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Comparative landscape genomics reveals species-specific spatial patterns and suggests human-aided dispersal in a global hotspot for biological invasions

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Abstract Biological invasions are a growing threat to native ecosystems, and genomic studies have become an increasingly useful tool for invasive species management by providing the ability to identify spatial population structure in the invaded range. In this study, we compared the spatial genetic structure of two ecologically distinct non-native lizard species both established and widespread throughout South Florida, a global hotspot for reptile invasions. We used an individual-based sampling approach to collect genetic samples of *Agama picticauda*, a rock specialist native to West Africa, and *Basiliscus vittatus*, a riparian specialist from Central and South America. We collected specimens across Miami-Dade County (the original site of introduction) and then genotyped ~4000 single nucleotide polymorphisms for each species. Both species exhibited fine-scale population structure at distances <5 km for *A. picticauda* and <10 km for *B. vitattus,* but at the county scale *B. vittatus* showed much stronger spatial structure compared to *A. picticauda*. Landscape genomic analysis revealed no significant landscape influence on *A. picticauda* genetic differentiation, while for *B. vittatus* low canopy cover was the best predictor of genetic connectivity. The genetic structure of both species may suggest human-aided dispersal is driving long distance movements, and *A. picticauda* appear more susceptible to these events likely due to their affinity for highly urbanized areas. By identifying variable dispersal patterns among two ecologically distinct species, we hope that this study will help combat the spread of these or similar species as they continue to arrive at urban centers across the globe.

Keywords Gene flow · Lizard · Population structure · ResistanceGA · Spatial genomics · Urban landscape

Introduction

Genetic studies are becoming increasingly useful to invasive species management, especially with the advent of next-generation sequencing allowing for large-scale genomic analysis of thousands of markers, which has been shown to identify fine-scale population structure more effectively (Spinks et al. 2014; McCartney-Melstad et al. 2018). Genetic analysis of non-native populations can be used to investigate the number of introduction events (Kolbe et al. 2004), pinpoint source populations (Kolbe et al. 2007; Fieldsend et al. 2021), and measure genetic diversity and

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identify genetic bottlenecks (Ma et al. 2020; Van-Wallendale et al. 2020). Landscape genetic analysis, which integrates population genetics and landscape ecology (Manel et al. 2003), can be used to identify the importance of different environmental factors to the facilitation or obstruction of spread and identify movement corridors as non-native species disperse throughout the newly invaded region (Arredondo et al. 2018; Low et al. 2018). In addition to the classic isolation by distance analysis (IBD (Wright 1943)), which compares the relationship between genetic distance and geographic distance, landscape genetics assesses the relationship with resistance distance (or isolation by resistance; IBR (McRae 2006)), where distance is calculated based on the resistance of the landscape to movement and gene flow.

Previous analyses have demonstrated that landscape resistance can be an accurate predictor of the spatial spread of invasive species (Lovell et al. 2021); however, this work did not assess local spatial scales relevant for management decisions. If there is human-aided dispersal within established populations or multiple source populations, this can confound the spatial signal or lead to high admixture within the invasive population, which in turn may increase genetic diversity and the ability for the species to adapt to the novel environment (Kolbe et al. 2004, 2007; Crawford and Whitney 2010; Fieldsend et al. 2021). The spatial genetic structure of non-native populations is vital to understanding such processes and to inform management decisions on how to deal with problematic invasive species. For example, landscape genomics has been used to assess both eradication units (areas of high gene flow that need to be eradicated simultaneously to prevent reinvasion) and population densities of invasive species to appropriately plan the amount of removal effort needed to be successful (Macdonald et al. 2019; Sjodin et al. 2020). While landscape genetics is a growing field with many possible applications (Balkenhol et al. 2015), few studies have used these methods on invasive species (Li et al. 2017; but see Medley et al. 2015; Arredondo et al. 2018; Combs et al. 2018; Low et al. 2018) or in urban landscapes (LaPoint et al. 2015), both of which are assessed in the present study.

The highly urbanized landscape of South Florida is a global hotspot for biological invasions and home to the world's largest community of non-native reptiles and amphibians (Krysko et al. 2016; Capinha et al. 2017). Success of non-native species introductions in this region is due to several factors, including South Florida's subtropical climate, which provides a close match to the native range of many introduced species (Mothes et al. 2019), the presence of major ports of entry, and the fact that South Florida is a global hub for the exotic pet trade, which could benefit from stricter law enforcement (Krysko et al. 2011). Lizards constitute a large majority of this non-native community, with established populations of at least 48 species (Krysko et al. 2019). Genetic studies have been conducted on a number of these non-native Florida lizards, such as the many *Anolis* (Kolbe et al. 2004, 2007) and gecko species (Short and Petren 2011a, 2011b; Fieldsend et al. 2021). However, within this non-native lizard community there are several relatively large predatory lizards that, due to their generalist diets and large adult body sizes, likely impact native species and food webs (Bartlett and Bartlett 1999; Enge et al. 2004) but are poorly studied in their Florida range.

For this study, we focused on the invasion patterns for two of these species, *Agama picticauda* and *Basiliscus vittatus*, both introduced to Miami in the 1970s and now common throughout Miami-Dade County (Figure S1). *Agama picticauda* is a rock specialist from West Africa, thought to be first introduced to South Florida in 1976, but was presumed to be extirpated from the original introduction site when it was demolished for the construction of a railway transport system (Wilson and Porras 1983). In the early 1990s, it was introduced again via a reptile dealer (possibly as a consequence of Hurricane Andrew) in the Homestead area (Enge et al. 2004). *Basiliscus vittatus* is a riparian specialist from Central and South America, introduced at the same original site as *A. picticauda* in 1976 and believed to have survived the site demolition as individuals were afterwards found along a nearby canal (Wilson and Porras 1983). Both species were subsequently identified in other counties throughout Florida, although these are assumed to be separate introduction events (Krysko et al. 2006; Nunez et al. 2016). For this study, we focus on Miami-Dade County, where both species were first introduced to Florida and are most abundant and widespread (Krysko et al. 2019).

While these species possess similar introduction histories, body sizes, and trophic roles (i.e., generalist predators; Krysko et al. 2019), they exhibit two extremes in habitat specialization, which we predict has influenced their dispersal across their non-native ranges and produced unique spatial genetic structure between species. For example, *A. picticauda* is a rock-specialist often observed making extensive use of anthropogenic impervious surfaces, and thus having close associations with disturbed and urbanized habitats in both its native (Krishnan et al. 2019) and non-native (Krysko et al. 2019) range along with observed use of transportation routes (e.g., hitchhiking on vehicles and trains; Moore 2019; Gray 2020). We therefore hypothesize that human-aided dispersal may be responsible for this species' rapid spread (ninefold increase in site occupancy and fourfold increase in local abundance across Miami-Dade County within five years; Clements et al. in prep). In addition to affinity to urbanized habitats (Bullock et al. 2018), lack of isolation by distance and high genetic similarity between geographically separated individuals would be further lines of evidence of human-aided dispersal (Short and Petren 2011a; Kelager et al. 2013; Meng et al. 2015). In contrast, *B. vittatus* is a known riparian specialist, and we predict the extensive network of canals in Miami-Dade County is a main mode of dispersal for this species (Krysko et al. 2006; Meshaka 2011). Comparing the population structure and inferred invasion patterns for these two species that exhibit such stark differences in their ecological traits, but are spreading throughout the same landscape, provides a unique way to identify how knowledge of species' natural history and ecology could help predict their dispersal throughout a new region. In this study, we use landscape genomic methods to understand spatial structure and dispersal patterns for these large predatory lizards, with the hopes of informing management decisions in South Florida and other regions where these or similar species may be introduced.

Materials and methods

Sampling and molecular procedures

We utilized an individual-based sampling approach, as this is the most powerful approach for detecting landscape influences on gene flow and is most appropriate for non-native species that are continually dispersing and have yet to reach equilibrium in the invaded range (Landguth et al. 2010; Shirk and Cushman 2014). We collected 45 *A. picticauda* and 50 *B. vittatus* individuals from sites spread throughout Miami-Dade County in 2018–2019 (Fig. 1) by hand or using a small lasso. Sample localities were chosen by collecting all records for each species in Miami-Dade County from the Global Biodiversity Information Facility (GBIF.org 2021a,b) and EDDMapS (EDDMapS 2021) databases and spatially filtering them to 1 km, so that all targeted sites were > 1 km apart. A few collection sites ended up being < 1 km apart due to opportunistic sampling.

Genomic DNA was extracted from tissues (liver or muscle) using Qiagen's DNeasy Blood and Tissue Extraction kit (Qiagen, Hilden, Germany), following the standard extraction protocol. DNA quality was checked by running 100 ng of each sample on a 1% agarose gel to confirm intact, unfragmented DNA. DNA samples were sent to University of Wisconsin-Madison's Biotechnology Center DNA Sequencing

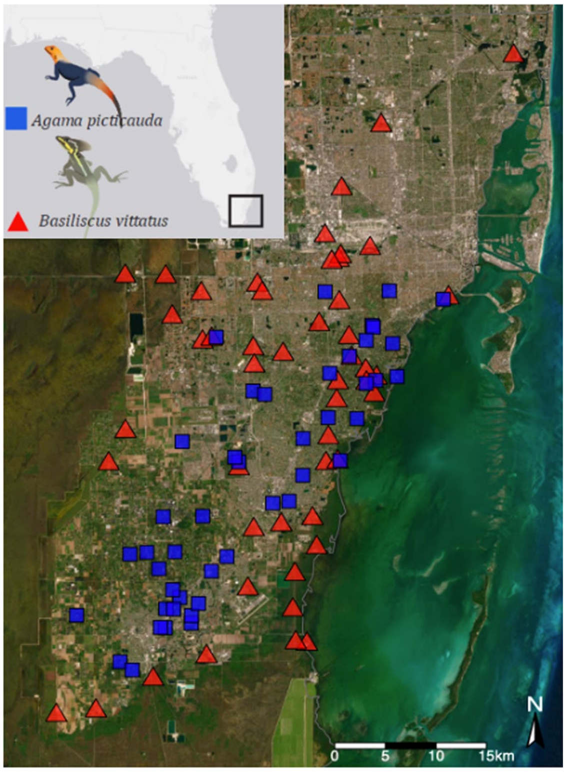

Fig. 1 Sample sites throughout Miami-Dade County, FL where *Agama picticauda* and *Basiliscus vittatus* were captured for this study

Facility for genotyping-by-sequencing using the restriction enzyme ApeKI for both species (following enzyme optimization). SNPs were called using the non-reference genome version of the Universal Network Enabled Analysis Kit (UNEAK) pipeline (Lu et al. 2013) implemented in Tassel 3.0 (Bradbury et al. 2007). This pipeline trims reads to 64 bp, merges identical reads into tags within each barcoded individual, and uses pairwise alignment to identify tag pairs with 1 bp mismatch (while probabilistically correcting sequencing errors using the error tolerance rate parameter set to 0.05). This resulted in 388,535 SNPs for *A. picticauda* and 497,346 SNPs for *B. vittatus*. These candidate SNPs were further filtered to only those present in $>90\%$ of individuals and those with $>5\%$ minor allele frequency, which left a final dataset of 4446 and 3952 SNPs for *A. picticauda* and *B. vittatus*, respectively, that was used for all analyses. We calculated observed heterozygosity (H_o), expected heterozygosity (H_e), and the inbreeding coefficient (F_{IS}; calculated as the averaged difference between the observed and expected heterozygosity) using the 'Hierfstat' package in R (Goudet and Jombart 2020; version 0.5–7).

Population structure analyses

Multiple analyses were used to identify the population structure for each species. First, we performed a STRUCTURE (Pritchard et al. 2000) analysis in STRUCTURE v.2.3.4 for values of K ranging from 1 to 10 for 500,000 iterations following 100,000 iterations of burn-in with five replicates. The best value for K was chosen using the Evanno method (Evanno et al. 2005) in the program STRUCTURE HARVESTER (Earl and vonHoldt 2012). Second, we used the R package 'conStruct' (Bradburd 2019; version 1.0.4), which is different from STRUCTURE as it is designed for dispersing species (incorporating isolation by distance) and compares spatial and non-spatial models. For this analysis, we assessed K from 1 to 10 with 10 replicates and 5000 iterations. To test for an effect of isolation by distance (IBD) on genetic structure, we performed a Mantel test between genetic and geographic distances, followed by a Mantel correlogram analysis to test for significance of spatial autocorrelation among individuals at different spatial scales using the R package "ecodist" (Goslee and Urban 2007; version 2.0.7). Spatial autocorrelation was assessed at intervals of 1 km (the minimum spacing at which samples were collected) and at larger intervals of 5 km. The genetic distance used was the proportion of shared alleles (D_{ps}; Bowcock et al. 1994) calculated in the 'adegenet' R package (Jombart 2008; version 2.1.3), which has shown to be an effective distance metric for individual-based sampling and landscape genetic analyses (Shirk et al. 2017), and outperformed other metrics when utilized on non-native populations (Medley et al. 2015). Finally, we conducted a spatial principal components analysis (sPCA), a spatially explicit ordination approach implemented in the "adegenet" R package (Jombart 2008). This analysis identifies eigenvectors that maximally explain both the genetic variance and trends in spatial autocorrelation.

Landscape influence on genetic structure

To understand how different landscape features shape the spatial structure of each species in the invaded range, we used the R package 'ResistanceGA' (Peterman 2018; version 4.0–0). ResistanceGA utilizes genetic algorithms to maximize the fit of resistance surfaces to the pairwise georeferenced genetic data and effective distances. The advantage of using 'ResistanceGA' for landscape genetics is that it does not require a priori knowledge of how resistant different landscape elements are to dispersal of the species, as most other methods do. Further, it can incorporate both categorical and continuous variables to delineate these landscape elements. The environmental variables we used include: (1) a categorical land cover layer from the Florida Fish and Wildlife Land Cover dataset (10 m resolution; Kawula and Redner 2018) with 15 land cover classes (e.g., agriculture, developed, transportation, vegetation types, water bodies), (2) a feature layer for the presence of roads, (3) a continuous layer for daily traffic intensity of each road (FDOT 2020), (4) a continuous layer of percent canopy cover (USDA Forest Service 2019; 30 m resolution), (5) a continuous layer for percent impervious (i.e., urbanized) surface (U.S. Geological Survey 2019; 30 m resolution), and (6) a feature layer for the presence of canals (USGS 2019), which are abundant throughout Miami-Dade County. The land cover, canopy cover, and impervious surface layers were aggregated to a resolution of 100 m to increase computational efficiency.

Landscape variables were optimized with pairwise resistance distances calculated in Circuitscape (Shah and McRae 2008) using default 'ResistanceGA' parameters and the D_{ps} genetic distance metric. All models were run twice to confirm similar results, as this is a stochastic process. After optimizing each surface independently with single-surface optimization, we ran multi-surface optimization pairing the top variable based on AIC_c (AIC corrected for sample size) with all other individual variables. We then conducted a bootstrap analysis to identify which combination of variables (single or multi-surface) was chosen most often as the top resistance surface explaining the genetic variation. This multi-surface analysis was only conducted for *B. vittatus*, as *A. picticauda* revealed no support for any spatial model (i.e., the null model was best supported).To further investigate each species' affinity for different landscape types, we extracted land cover data at all unique localities using the 10 m land cover layer included in the ResistanceGA analysis. The localities in this analysis included all capture locations for individuals in this study, as well as all georeferenced Miami-Dade County occurrences recorded in the GBIF (GBIF.org 2021a, b) and EDDMaps (EDDMaps 2021) databases. We then performed a contingency analysis to see if land cover associations differed between the two species. To account for spatial autocorrelation of the locality data, we followed recommendations in Cerioli (2002) to subsample our point datasets until spatial autocorrelation was no longer detected. We thinned each species dataset in increments of 50 m using the spThin R package (Aiello-Lammens et al. 2015; version 0.2.0) until there was no spatial autocorrelation based on a Join Count Test calculated using the spdep R package (Bivand & Wong 2018; verion 1.3–3). We then performed the contingency analysis on these thinned datasets, including only land cover classes that had ≥ 10 occurrences for at least one species. To further investigate which land cover types were significantly used by one species over another, we calculated 95% confidence intervals around the difference in proportion of each species' occurrences that were found in each land cover type. Cases where the confidence intervals do not overlap zero indicate a significant difference.

Results

Genetic diversity

Observed heterozygosity (H_o) was significantly lower than expected for both *A. picticauda* ($p < 0.0001$) and *B. vittatus* ($p < 0.0001$) throughout Miami-Dade County. *Agama picticauda* had an H_o of 0.31 and an inbreeding coefficient (F_{IS}) of 0.18, while *B. vittatus* had a lower H_o of 0.20 and a much higher F_{IS} of 0.38. Expected heterozygosity (H_e) was relatively similar for both species (*A. picticauda* = 0.38; *B. vitattus* = 0.31). These results suggest small, inbred populations for both species (Short and Petren 2011a; Mdladla et al. 2018), with *B. vittatus* exhibiting much lower genetic diversity and higher levels of inbreeding compared to *A. picticauda*.

Population structure

IBD and spatial autocorrelation

Isolation by distance (IBD) was not a significant predictor of *A. picticauda*'s overall genetic structure ($p = 0.83$); however, this varied across spatial scales. Using 1 km distance classes, the Mantel correlogram analyses revealed significant positive spatial autocorrelation at small distances around 2–3 km and at mid-high distances around 25–30 km (Fig. 2a). Negative spatial autocorrelation (i.e., individuals closer in distance being less genetically related) was found at mid-range distances of 12–18 km and at high distances of 37–38 km. When assessed using larger 5 km distance classes, there was only significant spatial autocorrelation at small < 5 km distances (Fig. 2b).

For the *B. vittatus* population, IBD was a significant predictor of overall genetic structure (Mantel $r = 0.17$, $p = 0.004$). Although not a strong correlation, this indicates greater spatial structure in *B. vittatus* compared with *A. picticauda*. The degree, and even direction, of spatial autocorrelation in *B. vittatus* genetic structure varied across spatial scales. At small distances ≤ 10 km there was significant positive spatial autocorrelation (Fig. 2c and d). However, at mid-range distances of 17–30 km there was significant negative autocorrelation.

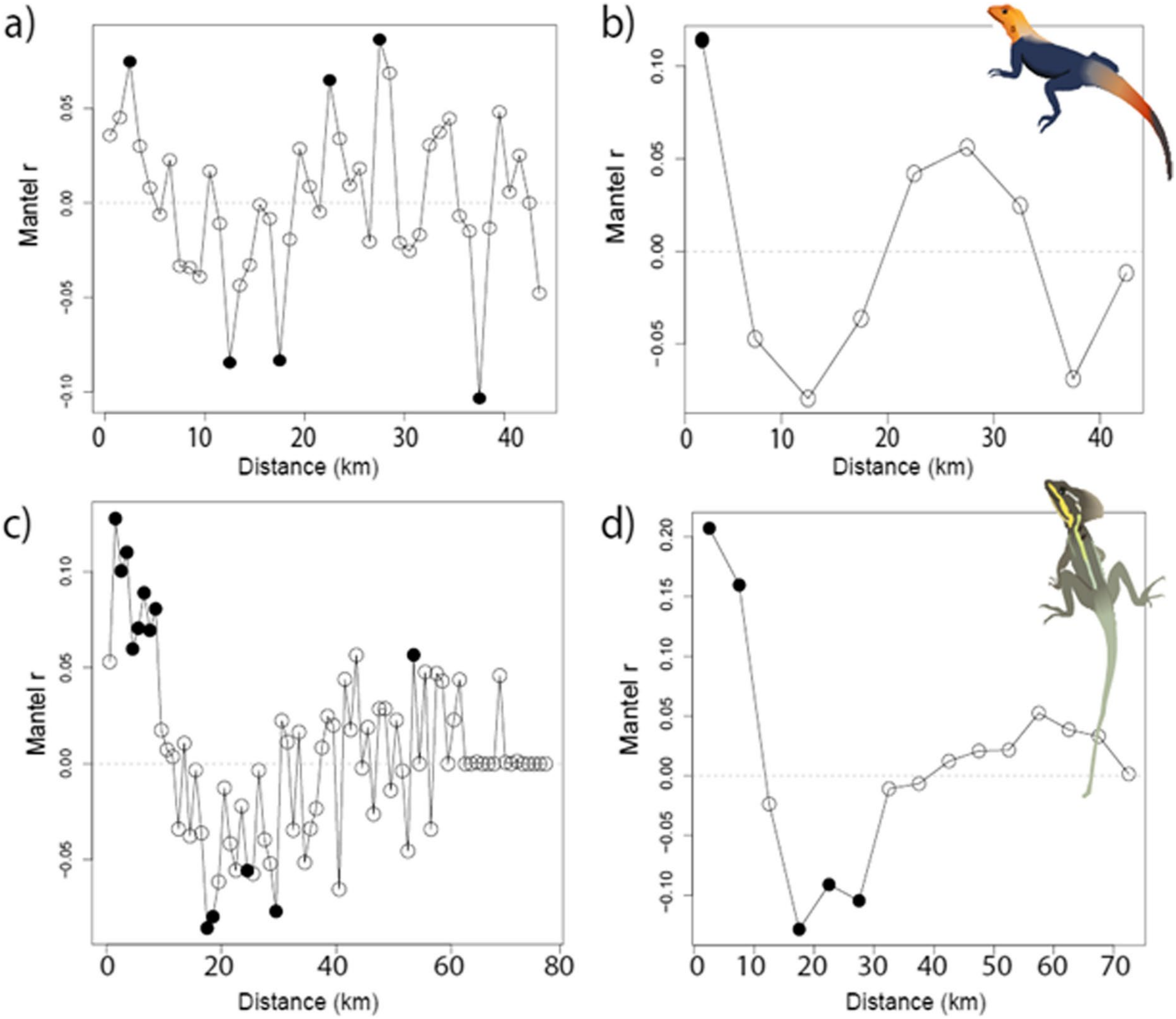

Fig. 2 Mantel correlogram results for *Agama picticauda* using 1 km (**a**) and 5 km (**b**) distance classes, and the same for *Basiliscus vittatus* in (**c**) and (**d**), where black circles indicate significant autocorrelation

STRUCTURE and conStruct analyses

The STRUCTURE analysis indicated K = 2 as the optimal number of clusters for *A. picticauda* based on the Evanno method. However, given that the Evanno method cannot assess when K = 1, it is suggested to also examine the likelihood distribution (L[K]; Evanno et al. 2005), and in this case it is important to note that L(K) for K = 1 is nearly as high as for K = 2 (Figure S2). At K = 2, only two individuals were separated into the second cluster, and K = 3 separated the remaining 43 individuals into relatively equal-sized groups (Fig. 3). For *B. vittatus*, the STRUCTURE analyses also revealed an optimal value of K = 2, but with a nearly equal split in population assignment (Fig. 4).

The conStruct analysis for *A. picticauda* showed minimal difference in model performance between spatial and non-spatial models (Figure S3a), except for K = 2, where the spatial model significantly outperformed the non-spatial model. In agreement with the STRUCTURE analysis, K = 2 appeared to be the best value of K for *A. picticauda*, as predictive accuracy showed little improvement after this value (Figure S3a). However, subsequent additional clusters showed substantial contribution to the covariance as

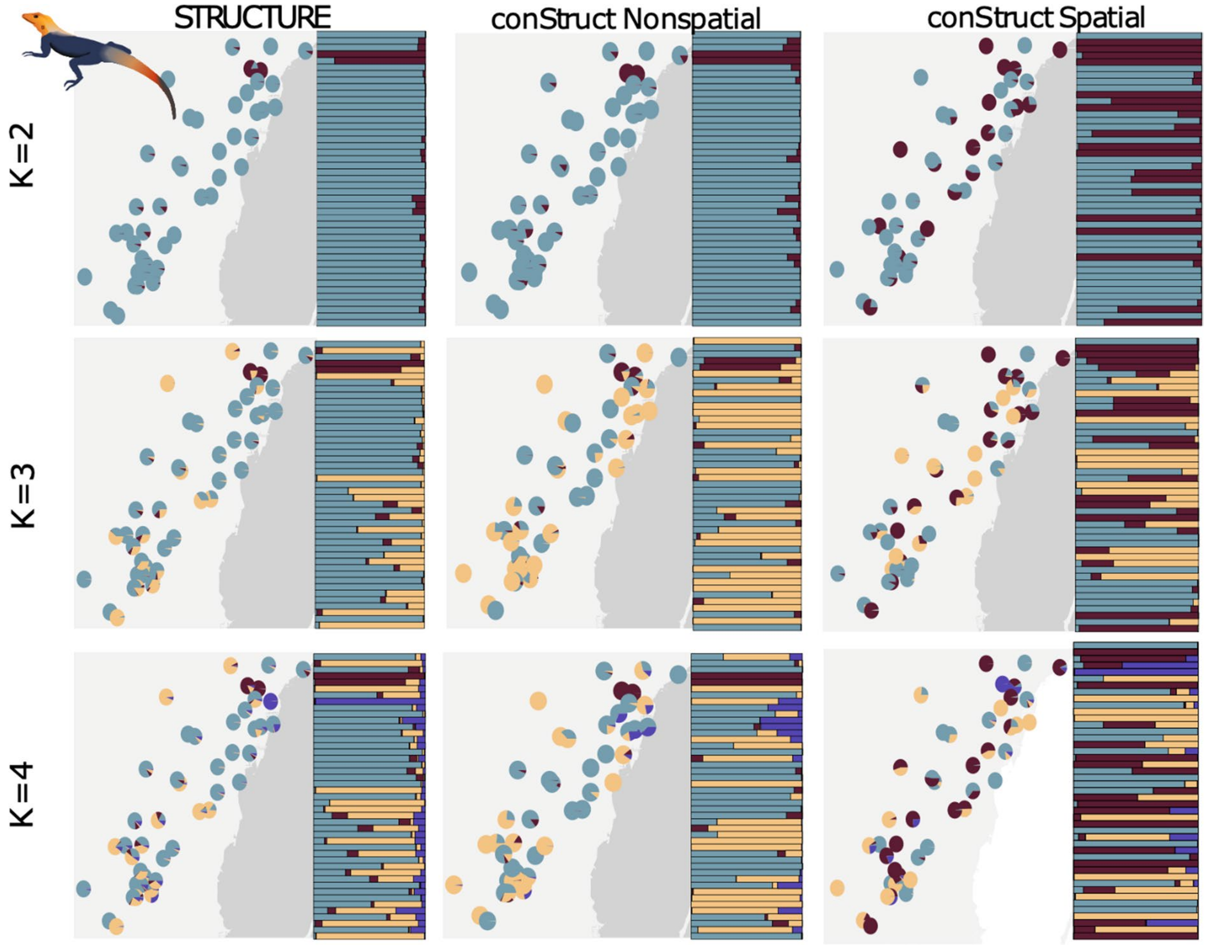

Fig. 3 *Agama picticauda* population assignments resulting from the STRUCTURE and conStruct non-spatial and spatial analyses across K=2–4 number of clusters. STRUCTURE analysis revealed K=2 as the optimal number of clusters, which is corroborated by the conStruct spatial model, while the conStruct non-spatial model showed the largest improvement in predictive accuracy at K=3. Note that across all models there is minimal spatial clustering of population assignments compared to *B. vittatus* in Fig. 4

K increased for both the spatial and non-spatial models (Figure S4a and b), suggesting more than two clusters may better define this population. The cluster assignments for the non-spatial model were the same as the STRUCTURE results, assigning the same two individuals to their own group at K=2, and for K=3 the remaining individuals were split relatively evenly into two groups (Fig. 3). However, the spatial model showed much higher mixed assignments at K=2.

For *B. vittatus*, the conStruct analysis indicated support for the spatial model over the non-spatial model across all values of K (Figure S3b), again indicating greater population structure in this species relative to *A. picticauda*. The biggest improvement in predictive accuracy occurred from K=1 to K=2, and performance increased very little after K=4. When examining the cluster contributions, for the spatial model there was little contribution of clusters > 4 (Figure S4c), and the non-spatial model showed hardly any additional contribution to covariance for layers > 2, until it reached high values of K=9 and 10 (Figure S4d). The cluster assignments for the non-spatial model were similar to the STRUCTURE model for K=2 and 3, with more variance at K=4. While cluster assignments were variable across all models, there appeared to be slight structure along the latitudinal gradient (Fig. 4).

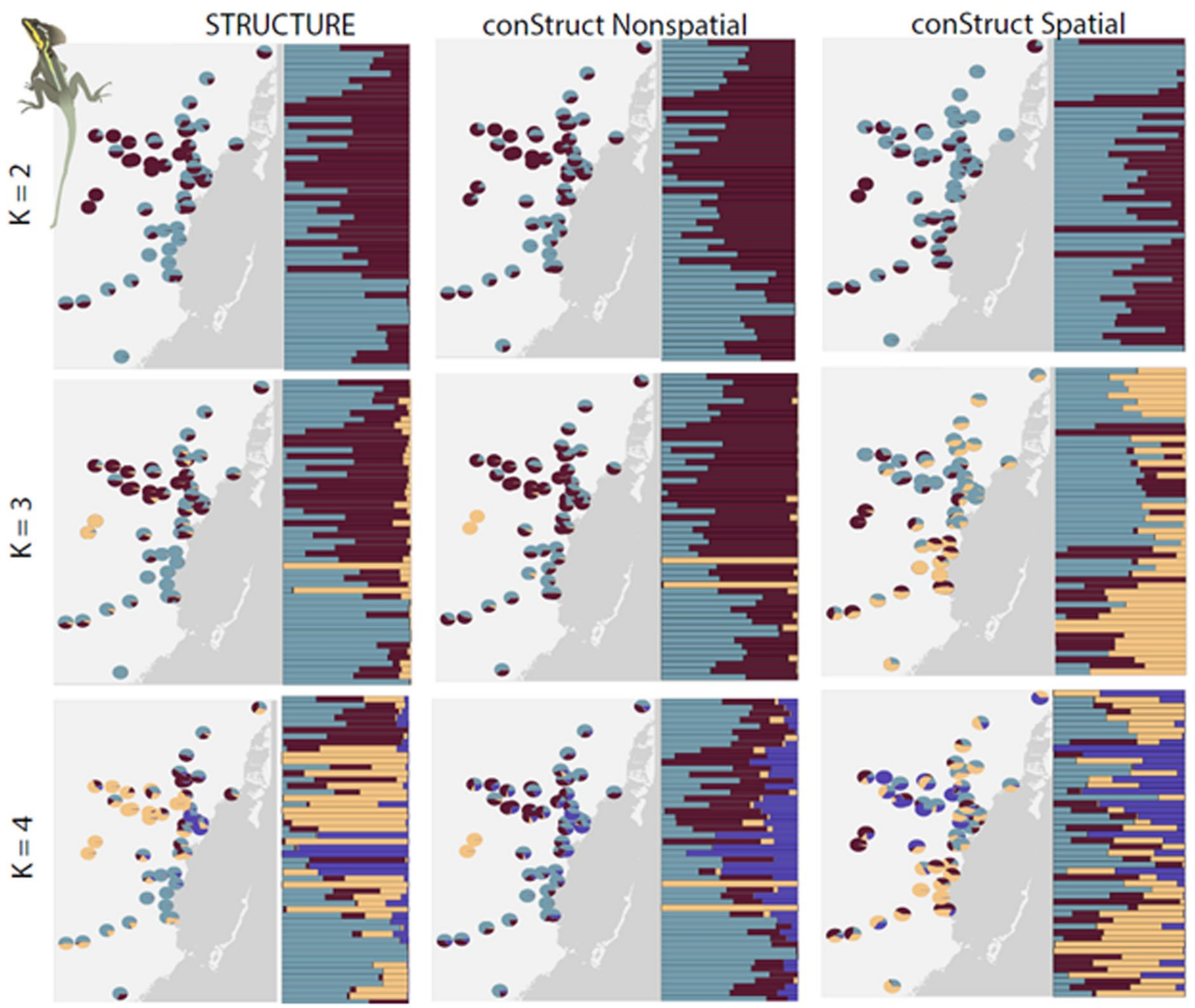

Fig. 4 *Basiliscus vittatus* population assignments resulting from the STRUCTURE and conStruct non-spatial and spatial analyses across K=2–4 number of clusters. STRUCTURE analysis revealed K=2 as the optimal number of clusters, while the conStruct models showed little improvement after K=4, with the spatial model showing higher predictive accuracy than the non-spatial model. Note that across all models there is higher spatial clustering of population assignments compared to *A. picticauda* in Fig. 3

sPCA analyses

Global structure in *A. picticauda* was only marginally supported ($p=0.07$) based on sPCA analysis, with a slight latitudinal structure seen when mapping these results (Fig. 5a–c). In contrast, sPCA analysis for *B. vittatus* identified significant global structure ($p=0.02$). The first global axis shows strong genetic differentiation between the mid-latitude group of individuals and those to the north and south (Fig. 5d), similar to the patterns seen in the population structure analyses (Fig. 4). The second global axis shows a clear east to west break in genetic connectivity (Fig. 5e), and plotting both axes together shows the mid-latitude group is genetically different from those to the north and south, and that within the mid-latitude group there is a gradual east to west genetic differentiation (Fig. 5f).

Landscape influence on population structure

The ResistanceGA analysis for *A. picticauda* revealed the intercept-only null model was best supported, showing no support for any spatial model,

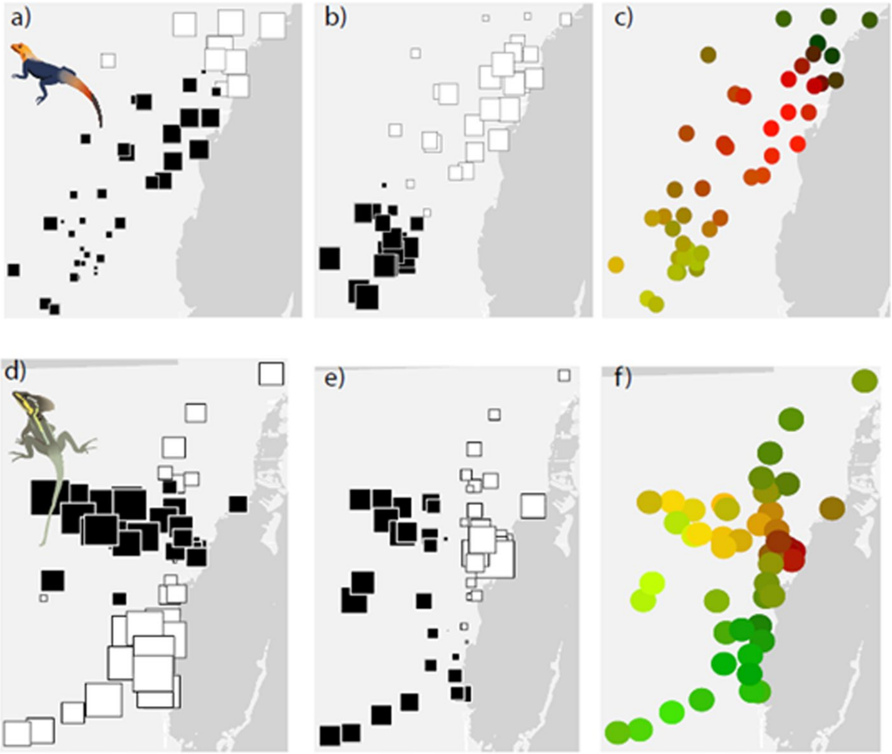

Fig. 5 First and second global axis scores from the sPCA analysis for *Agama picticauda* (**a**, **b**) and *Basiliscus vittatus* (**d**, **e**), respectively, followed by color plots combining the first two axes for *A. picticauda* (**c**) and *B. vittatus* (**f**). Larger squares represent higher genetic differentiation between sites of the opposite color, such that locations with large white squares are well differentiated from large black squares, while small squares represent sites with less genetic differentiation. Similar colors in c and f represent genetic similarity on a red-green color spectrum. Spatial genetic structure in *B. vittatus* has significant support ($p = 0.02$) while spatial structure in *A. picticauda* is only marginally supported ($p = 0.07$). This can be visualized in the overall larger size of squares for *B. vittatus* compared to *A. picticauda*

thus corroborating previous analyses suggesting that there is little spatial structure within this population (Table 1). In contrast, resistance surface optimization for *B. vittatus* revealed that canopy cover was the best predictor of genetic variation (Table 2), with lower resistance assigned to areas with lower percentages of canopy cover (Figure S5). Canopy cover was also the only variable that performed better than a Euclidean distance model.

The contingency analysis revealed significant differences in land cover association between the two species ($p < 0.001$, Fig. 6). The biggest

Table 1 *Agama picticauda* model selection results for resistance surface optimization

Surface	AIC$_c$	ΔAIC$_c$	Marginal R^2	Conditional R^2	Log liklihood
Null	−6628.96	0	0	0.417	3315.529
Distance	−6627.95	1.02	0.0076	0.423	3316.116
Roads	−6627.43	1.53	0.0256	0.435	3317.007
Canals	−6626.48	2.49	0.00552	0.419	3316.531
Traffic volume	−6625.71	3.26	0.0307	0.438	3317.353
Urbanization	−6624.82	4.15	0.0292	0.457	3316.907
Canopy	−6624	4.96	0.023	0.435	3316.5
Land cover	−6589.49	39.48	0.0854	0.491	3320.458

Highest support for the null model conforms with other evidence for lack of spatial structure

Table 2 *Basiliscus vittatus* model selection results for resistance surface optimization

Canopy cover was the most important variable for describing population structure in this species, with greater movement through areas with open canopy

Surface	AIC$_c$	ΔAIC$_c$	Marginal R^2	Conditional R^2	Log liklihood
Canopy	− 7441.2	0	0.313	0.532	3725.056
Distance	− 7432.01	9.19	0.266	0.474	3718.134
Roads	− 7429.94	11.26	0.263	0.472	3718.237
Canals	− 7429.31	11.90	0.263	0.472	3717.92
Traffic volume	− 7429.16	12.04	0.258	0.46	3719.034
Urbanization	− 7427.64	13.56	0.27	0.478	3718.274
Land cover	− 7398.69	42.51	0.306	0.503	3723.847
Null	− 7235.42	205.78	0	0.141	3618.754

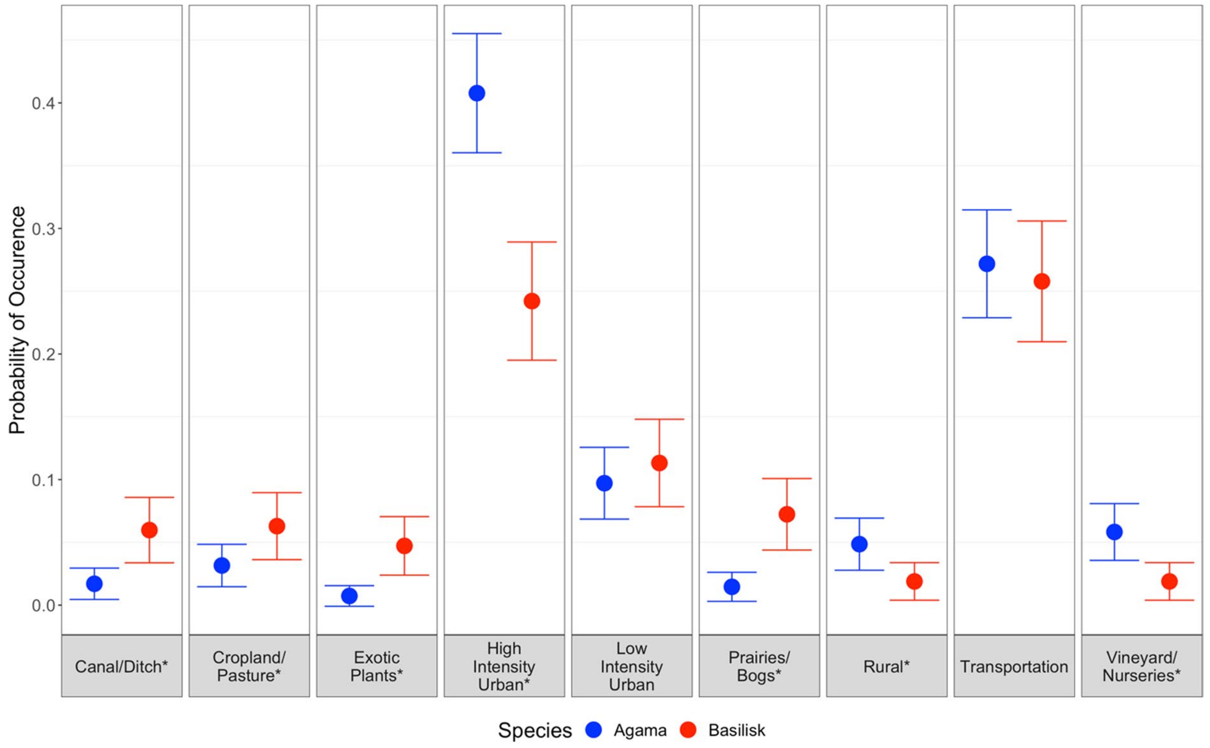

Fig. 6 Percentage of each species' occurrences found in each land cover type (only showing categories with ≥ 10 occurrences for at least one species). Error bars represent 95% confidence intervals, with * indicating significant differences between species' habitat associations. The localities in this analysis included all capture locations in this study as well as all georeferenced Miami-Dade County occurrences recorded in the GBIF and EDDMaps databases

difference in landscape association was in relation to urbanized land cover, where 41% of *A. picticauda* localities were from high intensity urban sites compared to only 24% of *B. vittatus* localities.

Discussion

Understanding invasion patterns via population genetic structure and landscape connectivity for established non-native populations serves as vital information for invasive species management (Kulhanek et al. 2011; Glen et al. 2013; Mačić et al. 2018). In this study we applied city-wide individual-based sampling in a multi-species comparative framework with thorough SNP genotyping, providing novel findings on the movement ecology of non-native species in a global hotspot for biological invasions. Our results show contrasting levels of genetic spatial structure between two non-native lizard species, with consistently higher levels of spatial structure in *B. vittatus* compared to *A. picticauda* across all analyses (IBD, conStruct, sPCA, ResistanceGA). This is mirrored by differences in habitat affinities, with *B. vittatus* more common near canals while *A. picticauda* is more common in high intensity urban habitat. *Agama picticauda*'s affinity for highly urbanized areas is the pattern of habitat association most expected to lead to human-aided dispersal (Bullock et al. 2018). Further, lack of isolation by distance (as seen in *A. picticauda*) is commonly found in invasive species in which human-mediated dispersal plays a prominent role in spread across the invaded range (Kelager et al. 2013). Perhaps the clearest support for human-aided dispersal is that the two most closely related *A. picticauda* individuals were found at sites that are ~ 30 km apart but connected by linear transportation routes (US 1 and the Metrorail). Still, while we view human-mediated dispersal as the most likely explanation of the genetic structure (or lack thereof) in *A. picticauda*'s invaded range, we cannot rule out the possibility that *A. picticauda* are so well adapted to Miami's urban environment that they are able to disperse themselves rapidly across such distances, experiencing essentially no barriers to gene flow. In this vein, *A. picticauda*'s ecological role as a rock-specialist may provide pre-adaptation to the urban environment due to similarities between anthropogenic impervious surfaces and rock.

It is important to note that these differences in genetic spatial structure between *A. picticauda* and *B. vittatus* occur despite the two species having similar invasion histories, body size, and trophic positions (i.e., generalist predators; Krysko et al. 2019), lending additional support to the prediction that their contrasting habitat affinities play an important role in dispersal patterns. However, there are other differences between the two species (e.g., continent of origin) that cannot be ruled out as influencing their dispersal patterns. Still, the evidence presented here supports the idea that a species' ecological characteristics shape its invasion patterns and such information should be taken into account when making management decisions. It is also important to note that even *B. vittatus* does not follow a continuous pattern of increased genetic differentiation from the known sites of introduction. This implies that there have either been more introduction events than previously thought, as is the case for nearly all other genetic studies of non-native reptiles in South Florida (Kolbe et al. 2004, 2007; Fieldsend et al. 2021), human-aided dispersal is spreading individuals of both species further than they would disperse on their own, and/or landscape features of the invaded range play a role in shaping spatial structure.

Variable dispersal patterns

All population structure and landscape analyses present contrasting evidence for how these two species have dispersed throughout the same invaded range. Previous landscape genetic work has demonstrated differing movement patterns for closely related but ecologically distinct invertebrates (Engler et al. 2014), and here we present the first evidence of this in non-native vertebrate species. One species, *A. picticauda*, showed insignificant or marginal spatial structure across Miami-Dade County for all analyses, with the exception of significant positive spatial autocorrelation at local (< 5 km) scales. In contrast, *B. vittatus* showed significant spatial structure across all analyses. The land cover association analysis emphasizes that the contrasting ecological characteristics of these two species may be the reason they exhibit different dispersal patterns. In particular, the finding that *A. picticauda* are found significantly more often in highly urbanized sites, increasing their susceptibility to human-aided dispersal, may explain the lack of spatial genetic signal in this species.

Agama picticauda

The lack of spatial structure seen in this study is also reflected in *A. picticauda*'s native range, where IBD was insignificant both range wide and within identified subpopulations (Krishnan et al. 2019). In its native range, it is believed the lack of structure is due to long-range dispersal events via hitchhiking on vehicles, leading to close genetic relatedness between distant locations (Krishnan et al. 2019). This hypothesis is corroborated by another study on the Miami-Dade County *A. picticauda* population based on locality data in the Homestead area, suggesting individuals are commonly dispersing via the railway system, in particular hitchhiking on plant exports as they were often found near nurseries (Gray 2020). As mentioned above, the two most closely related *A. picticauda* individuals were found at sites ~ 30 km apart that are connected by a linear transportation route. In terms of habitat associations, over half of *A. picticauda* localities in Miami-Dade County were from urbanized sites (mostly categorized as high intensity urban), and over a quarter (27%) were found at transportation-associated sites. This further emphasizes the likelihood that the lack of genetic structure in the Miami-Dade *A. picticauda* population is due to human-aided dispersal throughout the invaded range.

The population structure analyses supported K = 2 as the optimal number of clusters, and interestingly the two individuals that both the STRUCTURE and conStruct non-spatial model separated into their own cluster were both found on the University of Miami (UM) Coral Gables campus. While previous genetic work suggests that the Miami-Dade County *A. picticauda* populations come from a single source population (Nunez et al. 2016), sampling was limited to the area surrounding the introduction site in Homestead. The population structure results presented here may indicate that the UM campus population is the result of a separate introduction event. This would also not be the first time a non-native lizard species was introduced on the UM Coral Gables campus, where the Cuban knight anole (*Anolis equestris*) was believed to have been first introduced in 1952 (King and Krakauer 1966) and is now spread across 12 Florida counties (Krysko et al. 2011). Alternatively, it is possible that the original population introduced in 1976 was not truly extirpated as previously thought, and this northern genetic cluster reflects individuals from that first introduction near Miami International Airport.

Basiliscus vittatus

In contrast to *A. picticauda*, *B. vittatus* did show a significant IBD relationship over the entire Miami-Dade population, along with positive spatial autocorrelation at short distances and negative autocorrelation at mid-distance classes, which is indicative of restricted gene flow (Peakall et al. 2003) and evidence that the genetic structure is non-random. The STRUCTURE and conStruct analyses show a general latitudinal structure pattern (Fig. 4), however the east–west cluster at mid-latitudes appears to diverge from those to the north and south, reflected in the sPCA results (Fig. 6). This cluster at mid-latitudes is grouped around the original introduction site for *B. vittatus*, which suggests these are individuals dispersing from the original point of origin.

The spatial structure outside of this cluster is not as clear. The ResistanceGA analyses revealed canopy cover as the best predictor of spatial genetic structure (also the only variable explaining genetic variation better than Euclidean distance), giving low percentages of canopy cover the lowest resistance (Figure S5). The average percent canopy cover of all known *B. vittatus* localities was 28%, with a median of 23%, corroborating the ResistanceGA analyses and previous research within the species' native range, where *B. vittatus* was consistently found in more open canopy habitats (Brusch et al. 2016). In addition, 70% of the *B. vittatus* individuals captured for this study were found at or near (within 100 m) of a canal, which generally possess low canopy cover, being open water man-made structures running through urbanized areas. However, even though *B. vittatus* shows high fidelity to canals, the presence of canals was not shown to be a strong predictor of genetic variation (Table 2), suggesting canals may not be their main mode of dispersal throughout South Florida as previously postulated (Krysko et al. 2006; Meshaka 2011). One potential explanation is that *B. vittatus* move along canals at local scales, but their distribution at the county scale is shaped by other factors and canals are not modes of dispersal for long distances. Moreover, while *B. vittatus* shows fidelity to canals, the individuals found most often near the water's edge are juveniles, while adults spend more time further away from the water (Hirth 1963; Laerm 1974), suggesting that adults may not disperse via water bodies. The land cover association analyses found that this species was captured at transportation-associated sites 25% of the time, suggesting *B. vittatus* may also be subject to long distance translocations via human-aided dispersal, which may be the reason we find a lack of continuous spatial structure across the entire range.

Evidence and implications of human-aided dispersal

Human-aided dispersal is rewiring species spatial networks across the globe (Bullock et al. 2018), evident in both native (Perrigo et al. 2012; Valls et al. 2016) and invasive populations (Suarez et al. 2001; Medley et al. 2015; Arredondo et al. 2018), as postulated in this study. Human-aided dispersal within the invaded range complicates the reconstruction of invasion history, which is important for invasive species management (Cristescu 2015). Information on modes of dispersal is also vital to guide managers towards target areas that are identified as facilitators of spread. This study suggests that humans are one of those main facilitators. Studies demonstrating a human role in dispersing non-natives throughout the invaded range have primarily been conducted on plant (Rauschert et al. 2017; Arredondo et al. 2018) and invertebrate species (Medley et al. 2015; Robinet et al. 2016), and very few have investigated this in invasive vertebrates, which one would assume are less likely to be human-dispersed due to their size and conspicuousness. Examples of human-aided dispersal of vertebrates include wild pigs (*Sus scrofa*) in California, which are assumed to be spread as a result of hunting-related activities (Tabak et al. 2017), tropical house geckos (*Hemidactylus mabouia*) in Miami, which exhibit similar small-scale genetic structure likely accompanied by long-distance human-aided dispersal across the landscape (Short and Petren 2011a), and house sparrows (*Passer domesticus*) in Kenya, for which trucks and railways are theorized to be the leading cause of range expansion and population admixture throughout the invaded range (Schrey et al. 2014).

In this study, the lack of positive spatial autocorrelation at all but the shortest distances for both *A. picticauda* and *B. vittatus*, and their common association with transportation-related habitats (Fig. 6) strongly suggests that hitchhiking on vehicles is a main mode of long-range post-invasion dispersal. For *A. picticauda* especially, all lines of evidence indicate random population structure and high fidelity to urbanized areas, emphasizing that human-aided dispersal is likely the main mode of spread for this species, although further studies are needed to support this hypothesis. To prevent future spread of these species in South Florida and any future introduction sites, targeting transportation routes may be important for management action as additional evidence suggests both species may be of greater harm to natural ecosystems than previously thought (Gioeli and Johnson 2020). This targeting could consist of inspecting transportation hubs for new occurrences followed by removal measures, using network models to prioritize which transportation hubs are most important to search (Hulme 2009). Overall, this work demonstrates how landscape genetic analyses can be used to study the spatial structure and movement ecology of non-native vertebrate populations, which will be vital as biological invasions pose increasing detrimental impacts to native ecosystems.

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Author's contribution C.C.M. designed the study, collected and analyzed the data, and led the writing of the manuscript. C.A.S. provided conceptual guidance to the research and contributed to analysis and manuscript preparation. All authors read and approved the final manuscript.

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Data availability Raw sequence reads (fastq files) along with location and metadata for each specimen are available on Dryad at https://doi.org/10.5061/dryad.1jwstqk43.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

References

Aiello-Lammens ME, Boria RA, Radosavljevic A, Vilela B, Anderson RP (2015) spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. Ecography 38:541–545. https://doi.org/10.1111/ecog.01132

Arredondo TM, Marchini GL, Cruzan MB (2018) Evidence for human-mediated range expansion and gene flow in an invasive grass. Proc R Soc B 285:20181125. https://doi.org/10.1098/rspb.2018.1125

Balkenhol N, Cushman SA, Waits LP, Storfer A (2015) Current status, future opportunities, and remaining challenges in landscape genetics. In: Balkenhol N, Cushman SA, Storfer AT, Waits LP (eds) Landscape genetics. John Wiley & Sons Ltd, Chichester, pp 247–256

Bartlett RD, Bartlett PP (1999) A field guide to Florida reptiles and amphibians. Gulf Publishing, Houston, TX

Bivand R, Wong D (2018) Comparing implementations of global and local indicators of spatial association. TEST 27(3):716–748. https://doi.org/10.1007/s11749-018-0599-x

Bowcock AM, Ruiz-Linares A, Tomfohrde J, Minch E, Kidd JR, Cavalli-Sforza LL (1994) High resolution of human evolutionary trees with polymorphic microsatellites. Nature 368:455–457. https://doi.org/10.1038/368455a0

Bradburd G (2019) conStruct: models spatially continuous and discrete population genetic structure. R package version 1.0.4. https://CRAN.R-project.org/package=conStruct

Bradbury PJ, Zhang Z, Kroon DE et al (2007) TASSEL: software for association mapping of complex traits in diverse samples. Bioinformatics 23:2633–2635. https://doi.org/10.1093/bioinformatics/btm308

Brusch GA, Taylor EN, Whitfield SM (2016) Turn up the heat: thermal tolerances of lizards at La Selva, Costa Rica. Oecologia 180:325–334. https://doi.org/10.1007/s00442-015-3467-3

Bullock JM, Bonte D, Pufal G et al (2018) Human-mediated dispersal and the rewiring of spatial networks. Trends Ecol Evol 33:958–970. https://doi.org/10.1016/j.tree.2018.09.008

Capinha C, Seebens H, Cassey P et al (2017) Diversity, biogeography and the global flows of alien amphibians and reptiles. Divers Distrib 23:1313–1322. https://doi.org/10.1111/ddi.12617

Cerioli A (2002) Testing mutual independence between two discrete-valued spatial processes: a correction to pearson chi-squared. Biometrics 58:888–897

Combs M, Puckett EE, Richardson J et al (2018) Spatial population genomics of the brown rat (*Rattus norvegicus*) in New York City. Mol Ecol 27:83–98. https://doi.org/10.1111/mec.14437

Crawford KM, Whitney KD (2010) Population genetic diversity influences colonization success. Mol Ecol 19:1253–1263. https://doi.org/10.1111/j.1365-294X.2010.04550.x

Cristescu ME (2015) Genetic reconstructions of invasion history. Mol Ecol 24:2212–2225. https://doi.org/10.1111/mec.13117

Earl DA, vonHoldt BM (2012) STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. Conserv Genet Resour 4:359–361. https://doi.org/10.1007/s12686-011-9548-7

EDDMapS (2021) Early detection & distribution mapping system. The University of Georgia—Center for Invasive Species and Ecosystem Health. Available online at http://www.eddmaps.org/.

Enge KM, Krysko KL, Talley BL (2004) Distribution and ecology of the introduced African rainbow lizard, *Agama agama africana* (Sauria: Agamidae). Florida Florida Scientist 67(4):303–310

Engler JO, Balkenhol N, Filz KJ et al (2014) Comparative landscape genetics of three closely related sympatric hesperid butterflies with diverging ecological traits. PLoS ONE 9:e106526. https://doi.org/10.1371/journal.pone.0106526

Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals using the software structure: a simulation study. Mol Ecology 14:2611–2620. https://doi.org/10.1111/j.1365-294X.2005.02553.x

FDOT (2020) Annual average daily traffic. https://ftp.fdot.gov/file/d/FTP/FDOT/co/planning/transtat/gis/shapefiles/aadt.zip.

Fieldsend TW, Krysko KL, Sharp P, Collins TM (2021) Provenance and genetic diversity of the non-native geckos Phelsuma grandis Gray 1870 and Gekko gecko (Linnaeus 1758) in southern Florida, USA. Biol Invasions 23:1649–1662. https://doi.org/10.1007/s10530-021-02463-1

GBIF.org (2021a) GBIF occurrence download https://doi.org/10.15468/dl.xsktdp

GBIF.org (2021b) GBIF occurrence download https://doi.org/10.15468/dl.ujtbkh

Gioeli KT, Johnson SA (2020) Peters's Rock Agama in Florida. https://edis.ifas.ufl.edu/uw476. Accessed 2 Mar 2021

Glen AS, Pech RP, Byrom AE (2013) Connectivity and invasive species management: towards an integrated landscape approach. Biol Invasions 15:2127–2138. https://doi.org/10.1007/s10530-013-0439-6

Goslee SC, Urban DL (2007) The ecodist package for dissimilarity-based analysis of ecological data. J Statistical Software 22:1–19. https://doi.org/10.18637/jss.v022.i07

Goudet J, Jombart T (2020) Hierfstat: estimation and tests of hierarchical F-statistics. R package version 0.5–7. https://CRAN.R-project.org/package=hierfstat

Gray RJ (2020) Exotic hobos: release, escape, and potential secondary dispersal of African red-headed agamas (*Agama picticauda* PETERS, 1877) through the Florida railway systems. bioRxiv 2020.05.11.089649. https://doi.org/10.1101/2020.05.11.089649

Hirth H (1963) The ecology of two lizards on a tropical beach. Ecol Monogr 33:80–112

Hulme PE (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. J Appl Ecol 46:10–18. https://doi.org/10.1111/j.1365-2664.2008.01600.x

Jombart T (2008) adegenet: a R package for the multivariate analysis of genetic markers. Bioinformatics 24:1403–1405. https://doi.org/10.1093/bioinformatics/btn129

Kawula R, Redner J (2018). Florida land cover classification system. Final report to the state wildlife grants program, Florida fish and wildlife conservation commission.

Kelager A, Pedersen JS, Bruun HH (2013) Multiple introductions and no loss of genetic diversity: invasion history of Japanese Rose, Rosa rugosa, in Europe. Biol Invasions 15:1125–1141. https://doi.org/10.1007/s10530-012-0356-0

King FW, Krakauer T (1966) The exotic herpetofauna of southeast Florida. Quarterly J Florida Academy Sci 29:144–154

Kolbe J, Glor R, Schettino L et al (2004) Genetic variation increases during biological invasion by a Cuban lizard. Nature 431:177–181. https://doi.org/10.1038/nature02807

Kolbe JJ, Glor RE, Schettino LR et al (2007) Multiple sources, admixture, and genetic variation in introduced Anolis lizard populations: Anolis lizard introductions. Conserv Biol 21:1612–1625. https://doi.org/10.1111/j.1523-1739.2007.00826.x

Krishnan S, Ofori-Boateng C, Fujita MK, Leaché AD (2019) Geographic variation in West African *Agama picticauda* : insights from genetics, morphology and ecology. Afr J Herpetol 68:33–49. https://doi.org/10.1080/21564574.2018.1509139

Krysko KL, Burgess JP, Rochford MR, Gillette CR, Cueva D, Enge KM et al (2011) Verified non-indigenous amphibians and reptiles in Florida from 1863–2010: outlining the invasion process and identifying invasion pathways and stages. Zootaxa 3028:1–64

Krysko KL, Enge KM, Moler PE (2019) Amphibians and reptiles of Florida. University Press of Florida, Gainesville

Krysko KL, Seitz J, Townsend JH, Enge K (2006) The introduced brown basilisk (*Basiliscus vittatus*) in Florida. Iguana 13:24–30

Krysko KL, Somma LA, Smith DC et al (2016) New verified nonindigenous amphibians and reptiles in Florida, 1976 through 2015, with a summary of over 152 years of introductions. Reptiles & Amphibians 23:110–143. https://doi.org/10.17161/randa.v23i2.14119

Kulhanek SA, Ricciardi A, Leung B (2011) Is invasion history a useful tool for predicting the impacts of the world's worst aquatic invasive species? Ecol Appl 21:189–202. https://doi.org/10.1890/09-1452.1

Laerm J (1974) A functional analysis of morphological variation and differential niche utilization in basilisk lizards. Ecology 55:404–411. https://doi.org/10.2307/1935228

Landguth EL, Cushman SA, Murphy MA, Luikart G (2010) Relationships between migration rates and landscape resistance assessed using individual-based simulations: migration rates and landscape resistance. Mol Ecol Resour 10:854–862. https://doi.org/10.1111/j.1755-0998.2010.02867.x

LaPoint S, Balkenhol N, Hale J et al (2015) Ecological connectivity research in urban areas. Funct Ecol 29:868–878. https://doi.org/10.1111/1365-2435.12489

Li Y, Zhang X-X, Mao R-L et al (2017) Ten years of landscape genomics: challenges and opportunities. Front Plant Sci 8:2136. https://doi.org/10.3389/fpls.2017.02136

Lovell RSL, Blackburn TM, Dyer EE, Pigot AL (2021) Environmental resistance predicts the spread of alien species. Nat Ecol Evolution. https://doi.org/10.1038/s41559-020-01376-x

Low G, Chattopadhyay B, Garg K et al (2018) Urban landscape genomics identifies fine-scale gene flow patterns in an avian invasive. Heredity 120:138–153. https://doi.org/10.1038/s41437-017-0026-1

Lu F, Lipka AE, Glaubitz J et al (2013) Switchgrass genomic diversity, ploidy, and evolution: novel insights from a network-based SNP discovery protocol. PLoS Genet 9:e1003215. https://doi.org/10.1371/journal.pgen.1003215

Ma L, Cao L-J, Hoffmann AA et al (2020) Rapid and strong population genetic differentiation and genomic signatures of climatic adaptation in an invasive mealybug. Divers Distrib 26:610–622. https://doi.org/10.1111/ddi.13053

Macdonald N, Nugent G, Edge K-A, Parkes JP (2019) Eradication of red deer from Secretary Island, New Zealand: changing tactics to achieve success. New Zealand

Mačić V, Albano PG, Almpanidou V et al (2018) Biological invasions in conservation planning: a global systematic review. Front Mar Sci. https://doi.org/10.3389/fmars.2018.00178

Manel S, Schwartz MK, Luikart G, Taberlet P (2003) Landscape genetics: combining landscape ecology and population genetics. Trends Ecol Evol 18:189–197. https://doi.org/10.1016/S0169-5347(03)00008-9

McCartney-Melstad E, Vu JK, Shaffer HB (2018) Genomic data recover previously undetectable fragmentation effects in an endangered amphibian. Mol Ecol 27:4430–4443. https://doi.org/10.1111/mec.14892

McRae BH (2006) Isolation by resistance. Evolution 60:1551–1561. https://doi.org/10.1111/j.0014-3820.2006.tb00500.x

Mdladla K, Dzomba EF, Muchadeyi FC (2018) Landscape genomics and pathway analysis to understand genetic adaptation of South African indigenous goat populations. Heredity 120:369–378. https://doi.org/10.1038/s41437-017-0044-z

Medley KA, Jenkins DG, Hoffman EA (2015) Human-aided and natural dispersal drive gene flow across the range of an invasive mosquito. Mol Ecol 24:284–295. https://doi.org/10.1111/mec.12925

Meng JW, Zhu W, He MH et al (2015) High genotype diversity and lack of isolation by distance in the Alternaria solani populations from China. Plant Pathol 64:434–441. https://doi.org/10.1111/ppa.12275

Meshaka WE (2011) A runaway train in the making: the exotic amphibians, reptiles, turtles, and crocodilians of Florida. Monograph 1. Herpetol Conserv Biol 6:1–101

Moore JA (2019) Agama picticauda (Peter's Rock Agama) Dispersal. Herpetol Rev 50:360

Mothes CC, Stroud JT, Clements SL, Searcy CA (2019) Evaluating ecological niche model accuracy in predicting biotic invasions using South Florida's exotic lizard community. J Biogeogr 46:432–441. https://doi.org/10.1111/jbi.13511

Nuñez LP, Krysko KL, Avery ML (2016) Confirmation of introduced *Agama picticauda* in Florida based on molecular analyses. Bull Florida Museum Nat History 54(9):138–146

Peakall R, Ruibal M, Lindenmayer DB (2003) Spatial autocorrelation analysis offers new insights into gene flow in the Australian bush rat, *Rattus Fuscipes*. Evolution 57:1182–1195. https://doi.org/10.1111/j.0014-3820.2003.tb00327.x

Perrigo AL, Romeralo M, Baldauf SL (2012) What's on your boots: an investigation into the role we play in protist dispersal. J Biogeography 39:998–1003. https://doi.org/10.1111/j.1365-2699.2012.02691.x

Peterman WE (2018) ResistanceGA: An R package for the optimization of resistance surfaces using genetic algorithms. Methods Ecol Evol 9:1638–1647. https://doi.org/10.1111/2041-210X.12984

Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. Genetics 155:945–959. https://doi.org/10.1093/genetics/155.2.945

Rauschert ESJ, Mortensen DA, Bloser SM (2017) Human-mediated dispersal via rural road maintenance can move invasive propagules. Biol Invasions 19:2047–2058. https://doi.org/10.1007/s10530-017-1416-2

Robinet C, Suppo C, Darrouzet E (2016) Rapid spread of the invasive yellow-legged hornet in France: the role of human-mediated dispersal and the effects of control measures. J Appl Ecol 54:205–215. https://doi.org/10.1111/1365-2664.12724

Schrey AW, Liebl AL, Richards CL, Martin LB (2014) Range expansion of house sparrows (Passer domesticus) in Kenya: evidence of genetic admixture and human-mediated dispersal. J Hered 105:60–69. https://doi.org/10.1093/jhered/est085

Shah VB, McRae BH (2008) Circuitscape: a tool for landscape ecology. In: Proceeding of the 7th Python on science conference (eds Varoquaux G, Vaught T, Millman J), pp. 62–66.

Shirk AJ, Cushman SA (2014) Spatially-explicit estimation of Wright's neighborhood size in continuous populations. Front Ecol Evol. https://doi.org/10.3389/fevo.2014.00062

Shirk AJ, Landguth EL, Cushman SA (2017) A comparison of individual-based genetic distance metrics for landscape genetics. Mol Ecol Resour 17:1308–1317. https://doi.org/10.1111/1755-0998.12684

Short KH, Petren K (2011a) Fine-scale genetic structure arises during range expansion of an invasive Gecko. PLoS ONE 6:e26258. https://doi.org/10.1371/journal.pone.0026258

Short KH, Petren K (2011b) Multimodal dispersal during the range expansion of the tropical house gecko Hemidactylus mabouia. Ecol Evol 1:181–190. https://doi.org/10.1002/ece3.18

Sjodin BMF, Irvine RL, Ford AT et al (2020) Rattus population genomics across the Haida Gwaii archipelago provides a framework for guiding invasive species management. Evol Appl 13:889–904. https://doi.org/10.1111/eva.12907

Spinks PQ, Thomson RC, Shaffer HB (2014) The advantages of going large: genome-wide SNPs clarify the complex population history and systematics of the threatened western pond turtle. Mol Ecol 23:2228–2241. https://doi.org/10.1111/mec.12736

Suarez AV, Holway DA, Case TJ (2001) Patterns of spread in biological invasions dominated by long-distance jump dispersal: Insights from Argentine ants. PNAS 98:1095–1100. https://doi.org/10.1073/pnas.98.3.1095

Tabak MA, Piaggio AJ, Miller RS et al (2017) Anthropogenic factors predict movement of an invasive species. Ecosphere 8:e01844. https://doi.org/10.1002/ecs2.1844

U.S. geological survey (2019) NLCD 2016 Impervious surface conterminous United States. Sioux Falls, SD.

USDA forest service (2019) NLCD 2016 Tree canopy cover (CONUS). Salt Lake City, UT

USGS (2019) WMS flowing waters resource. https://gis-mdc.opendata.arcgis.com/datasets/ce5f90fd95d8472d85d8be6b434f890a_0/explore

Valls L, Castillo-Escrivà A, Mesquita-Joanes F, Armengol X (2016) Human-mediated dispersal of aquatic invertebrates with waterproof footwear. Ambio 45:99–109. https://doi.org/10.1007/s13280-015-0689-x

VanWallendael A, Alvarez M, Franks SJ (2020) Patterns of population genomic diversity in the invasive Japanese knotweed species complex. Am J Bot. https://doi.org/10.1101/2020.08.06.226886

Wilson LD, Porras L, Kansas U (1983) The ecological impact of man on the south Florida herpetofauna. University of Kansas, Lawrence. https://doi.org/10.5962/bhl.title.8435

Wright S (1943) Isolation by distance. Genetics 28:114–138