Predictors of Phylogeographic Structure among co-distributed taxa across the complex Australian Monsoonal Tropics

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Abstract

Differences in the geographic scale and depth of phylogeographic structure across co-distributed taxa can reveal how microevolutionary processes such as population isolation and persistence drive diversification. In turn, environmental heterogeneity, species' traits and historical biogeographic barriers may influence the potential for isolation and persistence. Using extensive SNP data and a combination of population genetic summary statistics and landscape genomic analyses, we explore predictors of the scale and depth of phylogeographic structure in co-distributed lizard taxa from the topographically and climatically complex monsoonal tropics (AMT) of Australia. We first resolve intraspecific lineages and then test whether genetic divergence across space within lineages is related to isolation by distance, resistance and/or environment, and whether these factors differ across genera or between rock-related versus habitat generalist taxa. We then test whether microevolutionary processes within lineages explain differences in the geographic scale and depth of intraspecific phylogeographic lineages. Results indicate that landscape predictors of phylogeographic structure differ between taxa. Within lineages, there was prevalent isolation by distance, but the strength of isolation by distance is independent of the taxonomic family, habitat specialization and climate. Isolation by environment is the strongest predictor of landscape-scale genetic divergence for all taxa, with both temperature and precipitation acting as limiting factors. The strength of isolation by distance does not predict the geographic scale of phylogeographic structure. However localized lineages had higher mean individual heterozygosity and less negative Tajima's D. This implies that finer-scale phylogeographic structuring within species is associated with larger and more stable populations and, hence, persistence.

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Running title: *Predictors of Phylogeographic Structure in the AMT*

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Abstract

Differences in the geographic scale and depth of phylogeographic structure across co-distributed taxa can reveal how microevolutionary processes such as population isolation and persistence drive diversification. In turn, environmental heterogeneity, species' traits and historical biogeographic barriers may influence

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Keywords

Population structure, gene flow, isolation by distance, geographic barriers, environmental limitation

Introduction

The immense variety of life forms that we observed today is a result of the speciation process- and all the factors that promote speciation initiation. Speciation is an extended process where the potential for persistence of population isolates is central to whether intraspecific lineages are ephemeral, or will eventually transition to full species under the protracted speciation model (Etienne et al., 2012; Rosenblum et al., 2012). Population isolation and high persistence of isolates manifests as a strong phylogeographic structure across the range of species (or parapatric species complexes). It follows that the phylogeographic structure of taxa depends on how a combination of species traits (e.g. specialization to spatially patchy habitats), environmental heterogeneity and biotic interactions (Harvey, Aleixo, Ribas & Brumfield, 2017; Riginos, Buckley, Blomberg, & Treml, 2014) influence isolation and/or persistence of populations (Funk et al., 2005; Oliveira et al., 2018; Pease et al., 2009). Understanding how genetic differentiation is shaped by environmental heterogeneity and dispersal limitation can help predict potential for adaptive divergence (Wang & Bradburd, 2014), in addition to informing how geographical and climatic barriers influence phylogeographic structure (Li, Huang, Sukumaran, & Knowles, 2018).

A broad spatial view of the population dynamics associated with species formation provides a bridge of two largely isolated research approaches – macro and microevolution (Harvey, Singhal & Rabosky, 2019). While macroevolution is broadly concerned with rates of speciation and extinction among groups, microevolutionary processes include intrinsic dispersal limitation, estimated using isolation by distance (Singhal et al., 2018; Strien, Holderegger, & Van Heck, 2015; Wright, 1943), extrinsic dispersal limitation related to the presence, currently or in the past, of geographic and physiological dispersal barriers (Myers et al., 2019; Pelletier & Carstens, 2018; Yannic, Hagen, Leugger, Karger & Pelissier, 2020), and population persistence through past climates (Bell et al., 2010; Ortego, Gugger, Riordan, & Sork, 2014; Vasconcellos et al., 2019).

Here we apply landscape genetics methods to a tropical reptile fauna in which most species have phylogeographic structuring, but with varying spatial and temporal scales. We explore whether dispersal within lineages is limited by geographic distance (isolation by distance (IBD); Wright, 1943), environmental heterogeneity (isolation by environment (IBE); Wang & Bradburd, 2014), or geographic barriers (isolation by resistance (IBR); Cushman, McKelvey, Hayden, & Schwartz, 2006; Spear, Balkenhol, Fortin, McRae, & Scribner, 2010), and how these relationships vary across rock-restricted vs. habitat-generalist species, or across genera, representing broader trait variation. We also test whether phylogeographic structuring is more geographically localized in taxa with lower dispersal (stronger IBD), larger local population size (higher average heterozygosity) or more stable population size assessed using departure from mutation-drift

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equilibrium (i.e. lower absolute Tajima's D). We apply this comparative approach to the lizard fauna of the Australian Monsoonal Tropics (AMT).

The AMT is a diverse and biologically rich region characterized by disjunct sandstone plateaus or areas of relatively high topographic relief separated by regions of flat savanna woodland (Figure 1). Aridity increases from north to south (Figure 1A). The AMT has strongly contrasting rainfall across wet and dry seasons, set against consistently warm temperatures (Figure 1B), and is the most fire-prone region in Australia (Bowman et al., 2010). Previous studies identified three biogeographically distinct areas within the AMT — the Top End, Kimberley and Cape York Peninsula (Figure 1A; Bowman et al., 2010; Woinarski, Mackey, Nix, & Traill, 2007), with the latter being the most biogeographically distinct (Fujita, McGuire, Donnellan, & Moritz, 2010; Lee & Edwards, 2008; Smith, Harmon, Shoo, & Melville, 2011). The Top End is more mesic than the Kimberley (Figure. 1A). Large river plains separate major plateaus in both regions (Figure 1A) and, along with climatic and edaphic barriers (e.g. the Gulf plains and Ord arid intrusion), represent a potential driver of allopatric divergence within terrestrial species (Catullo, Lanfear, Doughty, & Keogh, 2014; Eldridge, Potter, & Cooper, 2011).

Recent multilocus phylogeographic analyses of the AMT lizard fauna have consistently revealed strong phylogeographic structure within taxonomically recognized species. In some cases, cryptic species complexes have subsequently been taxonomically revised (Afonso Silva et al., 2017; Doughty et al., 2018; Melville, Date, Horner, & Doughty, 2019; Oliver et al., 2019; 2020), while assessments of species boundaries for other groups are still in progress (Catullo et al., 2014; Fujita et al., 2010; Laver, Doughty, & Oliver, 2018; Laver, Nielsen, Rosauer, & Oliver, 2017; Melville, Ritchie, Chapple, Glor, & Li, 2011; Potter et al., 2018). In some taxa (notably rock-specialist geckos; Laver et al., 2018; Moritz et al., 2018; Oliver et al., 2020) this phylogeographic structure can occur at very fine spatial scales, whereas in other taxa (e.g. more generalist *Carlia* skinks, Afonso Silva et al., 2017); *Diporiphora* dragons, Smith et al., 2011); and *Heteronotia* geckos, Moritz et al., 2016) the phylogeographic units typically span broader geographic ranges (Figure 1C). Phylogeographic lineages (whether or not now reclassified as separate species) are also much older in *Gehyra* than are those in the other genera (Figure 1C). There are also regional differences relating to climate and topography. Short-range phylogeographic lineages are concentrated in the more mesic regions of the Top End and west Kimberley, including on islands (Rosauer et al., 2016, 2018) and isolated karst limestones (Oliver et al., 2017). For Carlia, there were more variable demographic responses to past climate change in the drier Kimberley than the more mesic Top End (Potter et al., 2018).

This variation in the spatial and temporal scale of phylogeographic structure provides the opportunity to apply landscape genetics within lineages to test how intrinsic dispersal limits and ecological specialization interact with environmental heterogeneity in shaping the scale of phylogeographic structure within species. Using newly obtained SNP data and landscape-scale sampling with phylogeographic lineages, we 1) tested whether dispersal limitation within lineages (IBD) varies among taxa (families), ecologies (habitat requirement) or environmental condition; 2) explored what environmental features best explain genetic divergence within lineages (Isolation by distance/resistance/environment); and 3) tested whether microevolutionary processes, reflected in within-lineage genetic parameters, explain differences among taxa in the geographic scale and depth of phylogeographic lineages.

Material and Methods

Sequencing data

We selected species (or species complexes) that are widely distributed across the Top End and Kimberley regions, which also had geographic extensive genetic sampling with precise GPS coordinates, and which represented different genera and families of lizards. These include geckos (*Gehyra* and *Heteronotia* ; Gekkoninae), skinks (*Carlia* ; Scincidae) and dragons (*Diporiphora* ; Agamidae). All but *Heteronotia* (represented by the generalist *H. binoei*) include species with different habitat requirements and, from prior multilocus sequencing, varying scales of phylogeographic structure (Figure 1C; Supplementary Material S1), making them ideal for our study. Based on prior phylogeographic analyses and (except for rare cases of known

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mtDNA introgression) using mtDNA for lineage identification, we selected a subset of 579 samples (135 *Carlia* , 147 *Diporiphora,* 214 *Gehyra* and 83 *Heteronotia*) for the SNP screening, focusing on spatially unique individuals to maximize the number and geographic spread of sampled localities across the known range of each taxon (see Battey et al, 2020). We treat closely-related and parapatrically-distributed lineages as phylogeographic units, whether or not they have been recently revised taxonomically (Suppl. Mat. S1).

Our SNP detection method, Diversity Array Technology (DArT), uses restriction-enzyme reduction sequencing on Next-Generation-Sequencing platforms to identify SNPs within randomly distributed 75bp contigs (Jaccoud, 2001), and has proven valuable for detecting admixture between populations (Jane Melville et al., 2017; Unmack et al., 2017) and for landscape genetic studies (De Fraga, Lima, Magnusson, Ferrão, & Stow, 2017; Rossetto et al., 2019). Details of the SNP genotyping can be accessed in Georges et al. (2018) and Wells and Dale (2018). For samples from each genus, and within the older Gehyra radiation, the *australis, koira* and *nana* clades separately (Figure S3), the sequences were processed by proprietary DArT analytical pipelines to map reads and call SNPs. First, sequences are quality filtered using stringent selection criteria that compares the barcode region to the rest of the sequence. Next, using the DART fast clustering algorithm with a Hamming distance, sequences are aggregated into clusters. Then, SNP markers are identified in each cluster that will calculate an index of reproducibility for each locus. The resulting data contains the presence/absence of restriction fragments per SNP (SilicoDArT) and the final SNP calling with the position of a variant base related to the restriction fragment. To ensure the quality of our data, we filtered SNPs by repeatability across technical replicates (>98%), call rate (<10% missing data), and removed singletons, using the *dartR* package (Gruber, Unmack, Berry, & Georges, 2018) in RStudio (RStudio Core Team, 2015).

Sample design and population clustering

For landscape-scale analyses it is important to not confound diversity within meta-populations with divergence among historically isolated lineages, as have previously been identified in each of the species considered here (Suppl. Mat. S1). To visualize the population structure and divergence among samples using the SNP data, we first performed a principal coordinate analysis (PCoA) based on the genetic distance matrix between individuals using Euclidean distance to identify discrete clusters. We then ran two different analyses to verify clusters and test for admixture among them — *FastStructure* (Raj, Stephens, & Pritchard, 2014) and *conStruct* (Bradburd, Coop, & Ralph, 2018). *FastStructure* is a model-based clustering method that looks for the probability of an individual belonging to a cluster, considering the population structure, and was calculated with model complexity (K) between 1-7. The admixture proportions were visualized with a *Distruct* plot. *ConStruct* infers continuous and discrete patterns of population structure by estimating ancestry proportions for each sampled individual from two-dimensional population layers, where within each layer a rate at which relatedness decays with distance is estimated (Bradburd et al., 2018). In essence, this approach has IBD as a null-model, against which isolated populations are inferred, whereas *FastStructure* (and related methods) assumes panmixia within genetic clusters. For *ConStruct* we used spatial data (considering Isolation by distance), with a K between 1 and 7, and compared the predictive performance of the models by running cross-validation with 50 replicates. From here on, we will refer to these populations within described species with strong structuring as 'lineages', even if low admixture is observed between them in one or more of the above analyses (Table 1). These groups are well supported in previous studies using mitochondrial DNA and, in most cases, multilocus sequencing (more details in Suppl. Mat. S1).

Combining "landscape" and "genetics"

To investigate whether Isolation by distance (IBD) varies among lineages or regions we fitted a linear model between pair-wise log Euclidean geographic distance and genetic distance among individuals, calculated by "1 minus the proportion of shared alleles between each pair of individuals" using the *PropShared* function from the *adegenet* package (Jombart & Ahmed, 2011). The strength of IBD was measured within each of the taxa (species or intraspecific lineages) as identified above. The IBD slope is expected to increase with decreasing local population size and/or migration rate (Rousset, 1997) but is also reduced at large spatial scales by recent population expansion (Slatkin, 1994). Mantel tests were performed to calculate a p-value. We visualized slopes using the R package *jtools* (Long, 2019), and tested for differences across taxa (skinks,

geckos, and agamids), environments (more below), and between rock specialists vs habitat generalists. To represent climatic variation we focused on mean annual rainfall values, the dominant environmental variable of the region, from WorldClim (Hijmans, Cameron, & Parra, 2006) extracted from the convex hull polygons created from each species distribution locations, as the dominant environment variable of the region. To account for the influence of the precipitation, habitat preference and lizard group we performed a generalized linear model (glm; as our variables were non-normal) with the slope value of the IBD analysis and using 1-standard error as weighting.

To investigate the effect of environmental features on genetic difference among individuals (Isolation by Environment; IBE), we downloaded the 19 variables from WorldClim (Hijmans et al., 2006) at 30-s resolution. We tested for correlation among these variables using the *ENMTools* R package (Warren et al., 2019), keeping eight uncorrelated (r < 0.7) variables (Annual Mean Temperature, Mean Diurnal Range, Isothermality, Mean Temperature of Wettest Quarter and Driest Quarter, Precipitation Seasonality, Precipitation of Driest Quarter and Warmest Quarter) and extracting these variables for each locality per species. The value of each environmental variable per distribution point was used later as an environmental variable to relate to genetic divergence using generalized dissimilarity modelling, discussed above.

To avoid over-sampling our Isolation by Resistance (IBR) models we excluded occurrence records that were in islands (no-connectivity) or within the same resolution grid square at ~1km resolution. The resulting numbers of individuals used for each taxon are indicated in Table 1. We considered four landscape features to test the effect of resistance surfaces on species divergence: rivers, slope, evapotranspiration and potential environmental suitability based on species distribution models (SDM). Slope and rivers can represent physical and physiological barriers to dispersal for some of the species. We obtained a river shapefile from Geoscience Australia (1997), and considered major rivers as high resistance cells and intervening regions as low resistance. We extracted slope from altitude (CGIAR-CSI, 2019), using the package *raster* (Hijmans, 2019). Slope was obtained from the weighting coefficient for the altitude for each grid cell, helping to recognize flat areas that could facilitate dispersal of habitat generalist species or inhibit dispersal for rock-dependent species. All asci files were normalized from 0 to 1, with greater values indicating higher resistance. Global potential Evapotranspiration was obtained from CGIARC-CSI, 2019 (https://cgiarcsi.community/data/global-aridity-and-pet-database) and represents the water/productivity available for the organisms, which allows contrasting the mesic and dry conditions across the general north/south aridity gradient of the AMT (Figure 1A). Finally, we created SDMs for all species and lineages independently, based on the locality of genetically identified samples (see complete details in the Supplementary Material S1). We included all 19 WorldClim variables, running the Python 2.7 script (available at github.com/DanRosauer/phylospatial) to automate data preparation and modeling in *ArcGIS 10* (ESRI, 2011) and *MaxEnt v3.3* predictive approach (Phillips, Dudik, & Schapire, 2012). Following Elith et al. (2011), we retained even correlated variables, allowing *MaxEnt* to determine the required predictors for each model. To avoid over-prediction, background points were limited to a 3 degrees radius around the location records, with 25 bootstrap replicates for each SDM, and the result was exported as an asci file and normalized. The area under the curve (AUC) values for the SDMs vary between 0.95 and 0.71, indicating good model performance, except for the Kimberley lineage of *Diporiphora magna*, with an AUC of 0.61 (Table S1). Both precipitation and temperature related to the seasonality of the AMT appear to be important variables in most SDMs (Table S1). We used circuit theory to identify the most effective path by using the four landscape features described above in the software *Circuitscape* (McRae, Shah, & Mohapatra, 2013). This looks for all paths and averages them according to resistance values, where the SDM was used as a conductance surface (where higher values indicate greater ease of movement) and rivers, slope and evapotranspiration as resistances.

To investigate how IBD, IBE, and IBR contribute to genetic divergence, we based our analysis in part on the framework of Myers et al. (2019), using generalized dissimilarity modelling (GDM; Ferrier, Manion, Elith, & Richardson, 2007). This method calculates the relationship between nonlinear models associating the variation in the rate of genetic dissimilarity among individuals with distance variables. We ran seven independent tests for each species: first a full model, including geographic distance, environmental variables, and resistance surfaces; then, looking for the interaction between two of the datasets; and lastly looking at

each dataset alone (more details in Table 1). We used genetic divergence as the response variable and the geographic, environmental and resistance datasets as predictors in a GDM site-pair table, and quantified the predictor's importance and significance using a GDM matrix with 50 permutations.

Population-level predictors of phylogeographic diversity

To explore how microevolutionary processes (population size, dispersal restriction and population stability within lineages) relate to the geographic scale and depth of phylogeographic structuring within species (complexes), we estimated mean observed heterozygosity (*Ho*) and Tajima's D (Tajima, 1989), using the *dartR* package (Gruber, Unmack, Berry, & Georges, 2018), as well as the strength (i.e. slope) of IBD (as above). These measures provide us complementary information about persistence, where higher mean *Ho* is related to larger local effective population sizes (N_e), IBD slope to lower dispersal and/or smaller local N_e, and more negative Tajima's D values to stronger deviations from mutation-drift equilibrium, as could arise from population fluctuations. We note that our quasi-random sampling of individuals across space is expected to reduce confounding effects of spatial structuring on these summary statistics, assuming modest to large local effective population sizes as seems reasonable for these highly abundant lizards (Battey, Ralph, & Kern, 2020). To test whether lower dispersal (or local N_e) and more stable populations at the landscape scale translate to finer-scale or deeper phylogeographic structure across all lineages, we regressed (glm) lineage area and age (obtained from the mitochondrial DNA BEAST chronograms for each genus; Suppl. Mat. Figure S1-S4) against mean *Ho* , IBD slope and Tajima's D as predictor variables. Knowing that recent range expansion (as inferred by Tajima's D) could influence the relationship of range size with *Ho* , we also performed a generalized linear regression using Tajima's D values as a covariate. We also tested for effects of habitat preference and lizard group on mean *Ho* and Tajima's D values.

Results

Population differentiation and clustering

After stringent filtering, the average number of SNPs reduced from 52,693 to 3,729 for *Carlia* (N=135 across four lineages), from 150,178 to 7,472 for *Diporiphora* (N=147 across eight lineages), from 182,688 to 11,531 for *Gehyra* (N=214 across ten lineages) and from 185,704 to 10,017 for *Heteronotia* (N=83; three lineages). Values per lineage, the region of occurrence and habitat specialization are given in Table 1. After partitioning samples into major lineages, mean sample size was 23 individuals and, post-filtering, no lineages had more than 6% of missing data. As expected from prior studies, most species had deeply divergent intraspecific lineages, reflected in largely coincident patterns across the *PCo* A, *fastStructure* and either of the spatial or non-spatial *ConStruct* graphs (see Figure 2 for an example with *Carlia amax;* data for the other species are available in the Suppl. Mat. Figure S5-S8). The number of discrete lineages identified per species varied from one to three and these supported historically isolated lineages recognized in previous studies, mostly using different datasets (Suppl. Mat. S1). Our subsequent landscape genetic studies focused on variation within these lineages. However, some of these lineages as defined here could still comprise multiple less divergent but historically isolated populations that could confound some landscape genetic analyses but could not confidently resolved with the sampling here. These include *Diporiphora bilineata* and *D. perplexa* (Fenker et al, *unpublished data*), *Gehyra gemina* and *G. koira* (Oliver et al., 2020), *G. nana* 4 (Moritz et al., 2018), *H. binoei* TE (Moritz et al., 2016) and *Carlia munda* (Potter et al., 2018) (Suppl. Mat. S1).

Genetic diversity and Isolation by Distance

The Mantel tests showed a significant correlation between genetic and Euclidean geographic distance (IBD) for all lineages (glm; $p < 0.05$; Suppl. Mat. S1). As Mantel tests are prone to type I error (Wang, 2013) a visual exploration of the data was also done. In general, there was strong IBD, with slope estimates varying from 0.07 to 0.68 (Table 1; Figure 3; Figure S9). However, IBD slopes did not differ significantly across lizard genera, rock-dependent vs. habitat generalists, or in relation to annual mean precipitation (glms; all $p > 0.05$).

Mean individual *Ho* per lineage varies approximately 30-fold, between 0.007 to 0.192 (Table 1). Except for

the slightly positive value for *Gehyra gemina*, all lineages showed negative Tajima's D values (-0.058 to -1.376; Table 1) likely reflecting recent population fluctuations. *Heteronotia* geckos and *Carlia amax* in the Gulf region of the AMT exhibited the most negative values (Table 1); again, mean *Ho* was not related aridity, genera or habitat specialization (glm; p>0.05).

IBD, IBE, and IBR as limits of dispersal

The GDM models including isolation by distance, environment, and resistance together explained between 24% and 96% of variation in genetic divergence within lineages. Isolation by Environment (IBE) alone, or in combination with IBD or IBR, was the most important predictor of genetic divergence within lineages, while the principal environmental variables varied across taxa (Table 2). By contrast neither IBD alone, nor IBR alone, ever explained as much of the variation in genetic distances as did combined effects. Except for two lineages (*Diporiphora sobria* KIM and *Gehyra australis*), climatic variables were included among those contributing strongly to the models. Geographic distance (always in combination with environmental variables), was one of the most important variables for 13 of 25 lineages. For the remaining 12 lineages, eight have their genetic divergence limited by resistance surface, where four are related to cost-distance SDM; *Gehyra australis* and *G. lapistola* to the presence of a river, *Heteronotia binoei* NA6 to evapotranspiration, and *D. sobria* KIM to slope.

Population genetic predictors of phylogeographic structure

Testing for whether population size, stability or dispersal limitation predicted the scale of phylogeographic structure, geographically restricted lineages had higher *Ho* (AIC = -75.664; p = 0.005), but there was no significant relationship between range size and either Tajima's D (AIC= 24.025; p= 0.081) or the slope of IBD (AIC= -56.6; p = 0.212). When we add Tajima's D as a covariate (to control for possible reduction in *Ho* with range expansion) the negative relationship of heterozygosity and range size remained significant (p = 0.049). As in some taxa our estimates of IBD and Tajima's D could still be impacted by sampling across historically isolated lineages rather than metapopulations (Battey et al. 2020), we removed such potentially composite taxa (*Carlia munda* ; *Diporiphora bilineata* ,*D. perplexa* ; *Gehyra gemina* , *G. koira* , *G. nana* 4; *Heteronothia binoei* TE*; see Suppl. Mat. Info and Figure S10) and repeated tests. Excluding these taxa, more localised lineages now had less negative Tajima's D values (AIC= 52.351; p = 0.005); other results remained the same. Older clades (mostly*Gehyra*) have stronger IBD (Figure 4), but there is no relationship with either Tajima's D or *Ho* . When the above taxa are excluded, Tajima's D values did not differ across genera, region of occurrence or habitat specialization (p>0,05).

Discussion

Our SNP datasets support and extend previous evidence for strong phylogeographic structuring within these tropical lizard species complexes in the AMT. Compared with the smaller scale datasets available through traditional multilocus sequencing or exon capture, SNPs provide much higher resolution for studying the influence of environmental features on genetic divergence and population structure and admixture (Georges et al., 2018; Melville et al., 2017).

Intrinsic dispersal limitation, represented by the IBD slopes, was not related to the habitat specialization, genus or aridity. While populations of most of the rock-specialist lineages can be found on widely-dispersed flat rocks and open sandstone platforms (Melville et al., 2019; Oliver et al., 2019), only *Gehyra koira* and *G. lapistola* are associated with the more sparsely distributed tall rock escarpments (Oliver et al., 2019). That even these taxa, and especially the widely distributed *G. koira* , did not have stronger IBD than generalists is surprising. Similarly, there were no consistent differences among genera, which implicitly represent broader divergence in ecological traits. More insight into causes of the three-fold variation in observed intra-lineage IBD could come from inclusion of additional natural history attributes, such as body size and physiological tolerances, as well as more intensive sampling at finer spatial scales.

Isolation by Environment emerged as a stronger predictor of landscape-scale genetic divergence than Isolation by Distance or Isolation by Resistance. As IBE represents an interaction between species traits and

abiotic elements of the landscape (Myers et al., 2019; Paz, Ibáñez, Lips, & Crawford, 2015), we infer that local adaptation could be the principal driver of genomic divergence in these AMT lizards. Previous comparative studies showed that species-specific characteristics can be the main determinant of landscape genetic patterns (Myers et al., 2019; Reid, Mladenoff, & Peery, 2017; Robertson et al., 2018). But here, *Gehyra* and *Heteronotia*(Gekkonidae) have different determinants of population structure. Similarly, there is no overall differences in landscape genetic patterns between rock-specialists and generalist species. Yet, the distantly related *Diporiphora magna* KIM and *Gehyra nana4* lineages share a widely sympatric distribution and also have the same variables fall out as most important variables in explaining their genetic diversity - Average Annual Temperature and Average Daytime Range. These species have little in common and it is unclear why they might exhibit similar responses to environmental heterogeneity - they belong to different lizard families (Agamidae and Gekkonidae), and have different ecological requirements: *D. magna* KIM is a daytime habitat generalist dragon, while *G. nana* 4 is a nocturnal, rock-related gecko. Overall, the expected association between species traits and both landscape genetics and phylogeographic patterns (Zamudio et al., 2016) is elusive here.

Spatial variation in both temperature and precipitation emerged as important influences on landscape-scale diversification of these lizards. This supports findings that the environmental constraints are important drivers of genome-wide neutral differentiation patterns (Bothwell et al., 2017; Orsini, Vanoverbeke, Swillen, Mergeay, & De Meester, 2013; Sexton, Hangartner, & Hoffmann, 2014). This result is expected for ectotherm lizards, in which ecological traits are responsive to climate variation in space and time (Camargo, Sinervo, & Sites Jr, 2010; Pianka & Vitt, 2003). Additionally, the strong seasonality of rainfall across the AMT (Figure 1B) has direct impact on geographic (e.g. changes in the river regimes; Woinarski et al., 2007) and physiological barriers for organisms and further dispersal abilities. Spatial variation in seasonality variables were significant predictors of genetic distance within about half of the lineages examined here. This is not the first time seasonal variation in climatic condition is reported as a principal driver of genetic differentiation (Bothwell et al., 2017; Cushman et al., 2014; Yang, Cushman, Song, Yang, & Zhang, 2015), and should be investigated in the AMT in more detail. Other factors not considered in the present work are biotic interactions, such as competition, that could influence the resilience of the species/lineages in determined regions (Harvey, Aleixo, et al., 2017; Riginos et al., 2014), and spatial variation in long-term climatic stability (Potter et al., 2018), wherein past climate events affected species distribution and genetic structure (Vasconcellos et al., 2019).

While spatial variation in habitat suitability (IBR) is a significant predictor of genetic differentiation in some cases, it was never the best predictor, revealing that landscape features play a small role on differentiation of our co-distributed taxa. Rather, IBE, alone or in combination with IBD or IBR, was generally the best predictor. A deeper look into the IBD graphs shows that, for widely distributed taxa (e.g.*D. bilineata* and *G. gemina;* Figures S6 and S7), there is substantial population structure within lineages as landscape features (such as topographic variation and rivers) are not limiting the intrinsic dispersal. This does not necessarily result in formation of new phylogeographic lineages, as IBD is related to earlier stages of differentiation (Avise, 2000; Singhal et al., 2018). Yet, for other lineages, the structure within lineages is not clear on the IBD graphs, and environmental and landscape features could have a bigger influence on genetic divergence (Singhal et al., 2018).

While macroevolutionary patterns are presumably generated by population level (microevolutionary) dynamics (Harvey et al. 2019), it has proved challenging to discern the processes that connect the two scales (Li et al., 2018; Singhal et al., 2018; Harvey, Seeholzer, et al., 2017). A promising result here is that geographically restricted lineages had higher heterozygosity and (when removing taxa with cryptic lineage structure) lower deviations from mutation-drift equilibrium within lineages. This points to larger local effective population size and greater population stability as determinants of fine-scale phylogeogaphic structure, whereas the strength of IBD had no influence. Thus, population persistence, more than dispersal limitation, could be key to development of fine-scale phylogeographic structure and potential speciation. Finally, while other studies have shown that ecological preference can predict genetic diversity and divergence (Harvey, Aleixo, et al., 2017), this was not observed in our co-distributed taxa, emphasizing again that the divergence is

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species-specific and that effects of other ecological dimensions, such as physiological specialization and biotic interactions (e.g. range bloking) should be investigated. Methods incorporating microevolution into macroevolutionary analyses (and vice versa) are still limited, but recent developments promise a better integration of both fields (Harvey, Seeholzer, et al., 2017; Li et al., 2018; Price et al., 2014; Rabosky & Matute, 2013).

Conclusion

Our study on co-occurring taxa and well-sampled SNP datasets allows us to explore what intrinsic and extrinsic factors influence the development of fine-scale phylogeographic structuring within species. Population genetic statistics indicate the importance of population size and stability in promoting fine-scale phylogeographic structure. Local adaptation seems to be the strongest driver of phylogeographic structure in the AMT lizards, rather than family, habitat restriction and region of occurrence. Further examination of species-specific characteristics should help to elucidate which biogeographic and environmental features promote persistence and isolation between populations (Zamudio, Bell, & Mason, 2016). The strong seasonality of the AMT could also impact the propensity for genetic divergence and future studies should focus on local dispersal restriction across dry and wet seasons as these influence physiological and physical barriers.

Acknowledgements

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Data Accessibility

The data supporting the results are available at the Supplementary Material 1. Should the manuscript be accepted, the data supporting the results will be archived in an appropriate public repository (Dryad or Figshare) and the data DOI will be included at the end of the article.

Author Contributions

JF led conceptualization, data analysis and writing. JM and CM contributed substantial conceptual and editorial advice. LT contributed with conceptualization and data analysis. All authors contributed to writing and approved the final manuscript.

Figure legends

FIGURE 1. Introductory figure with data from the Australian Monsoonal Tropics (AMT). A) Map with elevation, rivers, and evapotranspiration, highlighting the location of the three principal regions — Kimberley, Top End and Cape York; B) Average monthly temperature (in degrees Celsius) and rainfall (in millimetres) values for the AMT region; and C) Generalized linear model between clade depth (based on number of

substitutions of ultrametric mtDNA trees) and clade distribution area (logkm2 values) for the four lizard genera included in the paper. This includes all known lineages present east of the Gulf break. Colours represent different lizard clade. Symbols represent different habitat preferences.

FIGURE 2. Species structure analysis for the AMT skink lizard clade *Carlia amax* , where A) Isolation by distance plot; B) Principal Coordinate Analysis; C) *ConStruct* analysis and D) *FastStructure* analysis. Colours represent three distinct species found in our dataset across all analyses.
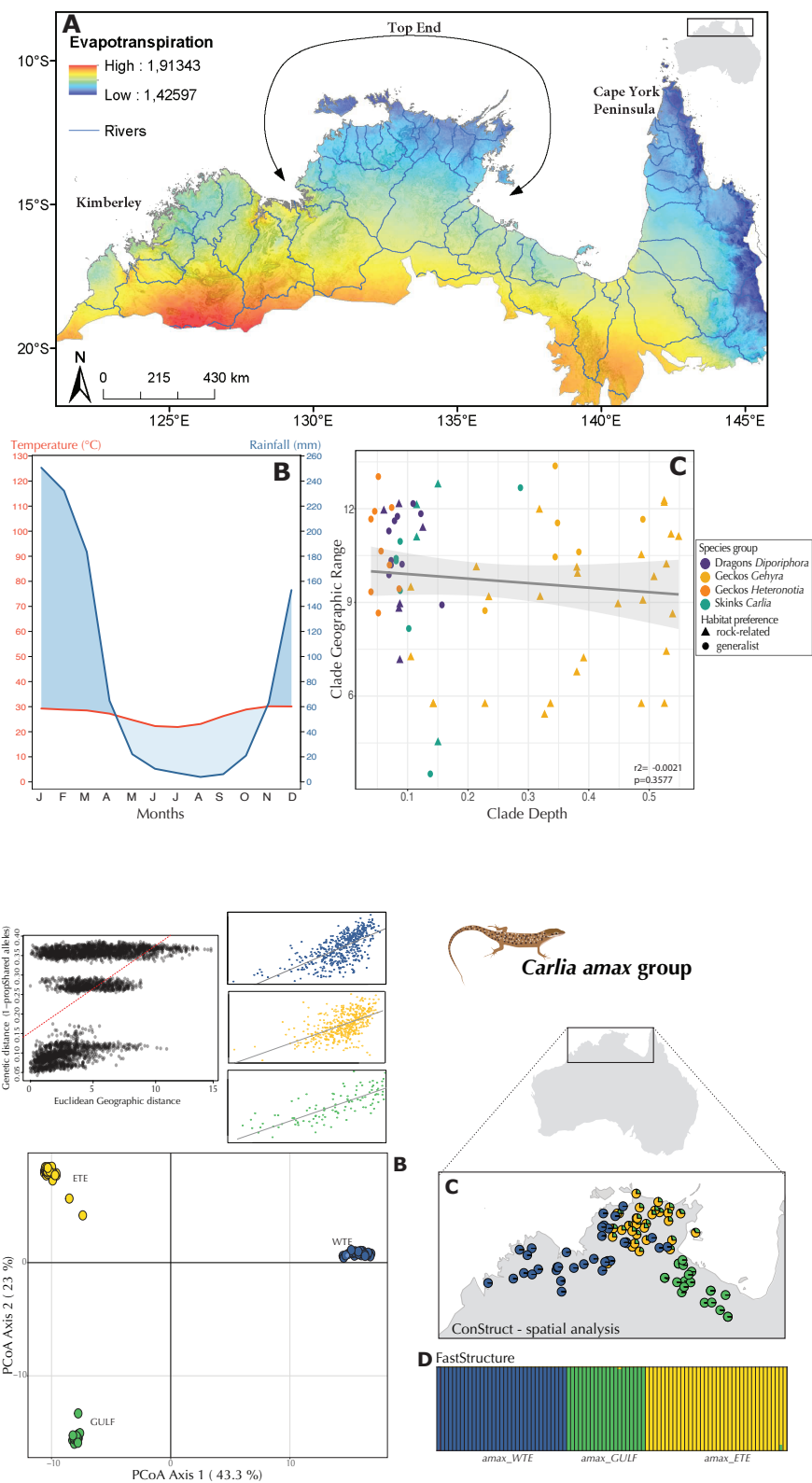
FIGURE 3. Isolation by distance graphs plotted across taxa (skinks, geckos and agamids), same environmental condition (using mean annual rainfall as a proxy; see Methods for more details) and habitat requirements (rock specialists vs. generalists). Higher values show stronger IBD relationship. Slopes represent the uncertainty (width) along the slope IBD estimate, where the circle is the point estimate.
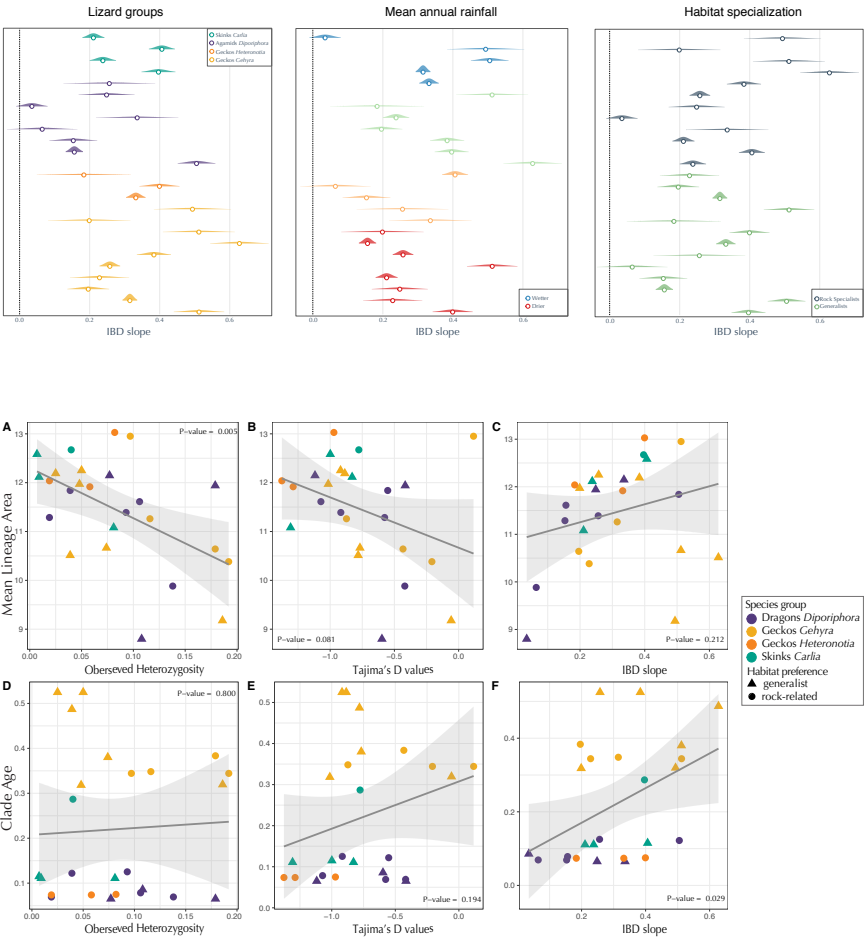
FIGURE 4. Regression plot of mean lineage distribution area and clade age against observed heterozygosity (Ho), Tajima's D values and isolation by distance (IBD) slope values. Colours represent different lizard clade groups. Symbols represent different habitat preferences. Significance values are indicated for each regression.

Table legends

TABLE 1. Lizard lineages included in our paper, including data on number of samples (N) used in most analyses, and samples used in the resistance models (IBR); habitat specialization; number of SNPs (Loc) before and after filtering; Observed heterozygosity (Ho), Tajima's D values and isolation by distance (IBD) slope (more information in the Methods section).

TABLE 2. Results from generalized dissimilarity modelling analyses, demonstrating the proportion (percentage) of genomic divergence explained by geographic distance (IBD), climate (IBE) and resistance surface (IBR), and the statistical significance of the full GDM model, with two particular variables that best explained genomic divergence in each of the full models. Model values in bold represent statistically significant (p<0.05) values. Shaded values represent the most significant results.

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`Table1.xlsx` available at https://authorea.com/users/370133/articles/488881-predictors-of-phylogeographic-structure-among-co-distributed-taxa-across-the-complex-australian-monsoonal-tropics

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`Table2.xlsx` available at https://authorea.com/users/370133/articles/488881-predictors-of-phylogeographic-structure-among-co-distributed-taxa-across-the-complex-australian-monsoonal-tropics