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LETTER

Evolutionary opportunity and the limits of community similarity in replicate radiations of island lizards

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Abstract

Ecological community structure ultimately depends on the production of community members by speciation. To understand how macroevolution shapes communities, we surveyed *Anolis* lizard assemblages across elevations on Jamaica and Hispaniola, neighbouring Caribbean islands similar in environment, but contrasting in the richness of their endemic evolutionary radiations. The impact of diversification on local communities depends on available spatial opportunities for speciation within or between ecologically distinct sub-regions. In the spatially expansive lowlands of both islands, communities converge in species richness and average morphology. But communities diverge in the highlands. On Jamaica, where limited highland area restricted diversification, communities remain depauperate and consist largely of elevational generalists. In contrast, a unique fauna of high-elevation specialists evolved in the vast Hispaniolan highlands, augmenting highland richness and driving islandwide turnover in community composition. Accounting for disparate evolutionary opportunities may illuminate when regional diversity will enhance local diversity and help predict when communities should converge in structure.

KEYWORDS
adaptive radiation, *Anolis*, beta diversity, biogeography, community structure, ecological limits, elevation, local versus regional richness, macroevolution, species pools

INTRODUCTION

A central goal in ecology is to determine what forces structure local communities, and why community membership varies across space. Local community composition reflects a balance between regional inputs of species, via speciation and dispersal, and local controls on their persistence, such as environmental filtering, competition and other drivers of extirpation (Leibold & Chase, 2018; MacArthur & Wilson, 1967; Rosenzweig, 1995; Vellend, 2016). If community diversity equilibria are primarily set by local forces, communities in similar environments should be similar in composition. Conversely, if regional forces predominate, regions with more species should also possess greater local-scale diversity (Ricklefs, 1987). Debate over whether local or regional forces dominate has reached an uneasy détente, as macroecological patterns suggest local control in some systems, and pervasive regional influences in others (Cornell & Harrison, 2014; Myers et al., 2013; Ricklefs & Schluter, 1993). What is thus crucial is to identify the reasons for this variation, and to establish a framework to explain why local processes determine local diversity in some systems, while regional species pools strongly influence others (Cornell, 1999; Harrison & Cornell, 2008; Lessard et al., 2012).

We approach this challenge by focusing on the mechanisms by which macroevolutionary inputs could ultimately determine community structure. First, we consider attributes of regions that foster (or limit) the evolution and persistence of diverse species pools (McPeek & Brown, 2000; Mittelbach &

Schemske, 2015; Rosenzweig, 1975; Swenson, 2011; Zobel et al., 2011). We then consider how diverse species pools may lead to saturated communities (competition-structured communities where species richnesses achieve stable equilibria; Rabosky & Hurlbert, 2015; Storch & Okie, 2019). The availability of unused resources, so-called "ecological opportunity," is often invoked to explain how lineages radiate into faunas whose members can coexist and fill available niches (Losos, 2010; Schluter, 2000). But ecological opportunity alone cannot explain the buildup of regional faunas (Rundell & Price, 2009). For lineages to take advantage of ecological opportunity, they must be able to speciate (Felsenstein, 1981; Rosenzweig, 1975). Speciation typically requires a period of allopatry (Coyne & Orr, 2004), so key determinants of species-pool diversity include a region's size, topography and age (Rosenzweig, 1995). Further, species pools arise from an interplay of ecological and evolutionary factors at spatial scales intermediate to the local versus regional scales of traditional assembly models (Emerson & Gillespie, 2008). Given the role of space in speciation, the hierarchical organisation of regions (large, evolutionarily-independent areas such as continents or oceanic islands) into environmentally-distinctive "sub-regions" (biomes) may shape the buildup of species pools, thereby influencing local community structure (Jetz & Fine, 2012; Mittelbach & Schemske, 2015; Qian & Ricklefs, 2000; Zobel et al., 2011).

Whether local communities are influenced by diversification depends on whether they are saturated. If communities are unsaturated, increased diversification within a region should elevate local richness by increasing species additions relative to losses (Hubbell, 2001; Leibold et al., 2004). Alternatively, if increased diversification produces species that specialise on attributes of particular sub-regions (Glor et al., 2003; Gray et al., 2019; Mayr, 1947), it may spur the emergence of local richness controls. Sub-regional specialists may better monopolise local resources, resulting in competition-structured communities resistant to generalist migrants (Cornell & Harrison, 2014; MacArthur, 1972). Therefore, whether local or regional forces predominate may depend on the availability of "evolutionary opportunity"—a term we use to describe the time and geographic space necessary for (allopatric) speciation, which in turn permits lineages to diversify and specialise on local ecological conditions (Algar & Mahler, 2015; Cornell, 2013; Losos & Parent, 2010).

If greater evolutionary opportunities indeed facilitate local control, we predict the emergence of several patterns in local-community abundance, species diversity and organisation across space (beta diversity). The concept of local control hinges on density dependence and community saturation, which can occur at the individual level (demographic carrying capacity), but also at the species level (as diversity increases, local extirpation eventually outpaces establishment, yielding an analogous carrying capacity for species; Storch & Okie, 2019). For communities to exhibit species-level saturation, they must be saturated at the level of individuals competing for limited resources (Cornell, 1999; Gaston, 2000). Thus, abundance in such communities should scale with resource availability, yielding correlations between local abundance and proxies of productivity, such as temperature or elevation (Wright, 1983). If individuals can efficiently utilise resources regardless of their evolutionary origins, the scaling of abundance and productivity should be similar across regions that differ in evolutionary diversity. Conversely, if greater diversification produces species that can access novel resources, regions with greater diversification should have higher local abundances (Cornell, 2013; Storch et al., 2018).

Next, if greater macroevolutionary diversity leads to the emergence of stronger local controls on species richness, the relationship between resources and local community richness should be similar across regions. However, this relationship will depend on whether clades in different regions have had sufficient opportunity to diversify into locally available niches—in other words, whether they have produced sub-regional specialists (i.e. endemics) that can saturate communities at the species level (Cornell, 2013; Jetz & Fine, 2012). If a given region has had insufficient time or space for diversification to fill sub-regional niches, we would expect local richness patterns across regions to diverge (MacArthur, 1972; Mittelbach & Schemske, 2015).

Finally, if evolutionary opportunity shapes communities by facilitating local control, we expect greater regional diversity to sort primarily among communities (as beta diversity) rather than within them (as elevated alpha diversity; Cornell, 2013; MacArthur, 1965). Evolutionary opportunity should precipitate the emergence of spatial structure within faunas through the evolution of endemic sub-regional specialists. When opportunity is substantial in similar environments, whole-community properties such as total richness and functional characteristics may converge, even among evolutionarily-independent regions (Cornell, 1999; Orians & Paine, 1983; Ricklefs, 2006). By contrast, faunas lacking in evolutionary opportunity should consist of environmental generalists, and the local communities within these faunas should exhibit little turnover and potentially low convergence between faunas.

Testing how diversification affects local communities is difficult, in part because of the challenge of locating systems that are ecologically similar but differ in evolutionary opportunity (Lessard et al., 2012). Regions differing in evolutionary richness often also differ in climate, habitat or the deep phylogenetic history of the biota, which may confound straightforward comparison (Price et al., 2000; Rosenzweig, 1995). Here, we leverage a natural experiment to examine the effects of macroevolution on local community structure: independent radiations of anole lizards (*Anolis*) distributed across similar environmental gradients on the Caribbean island of Jamaica and the northern paleoisland of adjacent Hispaniola (a biogeographically distinctive unit; Figure 1). These neighbouring islands share attributes that shape communities of anoles, including climate, vegetation type and macrohabitat diversity (Losos, 2009; Ricklefs & Bermingham, 2008). Both feature vast expanses of hot lowland tropical forest that grade into tall inland mountains featuring cool cloud-forest habitats. Accordingly, anoles have diversified to play similar ecological roles on both islands, even though they share no species and have been separated by tens of millions of years of evolution (Losos, 2009; Mahler et al., 2013). Despite their ecological similarity, northern Hispaniola is larger than and twice as old as Jamaica, likely affecting the evolutionary opportunity available to their faunas. In pioneering work, Williams (1983) suggested that the greater size of Hispaniola's highlands was crucial in elevating its evolutionary potential, resulting in the emergence of a distinctive endemic highland subfauna (see also Glor et al., 2003; Muñoz & Losos, 2018) and a richer fauna overall than Jamaica. Indeed, while the lowlands of both islands cover more than 3000 km^2, the minimum area required for *in situ* speciation in anoles (Losos & Schluter, 2000), only Hispaniola's highlands clear this threshold, leading to the expectation that Jamaica's highland communities should be evolutionarily constrained (Figure 2). Although it is possible that Jamaica's younger age (Donovan, 2002; Matos-Maraví et al., 2014; including its highlands, Buskirk, 1985) contributed to its diminished evolutionary opportunity, time's role is likely minor. After an initial burst of diversification, speciation on both islands has declined, and in Jamaica's case appears to have slowed to no net species additions for the last third of its history (Rabosky & Glor, 2010).

We conducted mark-resample surveys of *Anolis* communities across matched elevational gradients on Jamaica and Hispaniola to test whether greater macroevolutionary diversity, and especially differences in highland evolutionary opportunity, trickle down to structure local communities. We begin by asking (1) whether the abundance of *Anolis* within local communities across elevations is similar between islands, as predicted if local temperature is primarily responsible for controlling community size. Next, we ask (2) whether differences in sub-regional area trigger divergence in community structure at the species level, such that among-island community convergence exists in the lowlands (where evolutionary opportunity is substantial), but is lacking in the highlands (where Jamaica is limited). We then investigate (3) whether greater evolutionary opportunity in the Hispaniolan highlands leads to ecologically distinct subfaunas via the evolution of highland endemics. If so, we predict that Hispaniolan anole communities will exhibit greater beta diversity than their Jamaican counterparts. Finally, we (4) test the importance of sub-regional faunas in fostering convergence in abundance and richness between islands.

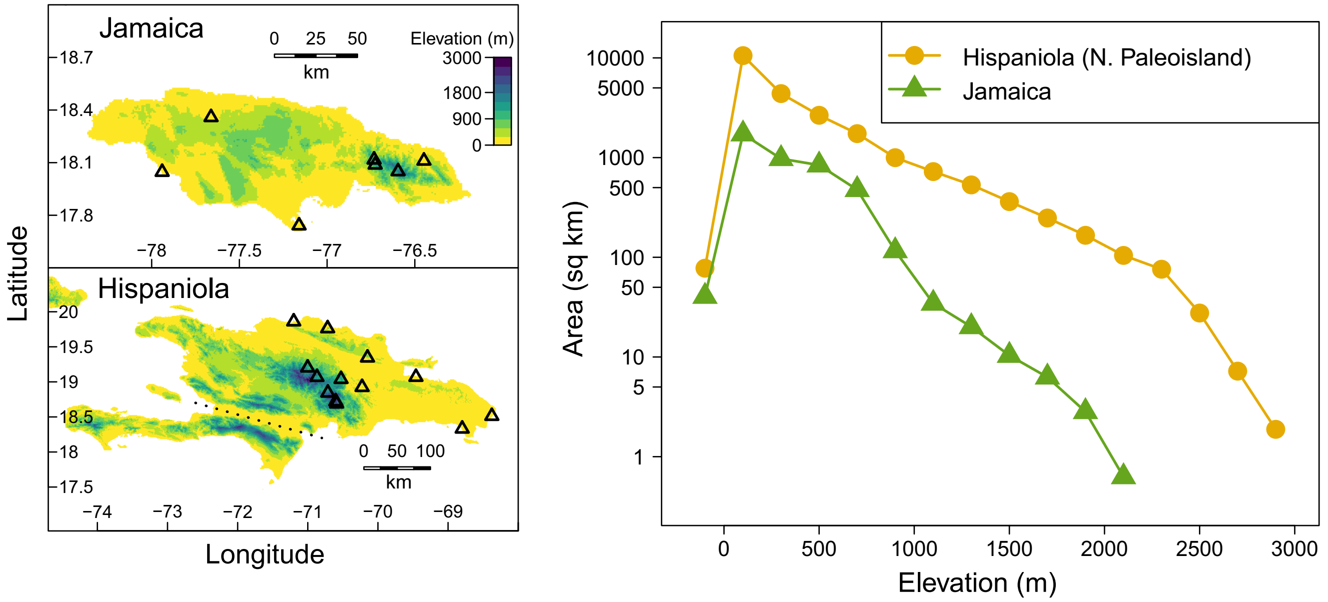

FIGURE 1 Left hand panels show maps of study landscapes (triangles) along the elevational gradients on both islands. Dashed line on Hispaniola separates the north paleoisland from the south paleoisland—areas that have had separate evolutionary histories during periods of higher sea levels, and which have different species pools. Note that maps of Jamaica and Hispaniola are not on the same scale. Right hand panel illustrates the total area (y-axis on log scale) in 200 m elevational bands on both islands. Note the steep drop-off in area on Jamaica above 700 m.

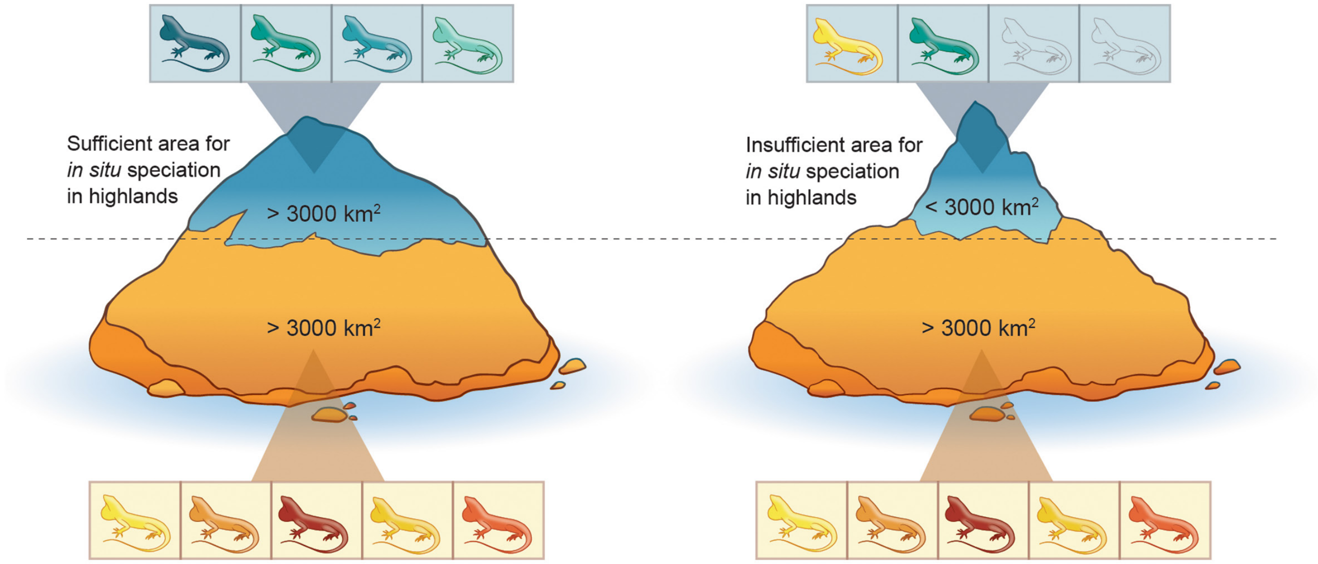

FIGURE 2 Schematic illustrating hypothesised influence of limited evolutionary opportunity in the highland sub-region on species-level composition within and between communities. On the island to the left, both lowland and highland sub-regions have sufficient space for speciation. As a result, diversification has filled available niches (boxes) with species (represented by different coloured lizards) in single examples of sub-regional communities (sets of joined boxes) for both the lowlands and highlands. On the right island, however, the limited highland area has prevented *in situ* speciation in that sub-region, resulting in (i) the evolution of only a single highland endemic (blue lizard), (ii) highland communities that include lowland-associated species (yellow lizard), and (iii) communities undersaturated at the species level (indicated by empty boxes). In the lowlands of both islands, sufficient evolutionary opportunity leads to convergence in niche-filling and the species diversity held within communities.

METHODS

Sampling

We surveyed *Anolis* communities in plots across northern Hispaniola (in the Dominican Republic) and Jamaica in June–August of 2016–2018. We surveyed plots in 20 landscapes (13 on Hispaniola, 7 on Jamaica), distributed over broad temperature and precipitation gradients. Landscapes spanned from 0 to 2380 m on Hispaniola (maximum elevation 3098 m) and 0 to 1923 m on Jamaica (maximum elevation 2256 m), an elevation range representing >99.5% of each island's total area. Sampled climates were broadly similar (Figure S1).

Each landscape contained two to four 30 m-diameter plots in forest habitat—the native climax vegetation ($N_{\text{Hispaniola}} = 35$, $N_{\text{Jamaica}} = 20$). An observer surveyed each plot six times, marking observed lizards with non-toxic paint following Heckel and Roughgarden (1979), allowing identification of resighted individuals.

Mark-resight model

We used mark-resight models to estimate each species' plot-level abundance, while accounting for detectability differences across species, time of day and observer. The model shared detectability and abundance information across plots and species, while allowing for plot and species-specific deviations via random intercepts and slopes (Frishkoff et al., 2019). Doing so permits robust abundance and detection estimates of both common and rare species. Species abundance was predicted based on plot canopy openness, measured using a spherical densiometer, and mean annual temperature and precipitation variables (from the CHELSA dataset; Karger et al., 2017).

We implemented mark-resight models in a Bayesian framework using rjags (JAGS: V4.2.0; R: V3.4.4; Su & Yajima, 2020). For every species at every plot the model estimated total abundance and parameters related to environmental variables (Tables S1–S6). A full model description is available in the supplement.

Hypothesis testing

To test whether community size scales identically with elevation on both islands, as predicted if communities are saturated at the individual level, we first regressed community size (total number of individuals in plots) against elevation. To assess whether greater regional diversity enhanced community-level species diversity across the same environmental gradient, we regressed plot-level species richness against elevation. We used posterior means from the resight model to represent best estimates of plot-level abundance and richness (because abundance and richness are Poisson-distributed, posterior medians and modes would be integers, resulting in loss of information about changes near 0).

We evaluated species abundance and richness trajectories across elevations using linear mixed-effects models (LMMs). Our full model predicted the response as a function of linear and quadratic elevation terms, with full interactions with island identity, and a random intercept of landscape to account for spatial clustering of plots. We iteratively dropped terms, comparing full and nested models until a likelihood-ratio test indicated all remaining terms were significant (alpha = 0.05). We square-root transformed resight-model-derived abundance and richness estimates to meet assumptions of residual normality and homoscedasticity (log transformation—more typical for richness and abundance data—failed to meet model assumptions). Because area declines with elevation, we validated that our results were not directly attributable to the species-area relationship by incorporating elevation-specific area into our best-fit models (see Table S7). We further tested whether richness and abundance trajectories were exceptionally similar across elevations using null models. In these models, we shuffled species identity between islands while maintaining gamma diversity, and simulated 1000 communities at plots (see Supplement).

Next, to test whether greater macroevolutionary diversity facilitates the evolution of specialised sub-regional endemics, thereby permitting greater partitioning of communities across space, we calculated abundance-weighted pairwise Bray dissimilarities between plots within each island using the betapart package (Baselga & Orme, 2012). We then examined abundance-weighted phylogenetic and morphological dissimilarity to assess whether differences in turnover had deeper evolutionary underpinnings, or resulted in ecomorphologically different community structures, respectively. To do so, we used the phylogeny and morphological measurements for anoles presented in Mahler et al. (2013). Measurements include body size and relative limb, tail and adhesive toepad dimensions, which correlate with the partitioning of structural microhabitats (Losos, 2009). We calculated phylogenetic dissimilarity of plots using abundance-weighted unifrac (Lozupone & Knight, 2005) in the abdiv package (Bittinger, 2020). For morphological dissimilarity, we calculated abundance-weighted mean pairwise distances between the species of all community pairs on each island using the four-dimensional PC-space of Mahler et al. (2013), which represents 93% of total morphological variation in Greater Antillean anoles. We assessed the rate at which pairwise community dissimilarities (taxonomic, phylogenetic or morphological) changed as a function of elevation differences between plots. We used linear regression models including both linear and quadratic elevation effects, an effect of island identity, and an island-by-elevation interaction.

Because sub-regional faunas formed to differing degrees on Jamaica and Hispaniola, we evaluated whether similar environments led to whole-fauna morphological convergence at both island and sub-region levels, gauged using community-mean morphology. We applied a threshold of 700 m to split islands into lowland and highland sub-regions. This elevation corresponded to the location of maximum turnover between highland and lowland species (results are not sensitive to the exact threshold). We assessed the abundance-weighted mean morphology along the four ecomorphological PC axes described above. To test whether morphology between subfaunas was more similar than expected by chance, we shuffled species morphologies 10,000 times and compared observed Euclidean distances between subfauna-mean morphologies to the null distribution.

Finally, given the potential distinctiveness of high-elevation subfaunas, we examined whether highland endemics drove any observed among-island differences in local diversity patterns. To do so we eliminated from the dataset all highland species (those with abundance maxima above 700 m, none of which occur at sea level). We then reassessed how abundance and richness of communities changed across the elevational gradient of each island using the same LMMs and model selection process described above. If among-island differences in the diversity-elevation relationship are attributable to the evolution of a richer highland subfauna on Hispaniola, deleting the highland fauna on both islands should reconcile these differences.

RESULTS

Local abundance and richness across islands

Abundances within local communities varied substantially, but community size declined monotonically on both islands as elevation increased (Figure 3a; best model: Elevation only, *Elevation* term: $p < 0.001$; marginal $R^2 = 0.57$). Despite the ~2-fold difference in gamma diversity between northern Hispaniola (11) and Jamaica (6), local communities at a given elevation possessed a statistically indistinguishable number of *Anolis* individuals (*Island* term: $p = 0.70$), and abundance declined with elevation at similar rates (*Island* × *Elevation* interaction $p = 0.11$). Null models confirmed that abundance trajectories between islands are more similar than expected by chance (Figures S2–S5).

But while among-island abundance patterns are similar, the partitioning of richness across elevations is not (*Island* × *Elevation* interaction $p < 0.001$, $Elevation^2$ term $p < 0.001$, marginal $R^2 = 0.86$). As predicted by the evolutionary opportunity model, Jamaica and Hispaniola have equivalent species richness in lowland communities. But above the lowlands, the trajectories diverge: Jamaica steadily loses species with elevation, while Hispaniola shows a mid-elevation hump, followed by a slow decline. Notably, above the lowlands (>500 m) communities are consistently richer on Hispaniola than on

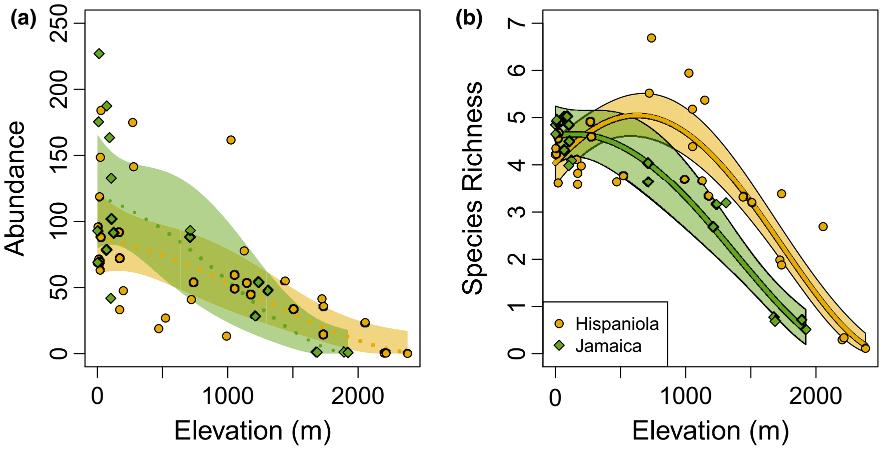

FIGURE 3 *Anolis* abundance and species richness across survey plots on both islands. (a) Total *Anolis* abundance declines monotonically with elevation and is statistically indistinguishable between islands. The depicted model includes linear and quadratic effects of elevation and full interactions with island identity, though only the effect of elevation is statistically significant after backwards model selection. (b) Species richness patterns along elevational gradients deviate between islands, ranging from rough equivalency in the lowlands to greater species richness in the Hispaniolan fauna upslope. Figure depicts model best-fit lines on Jamaica (green) and Hispaniola (yellow), with shaded regions representing standard error. Significant differences between islands are emphasised with black borders around best-fit lines and standard error regions in panel (b). Points represent posterior mean abundance and species richness at study plots derived from mark-resight models ($N_{\text{Jamaica}} = 20$, $N_{\text{Hispaniola}} = 35$).

Jamaica (Figure 3b). Null models suggest that species richness in the lowlands is indeed more similar between islands than expected by chance ($p < 0.05$ in most elevational bins below 500 m, Figures S2–S5).

Available area on both islands decreases with elevation, raising the possibility that area alone could be driving observed elevational trends (Figure S6). However, when controlling for available area (see Supplement), we observe qualitatively identical support for elevation terms, while area terms are non-significant (Table S7). Further, null models indicate that Hispaniola's mid-elevation richness hump is unlikely to have developed if species simply evolved to have temperature (elevation) optima in proportion to temperature availability based on area ($p = 0.004$, Figure S7).

Community partitioning into subfaunas

Geographic distance between plots has no effect on community dissimilarity, suggesting that dispersal limitation is not driving community structure (Figure S8). Instead, elevation drives beta diversity (Figure 4a). As predicted from Hispaniola's increased highland evolutionary opportunity, beta diversity is greater on that island. Further, Hispaniola's beta diversity derives primarily from among-site turnover, while much of Jamaica's stems from richness and abundance gradients (Table 1). This difference is a signature of the evolution of high-elevation endemics on Hispaniola. Specifically, the Hispaniolan fauna contains five species that are distributed across the lowlands, one lowland dry-habitat specialist and five found primarily above 700 m. By comparison, Jamaica has five species distributed across the lowlands, and only one high-elevation endemic.

Hispaniola's species comprise two distinct subfaunas: the lowest and highest communities share no species. In contrast, lowland species on Jamaica persist at its highest sites (Figure 4a–c). Interestingly, the elevated beta diversity of Hispaniola contains a strong phylogenetic signal linked to historical elevational specialisation. Hispaniola's highland endemics derive from a combination of *in situ* radiation and evolutionary colonisation from lowland ancestors. While two highland species each have a lowland species as their closest relative, the most abundant highland forest understory species primarily derive from a single clade, which colonised the highlands early in the history of the island, initiating an adaptive radiation in miniature (Figure 4d,e). This clade drives the formation of the sub-regional fauna on Hispaniola, resulting in substantial elevational turnover that is absent from Jamaica.

The evolution of Hispaniola's highland subfauna results in community-level differences in trait distributions. Average morphology diverges between lowland and highland communities on Hispaniola but remains undifferentiated on Jamaica (Figure 4f). Different environments should require different morphological solutions, and given ample evolutionary opportunity, communities in similar environments should converge. Indeed, the community abundance-weighted mean morphology in the lowlands of Jamaica and Hispaniola is more similar than expected by chance (Figure 4g and Figure S9; $p = 0.033$). In contrast, the highlands are morphologically distinct, without evidence for among-island convergence ($p = 0.44$).

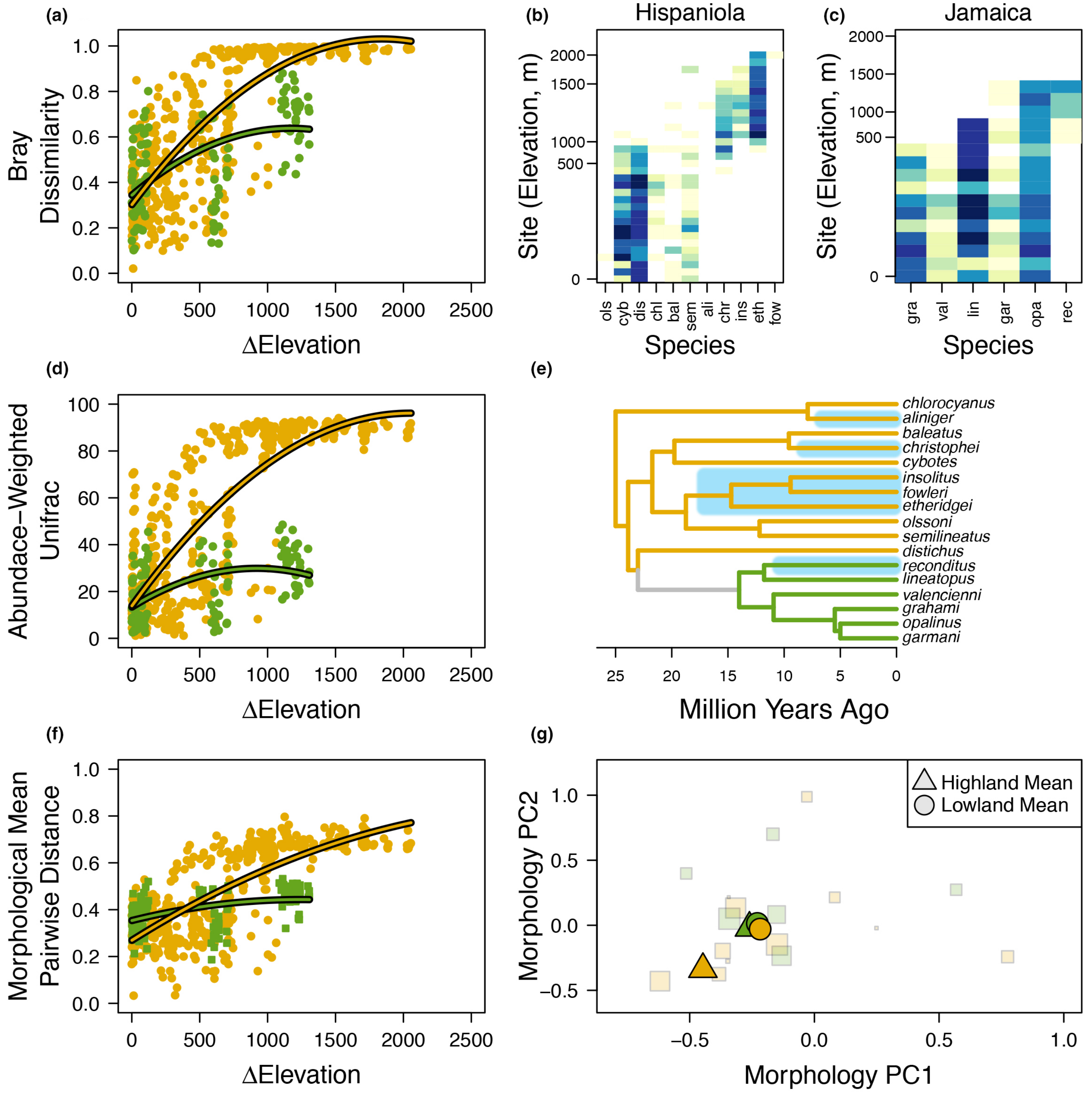

FIGURE 4 Greater macroevolutionary diversity on Hispaniola generates a distinctive high-elevation fauna. (a) Pairwise plot-level community dissimilarity based on species identity (balancing component) against the differences in elevation between plots. (b and c) Heat maps showing abundance of species in all plots along island elevational gradients. Plots are organised along the *y*-axis so that the lowest-elevation plots are on the bottom and the highest are on top. Tick marks along the *y*-axis show 500 m increments. Note that *y*-axes are not scaled uniformly within islands, because low elevation habitats are more common and thus better represented, and are not identical across islands, as sampling sites were not precisely matched by elevation. Species along the *x*-axis are ordered by mean elevation at which the species occurs. Note (i) the distinct highland species on Hispaniola, and (ii) differences between islands in elevation at which no anoles occur. (d) Pairwise phylogenetic dissimilarity of plots as in panel (a) highlighting the phylogenetic turnover with difference in elevation on Hispaniola. (e) Phylogeny of all *Anolis* species observed, with branches coloured according to island. Blue underlay highlights highland species (species not observed at sea-level); illustrated timescale obtained by setting the crown age of Jamaican *Anolis* in the ultrametric tree of Mahler et al., 2013 to 15 Ma, following Buskirk, 1985. (f) Pairwise morphological dissimilarity between plots as in panel (a) highlighting greater morphological dissimilarity between elevation zones on Hispaniola. (g). Location in morphospace of all observed species (transparent squares) along first two morphological principal component axes from 11 morphometric measurements. PC1 corresponds to limb length whereas PC2 corresponds to overall body size. Square size represents overall abundance of the species across all plots. Solid circles depict the abundance-weighted morphological means of all plots in the lowlands (<700 m asl) and triangles represent the highlands (>700 m asl). In all plots (except b and c) yellow indicates plots or species on Hispaniola whereas green indicates those on Jamaica.

Finally, the evolution of Hispaniola's high-elevation fauna apparently granted access to elevations that would otherwise go unoccupied. For example, on Hispaniola, three species were common above 1800 m and continued to occupy montane forests up until 2300 m (Figure 4b,c). But while Jamaica reaches 2250 m at its peak, we detected no anoles at or above 1800 m (note, resight models cannot rule out a small number of individuals, so model-predicted richnesses are non-zero; Figure 2b).

Community structure along environmental gradients

To understand the consequences of subfaunal emergence on local diversity, we examined elevational alpha diversity patterns on each island after eliminating all species that do not occur at sea level. With highland species absent, abundance trajectories are no longer statistically indistinguishable: total community size declines much more rapidly on Hispaniola than Jamaica (*Island* × *Elevation* interaction, $p = 0.021$; *Island* × *Elevation*^{2} interaction $p = 0.025$, $R^2 = 0.80$). Specifically, Hispaniola shows a lizard deficit at middle and high elevations with respect to Jamaica (Figure 5a).

TABLE 1 Islandwide beta diversity partitioning based on plot presence-absence (incidence) or abundance

Type	Component	Hispaniola	Jamaica
Incidence	Turnover	0.86	0.50
	Nestedness	0.03	0.17
	Total	0.90	0.67
Abundance	Balancing	0.86	0.59
	Gradient	0.07	0.22
	Total	0.93	0.81

Note: Total community dissimilarity is partitioned into a component deriving from species replacement between plots ("turnover" and "balancing"), versus from differences in richness or abundance between plots ("nestedness" and "gradient").

In contrast, eliminating highland endemics equilibrates elevational species richness trajectories between islands: the best-fit model includes only a linear elevation term (*Elevation* term $p < 0.001$, marginal $R^2 = 0.88$). Without highland species, Hispaniola loses its middle-elevation richness hump, and lowland species disappear from communities at roughly the same rate with increasing elevation on both islands (Figure 5b, All island effects non-significant: *Island* × *Elevation*^{2} interaction $p = 0.51$, *Island* × *Elevation* interaction $p = 0.43$, *Island* effect $p = 0.13$).

DISCUSSION

Diversification strengthens local controls on community structure

Analysis of a macroevolutionary 'natural experiment'—lizard radiations on neighbouring islands similar in environment but divergent in evolutionary opportunity—reveals complex signatures of macroevolutionary processes on local community structure. Specifically, greater diversification appears to (i) diminish the effect of regional diversity on local richness within biomes by saturating local communities, while simultaneously (ii) amplifying the importance of regional diversity for local richness at biome transition zones, where subfaunas

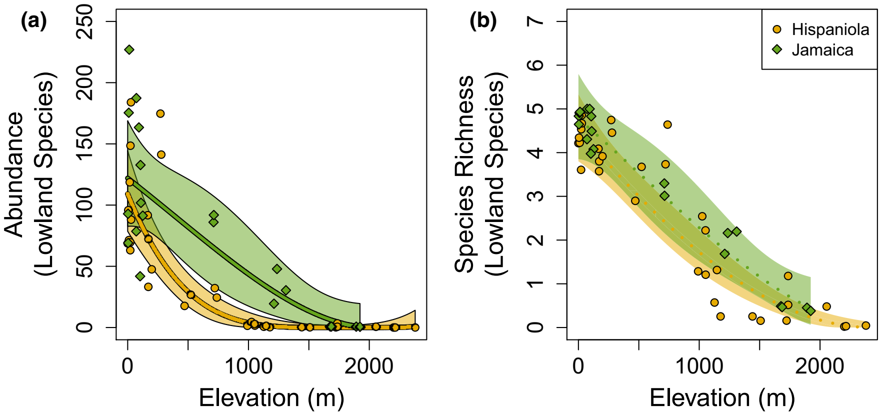

FIGURE 5 Species abundance and richness across elevation, excluding highland endemics from analysis. (a) Abundance of all lizard individuals in plots across elevations, evaluating only lowland species (those that have maximum abundances <700 m). When discounting the highland fauna, Hispaniola has fewer individuals at middle elevations, though total abundance is still equivalent between islands near sea level. Compare to Figure 3a, which analyses all species and shows equivalent abundance profiles by elevation across islands. (b) Species richness in plots, evaluating only lowland species. Removing the highland species yields remarkably similar alpha diversity trajectories between islands, suggesting that differences in species richness trajectories across islands observed in Figure 3b can be attributable to the presence of a diverse highland fauna on Hispaniola. Definitions of lines, shaded regions and points are the same as in Figure 3. Note that both panels depict models with linear and quadratic effects of elevation and full interactions with island identity, though only the effect of elevation was significant after backwards model selection for lowland species richness.

abut. Critically, the evolution of sub-regional ecological specialists may determine whether communities achieve local diversity controls at the species level.

The imprint of macroevolution on communities varies across levels of biological organisation. First, community abundances suggest local controls at the individual level regardless of macroevolutionary input. Abundances decline similarly with elevation on Jamaica and Hispaniola, despite a twofold regional diversity difference. Community sizes thus appear limited by competition—likely for dietary resources (energy). Interestingly, greater diversification did not raise individual-level carrying capacities by producing more efficient resource specialists (Cornell, 2013; Storch et al., 2018), although the slightly greater abundance of Hispaniolan anoles at the highest elevations may represent weak evidence for such an effect.

Second, community-level species richness was similar between islands where both provide ample opportunities for the evolution of endemic habitat specialists (the lowlands), but diverged in areas where opportunities differ starkly (the highlands). In the lowlands, species richness and average community morphology were nearly identical between islands despite the larger area and greater regional diversity of Hispaniola. Such similarity suggests that local richness limits have been reached (Cornell, 1999; Ricklefs, 2006). However, community structure diverged in the highlands, with species richness on Hispaniola exceeding that of Jamaica at elevations above ~700 m. Hispaniolan highland communities were also phenotypically distinctive, occupying a region of morphospace that differs from all sub-regions on either island. In contrast, Jamaica's highland communities were morphologically indistinct, largely due to the predominance of elevational generalists. This highland diversity difference suggests that Jamaica's high-elevation anole communities are undersaturated at the species level despite having similar abundances to those of Hispaniola (i.e. Jamaica's highlands could likely support additional species if their production were not limited).

Finally, as predicted if macroevolutionary inputs strengthen local controls on richness (Cornell, 2013), the greater diversity of species on Hispaniola was associated with greater beta diversity. This pattern was linked to the evolution of distinctive elevational subfaunas on Hispaniola, but not Jamaica.

Evolutionary opportunity and community assembly

Community abundance patterns suggest broadly comparable resources for anoles on Hispaniola and Jamaica. So why are Jamaica's montane communities less diverse? Ecological explanations such as dispersal limitation are not supported. Instead, diversity differences are explained by the paucity of Jamaican high-elevation specialists—indeed, computationally "deleting" highland species reconciles divergent richness-elevation relationships between islands. Thus, to understand Jamaica and Hispaniola's highland community differences, we must turn to the evolutionary buildup of their species pools (Mittelbach & Schemske, 2015).

Speciation-driven contributions to highland diversity could arise by colonisation-associated speciation, or alternatively by *in situ* radiation within the sub-region (Rosindell & Phillimore, 2011). The first mechanism involves either long-distance colonisation from a mountain-dwelling ancestor (the primary mechanism generating mountain endemics; Merckx et al., 2015), or colonisation by a lowland ancestor, accompanied by an evolutionary niche shift. The former requires the taxon have good dispersal capacity to cross unfavourable environments. Anoles, however, are poor dispersers, leaving niche shift as the only pathway. Such lowland-to-highland shifts occurred on both islands, but appear difficult, with one instance on Jamaica and a handful in northern Hispaniola. Indeed, evolutionary transitions of this sort are rare; speciation across biomes is ~25 times less likely than within them (Crisp et al., 2009).

The second mechanism, *in situ* highland radiation, occurred exclusively on Hispaniola, where a clade of highland endemics diversified into a variety of ecological types, raising the taxonomic, functional and phylogenetic uniqueness of the Hispaniolan highlands. Speciation in anoles is allopatric (Glor et al., 2004, 2005), and anoles need ~3000 km^2 to undergo *in situ* speciation (Losos & Schluter, 2000). The highland "sky island" in northern Hispaniola above 700 m clears this threshold with 4000 km^2, yet Jamaica's equivalent zone occupies less than 400 km^2. Thus, the rarity of cross-biome speciation, plus insufficient space for *in situ* radiation, appear to have deprived highland Jamaica of two to three additional species supported at similar elevations on Hispaniola.

In contrast, the lowlands on both islands easily exceed the 3000 km^2 threshold. Though the lowlands of northern Hispaniola are nearly 5× larger than Jamaica's (18,500 vs 3900 km^2), their alpha diversity is identical, suggesting that local diversity caps predominate, and have been reached. Northern Hispaniola's greater gamma diversity thus appears to come about not because it is larger *per se*, but because its high-elevation biome is large enough to generate an additional set of distinct species, boosting diversity from 6 species (lowland-only) to 11 (total).

Recent work has revealed the importance of geographical and environmental determinants of evolutionary radiation in setting regional diversity patterns (Fine & Ree, 2006; Jetz & Fine, 2012; Quintero & Jetz, 2018). Our work shows that "evolutionary opportunities" structure communities by producing species capable of maintaining local diversity equilibria. Such equilibria are consistent with temporal studies, which demonstrate stable community-level richness limits over timescales ranging from decades to epochs (Bambach, 1977; Brown et al., 2001; Close et al., 2019; Gotelli et al., 2017). However, they contrast with patterns in Hawaiian trees, one of few groups to be investigated for signatures of macroevolution on local community structure (Craven et al., 2019). In that system, greater island-level evolutionary diversity did correlate with local-scale diversity, suggesting that local diversity caps have not been reached, or are easily overridden. The likelihood that evolution will strengthen local controls may depend on system-specific mechanisms of dispersal, competition and coexistence. For example, compared to tropical trees, anoles are worse dispersers (Williams, 1969), engage in copious interference competition (Culbertson & Herrmann, 2019; Schoener, 1977), and, lacking dormancy, benefit less from temporal storage effects (Chesson & Warner, 1981), all of which favour local controls.

Regional contributions to diversity at biological suture zones

Even if communities are saturated with individuals, regional diversity may still augment local richness if processes that remove species with redundant niches (e.g. competitive exclusion) are slow relative to those that add them (e.g. immigration) (Cornell & Harrison, 2014). We see no evidence for such regional signatures across most of either island. However, where Hispaniola's distinct low-elevation and high-elevation subfaunas meet, local richness exceeds even lowland values, consistent with an ecotone-associated dynamic equilibrium (Storch & Okie, 2019). This richness boost is not accompanied by an increase in abundance, and deleting highland species results in a mid-elevation lizard deficit in comparison to Jamaica. Together, these observations suggest that density compensation allows for species additions in mid-elevation communities saturated at the individual level (MacArthur et al., 1972).

Middle elevations may be especially susceptible to richness peaks if fitness differences equilibrate between lowland and highland-adapted species with redundant dietary or structural niches, preventing clear competitive dominance (Chesson, 2000). Dispersal ability matters here also. As poor dispersers (Williams, 1969), anoles benefit little from mass- and rescue-effect driven persistence in unfavourable conditions. As such, the mid-elevation diversity peak on Hispaniola is fairly narrow. Ecotone peaks would be wider for stronger dispersers, and cross-ecotone supplementation could explain the frequent regional-local diversity correlations exhibited in some taxa (e.g. Ricklefs, 2000).

Generality and future prospects

The anole faunas of Jamaica and Hispaniola provide a rich opportunity for comparison because they represent a natural experiment: well-matched ecologically and phylogenetically, yet differing in their evolved diversities. Nevertheless, it remains a single comparison. Determining the generality of the evolutionary opportunity model we propose here awaits additional tests. Within anoles, a natural next step is to conduct local-community surveys in additional regions that either provide opportunities for independent sub-regional diversification (e.g. the Talamanca Mountains of Central America; the Andes and tepuis of South America; Moreno-Arias & Calderón-Espinosa, 2016) or lack them (e.g. Puerto Rico; Williams, 1983; the Amazon basin). More generally, the greatest potential for additional insight lies in clades that have repeatedly diversified in settings that differ in evolutionary opportunity. For systems in which evolutionary opportunity varies as a function of area, our model will be most useful for biotas featuring environmentally-defined sub-regional boundaries. Indeed, most terrestrial taxa fit this bill, exhibiting rapid species turnover at ecoregion boundaries (Smith et al., 2018). Time also influences evolutionary opportunity. "Hotspot" archipelagos, which represent chronosequences of ever-younger islands, will be uniquely well-suited for examining how temporal constraints on diversification shape local communities (e.g. Craven et al., 2019). Complementary insights may arise from invasions, as anthropogenic transplantations may equilibrate realised evolutionary opportunity across once-disjunct faunas. Anole invasions indeed strengthen island-level richness equilibria (Helmus et al., 2014), but how they affect local communities remains poorly understood.

Finally, while speciation generates species pools, extinction also sculpts regional diversity over time. A region's capacity for net diversification (speciation minus extinction) is likely what truly determines regional influence on communities. In practice, ascertaining the specific role of extinction in local diversity dynamics is difficult, especially when fossils are rare. In anoles, amber fossils document ecomorphological similarity between Hispaniola's Miocene fauna and today's, but this inference rests on a single fossil deposit (Sherratt et al., 2015). Phylogenetic analysis does not reveal a major role for extinction in these groups (Rabosky & Glor, 2010), but such signatures can be hard to detect from comparative data. Barring new fossil discoveries, insights into the importance of extinction for local anole communities will remain indirect. Paleontological studies of well-fossilised communities will be most informative. Such work remains rare, but a recent investigation of Phanerozoic tetrapod communities showed that once clades had initially radiated, community richnesses maintained stable long-term equilibria despite ongoing background extinction (Close et al., 2019).

CONCLUSION

Our results emphasise the role of macroevolutionary diversity in determining community structure. Over ecological time, communities at different compositional starting points converge to similar functional members, even if species identity varies (Fukami et al., 2005). We propose a similar process over evolutionary time—so long as evolutionary opportunity is available, speciation fills local communities, allowing them to achieve compositional similarity. Evolutionary opportunity permits sub-regional specialists to form, increasing beta diversity and supplementing alpha diversity at suture zones. Where speciation is limited, widespread species fill rare environments as best they can, but sub-regional faunas do not form, and local diversity in rare environments remains impoverished. Accounting for such dynamics may shed new light on how local or regional factors control community structure and diversity.

AUTHOR CONTRIBUTIONS

LOF and DLM designed the study, collected the data and wrote the first draft of the manuscript, LOF analysed the data with contributions from GLL, and all authors contributed to revisions.

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