait values are distributed among different species groups.

Response: Thanks for pointing out the potential issue arising from trait imputation. Motivated by your comments, we performed extensive additional analyses. First, we reran analyses with only those species for which we had complete empirical data for all eight traits ('complete cases' i.e., 237 out of 436 species (54%)). Second, we used species with a minimum of 5 empirically-measured traits ('near-complete cases'), which include 348 species or 80% of Tenerife's native flora. These species lack less than 5% of trait values in the species-by-trait matrix (Extended Data Figure 1a). As mentioned in our response to referee 1, we opted to present the results for near-complete cases, as results from 'complete cases' and from 'near-complete cases' were consistent. This allowed us to make the most of our field measurements and study 80% of Tenerife flora. Lastly, we analysed the distribution of missing and imputed trait values in the species-by-trait matrix and how the results in Extended Figure 1. Please note that there is only a maximum of 5.4% of missing trait values across groups (Extended Data Figure 1a). Thus, there is no group with a high percentage of missing traits. Please also note that these values are very low compared to accepted standards in functional ecological studies.

In general, seed mass and stem density were the traits with the lowest coverage at the island level as well as at the group level; these traits were also the most phylogenetically conserved ones (see the phylogenetic signal analysis we performed for this revision in the methods in Lines: 518-526 and results in Extended Data Table 2). Given their strong high phylogenetic signal we are confident about using the imputed values at such a low level.

Global trait data.

Why using the data from Díaz et al from 2016 ! It is likely that since 2016 there is way more species coverage, no ? Why not using TRY, BIEN, and data instead see for example <https://www.try-db.org/TryWeb/About.php>

Maybe you could even find some species that you imputed that are now in the latest TRY version (check BIEN database also ?)

Response: We thank you for this comment. We retrieved data from TRY but this only added 60 species to the global data set. Based on this updated and expanded dataset, we re-ran all analyses. Besides these few additions, the *Díaz et al. (2016)* dataset remains the most

comprehensive empirical trait data set at the species level that is publicly available. We also note that BIEN's trait data is largely restricted to the Americas.

D.Appropriate use of statistics and treatment of uncertainties

I am surprised to see that you did not analyze trait space divergence from expected distributions via the use of null models, which would have strengthened the results. I think that using well thought-out null models and providing statistics (e.g standardized effect size) of observed VS expected distribution would be beneficial to your work.

Response: We supplemented our analyses with additional null models (Extended Figure 2c), where we control for the difference of species number between global and island species pools, as well as for the potential underrepresentation of shrubs on the global data in order to have a more robust comparison between the island and global trait spaces. In Figure 3a, motivated by your suggestion, we additionally compare the five species groups to a null group to compare functional divergence and convergence of groups with respect to a null expectation. Therefore, if a group has a lower or higher value than the null group, it indicates functional convergence or divergence, respectively (see details in lines: 596-599; and see credible intervals across groups in Figure 3a).

E.Conclusions: robustness, validity, reliability

As said before, I think that the conclusions are a bit oversold given the fact that results are only based on description of trait space.

Response: Thanks for this comment. It was by no means our intention to oversell our results. In our revision, we work hard to present our results in a well-balanced and nuanced manner, and we have also toned down some statements. As mentioned before, we modified the abstract, main results and discussion, and the conclusions to make them more balanced (e.g., Lines: 38, 192 and 254).

F.Suggested improvements: experiments, data for possible revision

See section D.

G.References: appropriate credit to previous work?

As far as I know, I think that the references cited in the paper are appropriate

[Response: Indeed. Thanks.](#)

H.Clarity and context: lucidity of abstract/summary, appropriateness of abstract, introduction and conclusions

L38 : “our results reveal that long-distance dispersal, and the interplay between inter-island dispersal and archipelago-level speciation processes drive functional divergence and expand trait space. Conversely, speciation via cladogenesis has overall led to functional convergence, densely packing trait space around shrubbiness.”

I would suggest downgrading your statements in the abstract, as your results “suggest” the imprint of processes rather than “reveal” the effect of different processes.

[Response: We toned down this statement, as suggested \(see Line: 38\)](#)

Other comments on the main text and figures

Note that in the main text you generally interpret the results as patterns that suggest the influence of processes (rather than revealing or proving it), which I appreciate. There is still a few place where some strong statements could be downgraded, though.

[Response: Yes, as mentioned before we toned down strong statements.](#)

Also some minor comments:

L51 : isolation, as well as geographic and environmental factors

Isolation is a geographic factor, no ?

[Response: Yes, it is. We removed the word geographic to avoid redundancy \(Line: 52\)](#)

L69-75: “and may help identifying the factors that shape an assemblage [...] Ecological, biogeographical, and evolutionary forces may either expand or constrain trait space, thereby[...] leading to an incomplete and potentially biased understanding of the factors”

I agree with this text section, and you properly put the fingers of the limit of trait based approach. But I do think that such limits also apply to your study, hence precluding a formal test of the effect of eco-evolutionary processes on the Tenerife Flora.

Response: We agree with your comment. As we have been aware that we are not doing formal tests of the effect of eco-evolutionary processes on the flora of Tenerife, we talk about imprints of this process on the plant functional diversity of Tenerife (Line: 181).

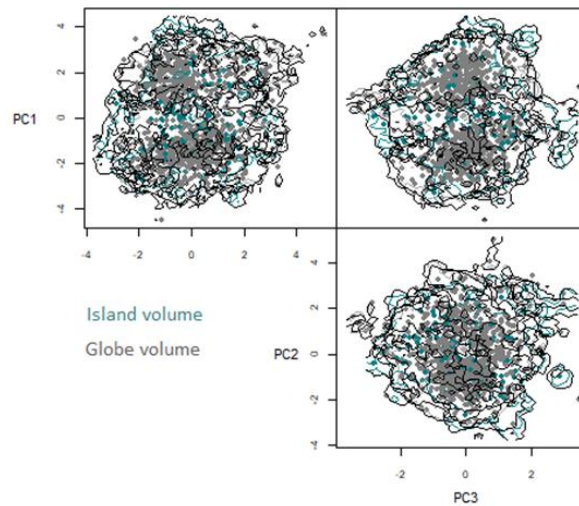
L81: “Biogeographical processes, such as long-distance dispersal, are thus expected to strongly constrain an island trait space, leading to functional convergence, where species share similar trait combinations”

You mean trait related to high dispersal ?

Response: We do not exclusively mean traits related to dispersal, but all trait combinations that might be missing on an island due to the limitation of certain plants for long-distance dispersal.

Figure 1. The difference between Tenerife/global trait space is not easy to catch. I would suggest showing and overlay 2D-density for each trait space (as done in Fig.2). You present the trait space resulting from PCA, but the overlap is computed from the hypervolume approach, where each trait is a dimension (right?). I do think that the hypervolume approach is the best way to measure trait space overlap as dimension reduction such as PCA will not consider empty space within the hypervolume, hence overestimating the overlap. My problem here lies in the difference between what is shown (PCA trait based) and what is computed (hypervolume overlap). I would suggest representing hypervolume instead (or both). For example only showing 3 dimensions (following Westoby’s LHS scheme ?) or so could be an option.

Response: Thank you for your suggestion about showing the contours and using 2D-density to visualize the global versus island trait spaces. However, the contours hide the data points, i.e., species, and thus decrease the interpretability of the figure (see the figure right below). We opted to present the main Figure 1 without the contours but we added them in the Extended Data Fig. 2c.



We do present all trait spaces resulting from the PCAs (i.e., Figure 1 and Figure 2). We computed the overlap between global and island trait spaces, as well as the functional diversity metrics in Figure 3, using hypervolumes (sensu Blonder et al. 2018), which we built using PC1, PC2 and PC3 from the PCA run with six traits (Figure 1) and with eight traits (Figure 2a). Due to computational constraints, Blonder et al. 2018 recommend using the lowest dimensionality possible (i.e., PC1-3) but using enough axes to ensure that a sufficient amount of variation is captured. This same hypervolume approach considers empty space within the trait space (ref. Blonder, 2016) and therefore controls for the overestimation of functional diversity metrics. In the revised version of this manuscript we edited the description of the methods to make clear the differences between what we show in the PCA (Figure 1 and Figure 2) (see section ‘Functional trait space visualisation’ line: 537) and what is computed using hypervolumes (see section ‘Trait spaces overlap and functional diversity estimation’ Lines: 545). We note that both the visualizations of the PCAs (trait space) and hypervolume estimation (functional diversity metrics) are linked. We use the PCA for visual inspections of the trait space, e.g., whether species are concentrated in a hotspot (as shown in Figure 1) or whether species are located in a particular part of the spectrum of traits.

Lastly, we opted for plotting PCAs instead of plotting the calculated hypervolumes. The hypervolume algorithm computes a stochastic description of a hypervolume, and we think that the contours of the computed hypervolume are not intuitive to interpret visually (see figure below)

L114: “Based on hypervolume overlap”. Based on PCA or trait axis ? How many dimensions did you consider ? This is important as the overlap might be largely influenced by these choices, and because on PC1 the two trait spaces seem quite different to me, maybe give a few details ? Also see previous comment.

Response: We edited the description of the methods to make clear how the hypervolume computation and overlap were done, i.e., we used the first three dimensions of the PCA. See our improvements in the section “Trait spaces overlap and functional diversity estimation”. Specifically, see lines: 549-552.

Pierre Gaüzère

Referee #3 (Remarks to the Author):

A. Summary of the key results

Barajas-Barbosa and colleagues measure a series of morphological traits for a large percentage of species from the flora of Tenerife. They study trait space for the whole seed plant flora of the island and separately for various elements of the flora, in order to examine the contribution of each of these groups to a variety of metrics. They compare the trait space of Tenerife to that obtained from a global dataset. The main result is the comprehensive description of the functional trait space for an insular flora. From this, the authors find that while there is an overlap between the island and the global trait space, the shape and distribution of trait space of Tenerife differs strongly from the global one. Another main finding is how different species categories (defined by endemism, biogeography and evolutionary origin) influence trait space in contrasting ways.

B. Originality and significance: if not novel, please include reference

As far as I am aware, this is the first comprehensive description of functional trait space for a large (diverse) insular flora, making this an original and very significant study. Most previous studies used patchier trait datasets, worked at smaller scales, and/or gathered data from existing trait databases. The authors of this study took a different approach – they measured most of the traits themselves for an impressive percentage of the flora of Tenerife, one of the most diverse oceanic islands in the world. Apart from describing the trait space of the seed plants of Tenerife, the study also presents a series of analyses examining different components of the flora which, when performed at this scale, provide unprecedented insight into how the native flora of an island is assembled. Some of the results are obvious (e.g., Tenerife is dominated by shrubs) and the methods used per se are not particularly novel (measuring plant traits and analyses of trait space), but the way in which they are used and interpreted is very comprehensive, sharp, and effective, and is likely to become a blueprint for how to execute these types of studies.

Response: We are thankful for your encouraging words and recognition of the hard-work and novelty of our study.

C. Data & methodology: validity of approach, quality of data, quality of presentation

See my comments under F.

D. Appropriate use of statistics and treatment of uncertainties

I am not an expert on the types of statistical analyses used (trait space metrics), so I prefer not to comment on their appropriateness and validity.

E. Conclusions: robustness, validity, reliability

As far as I can gather, from an island biogeographical perspective the results are rigorous and reliable and the conclusions are robust and have been interpreted with caution, without exaggerations.

F. Suggested improvements: experiments, data for possible revision

- The classification of the flora into five different groups is clear and appropriate, but some of the justifications are a bit odd. a) Why is relictualization singled-out as an important origin of Macaronesian endemics (e.g., why not also mention this for Canary endemics)? b) Why are Tenerife endemics singled-out as representing in-situ speciation (following the same logic as in a), they could be endemic following the extinction other islands); c) Why is intra-island dispersal singled out for Tenerife endemics? I assume it is equally important for the other groups.

Response: Thank you for this observation. We agree that the previous definitions were unclear. We clarified the definition for each group in lines 105-110. Regarding the Macaronesian endemics as well as other groups, we improved their description by explaining that this group 'mainly' is associated with relictualization (Line 106). It is correct that there are a few species among the Canary endemics that are also considered as relics. But among the Macaronesian endemics, there is a large number of species known to be the product of relictualization, much more than in other groups studied here. Thus, we treat Macaronesian endemics as a group that is primarily associated with relictualization (compare Fernández-Palacios et al. 2011). We also changed the part about Tenerife endemics by stating more clearly that Tenerife endemics are primarily associated with *in-situ* speciation and within-

island dispersal only (Line 110), as these species occur nowhere else but Tenerife (due to dispersal limitation, or the lack of suitable habitat elsewhere).

- More detail is needed regarding the group “cladogenetic species”. In order to establish whether species are cladogenetic, well sampled phylogenies are required, to prove that the species result from a single colonization. I guess phylogenies are available for many of these 21 lineages, so perhaps a good idea would be to have a table saying how these decisions of whether species are cladogenetic were made. It is not sufficient to say species are cladogenetic because they are endemic and belong to the same genus. There are multiple examples in which this does not apply. If phylogenies are not available, that’s fine, but it should be noted somewhere that these are “possible cladogenetic” or something like this. Note that it is also possible to have extant non-endemic species that are cladogenetic from the perspective of the islands (and there are some cases of this in the Canaries), if they result from cladogenesis on the Canaries followed by back-colonization of the continent. So the category cladogenetic needs further clarification. The cut-off of three species should also be explained, because clades of two species can also be cladogenetic.

Response: We carefully revised the information of the species belonging to each lineage (i.e., cladogenetic species) and added the references that support the lineage phylogeny (see updated Barajasetal_traits_status.csv in Data availability statement; also see improved description of the groups in Lines: 441-448). We now include in our analysis 63 lineages, which are present in Tenerife and have radiated within the Macaronesia (14 are Macaronesian endemics), Canary Islands (i.e., 104 are Canary endemic species) and Tenerife (i.e., 76 are Tenerife endemic species). Only one species has a wider distribution, *Dracaena draco*, which is considered a native non-endemic. Phylogenies were available for 57 lineages supporting their cladogenetic status. Only for six lineages no appropriate phylogenies were available and those were asserted based on morphology (by Jonathan Price, see explanation in Line: 444-445). Note that a total of 67 lineages are present in Tenerife, but we only studied 63 lineages, as we work only with the 348 Tenerife native species for which we have sufficient empirical trait data.

- The statement “most Tenerife endemics emerged via cladogenesis”. I would avoid statements like this, because, without fully sampled phylogenies, we do not know this. In

addition, it would be worth clarifying in this statement if by cladogenesis the authors mean within Tenerife, within the Canaries or within Macaronesia, because that matters in this context.

Response: As we previously described, the radiated lineages included now in our analysis have radiated within the Tenerife, Canary Islands, or Macaronesia (see improvement in line 442-444). Thus, we are confident - in this is also in line with the current floristic interpretation of these lineages - stating that most of the Tenerife endemics emerged via cladogenesis.

- The main figures are clear and appropriate. However, it would be nice to edit them a bit to make them more memorable. Maybe with some photos of plant species from Tenerife, or a topographical map of the island.

Response: Thanks for this suggestion. We added to Figure 2 botanical illustrations by artist Paulina Mocna of some iconic plants that illustrate some of the variation in plant functional traits and growth forms.

- As a general comment, throughout the manuscript I get the impression that the main point of view supported is that a lot of the traits and adaptations for the endemics evolved in situ on the islands (e.g. “adapted to the arid environments”). Without comparison with mainland ancestors and ancestral state reconstructions this can only be speculated, so I would recommend adding this note of caution.

Response: Thank you for this observation. We added a note in the conclusions to inform the reader about this limitation (see lines 236-238).

- Also in general, the main text is a bit plant- and Tenerife-centric, it would be nice to discuss the results in a more global context, perhaps with examples from other islands or even other taxa? There are a few papers on insular trait space in birds and snails, for example.

Response: Thanks for this observation. We found two examples that relate somewhat to our findings (Kraemer et al. 2022; Tejero-Cicuéndez et al. 2021). However, we have not included this in the text, as incorporating additional information and putting it in a context without extending too much the main text is challenging. We prefer to not stretch our conclusions to other taxa or islands, as we only have plant trait data for Tenerife at present.

- L130 - the time of aridification needs a reference.

Response: We included the reference for this statement (see line 135).

- L145 - I suggest adding “a general island syndrome for the island Tenerife”, as this is not the case for all islands.

Response: We modified the sentence following your suggestion (see line 152).

- L194 – promote (unclear whether this applies to species or habitat diversity).

Response: We modified the sentence to make the statement clearer (see lines 207-208).

- Trait measurements – for some cases multiple replicates per species were measured, so it would be useful to include the total number of samples measured (only the total number of species is given). I could not find the raw data for the measurements when there are multiple replicates per species. Perhaps this should be provided? It would be interesting to get an idea of how much variation there is within species. Finally, maybe this is mentioned but I missed how the final trait value for each species was computed (mean value across replicates?).

Response: Yes, we use species' means (calculated across replicates) for our analyses. We added a statement to clarify the resolution of the trait values we are using (see lines 466-467), but we have not added intra-specific data as our data was not collected to quantify this. Note that we are making all trait measurements at the individual level available via Figshare.

- L459 – L474 – The analyses of trait imputation are not very well explained and I did not fully understand them. The file “Trait_imputed_phylo8.csv” includes traits for all the species, but it is not clear how to identify which species had their traits imputed or which traits were imputed for a given species. Also, more details are needed regarding the analyses – we are told “we constructed the phylogeny using the mega-phylogeny” but it is not clear what “the” phylogeny is. Finally, is this imputation really necessary? It would be useful to know what the results would look like with only the species that were measured vs the dataset with the imputed species. In any case, I got confused as to whether the dataset shown in the main figures (e.g., Fig. 1 and 2) includes also points that are predictions, or just real measurements.

Response: Motivated by your observation, we now show the missing data in the species by trait matrix of the Tenerife flora (see Extended Data Figure 1). In the data shared via Figshare (see Data availability section), we provide the empirical data at species level (Barajasetal_traits_status.csv), with measured and missing values for Tenerife's flora (436 species). We also improved the description in the methods on how we built the phylogenetic tree (see Lines 506-510). As we previously explained (comment to Referee 1 and 2), we are now studying 80% of Tenerife flora (348 species out of the total 436), after performing extensive sensitivity analyses of the effects of using imputed data. That is, we performed the analysis with species that have complete trait data for the 8 traits, i.e., 'complete cases' composed by 237 species, and the set of Tenerife species with a minimum of 5 empirically-measured traits, i.e., 'near-complete cases', composed by the 348 species. The near-complete cases' miss less than 5% of trait values (Extended Data Figure 1a). Thus, we opted to present the results for 'near-complete cases' because they are consistent with the results of 'complete cases'; and this also allows us to study 80% of Tenerife flora and include as much as possible the empirical data that we collected on the island.

- L494 – what are the traditional approaches?

Response: We now cite *Villéger et al. 2008*. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, 89(8), 2290-2301.” (see line 547).

G. References: appropriate credit to previous work?

Yes.

H. Clarity and context: lucidity of abstract/summary, appropriateness of abstract, introduction and conclusions

The study is very well-written, clear, and easy to follow.

Luis Valente

New analysis summary

Main text

Figure 2a. Null model results for functional diversity indices that test for convergence or divergence (see detailed in Methods), i.e. functional richness, functional dispersion and functional evenness, across the five species groups.

Figure 2b. Comparison of functional contribution and originality across the five species groups.

Figure 2c. Functional contribution and originality of each species group in comparison to all other island species. We set this figure in the Extended Data in our first submission. Now, we present it in the main text.

Extended data

Extended data Fig. 1. Visualisation of missing and present data for Tenerife native seed plant flora.

Extended data Fig. 2c Displaying global trait space contours.

Extended data Fig. 2d. Null models assessing island and global trait spaces overlap.

Extended data Fig. 4. We added the phylogenetic analysis, i.e., hot nodes.

Extended data Fig. 6a. Tenerife map and biome representativity on the island.

Extended data Fig. 7. Sensitivity analyses using only cases (n= 237 species) with complete empirical data for all 8 traits.

Extended data Table 2. Phylogenetic signal of empirical trait values and phylogenetic signal of missing trait values

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Reviewer Reports on the First Revision:

Referees' comments:

Referee #1 (Remarks to the Author):

A. Summary of the key results

I have found the heavily revised version of the manuscript by Barajas-Barbosa et al. entitled "Assembly of functional diversity in an oceanic island flora" [MS number: 2022-02-02651A] greatly improved from the initial submission to Nature. I congratulate the authors for the massive amount of work they did to carefully revise their manuscript throughout, in terms of storytelling as well as new analyses. The authors, in my view, addressed successfully if not all, the vast majority of the comments and concerns arose by the three reviewers (see my suggestions and comments; point F). The general ecological, biogeographic, and evolutionary contextualization and inferences of key findings are now more balanced – this is also reflected in/produced by a more cautious use of the language all across the text. It constitutes a solid and inspiring study which showcases what type of eco-evolutionary insights can be gained by designing and implementing well pondered functional island biogeographic approaches.

B. Originality and significance: if not novel, please include reference

This is an original work in that implements concepts and approaches provided by the emerging field of functional island biogeography. The authors produced a remarkable dataset in terms of traits collected (in the field or extracted from literature and databases) for a high number of plant species native to the island of Tenerife, placing their research into a broader and global context. Thanks to their thorough functional and phylogenetic analyses, the authors were able to provide insights into which putative eco-evolutionary processes may be generating the interesting trait patterns they revealed for different biogeographic elements/floristic groups forming the island native flora. The significance of this work is therefore high, and could be extended to other islands and archipelagos (as well as other types of insular systems, such as terrestrial habitat islands) occurring in other regions and biomes.

C. Data & methodology: validity of approach, quality of data, quality of presentation

The new set of functional and phylogenetic analyses are suitable to tackle the research objectives. In my opinion, the approach is valid and sound, and the quality of the data and presentation of the key findings high and comprehensive.

D. Appropriate use of statistics and treatment of uncertainties

As per the previous point, I have found the statistical analyses dealing with the functional and phylogenetic facets of the story well designed. I have no issues with how the authors treated uncertainties, especially because the new analyses address this point thoroughly (e.g. sensitivity analysis, null models, hot note analysis of clades informing on phylogenetic structuring, phylogenetic signal on trait values). The more cautious and balanced language use also assisted in this task – as suggested by reviewers in the previous round, and tackled by the authors in this version (I have some suggestions how to possibly fine-tuning further, see point F).

E. Conclusions: robustness, validity, reliability

In light of what exposed in the preceding four points, I now see this work as a robust, valid and reliable piece of work.

F. Suggested improvements: experiments, data for possible revision

The only conceptual issue that still lingers concerns the functional spectra. I appreciate the reply of the authors on this regard, yet I remain unconvinced from a functional ecology viewpoint. I fully concur that comparing functional spaces and axes based on different number of traits is not fair from a stats perspective, but my point was a different one. The evidence that, in the PCA ran using 8 traits in Fig. 2a and Extended Data Fig. 3, LDMC does not align and does not form the second

axis related to the leaf economics spectrum as widely assumed/expected but it accounts for a great proportion of the first axis (which should be associated with plant size solely [plant height, leaf area, seed mass]) is still puzzling/challenging to reconcile, yet very interesting. This is the most striking example, but other instances concern e.g. LMA (1/SLA) being unrelated to LDMC (while generally SLA and LDMC trade-off, hence LDMC and LMA should be tightly/positively correlated).

Below, I indicate where the authors could consider further refining, and a few suggested edits – ordered by line numbering:

L1: in the title, what about adding “native” before “flora”?

L24: keywords – I do not think the authors can talk here about “community assembly” (they have not tackled this task, working at the level of different species groups/assemblages). I would suggest replacing this keyword with “native flora assembly”

L32: “native flora”

L53: in relation to the functional and evolutionary distinctiveness of islands, please see also: Veron, S., Kondratyeva, A., Robuchon, M. et al. High evolutionary and functional distinctiveness of endemic monocots in world islands. *Biodivers Conserv* 30, 3697–3715 (2021).

<https://doi.org/10.1007/s10531-021-02272-x>

L58: “irrespective of their traits” – this bit can be deleted

L60: “disentangle the putative processes”

L65: “communities” – I would say “assemblages” as more general and in fact the authors here worked at the scale of insular native plant species assemblage and different floristic groups – I would avoid referring to “community” in this paper as this level is not addressed

L67: in this instance, being a general statement, I would say also “seed mass, size, and volume”

L70: “in a community” – being a general notion, I would refer to “unit of study”

L79-80: “dispersal, establishment and persistence” – as formulated here, it suggests that these three main plant functions and challenges are all boosted on islands simultaneously. However, one open question in functional island biogeography is to examine an expected dispersal-local persistence trade-off over time, wherein plants on younger islands should be good dispersers whereas plants on older islands should be functionally good in persisting locally (as suggested by recent evidence of consistently larger seeds on New Zealand islands; Biddick et al. 2019 PNAS + Biddick & Burns 2021 *Ecol Lett*)

L80-84: I cannot grasp the logic link between these two sentences – expected functional divergence and convergence are mixed up. Please, rephrase for enhanced clarity

L86: replace “that fill” with “filling”? Also, I would delete “Iconic” as in the same sentence the magnitude of morphological changes is stressed + the same adjective is used 5 lines below

L93: “can affect”

L94: instead of “scrub” better saying “shrub”

L101: “may have”

L106: replace “mainly” with “primarily”?

L114: the header could be entitled “An oceanic island flora fits within global functional spectra”

L115: “native flora”

L134: “tends to favour”

L139: together with greater local persistence abilities, I would add “and more resource-conservative strategies”

L146: after “species”, I would add “, and with the evolution of insular woodiness (Zizka et al. 2022).” – this recent paper published in PNAS

L155: “persistence ability”

L168: “contrasting trait combinations” – contrasting to what? if related to the previous sentence, it is not necessarily contrasting. Leaf thickness may be linked to both sclerophylly (consistent) or succulence (contrasting). Please, specify or omit referring to idiosyncrasies

L181: “island native flora”

L208: “can promote”

L211: “hot node analysis” – I think that referring to the citation would suffice, i.e. without “sensu”

L218: “the constituent species” – not sure I fully get what the authors mean here

L226: consider rephrasing as "We interpret this result as a signal of"

L231-232: not sure I got your point here, and perhaps this entire sentence could be deleted?

L240-241: consider rephrasing as "To gain insights as to how speciation due to radiations may have shaped"

L242: "present on Tenerife. These are comprised" – this sentence is rather long. I suggest splitting here

L243: "the" before "Tenerife" can be deleted

L250-251: I think that the *Aeonium* and *Polycarpaea* clades should be in italics

L254-255: "Yet, it could also indicate that newly evolved species appear to be similar to those of co-occurring species" – hence, potentially functionally redundant for the traits examined in this study?

L260: "may have"

L261: "tends to lead"

L267: "better understanding"

L268: "island flora"

L382: consider rephrasing as "Trait space of the native flora of Tenerife fits within the global trait space"

L384: after "values" what about adding in brackets "(shrubby functional hotspot)"?

L385: "plant trait space known as the global" – this can be deleted

L405: "Contribution of putative biogeographical"

L406: "functional diversity of the native flora of Tenerife"

L445-448: something makes this sentence difficult to follow/incomplete to me; could you please rephrase for enhanced clarity?

L465: 350 or 436 species?

L470: "sun-exposed leaves"

L478: "Leaf thickness" – I guess measured with a (digital) caliper? please, mention it here or in the next sentence

L551 & L588: I think should be "ran" instead of "run"

L592: one of the two "calculated" should be deleted

Finally, I have spotted a few instances where American English has been used instead of British English (which I think the authors opted for), so please check throughout for consistency.

G. References: appropriate credit to previous work?
Also this task has been improved in the current version.

H. Clarity and context: lucidity of abstract/summary, appropriateness of abstract, introduction and conclusions

As for previous points, I see no issues. I congratulate the authors for the great effort they put into this revision, which produced a much-improved, clearer, and more balanced message all across.

Referee #2 (Remarks to the Author):

Dear Authors,

I carefully read your response to my previous concerns.

I am convinced by your revision as you address all the technical or methodological points previously raised. Reading the other's reviewers concerns and the new supplementary analysis provided have improved our manuscript and make our conclusion more robust.

I am sorry but I still have some reserves on the novelty and significance of the results in the context of a publication in *Nature*. To me, the main messages that "biogeography and evolution have jointly shaped island plant trait space" or that "biogeography and evolution leave imprints on island functional diversity" remains rather general and without large insight for Ecology science.

However, reading comments from reviewer #3 (Luis Valente), which is more into island biogeography than I do, it seems that it might be of broad interest for Nature readers. So, I am not against the publication of the study in Nature and I will let the editor make his choice on whether the paper is suited for publication, or not.

I hope you will understand my lack of support, although you provided a great study that will surely find its readership !

Thanks for the opportunity to review your ms.
Best regards,

Referee #3 (Remarks to the Author):

The authors have addressed all of my concerns. I appreciate the addition of the information on missing data (now visualised in Extended Fig 1), the clarifications regarding the species classifications and the revised methodology regarding trait imputation. I think this an interesting study that provides a quantitative and visual approach to understanding the assembly of an insular flora.

I have some minor suggestions:

L91 – avoid repeating iconic again.

L96-97 – something is not right with the grammar here.

L111 – all cladogenetic species are endemic to the region I think, so probably worth saying that.

L199 – add reference to the figure with the illustrations.

L242 – "originality of 63 immigrant lineages present on Tenerife, which are comprised of 191 species that have radiated on the Tenerife". It took me a while to figure out these are same species as those in the cladogenetic group. Or is that not the case?

L243 – delete "the"

L410 – delete "richness"

Extended Figure 4 – this figure is not very useful as it is not possible to see much. Also, in the legend, delete "than" after "expected".

Extended Figure 5 legend - add "radiated" to "d. Number of radiated lineages present in Tenerife..."

Extended Figure 7 – this figure is very busy. I would simplify if possible.

Luis Valente

Author Rebuttals to First Revision:

Responses to referees' comments

Referee #1 (Remarks to the Author):

A. Summary of the key results

I have found the heavily revised version of the manuscript by Barajas-Barbosa et al. entitled “Assembly of functional diversity in an oceanic island flora” [MS number: 2022-02-02651A] greatly improved from the initial submission to Nature. I congratulate the authors for the massive amount of work they did to carefully revise their manuscript throughout, in terms of storytelling as well as new analyses. The authors, in my view, addressed successfully if not all, the vast majority of the comments and concerns arose by the three reviewers (see my suggestions and comments; point F). The general ecological, biogeographic, and evolutionary contextualization and inferences of key findings are now more balanced – this is also reflected in/produced by a more cautious use of the language all across the text. It constitutes a solid and inspiring study which showcases what type of eco-evolutionary insights can be gained by designing and implementing well pondered functional island biogeographic approaches.

B. Originality and significance: if not novel, please include reference

This is an original work in that implements concepts and approaches provided by the emerging field of functional island biogeography. The authors produced a remarkable dataset in terms of traits collected (in the field or extracted from literature and databases) for a high number of plant species native to the island of Tenerife, placing their research into a broader and global context. Thanks to their thorough functional and phylogenetic analyses, the authors were able to provide insights into which putative eco-evolutionary processes may be generating the interesting trait patterns they revealed for different biogeographic elements/floristic groups forming the island native flora. The significance of this work is therefore high, and could be extended to other islands and archipelagos (as well as other types of insular systems, such as terrestrial habitat islands) occurring in other regions and biomes.

C. Data & methodology: validity of approach, quality of data, quality of presentation

The new set of functional and phylogenetic analyses are suitable to tackle the research objectives. In my opinion, the approach is valid and sound, and the quality of the data and presentation of the key findings high and comprehensive.

D. Appropriate use of statistics and treatment of uncertainties

As per the previous point, I have found the statistical analyses dealing with the functional and phylogenetic facets of the story well designed. I have no issues with how the authors treated uncertainties, especially because the new analyses address this point thoroughly (e.g. sensitivity analysis, null models, hot note analysis of clades informing on phylogenetic structuring, phylogenetic signal on trait values). The more cautious and balanced language use also assisted in this task – as suggested by reviewers in the previous round, and tackled by the authors in this version (I have some suggestions how to possibly fine-tuning further, see point F).

E. Conclusions: robustness, validity, reliability

In light of what exposed in the preceding four points, I now see this work as a robust, valid and reliable piece of work.

We thank the reviewer for their valuable feedback and the time invested in reviewing our manuscript. We are delighted that our revision was positively assessed and are grateful for those further comments.

F. Suggested improvements: experiments, data for possible revision

The only conceptual issue that still lingers concerns the functional spectra. I appreciate the reply of the authors on this regard, yet I remain unconvinced from a functional ecology viewpoint. I fully concur that comparing functional spaces and axes based on different number of traits is not fair from a stats perspective, but my point was a different one. The evidence that, in the PCA ran using 8 traits in Fig. 2a and Extended Data Fig. 3, LDMC does not align and does not form the second axis related to the leaf economics spectrum as widely assumed/expected but it accounts for a great proportion of the first axis (which should be associated with plant size solely [plant height, leaf area, seed mass]) is still puzzling/challenging to reconcile, yet very interesting. This is the most striking example, but other instances concern e.g. LMA (1/SLA) being unrelated to LDMC (while generally SLA and LDMC trade-off, hence LDMC and LMA should be tightly/positively correlated).

We thank the reviewer for this observation. We point out in several places in the main text that the native flora of Tenerife includes a large number of succulent species (lines 141-142, 168, 247-250, 264-266). Their high leaf water content and consequently low LDMC alters the commonly expected relationship between LDMC and SLA, as has been previously reported by e.g., Vendramini et al. (2002). In this study, they found that when succulent species (in central-western Argentina) were included there was no correlation between SLA and LDMC, yet the correlation between these two traits became statistically significant (and negative) as expected when excluding succulent species. Importantly, they also found a significant negative relationship between SLA and LDMC when analysing species from other regions. This explains the differences in the PCA axes presented in Figures 1 and 2a, and we clearly state the differences in the number of traits used in the PCAs in the text and figure captions for both (lines 160, 389, 403). Moreover, we discuss in the main text the importance of succulence in shaping the trait space of Tenerife (lines 141-143), which is due to the contributions of leaf-succulent lineages such as *Aeonium* (lines 247-248). While we appreciate this comment, we have decided not to change the main text significantly.

Reference: Vendramini, F., Díaz, S., Gurvich, D.E., Wilson, P.J., Thompson, K. and Hodgson, J.G. (2002), Leaf traits as indicators of resource-use strategy in floras with succulent species. *New Phytologist*, 154: 147-157. <https://doi.org/10.1046/j.1469-8137.2002.00357.x>

Below, I indicate where the authors could consider further refining, and a few suggested edits – ordered by line numbering:

L1: in the title, what about adding “native” before “flora”?

Thank you for this suggestion. We feel that “oceanic island flora” is already a long phrase. Therefore, we opted not to change the title but added the word native in the abstract (line 33), as a keyword (lines 23-24) and in the rest of the manuscript (e.g., line 117).

L24: keywords – I do not think the authors can talk here about “community assembly” (they have not tackled this task, working at the level of different species groups/assemblages). I would suggest replacing this keyword with "native flora assembly"

Thank you for this suggestion. We agree that the community is not the ecological scale analysed here; thus, we changed the keyword (line 23-24). We additionally checked the entire main text and are not using the term community.

L32: “native flora”

We think that “oceanic island native flora” would be problematic, but changed the text to “native flora of an oceanic island” (line 33).

L53: in relation to the functional and evolutionary distinctiveness of islands, please see also: Veron, S., Kondratyeva, A., Robuchon, M. et al. High evolutionary and functional distinctiveness of endemic monocots in world islands. *Biodivers Conserv* 30, 3697–3715 (2021).

<https://doi.org/10.1007/s10531-021-02272-x>

Thanks for pointing us to this paper that we now cite (line 55, citation number 14).

L58: “irrespective of their traits” – this bit can be deleted

We removed it as suggested (line 60).

L60: “disentangle the putative processes”

We tend to disagree and prefer to keep the original shorter and clearer wording (line 62).

L65: “communities” – I would say "assemblages" as more general and in fact the authors here worked at the scale of insular native plant species assemblage and different floristic groups – I would avoid referring to "community" in this paper as this level is not addressed

Thank you for this suggestion. We agree that assemblage better describes the level of our study. We changed this accordingly (line 67) and no longer use the term community in our manuscript.

L67: in this instance, being a general statement, I would say also "seed mass, size, and volume"

We added the suggested words (Line 69).

L70: “in a community” – being a general notion, I would refer to "unit of study"

We feel that “unit of study” is a very unspecific term. For consistency, we replaced the word with - assemblage- because concepts from community ecology can be applied to assemblages as well (line 72).

L79-80: “dispersal, establishment and persistence” – as formulated here, it suggests that these three main plant functions and challenges are all boosted on islands simultaneously. However, one open question in functional island biogeography is to examine an expected dispersal-local persistence trade-off over time, wherein plants on younger islands should be good dispersers whereas plants on older islands should be functionally good in persisting locally (as suggested by recent evidence of consistently larger seeds on New Zealand islands; Biddick et al. 2019 PNAS + Biddick & Burns 2021 *Ecol Lett*)

Thank you for this observation. We restructured this paragraph for clarity but due to space limitation refrain from expanding on these topics (lines 82-83).

L80-84: I cannot grasp the logic link between these two sentences – expected functional divergence and convergence are mixed up. Please, rephrase for enhanced clarity

We restructured and rephrased this entire paragraph to improve the clarity and the flow of our argumentation (see changes in lines 87-88).

L86: replace “that fill” with “filling”? Also, I would delete “Iconic” as in the same sentence the magnitude of morphological changes is stressed + the same adjective is used 5 lines below

We implemented the suggested change. We opted for using the expression “that fill” (line 86)

L93: “can affect”

Done (line 95).

L94: instead of “scrub” better saying “shrub”

The term “coastal succulent scrub” is commonly used for this vegetation type. We thus opted to keep it (line 96).

L101: “may have”

Done (line 104).

L106: replace “mainly” with “primarily”?

Done (line 108).

L114: the header could be entitled “An oceanic island flora fits within global functional spectra”

Thanks for this excellent suggestion. We changed this accordingly (line 116)

L115: “native flora”

Done (line 117).

L134: “tends to favour”

Done (line 135).

L139: together with greater local persistence abilities, I would add “and more resource-conservative strategies”

Many thanks. We added this (line 140).

L146: after “species”, I would add “, and with the evolution of insular woodiness (Zizka et al. 2022).” – this recent paper published in PNAS

Thank you for this suggestion. We feel that this addition would distort the flow of the sentence and think that the idea of insular evolution is implicit. We added the citation for Zizka et al. (2022, PNAS) in the line 148 (reference number 3).

L155: “persistence ability”

Changed (line 157)

L168: “contrasting trait combinations” – contrasting to what? if related to the previous sentence, it is not necessarily contrasting. Leaf thickness may be linked to both sclerophylly (consistent) or

succulence (contrasting). Please, specify or omit referring to idiosyncrasies

Thank you for this observation. Our original intent was to contrast these trait combinations with those associated with an acquisitive strategy. We realised that this was not clear and therefore deleted “contrasting”. Yet, please note that we updated the text (see lines 169-170), as Canary endemics species run along the LMA and leaf nitrogen content continuum; thus, these species include both conservative and acquisitive ecological strategies.

L181: "island native flora"

It is unclear to us what this suggestion refers to specifically. We infer that the referee suggests that we should change the title of the header to “island native flora”. However, we believe that such a change would decrease the readability of the header. Therefore, we opted not to implement the change (line 182).

L208: "can promote"

Done (line 209).

L211: “hot node analysis” – I think that referring to the citation would suffice, i.e. without “sensu”

Done (line 213)

L218: “the constituent species” – not sure I fully get what the authors mean here

We previously meant species that belong to the two groups Macaronesian endemics and Canary endemics. We are not using the former expression “the constituent species”. We now updated the paragraph (lines 218-219) to make it consistent with the final results after correcting for LDMC values, i.e., only Macaronesian endemics have a high evenness. There is no ambiguity about which group of species we are referring to as only Macaronesian endemics are mentioned (line 220).

L226: consider rephrasing as “We interpret this result as a signal of”

We cannot see how this rewording changes the meaning, so we opted for the shorter sentence (line 227).

L231-232: not sure I got your point here, and perhaps this entire sentence could be deleted?

We agree that this sentence was convoluted and have now rephrased for clarity it to: “This leads to newly evolved species that are functionally similar to the ancestral species” (line 232).

L240-241: consider rephrasing as “To gain insights as to how speciation due to radiations may have shaped”

Done (lines 241-242).

L242: “present on Tenerife. These are comprised” – this sentence is rather long. I suggest splitting here

Thanks for the suggestion. We now have split the long sentence into two separate sentences to improve clarity (line 244)

L243: “the” before “Tenerife” can be deleted

Done (line 245)

L250-251: I think that the *Aeonium* and *Polycarpaea* clades should be in italics

Yes, done (line 246-247).

L254-255: “Yet, it could also indicate that newly evolved species appear to be similar to those of co-occurring species” – hence, potentially functionally redundant for the traits examined in this study?
[Yes, that is a valid interpretation \(line 255-256\).](#)

L260: "may have"
[Done \(line 261\).](#)

L261: "tends to lead"
[Done \(line 262-263\).](#)

L267: "better understanding"
[Done \(line 268\).](#)

L268: "island flora"
[Done \(line 269\).](#)

L382: consider rephrasing as “Trait space of the native flora of Tenerife fits within the global trait space”
[Thank you for the suggestion. Done \(line 384\).](#)

L384: after “values” what about adding in brackets "(shrubby functional hotspot)"?
[Thank you for this suggestion. Added \(line 386\).](#)

L385: “plant trait space known as the global” – this can be deleted
[Done.](#)

L405: “Contribution of putative biogeographical”
[As described and discussed in detail in the main text, these groups stand for different biogeographical and evolutionary processes. We, therefore, opted to not follow this suggestion \(line 409\).](#)

L406: “functional diversity of the native flora of Tenerife”
[Thanks, this is a useful addition. Changed in line 410.](#)

L445-448: something makes this sentence difficult to follow/incomplete to me; could you please rephrase for enhanced clarity?
[Thank you for this suggestion. We have carefully read this sentence and think that its meaning is sufficiently clear. To ensure its clarity, we deleted “relative to mainland taxa” \(line 452\).](#)

L465: 350 or 436 species?

[To avoid confusion with the set of species we sampled, which we explain in line 454-455. We mention now the percentage of species sampled and their corresponding replicates \(line 469\).](#)

L470: “sun-exposed leaves”
[Changed \(line 474\).](#)

L478: “Leaf thickness” – I guess measured with a (digital) caliper? please, mention it here or in the next sentence
[We added a sentence mentioning this \(line 484\)](#)

L551 & L588: I think should be “ran” instead of “run”

Thanks for this observation, we changed it to the right tense (lines 556 and 593).

L592: one of the two “calculated” should be deleted

Done.

Finally, I have spotted a few instances where American English has been used instead of British English (which I think the authors opted for), so please check throughout for consistency.

We carefully checked English grammar and style and the consistent use of British English.

G. References: appropriate credit to previous work?

Also this task has been improved in the current version.

H. Clarity and context: lucidity of abstract/summary, appropriateness of abstract, introduction and conclusions

As for previous points, I see no issues. I congratulate the authors for the great effort they put into this revision, which produced a much-improved, clearer, and more balanced message all across.

We thank the reviewer for this positive message about our improvements.

Referee #2 (Remarks to the Author):

Dear Authors,

I carefully read your response to my previous concerns.

I am convinced by your revision as you address all the technical or methodological points previously raised. Reading the other's reviewers concerns and the new supplementary analysis provided have improved our manuscript and make our conclusion more robust.

I am sorry but I still have some reserves on the novelty and significance of the results in the context of a publication in Nature. To me, the main messages that "biogeography and evolution have jointly shaped island plant trait space" or that "biogeography and evolution leave imprints on island functional diversity" remains rather general and without large insight for Ecology science.

However, reading comments from reviewer #3 (Luis Valente), which is more into island biogeography than I do, it seems that it might be of broad interest for Nature readers. So, I am not against the publication of the study in Nature and I will let the editor make his choice on whether the paper is suited for publication, or not.

I hope you will understand my lack of support, although you provided a great study that will surely find its readership !

Thanks for the opportunity to review your ms.

Best regards,

We thank the reviewer for the time and thoughts put into evaluating our work.

Referee #3 (Remarks to the Author):

The authors have addressed all of my concerns. I appreciate the addition of the information on missing data (now visualised in Extended Fig 1), the clarifications regarding the species classifications and the revised methodology regarding trait imputation. I think this an interesting study that provides a quantitative and visual approach to understanding the assembly of an insular flora.

Many thanks for taking the time to review our manuscript and providing very helpful comments.

I have some minor suggestions:

L91 – avoid repeating iconic again.

We deleted the word ‘iconic’ used in the previous paragraph, right before “Adaptive island radiations,...” (see line 89). Now the word appears in the main text once (line 93).

L96-97 – something is not right with the grammar here.

We split this sentence into two and rephrased it for clarity (lines 97-100)

L111 – all cladogenetic species are endemic to the region I think, so probably worth saying that.

Good point. We added this (line 113)

L199 – add reference to the figure with the illustrations.

Done (line 200).

L242 – "originality of 63 immigrant lineages present on Tenerife, which are comprised of 191 species that have radiated on the Tenerife". It took me a while to figure out these are same species as those in the cladogenetic group. Or is that not the case?

We rephrased this sentence also in response to reviewer #1 to improve clarity. Please note that we also updated the text after fine-tuning our results (i.e., only *Aeonium* alliance and *Polycarphaea* actually expand the island trait space) once LDMC values were corrected (see lines 247 and 251).

L243 – delete “the”

Done

L410 – delete “richness”

Done (line 414).

Extended Figure 4 – this figure is not very useful as it is not possible to see much. Also, in the legend, delete “than” after “expected”.

Thank you for this suggestion. We updated Extended Figure 5 (previously Extended Figure 4) and also improved its quality. We deleted the word “than”.

Extended Figure 5 legend - add "radiated" to "d. Number of radiated lineages present in Tenerife..."

We added the suggested word. Note it is now Extended Figure 6.

Extended Figure 7 – this figure is very busy. I would simplify if possible.

Thanks for this suggestion. We are now showing only the most relevant results related to the sensitivity analysis in Extended Figure 7. Note that we also updated this figure after correcting LDMC values.

Luis Valente