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RESEARCH ARTICLE

Functional diversity and community convergence of land snails in the Aegean Sea islands

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Abstract

Aim: Island biological communities are considered to comprise non-random assemblages from surrounding source pools, but whether they converge towards predictable structural properties remains unclear. Here, we (i) test whether insular communities of land snails converge towards similar functional and/or taxonomic properties and (ii) evaluate whether island functional diversity is determined by island biogeographical characteristics such as area and distance to the pool as well as human-related variables.

Location: Sixty-six continental Aegean islands.

Taxon: Land snails.

Methods: We compiled a database of two morphological traits with functional significance (shell height and width) for 163 island species and 1529 species from the major species pools. We quantified inter-specific morphological dissimilarity between pairs of islands (turnover), using a modified index of the mean nearest taxon distance. We tested for functional and taxonomic convergence using null models and assessing whether overall mean turnover among islands and pairwise island-by-island turnover were lower than expected by chance. We performed multiple regression analyses to test whether functional diversity metrics scale with island biogeographical characteristics and human-related variables.

Results: Our analyses provide strong evidence that communities of land snails across the Aegean islands converge towards non-random functional properties and taxonomic structure. At the island level, a wide range of different shell shapes is observed, indicating greater functional richness than expected by chance. Regression analyses showed that island area is the only efficient predictor of functional diversity, indicating that available ecological/resource space is of central importance in driving the assembly of different shell shapes.

Main Conclusions: Our findings, consistent with previous studies of other taxa from oceanic islands, highlight that island species communities are not randomly assembled and display convergence in their functional and taxonomic composition. Integrating functional diversity metrics within biogeographic analyses has the potential to further our understanding of island biodiversity patterns.

1 | INTRODUCTION

How species assemble into spatially discrete communities has been a central research theme for decades. Islands, comprising geographically discrete spatial entities, have offered an amenable stage for research regarding the processes shaping community assembly (see Emerson & Gillespie, 2008; Whittaker et al., 2023). In essence, species can be added to a community through dispersal and colonization from surrounding species pools and through in situ evolutionary change, while extinction acts in the opposite direction, removing species from established assemblages. These processes operate continuously, generating an ever-changing dynamism in community composition, structure and the distribution of functional traits (Emerson & Gillespie, 2008; Gilbert & Levine, 2017). While chance and historical contingency (Chase, 2003) may, to some degree, influence these processes, there is much evidence that species assembly on islands is non-random under similar environmental conditions, with dispersal and environmental filters playing crucial roles (Simberloff & Wilson, 1970; Diamond, 1975; Tilman, 2004; and see Whittaker et al., 2023 for review).

The seminal Equilibrium Theory of Island Biogeography (MacArthur & Wilson, 1963, 1967) has proved invaluable in understanding patterns and processes in community ecology (Emerson & Gillespie, 2008; Warren et al., 2015; Santos et al., 2016), especially from the viewpoint of island species richness, which is described within the theory as being determined by a dynamic equilibrium between immigration, speciation and extinction, which in turn rely on island size and isolation. Although the equilibrium theory, in its simplest form, provides a form of 'null model' of ecological equivalence at the species level (i.e. no inter-specific variation in dispersal ability, competitiveness and probability of extinction), its authors were well aware of the importance of species functional traits (i.e. morphological, physiological and/or phenological characteristics of an organism

that express aspects of its ecological strategy) in shaping community structure. In recent work, such functional traits have been integrated into biogeographic analyses based on the quantification of particular traits on a per species basis (e.g. Jacquet et al., 2017; Schrader et al., 2023). One pattern that has been observed through such approaches is the convergence of island communities towards similar functional structures and/or taxonomic composition, in ways that make island species assemblages distinct from their respective species pools, but more similar to one another than expected by chance (e.g. Si et al., 2022; Triantis et al., 2022). This pattern is reflected in the lower turnover of taxonomic composition and/or functional characteristics of island assemblages than expected by chance (Triantis et al., 2022). The processes leading to island community convergence between/among islands with similar environmental conditions include: (i) the establishment on islands of a non-random subset of colonists with specific traits shaped by dispersal (i.e. species able to vreach islands) and/or environmental filtering (i.e. species adapted to environmental conditions on the islands); and/ or (ii) in situ evolutionary change, driven by the selection of specific morphological/functional traits (see Weigelt et al., 2015; Triantis et al., 2022). For example, dispersal and environmental filtering are likely to result in the underdispersion of traits (i.e. less trait variation than expected, based on a given source pool) that reflect dispersal ability and habitat or climatic controls (Weiher & Keddy, 1995; Fukami et al., 2005; Silva & Batalha, 2008).

The search for community-wide convergence thus becomes critical for deciphering the major processes leading to observed species assemblages because it can offer strong evidence in favour of a repeatable, predictable process. So far, insular community convergence has only been detected in relatively local-scale settings – such as nearby sets of islands (Losos et al., 1998; Mahler et al., 2013) and lakes (Seehausen, 2006; Muschick et al., 2012) – and oceanic islands (Gillespie, 2004; Si et al., 2022; Triantis et al., 2022), with the

number of studies addressing convergence at the community level across large scales of time and space remaining limited (see Moen et al., 2016; Triantis et al., 2022).

In the present work, we test for among-island functional community convergence in the land snails of the Aegean islands and examine the role of key environmental features as potential drivers of functional diversity at the island level. The islands of the Aegean Sea constitute one of the largest archipelagos on Earth (>7500 islands). They are located at the intersection of three continents and are mostly 'continental' islands (sensu Whittaker et al., 2023), having been connected to the current Greek and Turkish mainland. Due to their high topographic heterogeneity, complex geological and palaeogeographical history, highly diverse environmental properties and the presence of humans for at least 10,000 years, the Aegean islands have provided a globally unique natural laboratory for numerous ecological and biogeographic studies (Sfenthourakis & Triantis, 2017). We focus on 66 islands which share three key environmental features: (i) temperate latitude and Mediterranean climate; (ii) similar main vegetation types (arid to semi-arid Mediterranean vegetation, e.g. phrygana and maquis); and (iii) persistent change in geographical isolation, mainly due to long-term tectonic and eustatic events during the Pleistocene sea-level fluctuations, with most islands having experienced repeated connections between themselves and/or the mainland (Figure S1).

Land snails are valuable for identifying community assembly processes on islands as they are numerous – globally counting more than 11,000 insular species, with c. 75% being island endemics (Proios et al., 2021) – and exhibit a broad spectrum of shell shapes, resulting in high morphological diversity (Triantis et al., 2016) that is known to be linked to functional properties (Astor et al., 2014). For example, shell height and width, and their combined measurement as size (the geometric mean of height and width) and spirality (the ratio height/width) have been found to correlate with habitat preference (e.g. Cameron & Cook, 1989; Cook, 1997), niche differentiation among closely related species (e.g. Chiba, 2004) and extinction selectivity (e.g. Chiba & Roy, 2011). The land snails of the Aegean islands include more than 417 species – with c. 217 being island/archipelagic endemics – and they are found in various ecosystems, from typical (semi) arid Mediterranean vegetation (e.g. shrublands) and cultivations to bare rocky areas with scarce vegetation and urban/peri-urban ecosystems. These features, along with the Aegean archipelago's distinct biogeographical profile, provide a particularly useful stage for detecting island community assembly processes at the regional scale. We specifically address (i) whether functional diversity as measured through two morphological features (land snail shell height and width) reflects a deterministic mode of community assembly, that is whether land snail communities of different islands converge (i.e. functional convergence) towards predictable structural properties; (ii) whether functional convergence is matched by taxonomic convergence; and (iii) whether the functional diversity of insular land snails at the island level is driven by typical biogeographic processes (colonization, speciation and extinction) and thus related to island area, isolation, environmental heterogeneity and human influence.

2 | MATERIALS AND METHODS

2.1 | Data collation

We acquired complete species lists of the extant land snail faunas of 66 islands of the Aegean from a newly collated global database of insular land snails (Proios et al., 2021), and updated it with records kept at the Natural History Museum of Crete (NHMC). We excluded slugs and semi-slugs as they do not possess a fully developed shell. The malacofauna of these islands is well-studied, and reliable faunal lists for each of them are available (e.g. Maroulis et al., 2022; Mylonas & Vardinoyannis, 2022). We categorized islands into three island groups, namely, Northern, Eastern and Central Aegean islands, following the network-based bioregionalization provided in Triantis et al. (2018), spatial proximity and overall biogeographic affinity. We also collated complete species lists for three potential species source pools, namely, the Turkish coastline (Schütt, 2005), Greece (Bank & Neubert, 2017) and European countries around Greece, including countries of the Balkan peninsula and Italy (Bank & Neubert, 2017; Figure 1). We standardized species and genus names following MolluscaBase (2022).

For each species across the 66 islands ($n = 163$) and across the three species pools (892 species for the European, 673 for the Greek and 308 for the Turkish coastline), we retrieved morphological data of shell height and width from the AnimalBase Project Group (2023) database. When multiple measurements or ranges were provided for one species, we took the average value. For a small number of species ($n = 50$) not included in this database, we manually measured shell height and width from specimens kept at the NHMC. These measurements were taken parallel or perpendicular to the columellar axis (Cain, 1977). Although some measurements retrieved from AnimalBase may not have been taken following this method, such a discrepancy is commonly considered negligible relative to inter-specific morphological variation (Cowie, 1995).

We extracted geospatial data for the 66 islands from the Global Shoreline Vector dataset (Sayre et al., 2019). We considered six environmental variables as potential determinants of functional diversity: (i) island area (in km²), calculated as the two-dimensional planar surface of an island's polygon projected in a Mollweide equal-area projection; (ii) current closest distance to mainland (in km); (iii) past connection between an island and neighbouring mainland at a sea-level stand of 65m below present (a categorical variable classifying an island as being connected to mainland or not), which represents the median – most persistent – sea level of the last ~800 kyr, and has been shown to have the stronger imprint on the invertebrate native non-endemic species richness of Aegean land-bridge islands compared to
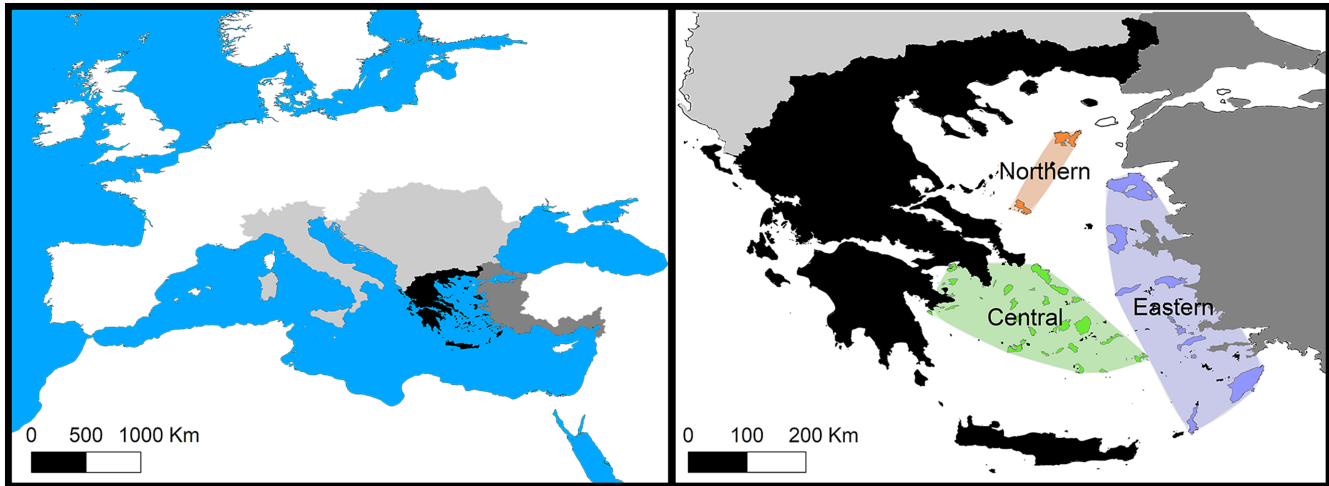
FIGURE 1 Left: The three species pools considered to determine community assembly in 66 Aegean islands. Black: Greece. Dark grey: coastline of Turkey. Light grey: European countries, including countries of the Balkan peninsula and Italy. Right: in colour, the 66 focal islands of the Aegean examined for community assembly processes: 16 islands in the Eastern Aegean group (blue), 8 islands in the northern Aegean group (orange) and 42 islands in the Central Aegean group (green).

island-mainland connections during the much briefer sea-level stand of the Last Glacial Maximum (i.e. 135m below present, see Hammoud et al., 2021); (iv) maximum elevation above sea level (in m), used as a proxy for environmental heterogeneity and extracted from the 30 arc-second (~1 km) digital elevation model of the Global Multi-resolution Terrain Elevation Data 2010 (GMTED2010; Danielson & Gesch, 2011); (v) human population density, obtained from the Gridded Population of the World version 4 (GPWv4; Doxsey-Whitfield et al., 2015) for most islands and complemented by national population censuses; and (vi) human extent of presence across an island, calculated as the proportion of island area covered by human activities, that is artificial and agricultural areas according to the Corine Land Cover 2018 dataset (European Union, 2018).

2.2 | Assessment of functional diversity

We quantified functional diversity of insular communities using two measures: (i) the morphospace (MS) calculated as the kernel density two-dimensional hypervolume (see Mammola & Cardoso, 2020) defined by shell height and width; and (ii) the mean morphological distance (MMD) between species on each island calculated by averaging the Euclidean distances between all species pairs in the two-dimensional MS defined by shell height and width. MS is a measure of functional richness, the amount of MS occupied by a given sample of species. MMD is a measure of the dispersion of different morphological species forms within a given sample of species (Foote, 1997). To calculate MS and MMD, we used the R package BAT (Cardoso et al., 2015) in R (R Core Team, 2022). For the MS hypervolume, we used a Gaussian kernel whose bandwidth was determined using a Silverman estimator applied to the entire species pool trait dataset (see Ali et al., 2023).

2.3 | Measurement of morphological turnover

We quantified differences in shell form among species between island pairs using a modified version of the mean nearest taxon distance (MNTD) sensu Triantis et al. (2022). This metric is designed to focus on morphological turnover (i.e. replacement of species traits among islands) and is usually referred to as $MNTD_{TURN}$ (Webb et al., 2008; Holt et al., 2018). For a pair of islands, A and B, $MNTD_{TURN}$ is calculated as:

$$MNTD_{TURN(A,B)} = min\left[\left(\frac{1}{n}\sum_{i=1}^{n}min(d_{iB})\right),\left(\frac{1}{m}\sum_{j=1}^{m}min(d_{jA})\right)\right]$$

where n and m are the species richness of islands A and B, respectively, $min(d_{iB})$ is the morphological distance between each species i of island A and the nearest (in terms of morphological distance) species of island B, and $min(d_{jA})$ is the distance between each species j of island B and the nearest species of island A. If the least diverse island has no unique species, then $MNTD_{TURN}$ is zero. On the other hand, if two islands have completely distinct species and their species richness is the same, $MNTD_{TURN}$ is equivalent to MNTD (see Triantis et al., 2022). The morphological distances between species in different islands, based on the two-dimensional MS defined by shell height and width, were calculated using Euclidean distances. The overall $MNTD_{TURN}$ across all 66 islands was taken as the mean value of all pairwise comparisons.

2.4 | Null model

To test for convergent community structure, we followed the method described in Triantis et al. (2022) and examined whether the overall mean $MNTD_{TURN}$ among the 66 islands, as well as pairwise $MNTD_{TURN}$ values between islands, were lower (i.e. convergence)

or higher (i.e. divergence) than expected by chance, respectively. To achieve this, we compared observed $MNTD_{TURN}$ values with those generated by a null model based on random morphological differentiation. We generated 1000 null communities for each island to simulate the expected morphological turnover values. Each island's null communities were constrained to have the same species richness as the observed one. Because the influence of each of the three species pools on each island is expected to differ due to different spatial proximities, we weighted the contribution of each species pool to each island's null community by calculating the inverse of the closest island-pool distance. In other words, for a given island, species from the closest pool had more chance to be selected during the null simulations than species from a more distant pool. Because different species pools might contain the same species, we ensured that null communities did not contain duplicated species from different pools. These simulated data were used to create 1000 random values for each pairwise $MNTD_{TURN}$ value and 1000 average pairwise $MNTD_{TURN}$ values across all island pairs. Deviation from the null expectation was assessed for each pairwise $MNTD_{TURN}$ value and for the overall mean $MNTD_{TURN}$ using the standardized effect size (SES). The SES was calculated as $(MNTD_{TURN} - \mu_{sim})/\sigma_{sim}$, where μ_{sim} is the mean of the simulated values, and σ_{sim} is the associated standard deviation. Negative and positive SES values indicate, respectively, lower and higher morphological $MNTD_{TURN}$ than expected by chance. Values greater than 1.96 or less than −1.96 were considered to be significantly higher or lower than expected, respectively (Gotelli & McCabe, 2002). We also assessed the significance of the deviations of the observed $MNTD_{TURN}$ values from the null distributions by identifying the proportion of null distribution values below or above the observed value.

To derive insights into whether community convergence patterns are differentially affected by the rates of endemism across islands, we ran the above analysis for all species and separately for endemic (as a proxy for in situ adaptation and speciation) and non-endemic faunas (as a proxy for dispersal and environmental filtering). We performed the last two analyses with a subset of 63 islands, after excluding three islands with no endemic species (see Figure S2 for the distribution of the number of endemic and non-endemic species across islands).

We also used the above null model method to simulate the null kernel density two-dimensional MS and the null MMD among species for each individual island. We derived the SES values for both MS and MMD for each island to test whether MS and MMD were lower or higher than expected by chance. Finally, to test for correspondence between morphological and taxonomical assembly patterns, we assessed whether the overall and pairwise genera compositional turnover between islands and island-specific genera richness and species/genus ratios were lower or higher than expected by chance using the same null model as detailed above. Deviations from the null expectation were assessed using SES values as specified above. We computed generic compositional turnover using the 'dist. prop' function of the 'ade4' R package (Thioulouse et al., 2018), applying the Manly method (Manly, 1994).

2.5 | Scaling of functional diversity with biogeographic variables

To test the relationship between functional diversity and the six biogeographic variables described above (area, distance to mainland, past island-mainland isolation, maximum elevation, human population density and human presence), we fitted two generalized linear mixed-effect models (GLMMs), using the SES values obtained for functional richness (MS) and dispersion (MMD) as response variables. SES values were preferred to the raw values because they allow testing of how biogeographical variables can explain trait-based assembly processes (functional clustering vs. overdispersion) and also because, unlike the raw values, SES values are statistically independent of species richness. The GLMMs were fitted with the 'glmer' function of the 'lme4' R package (Bates et al., 2015), using a Gaussian error structure and including island group (i.e. Northern, Eastern or Central Aegean islands) as a random (intercept) effect to account for spatial pseudoreplication (sensu Bunnefeld & Phillimore, 2012). Using the same random effect structure for all models, we performed model selection using the 'dredge' function in the 'MuMIn' R package (Barton, 2012) to fit all potential models and then considered those having similar empirical support based on the AIC_c being within <2 ΔAIC_c of the lowest value (Burnham & Anderson, 2002). We evaluated explained variance by computing marginal (fixed-effect only) and conditional (fixed and random effect) pseudo-R^2 values with the 'r.squaredGLMM' function of the 'MuMIn' package (Barton, 2012). Before applying the GLMMs, we checked for collinearity among the six explanatory variables by calculating pairwise Pearson correlations. Since no sign of collinearity was detected ($|r_z| < 0.7$; Figure S3, see Dormann et al., 2013), we subsequently $\log_{10}$-transformed all explanatory variables and standardized them to a mean of zero and unity standard deviation (SD; i.e., $(x - \bar{x})/SD$), which allowed for direct comparison of model coefficients.

3 | RESULTS

3.1 | Functional convergence

Regarding comparisons among islands, we found that the overall turnover in shell form among the 66 islands was significantly lower than expected by chance (SES = −18.53, $p = 0.002$, two-tailed), indicating convergence in community functional structure (Figure 2) at the whole archipelago scale. All islands exhibited significant shell form similarity (lower pairwise $MNTD_{TURN}$ than expected) with at least one other island and 87% (1862/2145) and 94% (2010/2145) of pairwise island comparisons exhibited significant convergence in functional and taxonomic structure, respectively (Figure 3a). Convergence in functional properties was more pronounced between islands of the same island group (i.e., Northern, Central, or Eastern; see Figure 3a). These results were also consistent for endemic and non-endemic faunas; for both, we found that the overall turnover in shell form across 63 islands was significantly lower than expected by chance
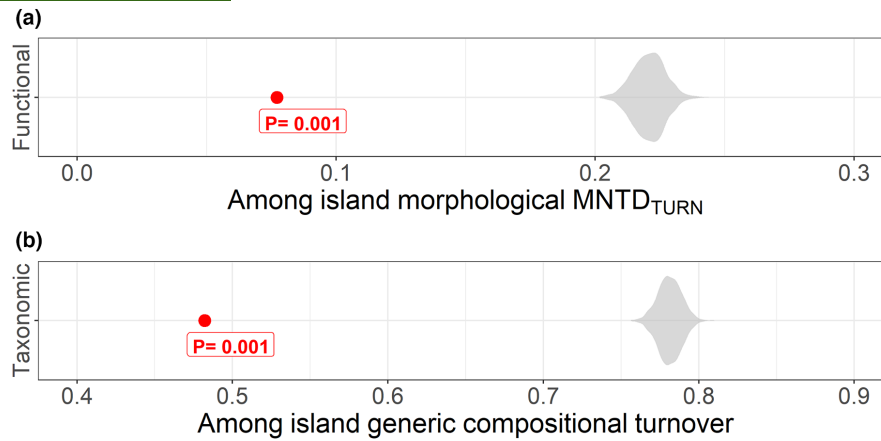
FIGURE 2 Land snail faunas of 66 Aegean islands converge on repeated patterns of (a) functional (in terms of shell height and width) and (b) taxonomic (in terms of genera composition) structure. Functional turnover (functional $MNTD_{TURN}$) is measured through the shell form defined by shell height and width (i.e. the Euclidean distances between species). Taxonomic turnover is measured in terms of genera composition, using the proportion of each genus on each island. Dots indicate observed average turnover between pairs of islands (among-island turnover). Violin plots show the distribution of average $MNTD_{TURN}$ calculated from 1000 simulations using a null model with random morphological and taxonomic structure. Red boxes show the p-values of the two-tailed tests.

(SES $= -17.17$, $p = 0.002$, and SES $= -7.13$, $p = 0.002$, respectively), with the turnover in endemic species (mean $MNTD_{TURN} = 0.33$) being higher than that of non-endemic species (mean $MNTD_{TURN} = 0.06$; see Figure S4). However, on a pairwise island-by-island basis, the functional convergence was much more pronounced for non-endemic faunas – for which all islands exhibited significant shell form similarity with at least one other island (1694 out of 1953 pairwise island comparisons; Figure S5a) – in comparison with endemic faunas, for which significant functional convergence was only observed for a minority of pairwise comparisons (187 out 1953 pairwise island comparisons; Figure S6a).
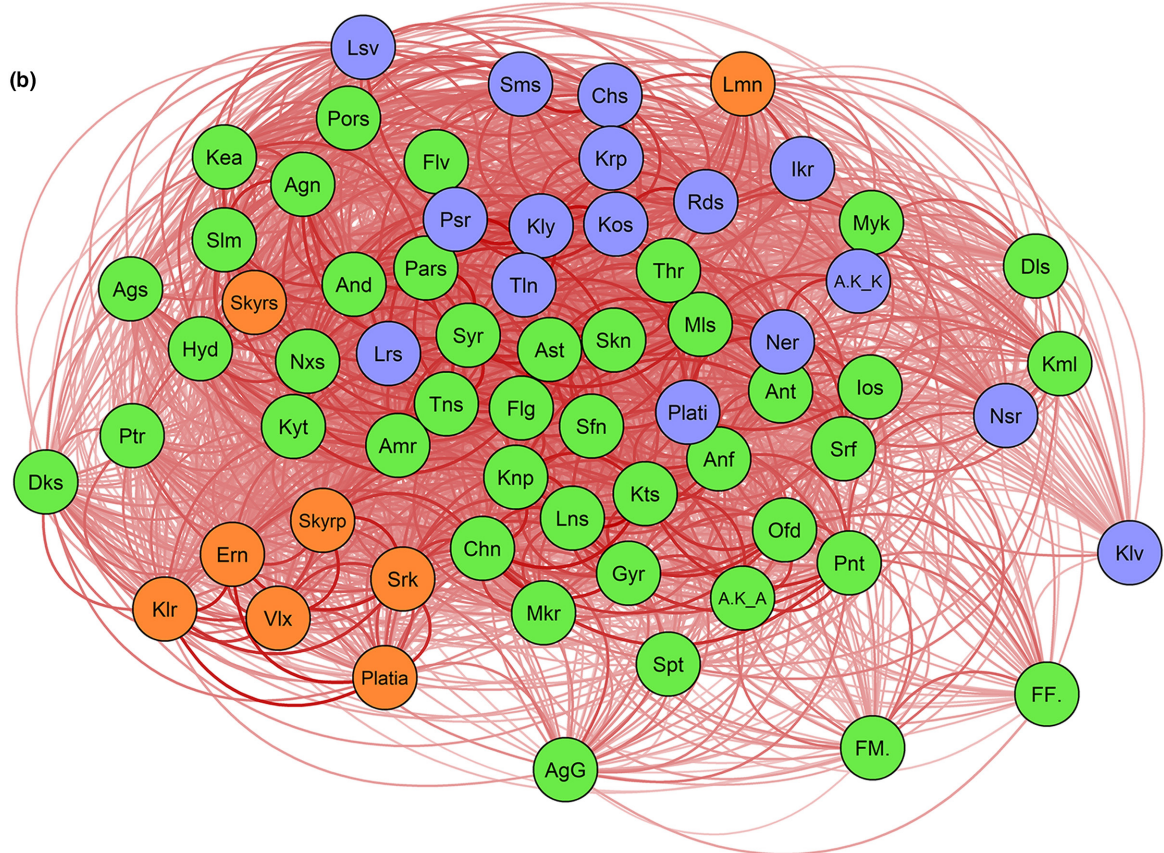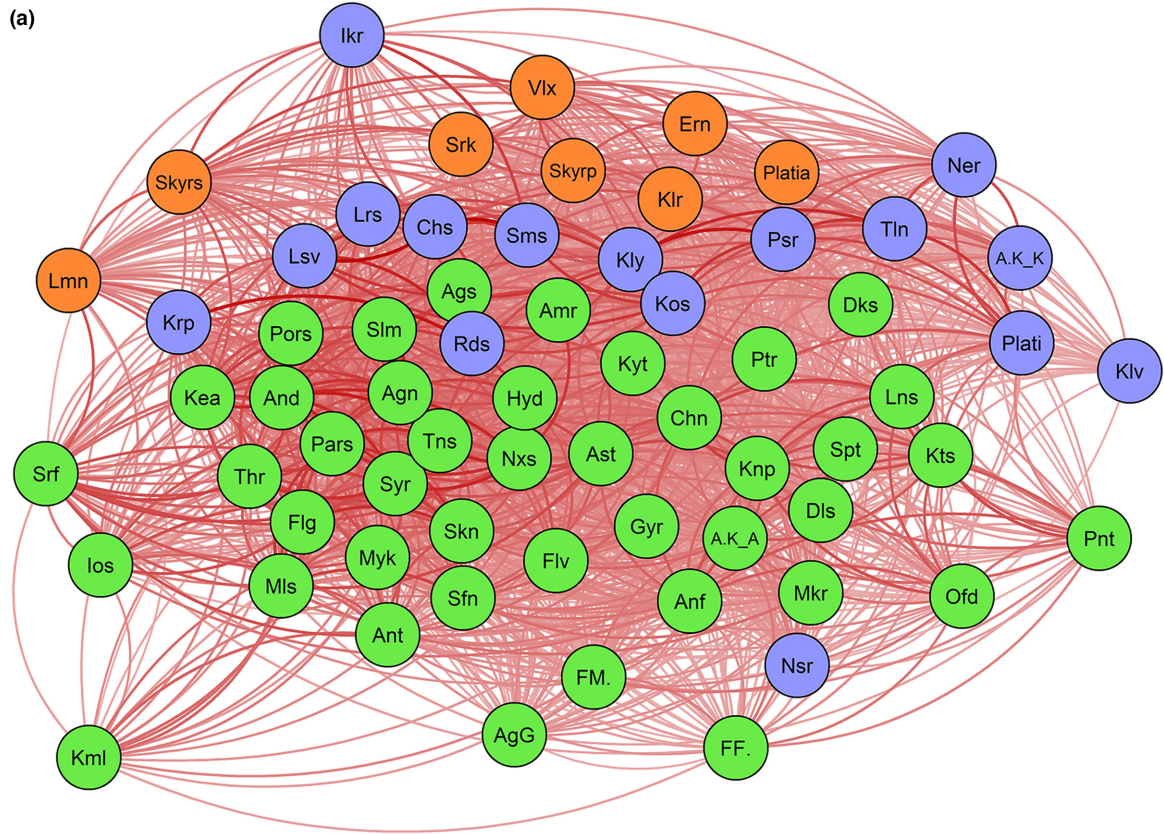
3.2 | Taxonomic convergence

The overall turnover in genera composition was significantly lower than expected by chance (SES $= -24.43$, $p = 0.002$, two-tailed), indicating convergence in community taxonomic structure (with regard to the

proportion of genera each island hosts; Figure 2b). All islands exhibited significant similarity in genera composition with at least one other island (2010 out of 2145 pairwise island comparisons; Figure 3b). As with functional diversity, convergence in taxonomic structure was more pronounced between islands of the same island group, except for a couple of islands – Limnos and Skyros, both belonging to the Northern Aegean island group – which exhibited more similarity with islands outside their island group (Figure 3b). These results were highly congruent when considering non-endemic and endemic faunas separately (Figures S5b and S6b, respectively).

3.3 | Island-level functional diversity and its scaling with biogeographic variables

The majority of islands had higher functional richness (MS) than expected by chance, indicating an overdispersion in shell height and width (SES > 1.96 for 62/66 islands; Figure 4a), and all 66 islands had

FIGURE 3 Convergent properties in (a) morphological and (b) taxonomic structure of 66 Aegean Island snail faunas. The networks show convergence properties in shell height and width (a) and genera composition (b). Nodes correspond to the 66 islands and colours of nodes correspond to island groups: blue = Eastern Aegean, orange = North Aegean, green = Central Aegean. A pair of connected nodes indicates significant convergence, with darker shaded lines indicating higher convergence than light shaded lines; the absence of connectors indicates no difference from null expectations. Convergence was estimated by comparing pairwise morphological and taxonomic turnover between pairs of islands against the distribution of values calculated from 1000 simulations using a null model with random morphological and taxonomic differentiation. A pair of islands was considered convergent when the observed dissimilarity was below the lower bound of the 95% confidence limits of the null model distribution (SES values below −1.96). Of all pairwise comparisons ($n = 2145$), 1862 pairs and 2010 pairs significantly converge in shell form and genera composition, respectively (SES < -1.96). Island names are as follows: A.K_A, Agia Kyriaki_Astypalaia; A.K_K, Agia Kyriaki_Kalymnos; AgG, Agios Georgios; Agn, Aegina; Ags, Agistri; Amr, Amorgos; And, Andros; Anf, Anafi; Ant, Antiparos; Ast, Astypalaia; Chn, Chondros; Chs, Chios; Dks, Dokos; Dls, Dilos; Ern, Erinia; FF, Fokionisi F.; Flg, Folegandros; Flv, Fleves; FM., Fokionisi M.; Gyr, Gyaros; Hyd, Hydra; Ikr, Ikaria; Ios, Ios; Kea, Kea; Klr, Koulouri; Klv, Kalavros; Kly, Kalymnos; Kml, Kimolos; Knp, Kounoupoi; Kos, Kos; Krp, Karpathos; Kts, Koutsomytis; Kyt, Kythnos; Lmn, Limnos; Lns, Lianos; Lrs, Leros; Lsv, Lesvos; Mkr, Makronisos; Mls, Milos; Myk, Mykonos; Ner, Nera; Nsr, Nisiros; Nxs, Naxos; Ofd, Ofidousa; Pars, Paros; Plati, Plati; Platia, Platia; Pnt, Pontikousa; Pors, Poros; Psr, Pserimos; Ptr, Patroklos; Rds, Rodos; Sfn, Sifnos; Skn, Sikinos; Skyrp, Skyropoula; Skyrs, Skyros; Slm, Salamina; Sms, Samos; Spt, Spetses; Srf, Serifos; Srk, Sarakino; Syr, Syros; Thr, Thira; Tln, Telendos; Tns, Tinos; Vlx, Valaxa.
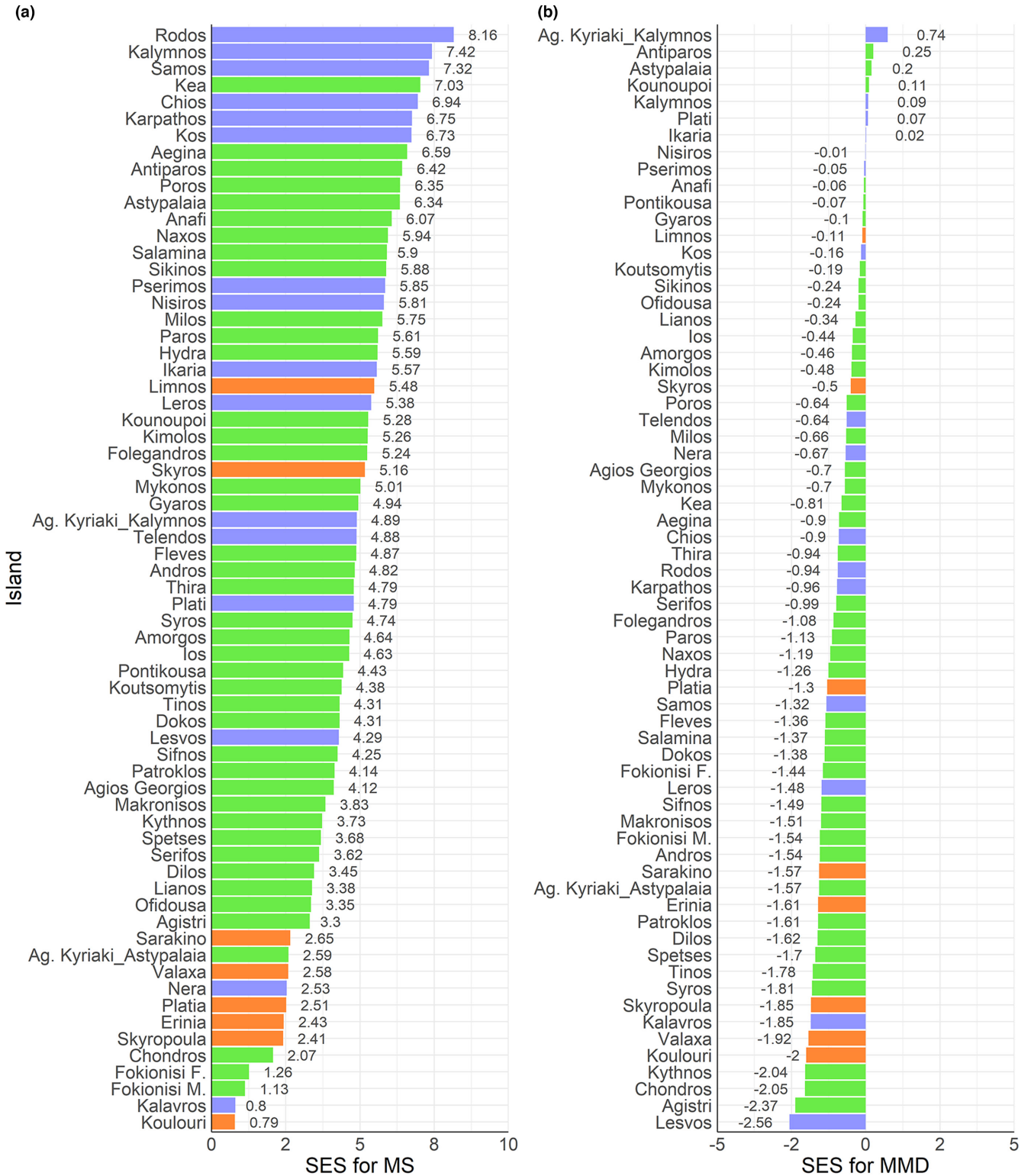
(a)

Island	SES for MS
Rodos	8.16
Kalymnos	7.42
Samos	7.32
Kea	7.03
Chios	6.94
Karpathos	6.75
Kos	6.73
Aegina	6.59
Antiparos	6.42
Poros	6.35
Astypalaia	6.34
Anafi	6.07
Naxos	5.94
Salamina	5.9
Sikinos	5.88
Pserimos	5.85
Nisiros	5.81
Milos	5.75
Paros	5.61
Hydra	5.59
Ikaria	5.57
Limnos	5.48
Leros	5.38
Kounoupoi	5.28
Kimolos	5.26
Folegandros	5.24
Skyros	5.16
Mykonos	5.01
Gyaros	4.94
Ag. Kyriaki_Kalymnos	4.89
Telendos	4.88
Fleves	4.87
Andros	4.82
Thira	4.79
Plati	4.79
Syros	4.74
Amorgos	4.64
Ios	4.63
Pontikousa	4.43
Koutsomytis	4.38
Tinos	4.31
Dokos	4.31
Lesvos	4.29
Sifnos	4.25
Patroklos	4.14
Agios Georgios	4.12
Makronisos	3.83
Kythnos	3.73
Spetses	3.68
Serifos	3.62
Dilos	3.45
Lianos	3.38
Ofidousa	3.35
Agistri	3.3
Sarakino	2.65
Ag. Kyriaki_Astypalaia	2.59
Valaxa	2.58
Nera	2.53
Platia	2.51
Erinia	2.43
Skyropoula	2.41
Chondros	2.07
Fokionisi F.	1.26
Fokionisi M.	1.13
Kalavros	0.8
Koulouri	0.79

(b)

Island	SES for MMD
Ag. Kyriaki_Kalymnos	0.74
Antiparos	0.25
Astypalaia	0.2
Kounoupoi	0.11
Kalymnos	0.09
Plati	0.07
Ikaria	0.02
Nisiros	-0.01
Pserimos	-0.05
Anafi	-0.06
Pontikousa	-0.07
Gyaros	-0.1
Limnos	-0.11
Kos	-0.16
Koutsomytis	-0.19
Sikinos	-0.24
Ofidousa	-0.24
Lianos	-0.34
Ios	-0.44
Amorgos	-0.46
Kimolos	-0.48
Skyros	-0.5
Poros	-0.64
Telendos	-0.64
Milos	-0.66
Nera	-0.67
Agios Georgios	-0.7
Mykonos	-0.7
Kea	-0.81
Aegina	-0.9
Chios	-0.9
Thira	-0.94
Rodos	-0.94
Karpathos	-0.96
Serifos	-0.99
Folegandros	-1.08
Paros	-1.13
Naxos	-1.19
Hydra	-1.26
Platia	-1.3
Samos	-1.32
Fleves	-1.36
Salamina	-1.37
Dokos	-1.38
Fokionisi F.	-1.44
Leros	-1.48
Sifnos	-1.49
Makronisos	-1.51
Fokionisi M.	-1.54
Andros	-1.54
Sarakino	-1.57
Ag. Kyriaki_Astypalaia	-1.57
Erinia	-1.61
Patroklos	-1.61
Dilos	-1.62
Spetses	-1.7
Tinos	-1.78
Syros	-1.81
Skyropoula	-1.85
Kalavros	-1.85
Valaxa	-1.92
Koulouri	-2
Kythnos	-2.04
Chondros	-2.05
Agistri	-2.37
Lesvos	-2.56

FIGURE 4 Standard effect sizes (SES) per island for (a) functional richness (MS), calculated as the kernel density two-dimensional morphospace defined by land snail shell height and width and (b) functional dispersion (MMD), calculated as the mean morphological Euclidean distance between species in each island in the two-dimensional morphospace defined by shell height and width. The SES values for MS and MMD were obtained through comparing the observed values with the distribution of values calculated from 1000 simulations using a null model with random morphological differentiation. Colours correspond to island groups: blue = Eastern Aegean, orange = North Aegean, green = Central Aegean.

positive SES values. In contrast, for most islands, functional dispersion (MMD) per island did not differ from that of the null communities (−1.96 < SES < 1.96 for 61/66 islands; Figure 4b), although 59 of the 66 islands had negative SES values. For most islands, the observed number of genera (ranging from seven to 46, mean = 22.82) did not differ from random (SES ranging from −0.79 to 1.93, mean = 1.09, Figure S7a), except for eight islands that exhibited higher than expected genera richness (SES ranging from 2 to 3.14, mean = 2.64, Figure S7b). These eight islands are all relatively close to mainland species pools: Lesvos, Aegina, Hydra, Poros, Salamina, Patroklos, Agistri and Makronisos (all but Lesvos, which is near the Turkish mainland, are located just off the coast of the central Greek mainland). Similarly, the observed species/genus ratio (ranging from one to 1.46, mean = 1.09) did not differ from that of the null communities for 61 islands (SES ranging from −1.86 to 0.74, mean = −1.02, Figure S7b), except for five islands, which exhibited a species/genus ratio lower than expected by chance (SES ranging from −2.41 to −2.09, mean = −2.27, Figure S7b). These five islands were a subset of the eight above-mentioned islands – namely, Lesvos, Salamina, Poros, Hydra and Aegina – and had a species/genus ratio higher than one (ranging from 1.04 to 1.1, mean = 1.07).

Functional richness (MS) was best explained by a model containing only island area, which had a significant positive effect (+ve) on, and accounted for 41% (i.e. $R^2_{marginal}$) of the variation in island SES values for MS (Table 1). The overall explanatory power of this model (i.e. $R^2_{conditional}$ including random effects) was 61%. The second-best model ($\Delta AIC_c = 1.5$) had roughly equal explanatory power ($R^2_{conditional} = 61\%$) and contained area and elevation but neither was significant (Table 1). The best model explaining functional dispersion (MMD) did not contain any of the six tested variables. The second-best model ($\Delta AIC_c = 0.9$) included only current distance to mainland (+ve), which offered marginal explanatory power ($R^2_{marginal} = 6\%$), with the overall explanatory power (i.e. $R^2_{conditional}$ including random effects) being 29% (Table 1).

4 | DISCUSSION

4.1 | Community convergence in Aegean island land snails

Our analysis of 66 Aegean island land snail communities provides strong support for convergence in both functional and taxonomic structure. This is, to our knowledge, the first time such a pattern has been reported, for continental islands. This pattern is revealed both as an overall mean across all islands (Figure 2) and on a pairwise island-by-island basis (Figure 3), in which case 87% (1862/2145) and 94% (2010/2145) of island comparisons exhibited significant convergence in functional and taxonomic structure, respectively, with islands belonging to the same island group clustering together under stronger convergence (Figure 3). These findings are in line with previous studies in oceanic island systems for other taxa, such as birds (Triantis et al., 2022), mammals (Si et al., 2022) and spiders (Gillespie, 2004), together showing that the processes guiding species assembly on islands are not wholly random and that island community convergence is rather a consistent pattern in nature, perhaps underlined by universal principles irrespective of the taxon or island system studied (cf. Gillespie, 2004).

Convergence in functional and taxonomic structure holds independently for endemic and non-endemic faunas at the whole archipelago scale, that is, across all islands (Figure S4). Functional convergence was more widespread in the case of non-endemic faunas (87% of pairwise island comparisons; Figure S5a), whereas, in endemic faunas, it was evident only for a minority of the island pairwise comparisons (9.6% of pairwise island comparisons; Figure S6a). Thus, non-endemic faunas seem to contribute substantially to the overall pattern (when considering all species together; Figure 3a), which might be due to the fact that the number of endemic species per island is much lower than the number of non-endemic species (Figure S2).

TABLE 1 Best models ($\Delta AIC_c < 2$) for functional richness (MS) and dispersion (MMD) standard effect sizes (SES).

	Intercept	Area	Elevation	Distance to mainland	R^2_M	R^2_C	ΔAIC_c
Response							
SES MS	4.50 (0.48)	1.12 (0.14)***	—	—	0.41	0.61	0
	4.51 (0.48)	0.77 (0.39)	0.37 (0.39)	—	0.42	0.61	1.5
SES MMD	−0.97 (0.17)	—	—	—	0.00	0.09	0
	−0.98 (0.25)	—	—	0.20 (0.09)*	0.06	0.29	0.9

Note: For each model, standardized regression coefficients (intercept and slope) are given along with their respective standard errors (in parentheses) and significance levels (***$p \leq 0.001$; *$p \leq 0.05$). Functional richness (MS) is calculated as the kernel density two-dimensional morphospace defined by land snail shell height and width, whereas functional dispersion (MMD) is calculated as the mean morphological Euclidean distance between species in each island in the two-dimensional morphospace defined by shell height and width. The SES values for MS and MMD were obtained through comparing the observed values with the distribution of values calculated from 1000 simulations using a null model with random morphological differentiation. Note that the SES values for MS for most islands are significantly positive, that is observed morphological richness is higher than expected by chance, whereas the SES values for MMD for most islands are not significant, that is observed morphological dispersion is not different from that expected by chance.

These findings indicate that in situ evolutionary change – as captured in the analysis of endemics – likely plays a minor role in the emergence of the observed island assembly patterns. In contrast, other processes captured in the analysis of non-endemic species seem to be more important in explaining functional convergence. We suggest four potential explanations. First, the existence of a dispersal/environmental filter leading to non-random colonization; land snails in the Aegean islands are mainly found in phrygana and maquis vegetation, whereas other habitats (e.g. dense forests, riparian habitats) – common in the mainland pools – are missing from most islands, resulting in an overall high inter-island similarity characterized by a limited range of environments. This inter-island habitat similarity is then likely to select for colonizers that are more similar in their functional traits than expected by chance. Second, a pre-existing inter-island faunal similarity; many of the focal 66 islands have been connected to each other, in some cases multiple times, and this is likely to have resulted in high faunal similarity, which is still evident among closely located islands (e.g. Triantis et al., 2008). Third, the existence of an environmental filter leading to non-random extinctions; because most of the Aegean islands we considered are of continental origin, a large part (at least) of their faunas may have established when they were part of mainland. Thus, functional convergence across entire and non-endemic faunas may be explained by ongoing relaxation processes (sensu Wilcox, 1978), assuming a faunal oversaturation at the time of isolation, followed by non-random extinctions driven by reduced carrying capacity of the islands after their isolation (see Triantis et al., 2008; Whittaker et al., 2023). Finally, in addition to the above-outlined natural non-random colonization and extinction, humans may also have had an effect on currently observed island snail communities and thus functional convergence. For example, their long presence in the broader Aegean region (see Sfenthourakis & Triantis, 2017) is likely to be linked with the spread of species on islands not previously present, either intentionally – as a food source (e.g. the case of *Levantina spiriplana*, see Korábek et al., 2022) – or unintentionally (e.g. the case of *Helix cincta*, see Korábek et al., 2021). These once introduced species have now become fully integrated within the observed 'native' faunas, raising faunal similarities among islands and thus leading to the emergence of functional convergence. Similarly, anthropogenic snail extinctions may also be non-random (Chiba & Roy, 2011). In practice, although there are not many recorded land snail extinctions across the Aegean islands, it is well established that the species being extirpated at the island level belong to specific genera (e.g. the genus *Zonites*; see Riedel, 1992). Which of these processes prevail in guiding community convergence in Aegean land snails requires further research.

Convergence in functional properties is matched by taxonomic convergence at the genus level (Figure 2); that is, the generic composition across islands represents a substantially distinct subset of the genera found in the species pools. Combined, these two findings support the view that genera, reflecting a deeper level of morphological divergence, relate more closely to niche occupancy – and thus functional traits – than speciation within genera (which is likely characterized by high trait conservatism). This recalls the concept of non-adaptive radiation (Gittenberger, 1991), in which geographically replacing species within a genus occupy the same functional niche, thus substantiating the view that genera rather than species are better at capturing the currency of functional diversity that matters (cf. Triantis et al., 2016). This finding is in line with previous pleas for the integration of functional diversity in island biogeographic studies, given that it has the potential to complement traditional taxonomic approaches and improve our understanding of the ecological processes driving island diversity patterns across time and space (Whittaker et al., 2014; Santos et al., 2016; Patiño et al., 2017; Schrader et al., 2021; Matthews et al., 2023).

4.2 | Explaining patterns of functional and taxonomic diversity at the island level

At the island level, functional richness (MS) is significantly overdispersed (Figure 4a). This means that the observed communities tend to be characterized by higher inter-specific trait variability compared to the variability of null communities derived from species pools, indicating that insular land snail communities of the Aegean occupy a broader morphological space than expected by chance based on their species richness. Considering that the two traits we used to measure functional diversity – shell height and width – have been shown to correlate with habitat preference (Goodfriend, 1986; Cameron & Cook, 1989; Cook, 1997), our findings are consistent with the hypothesis that the filling of ecological space by land snails on islands may be driven by niche partitioning. It is worth noting that overdispersion of functional traits underlies the theory of limiting similarity (i.e. species differing significantly in certain traits related to resource requirements are more likely to coexist; see MacArthur & Levins, 1967; Diamond, 1975) and has been invoked as a mechanism to explain niche differentiation in land snails (Chiba, 2004; Astor et al., 2014). In particular, Cain (1977, 1983) suggested that inter-specific variation in shell shape may indicate adaptation to different niches, while other authors have suggested that there is a strong association between shell shape and the nature of substrates on which they are active (e.g. Goodfriend, 1986). For example, Cameron and Cook (1989) argue for a mechanistic link between shell balance and the angle of substrate for optimized activity and resting, reporting that tall-spired Madeiran land shells are commonly found on vertical surfaces, flattened ones predominate on horizontal surfaces, while globular forms are more generalist in their preference for angle of substrate. Similarly, regarding the relative functional significance of shell size, Chiba (2004) reports that arboreal and semi-arboreal species of the genus *Mandarina* in the Bonin islands usually possess smaller shells than ground-dwelling ones. Finally, Cook (1997) reports that small and highly spired shells are more common in cooler and damper places than larger and flatter ones, pointing to the potential adaptation of different shell forms to different niches.

Notably, in our analyses, we used the raw values of shell height and width, as they provide a more direct measure of shell morphology compared to their transformation in size (the geometric mean of height and width) and spirality (height to width ratio). Other traits – such as microhabitat occurrence, diet or humidity preference (see Astor et al., 2014) – more directly related to niche occupancy could provide more solid foundations for examining these ideas; however, to date, such other traits are far less well quantified.

The number of genera and species/genus ratios did not differ from random for most of the island communities examined, except for a few islands ($n = 5$), which exhibited both a higher richness of genera and a lower species/genus ratio than expected by chance. Each of these islands is located close to mainland species pools, and therefore this inconsistency can potentially be attributed to the existence of a dispersal filter for more distant islands, which differentiates patterns of community assembly at a local (island) scale (Whittaker et al., 2023). This idea is supported by our findings of significant relationships between both the SES for genera richness and species/genus ratio with current distance to mainland (−ve for no. of genera and +ve for species/genus ratio; Table S1). Following this line of evidence, and as expected by the equilibrium theory of island biogeography (MacArthur & Wilson, 1963, 1967), islands closer to species pools should receive colonists more frequently than islands lying further away. Thus, communities on the former islands might be more likely to be characterized by greater numbers of genera. This pattern can also be explained on the basis of ongoing relaxation, with islands closer to the mainland likely having become isolated more recently than islands further away; hence, the implied extinction debt likely lags behind in the former islands, explaining why they still have a higher richness of genera and a lower species/genus ratio than expected by chance. It is worth noting that two of these five islands – Lesvos and Agistri – also exhibited convergence in functional dispersion MMD (lower dispersion than expected; Figure 4b), which indicates that communities might be getting denser in the height-width MS, possibly due to increased immigration compensating for any relaxation since the island became detached. Such immigration might be a consequence of mere propinquity, or be aided by human activity. Despite recent advances in our understanding of dispersal mechanisms (Cameron, 2016; Ożgo et al., 2016; Simonová et al., 2016; Roszkowska & Książkiewicz, 2022), evidence for species-specific-related dispersal traits remain scarce (e.g. Aubry et al., 2006; McKinney et al., 2019) and we lack a general framework for whether species with different shell height and width – and perhaps other traits such as shell size and shape – have a differential propensity for natural or anthropogenic dispersal.

4.3 | Scaling of functional diversity with biogeographic variables

Island area was the only predictor in the best model explaining the SES for functional richness, explaining 41% of its variation

(Table 1) and indicating that the processes leading to an overdispersion in trait variability across land snail communities of the Aegean islands likely depend solely on the available ecological space. Notably, island area is considered to be the single most consistent proxy for the available ecological space for species to establish (Triantis et al., 2012; Matthews et al., 2023), being able to capture, among other factors: (i) the direct effect of island size, that is the capacity of larger islands to support larger populations with lower extinction rates and therefore more species potentially with unique functional features; and (ii) the indirect effect of larger sizes, that is that larger islands have greater environmental heterogeneity and host a wider range of habitats/resources (Matthews et al., 2021; Whittaker et al., 2023). In this sense, area may still happen to be a better predictor of habitat variation than elevation (which we specifically included to capture the effects of environmental heterogeneity), so that some of the effects attributed to area could still be due to environmental heterogeneity (note that island area covaried with elevation at a level of $|r_\tau| = 0.68$; Figure S3). Taken together, these direct and indirect effects of island area on functional richness imply the potentially combined roles of (scale-dependent) chance and niche partitioning in guiding the co-existence of highly disparate morphological/functional shell forms at the island level. It is worth noting that the inclusion of island group as a random effect greatly improved the explanatory power of this model ($R^2_{conditional} = 61\%$), indicating that the processes determining functional richness in island land snail communities operate at a regional scale. This is also supported by our findings that convergence in both morphological traits and taxonomy is stronger between islands of the same island group (Figure 3), perhaps signalling the effects of regional variation in the available species pool. On the other hand, the SES for functional dispersion did not scale with any of the tested biogeographic predictors, consistent with the finding that the observed density of the MS is not different from that expected by chance (Figure 4b) and, thus, that the way it tends to be filled on islands of increasing area/richness is indistinguishable from random. However, this random filling might, to a certain degree, be influenced by the distance of an island to adjacent species pools, with islands closest to the mainland tending to have denser morphospaces (note the positive effect of distance to mainland in the second-best model for SES MMD; Table 1).

4.4 | Conclusions and future perspectives

Overall, our study suggests that the insular diversity of land snails across the Aegean is shaped through non-random, deterministic processes of community assembly and highlights that convergence in structural properties extends to both functional and taxonomic levels. These findings align with previous studies illustrating the utility of functional diversity in explaining patterns of island assembly (e.g. Triantis et al., 2022; Matthews et al., 2023; Schrader et al., 2023). Thus, the further integration of functional diversity into

the study of island biogeography is essential if we are to develop a generalized theory that extends to the study of island communities from the perspective of their traits.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are deposited in the Harvard Dataverse repository at https://doi.org/10.7910/DVN/40NUC0 (Proios, Maroulis et al., 2023), under an embargo of 2 years since the publication of the current manuscript.

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BIOSKETCH

The author team consists of biogeographers, evolutionary ecologists, biostatisticians and malacologists with diverse backgrounds and interests, including island biogeography, macroecology, community ecology and taxonomy.

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SUPPORTING INFORMATION

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