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Flying snails: immigrant selection and the taxon cycle in Pacific Island land snails

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Abstract

We tested the hypothesis that, for land snails, long-distance dispersal across oceans is primarily via aerial dispersal (i.e. wind- or bird-mediated), which likely favors so-called micromolluscs through immigrant selection for small (aerially buoyant) body size. Immigrant selection is a filtering process favoring phenotypes conferring greater capacities for long-distance dispersal. We also tested predictions of E. O. Wilson's taxon cycle, which hypothesizes that descendant species of island colonists are subject to a series of ecological and evolutionary dynamics, resulting over time in progressively more ecologically specialized island endemics with more limited dispersal capacity. We tested predictions of immigrant selection on aerial dispersal and the taxon cycle in native Pacific Island land snails of the Samoan Islands, Mariana Islands, and Lord Howe Island and neighboring small islands using geographic range, shell size, microhabitat, and elevation data compiled from primary and secondary literature. Single-archipelago endemic species found on multiple islands within an archipelago had significantly larger shell sizes than widespread species found in multiple archipelagos and single-island endemic species. Single-archipelago endemic and single-island endemic species were associated with vegetation and ground/rock microhabitats, respectively, whereas widespread species were more likely to be microhabitat generalists. Single-island endemic species were more likely to occur at high-elevation habitats, while widespread species were more likely to be confined to low-elevation habitats. Consistent with predictions of the taxon cycle and immigrant selection on aerial dispersal, Pacific Island land snails endemic to single islands or archipelagos (i.e. those assumed to be later in the taxon cycle) are more likely to have larger body size (archipelago endemics) and to occupy higher elevations (i.e. island interiors; island endemics) in more specialized microhabitats (all endemics).

Highlights

- Immigrant selection is a process that favors colonization of oceanic islands by better dispersers.

- Once established on islands, selection pressures may be reversed as descendant lineages become entrained in the taxon cycle, becoming increasingly more specialized and restricted to high-elevation, interior habitats.

- Pacific Island land snails disperse between islands either by aerial mechanisms (e.g. wind, birds) or by floating (e.g. on vegetation rafts), favoring smaller or larger dispersers, respectively.

- We find that widespread (presumably early taxon cycle) species are generally small-bodied microhabitat generalists inhabiting low elevations, single archipelago-endemic (mid taxon cycle) species are often large-bodied vegetation specialists, and single island-endemic (late taxon cycle) species are more likely to be ground/rock specialists inhabiting high elevations.

- This study confirms immigrant selection favoring smaller land snails as island colonists and is the first to test predictions of the taxon cycle in land snails across multiple families and archipelagos. Reversals in selection pressures during and after immigration may be pervasive phenomena influencing a broad range of island biotas.

Introduction

Land snails are indigenous to nearly all terrestrial biomes and biogeographic regions, including some of the least hospitable and most remote, like deserts and oceanic islands, respectively. Although famous for their limited abilities to disperse under their own power, many species of land snails can disperse great distances when carried by wind, flying animals, or ocean currents. As a result, hundreds of species of land snails occupy tropical forests in even the most isolated Pacific archipelagos, where many are highly endangered yet severely under-researched (Lydeard et al. 2004, Holland and Cowie 2009, Regnier et al. 2009, 2015, Hyman and Ponder 2016, Proios et al. 2021). Land snail dispersal to oceanic islands is a long-standing fascination for island biogeographers and malacologists, including Darwin himself (Orstan and Dillon 2009).

Studies of Pacific Island land snails (PILS) across multiple archipelagos yield invaluable insights into the biogeography, evolution, and phenotypic and ecological diversity of these animals (e.g. Parent 2012, Cameron et al. 2013). Across the isolated archipelagos of the Pacific, immigration of land snails appears to be primarily through aerial dispersal; that is, blown by wind or carried in plumage, attached to legs, or within the digestive tracts of flying animals. Although it may seem fantastical, wind-mediated land snail dispersal is a likely source of colonists to even the most isolated Pacific Islands (e.g. during storms; Mayr 1965, see also Dorge et al. [1999] for accounts of snails dropping from storms), especially for small micromolluscs (i.e. species < 5 mm in maximum shell dimension as adults; Geiger et al. 2007). The mass and diameter of neonate and juvenile micromolluscs are similar to those of inorganic particles collected in aerial plankton (e.g. < 5 mm^3 granite particles; Vagvolgyi 1975). PILS shells in good condition and containing soft tissue have been found in feces of wild-caught native Pacific Island birds (Kawakami et al. 2008, see also Wada et al. 2012 and Simonova et al. 2016), and aquatic birds are known to occasionally carry wetland molluscs in their feathers or, as Darwin (1859, 1878) observed, in the mud on their feet (Green and Figuerola 2005). Most PILS families are related to Australasian taxa (e.g. Goulding et al. 2023), and many show inter-archipelago differentiation (e.g. closely related genera and species found on different archipelagos and islands), consistent with dispersal patterns that may result from trade winds, jet stream, or birds occasionally carrying propagules from one archipelago to another (Gillespie et al. 2012).

Aerial dispersal is hypothesized to favor smaller land snails, since lighter snails are carried by a greater range of wind speeds, are better at hiding in bird plumage or bat fur without falling off (Vagvolgyi 1975), and are more likely to be swallowed whole by birds (and therefore less likely to be damaged during ingestion; Kawakami et al. 2008, Wada et al. 2012). Thus, immigrant selection, which favors phenotypes with greater probabilities of successful dispersal (Lomolino 1984, 1993), should result in colonists biased in favor of micromolluscs and those with broader ecological niches capable of adapting to a broad spectrum of coastal and low-elevation habitats (e.g. beachfront habitats of the source and focal islands). Immigrant selection favoring small propagule size may be present in other insular taxa, such as zoochorous Indo-Malayan angiosperms (Brodie et al. 2023).

Selective pressures following colonization are often counter to immigrant selection (Lomolino 2010). Inter-archipelago dispersal becomes disadvantageous as descendent species become locally adapted, whereas for species that maintain relatively high rates of inter-archipelago dispersal, immigration may swamp local adaptation. For endemic species, long-distance dispersal might at best land propagules in suboptimal habitats and at worst cause them to be lost at sea, particularly for non-directional dispersers like PILS (Gillespie et al. 2012). Alternatively, waning immigration abilities could stem from tradeoffs between the diminishing advantages for dispersal and *in situ* adaptations to island environments (Gillespie et al. 2012), which in PILS may include increases in body size and microhabitat specificity. These reversals in selective pressures following successful colonization may be integral to the taxon cycle (Wilson 1959, 1961), which predicts a progression in an island lineage from broadly dispersing, ecologically generalist species inhabiting coastal and low elevation habitats to descendant species with limited dispersal capacities and narrow niches that become increasingly specialized for high-elevation, interior habitats (Ricklefs and Bermingham 2002, Matos-Maravi 2020). Accordingly, we predict a trend in oceanic land snails from small-bodied microhabitat generalists broadly distributed across low elevations in multiple Pacific archipelagos to larger species restricted to a more limited range of microhabitats, high elevations, and single archipelagos or islands. These predictions describe possible general trends in PILS morphology, ecology, and geographic range sizes, rather than absolute rules; exceptions to the rule are expected.

We tested these predictions by comparing shell size, microhabitat breadth, and habitat elevation among widespread PILS species (i.e. species indigenous to multiple archipelagos and/or continental systems), single-archipelago endemic (SAE) species (i.e. found on multiple islands within an archipelago), and single-island endemic (SIE) species. These categories span a presumed chrono-sequence from early to late stages of the taxon cycle. We did not identify source populations for widespread and SAE species, nor did we compare fossil and descendant species or employ phylogenetic methods, because the necessary fossil and phylogenetic data are largely unavailable. Our dataset included 176 species from 22 families (Supplemental Table S1) inhabiting three Pacific archipelagos varying in their degree of isolation from Australasia. We limited our dataset to those archipelagos for which nearly complete species lists and ecological and morphological data are available: Lord Howe Island and some neighboring small islands, Mariana Islands, and Samoan Islands (780 km, 1795 km, and 2345 km from nearest mainland, respectively; see Supplemental Table S2 for islands list).

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We tested the predictions that SIE and SAE species are (1) larger-bodied, (2) more specialized in microhabitat use, and (3) found at higher elevations than widespread PILS are. We measured ecological breadth as breadth of microhabitat use (e.g. ground/rock- vs. vegetation-dwelling). Body size, microhabitat breadth, and habitat elevation were compared between confamilial species to partially control for phylogenetic effects.

Materials & Methods

Study system

This study focused on indigenous land snails of three Pacific archipelagos for which (nearly) complete species lists, field guides, annotated checklists, and/or identification guides were available: Lord Howe Island and some neighboring small islands (Hyman and Kohler 2020), Mariana Islands (Kerr and Bauman 2013, Kerr and Fiedler 2018, 2019), and Samoan Islands including American Samoa (Cowie 1998, Cowie and Cook 1999, Cowie et al. 2017). Data were primarily drawn from these sources. Additional species and morphological, ecological, and geographic range data were found in species descriptions, taxonomic revisions, family-specific studies, digital collections, and other primary and secondary literature (see Appendix S1 for full refences list and Supplemental Table S3 for compiled data). Families and binomial nomenclature were verified using Molluscabase[1] (except for *Pleuropoma* species, which were not listed in Molluscabase). Undescribed species were generally included if they were identified to the genus level.

Variables

Geographic range was expressed as degree of endemicity (island or archipelago extent). Species were considered SIE if they were believed to occur on only one island. Species were considered SAE if they are known from multiple islands within an archipelago but believed to be indigenous to one archipelago. Species indigenous to multiple Pacific archipelagos and/or continents in addition to Pacific Islands were considered widespread.

This study took a liberal approach to ambiguous occurrence data: uncertain occurrences were generally considered valid unless expert opinion expressed in the literature suggested otherwise. Similarly, species of uncertain indigeneity were generally considered indigenous. Very few, if any, species included in our analyses would have been likely subject to purposeful introduction by humans (e.g. certain large-bodied partulid land snails in Polynesia used in jewelry making; Lee et al. 2007). However, some small-bodied species (e.g. subfamily Subulininae, not included in this study) are suspected to have been accidentally introduced on multiple Pacific Islands both pre- and post-European colonization (e.g. Cowie 1998). Shell comparisons with collections from the Pleistocene fossil record, where available, can be useful to disentangle these from species with broad geographic ranges (Goulding et al. 2023), though doing so is beyond the scope of this study.

[1] https://www.molluscabase.org, last accessed 27 November 2023

Because Lord Howe Island and neighboring small island have been interconnected during Pleistocene sea level fluctuations, it could be argued that SAE species of the Lord Howe archipelago are more properly considered SIE. We repeated all analyses with SAE species from this archipelago reclassified as SIE. These species were *Placostylus bivaricosus* (Gaskoin, 1855), *Gudeoconcha sophiae* (Reeve, 1854), *Innesoconcha catletti* (Brazier, 1872), and *Innesoconcha delecta* (Iredale, 1944). Reclassifying these four species to SIE did not substantially change results (see Appendix S2).

Species body size was measured as maximum shell dimension. Slugs and semislugs, for which shell size is a poor indicator of overall body size, were excluded from the dataset. If more than one maximum shell dimension for a species was found in the literature, the largest size reported was typically used in the dataset. Maximum shell dimension has drawbacks for datasets like ours that include morphologically and taxonomically disparate taxa. As an estimate of external shell volume, maximum shell dimension performs similarly to other functions of shell height and width, such as geometric mean of height and width (Osborne and Stehman 2022). We used maximum shell dimension as our body size measurement, because it is most readily available in the literature and comparable to other land snail biogeographic studies. For over 85% of species, we compared results using maximum shell dimension to those using conical volume (i.e. volume of a cone with height equal to shell height and width equal to shell width), which is a more appropriate shell size measurement for data such as ours (Osborne and Stehman 2022). There were no qualitative differences in results between these shell size measurements (see Appendix S3).

Land snail microhabitats were characterized as vegetation-dwelling, ground/rock-dwelling, and generalist. Species known to inhabit live vegetation, including arboreal species, were classified as vegetation-dwelling. Species found on the ground, in organic litter including dead vegetation, buried in soil, on or under rock, on limestone cliffs or rubble, and in similar microhabitats were considered ground/rock-dwelling. The grouping of ground- and rock-dwelling land snails reflects the information available and overlap in microhabitat use for some species (e.g. "under rock" could be considered both ground-dwelling and rock-associated, several species inhabit both organic litter and rocks). This grouping should be regarded with some caution and not as a claim that ground- and rock-dwelling land snails are ecologically equivalent. Species found in both vegetation and ground/rock microhabitats were considered microhabitat generalists.

Elevation data were drawn primarily from collection locality elevations and qualitative descriptions in the literature. Low-elevation qualitative descriptions included near-shore habitats, lowlands, river mouths, or similar habitats. Islands with low maximum elevations (i.e. Dano, Alupat, Blackburn, Gower, Nuulua, Roach, Aunuu, Aguiguan, Tinian, Nuutele, Maug, and Guguan) and two low-elevation geographic markers on Lord Howe Island (i.e. Mutton Bird Point and Intermediate Hill) were also considered low-elevation habitats.

High-elevation descriptors included highlands; island interiors; heights, upper slopes, and summits of mountains; and other high-elevation geographic features. The Mataulano Lake area on Savaii, Samoan Islands, was also considered a high-elevation habitat. Mid-elevation habitats included those described as slopes or mid-slopes. Mid-elevation habitats were combined with low-elevation habitats due to a paucity of mid-elevation species and constriction of low- and mid-elevation ranges compared to high-elevation species and ranges.

Numerical elevation data were gathered primarily from published collection locality descriptions or species ranges. Hyman and Kohler's (2020) occurrence maps were cross-referenced with a topological contour map[2] to estimate elevations for many Lord Howe Island species. For 17 species, elevations of collection locality GPS coordinates were estimated using Google Earth Pro (i.e. we recorded numerical elevation data reported in Google Earth Pro for collection locality coordinates). This method could not be used for more species because of lack of precision in reported coordinates (e.g. reported coordinates map to ocean in Google Earth Pro) and inaccuracies in Google Earth Pro's elevation data (e.g. for Mt. Gower of Lord Howe Island).

Numerical and qualitative elevation data were compared for 55 species for which both were available. These 55 species produced 49 numerical elevation values that could be coded as either high or low elevation based on qualitative descriptions. Conflicting qualitative descriptions were available for six elevations (50 m, 200 m, 277 m, 300 m, 500 m, 610 m); these were assigned a percentage value representing how often they were associated with low- or high-elevation qualitative descriptions. Logistic regression was performed using the "glm" function in the statistical program R (R Core Team 2023) with "family" set to "binomial" (i.e. numerical elevation as explanatory variable, proportion of "high elevation" qualitative descripts as response variable). Regression coefficients were then used to estimate inflection point (321 m) beyond which elevations were most likely to be qualitatively considered high-elevation habitat.

Species with numerical elevation ranges of 0 to 321 m were categorized as low-elevation species. Similarly, species with ranges above 321 m were categorized as high-elevation species. Species whose lower elevation limit was reported as "above 300 m" were also considered high-elevation. Species with ranges spanning 321 m were categorized as broad-elevation species. Species with both qualitative and quantitative elevation data were categorized based on quantitative data. Species with only qualitative elevation data were similarly categorized as low-, broad-, or high-elevation species based on habitat descriptions.

We were unable to find shell size, microhabitat, and elevation data for all species in any archipelago (excepting shell size data for Lord Howe species).

For both microhabitat and elevation data, habitat descriptions outside of Pacific Islands were generally excluded from the dataset.

Analyses

All analyses were performed in the statistical program R version 4.3.2, and all statistical tests were two-sided. Because all snail shell size distributions were significantly non-normal (Shapiro-Wilk normality test performed using function "Shapiro.test", $W < 0.82$, $p < 0.001$ for all tests), we compared median shell sizes between degrees of endemicity using a Kruskal-Wallis rank sum test ("kruskal.test" function). Pairwise Wilcoxon rank sum tests ("pairwise.wilcox.test" function) were used for post-hoc pairwise comparisons of medians. Wilcoxon rank sum test statistics, effect sizes, and confidence intervals were estimated using the "wilcox.test" function. Shell size distributions were visualized using the "geom_violin" function from R package *ggplot2* version 3.4.4 (Wickham 2016).

Comparisons of shell size distributions were confirmed using one-way ANOVA ("aov" function) on log-transformed shell size data. Post-hoc pairwise means comparisons of log-transformed data were performed using Tukey's honest significant difference test ("TukeyHSD" function). Log-transformed shell size data were not significantly different from normal (Shapiro-Wilk normality test performed using function "Shapiro.test", $W > 0.96$, $p > 0.3$ for all tests).

Tests of association between degree of endemicity and microhabitat or elevation category were conducted using Chi-squared tests ("chisq.test" function). Effect sizes were measured using Cramer's V. Chi-squared test residuals were visualized using the "geom_bar" function from *ggplot2*.

Within-family analyses were conducted for families with species representing at least two levels of endemicity (i.e. widespread, SAE, and SIE confamilial species; both widespread and SAE species; both widespread and SIE species; both SAE and SIE species). This allowed us to partially control for phylogenetic effects on shell size, microhabitat specificity, and habitat elevation specificity.

To determine whether shell sizes differ within families based on degree of endemicity, ANOVA tests with family as a blocking factor ("aov" function) were performed on a subset of species from families with multiple degrees of endemicity and for which shell size data were available. Pairwise differences in means were visualized using the "ggpaired" function from the package *ggpubr* version 0.6.0 (Kassambara 2023).

Within-family associations between degree of endemicity and microhabitat or elevation category were performed using Cochran-Mantel-Haenszel Chi-squared tests with families as strata ("mantelhaen.test" function) on subsets of species in families for which confamilial species have multiple degrees of endemicity and inhabit multiple microhabitat or elevation categories, respectively. In this context, strata are analogous to blocking factor. The appropriateness of Cochran-Mantel-Haenszel Chi-squared tests was supported by Woolf tests of homogeneity of odds ratios ("woolf_test" function from the package *vcd* version 1.4-11 [Meyer et al. 2023],

$p > 0.99$ for both tests). Where results of Cochran-Mantel-Haenszel Chi-squared tests were significant, results were then interpreted by performing Chi-squared tests on data subsets ignoring strata.

Figure colors were generated by the *NatParksPalettes* package version 0.2.0 (Blake 2022).

Results

Consistent with predictions of the taxon cycle and reversals in selection pressures following long-distance dispersal, median shell size of SAE species was significantly larger than that of widespread species, which are presumably earlier in the taxon cycle (Kruskal-Wallis rank sum test, $X^2 = 11.03$, df = 2, $p = 0.004$, n = 167 species for which both endemicity and shell size were determined; Pairwise Wilcoxon rank sum test, W = 455.5, $p = 0.009$, median$_{SAE}$ = 12.4 mm, median$_{widespread}$ = 6.0 mm, difference in location = 5.0 mm, 95% confidence interval 1.0 to 10.0 mm; Fig. 1a). Contrary to a related prediction, however, SIE species were significantly smaller than SAE species, even though SIE species presumably represent a later stage in the taxon cycle (pairwise Wilcoxon rank sum test, W = 888.5, $p = 0.005$, median$_{SAE}$ = 12.4 mm, median$_{SIE}$ = 6.0 mm, difference in location = 5.0 mm, 95% confidence interval 1.5 to 9.0 mm; Fig. 1a).

Further, there was no detectable size difference between SIE and widespread species (pairwise Wilcoxon rank sum test, W = 2,025.5, $p = 0.922$, median$_{SIE}$ = 6.0 mm, median$_{widespread}$ = 6.0 mm, difference in location > -0.001 mm, 95% confidence interval -1.4 to 1.3 mm; Fig. 1a). Log-transforming shell size data produced similar results (one-way ANOVA comparing all degrees of endemicity, F = 7.715, df = 2, 164, $p < 0.001$; pairwise Tukey's honest significant difference tests, SAE vs widespread: $p = 0.003$, difference in location = 0.57, 95% confidence interval 0.17 to 0.98; SAE vs SIE: $p < 0.001$, difference in location = 0.58, 95% confidence interval 0.22 to 0.95; SIE vs widespread: $p = 0.998$, difference in location = -0.009, 95% confidence interval -0.33 to 0.31).

The largest species in the dataset were *P. bivaricosus* (80.0 mm), *G. sophiae* (38.4 mm), and *Epiglypta howeinsulae* (J. C. Cox, 1873) (34.8 mm). All three species are endemic to Lord Howe Island (*E. howeinsulae*) or the Lord Howe archipelago (*P. bivaricosus*, *G. sophiae*). *Placostylus bivaricosus* is a representative of a large-shelled family (Bothriembryontidae; Hyman and Kohler 2020). *Epiglypta howeinsulae* and *G. sophiae* are some of the largest members of the family Helicarionidae, which includes micromolluscs, large shells, and semislugs (Hyman and Kohler 2020).
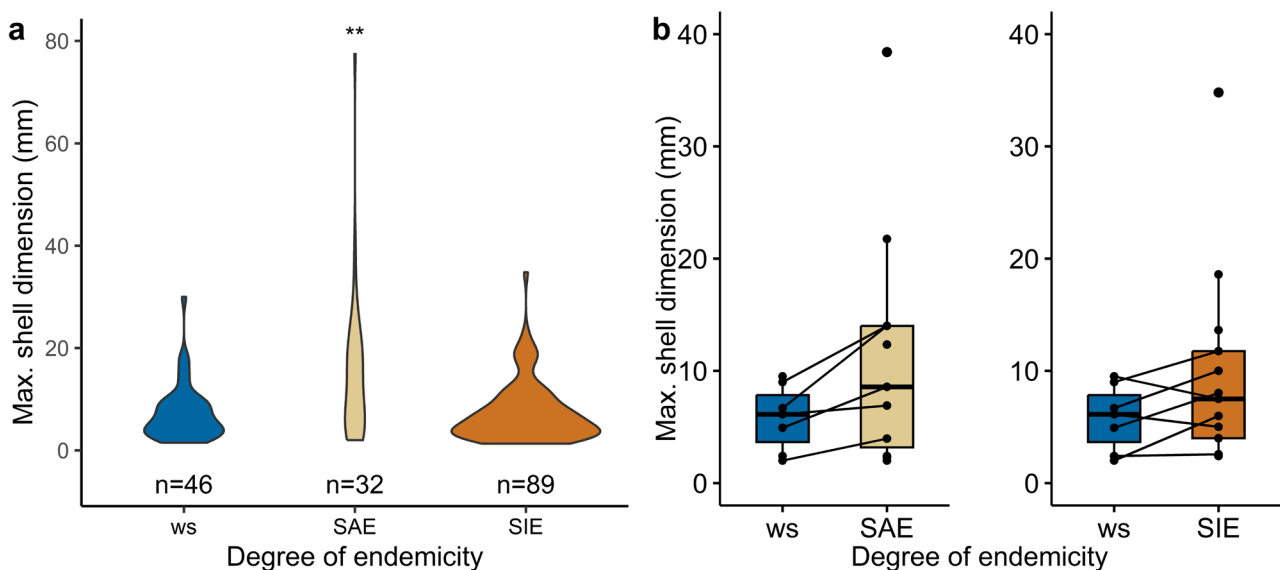

Figure 1. Maximum shell dimension compared to degree of endemicity for native land snails of Samoan Islands, Mariana Islands, and Lord Howe Island and neighboring small islands. **a** Maximum shell dimension distributions for all land snails in the dataset. Distributions scaled by sample size for each degree of endemicity. Data shown for 46 widespread species, 32 single-archipelago endemic species, and 89 single-island endemic species. Asterisks indicate the statistically significantly different group (Kruskal-Wallis rank sum test, $X^2 = 11.03$, $p = 0.004$; Pairwise Wilcoxon rank sum tests, W$_{SAE \, vs \, ws}$ = 455.5, p$_{SAE \, vs \, ws}$ = 0.009, W$_{SAE \, vs \, SIE}$ = 888.5, p$_{SAE \, vs \, SIE}$ = 0.005, W$_{SIE \, vs \, widespread}$ = 2,025.5, p$_{SIE \, vs \, widespread}$ = 0.922). **b** Within-family comparisons of maximum shell dimension (ANOVA, F = 1.79, p = 0.171). Diagonal lines connect means of maximum shell dimension of confamilial species with different degrees of endemicity. Data shown for 7 families with widespread species, 11 families with single-archipelago endemic species, and 13 families with single-island endemic species (n = 140 species total). Center line = median, box limits = upper and lower quartiles, whiskers = points within 2 SD of the mean, bolded points = outliers. Abbreviations: ws = widespread, SAE = single-archipelago endemic, SIE = single-island endemic.

Breadth of microhabitat occupancy was significantly associated with level of endemicity, with microhabitat niche breadth decreasing along a series from widespread to SAE to SIE land snails (Chi-squared test, X^2 = 28.35, df = 4, p < 0.001, Cramer's V = 0.24, n = 128 species for which both endemicity and microhabitat were determined). Over half of widespread species were generalists (i.e. ground/rock- and vegetation-dwelling); SAE species were more specialized, with a plurality found in vegetation; while most SIE species were ground/rock-dwelling, and few were microhabitat generalists (Fig. 2a).

As predicted, habitat elevation occupied was significantly associated with degree of endemicity (Chi-squared test, X^2 = 23.65, df = 4, p < 0.001, Cramer's V = 0.21, n = 135 species for which both endemicity and habitat elevation were determined). Over two-thirds of widespread species occurred only at low elevations (i.e. 0 to 321 m), and no widespread species occurred only at high elevations (i.e. > 321 m; Fig. 2b). In contrast, most high-elevation species were SIE, and relatively few SIE species were restricted to low elevations.

Based on within-family analyses, there were no significant differences in body size based on degree of endemicity (ANOVA, F = 1.79, df = 2, 125, p = 0.171, n = 140 species in 13 families), although the means of confamilial widespread species' shell sizes were generally smaller than means for both SAE and SIE

confamilials (Fig. 1b). Log-transforming shell size data did not change conclusions (ANOVA, F = 1.40, df = 2, 125, p = 0.249). There was a significant association between endemicity and microhabitat within families (Cochran-Mantel-Haenszel Chi-squared test, M^2 = 9.50, df = 4, p = 0.050, n = 77 species in 7 families with species representing at least two levels of endemicity in at least two microhabitat categories). Species included in within-family analysis of microhabitat specificity showed the same pattern of association as found in the full dataset (Supplemental Fig. S1a). Within families, endemicity was significantly and positively associated with elevation (Cochran-Mantel-Haenszel Chi-squared test, M^2 = 9.69, df = 4, p = 0.046, n = 104 species in 11 families with species representing at least two levels of endemicity in at least two elevation categories). Species included in within-family analysis of habitat elevation exhibited a significant association between widespread and SAE species and low elevations and between SIE species and high elevations (Supplemental Fig. S1b).

Discussion

Our results were generally consistent with the aerial dispersal and taxon cycle hypotheses, revealing possible reversals in selection pressures for island land snails. Widespread species (presumably early taxon cycle) exhibited a high prevalence of relatively small-shelled microhabitat generalists occupying low elevations (Fig. 3a).
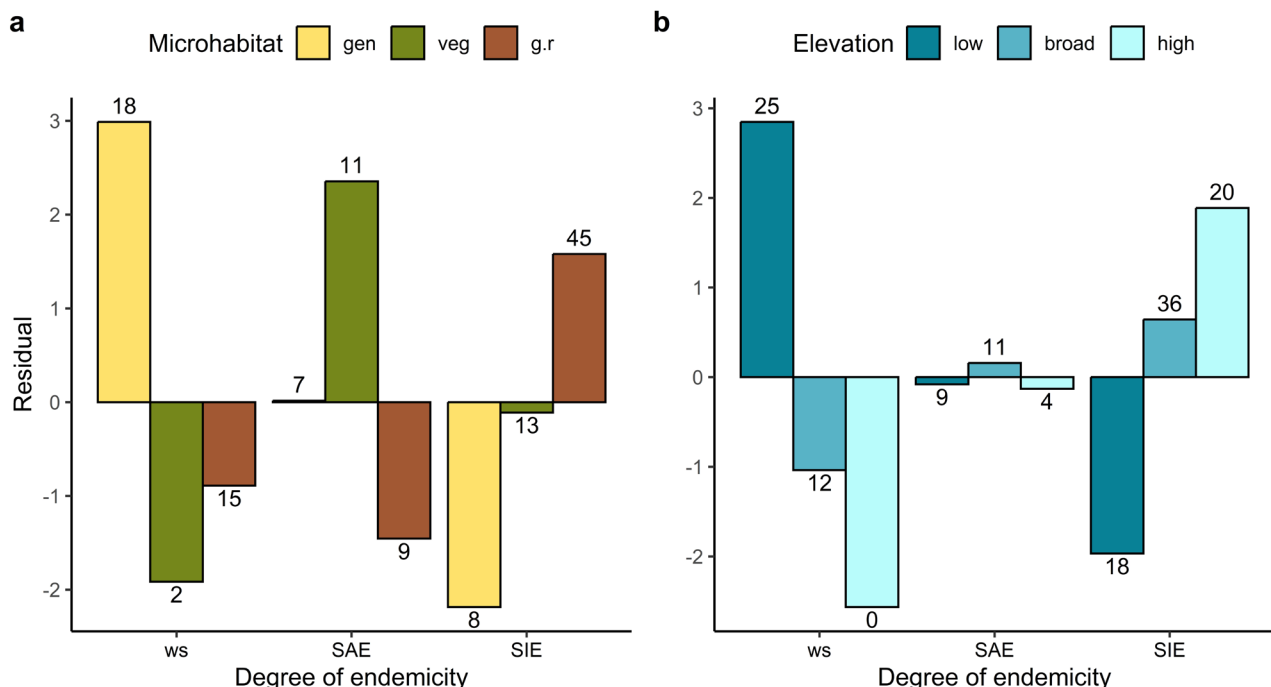

Figure 2. Strength of association between degree of endemicity and **a** microhabitat and **b** habitat elevation (Chi-squared tests, X^2 > 23, p < 0.001 for both) in native land snails of Samoan Islands, Mariana Islands, and Lord Howe Island and neighboring small islands. Bars show magnitudes and signs of Chi-squared test residuals. Numbers above or below bars indicate numbers of Pacific Island land snail species in each category (data shown for 128 species in **a** and 135 species in **b**). Abbreviations: ws = widespread, SAE = single-archipelago endemic, SIE = single-island endemic, gen = generalist, veg = vegetation-dwelling, g.r = ground/rock-dwelling.

By contrast, SAE and SIE species were larger-shelled (in the case of SAE species) with greater degrees of microhabitat specialization in high-elevation, interior habitats (in the case of SIE species; Fig. 3b-c). Within-family analyses (i.e. analyses that roughly account for phylogenetic relatedness) also support these findings.

Similar patterns consistent with the aerial dispersal and taxon cycle hypotheses have been anecdotally observed for PILS in other archipelagos. Hawaii-endemic Achatinellidae can be nearly an order of magnitude larger than more widespread, confamilial species (median shell size of genera in the Hawaii-endemic Subfamily Achatinellinae: 20 to 22 mm [Vagvolgyi 1975]; maximum shell dimension of widespread achatinellids in our

dataset: 2.6 to 4.0 mm). Phylogenetic evidence lends tentative support to the hypothesis that Hawaiian achatinellines are descended from a small, aerially dispersing ancestor (Holland and Hadfield 2004). Further, Hawaiian achatinellines are arboreal habitat specialists, whereas most widespread achatinellid species in our dataset are microhabitat generalists, again suggesting a potential association between degree of microhabitat specialization, endemicity, and shell size in Achatinellidae.

In the Galápagos, older islands are inhabited by larger *Naesiotus* species (a genus endemic to the archipelago; Kraemer et al. 2021); this presumably results from longer periods of evolution in isolation and consequent declines in dispersal ability.
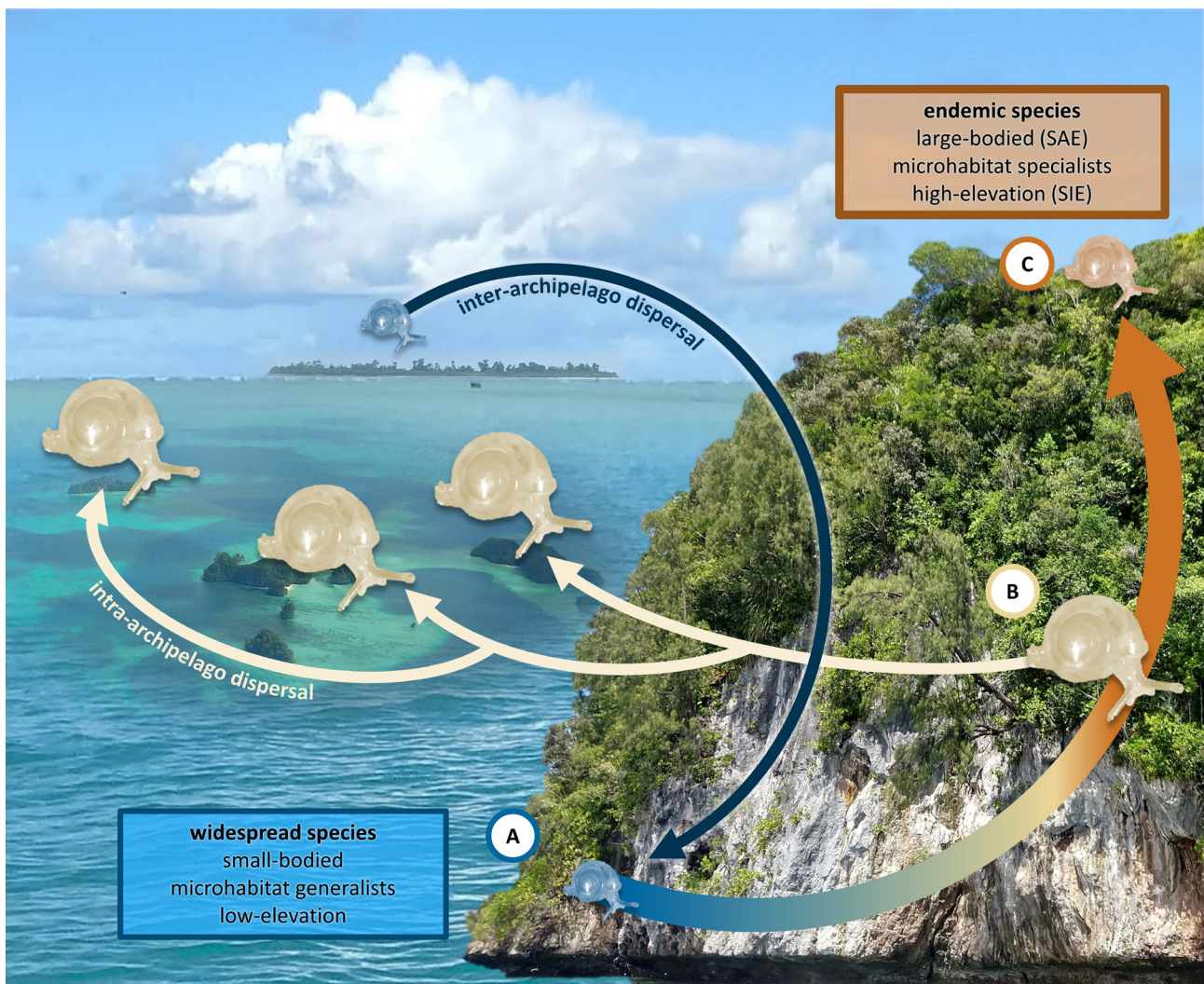

Figure 3. Conceptual model of immigrant selection and the taxon cycle in Pacific Island land snails proposed by this study. **a** For widespread species, inter-archipelago aerial dispersal favors small body size and microhabitat generalism. Competition with locally adapted endemic species largely excludes widespread species from high-elevation habitats. **b** For single-archipelago endemic species, intra-archipelago rafting dispersal may select for large body size. As single-archipelago endemic species become locally adapted, they tend to specialize in vegetation-dwelling. **c** Single-island endemic species are most ecologically specialized, predominating in ground/rock microhabitats and in high-elevation island interior habitats. Abbreviations: SAE = single-archipelago endemic, SIE = single-island endemic.

This pattern of larger PILS on relatively older islands holds across Pacific archipelagos (Kraemer et al. 2021). *Naesiotus* are all SIE species, and various species in the radiation are found in all Galápagos habitat types, except for lava boulders and sandy coastal zones (i.e. marginal coastal habitat; Parent and Crespi 2009). On Rarotonga, at least eight of 14 widespread species found in late-Holocene fossil land snail fauna were apparently restricted to that island's lowlands (Brook 2010), consistent with the association we found between degree of endemicity and elevation.

Immigrant selection on aerial dispersal may be present in Atlantic Island land snails, continental land snails, and even marine snails as well. In Eastern Europe and the Western Caucasus region, micromollusc species are more likely to have broad geographic ranges than large species are (Cameron et al. 2010, Pokryszko et al. 2011), consistent with aerial dispersal favoring small snails. Phylogenetic evidence suggests that members of the *Balea perversa* (Linnaeus, 1758) species group have repeatedly dispersed between mainland Europe and far-flung Atlantic Islands of Iceland, the Azores, Madeira, Tristan da Cunha, and Gough Island (Gittenberger et al. 2006), with ample opportunities for immigrant selection during aerial dispersal. Similarly, genetic data show that Neotropical intertidal snails in the genus *Cerithideopsis* have repeatedly dispersed across the Isthmus of Panamá, presumably transported by seabirds (Miura et al. 2012).

Counter to one of our predictions, we found that SIE species were smaller than SAE species. We can only speculate that this apparently anomalous result may stem from more prolonged selection during dispersal among islands within archipelagos, coupled with selection against inter-archipelago dispersal. In such cases, rafting on vegetation or floating directly in sea water may be more common means of intra-archipelago dispersal, favoring larger snails with greater energy stores to survive the rafting (i.e. non-aerial) voyage. Darwin demonstrated that some land snails can survive 2-3 weeks in sea water (Darwin 1859, Orstan and Dillon 2009), perhaps long enough to occasionally drift between neighboring islands. Hawaiian-endemic *Succinea caduca* (Mighels, 1945) can survive up to 12 h of emersion in sea water while attached to bark, suggesting that *S. caduca* may disperse among the Hawaiian Islands on vegetation washed to sea (Holland and Cowie 2007). Alternatively, some aspects of high-elevation sites and/or ground/rock microhabitats may favor smaller species while simultaneously inhibiting inter-island dispersal, producing a preponderance of small, SIE, high-elevation ground/rock specialists. Clearly, differences between inter- and intra-archipelago land snail dispersal and their ecological and evolutionary consequences warrant further study.

Though not conclusive, our data indicate that the taxon cycle cannot be ruled out as a working hypothesis to explain PILS geographic distributions. Without phylogenetic or fossil evidence, we were unable to test the assumption that SAE and SIE species are descended from widespread ancestors (Ricklefs and Bermingham 2002, Matos-Maravi 2020). Unfortunately, requisite fossil and phylogenetic data are lacking for many PILS. For example, a recent multi-archipelago, multi-taxon phylogenetic examination of the taxon cycle identified only four land snail genera from two families with sufficient phylogenetic data for inclusion in analyses (the bulimulid genus *Naesiotus* and partulid genera *Eua*, *Partula*, and *Samoana*; Keppel et al. 2023). Given the state of knowledge, this key assumption that widespread, SAE, and SIE species represent a chrono-sequence is largely inescapable. This study is therefore a starting point in assessing the taxon cycle in PILS, not a definitive demonstration of the phenomenon. We encourage future studies to re-evaluate this question using data from additional archipelagos, phylogenetic analyses, and/or fossils.

That said, some of our results cannot be explained without invoking the taxon cycle. There is no compelling reason why aerial dispersal alone would result in widespread species occupying low elevations; indeed, aerial dispersal might be expected to favor high-elevation species (Gillespie et al. 2012). The taxon cycle explains this seeming contradiction: because they lack local adaptations, widespread species incur a competitive disadvantage in more favorable high-elevation habitats. This competitive disadvantage may increase with island age, as greater niche filling interferes with colonization and diversification by new taxa (Keppel et al. 2023). Thus, the taxon cycle – but not immigrant selection alone – predicts that widespread species would be more common at lower elevations (Ricklefs and Bermingham 2002, Matos-Maravi 2020).

Island land snails are at the forefront of the anthropogenic extinction crisis. Many Pacific-endemic snails are probably extinct (Regnier et al. 2015, Proios et al. 2021) or remain extant in the wild only in high-elevation refugia (Lydeard et al. 2004). Extinct and refugial PILS species remain invisible to much of the scientific community because of disproportionately low research effort or limited publicity compared to other imperiled taxa (Lydeard et al. 2004) and, as a result, are underrepresented in databases like the *IUCN Red List of Threatened Species* (Regnier et al. 2009). Yet both the taxon cycle and the contagion hypothesis of anthropogenic geographic range contraction suggest that range-restricted, high-elevation species like many endemic PILS are at increased risk of extinction (Lomolino 2023). Studies like ours demonstrate the potential for insightful biogeographic research on island land snails (see Beck and McCain [2020] on the value of invertebrate macroecology). Unfortunately, these diverse and highly endemic assemblages are being replaced by a limited and redundant set of synanthropic species, exacerbating the ongoing homogenization of nature in general (McKinney and Lockwood 1999, Lydeard et al. 2004).

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Author Contributions

T.R.O. and M.V.L conceived the ideas; T.R.O. compiled and analyzed the data; T.R.O. and M.V.L led the writing. R.J.R. supervised the project.

Data Accessibility Statement

All references from which data were drawn are listed in Supplementary Material (Appendix S1). Compiled taxonomic, geographic, morphological, and ecological data are available in Supplemental Table S3.

Supplementary Material

The following materials are available as part of the online article at https://escholarship.org/uc/fb
Figure S1. Strength of association between degree of endemicity and a microhabitat and b habitat elevation for species included in within-family analyses.
Table S1. Number of species per family included in analyses.
Table S2. Islands from each focal archipelago included in analyses.
Table S3. Geographic, morphological, ecological, and taxonomic traits and presence-absence matrix of included species.
Appendix S1. All references for Pacific Island land snail morphological, ecological, and geographic range data.
Appendix S2. Results of analyses in which single-archipelago endemic land snails of Lord Howe Island and neighboring small islands are reclassified as "single-island endemic" species to reflect historical interconnectedness of islands.
Appendix S3. Comparison of shell sizes between widespread, single-archipelago endemic, and single-island endemic species using maximum shell dimension and conical volume as shell size measurements.

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