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Research article

Spatial phenotypic variability is higher between island populations than between mainland populations worldwide

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Spatial isolation is a key driver of population-level variability in traits and genotypes worldwide. Geographical distance between populations typically increases isolation, but organisms face additional environmental barriers when dispersing between suitable habitat patches. Despite the predicted universal nature of the causes of isolation, global comparisons of isolation effects across taxa and geographic systems are few. We assessed the strength of isolation due to geographic and macroclimatic distance for paired marine island and paired mainland populations within the same species. Our meta-analysis included published measurements of phenotypic traits and neutral genetic diversity from 1608 populations of 108 plant and animal species at a global scale. As expected, phenotypic differentiation was higher between marine islands than between populations on the mainland, but we found no consistent signal for differences in spatial patterns of neutral genetic diversity between the two systems. Geographic distance had comparatively weak effects on the spatial patterns of phenotypes and neutral genetic diversity. These results suggest that spatial patterns of phenotypic variation are determined by eco-evolutionary pressures that differ more between islands than between mainland populations, while the spatial variability of neutral genetic diversity might be shaped by rather similar processes in the two systems. Our approach demonstrates that global biodiversity models that include island biology studies may progress our understanding of the interacting effects of spatial habitat structure, geographic- and environmental distances on biological processes underlying spatial population variability. We formulate future research directions for empirical tests and global syntheses in the field.

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Introduction

Understanding mechanisms governing spatial patterns of biodiversity at biogeographical scales is a challenging theme in ecology. Spatial isolation between populations can decrease connectivity and limit gene flow and therefore plays a major role in shaping inter-population variability and speciation processes (Orsini et al. 2013, Sexton et al. 2014, Pironon et al. 2017). Comparative analyses of natural systems characterised by spatially discontinuous habitats such as islands separated permanently by saltwater (hereafter referred to as marine islands) with those where isolation can be driven by increasing geographic distance between populations within a comparatively benign landscape matrix (e.g. the mainland) have been encouraged, as they can advance our understanding of the consequences of spatial isolation for phenotypes and genotypes (Haila 2002, Laurance 2008, Santos et al. 2016, Martín-Queller et al. 2017, Patiño et al. 2017, Flantua et al. 2020).

To date, comparing marine island populations to mainland populations has been a classic approach to understanding the drivers of isolation due to the obvious geographic separation of islands from the mainland, particularly for oceanic rather than continental islands (Weigelt and Kreft 2013). On islands, organisms can be subject to strong selection pressure due to a large variety of eco-evolutionary forces that include lowered gene flow, founder effect, genetic drift and high extinction rates due to smaller population sizes, modified abiotic and biotic conditions (Santos et al. 2016, Patiño et al. 2017). These factors have been linked to shifts in body and organ size (the 'island rule', Foster 1964, Lomolino et al. 2013, Benítez-López et al. 2021), decreased dispersal (Burns 2018), slower growth rates and increased life span (Andrews 1976, Lens et al. 2013), and changes in reproductive strategies and behaviour (Covas 2012, Morinay et al. 2013) in island populations. Such changes associated with island populations are known as the 'island syndrome' (Whittaker and Fernández-Palacios 2006). In conjunction with such life history, physiological and behavioural changes, spatial equilibrial processes (founder effects, restricted dispersal, small population sizes, higher extinction rates) should theoretically reduce the neutral genetic diversity of island populations in comparison to mainland populations. However, while such patterns are predicted, this observation is not generally applicable across all island systems (Frankham 1997, Woolfit and Bromham 2005, García-Verdugo et al. 2015).

While islands have been the classic focus of isolation effects, isolation can also emerge on the mainland, due to either large geographic distances between populations (in continuous and recently fragmented habitats, McIntyre and Hobbs 1999, Watson 2002, Laurance 2008), or environmental discontinuities between suitable habitat patches in ecological islands (Csergő et al. 2014, Tapper et al. 2014, Steinbauer et al. 2016). However, mainland isolation is likely to differ from classic marine island isolation, as mainland habitat islands lack an abrupt saltwater barrier and experience higher spatial or temporal connectivity (Haila 2002, 2002, Driscoll et al. 2013, Ó Marcaigh et al. 2021). As a result of this difference, their analogy with marine islands has been questioned (Flantua et al. 2020). This calls for further comparative investigations to better understand the spatial mechanisms governing the biodiversity of island versus mainland systems, and for the conceptual unification of isolation research across systems (Haila 2002, Laurance 2008, Santos et al. 2016, Patiño et al. 2017, Flantua et al. 2020).

Geographic distance may be key determinant of spatial isolation, as well as an important driver of spatial variability, and it is perhaps the most commonly used metric of geographic isolation (Wright 1943, Orsini et al. 2013, Sexton et al. 2014). But geographic distance is not an exclusive determinant of spatial patterns in phenotypic traits and neutral genetic diversity. While strict isolation by distance emerges due to limits to dispersal and genetic drift (Wright 1943), the role of environmental conditions in fostering spatial population variability may override the direct effects of geographic distance (Kalmar and Currie 2006, Shafer and Wolf 2013, Orsini et al. 2013, Sexton et al. 2014). Environmental heterogeneity modified biotic interactions and habitat disturbance often shape the course of ecological and evolutionary processes in populations worldwide and have sculpted much of the individuality of island populations (Kalmar and Currie 2006, Heaney 2007, Triantis et al. 2010, Lens et al. 2013, Weigelt and Kreft 2013, Stuessy et al. 2014, Borregaard et al. 2017). Environmental factors are key determinants of intraspecific body size variation in vertebrate groups globally (Henry et al. 2023). Increasing evidence indicates that even the spatial patterns of neutral genetic diversity are heavily influenced by environmental conditions in addition to the geographic position of populations (Lira-Noriega and Manthey 2014, De Kort et al. 2021). Despite significant advances in understanding these two major drivers of biodiversity at different levels of organisation, global comparative evidence for differential effects in island versus mainland systems is still lacking.

A complicating circumstance is that significant differences in responses may exist across different traits or groups of species, some being more responsive to geographic forces, while others responded more readily to environmental conditions (Orsini et al. 2013, Sexton et al. 2014, Pironon et al. 2017, Henry et al. 2023). For example, the genetic diversity of plants responds more readily to geographic, than environmental drivers compared with animals (Sexton et al. 2014). As a result, a series of geographic, environmental and taxonomic factors need to be considered for a better understanding of the links between life histories and spatial isolation (Dupré and Ehrlén 2002, Sutherland et al 2013) and in order

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to detect the effect of system type (e.g. island or mainland) on inter-population variability (García-Verdugo et al. 2015, De Kort et al. 2021). Due to the difficulties in disentangling these influencing factors, the development of global biogeographic models of population variability has been slow, despite major advances in functional biogeography and population macroecology (overviews by Schrader et al. 2021a, b, Buckley and Puy 2022, Vasconcelos 2023).

Here we conducted a global meta-analysis of multiple plant and animal populations studied in both island and mainland systems, in which we test how geographic distance and macroclimatic distance relate to phenotypic and neutral genetic diversity variation between populations of marine island systems and between populations of mainland systems (Fig. 1). While neutral genetic diversity results from spatial processes such as gene flow, migration or dispersal, it has mostly indirect effect on fitness through e.g. inbreeding depression or founder effects (Holderegger et al. 2006). In contrast, phenotypic variability is mainly influenced by a mixture of adaptive and plastic responses to the environment, and it is only partially related to neutral (standing) genetic diversity (see Hoban et al. 2016, Jensen et al. 2016 for relationships between neutral genetic markers and phenotypic variability and approaches to identify loci under selection on the basis of putatively neutral loci). Therefore, the two measures provide complementary insights into processes underlying spatial diversity patterns. While we expected populations to show greater differences in phenotypic traits and neutral genetic diversity with increasing geographic distances between populations, we predicted that these effects would be stronger within island systems, which show consistent spatial structure compared to the mainland systems. We further expected greater differences in phenotypic traits and neutral genetic diversity with increasing macroclimatic differences between populations, but we did not expect macroclimate effects to differ between the two system types. Finally, we predicted that phenotypic traits would show higher levels of spatial variation across populations compared to neutral genetic diversity, because the former are more strongly influenced by natural selection and may be modulated by plastic responses to environmental heterogeneity.

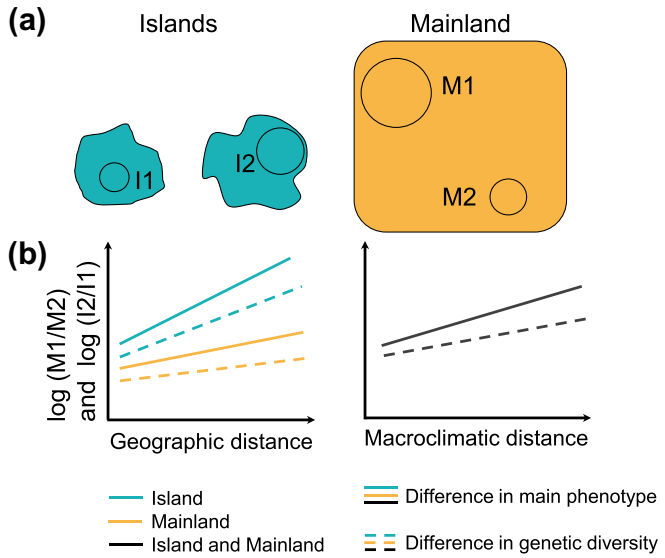

Figure 1. (a) Figure showing the main study selection criterion. The population (marked with circle) was the observation level for analysis, and only study systems with a minimum of two islands (I1, I2) and two mainland populations (M1, M2) were considered. Circle size indicates possible differences between the mean of a specific phenotypic trait or a neutral genetic diversity measure. We calculated the log ratio between the largest and the smallest values for paired island populations and paired mainland populations respectively for each phenotypic trait and neutral genetic diversity measure (y-axis in b). (b) Expectations for a positive effect of geographic and macroclimatic distances on the calculated response variables within island and mainland systems. We expected stronger effects of geographic distance on mean phenotypes and neutral genetic diversity in island systems compared to the mainland systems, and we did not expect the effects of macroclimatic distance to differ between the two system types. We expected stronger responses of phenotypic traits compared to the neutral genetic diversity.

Material and methods

Database compilation

We searched the ISI Web of Science in March 2017 for comparative studies that included data on phenotypic traits and/or neutral genetic diversity of populations on marine islands and on mainland sites in any taxonomic group. Search terms were 'island' and ('mainland' or 'continental') and 'population*' and ('demograph*' or 'fitness' or 'survival' or 'growth' or 'reproduc*' or 'density' or 'abundance' or 'size' or 'genetic diversity' or 'genetic structure' or 'population genetics') and ('plant*' or 'tree*' or 'shrub*or 'animal*' or 'bird*' or 'amphibian*' or 'mammal*' or 'reptile*' or 'lizard*' or 'snake*' or 'fish'), subsequently refined to the Web of Science categories 'Ecology' or 'Evolutionary Biology' or 'Zoology' or 'Genetics Heredity' or 'Biodiversity Conservation' or 'Marine Freshwater Biology' or 'Plant Sciences' or 'Geography Physical' or 'Ornithology' or 'Biochemistry Molecular Biology' or 'Multidisciplinary Sciences' or 'Environmental Sciences' or 'Fisheries' or 'Oceanography' or 'Biology' or 'Forestry' or 'Reproductive Biology' or 'Behavioral Sciences'. The search included the whole text including abstract and title, but only abstracts and titles were searchable for older papers depending on the journal. The search returned 1237 papers which were distributed among co-authors for further analyses.

We chose papers for inclusion in the dataset if the same species was studied on a minimum of two marine islands and two sites on the mainland (Fig. 1). While we accepted the authors' judgement about island versus mainland status, we made our own judgement based on the relative size of the island or position relative to the mainland i.e. some islands were reinterpreted as mainland if they were at least four times larger than smaller islands within the same study, with the median size difference for islands reclassified as mainland being 249 times larger than other islands in the study (17

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papers), or if the distance of the island from the continent was very low compared to the rest of the islands within the same study (4 km versus 1700 km in one paper, and 300 m versus 11 km in another paper; Supporting information). We eliminated studies comparing populations on several islands where there were no clear island versus mainland comparisons even after reinterpreting the island status, studies referring to migratory species, recent invasions (< 50 years), marine species (including coastline organisms), studies on lake or river islands and ex situ populations. The complete selection criteria are presented in the Supporting information. The initial filter resulted in 234 papers which were then redistributed among co-authors for a second round of filtering. In the second filter, we excluded papers that did not provide both population geographic coordinates and population-level quantitative data based on individual measurements, unless data were provided upon contacting the authors or could be obtained from figures using DataThief (Tummers 2006). We visually inspected maps plotted for each study separately and we made minor adjustments to the GPS coordinates when the coordinates placed the focal population off the island or mainland. For this study, we included only responses measured at individual level, therefore we removed papers referring to demographic performance, and we also excluded traits such as immunity, behaviour and diet that are heavily reliant on ecosystem context. We extracted data on population level mean for two broad categories of response: 1) broad phenotypic measures, which included traits such as size and weight of entire body or body parts, morphology (e.g. mandible shape, number of stamens, wood density), metabolism products (e.g. colour of skin), physiology (e.g. digestive efficiency), vital rates (growth, survival, reproduction) and mean age of sampled mature individuals; and 2) genetic diversity, which included heterozygosity, allelic richness, number of alleles per locus (Supporting information). The final dataset included 112 studies of 108 species (72 animals and 36 plants) in 868 island populations and 760 mainland populations, with population-level taxonomic and biogeographic information, totalling 7438 records (Fig. 2, Supporting information). The dataset and the corresponding bibliography are available in the Dryad data repository (Csergő et al. 2023).

Calculation of pairwise distances between population parameters

To test how genetic and phenotypic measures vary within island and mainland systems, we calculated the pairwise difference between population mean values for each phenotypic and genetic measure for each species 1) between island populations and 2) between populations on the mainland. To allow comparisons across the range of different measures, the pairwise difference between populations was expressed as the log response ratio of the paired measures, as follows: $x_{ij} = \log_{10}\left(\frac{m_{ij}}{n_{ij}}\right)$, where m = larger population mean value and n = smaller population mean value, i = population measure type, j = species. Higher log ratios indicate stronger differences between sites for phenotypic or genetic values (cf. Hedges et al. 1999). In this metric there was no directional structuring of the pairwise distances between populations, and values ranged between $\log_{10}(1)$ and $\log_{10}(\infty)$. This dimensionless metric did not require further standardisation across different types of genetic and phenotypic variability measures, enabling meaningful comparisons between populations. The pairwise distance in genetic diversity between populations 1) quantifies the difference in genetic diversity between populations, not genetic differentiation e.g. two populations with strongly differentiated genotypes could have identical genetic diversity and thus, a low value for the metric; 2) It quantifies the scale of the difference, not the level of diversity e.g. comparing equally high diversity populations can be identical to comparing equally low diversity populations.

The non-independence of pairwise distance measures was accounted for in the statistical analysis (below).

Calculation of geographic and macroclimatic distances between populations

We calculated the pairwise geographic distance between island populations and between mainland populations as geodesic distance (shortest distance on the WGS84 ellipsoid) based on the GPS coordinates of the populations, using the *distGeo* function in the 'geosphere' package (Hijmans 2019) in R, ver. 3.4.4 (www.r-project.org). Geographic distances were similar between island and mainland populations (Supporting information).

To calculate the macroclimatic distance between each population pair, we performed a principal component analysis (PCA) of four climate variables reflecting mean and variation in temperature and precipitation available in CliMond ver. 1.2 (Kriticos et al. 2012) at 10 min resolution: mean annual temperature (Bio1), annual precipitation (Bio12), temperature seasonality (CV) (Bio4) and precipitation seasonality (CV) (Bio15), using the *prcomp*' function in the 'stats' package in R. For populations where climate variables were not available on the global climate maps mostly due to small island size not captured in CliMond, we extracted data from the geographically closest grid cell with available climate values, which was available within 3.5 km away from the focal grid cell for all localities. Variables were centred on zero and scaled to unit standard deviation prior to the analyses. Island and mainland populations occupied a broadly similar climatic space and were best represented in three regions of the PCA corresponding to 1) wet, cold climate with constant precipitation and seasonal temperature i.e. temperate oceanic climate, 2) dry climate and seasonal precipitation i.e. temperate continental climate, and 3) wet, hot climate with constant temperatures i.e. tropical oceanic climate (Supporting information). We calculated the pairwise macroclimatic distances between populations on the first two axes of the PCA space using the '*dist*' function and '*euclidean*' distance measure in R.

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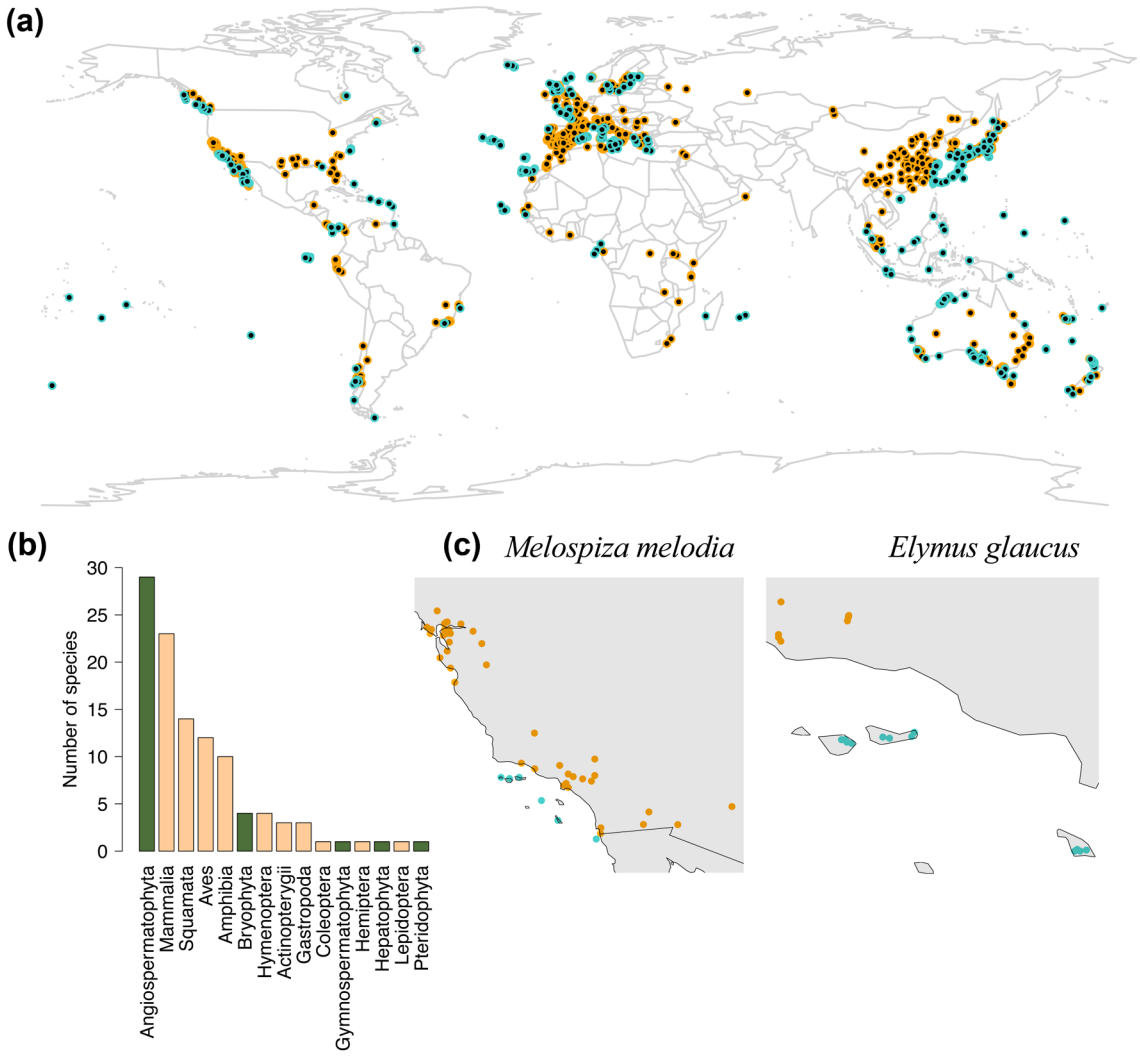

Figure 2. (a) The global representation of 868 island (turquoise dots) and 760 mainland populations (orange dots) with population-level phenotypic traits and genetic diversity data studied comparatively in island and mainland systems for 108 species. (b) Number of species in different taxonomic groups included in this study. Animals are indicated with light brown, and plants with green colour. (c) Two sample maps showing the geographic distribution of populations studied comparatively in island and mainland systems for a bird (*Melospiza melodia*) and a plant (*Elymus glaucus*) species.

Statistical analyses

To investigate how the pairwise log response ratio of the mean population parameters was affected by geographic and macroclimatic distance between populations, system type (island versus mainland) and taxonomy, we fitted Bayesian phylogenetic mixed models using the 'MCMCglmm' package (Hadfield 2010).

We ran two general models, corresponding to phenotypic variability and genetic diversity respectively. For these general models, the model structure was: *log_ratio(phenotypic trait or genetic diversity) ~ factor(mainland vs island) + log_{10}(geographic distance) + Kingdom (plant vs animal) + macroclimatic distance + interaction (mainland vs island) : log_{10}(geographic distance) + interaction (mainland vs island): macroclimatic distance*. The models included phylogeny, study ID and the response variable type (e.g. size, heterozygosity, totalling 16 levels for genetic diversity and seven levels for phenotype variability, see the Supporting information) as random intercepts. Our models accounted for potential pseudoreplication issues associated with the process of pairwise comparison across populations and the phylogenetic structure of the data. If a population was represented in more than one pairwise comparison, using the full set of pairwise combinations for any group of populations would result in pseudoreplication. To avoid this, we used random pairwise comparisons between populations without replacement to create datasets where each population can only be represented once. For example, for comparisons in a system with three island populations, each dataset would only include one pairwise comparison to avoid any given population being represented more than once. If more than one population was present on an island,

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which was the case for some larger islands, one population was chosen at random for each round of creating pairwise comparisons. To capture the full set of possible pairwise comparisons, we created 100 pairwise datasets, and each was then used to independently test our hypotheses. To ensure that the results were not due to the evolutionary history of species, phylogeny was included in the MCMCglmm model as a random effect (Hadfield 2010). Rather than using one phylogenetic tree and assuming no error in the tree structure or branch length, we created a distribution of 100 phylogenies from various sources that incorporated the errors associated with building phylogenetic trees (Supporting information). As a result of accounting for pairwise pseudoreplication and phylogenetic uncertainty, we ran 100 MCMCglmm models as described in the 'Multree' package (Guillerme and Healy 2014), with each separate run associated with an independent pairwise dataset and a random phylogeny. As the posterior outputs of MCMC models are combinable, coefficient distributions were created by amalgamating coefficient posterior distributions from all runs.

The general phenotypic variability model included 47 species (7 plants, 40 animals) and the general genetic diversity model included 72 species (31 plants, 41 animals). Due to the different numbers of populations studied per species, each replicate model of the phenotypic and genetic models included a different number of associated pairwise measures between populations, ranging between approximately 1073–1089 and 1608–1633, respectively.

To assess the robustness of our results, we ran a series of additional models for both the phenotypic variability and neutral genetic diversity datasets, each exploring different limiting aspects of our data: 1) as zero values are common in measures of genetic diversity and biological phenotypes (e.g. lack of polymorphic loci in a population), and log ratio values cannot be calculated if any values are zero, these values were dropped from the main models (and from the results presented in the main text). To test the effect of zero-values on our analyses, we ran separate, 'zero-adjusted' general models for both the phenotypic variability and neutral genetic diversity, in which we added 10% of the mean of the respective variable to all individual measurements. 2) To explore the extent to which the general models were influenced by the response variables more frequently represented in the database, we ran separate models on the two most commonly measured variables in the dataset: body (or body part) size and heterozygosity. These models were fitted following the same method as the general models but had one random term (the response variable type) removed. Additionally, because in the main models some of the selected variables were present in only one or two species, we performed analyses of phenotypic distance and genetic diversity where only measures represented by at least five species were included. 3) As macroclimatic distance and geographical distances were correlated (Supporting information), we also refitted each of the main models with either the macroclimatic distance or geographical distance excluded. 4) In the main models, we tested for non-linear responses of differences in phenotypic traits and genetic diversity to geographic distance. 5) To test whether the origin of islands may have influenced the results, we refitted the main models splitting islands into continental and oceanic formation for species where this information was available in the original papers, interpreting all islands reported volcanic as oceanic and hence never connected to the continent. 6) To investigate whether the effects of system type, geographic and macroclimate depended on the Kingdom, we refitted the main models separately for animals and plants (but due to low sample size, phenotypic distance models could not be fitted for plants).

Models built this way could not accommodate non-neutral genetic differentiation between populations, because differentiation is a property of a pair of populations but the unit of observation in our study was the population itself. Likewise, the models did not accommodate existing models of population variability developed specifically for island systems, such as the effect of island size or distance of islands from the mainland, which are difficult to correspond to mainland systems, and fell beyond the scope of this analysis.

The structure of all models together with the number of species and corresponding pairwise population measurements is presented in the Supporting information.

Results

Determinants of phenotypic difference between populations

The log ratio values for the phenotypic traits included in the analysis ranged from 0, indicating cases with no difference between populations, to 3.7 which, when back transformed from log space, corresponds to a ratio of approximately 39:1 between populations for the given measure. As expected, we found higher differences in phenotypic traits between island populations than between mainland populations, mainland populations having a log ratio 0.189 lower than island populations (mode = −0.18, 95% CI = −0.39, −0.01, Table 1a, Fig. 3, Supporting information). This difference in the level of variation corresponds to a ratio of trait values of approximately 1.44:1 between island populations and 1.15:1 for mainland populations. We found some support for an interaction between system type (island or mainland) and geographic distance, i.e. phenotypic variability between populations tended to increase with increasing geographic distance on the mainland, but it was constant for all geographic distances on islands. This effect size corresponds to variation between mainland populations approximately 500 km apart matching the variation found between island system populations regardless of geographic distance between islands (Table 1a, Supporting information). The effect of other variables was even weaker (Table 1a, Supporting information). Across the random terms included in the model, most of the variation was associated with the residual terms, less variation was associated with the study or the species, and very little effect was attributed towards the phylogenetic term and response type

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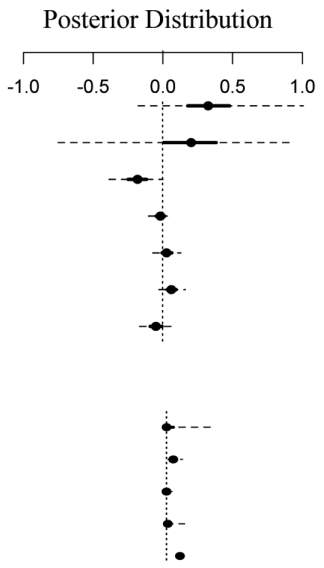
Table 1. Model terms, estimates, confidence intervals and posterior coefficient estimates of the Bayesian model of (a) phenotypic distance and (b) genetic diversity distance between populations in island and mainland systems. Positive values indicate positive, and negative values indicate negative effect of the tested variables on the log-ratio of response variables. The posterior distribution of coefficients for the fixed effects are shown across 100 models, with horizontal continuous lines representing the 50 and 95% posterior density intervals. All variables were standardised to zero mean and unit variance prior analyses. Random effects included variation associated with phylogeny (Phylogeny), the study from which data was derived (Study), within species variation (Species) and the sub-category of the response type (Response type), while Units represent residual variation.

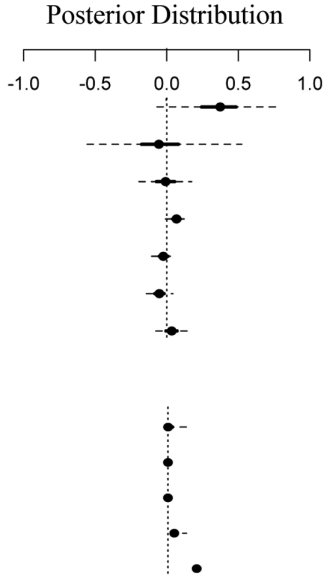
(a) Phenotypic distance model

Model term	Estimate (β)	Lower CI	Upper CI	Posterior Distribution
Fixed effects				
Intercept	0.33	−0.18	1.00	
Kingdom effect	0.21	−0.75	0.93	
System effect mainland	−0.18	−0.39	−0.01	
Geographic distance	−0.02	−0.10	0.07	
Environmental distance	0.03	−0.07	0.13	
Geographic distance: System effect	0.07	−0.02	0.16	
Environmental distance: System effect	−0.05	−0.17	0.08	
Random effects				
Phylogeny	0.01	0.00	0.31	
Study	0.05	0.01	0.11	
Species	0.01	0.01	0.04	
Response type	0.01	0.00	0.13	
Units	0.10	0.07	0.12	



(b) Genetic diversity distance model

Model term	Estimate (β)	Lower CI	Upper CI	Posterior Distribution
Fixed effects				
Intercept	0.37	−0.07	0.76	
Kingdom effect	−0.07	−0.56	0.53	
System effect mainland	−0.01	−0.20	0.17	
Geographic distance	0.07	−0.01	0.15	
Environmental distance	−0.02	−0.11	0.06	
Geographic distance: System effect	−0.05	−0.14	0.04	
Environmental distance: System effect	0.03	−0.08	0.15	
Random effects				
Phylogeny	0.01	0.00	0.13	
Study	0.01	0.00	0.03	
Species	0.01	0.00	0.03	
Response type	0.05	0.02	0.13	
Units	0.20	0.18	0.23	



(Table 1a). The zero adjusted models, the reduced model that included phenotypic traits associated with size, the reduced model that included specific phenotypic traits represented by at least five species, the models which excluded the macroclimatic or geographic distance, and the models fitted separately for animals produced qualitatively similar results to the main phenotypic model (Supporting information), but the animal-only model found no statistical support for the system effect. We find no support for a nonlinear effect of geographic distance on phenotypic traits (Supporting information). In the models testing the effect of island origin, while both island types were associated with higher phenotypic trait variation when compared to mainland populations, with oceanic islands having a higher level of difference, these effects were no longer significant (Supporting information). This result likely reflects the lack of power due to splitting island samples into two groups, while omitting studies where island origin was mixed or unknown.

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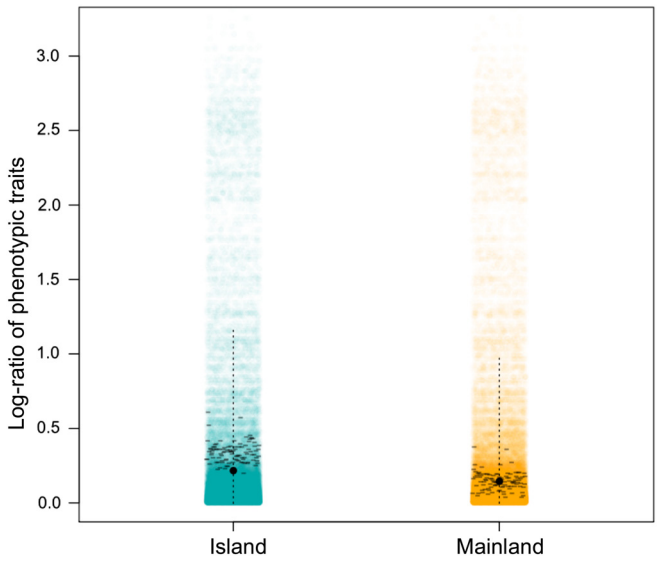

Figure 3. Log-ratio of phenotypic trait values between island populations (turquoise) and between mainland populations (orange) for 100 sampled datasets. Horizontal black lines represent intercept estimates for each of the 100 sampled datasets, and the point with a vertical dashed line represent the mean and the overall 95% credibility interval. Points are jittered horizontally for better visualisation.

Determinants of difference in genetic diversity between populations

The log response ratio values for the genetic diversity measures included in our analysis ranged from 0, indicating cases with no difference between populations, to 4.32, which corresponds to a ratio difference of approximately 75:1 between measures of genetic diversity between two populations. In the main model we found no evidence for a strong effect of geographic or macroclimatic distance, system type or kingdom on the log ratio of mean genetic diversity measures between populations, as the posterior distributions of all parameters overlapped with zero (Table 1b, Supporting information). Of all variables, geographic distance had a weak, positive influence on the difference in mean genetic diversity between populations, with the posterior distribution for all 100 combined models slightly overlapping zero, and an increasingly larger range of inter-population differences in neutral genetic diversity observed at higher geographic distances (Table 1b, Supporting information). Across the random terms included in the model, most of the variation was associated with the residual terms, less variation was associated with the response type, and very little effect was attributed towards the phylogenetic term, study and species (Table 1b). The random term response type absorbed the variation due to the different measurement types and genetic markers used, which likely differed regarding their ability to detect fine-scale genetic variation, and thus our analysis provided a good overview across a range of measures with different sensitivities.

In the model that did not include geographic distance, we detected higher differences in genetic diversity between islands than between mainland populations, but this effect did not persist in the model that included geographic distance (Supporting information). Likewise, in the model that included the polynomial term for geographic distance, we detected higher differences in genetic diversity between islands than between mainland populations, but the non-linear effect of geographic distance was not statistically supported (Supporting information). The zero adjusted model, the reduced model of heterozygosity, the reduced model that included specific genetic diversity measures represented by at least five species, the models which excluded environmental distance, the models where islands were split into continental and oceanic, and the models fitted separately for animals and plants produced qualitatively similar results to the main genetic diversity model (Supporting information).

Discussion

Using a global dataset of phenotypic differences and differences in neutral genetic diversity for 1608 populations of 108 species studied comparatively in marine island and mainland systems, we showed greater differences in phenotypic traits between islands than between equivalent populations on the mainland, and no differences in the spatial patterns of neutral genetic diversity between the two systems.

As expected, mean phenotypic differences were higher between island populations than between mainland populations. On the mainland, more populations are likely to benefit from higher connectivity between habitat patches compared to islands (Pușcaș et al. 2008, Driscoll et al. 2013, Martín-Queller et al. 2017), which could lower the magnitude of spatial phenotypic variability. In island systems, the effective isolation due to the saltwater matrix and its consequences e.g. lowered gene flow, can amplify opportunities for phenotypic differentiation between populations, which has been linked to accelerated rates of speciation and high levels of island endemism (Whittaker and Fernández-Palacios 2006, Kier et al. 2009). Evolutionary pressure promoted by niche differentiation following colonisation of islands with different natural history may also underly the stronger phenotypic differentiation between islands compared to mainland populations (O'Connell et al. 2019). Due to our modelling framework, we could not derive to what extent the phenotypic differentiation was due to genetic differentiation, because our genetic diversity metric quantified differences in neutral genetic diversity between populations. However, the demonstrated genetic differentiation between islands and mainland sites (reviewed by Stuessy et al. 2014) strongly suggest that genetic differentiation may underly the accentuated phenotypic differences between individual islands compared to mainland systems. The result could also be due to the fact that on islands smaller population sizes are more frequent than on the mainland due to constraints of island size (Woolfit and Bromham 2005, Triantis et al. 2010). As a result, genetic drift is more frequent on islands (Woolfit and Bromham 2005), which can set populations on distinct evolutionary courses and enhance their phenotypic

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differentiation. The effect of island system on phenotypic differentiation emerged despite us analysing oceanic islands together with continental islands. Continental islands have a different history (they are often closer to the mainland, benefiting from more frequent immigration opportunities that stabilize the selection on phenotypic traits) that may have lowered to some extent the effect of the island system type. While suffering from lack of power, our additional analysis of island system type split between continental and oceanic suggests this was indeed the case.

In line with our expectations, we found a tendency for increased mean phenotypic differences between populations with increasing geographic distance on the mainland, but contrary to our expectations we did not find a similar trend in island systems, and we found no effect of macroclimatic distance on the phenotypic differences. While geographic distance and macroclimatic distance were correlated in our data, which is frequently the case in spatial analyses (Bahn and McGill 2007, Coutts et al. 2016), models excluding either the geographic or macroclimatic distance did not change the results. The lack of any geographic distance effects on phenotypic differences between islands reinforce that other spatial constraints as detailed above (isolation due to saltwater, niche differentiation, island size etc.) may be more effective at promoting phenotypic variability in island systems compared to the simple isolation by distance. On the mainland on the other hand, the signal, albeit weak, of a positive effect of geographic distance on phenotypes suggests that isolation by distance may play a relatively more important role in emerging spatial trait variability compared to island systems (De Vriendt et al. 2017). The lack of macroclimate effects in both systems suggests no effect of isolation by macroclimate in driving mean population-level phenotypic variation. However, evidence exists for the contrary at least for particular groups of organisms (e.g. in endothermic, but not in ectothermic vertebrates, mean temperatures were associated with smaller intraspecific body size globally; Henry et al. 2023, but see Rubalcaba et al. 2023). Therefore, the role of macroclimate in generating isolation is likely idiosyncratic in terms of the taxonomic groups it affects, and in contrast to geographic forces (spatial habitat structure, geographic distance) its effects on spatial phenotypic variability are harder to generalise. However, as sites for island–mainland population comparisons are primarily not selected to test variation determined by environmental differences, we suspect that in our dataset the macroclimatic distance between populations was too small, as the most frequent paired distance represented only 2% of the largest potential environmental distance found in our data. Finally, macroclimate represents only one dimension of environmental distances between populations, while other environmental variables that more directly capture the environments experienced by populations, such as the heterogeneity of vegetation types, could be potentially more influential on the measured phenotypic traits.

There was no effect of the system (island or mainland) on differences between population-level neutral genetic diversity, except when the geographic distance was omitted from the model and when we tested for the nonlinear response to geographic distance. This is surprising, because we expected greater variation in neutral genetic diversity between islands beyond the effect of geographic distance due to e.g. disproportionate dispersal difficulties when traversing larger saltwater barriers, or the hypothesised larger differences in population sizes between different islands compared to populations on the mainland. The geographic and macroclimatic distances potentially underlying the variation in neutral genetic diversity had no system-dependent effects either, because the interaction between these variables and the system type was not significant. Other relevant factors for neutral genetic diversity not tested here such as effective population size or population dynamics and stability could still differ between island and mainland systems. Nevertheless, none of the potentially involved factors caused consistent between-population differences in neutral genetic diversity in island versus mainland systems in our study. Consequently, the spatial patterns of neutral genetic diversity are driven, at least partially, by different mechanisms compared to the spatial patterns of phenotypic traits, which are clearly governed by forces that differ between island and mainland systems (Whittaker and Fernández-Palacios 2006, Santos et al. 2016). These results provide support for the universality of neutral processes across systems.

In line with our expectations, we captured a weak signal of a positive influence of geographic distance on the mean differences in neutral genetic diversity between populations, which was similar across islands and mainland populations. While spatial isolation is typically a much stronger driver of genetic differentiation between populations due to limits to dispersal and genetic drift (Sexton et al. 2014), the effects of geographic distance on spatial patterns of neutral genetic diversity seem globally weak and may be more heavily influenced by organismal life histories combined with environmental conditions, as advanced earlier by Orsini et al. (2013) and Lira-Noriega and Manthey (2014). Gene flow underlying genetic diversity is often not correlated with geographic distance between populations, but instead with the so-called 'resistance distance' (Unnithan Kumar et al. 2022), meaning that other physical barriers, such as topological features (rivers and mountains) or environment (forest versus open habitat) are much more important. Such features are taxon-specific and would hard to be measured with the current study design. Nevertheless, the simple geographic distance may still determine parallel patterns of neutral genetic diversity in both island and mainland system, despite the responses being overall weak.

The effects of environmental distance can override the effects of geographic distance on differences in neutral genetic diversity between populations (Lira-Noriega and Manthey 2014), but in our study, contrary to our expectations, macroclimate had no such effect in either system. As with the phenotypic differences, contrasting climatic requirements of different groups of species may make it difficult to distil generalisations over the course of global approaches. Extending the sampling design of island–mainland studies to

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evaluate responses across larger environmental gradients may be needed to strengthen signals of global macroclimate effects on neutral genetic diversity, as also suggested by the range of results in Lira-Noriega and Manthey (2014).

Reconciling island biogeography theories with complementary ecological and evolutionary theories has a high priority in the future agenda of island biology (Patiño et al. 2017). Our findings suggest that comparative tests of general isolation-by-distance and isolation-by-environment expectations in island and mainland systems, on populations of the same species, offer promise in achieving such a reconciliation. In global comparative analyses, there is an outstanding amount of unexplained variability (e.g. 40–70% random species effect in De Kort et al. 2021). This was also the case for our dataset, with effects due to system type or variation associated with factors such as taxonomic diversity only capturing a small fraction of the variation between populations. While macroecological studies spanning global scales and across kingdoms, such as ours, typically have large levels of unexplained variation, they are expected to uncover fundamental spatial phenomena with large effect sizes. We found only relatively small effects of geographic distance in both island and mainland systems, indicating that the effect of this simple isolation measure, commonly used to explain between-population variation, is difficult to generalise or not as universal as previously thought. Context dependencies associated with different life histories, such as dispersal ability of particular species, biotic interactions, variable population sizes, specific colonisation and isolation histories etc. (De Kort et al. 2021) may weaken the effects of geographic distance on phenotypes and genetic diversity. For example, in our island systems the effect of geographic distance was lowered because we analysed oceanic islands together with continental islands that benefit more from the spatio-temporal connectivity with the mainland. Further, a nonlinear response of phenotypes and genetic diversity to geographic distance could be expected to indicate limits to the effects of geographic distance on particular phenotypes or on the genetic diversity of certain species, however we find no statistical support for it in this study.

We also expected stronger effects of kingdom (plant or animal), species or the phylogenetic relationships between species as in, e.g. Sexton et al. (2014), who found differences between plant and animal genetic responses to geographic and environmental distances. Because this was not the case in our dataset, we suspect that the low sample size (e.g. only seven plants in the phenotypic differentiation models) and the large range of traits each more or less responsive to geographic distance and/or correlated with each other to different extents might have hindered our ability to reveal general patterns. The magnitude of the differences between populations varied largely depending on the response type, but the amount of data available for particular response types was generally low, with the exception of body size for the phenotypic traits and heterozygosity for the neutral genetic diversity. We therefore call for a careful investigation of context-dependent drivers of population variability across fundamentally different geographic systems, commensurate with the life history of particular organisms. Comparative functional connectivity studies are a promising avenue in this direction (Juhász and Oborny 2020, Kimberley et al. 2021).

The knowledge transfer between island and mainland systems is still limited. In a horizon scan of the state-of-the-art of island biogeography by Patiño et al. 2017, only 10.2% of respondents worked in both system types. We echo earlier calls (Patiño et al. 2017) for a better replication of the control mainland populations, which may massively improve the applicability of island biology studies in developing global biogeography models. Alternatively, studies could investigate spatial isolation mechanisms comparatively across different types of mainland systems ranging from ecological islands to continuous habitats, while perhaps benefiting from larger datasets. Further studies could explore differences in phenotypic traits and genetic diversity between different populations of the same island, having the potential to reveal parallel mechanisms building the variability of island and mainland populations.

Conclusions

We conducted a strong test of the generality of isolation effects, by comparing geographic and macroclimatic distance effects in paired island and paired mainland populations within the same species, on a diversity of response variables measured on a range of taxa. Our results suggest that while eco-evolutionary pressures that shape phenotypic traits are likely to differ more between different islands than between mainland populations, they do not cause consistent between-population differences in neutral genetic diversity across island and mainland systems. These findings have deep implications for future models of population variability at biogeographic scales, which we show can be improved by considering the spatial structure of species' habitats in addition to the commonly employed predictors of environmental conditions or geographic distances between populations. While small marine islands are situated at the extreme end of a spatial isolation continuum, they can serve to understand the interacting causes of spatial population variability globally. Our findings may also be useful guides in conservation decisions. The spatial extent of protected areas could be tailored to preserve system-dependent biological processes, thus larger areas may be necessary to preserve similar levels of phenotypic variability in homogeneous than in spatially more structured habitats.

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.h18931zqg (Csergő et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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