

Dispersal restriction and facilitation in species with differing tolerance to development: A landscape genetics study of native and introduced lizards

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Abstract

Aim: The development of natural habitats into urban land uses has greatly accelerated in the recent past due to human activities. This habitat development disrupts species' natural dispersal processes and can lead to both direct and indirect impacts on dispersal. Whether human activities result in restricted or facilitated dispersal may depend on a species' development tolerance; however, this premise has not been tested. We examined the impact of urbanization and road networks on the dispersal of three lizard species in the context of their development tolerance.

Location: Curaçao.

Methods: To quantify species' development tolerance, we modelled three lizard species abundances at sites based on surrounding landscape development. Using micro-satellite genotypes, we conducted individual-based resistance surface analyses and modelled the effect of habitat development on genetic admixture to assess indirect dispersal restriction and facilitation. We explored direct facilitation of dispersal using network analysis of mitochondrial haplotypes.

Results: *Phyllodactylus martini*, a native gecko species, was the least tolerant of development and experienced indirect dispersal restriction due to roads, according to resistance surface analyses. *Anolis lineatus*, a native anole species, exhibited a neutral relationship with development. Resistance surfaces and Structure analyses showed that *A. lineatus* faced indirect dispersal restrictions from roads and developed areas, while mitochondrial haplotype networks suggested they benefited from occasional human-facilitated long-distance dispersal events. *Hemidactylus mabouia*, an introduced gecko species, was the most tolerant of development, and experienced no dispersal restriction, but mitochondrial haplotypes suggest direct long-distance dispersal facilitation.

Main Conclusions: Our findings highlight development tolerance as a key predictor of dispersal impact for these species and future work should test whether these patterns are upheld in other systems. Understanding how human activities affect species'

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dispersal will aid in managing introduced species while promoting connectivity for native species navigating dispersal challenges in dynamic landscapes.

KEYWORDS

gene flow, human-mediated dispersal, invasive species, isolation by resistance, jump dispersal, reptile

1 | INTRODUCTION

Over the past century, the rate at which humans have developed habitats across the globe, transforming them from natural to agricultural and urbanized land uses, has greatly accelerated (Gleditsch et al., 2023). As habitat development and associated transportation networks expand globally, species dispersal processes are fundamentally impacted. Human-induced changes to dispersal affect species' genetic connectivity and diversity (Miles et al., 2019), local adaptation and speciation (Crispo et al., 2011), metapopulation dynamics (Bullock et al., 2020), community assembly (Perry et al., 2020) and interspecies interactions (Duckworth & Badyaev, 2007). However, the strength, direction and type of impacts on dispersal are not felt equally by all species (Bullock et al., 2018). Therefore, it is imperative to understand not only how human activities affect dispersal, but also the factors that drive different responses among species.

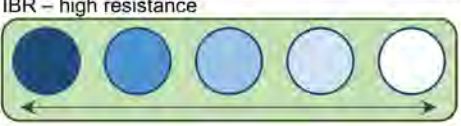
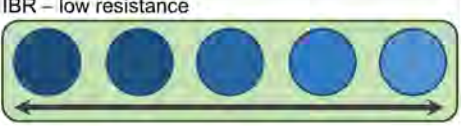
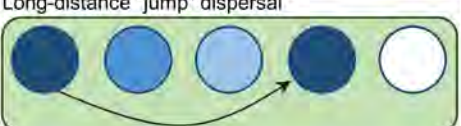
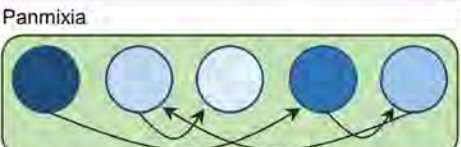
Over time, dispersal generates spatial genetic patterns that vary based on the geographic proximity of related individuals (Figure 1; David, 2018; Jordano, 2017; McRae, 2006; Wright, 1943). Identifying the spatial genetic patterns exhibited by a species can indicate the influence of natural versus anthropogenic processes on dispersal. While natural landscape features can result in dispersal restriction or facilitation, human activities can directly and indirectly modify the spatial and temporal scales at which dispersal occurs (Figure 1). Land use change, such as habitat development, results in the *indirect* restriction or facilitation of dispersal. Habitat development restricts dispersal by separating preferred habitat patches with unsuitable habitat and barriers that limit movement and ultimately gene flow (Tucker et al., 2018). Conversely, habitat development can also indirectly facilitate dispersal for development-tolerant species or invasive species (Brown et al., 2006).

Human activity also results in the *direct* facilitation of dispersal. Within developed habitat, species have a higher likelihood of interacting with, and being taken up by, human transportation infrastructure that can move them long distances (Bullock et al., 2018). Direct facilitation of long-distance dispersal, via both intentional and accidental transport, is well-known for moving species outside their native ranges and is gaining recognition as a predominant way non-native species also disperse within their introduced ranges (Gatto-Almeida et al., 2022). Comparatively, the direct transport of species within their native range is largely undetectable without genetic methods. While this phenomenon has been documented in plants (e.g., Sonkoly et al., 2022), the frequency with which it occurs is unknown for most other taxa. A species' use of developed habitat

may predict the likelihood of direct facilitation of dispersal within their native range (Figure 1; Miles et al., 2018, 2019). However, the broader link between species' tolerance of habitat development and the impact that human activities have on dispersal has not been well-explored. At present, the factors that influence which species will be directly transported by humans are not well-established. Identifying the links between development tolerance and direct transport by humans would be especially valuable for predicting species' likelihood of being transported outside its native range (Pyšek et al., 2020).

We examine the link between development tolerance and both direct and indirect human-modified dispersal. We define development tolerance as a species' ability to persist in developed habitats, as indicated by their abundance. Since species abundances integrate both the survival and dispersal components of population dynamics, they may provide a useful metric for predicting how species' dispersal responds to a gradient of human activities, like habitat development. We use as our study system three lizard species that co-occur on the Caribbean island of Curaçao and vary in their colonization history and putative tolerance to development. *Phyllodactylus martini* is a native gecko that has no introduced populations outside its native range, nor do any other *Phyllodactylus* species, indicating a potential lack of direct dispersal facilitation. We expect *P. martini* will have a low tolerance to development and experience restricted dispersal (Figure 1). *Anolis lineatus* is a native anole that has been introduced to neighbouring Bonaire island (van Buurt & Debrot, 2012) and Suriname (Hoogmoed, 1980). Given the history of *A. lineatus* as an introduced species, we predict it is tolerant to development and has the potential for facilitated dispersal within its native range (Figure 1). Finally, *Hemidactylus mabouia* is a gecko introduced to Curaçao in the 1980s that is one of the most globally successful invading reptile species (Bomford et al., 2009) and is tolerant of development (Short & Petren, 2011b). We predict that *H. mabouia* will experience dispersal facilitation, including instances of direct, human-assisted movement (Figure 1).

We first quantify the relative tolerance of development for the three species to provide a context for interpreting their dispersal patterns. We then use landscape genetic techniques to reveal human influences on dispersal patterns within Curaçao. Specifically, we investigate the indirect influence of habitat development on dispersal restriction and facilitation. In addition, we investigate direct facilitation of long-distance dispersal by identifying spatial outliers in genetic relatedness. By contrasting the dispersal patterns of these three species, we provide a multifaceted view of how humans are directly and indirectly modifying dispersal for species with differing tolerances to habitat development.

Spatial genetic patterns of dispersal	Human modifications to dispersal			
	Effect	Hypothesis	Mechanism	Examples
 <p>IBR – high resistance</p>	Restriction of dispersal	Species <i>intolerant</i> to development experience restriction	Indirect – Human activities alter dispersal.	Developed habitat has high resistance to ground sparrow dispersal. ¹
 <p>IBR – low resistance</p>				Urban greenspaces have low resistance to white-footed mouse dispersal. ²
 <p>Long-distance "jump" dispersal</p>	Facilitation of dispersal	Species <i>tolerant</i> to development experience facilitation	Direct – Humans transport (vector) individuals.	Termites are directly transported in wood throughout their native range, but genetic structure is maintained. ³
 <p>Panmixia</p>				Invasive polychaete pests are frequently directly transported via aquaculture, removing genetic signature. ⁴

¹Rodríguez-Bardía et al. 2022 ; ²Munshi-South 2012 ; ³Eyer et al. 2020 ; ⁴David et al. 2016

FIGURE 1 Examples of spatial genetic patterns resulting from natural- and human-modified dispersal. Circles represent individuals of the same species where the similarity in shading of the circles indicates similarity in genetic relatedness. Arrows indicate directionality and strength (thickness) of gene flow due to dispersal. Isolation-by-resistance (IBR) occurs where closely related individuals are proximal to each other, and relatedness decreases as landscape resistance increases. Factors that have high resistance to movement result in dispersal restriction and limit the spatial scale over which closely related individuals occur (Row 1: IBR – high resistance). We hypothesize that human activities will indirectly create dispersal restriction in the form of landscape resistance for species intolerant to development. Conversely, factors which lower resistance facilitate dispersal and expand the spatial scale over which closely related individuals occur (Row 2: IBR – low resistance). We hypothesize that human activities will indirectly create dispersal facilitation by lowering landscape resistance for species tolerant to development. Species that are tolerant to development are also more likely to experience long-distance dispersal, in which humans directly facilitate individual movements, often unintentionally. Factors that facilitate long-distance, or 'jump', dispersal are infrequent events that begin to erode the IBR pattern but can still be detected by discontinuities in an IBR background (Row 3: Long-distance dispersal). Finally, panmixia, an absence of spatial genetic structure, is an extreme case of facilitation, resulting from frequent long-distance dispersal events (Row 4: Panmixia). We hypothesize that this pattern, which can result from the direct facilitation of movement by humans, is more likely to occur in species which are tolerant to development. Any of these patterns may result from natural dispersal processes; however, human activities (see examples) directly and indirectly alter the temporal and spatial scales at which they occur. In addition, a single species may experience both restriction and facilitation, as well as direct and indirect impacts on dispersal due to humans.

2 | MATERIALS AND METHODS

2.1 | Study system and lizard sampling

We sampled three lizard species, *P.martini*, *A.lineatus* and *H.mabouia*, on Curaçao, a mid-sized (444 km²) Caribbean island north of Venezuela. Curaçao's natural vegetation consists of remnant manchineel (*Hippomane mancinella*) forest and xeric scrub vegetation. Development in the form of urbanization has replaced natural vegetation across the island; due to the arid climate and lack of freshwater sources, agriculture is scant. The southern half of Curaçao, in and around the city of Willemstad, is the most developed portion of the island, while the northern half of Curaçao has a higher proportion of remaining natural vegetation.

We structured our effort to sample sites along the gradient of habitat development across the entire island (Figure 2, Table S1). All three lizard species were surveyed as part of a larger biodiversity survey from 27 January 2017 to 11 March 2017. We sampled geckos between 18:00 and 23:00, and anoles between 08:00 and 18:00, which corresponds to their daily peak activity times. To sample species abundances for quantifying development tolerance, we conducted area constrained surveys of ~400 m² and recorded the number of individuals of each species we encountered at 30 study sites varying in habitat development. To minimize factors known to influence detectability in lizard surveys (Lardner et al., 2015), surveys were consistently conducted by the same searchers using the same search equipment in the same weather conditions within the same season. In total, we counted 188 *P.martini*, 379 *A.lineatus*, and 233 *H.mabouia* across the 30 sites.

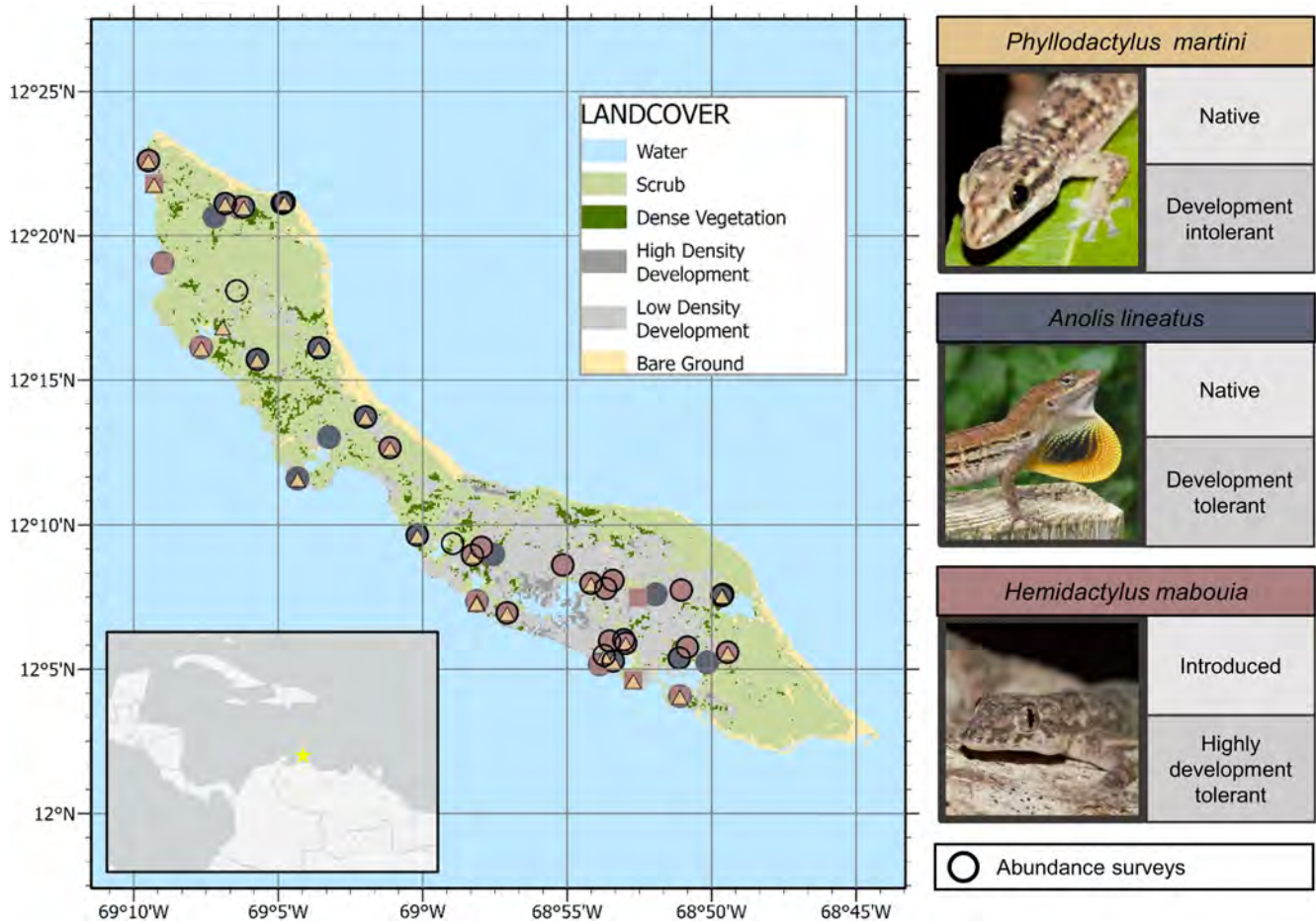


FIGURE 2 Locations on Curaçao where tissue was sampled for DNA extraction from a native gecko (*Phyllodactylus martini* – represented by yellow triangles), a native anole (*Anolis lineatus* – represented by dark blue circles) and an introduced gecko (*Hemidactylus mabouia* – represented by pink squares). Thirty of the 50 locations were also surveyed for lizard abundance to estimate the tolerance of each species to development (Figure 3).

Following the abundance surveys, we conducted additional lizard sampling to obtain tissue samples for genetic analyses so that the tissue collection would not affect the abundance data. At the 30 sites where we conducted area-constrained surveys plus 20 additional sites around the island, we captured lizards by hand and collected a tail tip (~1 cm) for landscape genetic analyses, stored the tail tip in 95% ethanol, and released individuals alive at the point of capture. We collected samples from 100 individuals per species across these 50 locations. Since our analyses were at the individual rather than site level, this sample size is sufficient given the strong power of individual-based analyses to detect spatial-genetic structure even with as few as 3–4 individuals per patch (Balkenhol & Fortin, 2015). Upon sequencing the DNA, five individuals that were putatively identified as *H. mabouia* in the field at two sites were revealed as *H. frenatus* (Behm et al., 2019), leaving 95 individuals for genetic analyses. All individuals for all species were successfully sequenced at the mitochondrial *cytochrome b* gene. We were able to obtain genotypes for 94 *P. martini* at 11 microsatellite markers, 96 *A. lineatus* at 11 microsatellite markers and 93 *H. mabouia* at 10 microsatellite markers (Methods S1 in Appendix S1).

2.2 | Tolerance to development

We quantitatively assessed species-specific tolerance to development by regressing the relative abundance (i.e., count data) of each species against the amount of developed habitat in the landscape surrounding each sample point. Since we sampled sites across the continuum of development in Curaçao, this approach allowed us to identify how abundances changed with increasing development intensity. We calculated the proportion of high- and low-density development in each 100, 250, 500, 750 and 1000m buffer around our study sites from a 30m resolution land cover raster (Behm et al., 2023) using ArcGIS Pro (Esri Inc. Redlands, CA, version 2.9.0). High density development was categorized as developed land cover where impervious surface accounted for greater than 50% of the cover, and low-density development was developed land cover with less than 50% impervious surface cover (Zhu, 2016). Because development values were highly correlated across buffers, we calculated the mean total development (high- and low-density development combined) across all buffers for each site. We then regressed the log-transformed abundance of each species against mean development

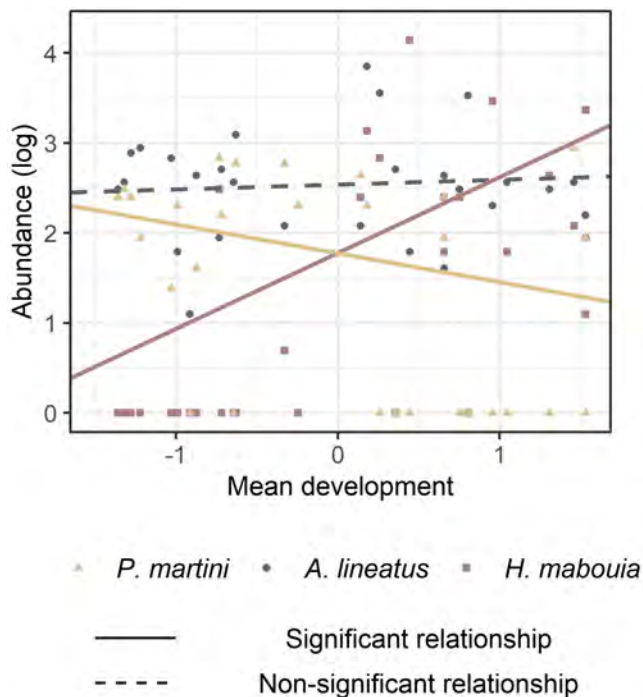


FIGURE 3 Tolerance to development, represented as the relationship between mean habitat development and lizard relative abundances on Curaçao for a native gecko, *P. martini*, a native anole, *A. lineatus*, and an introduced gecko, *H. mabouia*. Mean habitat development represents the mean proportion of habitat development in 100, 250, 500, 750 and 1000m radius buffers surrounding each survey site, with higher values on the x-axis indicating higher development. Overall, *P. martini* showed low development tolerance, *H. mabouia* showed a high development tolerance, and *A. lineatus* showed no significant relationship between relative abundance and mean habitat development.

using a separate generalized linear model with a Poisson distribution for each species. Mean development was scaled to facilitate direct comparisons of coefficients across models to show the relative tolerance of development for each species. Analyses were conducted in R version 4.0.2 (R Core Team, 2021).

2.3 | Restriction and facilitation (IBR) – resistance surfaces

To evaluate the effect of landscape features on dispersal facilitation and restriction, we used the R package ResistanceGA to optimize and select resistance surfaces (Peterman, 2018; Peterman et al., 2014). ResistanceGA uses genetic algorithms to optimize the relationship between pairwise landscape resistances, calculated in Circuitscape (McRae et al., 2008), and pairwise individual genetic distances. Models are fit using maximum-likelihood population effects (MLPE) which account for nonindependence among pairwise distances (Clarke et al., 2002) following an optimization process (Methods S2 in Appendix S1; Cushman & Landguth, 2010; Khimoun et al., 2017).

Our chosen genetic distance measure was a principal components analysis (PCA)-based genetic distance metric on individual microsatellite genotypes (Shirk et al., 2010). This method relies on a genetic data matrix of allele usage, where rows represent individuals and columns represent the number of alleles present in the population per allele with values of 0, 1 or 2 per individual. We calculated principal components from this matrix and then measured Euclidean distance among 64 PC axes, as including multiple PC axes greatly improves model selection in downstream analyses (Shirk et al., 2017). We assessed the influence of two landscape variables, land cover and road network, on genetic distance between pairs of individuals. The optimal thematic resolution for land cover included development, vegetation and bare ground (sand) categories and no aquatic pixels (Figure S1). To reduce computational time, we resampled the original 30m raster to 100m pixels because the inference of landscape genetic patterns is robust to rescaling land cover raster resolution (McRae & Beier, 2007). For the road surface, we extracted road line shapefiles from the OpenStreetMap dataset via the Humanitarian Data Exchange and rasterized them at the same 100m resolution as the land cover data. The optimal thematic resolution indicated the presence or absence of any road (Figure S1).

We used the optimal land cover and road network rasters to assess isolation by resistance (IBR). We used the 'all_comb' function in ResistanceGA to simultaneously perform single-surface and multi-surface optimization, which combines the land cover and road surfaces into a single composite surface. The best model (null [intercept-only], geographic distance, single surfaces – road or land cover, or combined surface) is selected using AIC. All optimizations, including those in the preliminary analysis, were performed using the Julia build of ResistanceGA (Hall et al., 2021). We ran all optimizations with an input file restricting the comparison of pairs to those greater than 100m apart to prevent the comparison of individuals sampled within the same grid cell. Three independent runs were conducted to ensure parameter estimates converged.

2.4 | Restriction and facilitation (IBR) – determinants of admixture

To understand how the relatedness of individuals clusters spatially across the landscape, we first assessed population structure based on microsatellite DNA using the Bayesian clustering program Structure 2.3.4 (Pritchard et al., 2000), implemented through the R package ParallelStructure (Besnier & Glover, 2013). We evaluated the presence of genetic clusters $K=1-n$ (n =number of sites sampled for each species), under the admixture model. We performed five independent runs of 500,000 Markov chain Monte Carlo repetitions following a burn-in of 100,000 iterations. The optimal number of clusters was determined in Structure Harvester (Earl & vonHoldt, 2012) using maximum likelihood (Pritchard et al., 2010) and Evanno's ΔK (Evanno et al., 2005). We further evaluated each identified cluster using Genepop on the Web to test for global

heterozygote deficiency, which can indicate the presence of potential unidentified population structure (Raymond & Rousset, 1995; Rousset, 2008).

The assignment of individuals to discrete clusters indicates genetic sorting; however, in many cases, substantial portions of individual genotypes may be associated with multiple genetic clusters, signifying genetic admixture. In human-dominated landscapes, high levels of admixture may be indicative of dispersal facilitation, while low levels of admixture may represent dispersal restriction across the landscape. We used generalized linear mixed models (GLMM) to infer the relationship between landscape variables and admixture to inform whether landscape variables resist or facilitate dispersal at the population level to complement the individual pairwise comparison in the resistance surface analyses.

We used the land cover and road rasters described in the above analyses to derive two landscape-level descriptors of each site for these models. We calculated the percent cover of each land cover type (high-density development, low-density development, forest and shrub) from our land cover map within 100, 250, 500, 750, 1000, 2000, 3000, 4000 and 5000m buffers around each study site in ArcGIS Pro. Due to correlations among variables across buffer sizes, we conducted a PCA of the proportion of each land cover type in each buffer. We retained the first two axes (landPC1 and landPC2); positive values on landPC1 were associated with higher development, while positive values on landPC2 corresponded with denser forest vegetation (Figure S2). We then calculated road density within the same buffers, summarized road density variables using a PCA, and again retained the first two axes (roadPC1 and roadPC2). Positive values on roadPC1 represented sites with increasing road density at broad spatial scales (>750m buffer), while positive values on roadPC2 represented increased road density at smaller scales within in the immediate vicinity of the site (<250 buffer; Figure S3). We also included two additional site-specific categorical variables not included in the resistance models. First, we recorded whether each study site was developed (<20m from buildings or paved surfaces) or undeveloped (>100m from buildings or paved surfaces), regardless of the surrounding landscape context. Second, we categorized each site as having high (resorts, parks) or low (private residences, hiking areas) public accessibility based on the ease and level of visitation.

We evaluated the effect of these variables on cluster membership with GLMMs using the lme4 package with the afex wrapper in R (Bates et al., 2015; Singmann et al., 2021). The response variable was a binary indicator of whether an individual was assigned to a cluster or admixed. We chose a conservative estimate of >80% membership probability in a single cluster as the cutoff for assignment, which should allow for detection of any admixture within recent generations. The fixed effects were the landscape and road PC axes and the two categorical site descriptors. The random effect represented site to account for multiple individuals collected from the same location. We also accounted for spatial autocorrelation among samples with Spatial Eigenvector Mapping using the ME function in the spatialreg package (Bivand et al., 2021; Dormann et al., 2007). We compared models with and without spatial autocorrelation variables using AIC.

We reduced the best model to a simplified model including only the variables with significant *p*-values (Zuur et al., 2009). We checked model assumptions in the DHARMA package (Hartig, 2022). Positive estimates in the final model indicate a positive relationship with admixture, but the interpretation of this relationship as dispersal facilitation or restriction is variable-dependent (Table S3).

2.5 | Direct facilitation – long-distance dispersal

To explore the direct facilitation of long-distance dispersal, we conducted an outlier analysis on the spatial genetic structure of mitochondrial DNA haplotypes, which demonstrated clear spatial clustering. We determined the number of haplotypes present and created maximum parsimony trees of those haplotypes using the R package haplotypes (Aktas, 2020). For *P. martini* and *A. lineatus*, we identified dozens of haplotypes; therefore, we conducted network analysis on the maximum parsimony tree to group individuals into modules. These haplotype modules represented subset communities of the network in which nodes were more densely connected to each other than to nodes in the rest of the network, in this case suggesting closer relatedness. We used the infomap clustering algorithm in the igraph R package, which relies on random walks across the network, for clustering (Csardi & Nepusz, 2006; Fortunato & Hric, 2016). We assessed whether individuals within the haplotype modules were geographically clustered using GLMMs where pairwise geographic distance between individuals was the response variable and the fixed effect was a binary indicator of whether the two individuals were in the same module or not. The random effect accounted for multiple individuals representing one module.

To test long-distance dispersal, we examined the geographic distribution of each module for outliers, essentially identifying genetically similar individuals at greater-than-expected distances (Eyer et al., 2021). Such outliers indicate 'jumps' beyond natural dispersal capabilities, therefore potentially indicating direct facilitation of dispersal by humans. For each module, we calculated a centroid based on the average geographic coordinates of all individuals within that module and calculated the distance of all individuals from the centroid. We then identified statistical outliers from modules with greater than four individuals using boxplots of the distribution of individual distances from the centroid for each module. We excluded outliers that were below the median distances because these represent individuals that are closer to the centroid than average.

For modules containing outliers, we performed hierarchical clustering of the relatedness of individuals within those modules to trace the potential geographic origin of the outlier individual. We built trees with the microsatellite genotypes using the hclust function in base R and tested single, complete and average clustering strategies. We compared the resulting trees with the cophetic function in base R, which finds the estimated dissimilarity between each point on the tree and then correlates the estimated distances and the genetic distances. A higher correlation indicates that the given clustering method accurately represents the data.

We created trees using the best performing strategy (average linkage for all species) for all modules with outliers for *P. martini* and *A. lineatus*. Because *H. mabouia* had only three haplotypes, we did not conduct outlier identification but did create a tree for the rarer haplotype with the goal of understanding its potential introduction and spread on the island.

3 | RESULTS

As expected, *P. martini* was the species least tolerant to development as indicated by a negative relationship between abundance and habitat development (coefficient = -0.32, $p < .001$; Figure 3). In the landscape genetic resistance surface analysis, geographic distance alone was the best model for *P. martini* (Table 1). The resistance surface based on road presence had $\Delta AIC < 2$, though geographic distance was found to be the top model 84.0% of the time. The competing roads model showed that roads increased resistance to movement by 272.8 times (Table 1). We detected no population structure ($K = 1$) for *P. martini* (Figure S4) making the analysis of environmental determinants of admixture impossible. However, we detected global heterozygote deficiency in this cluster ($p < .001$). Combined with the resistance surface analyses, a single genetic cluster suggested a widespread species with low dispersal following an isolation by distance spatial genetic pattern. However, this species also experienced dispersal resistance due to roads.

We identified 54 mitochondrial haplotypes for *P. martini*, which grouped into nine modules (Figure S5). These modules were geographically clustered, meaning that individuals were closer to members of the same module than to individuals of different modules (distance = -11,403.8m, SE = 753.7m, t -value = -15.13). We detected a single outlier in Module 5; however, compared to other modules, this was a tightly distributed cluster of individuals spatially (Figure S5c). So, while the individual was a statistical outlier, it was still geographically close to the locations of all other individuals when mapped; therefore, it seems unlikely that this outlier constitutes a long-range dispersal facilitation event.

Development had no significant impact on *Anolis lineatus* relative abundance (coefficient = .05, $p = .31$; Figure 3). Resistance surfaces optimized based on roads or land cover type provided a better explanation of genetic distance compared to geographic distance alone (Table 1). These two competing models had $\Delta AIC < 2$, but bootstrap analyses indicated the presence of roads as the top model 64.5% of the time. The presence of roads was approximately 10,000 times more resistant to *A. lineatus* movement than pixels without roads. In the land cover resistance surface, vegetation was the most conductive habitat, with developed areas being nearly 8.6 times more resistant to movement. The bare ground land cover category was the most highly resistant to movement by *A. lineatus* (and the other two species), as expected since bare ground provides few available resources (Rand & Rand, 1967). The results of the resistance surface optimization indicated that roads and developed land cover restricted *A. lineatus* dispersal.

TABLE 1 Results of landscape genetic analysis evaluating the influence of landscape resistance on genetic differentiation in three lizard species. Resistance values were optimized for each surface using ResistanceGA. Model performance was evaluated based on average AIC_c across 1000 bootstrap replicates, with the top supported models ($\Delta AIC < 2$) indicated in bold.^a

Species	Surface	AIC_c	ΔAIC	R_m^2	R_c^2	%top	Feature 1 ^b	Feature 2	Feature 3
<i>P. martini</i>	distance	10,364.1	0	0.001	0.878	84.0			
	roads	10,365.4	1.2	0.002	0.878	11.7	1	272.8	NA
	land cover	10,368.2	4.1	0.002	0.877	4.3	1	13	11,183.6
	combined	10,370.9	6.8	0.001	0.877	0			
	null	10,396.9	32.8	0.000	0.875	NA			
<i>A. lineatus</i>	roads	12,411.4	0	0.009	0.829	64.5	1	10,000	NA
	land cover	12,412.7	1.3	0.008	0.828	26.1	1	8.6	10,000
	distance	12,420.1	8.7	0.006	0.830	9.3			
	combined	12,492.5	81.1	0.313	0.902	0.1			
	null	12,530.2	118.8	0	0.824	NA			
<i>H. mabouia</i>	null	10,488.0	0	0	0.795	NA			
	distance	10,489.4	1.5	<0.001	0.794	81.3			
	roads	10,489.7	1.8	0.024	0.797	18.3	4928.7	1	NA
	land cover	10,493.7	5.8	<0.001	0.794	0	3.0	1	9881.7
	combined	10,495.4	7.4	0.046	0.799	0.3			

^a%Top represents how often each surface was chosen as the top model in bootstrap replicates. Marginal R^2 (R_m^2) represents the overall proportion of variation explained by the fixed effects in the model alone, while the conditional R^2 (R_c^2) represents the overall variation explained by the model.

^bThe optimized resistance values for each category in the univariate surfaces are relative to 1; values higher than 1 indicate increased resistance to movement. Since values were consistent across three replicates, we show average values. For the land cover surface, Feature 1 = vegetation, Feature 2 = development, and Feature 3 = bare ground. For the road surface, Feature 1 = road absence and Feature 2 = road presence.

In the analysis of genetic admixture, both maximum likelihood and Evanno's ΔK supported $K=2$ populations (Figure S6) for *A. lineatus*. One cluster was more common on the southern, developed

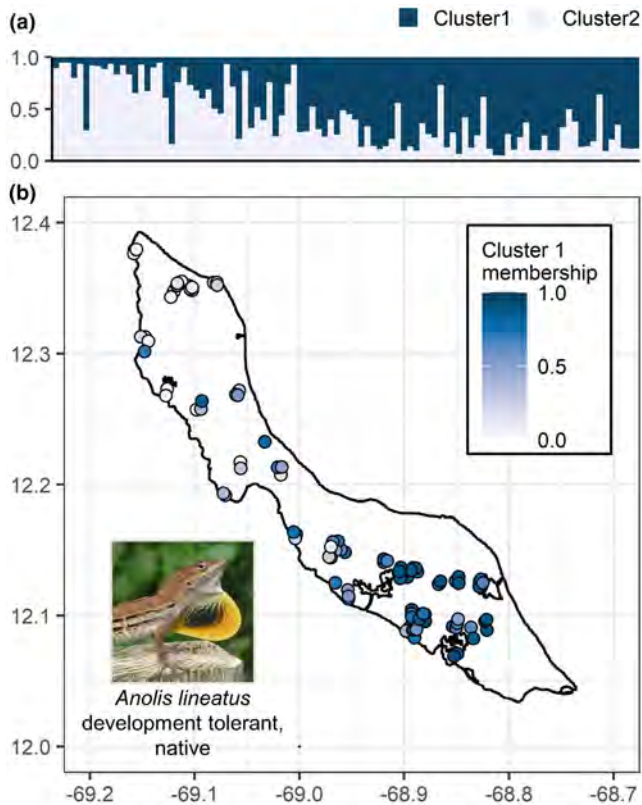


FIGURE 4 Membership in two genetic clusters identified by structure for *A. lineatus*. (a) Q-plot showing the proportion of each individual genotype (vertical bars) belonging to Clusters 1 and 2. Individuals are arranged from left to right by longitude. (b) Individuals mapped across Curaçao, with blue colouring indicating a higher membership in Cluster 1. Individual position is jittered to show individuals collected from the same location.

half of the island, while the other was more common on the northern, natural half, though admixture was common (Figure 4). In our models exploring the effect of landscape variables on admixture, the development status of a site, landPC1 and roadPC2 were significant predictors (Table 2). All predictors had a negative relationship with single cluster membership, suggesting that *A. lineatus* individuals were more likely to be admixed at sites categorized as 'undeveloped', in areas that have high surrounding development, and a high density of roads in the immediate vicinity, such as parks in developed areas.

We identified 65 mitochondrial haplotypes in *A. lineatus* individuals, which grouped into 12 geographically clustered modules (Figure 5a, Figure S7a) (distance = -10,011 m, SE = 670 m, t-value = -14.94). We detected upper outliers from modules 1, 3, 8 and 11 (Figure 5b, Figure S7b). We did not interpret the outliers for Module 3 or 8 because of their broad and limited spatial distributions, respectively. The outliers for Module 1 and Module 11 were on opposite ends of the island from all other individuals sharing the same module (Figure 5c,d), indicating potential long-distance dispersal facilitation. Module 1 encompassed individuals from sites on the south end of the island, and the outlier was sampled at a public beach on the north end of the island. Hierarchical clustering indicated that this individual was most closely related to another individual from a private residence (Figure 5e). The outlier in Module 11 was sampled on the property of the Curaçao Zoo. Hierarchical clustering based on genetic distances calculated from microsatellites reinforced that this individual clusters within more northern genotypes (Figure 5f).

Hemidactylus mabouia relative abundance increased with human development (0.84, $p < .001$; Figure 3), indicating a tolerance of development. In the resistance surface analysis, the null model, geographic distance and roads were the top competing models (Table 1). The bootstrap analysis does not include the null model but found geographic distance to be the top model >81.3% of the

Predictors	Model 1 - Global w/autocorrelation		Model 2 - Global		Model 3 - Final	
	Estimate	p-Value	Estimate	p-Value	Estimate	p-Value
Intercept	-0.26	.31	-0.27	.29	-0.28	.29
Public access status ^a	-0.41	.18	-0.23	.40		
Developed status ^b	-0.85	.05	-0.94	.03	-0.91	.03
Land PC1 - Development	-1.38	.06	-1.65	.02	-0.78	.03
Land PC2 - Vegetation	-0.56	.07	-0.56	.08		
Road PC1 - Landscape	1.03	.13	1.04	.13		
Road PC2 - Local	-0.82	.04	-0.96	.02	-0.78	.04
Spatial eigenvector 1	3.87	.20				
Spatial eigenvector 2	3.10	.24				

^aFirst level of public status is 'high', and the second level is 'low'.

^bFirst level of developed status is 'undeveloped', and the second level is 'developed'.

TABLE 2 Generalized linear mixed models relating landscape variables to whether an individual *A. lineatus* is a member of a genetic cluster or is admixed. A negative estimate indicates that a variable has a negative relationship to group membership and is therefore positively related to admixture. Significant p-values are indicated in bold.

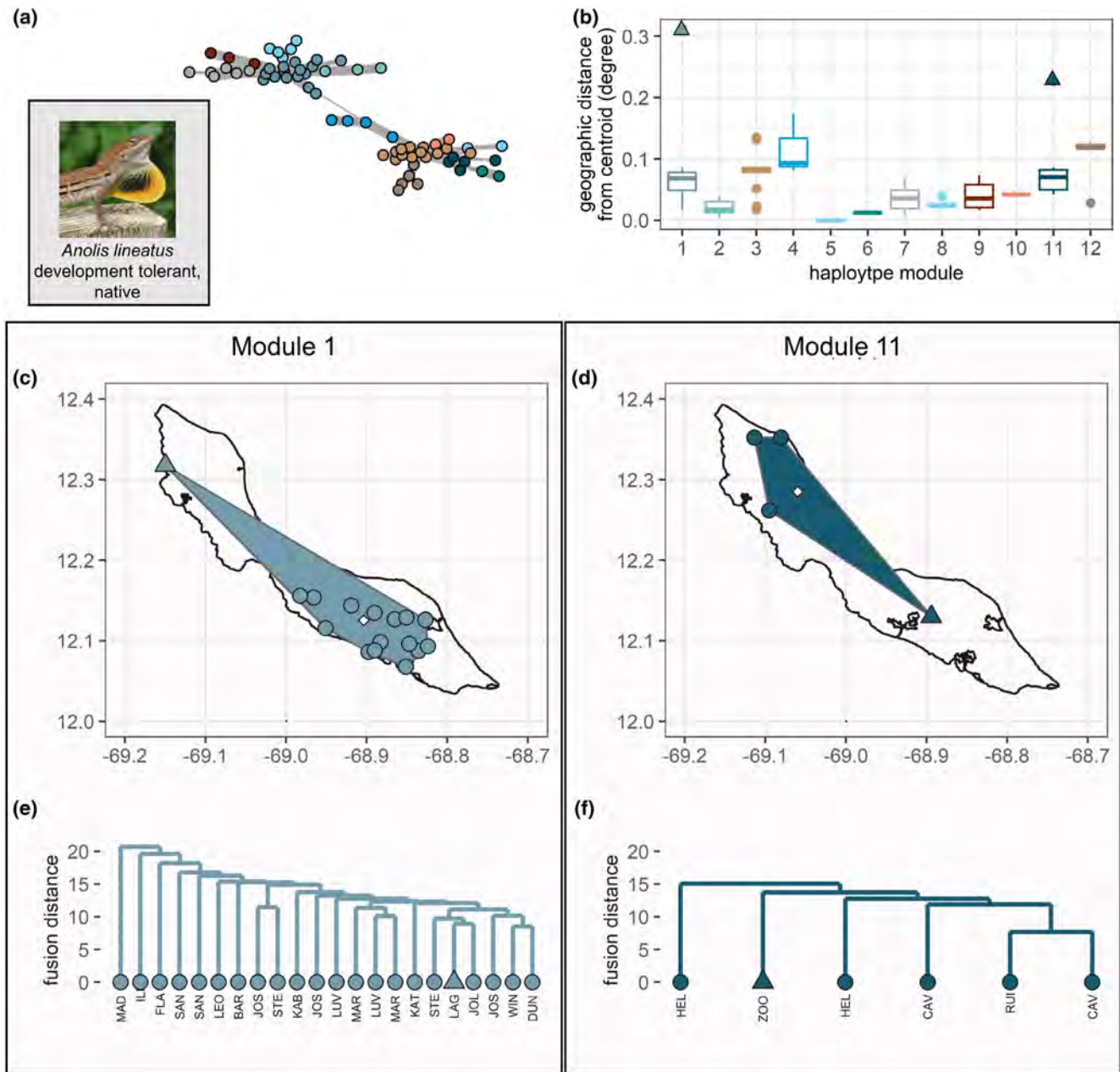


FIGURE 5 Identification of geographic outliers from *A. lineatus* haplotype modules. (a) We grouped 65 mitochondrial haplotypes into 12 modules based on clustering within a maximum parsimony network. Edge thickness and length indicate base-pair differences (1–6) between haplotypes, with thicker lines indicating fewer differences and thus increased similarity. (b) We identified outliers (triangles) from the geographic centres (shown in c and d with white diamonds) of (c) Module 1 and (d) Module 11. We used hierarchical clustering of microsatellite data to examine how the outliers from (e) Module 1 and (f) Module 11 related to individuals collected from other sites within the same module. On the dendrograms in (e) and (f), individuals are labelled with the name of the site they were collected from. A full summary of site names can be found in the [Table S1](#).

time compared to other resistance surfaces. We found no population structure ($K=1$) for *H. mabouia* (Figure S8), making the admixture analysis impossible. However, we detected global heterozygote deficiency in this cluster ($p < .001$). Like *P. martini*, the lack of population structure, combined with the support for the geographic distance model, indicated a species with limited dispersal following an isolation by distance model. However, the support for the null model showed that *H. mabouia* dispersal was more random and

unconstrained by habitat. Interestingly, for *H. mabouia*, areas with roads were 4928.7 times more conductive than areas without roads.

We detected only three haplotypes in *H. mabouia*. One was common and distributed across the island while the second differed from the first haplotype by only one base-pair and occurred in only one individual, representing a recent mutation. The third haplotype differed from the common haplotype by 22 base-pairs and occurred at only six locations (Figure 6a). For this rare third haplotype, hierarchical

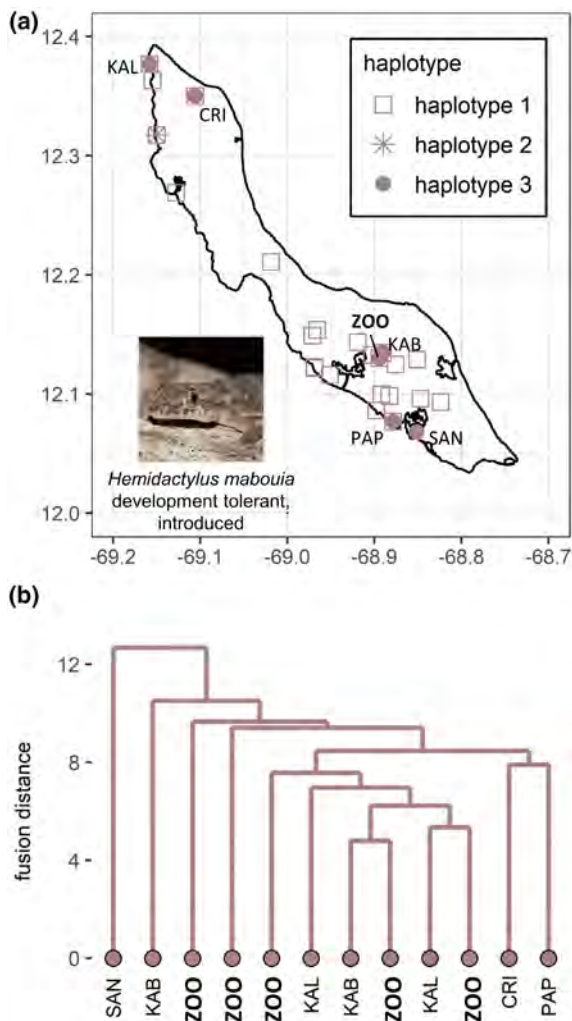


FIGURE 6 We identified (a) three mitochondrial haplotypes for *H. mabouia* on Curaçao – haplotype 1 was common across the island, whereas haplotype 2, which differed by only one nucleotide from haplotype 1, occurred in a single individual. Haplotype 3 was found at a handful of sites across the island. (b) Hierarchical clustering based on microsatellite relatedness data for haplotype 3 reveals that individuals collected from the Zoo are related to individuals collected at many sites across the island.

clustering indicated that individuals with this haplotype were more closely related to individuals at other sites than individuals at the same or geographically proximal sites (Figure 6b). Across multiple sites, individuals were closely related to individuals sampled at the Curaçao Zoo.

4 | DISCUSSION

There is an increasing need to understand and predict how species dispersal will be modified in the face of global change, especially given the implications for predicting species invasions. Our results support the hypothesis that development tolerance can predict how a species experiences dispersal restriction or facilitation resulting from human activity.

4.1 | Dispersal restriction

The presence of roads restricted the dispersal of the development-intolerant native gecko species, *P. martini*. This finding aligns with a large body of literature showing that roads impede dispersal for a variety of taxa, often leading to reduced population sizes and genetic drift (Holderegger & Di Giulio, 2010). Reptile species are subject to direct mortality on roads (Andrews et al., 2015), and roads act as a barrier to gene flow for small-bodied, dispersal-limited reptiles (Delaney et al., 2010).

Our structure analysis of microsatellite data suggested an island-wide panmictic population of *P. martini*, while mitochondrial DNA showed a high degree of differentiation and spatial structuring. We did detect heterozygote deficiency in the single genetic cluster identified with microsatellites, which may indicate a Wahlund effect, suggesting cryptic population structure at small scales which we are unable to detect in this analysis. Such cryptic population structure could also indicate the recent influence of development in limiting dispersal of a previously panmictic population. While no studies have directly examined dispersal in *P. martini*, the dispersal of a closely related species (*Phyllodactylus tuberculatus saxatilis*) is limited to <20km in a continental system (Blair et al., 2015). However, the small size of Curaçao (<60km at the longest distance) could easily allow gene flow over several generations, and panmictic genetic clusters have been identified at similar spatial scales in a related species (*P. benedetti*; French et al., 2022). The diversity and spatial sorting of mitochondrial haplotypes likely results from long-term female philopatry, which can result in spatial genetic structuring even in the absence of geographic barriers (Blair et al., 2015; Irwin, 2002). Anoles also exhibit similar patterns of male-biased dispersal (Johansson et al., 2008), which likely account for the large number of mitochondrial haplotypes found in *A. lineatus*, compared to only two microsatellite genetic clusters.

Like *P. martini*, roads restricted the dispersal of *A. lineatus*, the other native species in our study, which had a neutral relationship to development. In addition, developed habitat restricted *A. lineatus* dispersal relative to vegetated habitat. This finding aligns with research showing that development and urban habitat fragmentation reduces gene flow for other small-bodied, dispersal-limited lizard species (Wenner et al., 2022). Although our results show that *A. lineatus* can tolerate development, they likely prefer irrigated gardens (Rand & Rand, 1967); therefore, their ability to move through other habitats in the developed matrix may be limited. Additionally, biomechanical research suggests that running speeds for other *Anolis* species dramatically decline on man-made surfaces, with negative consequences for predator avoidance and fitness in urban environments (Winchell et al., 2018).

For native species such as *P. martini* and *A. lineatus*, understanding how habitat development restricts dispersal is an important conservation concern. Reduced connectivity and habitat fragmentation can lead to lower effective population sizes (Fusco et al., 2021) and genetic diversity (Munshi-South et al., 2016), and increased rates of inbreeding (Richardson et al., 2021). In some species, lower gene flow, combined with the selective pressure of developed environments, may lead to

local adaptation that allows species to better persist in their novel habitats. For instance, anoles (*Anolis cristatellus*) in urban environments show morphological and genetic adaptations associated with movement, immune function, motor regulation, and metabolism (Winchell et al., 2016, 2023). However, for other species, particularly those like *P. martini*, that are sensitive to development, decreased gene flow and related population-level effects may decrease population persistence in developed areas (Munshi-South et al., 2013).

4.2 | Dispersal facilitation

For dispersal-limited species threatened with reduced gene flow in the face of development, human-mediated dispersal facilitation can present a potential rescue by increasing connectivity and gene flow. Our analyses of population admixture and mitochondrial haplotypes revealed evidence for facilitated dispersal in *A. lineatus*. Our finding of increased admixture in developed green spaces suggests higher gene flow in these areas due to two possible explanations. First, *A. lineatus* may preferentially use urban green spaces if these areas represent high-quality habitat (Rand & Rand, 1967) in the midst of inhospitable matrix, resulting in indirect facilitated dispersal (Munshi-South, 2012). This explanation aligns well with the results of the resistance surfaces, which suggested that vegetated habitat provides low resistance to *A. lineatus* movement. Alternatively, increased admixture for anoles in developed green spaces on Curaçao may result from vectored dispersal in which anoles 'hitchhike' with humans visiting these locations. Anoles have a rich history of hitchhiking in the transport of plants and building materials (Helmus et al., 2014; Williams et al., 2019). Unfortunately, our admixture analysis cannot distinguish between these two mechanisms.

Our spatial analysis of mitochondrial haplotypes, however, is aimed specifically at detecting direct facilitation, in the form of long-distance dispersal. This analysis detected two examples of direct facilitation, both to opposite ends of the island, for *A. lineatus*. At these distances, human-facilitated dispersal is the most parsimonious explanation over other possible mechanisms. This is likely a conservative estimate of direct transport for *A. lineatus* on Curaçao. People make more short distance trips than long ones (Alessandretti et al., 2020), meaning that they are likely also moving *A. lineatus* shorter distances than we can detect.

Long-distance dispersal, especially human-vectored, is generally considered rare in comparison to diffusive dispersal but can be an important source of gene flow, introducing and maintaining genetic diversity within a species' native range (Converse et al., 2017; Jordano, 2017). In some ways, unintentional human-vectored long-distance dispersal mirrors intentional translocation for conservation, which is an essential tool for maintaining genetic diversity and population viability for species with low gene flow (Michaelides et al., 2015). Unlike planned translocations for conservation, accidental human-vectored dispersal usually goes undetected without genetic methods. Our study is one of the few that shows unintentional hitchhiking of vertebrate species within their native range.

The lack of evidence for accidental human-vectored dispersal in native species contrasts sharply with that of introduced species, which have a history of hitchhiking both to new areas (Perella & Behm, 2020) and within their introduced ranges (Short & Petren, 2011b). The propensity of invasive species to be transported by human-activities is related to the ease with which they live and interact with human spaces (Bullock et al., 2018). In our study, *H. mabouia* showed a positive association with human development, which matches previous observations of this species (van Buurt & Debrot, 2012). Our analysis of population structuring showed no genetic clustering based on microsatellites. However, we did detect heterozygote deficiency in the population, suggesting either cryptic population structure or potential inbreeding from a small population being introduced to Curaçao. A similar analysis of introduced *H. mabouia* populations in Florida found strong genetic clustering, even between adjacent buildings, in newly colonized areas, but found no genetic clustering in areas colonized earlier (Short & Petren, 2011a). *Hemidactylus mabouia* was likely introduced to Curaçao in the 1980s (van Buurt & Debrot, 2012), nearly a decade earlier than it was introduced to Florida (Butterfield et al., 1993). Therefore, *H. mabouia* populations on Curaçao may have experienced sufficient dispersal since colonization to reach equilibrium and lose any population structuring (Detwiler & Criscione, 2014), similar to the established Florida populations. The panmictic nature of the Curaçao population is supported by the landscape resistance analysis, in which the null model was the best supported model. However, the lack of landscape resistance is somewhat unexpected given that previous observations of *H. mabouia* on Curaçao have suggested that they are unable to penetrate far from homes and gardens into the natural habitat (van Buurt & Debrot, 2012).

The panmictic population of *H. mabouia* is likely explained by sufficient time and dispersal following colonization, which may have been helped along by human-vectored dispersal, as identified using mitochondrial DNA haplotypes. Given the restricted distribution of the rarer haplotype relative to the most common, it may represent a more recent, cryptic introduction. This finding is congruent with worldwide analyses which show multiple introductions to the Caribbean from *H. mabouia*'s native range in Africa (Agarwal et al., 2021). Our findings show that individuals with *H. mabouia*'s rarer haplotype were closely related to individuals collected at other, often distant sites and that most sites where we encountered these individuals were developed locations, suggests that *H. mabouia* is likely frequently moved between sites via hitchhiking. In Florida, *H. mabouia* is panmictic at the state level likely due to frequent human-vectored dispersal in the form of mass shipments of goods and containers between locations within the state (Short & Petren, 2011b).

Given the rapid acceleration of reptilian introductions worldwide (Capinha et al., 2017), understanding how humans facilitate such dispersal is important for management actions, including population control and limiting range expansion. One potential way of controlling invasive species spread is to identify hotspots of human-vectored dispersal (Hulme, 2009). In our analysis, we identified the Curaçao Zoo as a location related to human-vectored dispersal in

both *H. mabouia* and the native *A. lineatus*. The Curaçao Zoo has been identified as an introduction point for other recently identified species, including another Hemidactylus gecko, *Hemidactylus frenatus*, as well as the ladybird beetle, *Cheilomenes sexmaculata* (Assour & Behm, 2019; Behm et al., 2019). Our results show that the movement of people and goods away from the Zoo also has the potential to spread introduced species to other parts of the island. Increased inspection of shipments could allow for early detection and the implementation of effective control measures (Scholte et al., 2010).

5 | CONCLUSIONS

Our study demonstrates the potential power of using development tolerance as an indicator for predicting the impacts of human development on species' dispersal. We expect that other species with a negative relationship between abundance and development will also experience dispersal restriction, whereas those with a positive relationship will experience dispersal facilitation. Although neutral relationships with development can arise from multiple factors, we still predict a likelihood for dispersal facilitation if the species is found in developed habitat. While our study shows a clear pattern between development tolerance and the impacts of humans on dispersal, our patterns are based on only three species. However, these patterns should not be unique to Caribbean lizards and future work should test the consistency of these patterns across systems.

The need to understand species dispersal in a changing world and to predict species responses has become increasingly apparent in recent years (Rodríguez-Bardía et al., 2022). The ability to predict how species will respond to development is increasingly important in the face of urbanization, land use and human activities. The impact of humans on the landscapes around them continues to rise with consequences for species dispersal. For some species, land cover change and development restrict dispersal and reduce connectivity. Increasingly though, the interconnectedness of the human world has resulted in the introduction and spread of species to new locations through human facilitated dispersal (Gleditsch et al., 2023). Development tolerance may be an important but overlooked trait for predicting species dispersal both within and beyond their native ranges.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.13858>.

DATA AVAILABILITY STATEMENT

Individual genotype data, as well as corresponding habitat data, are publicly available on DataDryad (<https://doi.org/10.5061/dryad.w9ghx3fvz>).

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SUPPORTING INFORMATION

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