

Niche conservatism predominates in adaptive radiation: comparing the diversification of Hawaiian arthropods using ecological niche modelling

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The role of the environmental niche in fostering ecological divergence during adaptive radiation remains enigmatic. In this study, we examine the interplay between environmental niche divergence and conservatism in the context of adaptive radiation on oceanic islands, by characterizing the niche breadth of four Hawaiian arthropod radiations: *Tetragnatha* spiders (Tetragnathidae Latreille, 1804), *Laupala* crickets (Gryllidae Otte, 1994), a clade of *Drosophila* flies (Drosophilidae Fallén, 1823) and *Nesosydne* planthoppers (Delphacidae Kirkaldy, 1907). We assembled occurrence datasets for the four lineages, modelled their distributions and quantified niche overlap. All four groups occupy the islands in distinct ways, highlighting the contrasting axes of diversification for different lineages. *Laupala* and *Nesosydne* have opposite environmental niche extents (broad and narrow, respectively), whereas *Tetragnatha* and *Drosophila* share relatively intermediate tolerances. Temperature constrains the distributions of all four radiations. Tests of phylogenetic signal suggest that, for *Tetragnatha* and *Drosophila*, closely related species exhibit similar environmental niches; thus, diversification is associated with niche conservatism. Sister species comparisons also show that populations often retain similar environmental tolerances, although exceptions do occur. Results imply that diversification does not occur through ecological speciation; instead, adaptive radiation occurs largely within a single environment.

ADDITIONAL KEYWORDS: adaptive radiation – *Drosophila* – insects – *Laupala* – *Nesosydne* – niche conservatism – oceanic islands – species distribution modelling – spiders – *Tetragnatha*.

INTRODUCTION

Known to produce spectacular arrays of biodiversity, adaptive radiation has long captivated the attention of evolutionary biologists. Adaptive radiation occurs when lineages experience high levels of niche diversification over relatively short timescales via ecological, behavioural or physiological differentiation, e.g. diversification in concert with adaptation (Schluter,

2000). Owing to the complexity of this process, the full array of mechanisms driving radiations and, in particular, the differences among comparable radiations have not yet been fully disentangled (Rundell & Price, 2009). Particularly enigmatic is the relative importance of shifts in the landscape-level environmental niche associated with speciation. Among systems pertinent to the study of adaptive radiation, isolated insular systems, including lakes and oceanic islands, are the most renowned (Losos & Ricklefs, 2009). These regions serve as microcosms of evolution owing to their small sizes and extreme isolation. Here, we use a comparative framework to examine the ecological context within which adaptive

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radiation takes place, by characterizing the relative role of niche shifts between different environments and niche shifts within a given environment across multiple lineages.

Crucial to understanding the influence of environmental niche shifts in the course of adaptive radiation is a clear grasp of the relative importance of the primary processes involved in lineage segregation and divergence. First, differentiation can arise owing to shifts in the environmental aspect of a species' niche as determined by physiological limitations, including landscape-level climate or habitat associations (De Busschere *et al.*, 2015; Lescak *et al.*, 2015), frequently associated with ecological speciation (Nosil, 2012). Second, geographical isolation may allow divergence in the same environmental conditions, with the two isolated populations differentiating through neutral processes, such as drift in geographical isolation (Schluter, 2009). Lineages that diverge initially through geographical isolation may subsequently undergo shifts in the biotic aspect of a species' niche as determined by their ecological, behavioural or microhabitat preferences within a given environment (Gillespie, 2016; Stroud & Losos, 2016); such shifts may be associated with character displacement when ecologically similar species come into secondary contact (Cotoras *et al.*, 2018). In some systems, all three factors may play a role (e.g. Salzburger *et al.*, 2014). Diversification in Hawaiian arthropods has been linked to shifts in biotic interactions and dispersal to new islands (Roderick & Gillespie, 1998; Jordan *et al.*, 2003; Cowie & Holland, 2008; Rubinoff & Schmitz, 2010; Bennett & O'Grady, 2012; Goodman *et al.*, 2014), whereas the association of shifts in landscape-level environment with adaptive radiation remains largely unknown. Given that environmental niche shifts are crucial in other well-studied adaptive radiations, in particular stickleback fish (Rundle *et al.*, 2000), an assessment of the relative importance of microhabitat and environmental niche shifts in understanding Hawaiian radiations is long overdue.

In remote insular systems, niches may remain 'open' for comparatively long periods of time owing to the rarity of successful colonization. As a result, niches may be filled more rapidly by endemic progenitors adapting to novel environments or microhabitats within the system than by dispersal from external areas by preadapted taxa (Stroud & Losos, 2016). Thus, the phenomenon of adaptive radiation on remote insular systems can be explained largely by the interplay between speciation and ecological niche shifts (Roughgarden, 1972). Within this framework, the origin of diversity depends on the relative rates of dispersal and adaptation in filling empty niches. Given sufficient dispersal, taxa preadapted to the environment can successfully establish in new areas.

However, lower dispersal rates can provide the time needed for expansion into novel environments or niche shifts within an environment by taxa already present on a given island (Roughgarden, 1972; Losos & Ricklefs, 2009).

STUDY SYSTEM AND AIMS

In the case of extremely isolated oceanic islands of volcanic origin, such as the Hawaiian archipelago, the balance between dispersal and adaptation varies considerably between lineages. Some lineages occupy a similar niche, in terms of both environment and microhabitat, across the entire archipelago (so-called 'non-adaptive' radiation), whereas others show a single episode of niche expansion at the base of the radiation, with further species exhibiting little ecological change, and yet others show repeated episodes of niche expansion or shifting (Gillespie, 2016). The Hawaiian Islands are especially useful for comparative studies because multiple lineages have speciated within and across environments over the same time frame, with diversity resulting largely from *in situ* speciation on evolutionary timescales involving a small number of parental lineages (Baldwin & Sanderson, 1998; Roderick & Gillespie, 1998; Eldon *et al.*, 2013). Terrestrial arthropod faunas, which constitute > 75% of the endemic Hawaiian biota (Eldredge & Miller, 1997), are particularly amenable to comparative studies of adaptive radiation across the same geological setting (Shaw & Gillespie, 2016).

Ecological niche modelling, or species distribution modelling (SDM), offers a powerful way to examine the influence of niche dynamics in diversification (Guisan & Zimmermann, 2000; Elith & Leathwick, 2009). By correlating occurrences with spatial environmental covariates (see examples in the [Supporting Information, Table S1](#)), it allows analysis of shifts in climate and habitat over the evolutionary history of a lineage. The present study uses SDM to explore whether environmental shifts accompany divergences in four Hawaiian arthropod lineages. The target lineages are a radiation of long-jawed spiders of the genus *Tetragnatha* (Tetragnathidae), sword-tailed crickets of the genus *Laupala* (Gryllidae), the antopocerus, modified tarsus and ciliated tarsus (AMC) clade of fruit flies in the genus *Drosophila* (Drosophilidae) and planthoppers of the genus *Nesosydne* (Delphacidae). Lineages were selected to represent a spectrum of functional roles: predators, detritivores, fungivores and herbivores, respectively. Previous work suggests that these groups speciated by shifts in different biotic interactions: microhabitat specificity in response to predation in the spiders (Gillespie, 2004, 2016), sexual communication behaviour in the crickets (Mendelson & Shaw, 2005), secondary sexual morphological

characteristics in the flies (Lapoint *et al.*, 2014) and shifts in plant hosts in the planthoppers (Goodman, 2010; Goodman *et al.*, 2012). Thus, a diversity of mechanisms is implicated in shaping diversification across this suite of taxa.

To examine whether diversification during adaptive radiation is associated with shifts in environmental tolerance, as through ecological speciation, or whether diversification is solely a factor of shifts in biotic interactions within a conserved range of environmental tolerance, we asked three questions.

1. What are the climatic bounds and associated constraints on distributions within which diversification has occurred?
2. Do the lineages show a phylogenetic signal of environmental niche evolution?
3. Within a lineage, do any pairwise comparisons of closely related taxa or populations show a pattern of niche conservatism or divergence?

MATERIAL AND METHODS

COMPILED SPECIES LOCALITIES

Occurrence datasets were compiled from museum records, published literature and unpublished field notes (a list of published data sources is given in [Supporting Information, Appendix S1](#); and museum specimen numbers in [Supporting Information, Table S2](#)). We georeferenced all records that had no coordinates using recommended protocols (see Global Biodiversity Information Facility and detailed below; Chapman & Wieczorek, 2006; Hiller *et al.*, 2016). We recorded coordinate uncertainty in metres following the point-radius method through the GEOLocate Web application (Bart *et al.*, 2010; additional georeferencing protocol details are given in [Supporting Information, Appendix S2](#)).

In total, we obtained > 5000 specimen records. We filtered the data by removing duplicate points and points with a coordinate uncertainty > 3 km, thus reducing spatial autocorrelation and erroneous localities (for discussion, see Phillips *et al.*, 2006). The resulting points were mapped, visually checked for accuracy, and removed if likely to reflect a georeferencing error (e.g. mapping in the ocean). For each group, > 50% of the data fell under a 1 km radius of error and > 75% fell under a 2 km radius of error, sufficiently matching the resolution of the environmental layers. Given that our environmental layers were at a coarse (~1 km²) resolution, we did not spatially filter our data, because any adjacent grids with occurrence points would be likely to reflect real biological occurrences. The final number of unique occurrence records used per species is

recorded in the [Supporting Information \(Table S3\)](#). Across all groups there was an average of seven records per species.

ASSEMBLY OF ENVIRONMENTAL LAYERS

Environmental datasets were obtained from the Rainfall Atlas of Hawaii and Climate of Hawaii (Giambelluca *et al.*, 2013, 2014). Layers were from 1978–2007, which corresponds to the collection dates of > 75% of the points used in this study. We resampled, clipped, and converted the vegetation height layer from a polygon layer to a raster using ArcGIS v.10.2 (ESRI, 2011). Layers were resampled from a ~250 m² to a ~1 km² resolution using smoothing for quantitative variables and nearest neighbour resampling for categorical variables. This spatial resolution was most appropriate given the uncertainty of occurrence localities and our focus on landscape-level climate trends, not microclimate.

Only four layers were ultimately used, to prevent overfitting, where highly complex models are so specific to the training data that they fail to predict a species general niche accurately. To check for correlation between variables, we computed pairwise Pearson correlation coefficients in ArcGIS (ESRI, 2011). We removed one variable per pair with a correlation > 0.60 (Braunisch *et al.*, 2013; correlation matrix of all layers is given in [Supporting Information, Table S1](#)), and kept uncorrelated variables that improved model area under the curve (AUC) values: mean annual air temperature (in degrees Celsius), mean annual rainfall (in millimetres), vegetation height (in metres) and normalized difference vegetation index (NDVI; reflectance scale ranging from minus one to plus one). We included vegetation height to capture structural differences in canopy, and NDVI to capture vegetation density (less dense, 0.1–0.3, scrubland; 0.3–0.6, dry or mesic forest; most dense, > 0.6, rainforest). Additional details on layer selection are presented in the [Supporting Information \(Appendix S2\)](#).

SPECIES DISTRIBUTION MODELLING

MaxEnt (v.3.3.3k) was used to quantify the suitable habitat for each taxon (Phillips *et al.*, 2006). This method was most appropriate for our study because MaxEnt does not require absence data, which is difficult to obtain from historical records (Phillips *et al.*, 2006). MaxEnt has been shown to be the most capable presence-only SDM approach for small sample sizes, producing meaningful models when tested with five occurrences (Hernandez *et al.*, 2006). It is thus best equipped to handle the small, incomplete datasets most frequently available for endemic arthropods. In general, MaxEnt also offers improved

accuracy for species with narrow geographical ranges, characteristics of our focal groups and of characteristics of island-restricted organisms in general (Hernandez *et al.*, 2006; Pearson *et al.*, 2007; Wisz *et al.*, 2008).

MODELLING AT THREE TAXONOMIC LEVELS

Genus-level estimation of environmental tolerance

We modelled niches for each lineage across all islands by including all localities in the model to estimate the environmental niche breadth of each of the four genera. Models were run under default settings, with a random test percentage of 25 and ~10 000 background points, because Phillips & Dudik (2008) found that default settings work sufficiently well for modelling potential niches. Given that we are interested in four radiations modelled in the same way using the same data sources (museum collections often have spatial autocorrelation biases and do not contain taxa that went extinct before colonial times; Merow *et al.*, 2013; Muscarella *et al.*, 2014), our approach provides a robust comparative framework, despite biases.

We tested which environmental variable best explained the range of each group using a jackknife test of variable importance for ranking (as suggested by Braunisch *et al.*, 2013; Supporting Information Fig. S1). Using the 'phyloclim' R package, we then generated predicted niche occupancy (PNO) profiles of each group for each environmental input (Heibl & Calenge, 2013; R Core Team, 2015). Predicted niche occupancies plot the probability of occurrence against a given value of the environmental variable, to create niche profile graphs. The PNOs in this study used 100 statistical bins set to a width of one.

Species-level variation in environmental tolerance and tests of phylogenetic signal

To understand the environmental space occupied by each lineage on each island, we performed a principal components analysis (PCA) on the samples across all species, joining the occurrence points with the selected environmental variables using R Statistics (Supporting Information, Table S4; R Core Team, 2015, base package). Next, to test whether our datasets showed phylogenetic signal, we used the 'phylosig' calculation in the R package 'phytools' (Revell, 2012). We ran this analysis on the three lineages (*Tetragnatha*, *Laupala* and AMC *Drosophila*) that have published phylogenies (Supporting Information, Fig. S2). This calculation examines whether trait evolution, in this case the environmental variable value found at a given occurrence point (Supporting Information, Table S4), resembles Brownian motion as measured by Pagel's λ , chosen because Molina-Venegas & Rodríguez (2017) found that Pagel's λ was

more robust to incompletely resolved phylogenies than Blomberg's K , the alternative metric implemented in phytools.

Population-level examples of niche dynamics

To determine whether any taxa exhibited evidence of environmental niche conservatism or divergence, we compared populations of the same species and populations of sister species that occur on the two youngest island groups, Maui Nui (Molokai, Lanai and Maui) and Hawaii. We modelled niches of all population pairs in MaxEnt, but owing to the small sample size of several species, we chose not to run test data and instead filtered resulting models by AUC values. Jackknifing-based models are also not ideal given < 20 records per species (Shcheglovitova & Anderson, 2013). Although our models are undoubtedly oversimplified, many of these species are highly range restricted, sometimes to a single bog or mountaintop. Omitting these species because of the small number of occurrence records would be to ignore a large amount of the rare diversity in these groups. Therefore, we elected to run all data points in an effort not to bias our results in favour of more common species with larger ranges. Recent work has shown that using small sample sizes, consistent with our sampling, is justified when the species are narrowly endemic and have low prevalence (here, the fraction of the study area occupied by the species) or, in other words, when the samples are representative of the species niches (van Proosdij *et al.*, 2016).

We then characterized the pairwise genetic relationships as two populations within the same species, sister species or 'successive sister species' based on the phylogenetic data available for Hawaiian *Tetragnatha* (Ingram & Mahler, 2013), *Laupala* (Mendelson & Shaw, 2005), *Nesosydne* (Goodman, 2010) and *Drosophila* (Lapoint *et al.*, 2014). Although incomplete sampling, especially for *Laupala* (> 40% incomplete) and *Nesosydne* (> 60% incomplete), could potentially lead to incorrect conclusions here, in general we expect these comparisons to represent relatively closely related lineages. We also noted whether the comparisons occurred within an island (Maui Nui–Maui Nui or Hawaii–Hawaii) or between islands (Maui Nui–Hawaii). Specifically, we assessed whether species occurring on the same island and on different islands show niche conservatism or divergence.

We generated niche models by clipping environmental layers to single islands and then creating models on all species localities that fell within those islands. Next, we projected the SDM to all islands to create theoretical range maps if the groups were not constrained by inter-island barriers (Phillips & Dudik, 2008). We used clamping, or limiting model extrapolations to

the environment present in training models, without accounting for differing environmental conditions, because conditions between islands overlap extensively (Fig. 2B), and default settings with background points ranging from ~2000 for range-restricted species to ~10 000 for widespread species. We used the R package 'ENMeval' (Muscarella *et al.*, 2014) to quantify percentage niche overlap combined across all four variables and to compare species occurring on different islands directly. To examine the role of environmental niche evolution in adaptive radiation further, we looked for examples of both environmental divergence and conservatism, as measured by combined niche overlap (all four variables together as measured in ENMeval rather than each variable separately in phylclim). We also calculated PNOs and generated pairwise niche overlap for each environmental variable for each species combination using the 'niche.overlap' tool in phylclim (Heibl & Calenge, 2013). Overlap measures describe environmental niche similarity, based on a scale of zero (no overlap) to one (perfect overlap) (metric Schoener's *D* used based on recommendations of Warren *et al.*, 2008; Rödder & Engler, 2011).

RESULTS

GENUS-LEVEL ESTIMATION OF ENVIRONMENTAL TOLERANCE

Habitat suitability maps and PNOs for each genus are presented in Figure 1. In order of importance, the top variables constraining distributions across lineages, in both training and test data, were temperature and vegetation height in *Tetragnatha*; rainfall, NDVI and temperature in *Laupala*; and temperature and rainfall in *Drosophila* and *Nesosydne*. All genus-level models had significant *P*-values of < 0.05 when set to 25% test data.

The results indicate that *Nesosydne*, as a lineage, has access to the largest amount of suitable habitat and the widest range of temperature tolerances (Fig. 1). The modelled range for *Laupala* was the smallest of the four groups and had the most constrained thermal range, needing higher temperatures, rainfall and NDVI. Based on PNOs, *Tetragnatha* and *Drosophila* both had highest probabilities of occurrence at mid-level temperatures. *Tetragnatha*, *Drosophila* and *Nesosydne* all had high probabilities of occurrence at both low and mid-levels of rainfall (Fig. 1A).

SPECIES-LEVEL VARIATION IN ENVIRONMENTAL TOLERANCE AND TESTS OF PHYLOGENETIC SIGNAL

In the PCA, 58.8% of the variation was driven by NDVI and vegetation height, with mean temperature

and rainfall close behind (Fig. 2A; Supporting Information, Table S5). The four lineages did not show strong differentiation along these axes, but the PCA results of high conservatism generally agree with the habitat suitability maps and PNOs. We found high overlap in environmental niche space both between lineages and within the lineages between islands (Fig. 2B).

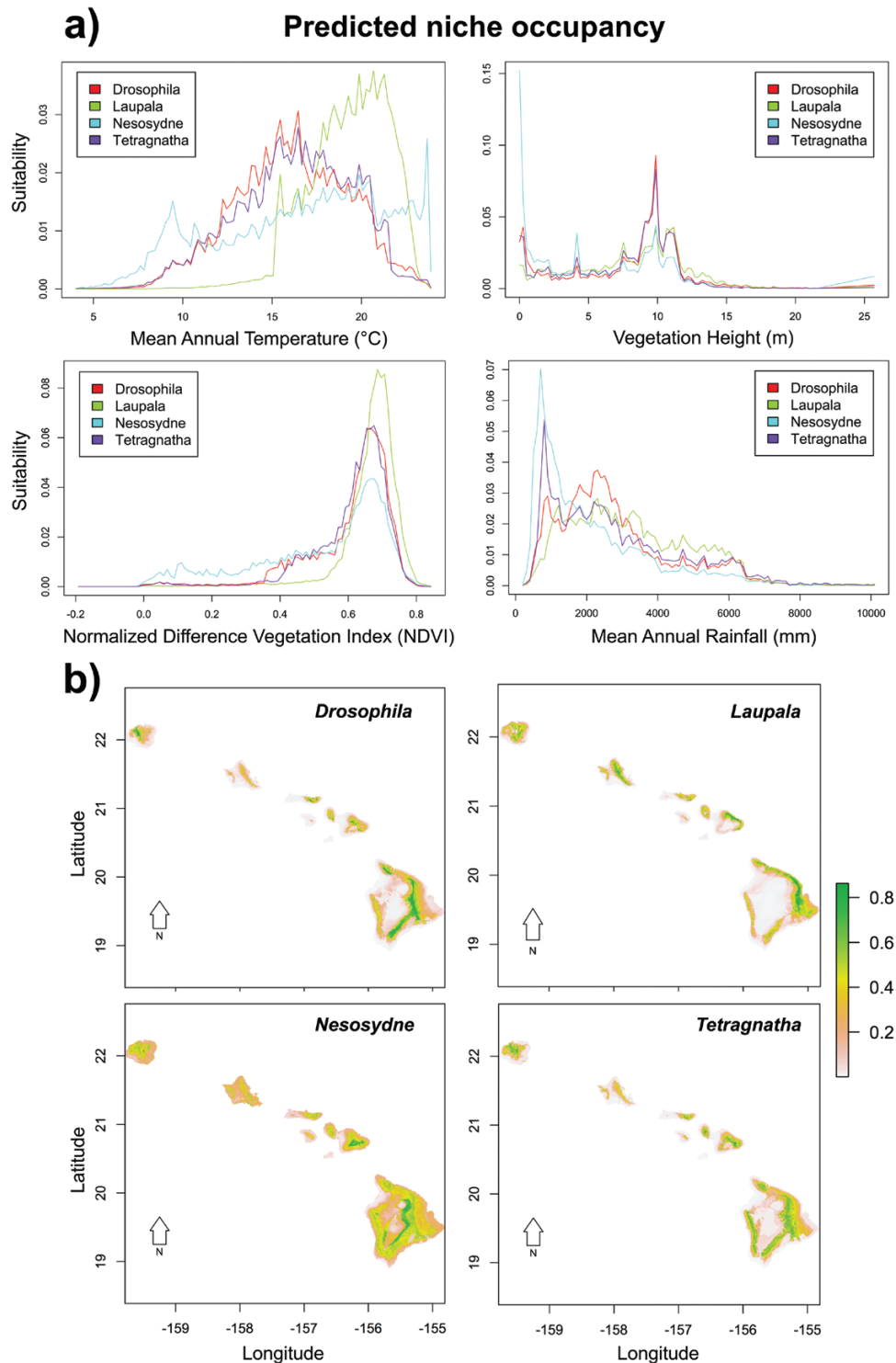
Results from the phylosig tests showed that our datasets were robust for *Drosophila* and *Tetragnatha*. For *Drosophila*, we found that rainfall, vegetation height and NDVI niche axes contain statistically significant ($P < 0.05$) phylogenetic signals. *Tetragnatha* showed statistically significant ($P < 0.05$) phylogenetic signal for the same variables and for temperature (Supporting Information, Table S6). The *Laupala* dataset was not robust ($P = 1.0$) and contained no significant phylogenetic signal, probably owing to > 40% incomplete taxon sampling in the phylogenetic tree. The available *Nesosydne* tree had > 60% incomplete taxon sampling; therefore, we did not attempt a phylosig analysis.

POPULATION-LEVEL EXAMPLES OF NICHE DYNAMICS

Comparing populations of species that occur on different islands (between Hawaii and Maui Nui), all four groups had instances of pairwise comparisons which showed low environmental niche overlap between allopatric populations, and all groups except *Laupala* had instances of pairwise comparisons that showed extremely high environmental niche overlap between allopatric populations (Fig. 3A). *Laupala* contained no population pairs with extremely high overlap (> 80%). Most interestingly, however, we found examples of divergence in environmental niche between allopatric populations within single islands in addition to examples of environmental niche conservatism (Fig. 3A). Thus, the population comparisons revealed generally high environmental niche overlap across lineages and islands, but also some pairwise comparisons with low overlap.

DISCUSSION

As predicted, we found that environmental niches and, in particular, NDVI and vegetation height are largely conserved between species (Figs 1A, 2A). This suggests that, for the most part and despite some exceptions (Fig. 3A), diversification has occurred as a result of partitioning by biotic interactions, such as microhabitat choice or host plant specialization within a given environment, consistent with our current understanding of these radiations.



DIFFERENT GENUS-LEVEL DISTRIBUTIONS AND SPECIES-LEVEL NICHE BETWEEN RADIATIONS

Despite occurring in the same archipelago and across islands containing similar niche space (Fig. 2B), each focal lineage has occupied the available environmental niche space in distinctive ways. Comparison of PNOs across genera revealed telling differences among them (Figs 1A, 2A). *Tetragnatha* and *Drosophila* had similar thermal tolerances, corresponding to the cool temperatures found in their mid-elevation forest habitats. The two lineages generally co-occur except in areas of suitable temperature that also have extremely low rainfall. For example, unlike *Drosophila*, certain species of *Tetragnatha* occurred on the southwest side of Hawaii Island, an area with relatively low rainfall (Fig. 1B), possibly because *Tetragnatha* are generalist predators (Gillespie, 1999), whereas AMC clade *Drosophila* are fungivores that rely on the presence of decaying plant material (Lapoint *et al.*, 2014), which might be less abundant in drier areas.

Laupala had a narrow range of thermal tolerance, with a much higher probability of occurrence at warmer temperatures, indicative of their restriction to lower to mid-elevation sites. *Laupala* also had a low probability of occurrence at low levels of rainfall and the highest probability of occurrence at high levels of rainfall of any group (Fig. 1A). This suggests that both temperature and rainfall are constraining factors for *Laupala*, much like *Drosophila* and *Tetragnatha* but at lower elevations, and that diversification within this genus occurred within a narrow band of suitable climate.

In contrast, *Nesosydne* had an exceptionally wide range of temperature tolerances, corresponding to some species at the highest elevations on Maui and others close to sea level, on Oahu (Fig. 2A), consistent with the hypothesized pattern of ecological release (Goodman, 2010). This indicates that temperature may not inherently constrain this group. It also suggests that host plants may be a better predictor of distribution than any climatic variable at deeper phylogenetic levels. *Nesosydne* also occupied a broader range of vegetation height, in contrast to the other lineages, which showed a strong conservatism of vegetation height (Figs 1A, 2A). This again signifies niche lability in *Nesosydne* consistent with the lineage having diversified into a variety of habitats, not only forest, unlike *Drosophila*, *Tetragnatha* and *Laupala*, which are generally forest-restricted taxa (Gillespie, 2004; Mendelson & Shaw, 2005; Lapoint *et al.*, 2014).

Dispersal might play a role in these observed niche patterns, because *Nesosydne*, which shows extremes of both winged and flightless species (Goodman, 2010), has the greatest niche breadth (Figs 1A, 2A). However, dispersal ability is intimately connected to niche occupancy (Gillespie *et al.*, 2012), and its role in constraining or promoting niche differentiation would be speculative without additional data.

Based on jackknife tests (Supporting Information, Fig. S1), mean annual temperature was an important factor in predicting the distributions of all groups studied, consistent with the findings of other studies that temperature determines ranges at a landscape level (e.g. Guisan & Zimmermann, 2000). Rainfall also constrained the distribution of *Laupala*. These results highlight the potential for dramatic range shifts or extinctions if temperature or rainfall fluctuates in the Hawaiian Islands owing to global warming (Harter *et al.*, 2015). In particular, we would expect dire consequences if environmental changes occur in the core areas identified in the genus-level SDMs (Fig. 1B).

SIGNALS OF ENVIRONMENTAL NICHE CONSERVATISM AND DIVERGENCE, WITHIN AND BETWEEN ISLANDS

Our results reveal strong phylogenetic signals of environmental niche conservatism in Hawaiian arthropods, although only the *Drosophila* and *Tetragnatha* datasets contained sufficient information to test for phylogenetic signal based on the phylslog function (Supporting Information, Table S6). For each of these, we found that closely related species tended to have more similar environmental niche characteristics than expected by chance alone. Thus, in *Drosophila* and *Tetragnatha*, closely related species tend to possess especially similar environmental niches compared with more distantly related species. This was also true at the population level, with examples of environmental niche conservatism between populations within the same island, both on Maui Nui and Hawaii, as measured by combined niche overlap calculated from all four variables. This observation agrees with recent work showing that ecologically similar and closely related species of Hawaiian *Tetragnatha* co-occur on the younger Hawaiian Islands (Cotoras *et al.*, 2018).

Our results revealed high environmental niche overlap between closely related and geographically co-occurring taxa, suggesting that these species boundaries must be maintained exclusively through biotic interactions (Cotoras *et al.*, 2018; Gillespie, 2016). For example,

groups. Most notably, *Nesosydne* has an extremely wide range of suitable temperature and *Laupala* has higher probability of occurrence at higher temperatures and higher rainfall levels compared with *Tetragnatha* and *Drosophila*. B, species distribution models show maps of habitat suitability on a scale of 0–100% suitable, reflecting the core of the distribution of each group. Note the particularly wide distribution for *Nesosydne*.

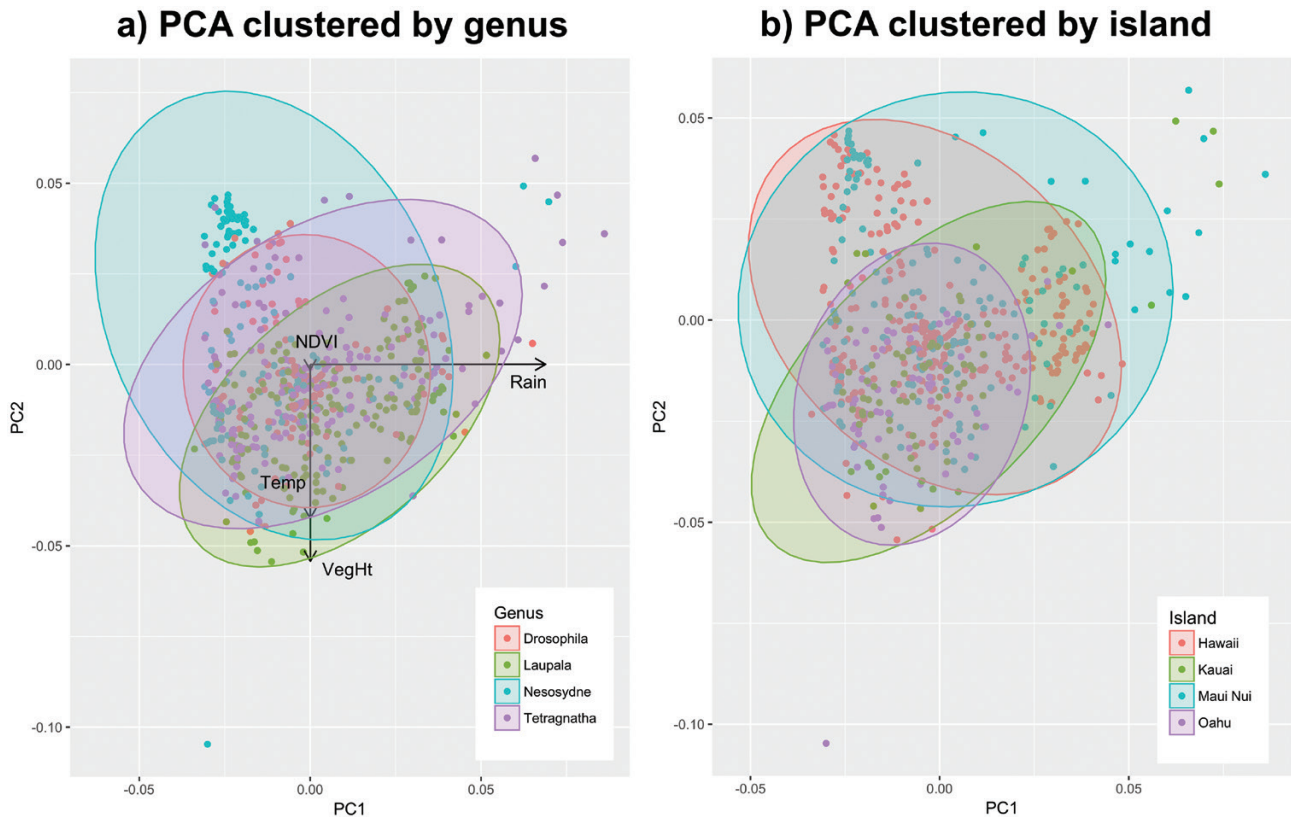


Figure 2. Principal components analyses (PCAs) of niche variation. A, principal component PC1 explains 58.8% of the variation and is correlated most with normalized difference vegetation index (NDVI) and vegetation height, followed by mean temperature and rainfall (see [Supporting Information, Table S5](#)). Principal component PC2, which explains 20.9% of the variation, is positively correlated with rainfall and negatively correlated with temperature. *Tetragnatha* and *Laupala* are most impacted by the first dimension of positive correlation with vegetation, NDVI and mean temperature, whereas variation in *Nesosydne* is best explained by a positive correlation with rainfall and negatively with temperature. *Drosophila* has a narrower association with these variables, centred on mid-level values of temperature and rainfall. B, grouping points by island revealed a high overlap in niche space, leading us to investigate patterns of occupation by the lineages and by pairs of sister taxa.

among species that occur on the same island with high environmental niche overlap, *Tetragnatha stelarobusta* (Gillespie, 1991) and *Tetragnatha eurychasma* (Gillespie, 1991) differ in web architectures ([Fig. 3A](#), comparison 1; [Blackledge & Gillespie, 2004](#)), whereas *Nesosydne bridwelli/osbornii* (Muir, 1919, 1916) and *Nesosydne nigrinervis* (Muir, 1919) specialize on different host plants ([Fig. 3A](#), comparison 5; [Goodman, 2010](#)). Additionally, *Drosophila prodita* (Hardy, 1965) and *Drosophila redunda* (Hardy, 1965), and *Drosophila conformis* (Hardy, 1965) and *Drosophila sordidapex* (Grimshaw, 1901), show morphological differences consistent with sexual selection ([Fig. 3A](#), comparison 14; [Kaneshiro, 1997](#)).

Comparison of closely related allopatric populations across the young Hawaiian Islands (Maui Nui and Hawaii) produced examples of both high and low niche overlap, as expected when taxa are at different

stages of lineage divergence in the course of adaptive radiation. As illustrated in [Fig. 3A](#) (comparisons 8 and 16), dispersal to, and subsequent divergence on, novel islands can sometimes be associated with a shift into a new habitat or climate, although it is not clear whether these shifts in environment precede co-occurrence as expected if taxa are diversifying through ecological speciation. However, we also found that environmental niches are commonly conserved when species jump islands, such as *T. stelarobusta* vs. *Tetragnatha perkinsi* ([Fig. 3A](#), comparison 3; Simon, 1900). In particular, when we modelled the environmental niches of populations of multi-island species independently and then calculated fundamental environmental niche overlap, we discovered many clear instances of environmental niche conservatism across islands between allopatric taxa ([Fig. 3A](#), comparisons 2, 6 and 13). This adds to the evidence (see [Gillespie *et al.*, 2012](#)) that when species

first colonize new islands (e.g. assuming the progression rule of colonization moving from older to younger islands; [Wagner & Funk, 1995](#); [Shaw & Gillespie, 2016](#)) they may initially retain the environmental niche of their ancestral population. A similar result, that more closely related species are allopatric yet found within similar environments, rather than geographically proximate locations, has also been found in Hawaiian *Thyrocopa* moths ([Medeiros et al., 2015](#)).

In addition to the many examples of environmental niche conservatism, we documented some clear examples of environmental niche divergence between populations within the same island, despite overall niche space summarized across all species being relatively similar within lineages between islands ([Fig. 2B](#)). *Tetragnatha brevinatha* (Gillespie, 1992) and *Tetragnatha macracantha* (Gillespie, 1992) share the same microhabitat niche ([Gillespie, 1991](#), [Cotoras et al. 2018](#)), and *Nesosydne eeke* (Muir, 1919) and *Nesosydne argyroxiphium* (Kirkaldy, 1908) live on the same genus (*Argyroxiphium*) of silversword host plant ([Goodman, 2010](#)). *Tetragnatha brevinatha*, *T. macracantha*, *N. eeke* and *N. argyroxiphium* also all occur on Maui. However, these comparisons show only moderate environmental niche overlap, lending support to

divergence associated with an environmental niche shift rather than a biotic interaction. Comparisons of populations and sister species within *Laupala* also show several cases of environmental niche divergence within a single island ([Fig. 3A](#), comparisons 9–12). Often, these examples are associated with one of the two populations occurring on the leeward, more arid part of the island; the comparison with the lowest climatic overlap of all, *Laupala nigra* (Otte, 1994) and *Laupala kona* (Otte, 1994), involved ranges from different sides of Hawaii Island, rather than different islands ([Fig. 3B](#)). When we tested for specific niche characteristics, we indeed found that the two species occupy different rainfall regimes ([Fig. 3B](#)).

Intra-island shifts, not only colonization of new islands, can thus provide sources of divergence in environmental niche in some cases, particularly in less dispersive taxa ([Gillespie et al., 2012](#)), such as flightless *Laupala*. Speciation events and genetic divergence within single islands have been documented in other Hawaiian radiations (e.g. [Jordan et al., 2003](#); [Goodman et al., 2014](#)) and in other oceanic archipelagos (e.g. [Brown et al., 2017](#)). However, the corresponding shifts in environmental or climatic niches that can occur in allopatry have been underappreciated as potential

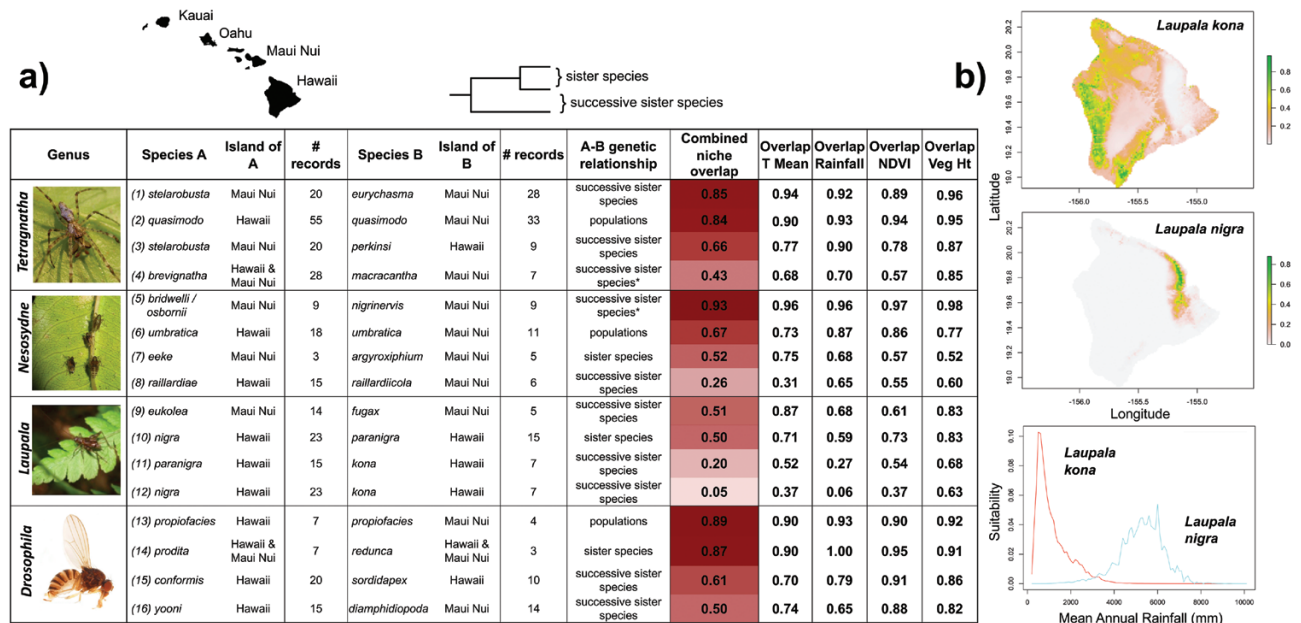


Figure 3. Population-level examples of niche dynamics. A, specific examples of niche conservatism (e.g. species comparisons 1, 2, 5, 13 and 14) and examples of niche divergence (e.g. comparisons 4, 8, 11, 12 and 16) based on combined, projected (see Material and methods) niche overlap are presented in table form. Typical thresholds, as used by [Rödder & Engler \(2011\)](#), are as follows: (white) 0.0–0.2, ‘no overlap’; (light pink) 0.2–0.4, ‘low overlap’; (pink) 0.4–0.6, ‘moderate overlap’; (dark pink) 0.6–0.8, ‘high overlap’; and (red) 0.8–1.0, ‘extremely high’ overlap. Note whether these comparisons occur on the same or across different islands within the Hawaiian archipelago. *Species pairs whose phylogenetic relationships are incompletely resolved. B, predicted niche occupancy models illustrating one particularly striking example: how two closely related species of *Laupala* crickets have diverged within the same island associated with two different rainfall regimes.

sources of selective pressures. Our results (Fig. 3A) show evidence of environmental niche expansion (in rainfall, temperature and NDVI) in the context of adaptive radiation, namely that one of the ways species can diversify is by undergoing ecological release via expansion in climatic tolerance on individual islands.

CHALLENGES TO SPECIES DISTRIBUTION MODELLING ON ISLANDS

Here, we outline our framework for examining niche conservatism and divergence in island radiations. In the

face of inherent challenges, both methodological (Fig. 4, challenges 2a and 3a; to which we propose solutions Fig. 4, solutions 2b and 3b, respectively) and institutional (Fig. 4, challenge 1a), we present a comprehensively compiled dataset for four lineages of invertebrates for the Hawaiian archipelago and demonstrate their use in the evolutionary analysis of niche divergence. Despite our best efforts to compile the most comprehensive set of georeferenced occurrence records available for these taxa, localities were not numerous or detailed enough for us to draw specific conclusions for all species in each group or to use testing data on species-level models

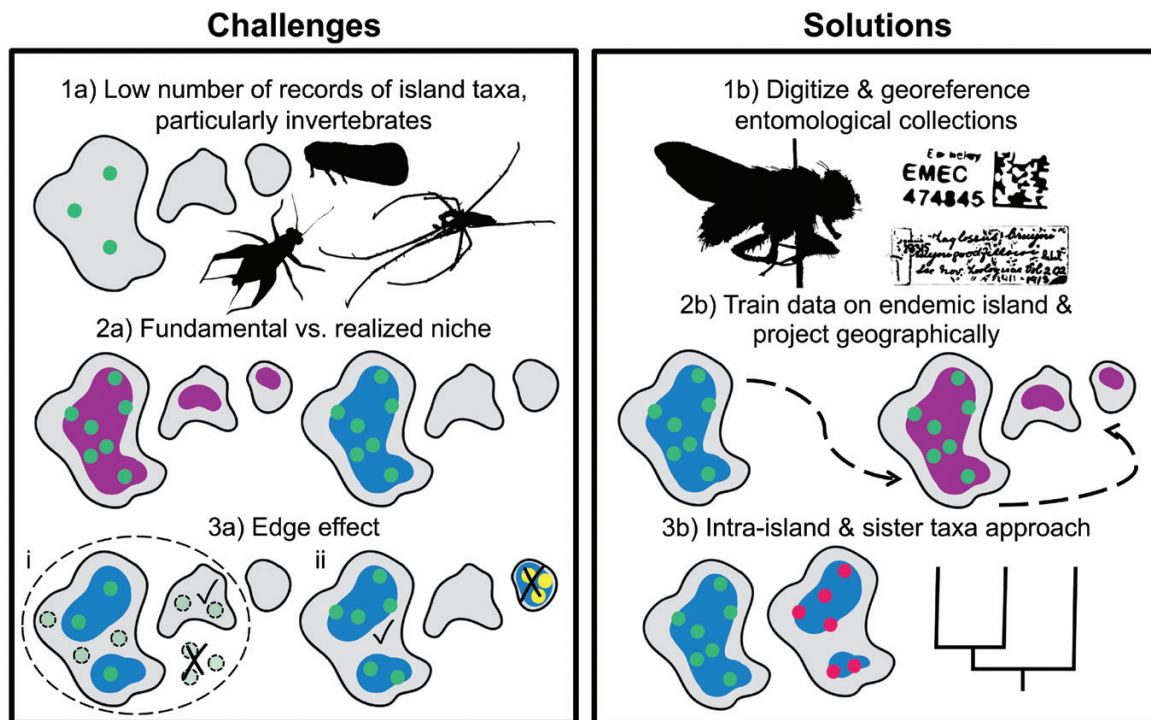


Figure 4. Challenges of species distribution modelling on islands. Challenge 1a, many taxa of interest on oceanic islands, such as Hawaii, are arthropods. Modelling invertebrates is generally more difficult than for vertebrates owing to the lack of high-quality sampling data. Solution 1b, we addressed this challenge by digitizing and georeferencing data from natural history collections. Challenge 2a, modelling the fundamental niche (first series of three islands, purple distribution) vs. the realized niche (second series of three islands, blue distribution) are conflated in the face of the geographical barriers that islands naturally represent; in other words, the fundamental and realized niches may be the same but often are indistinguishable because the realized niche is defined by the geographical limits of the island. Solution 2b, we attempted to address this in island endemic species by training on its endemic island and projecting geographically to other islands in the archipelago. Challenge 3a, modelling in island systems exacerbates the edge effects of modelling along a geographical barrier. Edge effects have well-known impacts on species distributions and interactions in ecology but have less well-documented impacts on niche modelling. Edge effects affect modelling in three ways: (1) individuals can be harder to detect if they are at lower abundance near the edge of their range, thus being missed by collectors and not included in models (3a.i, only three occurrences in distribution centre); (2) background sampling is defined by the extent of the islands (3a.i, background points in dotted circles, extent of raster large dashed circle), excluding potentially suitable climatic areas; and (3) if a species is spread across an entire island (3a.ii, yellow species), as often happens on small islands, their distribution is best defined by the limits of the island rather than any environmental variable. Solution 3b, we attempt to address this with intra-island niche comparisons of sister taxa on larger islands (e.g. Hawaii, Maui Nui), thereby limiting comparisons to taxa that experience similar impact and can be modelled more reliably (see discussion by Saupe *et al.*, 2012).

(Fig. 4, challenge 1a), a requirement for validating SDMs. Nevertheless, the correlative data produced by this study can be used to generate species-specific hypotheses, because we identified several examples of both niche conservatism and divergence between species (Fig. 3A; Fig. 4, solution 3b).

At present, entomological museums, in particular, face challenges from a shortage of funding and difficulties in generating digitized specimen-level data (Vollmar *et al.*, 2010). This study highlights the benefits of investing in the databasing and georeferencing of arthropod collections (Fig. 4, solution 1b), by showing how these efforts provide data key to understanding the mechanisms of adaptive radiation. Given the inaccuracy of models with small datasets (Muscarella *et al.*, 2014), we did not attempt to hindcast or to generate predictions with future climate scenarios in this study. However, owing to the vulnerability of the Hawaiian Islands, modelling the distributions of additional endemic species and the potential consequences of anthropogenic change when more data become available through the digitization of collections is of paramount interest.

CONCLUSION

Our results point to three key new insights into adaptive radiations.

1. Environmental shifts are likely to be rare (phylogenetically conserved), especially regarding habitat type. In other words, adaptive radiation occurs largely within a given environment. We found little evidence that taxa mainly diverge between habitats, which is the expectation if ecological speciation is the primary driver of adaptive radiation (Losos & Ricklefs, 2009).
2. Lineages differ in the environmental niche that they occupy and within which they diversify.
3. Environmental shifts do happen, also to varying degrees in different groups, usually when a given lineage successfully occupies a novel climatic regime; this can occur both within single islands and during colonization of new islands, and commonly involves retention of the same microhabitat or biotic niche.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

Appendix S1. Data sources.

Appendix S2. Supplementary methods and references.

Figure S1. Jackknife tests of variable importance.

Figure S2. Input phylogenetic trees for phylosig function.

Table S1. Pearson correlation matrix of environmental layers.

Table S2. Museum specimens used in the occurrence dataset.

Table S3. Number of occurrence records per species.

Table S4. Principal components analysis (PCA) and phylosig function input values.

Table S5. Principal components analysis loading data.

Table S6. Phylosig function results.

SHARED DATA

All occurrence points (as coordinates with degree of error) and MaxEnt model statistics are available for download from Pangaea: <https://doi.pangaea.de/10.1594/PANGAEA.865181>. We also present species-level SDM maps (as raster grids in ASCII format), which should be used as a preliminary hypothesis of potential distribution (e.g. range maps for conservation purposes) because these models have not been validated. Published occurrence record sources are available in the [Supporting Information \(Appendix S1\)](#). Individual museum records are available from the respective collections ([Supporting Information, Table S2](#)).