

Why studying the response of trait coordination to insularity matters?

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Abstract

Functional island biogeography can provide eco–evolutionary insights into which main drivers contribute to shaping the distribution of organisms' forms and functions on islands. It does so by examining trait patterns. As a result, traits are increasingly studied on islands, either along insularity gradients or by comparing patterns of island versus mainland biota. So far, functional island biogeography has investigated trends of trait values (i.e., average, functional diversity), whereas coordination between pairs of traits remains unexplored along insularity gradients. Yet, trait coordination analyses constitute the foundational tool to detect main functional spectra and strategies of organisms. In this perspective, we set out to offer a conceptual and analytical framework that should facilitate the inclusion of trait coordination (i.e., the co–variation of traits both at the intra- and interspecific level) in functional island biogeography. We illustrate, with a case study focused on persistence traits of edaphic island plant specialists, what type of insights can be gained by examining the response of trait coordination to variation in insularity. We asked two questions, namely whether, with increasing insularity, the strength of the relationship (R^2) increases (Q1), and the direction of the relationship (slope) decreases (Q2). We positively answered our research questions, with lines of evidence suggesting a selective “forcing” towards tighter and more strongly coordinated strategies (Q1), and functional trade-offs (Q2). We infer which ecological and biogeographic drivers could be behind the observed patterns, while acknowledging possible drawbacks. We conclude by identifying three main take-home messages and related future directions for integrating trait coordination in functional island biogeography to further advance the field.

KEYWORDS

functional island biogeography, insular systems, interspecific differences, intraspecific variability, plant persistence strategies, trait co–variation

1 | THE EMERGENCE AND USEFULNESS OF FUNCTIONAL ISLAND BIOGEOGRAPHY

Functional biogeography provides a conceptual and methodological framework to gain insights into which drivers contribute to shaping

the distribution of organisms' forms and functions across different spatial scales and organizational levels (Violle et al., 2014; Whittaker et al., 2014). The fundamental investigative tools of functional biogeography are functional traits, which inform on organismal performance and fitness in terms of growth, survival and reproduction

Gabriele Midolo and Gianluigi Ottaviani contributed equally to this work and share first authorship.

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success (Violle et al., 2007). Trait-based approaches can, in turn, capture how organisms face different ecological challenges (Weiher et al., 1999). For plants, these challenges include (i) acquire, use and conserve above- and below-ground resources, (ii) reproduce sexually versus vegetatively, (iii) ability to disperse propagules, (iv) tolerate, avoid or resist major biotic and abiotic disturbances and stressors (Klimešová et al., 2018; Ottaviani et al., 2020).

More recently, functional ecologists and biogeographers are increasingly implementing trait-based approaches to identify which drivers can affect the distribution and eco-evolutionary dynamics of island biota forms and functions, giving rise to the field of functional island biogeography (Ottaviani et al., 2020; Schrader et al., 2023; Schrader, Wright, et al., 2021). This growing research interest is linked to the potential of trait-based studies to address the majority of the most pressing questions in island biogeography (Ottaviani et al., 2020; Patiño et al., 2017; Santos et al., 2016). Insular systems—conceptually including both true (e.g., oceanic) islands and terrestrial habitat islands (see Itescu, 2019; Méndez-Castro et al., 2021)—represent indeed excellent models to address fundamental questions in ecology, biogeography, and evolution (Warren et al., 2015; Whittaker et al., 2008, 2017). Being spatially and temporally confined, the insular setting facilitates better accounting for the effects of different abiotic and biotic factors on island biota compared to their mainland counterparts (Warren et al., 2015; Whittaker et al., 2017; Wilson & MacArthur, 1967). For example, a multifunctional trait-based approach may help explain what contributes to form the long-observed island syndrome (Burns, 2019; Carlquist, 1974) by identifying major functional components of the syndrome in terms of trait values, diversity, and their coordination forming functional axes (Ottaviani et al., 2020).

However, the basic determinants of these functional axes (such as trait coordination) remain largely overlooked in functional island biogeography (Figure 1; but see Burns, 2016).

For plants, most of the flourishing interest in functional island biogeography is using two main approaches. The first compares trait patterns of island versus mainland biota. For example, such comparative approach provided key eco-evolutionary insights into what (i) could be behind the island disharmony (i.e., the over- or under-representation of certain lineages, growth forms or life histories on islands compared to mainland; Grossenbacher et al., 2017; König et al., 2021; Taylor et al., 2019, or (ii) may (or may not) explain the island rule (i.e., the tendency towards intermediate sizes on islands), suggesting that this pattern may be driven by an evolutionary drift for leaf and plant size (Biddick et al., 2019; Biddick & Burns, 2021; Burns, 2022). The second approach analyzes trait patterns (trait average or diversity) along insularity gradients (Conti et al., 2022; Ottaviani et al., 2022; Schrader, Westoby, et al., 2021; Walentowitz et al., 2022; Figure 1a,b). For example, insights into which functional strategies plants tend to deploy to successfully persist locally (hence possibly counteracting local extinction risk; Auffret et al., 2017) have been obtained for specialist species of different types of terrestrial habitat islands. These species are consistently distinguished by better persistence abilities (e.g., better protected bud banks, more resource-conservative strategies) and having more similar trait values (i.e., lower functional diversity) with increasing insularity (Conti et al., 2022; Ottaviani et al., 2022). These examples highlight the potential of functional island biogeography to better understand drivers of island species' distribution, persistence, diversity, and evolution.

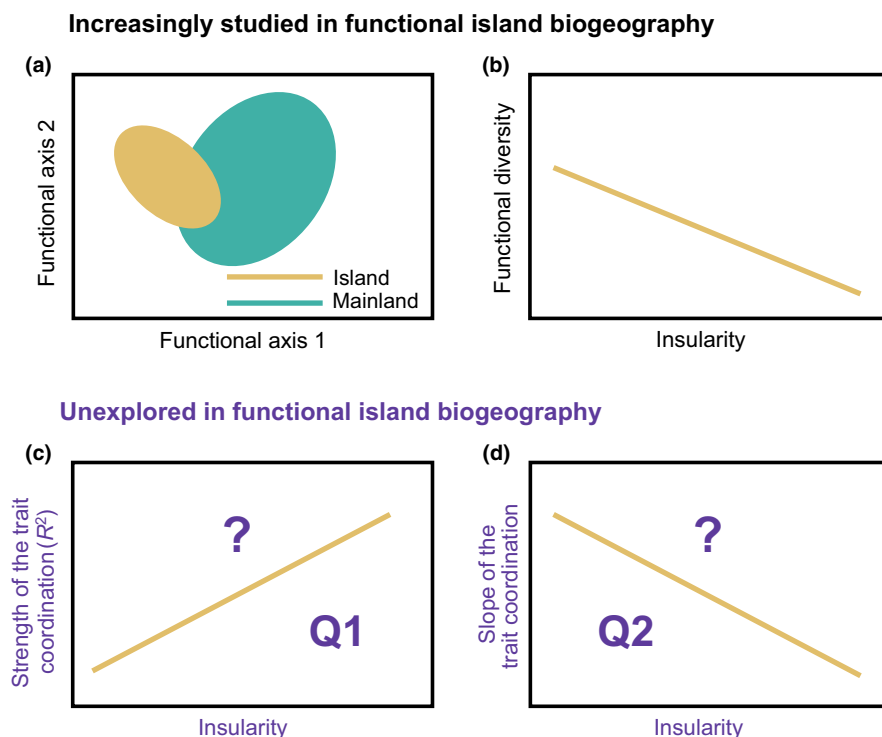


FIGURE 1 Conceptual scheme showing, in the upper panels (a, b), the main research interests and approaches in functional island biogeography so far. These use comparative studies examining trait patterns between island biota and their mainland counterparts (a), and how functional diversity varies with insularity, with indications showing a decline, paralleling what is typically observed for taxonomic diversity (b). In the lower panels (c, d), the knowledge gaps associated with the variation of trait coordination with insularity, in terms of changes in the strength (c) and slope (d) of the relationship, are displayed—with the expected patterns presented as questions addressed in this study (Q1 and Q2, respectively).

2 | WHAT CAN THE ANALYSIS OF TRAIT COORDINATION ON ISLANDS TELL US?

Trait coordination describes how pairs of traits co-vary, and symmetric bivariate linear regressions are used as the primary analytical tool. These relationships can be estimated through different model parameters linked to the proportion of variation explained by the coordination (strength of the link; such as R^2) and the model estimate (direction of the link; slope). Trait relationships are useful tools as they can detect fundamental functional strategies (Givnish, 1986; Reich et al., 1999; Westoby et al., 2002). For plants, examples include: (1) a trade-off between the speed of resource acquisition and utilization versus conservation (e.g., between specific leaf area and leaf dry matter content) which, in turn, can affect the longevity of organs and individuals (e.g., a trade-off between specific leaf area and leaf lifespan; Klimešová et al., 2016; Westoby et al., 2002; Wright et al., 2004), and (2) a positive coordination between size-related traits, such as between plant height and leaf area (Burns, 2016). Similar questions have also been addressed on other organisms (such as animals; Santini et al., 2018; Voje, 2016). Additionally, most of the research on trait coordination and their response to variation in environmental conditions tended to concentrate on interspecific differences so far (e.g. Reich et al., 1999; Westoby et al., 2002; Wright et al., 2004, 2005); yet, recent studies stressed the relevance of including intraspecific variability (Burns, 2016; Fajardo et al., 2020, 2022; Midolo et al., 2019; Westerband et al., 2021).

Despite their importance to detect fundamental functional axes and strategies, analyses of trait relationships along insularity gradients (i.e., if and how the coordination varies) remain completely unexplored (Figure 1c,d). In this research, we aim to offer a perspective about this still untapped source of information. First, we set out to provide a case study focused on plant specialist species of terrestrial habitat islands (edaphic islands), illustrating how trait coordination can vary with insularity. We do so by implementing an integrative intra- and interspecific approach, that is, accounting for both intraspecific variability (among-islands) and interspecific differences (within- and among-islands) in trait coordination (see Section 3).

Based on (1) basic assumptions of island biogeography theory predicting an increasing selective pressure with increasing insularity on species diversity (Ibanez et al., 2018; Wilson & MacArthur, 1967), and (2) previous studies examining trait patterns on islands showing a decrease of functional diversity with insularity (Conti et al., 2022; Schrader, Westoby, et al., 2021) and better local persistence strategies (Biddick et al., 2019; Biddick & Burns, 2021; Ottaviani et al., 2022), we asked the following questions:

(Q1) Does the strength of the trait coordination (i.e., model R^2) increase with increasing insularity (Figure 1c)?

(Q2) Does the slope of the trait coordination decrease with increasing insularity (Figure 1d)?

Positively answering the first question would suggest a “forcing” effect of insularity towards tighter and better coordinated

strategies, whereas for the second question would indicate an increasing “push for trade-off” among different plant traits and related functions. We then make some inferences linked to the revealed patterns, illustrating what type of ecological and biogeographic insights can be gained. We conclude by identifying key take-home messages in the guise of future avenues that may stem along this research pathway.

3 | CASE STUDY: THE RESPONSE OF TRAIT RELATIONSHIPS OF EDAPHIC ISLAND PLANT SPECIALISTS TO INSULARITY

We based our case study on the data presented in Ottaviani et al. (2022). This dataset refers to 13 perennial plant specialist species of temperate dry grasslands. These grasslands are found on resource-poor and shallow soils associated with granite outcrops in Central Europe (southern Czech Republic). They constitute a special type of terrestrial habitat islands, namely edaphic islands (hereinafter, ‘islands’), being patchily distributed in a dissimilar arable landscape matrix (limiting dispersal, gene flow, and establishment; Figure 2a; Ottaviani et al., 2022). The selected species are specialized and confined to the edaphic islands, hence are expected to conform to island biogeography predictions (Méndez-Castro et al., 2021; Ottaviani et al., 2020). Among the 13 specialist species, five are clonal and eight are non-clonal plants, representing ~45% of the regional pool of habitat specialists (Conti et al., 2022; Méndez-Castro et al., 2021).

We collected functional traits on 20 islands. We selected seven plant functional traits that are tightly linked to local persistence strategies: age, belowground dry matter content (BDMC), lateral spread, plant height, radial growth, storage tissue, and vessel size (Klimešová et al., 2019) – refer to Ottaviani et al. (2022) for further methodological details on sampling design and data collection. In brief, we generally sampled three undamaged individuals per species per island during the vegetative and flowering peak season in 2019. The total number of sampled individuals was 538 (because not all species were present at all study islands, and in a very few instances we could sample only two individuals because of small population sizes). We averaged trait values for each species on each island (Figure 2).

Then, we quantified trait coordination for each pair of traits on each island by fitting standardized major axis (SMA) regression models using the ‘sma’ function of the *smatr* R package (Warton et al., 2012; Figure 2b). SMA is the most suitable approach when dealing with trait coordination wherein no dependency of Y on X is expected (Warton et al., 2006). Finally, we used ordinary least squares linear models to assess the effect of insularity on both R^2 (Q1) and slope (Q2) of the SMAs (Figure 2c). As a measure of insularity, we selected target effect (calculated as the ratio between the spatial isolation [distance to the putative species source] and the size of the target island; for details, see Méndez-Castro et al., 2021), which proved to capture multiple dimensions of insularity in the study system (Ottaviani et al., 2022). Our analyses integrated intra- and interspecific variation because: (1) on

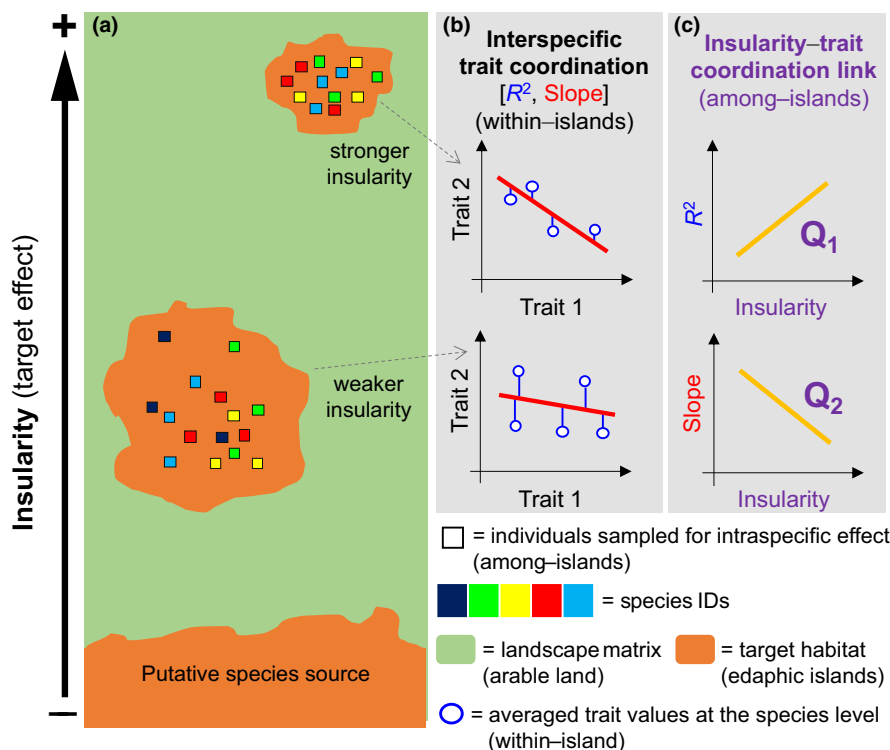


FIGURE 2 Simplified visual representation of the sampling design and analytical framework of the case study devised to examine shifts in the strength (R^2) and direction (slope) of trait coordination with insularity. Panel (a) displays a stylized schematic showing how traits of different plant species were sampled on three individuals per island along an insularity gradient (putative species source is identified on island size and specialist species richness; see Méndez-Castro et al., 2021). Panel (b) illustrates how trait coordination were computed across pairs of traits averaged for each species and analysed within each island (through standardized major axis linear models). Panel (c) displays the link between insularity (set as predictor) and trait coordination parameters (R^2 , slope; set as response variable) addressing the two research questions, using ordinary least squares linear models (see also Figure 1c,d).

each island, we ran bivariate trait regression across all species present on that edaphic island (averaging trait values collected on 3 individuals/species/island), but (2) trait values of individual species varied across islands (hence accounting for intraspecific variability and interspecific differences; see Figure 2a,b). We discuss significant ($p \leq 0.05$) and marginally significant ($p \leq 0.1$) relationships between trait coordination and insularity (Figures 3 and 4). Additional methodological details (Appendix S1) and within-island trait-coordination regression plots for each pair of trait (Appendix S2) are reported in the Supporting Information.

Results tended to positively answer our questions—yet we acknowledge that most patterns were not significant, possibly linked to the relatively small sample size or because other factors than insularity (such as soil conditions; Ottaviani et al., 2022) may affect trait coordination. The positive coupling between the strength of the trait coordination (SMA R^2) and insularity (Q1) was supported in three pairs of traits (Figure 3), whereas only for age~storage tissue link we found a negative relationship (opposing our expectation). Consequently, plants on more insular islands tend to better coordinate the functions of resource acquisition, structural support, and individual longevity—as highlighted by the increase in R^2 for the age~BDMC, age~vessel size, and plant height~radial growth relationships. At the same time, the contrasting patterns revealed for age~BDMC versus age~storage tissue relationships corroborate the idea that BDMC is a trait that can better capture the function of structural support rather than resource conservation (e.g., water, carbohydrates), which is more tightly associated with storage tissue in the studied temperate dry grassland species (Ottaviani et al., 2022). Insularity therefore tended to strengthen the trait coordination towards tighter and better coordinated strategies—similar to what is

observed for plants under increasingly constraining environmental conditions (e.g., Anderegg et al., 2021; Ottaviani et al., 2018). This evidence seems also to align with previous works suggesting how insularity may operate as a selective “forcing” pressure on species diversity (Ibanez et al., 2018) and persistence-related trait values (average and diversity; Conti et al., 2022).

Additionally, we found that island plant specialists under stronger insularity tended to shift towards functional trade-offs, i.e., a tendency of the coordination to shift from a positive to a negative relationship, as revealed for four pairs of traits (Figure 1d [Q2]; Figure 4). This result may have some important implications, both for functional island biogeography and trait-based functional ecology. By including intraspecific variability and interspecific differences in the analysis of trait coordination, we could detect how functional coordination between pairs of traits affecting the local persistence of island plant specialists may vary along a biogeographic (insularity) gradient. This pattern may occur also across other types of gradients, for example with aridity (see Anderegg et al., 2021). On its own, our finding that stronger insularity tends to be associated with functional trade-offs (Figure 4) challenges the notion that fundamental functional spectra of plants remain consistent across different organizational levels and spatial scales, as postulated, for example, by the leaf economics spectrum (which orders plants across a resource conservation–acquisition continuum; Wright et al., 2004).

Interestingly, we positively answered our questions for different pairs of traits. For instance, with increasing insularity, age was more tightly linked to BDMC and vessel size suggesting a reinforced coordination between these traits (Figure 3); yet, the “push for

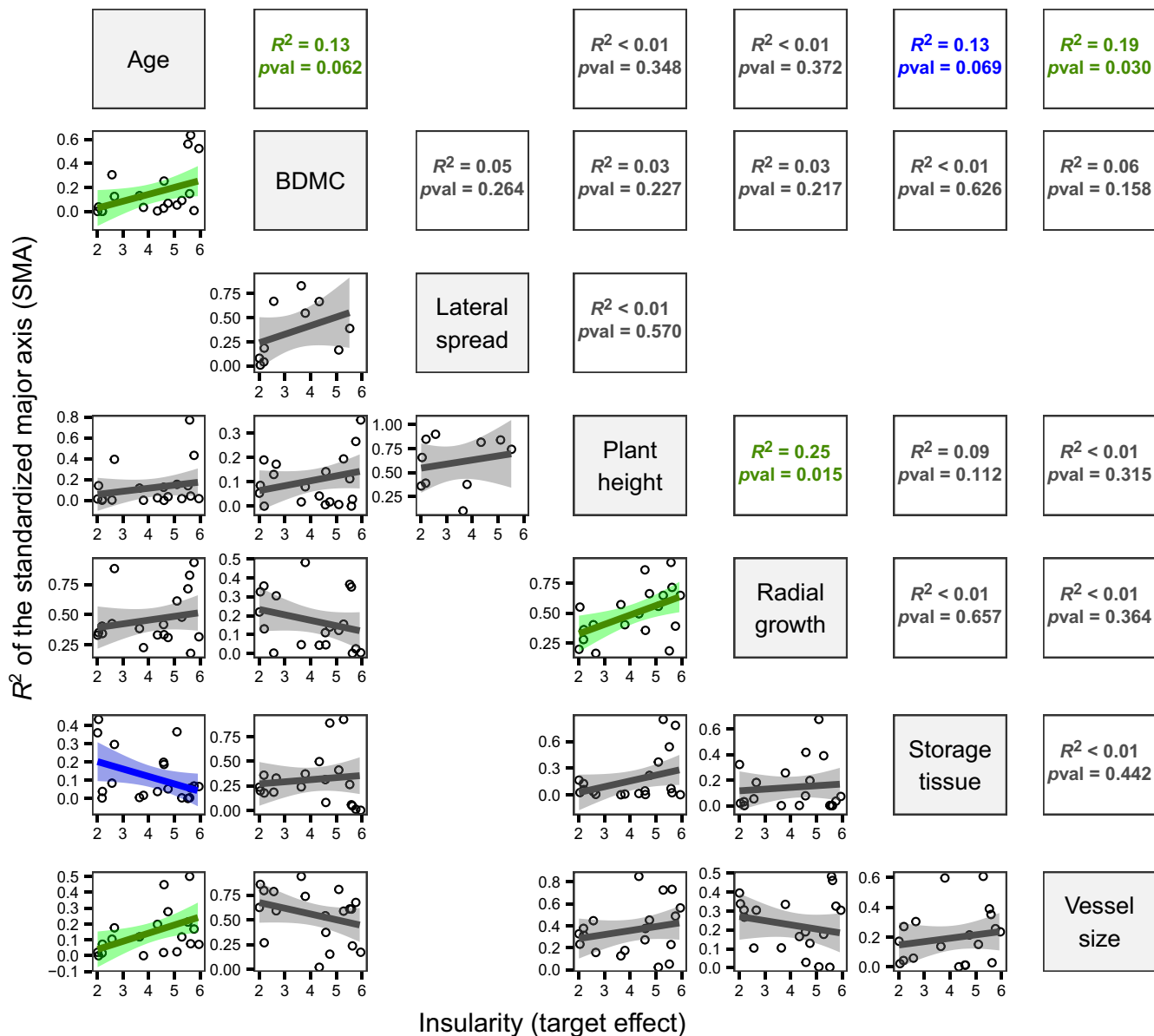


FIGURE 3 The effect of insularity on the strength of trait coordination (= the R^2 of the standardized major axis [SMA]) for each studied pair of traits. The relationships positively answering our question (Q1; namely a positive coupling between R^2 of SMA and target effect) are shown in green, whereas the relationships (only one, marginally significant) opposing our expectation are in blue. The bottom-left panels display the scatter plots, while the top-right panels show the adjusted R^2 and p -values of each model.

trade-off" effect with insularity for this longevity-related trait was observed with plant height (Figure 4). This may imply that the slopes of age~BDMC and age~vessel size respond to other factors than insularity, such as biotic interactions or environmental conditions—especially soil parameters that can largely affect plant trait patterns and local persistence strategies on edaphic islands (Hulshof & Spa-sojevic, 2020; Kazakou et al., 2008; Ottaviani et al., 2022).

Overall, we have obtained various lines of evidence that point towards a predictable effect of insularity on the strength and direction of trait coordination. However, we acknowledge that correlation does not necessarily involve direct causality, and that the studied trait coordination are based on a relatively small sample size. Nevertheless, traits were measured on samples (individuals) collected

in-situ and selected to accurately capture local persistence strategies of plants (Ottaviani et al., 2022).

4 | LOOKING FORWARD: FUTURE DIRECTIONS FOR INTEGRATING TRAIT COORDINATION IN FUNCTIONAL ISLAND BIOGEOGRAPHY

In this perspective, we attempted to offer a rationale as to how studying trait relationships along insularity gradients is a relevant gap for functional island biogeography. Our approach can be applicable also to other organisms than plants. With the case study, we have shown

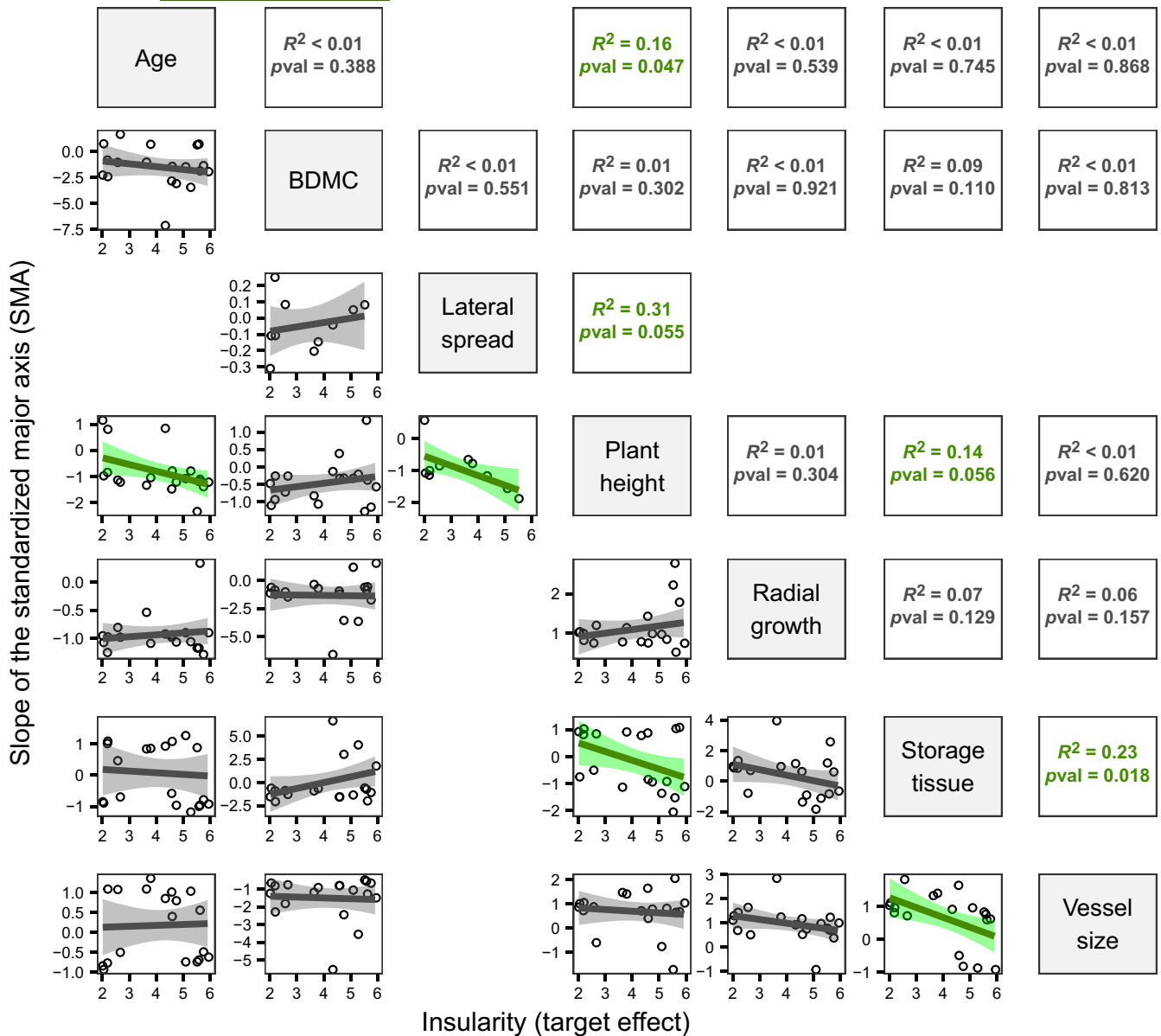


FIGURE 4 The effect of insularity on the direction of trait coordination (= the slope of the standardized major axis [SMA]) for each studied pair of traits. The relationships positively answering our question (Q2; namely a negative coupling between slope of SMA and target effect) are shown in green (we revealed no opposing trends). The bottom-left panels display the scatter plots, while the top-right panels show the adjusted R^2 and p -values of each model.

what type of ecological and biogeographic insights can be gained by implementing an approach which integrates intraspecific variability and interspecific differences into a coherent conceptual and analytical framework. We want to leave the reader with three main take-home messages and directions for future research that we consider most relevant and promising to further push the field of functional island biogeography forward.

4.1 | Including intraspecific trait variability

We advocate for incorporating intraspecific variability in trait relationships (Fajardo et al., 2020, 2022). In our case study, we got

indications that by integrating intra- and interspecific levels, we could gather deeper insights as to how individuals of the same and different species can adjust their fundamental functional spectra and strategies with increasing insularity. This is illustrated by shifts in trait coordination (e.g., from positive to negative relationships) that may allow plants to fine-tune their responses to variation in insularity. In other studies not dealing with insularity, such adjustments have been shown to be associated with non-independent functional traits co-varying within their spectrum in response to bioclimatic filters (e.g., Midolo et al., 2019). Additionally, the potential role played by ontogeny could be considered, since less developed/younger individuals may be distinguished by different trait values and coordination than more developed/more mature individuals (Burns, 2016;

Dayrell et al., 2018; Fajardo et al., 2020). Here, we could not gather more detailed data on within-island shifts in intraspecific trait coordination (due to logistic and conservation constraints), which could provide additional functional insights (see Burns, 2016).

4.2 | Tailoring the study design

In our case study, we illustrated that the detection of insularity effect was influenced by the selection of traits (reflecting our expectations) and sample size. Consequently, trait coordination should be further examined with a greater sample size and include more traits able to capture major functions (i.e., beyond persistence, such as dispersal abilities, reproduction type and effort; Ottaviani et al., 2020). We further stress that it is key to analyse traits reflecting an established or hypothesized functional correlation; otherwise, testing the effects of insularity on traits for which no meaningful ecological link can be expected, may lead to spurious evidence of predictors' effect on trait coordination. Also, we suggest that trait coordination should be comparing trait relationships of island versus mainland biota, for example between closely related species to control for possible effect of shared evolutionary history on trait patterns (Biddick et al., 2019; Biddick & Burns, 2021; Burns, 2016, 2022). Finally, it is important to tailor the study design in a way that facilitates disentangling and quantifying the net effect of insularity on trait coordination (by accounting for covariates and their interaction with insularity).

4.3 | Addressing conservation biogeography of insular systems

Trait coordination can also inform upon potential adaptations of organisms to global environmental changes (Santini & Isaac, 2021). Islands and terrestrial habitat islands constitute priority elements in conservation as they harbour highly specialized biota, including many endemics and species threatened by environmental changes (Barton & Fortunel, 2023; Macinnis-Ng et al., 2021; Veron et al., 2019). Coordination between key plant functional traits related to local persistence and dispersal may affect the capacity and vulnerability of populations, species, and assemblages to cope with changing environmental conditions, including global warming, land-use alterations, and invasions. For example, plant populations in refugia or at the edge of the species range (or environmental niche) may abandon sexual reproduction in favour of vegetative modes. This pattern, called 'functional extinction' (Jiménez-Alfaro et al., 2016), can have far-reaching consequences because remnant populations may have reduced or hindered dispersal abilities as well as lower genetic diversity generated by such functional trade-off promoting vegetative strategies to persist *in-situ*.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The dataset used in this study is available from the Figshare Digital Repository: (<https://doi.org/10.6084/m9.figshare.19698970.v4>; Ottaviani et al., 2022).

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BIOSKETCHES

Gabriele Midolo is a plant ecologist interested in the response of plant species and functional traits to environmental changes and how this knowledge can be applied to aid ecosystem management and conservation.

Francisco E. Méndez-Castro is an island biogeographer focusing on different types of insular systems and organisms, examining which traits and insularity metrics affect the distribution of species.

Gianluigi Ottaviani is a plant functional ecologist using trait-based approaches to gain insights into (i) which factors shape species' persistence and distribution (in insular habitats primarily), and (ii) plant responses to environmental changes.

Author Contributions: Gianluigi Ottaviani conceived the original idea, and Gabriele Midolo provided key insights to further develop it. Gabriele Midolo conducted the statistical analyses. Gianluigi Ottaviani and Francisco E. Méndez-Castro collected the data. Francisco E. Méndez-Castro calculated the insularity metrics. Gabriele Midolo and Gianluigi Ottaviani led the writing of the manuscript, with inputs from Francisco E. Méndez-Castro.

SUPPORTING INFORMATION

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

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