RESEARCH ARTICLE

Does island ontogeny dictate the accumulation of both species richness and functional diversity?

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Abstract

Aim: The accumulation of functional diversity in communities is poorly understood. Conveniently, the general dynamic model of island biogeography (GDM) makes predictions for how such diversity might accumulate over time. In this multiscale study of land snail communities on 10 oceanic archipelagos located in various regions of the globe, we test hypotheses of community assembly in systems where islands serve as chronosequences along island ontogeny.

Location: Ten volcanic archipelagos.

Time period: From 23 Ma to the present.

Major taxa studied: Endemic land snails.

Methods: Initially, we assembled geological island characteristics of area, isolation and ontogeny for all studied islands. We then characterized island-scale biotic variables, including the species diversity and functional diversity of snail communities. From these data, we assessed relationships between island and snail community variables as predicted by the GDM, focusing initially on the islands of the Galápagos archipelago and thereafter with a broader analysis of 10 archipelagoes.

Results: As in other studies of island assemblages, in Galápagos we find a hump-shaped curve of species richness, with depauperate snail faunas on early-ontogeny islands, increasing species richness on mid-ontogeny islands and low species richness on islands in late ontogeny. We find exceptionally low functional diversity on early-ontogeny islands that increases through mid-ontogeny, whereas late-ontogeny islands exhibit a range of functional diversity. The analysis including all 10 archipelagos indicates a major role of archipelago-specific factors. In both sets of analyses, functional diversity is exceptionally low on early-ontogeny islands, and island ontogeny is a significant predictor of morphology.

Main conclusions: Consistent patterns of functional diversity across island ontogeny on all examined archipelagos indicate a common role for habitat filtering, ecological opportunity and competition in a diversity of systems, leading to predictable changes in functional diversity and average morphology through island ontogeny, whereas patterns of species richness appear subject to archipelago-specific factors.

KEYWORDS
community assembly, geometric morphometrics, island biogeography, shell shape

1 | INTRODUCTION

The diversity of species in communities can be noteworthy at both extremes [e.g., biodiversity hotspots (Myers et al., 2000) versus recently deglaciated regions (Montoya et al., 2007)]. Communities actively transitioning between low and high diversity can shed light on the processes driving this change. Consequently, the accumulation and contraction of species in communities has been studied extensively through theory and simulation (MacArthur & Wilson, 1963, 1967; Whittaker et al., 2001, 2008), large natural stochastic events [e.g., Krakatau islands after the 1883 eruption (Ernst, 1908)], chronosequences of years to decades (reviewed by Walker et al., 2010), and in broader synthesis (Ricklefs, 1987). Although the number of species is a common focus of these studies, somewhat less attention has been given to the morphological variation within communities, particularly as that variation changes through evolutionary time (but see Fryer & Iles, 1972; Losos, 1992; Price et al., 2000).

The factors that determine community-level species richness are complex (Fine, 2015; Harmon & Harrison, 2015; MacArthur & Wilson, 1963, 1967; Ricklefs & Schluter, 1993). Abiotic features, such as intercommunity connectivity, habitat size, environmental complexity and total energy flowing into the system, can each influence overall species richness (Diamond, 1975; Gravel et al., 2011; Roell et al., 2021). Biotic features can also affect the species richness of communities [e.g., interspecific interactions (Carvajal-Enderas et al., 2017; Cottenie & De Meester, 2004; Diamond, 1975)]. Additionally, species morphology has the potential to direct evolutionary trajectories and influence patterns of species richness within and across communities (Losos, 2009; Sherratt et al., 2016). One measure of morphological variation that might be particularly important for both species ecology and evolution is functional diversity, which summarizes those species attributes that directly influence ecosystem processes (Tilman, 2001). However, the factors affecting such morphological variation within and among communities remain poorly understood (Borregaard et al., 2017).

Stimulated by the realization that species richness represents an oversimplified and incomplete quantification of biodiversity, recent empirical and theoretical studies have integrated additional evolutionary and ecological axes of diversity, such as phylogenetic, morphological, ecological and functional diversity (e.g., Flynn et al., 2011; Jacquet et al., 2017). One general consensus emerging from studies combining functional diversity with species richness is that these measures do not always coincide. In a recent biodiversity study of mammals from 782 terrestrial ecoregions across the globe, Mazel and colleagues (2014) found that functional and phylogenetic diversity saturate with increasing area more quickly than does species richness. Likewise, the functional diversity of bats on islands and nearby continental ecosystems in Panama was found to be less sensitive to habitat loss (i.e., decrease of area) than species richness (Farneda et al., 2020). Farneda et al. (2020) also found that both biodiversity metrics scaled in a fundamentally different manner with area depending on the ecosystem examined, suggesting that some key functions might be lost more quickly with habitat reduction on insular compared with continental ecosystems.

On islands, the simultaneous influence of colonization, speciation and extinction play out over recent geological time, and the relative simplicity of island over continental systems facilitates study (MacArthur & Wilson, 1963, 1967; Whittaker et al., 2008), particularly given that the mechanisms driving evolutionary change on islands are not thought to be unique to insular systems (e.g., Pinto et al., 2008). Oceanic volcanic hotspot archipelagos, in particular, are valuable in studying the accumulation of diversity because each island follows a natural life span of birth, growth, subsidence and eventual death. Thus, islands of varying ages across single archipelagos can serve as a series of snapshots through island life span, or ontogeny (Lim & Marshall, 2017; Nunn, 1994; Stuessy et al., 1998). Therefore, in addition to serving as study systems for understanding the effects of area and isolation on biodiversity, oceanic islands are particularly useful for untangling the dynamics associated with individual axes of ecological and evolutionary diversity as communities assemble, particularly through the general dynamic model of island biogeography (GDM; Whittaker et al., 2008).

The GDM makes clear predictions for the trajectory of environmental complexity and habitat diversity through island ontogeny. They are expected to be low when the island is newly formed and not yet shaped by erosion or other geological phenomena, higher as erosion and downcutting introduce both physical barriers and novel local environments, and lower again as erosion and island subsidence continue until the island founders (Whittaker et al., 2008). Species richness is predicted likewise to rise and fall along this trajectory: Few colonists comprise the low richness of young volcanoes; additional colonization and intra-island speciation events ensure a higher species richness on middle-stage islands; and high rates of extinction result in low species richness on sinking and eroding late-stage islands (Borregaard et al., 2017; Cameron et al., 2013; Triantis et al., 2015; Whittaker et al., 2008). When inter-island colonization remains low, the GDM predicts that species richness reaches a single peak approximately midway through island ontogeny.

Predictions for how morphological variation might change through island ontogeny can be more complicated and remain to be explored fully (Borregaard et al., 2017). At the broadest scales, species richness and morphological diversity are thought to evolve in concert (e.g., Rabosky et al., 2013). Likewise, at smaller scales, under the assumption that the youngest and oldest islands exhibit limited ecological opportunities for species, ecologically relevant morphological variation (hereafter termed "functional diversity") may be predicted to be lowest on these youngest and oldest islands, leading to a hump-shaped curve of functional diversity through island ontogeny (Mahler et al., 2010). Alternatively, competition among closely related species might be particularly high on eroding islands, preventing a decline of functional diversity as islands age (Borregaard et al., 2017; Whittaker et al., 2008). The phenomenon of competitive exclusion on declining islands can prevent multiple species from converging on one or a small number of morphological optima, instead maintaining a high degree of functional diversity even when species richness is low (Grant & Grant, 2006).

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Large-scale explorations of these hypotheses often combine datasets across multiple archipelagos (e.g., Jõks et al., 2021; Triantis et al., 2016; Weigelt & Kreft, 2013). Such examinations add much-needed power to hypothesis tests, typically involving hundreds of species across dozens of islands. Statistical power is necessary in these studies because comparisons between hypotheses frequently involve statistical models with eight or more parameters. A potential drawback to such analyses is that direct comparisons across archipelagos can obscure patterns specific to single archipelagos and particular lineages. Furthermore, measures of morphological diversity are not as easily compared among distantly related lineages as species diversity. Thus, a combined approach that identifies global-scale patterns among archipelagos while further interrogating highly detailed datasets from a single archipelago holds the most promise for testing complex hypotheses of species and morphological diversification on islands while simultaneously evaluating their generalizability at a broader scale.

Here, we initially characterize species richness and functional diversity of land snails in the Galápagos archipelago and thereafter test ideas related to their accumulation over time. Galápagos is a volcanic hotspot archipelago with islands of varying ages dotting the eastern Pacific Ocean, from the massive young volcanoes in the west to the highly eroded oldest islands in the east (Figure 1). Of all the species found in Galápagos, perhaps none has diversified to the extent of the land snail genus *Naesiotus*, with > 60 described species (and several currently undescribed species) occupying nearly every terrestrial habitat in the archipelago. Of note, snail populations on the youngest islands tend to be clustered at the highest elevations, where the environments are generally humid and plant diversity is highest (ACK & CEP, pers. obs.), whereas the lower maximum elevations of the oldest islands prevent the maintenance of humid habitat over large areas. Consequently, selection on morphological traits might differ for species on islands of different ages as availability of suitable habitats trend from primarily humid to primarily arid. Furthermore, a direct measure of ecological complexity (an analogue of ecological opportunity) is difficult for *Naesiotus* snails, but a reasonable approximation can be made by quantifying plant species richness and vegetated area, each of which is likely to contribute to ecological complexity (Lomolino, 2001). In *Naesiotus*, shell shape variation is tightly linked to environmental variation (Parent & Crespi, 2009), and might therefore best reflect changes in selective regimes along island ontogeny. For example, species found in arid regions of the archipelago often have relatively smaller apertures, presumably to reduce rates of water loss, whereas those found in humid regions have shell shapes that might minimize the use of shell material. Within communities, microhabitat variation may provide still more opportunities for ecologically relevant morphological evolution, which may, in turn, allow these snails to play a significant role in nutrient cycling and as prey (Kraemer et al., 2019). Notably, *Naesiotus* species dominate by far the malacofauna of these islands, in the number of species, extent of geographical distribution and population abundances (Chambers, 1986; Coppois, 1984; Miquel & Herrera, 2014; Smith, 1966). Here, we expand the dataset of Parent

and Crespi (2009) of shell morphology for 30 putative *Naesiotus* species to a total of 69, focusing on species and morphological variation along island ontogeny. An independent set of analyses for Galápagos is possible only with the diverse and detailed datasets described here. Future similar analyses might evaluate multiple archipelagos concurrently with the expansion of existing datasets.

We also use an existing dataset (henceforth referred to as the "global dataset") on land snail biodiversity from Triantis et al. (2016) to identify broader patterns of morphological variation across island ontogeny and to place the results of the Galápagos analyses in a global context. Relevant variables for the present study included in the global dataset are land snail species richness for all islands, island age, and the average height and width of the shell of each snail species. Perfect comparisons between this dataset and the Galápagos-specific dataset are not possible, although analogies can be drawn. For example, both datasets include measurements of shell morphology: The Galápagos dataset includes shell shape measurements, whereas the global dataset summarizes shell height and width for all species. Although these measures are not perfectly comparable, they allow us to compare morphological variation among distinct multispecies communities, focusing on the patterns found within rather than between datasets. We also evaluate hypotheses at the generic level, because previous studies identified different diversity patterns at the generic level compared with species (Triantis et al., 2016).

In this study, we test several predictions of the accumulation of species richness and functional diversity on volcanic mid-ocean islands. We predict that (1) snail species richness will rise and fall with island ontogeny. Under the hypothesis that ecological opportunity drives morphological variation along island ontogeny, we predict that (2a) the ecological complexity of snail habitats (as measured by plant species richness and size of vegetated area) will rise and fall with island ontogeny, and (2b) snail functional diversity will covary with plant species richness. Under the hypothesis that ecological opportunity is the main driver of functional diversity, we predict that (3a) snail functional diversity will rise and fall with island ontogeny. In contrast, under the hypothesis that competition drives the maintenance of functional diversity late in island ontogeny, we predict that (3b) snail functional diversity will rise with island ontogeny (without a subsequent decline). Finally, under the hypothesis that selection on snail morphology depends on local ecological conditions that change over the course of island ontogeny, we predict that (4) island ontogeny will be a significant predictor of snail morphology.

2 | METHODS

2.1 | Data collection: Galápagos data

2.1.1 | Island ontogeny

The major islands of the Galápagos Archipelago consist of seven young volcanoes and between nine and 11 major older islands.
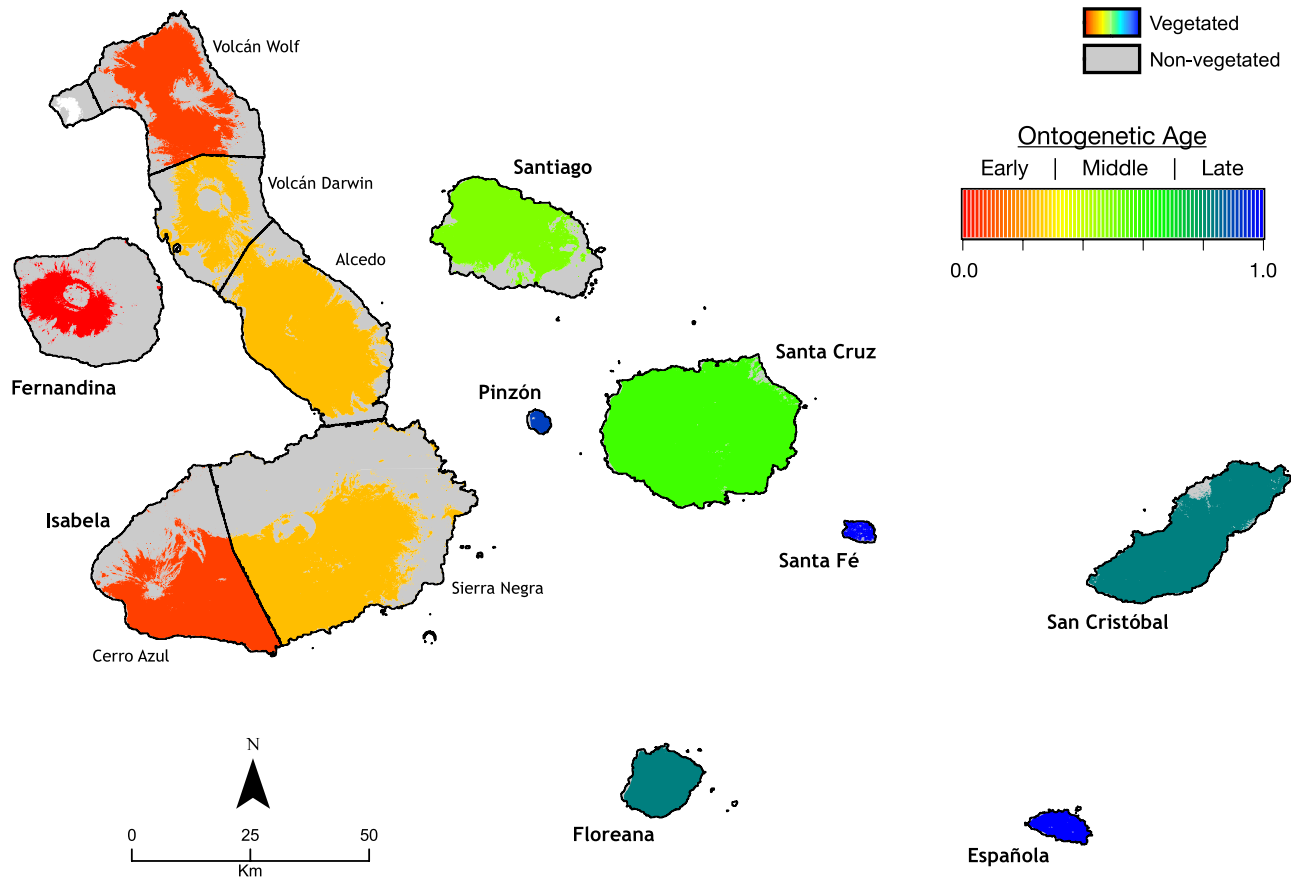
FIGURE 1 Map of the studied portion of the Galápagos Archipelago. Note how the young volcanoes of the western islands are partly vegetated, whereas the older eastern islands have become fully vegetated. Relative ages of islands are colour coded, with hotter colours indicating early ontogeny and cooler colours late ontogeny

Although six of the seven young volcanoes have merged to form the single landmass of Isabela Island, each volcano is separated from the others by barren lava flows that form impassible barriers for many species, including land snails. Any movement of snails from one volcano to another on Isabela would probably occur through the same modes of transport as inter-island colonization (e.g., through birds). We therefore consider these volcanoes effectively to be isolated islands in our analyses. We estimated relative ontogenetic age as the proportion of the life span of each island currently completed. This value was calculated using a Galápagos island subsidence model (Geist et al., 2014). Using known geological processes of thermal subsidence in volcanic archipelagos, the subsidence model identified an archipelago-wide rate of island subsidence, which, when combined with current island age and elevation, can be used to estimate the relative ontogenetic age of a given island. This is particularly valuable for testing biological predictions because some features of communities on islands may depend not only on strict community age, but also on other local features considered by island ontogeny, such as current elevation (Mahler et al., 2010).

Our goal here is to track the accumulation of diversity throughout the life span of islands, from the time they emerge until they disappear under the ocean surface. As such, to be comparable, the ontogenic progress of each island needs to be pinpointed on a common ontogenic time-scale. Using this approach, San Cristóbal and Española, two islands that are of similar geological ages, are revealed to be at distinct points along their ontogenetic life span (Figure 1). The former has a relatively complex landscape, large area and higher elevation, all typical of an island midway through its life span, whereas the latter has the simple landscape, small area and lower elevation typical of an island nearing the end of its life span. Using this framework, the island of Fernandina and the volcanoes of Isabela are considered early ontogeny, Santiago and Santa Cruz are midway through their life span, and Floreana, San Cristóbal, Santa Fe, Pinzón and Española are considered late ontogeny.

Our estimates of relative ontogenetic age make several important assumptions. Most importantly, the subsidence model we use assumes a common subsidence rate across the archipelago (Geist et al., 2014). This is likely to be an oversimplification, because subsidence can be influenced by factors such as stochastic geological events for each island, island placement relative to the Galápagos hotspot, thickness of the crust and maximum elevation reached. Until these factors can be measured at an island-level resolution, however, we will use a common subsidence rate for the archipelago.

2.1.2 | Island area and isolation

For each island and the volcanoes that form Isabela, we estimated area and isolation *sensu* Roell et al. (2021). Briefly, we used ArcMap v.10.3.1 (Esri, 2014) to identify boundaries between the volcanoes of Isabela, using the lowest elevation of the lava fields separating the volcanoes as biogeographical boundaries. We calculated isolation by averaging the shortest pairwise distance (coast to coast) from each focal island to every other island.

2.1.3 | Plant diversity

To quantify plant diversity, we used the total number of native and endemic species of vascular plants from the Galápagos checklist published by Lawesson et al. (1987), which is the most accurate voucher-backed checklist available that partitions the diversity on Isabela by individual volcano (see *Choice of plant species richness dataset* in Supporting Information).

2.1.4 | Plant vegetated area

For each island, we calculated the size of the area that was vegetated, and therefore potentially suitable for snail habitat, using a normalized difference vegetation index (NDVI; see *Island area calculations with NDVI* in Supporting Information).

2.1.5 | Snail diversity

We quantified snail diversity as the number of operational taxonomic units (OTUs) per island or volcano using an integrative, collections-based approach that takes into account all known published and unpublished data on the anatomy, morphology and phylogeny of Galápagos *Naesiotus* species. N.F.S. has examined all known museum material and is in the process of preparing taxonomic revisions of the group, which will be published separately (Shoobs, in prep.; Shoobs et al., in prep.). We determined OTUs in accordance with a conception of species as biological lineages with unique, diverging evolutionary trajectories (the unified species concept *sensu* de Queiroz, 2007). All OTUs we consider here are recognizable by their island of origin and a fixed (albeit arbitrary) degree of morphological difference, most frequently by unambiguous species-specific apomorphy in at least one shell trait. For the majority of OTUs, the taxonomic utility of these characters for the purposes of delimitation is supported directly by mitochondrial and genomic phylogenetic data (Parent & Crespi, 2006; Phillips et al., 2020), although the robust delimitation of species is neither the object nor the result of the present paper.

2.1.6 | Snail habitat

Vegetation in Galápagos has been divided according to various zonation schemes (e.g., Wiggins & Porter, 1971), although in nearly all cases these divisions have been made along elevation, with vegetation zones on each island forming concentric rings at particular elevations, owing largely to differences in precipitation at different elevations. Although several different partitioning schemes have been proposed, nearly all identify a low-elevation arid zone and a high-elevation humid zone, with few species shared between them. Although most other habitat designations present some species overlap, in *Naesiotus* all species are restricted to only the arid or the humid zone. Therefore, here we categorize all *Naesiotus* species as either belonging to the arid zone or the humid zone (*sensu* McMullen, 1999; Parent & Crespi, 2009).

2.1.7 | Shell morphology

We collected radiographs of individual shells for morphological analyses (number of shells = 1,789; 2–101 per species, with a mean of 25.9; number of species = 69). Shells were imaged with the axis parallel to the imaging plane, with the aperture facing up. We characterized shell shape and size using landmark-based geometric morphometrics (Adams et al., 2013; Bookstein, 1991; Mitterocker & Gunz, 2009; Sheratt et al., 2016). We used a combination of eight fixed landmarks representing homologous points and seven sliding semi-landmarks along the curved aperture or opening of the shell (Figure S1). We digitized all shells twice, using the R package Geomorph (Adams et al., 2020). We then aligned the landmark data using a generalized Procrustes superimposition, in which semi-landmarks were permitted to slide along their tangent directions to minimize Procrustes distance between specimens (Rohlf & Slice, 1990). The resulting Procrustes shape coordinates were averaged per specimen to reduce digitization error, and the subsequent reduced dataset of shape coordinates was used as variables for the shape analyses described below. Procrustes variance was used to calculate functional dispersion (Laliberté & Legendre, 2010), a distance-based measure of functional richness and divergence, in subsequent analyses. We used centroid size as an estimate of shell size for each individual (calculated as the square root of the sum of squared distances of all landmarks from their centroid; Rohlf & Slice, 1990).

2.2 | Data collection: Global archipelago dataset

From a multi-archipelago dataset assembled by Triantis et al. (2016) and Norder et al. (2019), we extracted data relevant to the hypotheses and predictions for the present study, including island age, island species richness, island area, and the height and weight of snail species for each island. From these morphological measurements, we calculated the convex hull volume, which is the minimum volume of functional trait space required to include all species within a community (Mason & Mouillot, 2013). To avoid complications arising from the extreme

variation in island ages among archipelagos, we set island ages by the oldest island in each archipelago. Thus, the oldest island in each archipelago received a relative age of one, and other islands received a relative age determined by a comparison to the oldest island in their archipelago. We supplemented the dataset assembled by Triantis et al. (2016) and Norder et al. (2019) with information regarding island isolation *sensu* Weigelt and Kreft (2013). More specifically, we used the metric "N16a" from that publication, which corresponds to the neighbor index of Kalmar and Currie (2006) and is calculated as the sum of the area of all neighbouring islands closer than the nearest mainland weighted by their squared distances.

2.3 | Statistical analysis

2.3.1 | Prediction 1: Snail species richness will rise and fall with island ontogeny

Galápagos dataset
We built a series of linear models to test this prediction, using the natural logarithm of snail species richness on each island as the response variable, with isolation, area and island ontogeny serving as predictor variables (with a squared island ontogeny term simulating the predicted rise and fall of diversity through island ontogeny). We then used the "*step*" function in R to identify the best-fitting model to predict snail species richness.

Global archipelago dataset
Prediction 1 was tested using the global dataset by incorporating archipelago as a random effect. Like Cameron et al. (2013), we began with a full model containing all possible fixed effects and evaluated the fit of all variations of models containing archipelago as a random effect. After choosing the best full model with a random structure, we identified the best model among the possible combinations of fixed effects using the corrected Akaike information criterion (AICc).

2.3.2 | Prediction 2

(a) The ecological complexity of snail habitats will rise and fall with island ontogeny
To test this prediction, we built two series of linear models with isolation, area and island ontogeny as predictor variables. In the first set of models, plant species richness served as the response variable, whereas in the second set of models the vegetated area served as the response variable. As with prediction 1, we used a squared island ontogeny term to simulate the predicted rise and fall of complexity through island ontogeny.

(b) Snail functional diversity will covary with plant species richness
In this analysis, we built a linear model with the natural logarithm of snail functional diversity for each island as the response variable and plant richness as the predictor variable.

2.3.3 | Prediction 3: (a) Snail functional diversity will rise and fall with island ontogeny, or (b) snail functional diversity will rise with island ontogeny

Galápagos dataset
To test these alternative predictions, we built a series of linear models, with snail functional diversity as the response variable and isolation, area and island ontogeny as predictor variables. As with predictions 1 and 2, we used a squared island ontogeny term to simulate the rise and fall of variation through island ontogeny as predicted by prediction 3a or a linear island ontogeny term for the model in prediction 3b. We then used the "*step*" function in R to identify the best-fitting model to predict snail functional diversity.

Global archipelago dataset
Prediction 3 was tested using the global dataset by incorporating archipelago as a random effect, as with prediction 1.

Simulation analysis
Owing to the limited statistical power for distinguishing between predictions 3a and 3b with the Galápagos dataset ($n = 13$ islands and volcanoes), we also tested the hypothesis that ecological opportunity drives community-level functional diversity using a permutation-based analysis. Briefly, we sampled species randomly from the archipelago-wide species pool to simulate snail communities matching the species richness encountered on islands with two or more species ($n = 2$–30). We tested the alternative hypothesis that the accumulation of functional diversity is driven by ecological opportunity (the null model in this procedure assumed that functional diversity accumulates via neutral processes) by comparing the observed functional diversity on each island with the sampling distributions constructed in this permutation procedure. In addition to using the observed shell shape dataset, we repeated this analysis by simulating shell shapes within the observed shape morphospace to make sure our findings were not constrained by the observed shell shape diversity in our dataset.

This analysis framework was repeated for the global dataset, but instead of identifying particular islands that are significantly more or less morphologically diverse than expected, we initially calculated the disparity between the observed morphological diversity and the mean expected morphological diversity simulated for each island (given the observed species and generic richness). Relative island age was then used to predict this disparity to test the hypothesis that environmental filtering early in island ontogeny leads to less

TABLE 1 Best-fitting linear models for predictions 1–4 using the Galápagos dataset

Predictions and best model	R^2	$F_{(d.f.)}$	p-value
Prediction 1: Snail species richness rises and falls with island ontogeny (Figure 2a)			
Species richness: $T_o + T^2_o$	.39	4.77(2,10)	.035
Prediction 2a: The ecological complexity of snail habitats rises and falls with island ontogeny (Figure 2b,c)			
Plant richness: $A + T_o + T^2_o$	.53	5.53(3,9)	.020
Vegetated area: $A + T_o + T^2_o$	.79	16.13(3,9)	< .001
Prediction 2b: Snail functional diversity covaries with plant species richness (Figure 2d)			
Functional diversity: PR	.37	7.44(1,10)	.021
Prediction 3: (a) snail functional diversity rises and falls with island ontogeny, or (b) snail functional diversity rises with island ontogeny (Figure 2e)			
Functional diversity: $A + T_o$	.51	6.83(2,9)	.016
Prediction 4: Island ontogeny is a significant predictor of snail morphology (Figures 2f and 3)			
Morphology: Snail shell shape: T_o	.39	7.02(1,11)	.013
Morphology: Snail shell size: T_o	.52	14.15(1,11)	.003

Note: Predictor variables are abbreviated as follows: A = area; I = isolation; PR = plant species richness; T_o = linear island ontogeny; $T_o + T^2_o$ = nonlinear island ontogeny.

morphological diversity than expected, whereas competition among species leads to more morphological diversity than expected late in island ontogeny. The global analysis included archipelago as a random effect, as with prediction 1.

2.3.4 | Prediction 4: Island ontogeny will be a significant predictor of snail morphology

Galápagos dataset
To test this prediction, we performed a permutational multivariate analysis of variance (MANOVA), with the average snail shape for each island as the response variable and island ontogeny as the predictor variable. We also performed a linear regression, with the average snail size for each island as the response variable and island ontogeny as the predictor variable.

Global archipelago dataset
To test this prediction, we performed a MANOVA, with the average snail height and width for each island as the response variable, island ontogeny as the main predictor variable, and archipelago as a nested factor.

3 | RESULTS

3.1 | Tests of predictions

Predictions 1–4 using the Galápagos dataset are summarized in Table 1. Predictions 1 and 3 using mixed effects models and the global dataset are summarized in Table 2 and Figure 3. We found support for prediction 4 with the global dataset (species: $R^2 = .62$, $F_{(10,53)} = 8.81$, $p < .001$, Figure 4a; genus: $R^2 = .46$, $F_{(10,53)} = 4.43$, $p < .001$), with the snail faunas on most archipelagos growing larger

over time. In Hawaii, however, snail communities from the oldest islands were among the smallest observed.

3.2 | Subsequent analyses

The significant area and island ontogeny terms from prediction 3 led us to perform an additional analysis directly comparing island area with snail functional diversity at different points of island ontogeny. Here, we found a significant relationship between island area and functional diversity on Galápagos islands in the first 30% of their life span ($r = .84$, $t = 3.15$, d.f. = 4, $p = .034$), and a trend between island area and functional diversity on Galápagos islands in the last 25% of their life span ($r = .92$, $t = 3.40$, d.f. = 2, $p = .077$), with the slope of the area–functional diversity relationship being significantly steeper on older compared with younger islands ($t = -11.26$, $p < .001$; Figure 2g). We found a similar pattern when evaluating the global dataset, albeit with some important differences. When evaluated individually, there appeared to be real differences in the relationships between island area and functional diversity for early-ontogeny islands ($b_{early} = 0.39$ at the species level and $b_{early} = 0.30$ at the generic level, where b denotes the slope of the least squares regression line) and late-ontogeny islands ($b_{late} = 0.79$ at the species level and $b_{late} = 0.28$ at the generic level). However, when archipelago was included as a random effect, as with prediction 3, we found no significant effect of early versus late ontogeny.

The permutational sampling procedure of Galápagos islands indicated that all early-ontogeny islands exhibited significantly less functional diversity than expected given a random colonization and diversification process from older islands, while the three late-ontogeny islands exhibited all possible levels of functional diversity (i.e., lower, predicted and higher) in comparison to a random extinction process (Figure 2h; Table S1; Table S2).

The permutational sampling procedure of the global dataset revealed a positive relationship between island ontogeny and the

TABLE 2 Best-fitting mixed effects models for predictions 1 and 3 using the global dataset

Response	Random structure	Intercept	Ln(Area)	Ln(Isolation)	Time	Time^2	Parameters	AIC$_c$
Prediction 1: Snail species richness rises and falls with island ontogeny								
Species richness	Isolation	1.396	0.368	NI	NI	NI	6	152.85
Generic richness	Area	1.315	0.202	NI	NI	NI	6	114.03
Prediction 3: (a) snail functional diversity rises and falls with island ontogeny, or (b) snail functional diversity rises with island ontogeny								
Ln(Morphospace$_{Species}$)	Isolation	2.482	0.398	NI	NI	NI	6	176.03
Ln(Morphospace$_{Genera}$)	Intercept	1.187	0.248	0.079	NI	NI	5	120.70
Ln(Morphospace$_{Genera}$)	Intercept	0.937	0.274	NI	NI	NI	4	120.92

Note: These analyses were also calculated using two modified isolation measures (Supporting Information Tables S3 and S4). The results are largely concordant with results presented in this table.

Abbreviation: NI = variable not included in model.

AIC$_c$, corrected Akaike information criterion.

disparity between observed and expected functional diversity, with early-ontogeny islands generally being less functionally diverse than expected and late-ontogeny islands generally more functionally diverse than expected, even when archipelago was included as a random effect (species: estimate = 102.76, d.f. = 55.89, t = 2.90, p = .005, Figure 4b; genus: estimate = 77.34, d.f. = 45.79, t = 3.41, p = .001).

4 | DISCUSSION

There are many factors contributing to the formation and maintenance of biological diversity, and their potential interactions are complex and challenging to study. Islands are naturally simplified systems where these factors are tractable and their effects easier to quantify. As an example, species richness has repeatedly been found to rise and fall predictably on volcanic islands through their ontogeny (Cameron et al., 2013; Lim & Marshall, 2017; Whittaker et al., 2008). However, less attention has been devoted to how the dynamics of island geological formation might affect the accumulation, maintenance and loss of functional diversity within communities. When considering Galápagos *Naesiotus* snails, we find a characteristic hump-shaped curve of species richness over time, and we also find this in the native and endemic plant species that make up their habitats. The relationship between functional diversity in *Naesiotus* snails and island ontogeny is more complex. We find that snail communities begin with very little functional diversity on young volcanoes, gain variation in mid-ontogeny and, depending on the island, either continue to gain, maintain or lose much of their functional diversity in late ontogeny. Finally, through island ontogeny, the average island snail morphology shifts unidirectionally with changes in habitat availability.
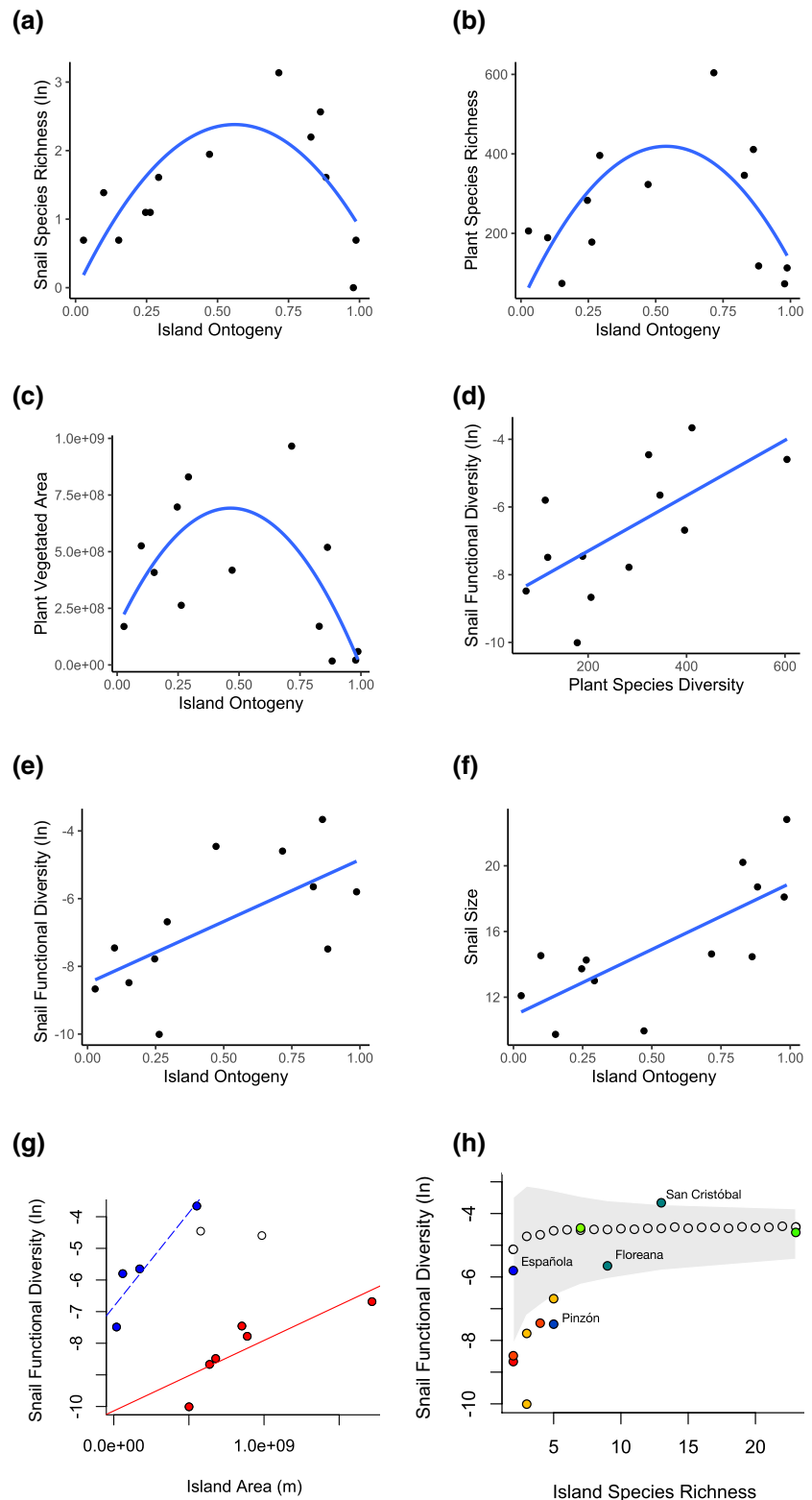
At the global scale, we find island area and isolation to be the most important predictors of species and generic richness on

islands. We find that even though functional diversity reaches a peak part-way through island ontogeny, island age is not a significant predictor of functional diversity on islands. We do find that snail communities tend to be functionally less variable early in island ontogeny and more variable late in island ontogeny compared with what would be expected from random species assembly. Finally, as with the Galápagos analysis, through island ontogeny the average island snail morphology shifts unidirectionally.

4.1 | Species richness

Low species richness in comparatively young and old island communities has been found in other systems (Lenzner et al., 2017; Lim & Marshall, 2017) and is expected from theory (Whittaker et al., 2008) and simulation (Valente et al., 2014). With the Galápagos dataset, we identified a significant effect of island age on species richness. Low species richness early in island ontogeny has a simple biological basis: Younger islands have less time for species to accumulate, given the rarity of colonization events and the time needed for *in situ* speciation to complete. Species richness is expected to build in mid-ontogeny as species accumulate by both colonization and intra-island speciation. Previous phylogenetic work supports both modes of species accumulation in Galápagos *Naesiotus* (Parent & Crespi, 2006; Phillips et al., 2020). The decline in species richness on older islands is thought to result from the loss of physical space, ecological habitat, or both, as islands erode and subside. In Galápagos, as island size and elevation decline, the first major habitat to disappear is the humid zone, which requires an elevation of several hundred meters above sea level (McMullen, 1999). For *Naesiotus* snails, the availability of refugia, both from predators and from solar radiation, might be especially limiting as islands get smaller, lower and more arid, possibly leading to accelerating extinction rates on late-ontogeny islands.

FIGURE 2 (a–c) Results of comparisons between island ontogeny and (a) snail species richness, (b) plant species richness, and (c) plant vegetated area. (d) Comparison between plant species richness and snail functional diversity. (e,f) Comparison between island ontogeny and snail functional diversity or snail size (measured as centroid size from the shape analysis), respectively. (g) Relationship between island area and snail functional diversity. Note the low slope of the relationship among early-ontogeny islands (red, continuous line) in comparison to the relationship among late-ontogeny islands (blue, dashed line). (h) Comparison between island species richness and variance in snail shape, with observed data coloured by island ontogeny. Open circles represent the mean shape variance expected if species morphology were distributed arbitrarily across the archipelago. The four late-stage islands with more than one species are identified by name. Note the exceptionally low shape variance found among all early-stage islands (coloured in red)

In contrast, the global analysis did not identify a significant rise and fall of species or generic richness through island ontogeny. Instead, island area and isolation appear to be major factors determining species richness, and much of the remaining variation in species richness is explained by the random effect of archipelago.

4.2 | Ecological complexity

The building of ecological space early and its subsequent loss late in Galápagos island ontogeny are supported in our data, through changes in both total vegetated area and plant species richness over time. On young volcanoes, the cool and humid environments at high elevations
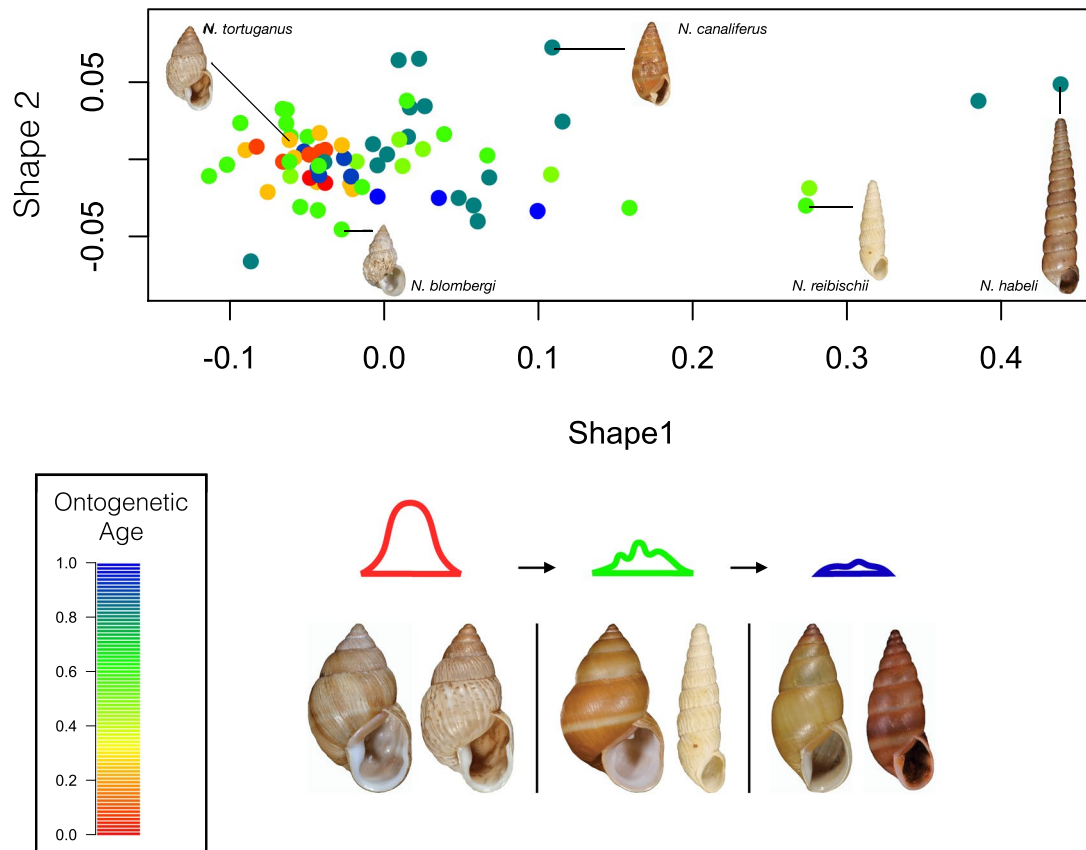
FIGURE 3 Morphological variation of Galápagos *Naesiotus*. Top: Functional diversity of 69 putative *Naesiotus* species, presented as the average shell shape for each. Species are coloured by the ontogenetic age of their respective island. Note how all species from early-ontogeny islands (red and yellow) cluster in one small region of morphospace. Bottom: Species pairs from left to right show the extremes of morphological shape variation of representative early-, middle- and late-ontogeny islands (represented by Sierra Negra, Santa Cruz and Española, respectively; shell size not to scale). Note the shift from shells with relatively large to relatively small apertures through island ontogeny

give way to harsh environments at low elevations, which are dominated by barren lava fields. As a result, terrestrial plant communities generally appear to build from the top down (Mueller-Dombois & Fosberg, 1998). This is reflected in the positive relationship between island ontogeny and vegetated area for the initial growing phase of island life span (Figure 2c). Past their peak size, a negative relationship between island ontogeny and vegetated area is driven by the decline in total island area on older islands. The vegetated area on older islands is a stark contrast to young volcanoes where, typically, a small proportion is vegetated. Plant species richness follows a similar hump-shaped curve through time, with an initial species build-up followed by a decline, paralleling the rise and fall of island area.

4.3 | Ecological opportunity and functional diversity

Support for the hypothesis that ecological opportunity drives functional diversity at the island scale should be revealed by a

positive relationship between island snail functional diversity and plant species richness. We find support for this relationship in the Galápagos land snail dataset (Figure 2d). A subsequent prediction of this hypothesis is that functional diversity will follow a similar hump-shaped curve through island ontogeny to that found for plant species richness. We find strong support for this hypothesis from early to mid-ontogeny. On young volcanoes, we find very little functional diversity in *Naesiotus* snails; nearly all species cluster tightly in morphospace. Up to mid-ontogeny, functional diversity increases with plant species richness, leading to a remarkable variety of shell shape on middle-aged islands. In late ontogeny, however, although both plant and snail species richness decline, we do not find a consistent loss of functional diversity. Instead, a more complex picture emerges on the four major islands at the end of their life span.

We find that the five species on Pinzón Island form a community with low functional diversity, significantly lower than what would be expected from a community composed of a random set of five *Naesiotus* species. This low functional diversity parallels the low
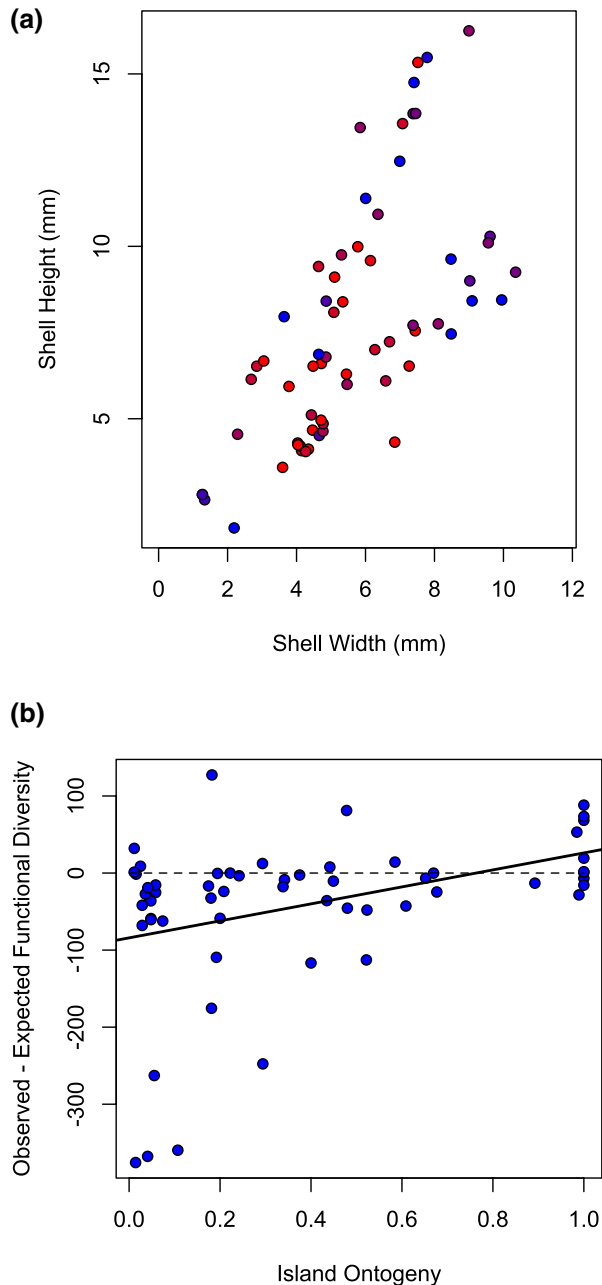
FIGURE 4 (a) Average height and width of snail species from each island from the global dataset. Islands are colour coded by the archipelago-specific relative ontogeny of the island. Younger islands with ontogeny scores close to zero are red, whereas older islands with ontogeny scores close to one are blue. Note how extreme morphologies tend to be found on relatively older islands. (b) Disparity between observed and expected functional diversity on islands along island ontogeny. The dashed line indicates a match between observed and expected diversity. Points below the dashed line indicate islands with snail communities with less functional diversity than expected, whereas points above the dashed line indicate islands with snail communities with more functional diversity than expected. The continuous line marks the least squares regression line of island ontogeny on functional diversity disparity

snail and plant species richness found on that island and supports the hypothesis that ecological opportunity constrains functional diversity. Under this hypothesis, we predict that surveys of comparable patches of habitat on late-stage islands would find that at local scales, Pinzón Island has lower alpha and beta diversity, lower population level functional diversity and less diverse snail refugia from predators and solar radiation than other late-stage islands.

San Cristóbal Island is also well advanced in ontogeny and hosts a snail community of 13 species. However, in stark contrast to Pinzón, San Cristóbal boasts a remarkably high degree of functional diversity, well beyond what would be expected from a randomly assembled 13-species snail community (Table 1). The pattern of high functional diversity at the community level on San Cristóbal Island is consistent with the hypothesis that increasing interspecific competition on older islands drives character displacement and an increase in total functional diversity (Whittaker et al., 2008). Under this hypothesis, we predict that future research will find an overdispersion of snail morphology among species at the local scale, as those species with similar functional morphology and therefore most likely to compete become the least likely to co-occur within the same patch of habitat.

The snail species found on Española and Floreana islands have retained more functional diversity than the community on Pinzón, yet less than San Cristóbal. Instead, the land snail communities on these islands have similar functional diversity to what would be expected from communities randomly chosen from the Galápagos *Naesiotus* species pool (Table 1). Our null expectations for functional diversity on islands are driven mainly by the availability of physical space. As islands erode and subside over time, area is reduced, which may lead species increasingly to come into contact with one another and progressively to decline in population size, if species have spatially limited distributions. We predict that this decrease in area would lead to extinction, hence a reduction in species richness, but not necessarily a steep decline in morphological variation until island area is significantly reduced. Any predictions made about the mechanisms driving functional diversity on Pinzón or San Cristóbal might be able to use Española and Floreana as control islands, because they appear to follow these null expectations. Although it might be that ecological opportunity alone drives the accumulation of functional diversity early in island ontogeny, several island-specific factors and historical contingency might together determine morphological variation on older islands. More focused research on the differences among these four islands will help to test these hypotheses more directly.

The global archipelago dataset reveals that island area and isolation are important predictors of functional diversity, and island age might be important both at the species and generic levels, depending on the island isolation measure (Table 2; Supporting Information Tables S3 and S4). Generally, although we observe a wide range of functional diversity on the oldest and youngest islands, nearly all islands midway through island ontogeny are at the upper bound of morphological diversity. More interestingly, through the simulation

procedure we find that from the global dataset young islands tend to be less morphologically variable, hence supporting lower functional diversity, whereas old islands tend to be morphologically more variable than expected based on random species assembly. This result strongly supports our findings from the Galápagos dataset, indicating that island colonization is a filtering process, leading to less functional variation than would otherwise be expected, and that the functional variation found on older islands might be the result of competition among persisting species.

Formalized and largely fuelled by the theory of island biogeography (MacArthur & Wilson, 1963, 1967), studies on islands have long focused on the relationship between species richness, area and isolation. More recently, this static and species-centric view has been expanded to consider how the dynamic nature of island geology itself might shape these relationships (Whittaker et al., 2008), and to include additional ecological and evolutionary features of diversity, such as functional and phylogenetic diversity (Sanmartín et al., 2008; Valente et al., 2014; Whittaker et al., 2014). Studies have found conflicting results regarding the scaling of functional diversity; in some cases, it might scale linearly with species richness (e.g., Whittaker et al., 2014), and in others the increase in the number of species is not associated with increased function in the community, suggesting functional saturation (e.g., Farneda et al., 2020). Our study adds to this range of findings and, more importantly, offers a framework capitalizing on non-equilibrial systems (*sensu* Gillespie, 2013) to investigate further the processes responsible for the divergent trajectories along which species richness and functional diversity accumulate as communities assemble.

4.4 | The role of morphology in colonization

Before the present study, field observations and collections suggested that early-ontogeny snail communities were primarily situated in humid zone environments, mid-ontogeny snail communities were highly diverse and widely distributed, and late-ontogeny snail communities were limited to arid environments (Coppois, 1984; Dall, 1896; Dall & Ochsner, 1928; Smith, 1966). This pattern was thought to be driven by the limited range of vegetation on young volcanoes and the lack of a significant humid zone on most late-ontogeny islands. We find that this shift in habitats available to and occupied by snails leads to a directional shift in the morphospace occupied by snails through island ontogeny, which might have implications for the colonization process on islands. The extremely narrow region of morphospace occupied by young volcano species suggests that colonization acts as a filter of potential morphologies or the environments on young volcanoes strongly select for particular morphologies or, perhaps most likely, some combination of the two. This finding is in contrast to what Karadimou and colleagues (2015) have found in vascular plant assemblages on volcanic islands. In their study, the authors found multiple patterns of community assembly across and within the four communities they considered and, in particular, no common species assembly mechanism was inferred on all younger islands, which led the authors to conclude that

stochastic processes might dominate early in community assembly. Conversely, Carvajal-Endara et al. (2017) found a strong signature of habitat filtering in the initial colonization of lineages to isolated archipelagoes. Here, we also find evidence of habitat filtering during the colonization process, although in this case the colonization events in question are the result of intra-archipelago movement. We find that the multiple independent lineages of *Naesiotus* snails that have recently colonized separate volcanoes all share a common morphology, which suggests that subsequent convergence in the assembly of functional diversity as communities mature might not be constrained by historical contingencies, as it has been suggested in other systems (Blount et al., 2018; Gould, 1989; Losos et al., 1998).

4.5 | Evolutionary trajectories in morphospace

Although we do not find a consistent decline of morphological variation on late-ontogeny islands, we do see a directional shift in average morphology both in the global dataset and in the Galápagos dataset. In the Galápagos dataset, we find that not only do snails tend to become larger through time, but also snail shape tends to become more elongated along the central axis. This continued shift might occur as the extant snail diversity skews toward arid-adapted species. In snails, adaptation to arid environments often includes a change in shell morphology toward an elongated shell, which facilitates the evolution of a relatively smaller aperture, probably reducing water loss (Goodfriend, 1986). In accordance with this hypothesis, all elongated Galápagos snails are restricted to the arid zone and are found predominantly on late-ontogeny islands. It is unclear whether this shift in morphological variation is the result of non-random extinction based on morphology or continued morphological evolution through island ontogeny, but a focused study combining the evolutionary history of Galápagos *Naesiotus* with this morphological dataset might clarify that question. For the global data, snails tend to get larger through island ontogeny, except in the Hawaiian archipelago, where we instead see that snails from the oldest islands are among the smallest species found on this archipelago. These patterns across datasets are concordant with a predictable, directional shift in the adaptive landscape along island ontogeny, although archipelago-specific factors are likely to direct the trajectory of these shifts.

4.6 | Conclusions

Empirical studies on the dynamics of morphological variation have largely focused on single lineages rather than entire communities. Across long time-scales of tens to hundreds of millions of years, morphological diversification in radiating lineages follows a pattern similar to species richness, with a peak part-way through the life span of the radiation [e.g., trilobites (Foote, 1993; Roy & Foote, 1997)]. At somewhat shorter time-scales of millions to tens of millions of years, several studies have shown that morphological variation continues to rise consistently as the radiation proceeds

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[e.g., cichlids (Fryer & Iles, 1972); *Anolis* (Losos, 1992); warblers (Price et al., 2000)]. In contrast, other studies have found that the increase in the number of species is not necessarily accompanied by an increase in morphological variation (Losos & Miles, 2002; Ricklefs, 2012; Warheit et al., 1999). Although single-lineage studies have the advantage of being tractable, studying the accumulation of morphological diversity at the community level can shed light on how biotic interactions might influence this process. Thus, systems on depauperate islands, such as Galápagos *Naesiotus* land snails, where a single lineage dominates a community and has diversified into a wide range of co-occurring and potentially competing species, offer the opportunity to study the role of biotic interactions in shaping communities.

AUTHOR CONTRIBUTIONS

A.C.K. conceptualized and designed the study. A.C.K. performed the analyses. A.C.K. and C.E.P. wrote the first manuscript draft. All authors contributed to data collection and manuscript revision.

DATA AVAILABILITY STATEMENT

We provide all analyses and corresponding data as Supporting Information.

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