Title: Demographic expansion and panmixia in a St. Martin endemic, *Anolis pogus*, coincides with the decline of a competitor

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Abstract

Understanding patterns of differentiation at microgeographic scales can enhance our understanding of evolutionary dynamics and lead to the development of effective conservation strategies. In particular, high levels of landscape heterogeneity can strongly influence species abundances, genetic structure, and demographic trends. The bearded anole, *Anolis pogus*, is endemic to the topographically complex island of St. Martin and of conservation concern. Here, we examined genetic diversity and inbreeding, assessed which features of the landscape influence population abundances, tested for population genetic structure across St. Martin, and inferred historical demographic trends. We found minimal inbreeding or low genetic diversity in *A. pogus*. We found that suitable habitat occurs broadly across the island and that population abundances were largely predicted by canopy cover. However, there was no signature of population genetic structure across the distribution, in contrast to the co-distributed anole species (*Anolis gingivinus*). Historical demographic trends in *A. pogus* were in sharp contrast to *A. gingivinus*, with effective population sizes of *A. pogus* increasing in the recent past while *A. gingivinus* population sizes have declined. We posit that declines in a competitor species allowed for population size expansion in *A. pogus*. Overall, these analyses suggest that *A. pogus* is unlikely to be of immediate conservation concern. Further, we highlight the role of demographic history and ecological interactions in shaping population structure.

Keywords: Lesser Antilles, Caribbean, population genomics, abundance modeling, conservation genomics, *Anolis gingivinus*

Introduction

Island systems have long contributed to our fundamental understanding of evolution (Grant and Grant 2011; Shaw and Gillespie 2016; Patton et al. 2021) but they are also highly threatened and have become a focus of extensive conservation efforts (Graham et al. 2017; Russell and Kueffer 2019). Gene flow is generally strong over small spatial scales, which is thought to inhibit the formation of landscape-level variation on small islands (Wright 1943; Lenormand 2002). Consequently, species on smaller islands are often treated as homogeneous populations. Yet, a growing literature on 'microgeographic' differentiation (i.e., differentiation within dispersal capabilities of a species) in genetics, phenotypes, ecology, and abundance have challenged this paradigm (e.g., Malhotra and Thorpe 1991; Richardson et al. 2014; Denney et al. 2020; Scotti et al. 2023; Yuan et al. 2023). Characterizing this microgeographic differentiation has implications for our understanding of evolutionary dynamics on small islands.

Many oceanic islands are volcanic in origin, which can generate topographically complex landscapes over short spatial distances. Variable topology can in turn lead to high degree of variation in both abiotic and biotic heterogeneity that shapes patterns of abundance, genetic structure, and demography across the landscape (Wang and Bradburd 2014; Chandler and Hepinstall-Cymerman 2016; Gurevitch et al. 2016). For example, mountainous terrain can generate population structure by inhibiting gene flow and increasing genetic drift across the landscape due to topography directly (Wright 1943; Wang 2009; Steinbauer et al. 2012; Irl et al. 2015; Verboom et al. 2015) or because of its impact on other environmental variables such as climate and habitat (Wang 2013; Wang et al. 2013; Wang and Bradburd 2014). Species that respond differently to environmental variation across the landscape are also likely to exhibit variation in local abundance (Renjifo 2001; Young and Carr 2015; Chandler and Hepinstall-

Cymerman 2016; Jesse et al. 2018). Furthermore, community composition also varies in heterogeneous landscapes leading to situations in which local abundances and population structure of a given species are shaped by the local influence of their competitors or predators (Andren 1992; Buckley and Roughgarden 2005; Kahilainen et al. 2014). Finally, islands inhabited by humans are also subject to strong land use pressure, which can alter the existing environmental landscape (Graham et al. 2017). For species with limited urban tolerance, changes in land use can lead to population declines (Selwood et al. 2015) and reduced gene flow from habitat fragmentation (Young et al. 1996; Alcaide et al. 2009; Burriel-Carranza et al. 2024). The ability for any of these environmental features to form population structure is influenced by historical demographic fluctuations which can strengthen or weaken the relative effects of genetic drift, gene flow, and selection (Slatkin and Hudson 1991; Slatkin 1993; Hutchison and Templeton 1999). Understanding how species respond to heterogeneous landscapes is vital to our understanding of evolutionary biology and informing conservation management. Integrative studies drawing from a range of ecological and genomic data can provide valuable insights into how species respond to different levels of landscape level variation.

Here, we assess landscape-level population abundance, genetic structure, and historical demography of the bearded anole, *Anolis pogus*, a species of conservation concern endemic to the island of St. Martin (Powell et al. 2020). *Anolis pogus* is a protected species under both Sint Maarten and French regulations that was recently moved from Vulnerable to Near Threatened on the IUCN Red List (Powell et al. 2020). Still, both Red List assessments were based on limited empirical studies. Given the fluctuating conservation status and consistent patterns of microgeographic variation in its regional congenerics (Stenson et al. 2002; Jung et al. 2024), this species presents a compelling opportunity to examine microgeographic drivers of abundance and

genetic structure in a species of conservation concern. Although the island of St. Martin is only ~87 km^2, the co-distributed *Anolis gingivinus* exhibits isolation-by-distance at this scale (Jung et al. 2024) as do several other Lesser Antillean animals distributed on similarly sized islands (e.g., Stenson et al. 2002; Yuan et al. 2022; Daniel et al. 2023). Furthermore, several Lesser Antillean anoles exhibit variable abundance across the landscape in relation to habitat (Buckley and Roughgarden 2005). Observational reports suggest that *A. pogus* abundances are higher at forested sites (Lazell 1972; Schwartz and Henderson 1991; Powell et al. 2005). However, systematic assessments of potential drivers of abundance variation in *A. pogus* are sparse (Jesse et al. 2018) despite being fundamental for understanding the species' ecology and identifying target areas for potential conservation. Finally, *A. pogus* and *A. gingivinus* are strong competitors (Pacala and Roughgarden 1982, 1985), with *A. gingivinus* thought to be more open canopy and urban adapted despite the two species overlapping throughout the entirety of their ranges on St. Martin (Eaton et al. 2002; Powell et al. 2005). On St. Kitts and Grenada, habitat partitioning between their two anole species drives differential abundances across the landscape (Buckley and Roughgarden 2005). Because habitat partitioning also occurs on St. Martin with *A. pogus* preferring shaded microhabitats in sympatry (Pacala and Roughgarden 1982, 1985), we expect *A. pogus* abundances to be higher in forest habitats where competition from the more open canopy adapted *A. gingivinus* should be weaker. These dynamics may have shifted over time due to historical changes in landcover, allowing us to compare the effects of competition and urbanization on genetic structure and demographic trends. In particular, we predict that European arrival on St. Martin caused population declines in *A. pogus* due to deforestation associated with sugar plantation agriculture and urbanization (Boldingh 1909; Watts 1993) as well as increased competition with the urban tolerant *A. gingivinus*.

Overall, our study has three main aims. First, we tested the hypothesis that *A. pogus* abundances are higher in forested sites across the landscape. Second, we tested the hypothesis that *A. pogus* exhibits microgeographic population structure similar to other species of Lesser Antillean anoles. Third, we inferred recent demographic history in *A. pogus* and *A. gingivinus* with the expectation that the former has experienced recent declines due to deforestation whereas the latter did not. We discuss the implications of our results for the conservation of *A. pogus* and for our understanding of the interaction between demography and landscape-level ecology and genomics.

Methods

Abundance-based species distribution modeling

We performed abundance-based species distribution modeling using data collected from 100 plots (80 m^2) surveyed between 30 November 2018 until 08 February 2019 and distributed throughout the island of St. Martin (Fig 1B). Surveys followed the protocol of McDiarmid et al. (2012). In brief, plots were 8x10m and visually surveyed by walking parallel 10m transects for 40 person minutes. We surveyed all plots during daylight hours (between 0830 and 1800 hours). All survey plots were separated by a minimum of 100m. We determined abundance as the number of *A. pogus* encountered in each plot. We also included 12 additional absence-only sites that were extensively surveyed (>2 person hours) explicitly for *A. pogus* as part of our genetic sampling. We performed analyses with and without these absence-only sites to determine their influence on our results. As environmental layers, we downloaded global canopy cover (Hansen et al. 2013), mean annual temperature (BIO1) and temperature seasonality (BIO4) from WorldClim2 (Fick and Hijmans 2017), land use from WorldCover2.1 (Zanaga et al. 2022), and

126 elevation from the Shuttle Radar Topography Mission (SRTM) (Farr and Kobrick 2000). We
127 converted land use data into urban coverage using the proportion of cells classified as 'built-up'.
128 All predictor rasters were resampled to 1 arc-second resolution. We selected environmental
129 variables based on previous hypotheses about the preferred habitat of *A. pogus*. Specifically, that
130 the species preferred upland, closed canopy, and cooler sites (Lazell 1972). We included
131 urbanization due to our particular interest in the influence of land use on this species. For
132 distribution modeling, we extracted values from each raster layer for all survey plots.
133 We constructed abundance-based species distribution models using two approaches:
134 random forest (RF) and Generalized Linear Model (GLM). We treated abundance data as per
135 plot using the centroid of the plot as its location. For RF models, we assessed variable
136 importance as the decrease in mean squared error (MSE) and selected important variables using
137 the *Boruta* package (Kursa and Rudnicki 2010). This method iteratively compares each variable
138 importance with random importance generated by permuting across variables. Variables that are
139 less important than random are progressively dropped until only important variables remain.
140 Because urbanization and elevation were negatively correlated ($\rho = -0.432$), we tested their
141 importance both together and separately. Collinearity can influence estimates of importance;
142 however, RF models should otherwise be robust to collinearity (Breiman 2001). Thus, we still
143 included both variables in our model fit. We fit our RF model using 1000 trees and a mtry of 1
144 (mtry is the number of variables sampled as candidates at each split in a RF model). For our
145 GLM approach, we first assessed dispersion using a Poisson distribution. Because our full model
146 using a Poisson distribution was substantially over-dispersed (dispersion = 3.25), we fit our
147 GLM using a negative binomial distribution (dispersion = 0.93). To allow more direct
148 comparison, we refit each of our RF and GLM models using the inclusive set of variables

149 determined as important in our RF or significant in our GLM. We used each of our refit models
150 to predict the abundance of *A. pogus* across the landscape of St. Martin. We assessed the
151 accuracy of our models using out-of-bag validation for RF (Breiman 2001) as well as using 20%
152 of our data as validation for both RF and GLM. Accuracy was calculated as root mean squared
153 error (RMSE). Analyses were performed in R v4.3.2. We performed RF analyses using the
154 *randomForest* package (Liaw & Weiner 2002) and GLM analyses using the *MASS* package
155 (Venables and Ripley 2002).
156
157 *Whole genome sequencing*
158 To characterize population structure and landscape genomics, we implemented a low
159 coverage whole genome sequencing (WGS) approach. Between 2018 and 2023, we sampled 54
160 tail tips from *A. pogus* on the island of St. Martin (Fig 2). We also included 8 samples of the co-
161 distributed *A. gingivinus* (3 from Anguilla and 5 from St. Martin) to assess comparative historical
162 demography as described below. The population structure and landscape genetics of *A.*
163 *gingivinus* on St. Martin is described elsewhere (Jung et al. 2024). We extracted whole genomic
164 DNA from these tissues using the Qiagen DNeasy Blood & Tissue Kit. We prepared whole
165 genome sequencing libraries using $1/4^{th}$ reactions of the NEBNext Ultra II FS DNA Library Prep
166 Kit. We then performed 150bp paired-end sequencing on the Illumina Novaseq X platform.
167 Following QC and adapter trimming, we aligned raw reads to the *A. sagrei* genome (AnoSag2.1;
168 Geneva et al. 2022) using BWA-MEM (Li 2013). After removing PCR duplicates, we called
169 SNPs in ANGSD (Korneliussen et al. 2014) retaining SNPs present in a minimum of 90% of
170 samples, having a minimum of 108X pooled coverage, and a *P*-value less than 10^{-6}. We

171 estimated SAMtools model genotype likelihoods (Li 2011) which were incorporated into all
172 downstream genomic analyses unless otherwise stated.
173
174 *Genetic Diversity*
175 We calculated metrics of genetic diversity to assess the conservation status of *A. pogus*.
176 Using the folded SFS calculated in realSFS (Nielsen et al. 2012), we determined genome-wide
177 Tajima's D and nucleotide diversity (π) across all samples. We also assessed average inbreeding
178 coefficients (Jacquard 1974) and pairwise relatedness in ngsRelate (Korneliussen and Moltke
179 2015). Relatedness estimates were used to determine if sibling, or equivalent, pairs (i.e., $r > 0.5$)
180 were sampled which may influence our other analyses. As another estimate of potential
181 inbreeding, we assessed runs of homozygosity (ROH) using bcftools (Narasimhan et al. 2016).
182
183 *Population structure and landscape genomics*
184 We assessed overall population structure agnostic of landscape features using several
185 methods. First, we performed a principal component analysis (PCA) using genome-wide allele
186 frequencies in PCAngsd. Second, we performed multidimensional scaling (MDS) using the
187 identity-by-state (IBS) matrix generated in ANGSD. Third, we conducted admixture analyses
188 using NGSadmix for ten iterations of $K = 1$ through $K = 6$. We then selected a best K using the
189 ΔK likelihood method from Evanno et al. (2005).
190 Next, we used landscape genomics methods to assess the effect of environmental
191 variation on genetic diversity. We then compared the relative effects of isolation-by-distance and
192 isolation-by-environment using multiple matrix regression with randomization (MMRR) (Wang
193 2013). Following the theoretical framework of Hutchison and Templeton (1999), we graphically

assessed the relationship between genetic and environmental distance to determine if gene flow and genetic drift were in equilibrium using the *graph4lg* package in R (Savary et al. 2021). We calculated genomic distance as both IBS in ANGSD and raw p-distances in ngsDist (Vieira et al. 2016). We converted IBS from a similarity to a dissimilarity matrix using 1-IBS for ease of interpretation. To compare with our abundance modeling results, we selected the same set of predictor variables for tests of IBE.

Additionally, we estimated effective migration surfaces (EEMS) across the island of St. Martin (Petkova et al. 2016). This method models continuous genetic diversity across a specified landscape and is based on a stepping-stone model where migration is modeled between demes with migration rates varying by location. Using the genetic dissimilarity matrix calculated from ngsDist, we ran EEMS using a deme size of 400, with three independent starting chains for $2x10^6$ MCMC iterations following an initial burn-in of $1x10^6$ and thinning of 9,999. Posterior plots were compared across the three independent runs to ensure convergence, these three runs were then combined and visualized in the *reemsplots2* R package (https://github.com/dipetkov/reemsplots2).

Demographic modeling

To assess the demographic history of *A. pogus* and *A. gingivinus* on the island of St. Martin, we used ngsPSMC (Shchur et al. 2017). This method allowed us to incorporate genotype likelihood values into our demographic reconstruction. We estimated θ as $2N_0\mu$*bin where N_0 was 10,000, bin size was 100, and μ was 1.73×10^{-9}. Mutation rate, μ, was the average estimated rates from the genomes of six species of anoles (Kanamori et al. 2022). We set recombination rate, ρ, as 0.002 (Bourgeois et al. 2019; Moran et al. 2024). We scaled our results using a

generation time of 1 year (Kanamori et al. 2022). PSMC methods produce estimates of demographic history using a single genome. However, because ngsPSMC cannot currently perform bootstrapping, we assessed if demographic patterns were consistent across multiple individuals (e.g., Sarabia *et al.* 2020; Moran *et al.* 2023). Specifically, we analyzed 6 *A. pogus* with the highest coverage (>5X) distributed across the island using 20 iterations each and a PSMC pattern of 4+30*2+4+6+10 (Nadachowska-Brzyska et al. 2015; Kanamori et al. 2022). For *A. gingivinus*, we analyzed 5 individuals from St. Martin and 3 from Anguilla using the same parameters. All *A. gingivinus* individuals had coverage >10X and we selected higher coverage individuals of *A. pogus* to improve performance. Our sample size is consistent with general implementation of these methods (e.g., Sarabia *et al.* 2020; Moran *et al.* 2023).

Mitogenome analyses

To compare with nuclear genomic results, we reconstructed the mitogenome for each individual from our WGS data. We implemented a two-step approach to generating whole reference mitogenomes. First, we aligned reads from a single individual to a whole mitochondrial reference genome for *A. schwartzi* (Yuan ML, unpublished data) using BWA-MEM. Both species are part of the *A. wattsi* species complex and are closely related (Lazell 1972). This process yielded an incomplete and non-contiguous mitochondrial genome spanning ~82% of the *A. schwartzi* mitogenome. Second, we used our first pass assembly as a bait to refine the *A. pogus* mitogenome (1096X coverage) for the same individual using MITObim (Hahn et al. 2013). We then mapped reads for each individual to our final reference mitogenome.

We analyzed our mitochondrial data using consensus genotypes. These mitogenomic analyses were intended to directly complement our nuclear genomic analyses described above.

We calculated π and Tajima's D across all samples. To assess IBD and IBE, we calculated Kimura's three-parameter distance (Kimura 1981) and fit MMRR models following our genomic data analyses. We estimated the mitogenome phylogeny using BEAST2 (Bouckaert et al. 2014). To calculate divergence times, we implemented a random local clock using a 1.3% divergence per million years rate estimated for vertebrate mitochondria (Macey et al. 1998), a GTR+I substitution model selected by PartitionFinder2 (Lanfear et al. 2017), and a coalescent exponential tree prior.

Results

Abundance-based species distribution modeling

Our GLM and RF models were largely concordant with each other. We also found that models were similar whether or not additional absence-only sites were included. Thus, we only report results of our full dataset. For our RF models, we found that urbanization, canopy cover, and elevation were important. Urbanization was marginally supported in the full model (Fig 1A), but significantly supported when excluding collinear elevation (Fig S1). Our full RFmodel explained 23.59% of variation (out-of-bag RMSE = 3.52; validation RMSE = 2.87). Canopy cover was the primary predictor of *A. pogus* abundance on St. Martin (28.94%) with higher abundance in sites with more closed canopy (Fig 1A-C). Abundance was also higher in higher elevation (17.05%) and less urbanized sites (8.54%). In our GLM models, only canopy cover ($z = 3.28$; $P = 0.001$) and urbanization ($z = -2.55$; $P = 0.011$) were significant predictors of abundance. Specifically, *A. pogus* was more abundant in closed canopy and less urbanized sites. Our validation data estimated an RMSE of 3.42 for our GLM.

Genetic Diversity

Our *A. pogus* WGS data had an average mapped coverage of 3.35X and an average mapping efficiency of 94.9% to the *A. sagrei* genome. Nucleotide diversity per chromosome ranged from 0.014 to 0.016. We recovered low levels of relatedness ranging from 0 to 0.095 across our sampling. Thus, we did not remove any samples for being closely related. Mean pairwise relatedness was 0.0255 ± 0.0004. Inbreeding coefficients were also low across our sampling with a mean of 0.0024 ± 0.0023 and a range of 0 to 0.122. Our ROH analyses are consistent with our estimated inbreeding coefficients (mean F_{ROH} = 0.0037 ± 0.0020). We did not find any ROH greater than 1Mbp and only 28 individuals had ROH greater than 100 kbp.

Population structure and landscape genomics

Spatial clustering was not evident in our PCA, MDS, or admixture analyses (best K = 5; Fig 2, S2). Consistent with these results, we found no evidence for either IBD or IBE using either p-distances (MMRR: R^2 = 0.036, P = 0.678, Table 1) or IBS (MMRR: R^2 = 0.013, P = 0.830, Table 1). Our graphical analyses also showed no pattern of IBD (Fig 3B). Rather, the overall curve followed a case II curve which is characterized by a relatively horizontal slope with a tight overall spread of genetic distances and implies a dominance of gene flow over drift (i.e., panmixia; Hutchison and Templeton 1999). Estimated effective migration surfaces suggest that the variation in gene flow across St. Martin is low (Fig S3). Regions where gene flow is suggested to be reduced correspond to regions inferred to having lower abundances of *A. pogus*, likely associated with lower elevation and less canopy cover in these areas (Fig 1B-C).

Demographic modeling

We found consistent support for recent population expansion in *A. pogus* among our demographic analyses. Tajima's D was negative across chromosomes (range: -1.13 to -1.02). We inferred consistent demographic histories from ngsPSMC across all six individuals suggesting relatively robust results. We inferred two periods of major population expansion (Fig 3A). The older expansion occurred during the Pleistocene from ~55–80 kya and was followed by a major population decline from ~10–55 kya, both during the last glacial period. The most recent population expansion began during the Holocene ~2–3 kya and persists to the present. For *A. gingivinus*, our ngsPSMC analyses inferred historical population declines from ~30–80 kya and ~3000 kya to the present. We also inferred a population expansion from ~3–26 kya. Our results for *A. gingivinus* were similar for the Anguilla and St. Martin populations.

Mitochondrial comparison

Mitogenome nucleotide diversity was 0.004. Consistent with our nuclear results, we recovered no mitochondrial spatial structure across the island of St. Martin for *A. pogus*. Specifically, we did not find evidence of either IBD or IBE (MMRR: $R^2 = 0.006$, $P = 0.951$, Table 1). Our mitogenome phylogeny was well-supported but clades did not correspond to populations or geographic regions (Fig 2). The last common mitochondrial ancestor of our extant samples was estimated to 1.80 Ma [1.62–1.98 Ma]. As with our genomic results, our mitochondrial analyses also detected signatures of a recent population expansion (Tajima's D = -2.19).

Discussion

We did not find evidence of range restriction, population decline, or genetic structure in *A. pogus* on the island of St. Martin. Rather, *A. pogus* was inferred to occur broadly throughout the island, albeit with variable abundances primarily predicted by canopy cover. The species was also inferred to be undergoing a recent demographic expansion that likely has not reached equilibrium with genetic drift, resulting in panmixia. In comparison, the more widespread, urban adapted (Lazell 1972; Schwartz and Henderson 1991; Eaton et al. 2002; Powell et al. 2005), and spatially-structured (Yuan et al. 2023; Jung et al. 2024) *A. gingivinus* exhibited an unexpected signal of recent population decline both on St. Martin and on neighboring Anguilla. We discuss our findings and how they inform our understanding of the interaction between microgeographic adaptation, interspecific competition, and demographic responses to shared stressors in the system.

Landscape ecology and genomics

Although *A. pogus* exhibited microgeographic patterns of increased abundance with increasing canopy cover, we did not find any evidence of population structure or landscape effects in *A. pogus* for either our nuclear genomic or mitogenomic data (Fig 2, Table 1). This lack of microgeographic genomic structure may not be surprising as gene flow is expected to be stronger across short distances (Wright 1943) and St. Martin is only ~87 km^2. Yet, microgeographic population structure has been documented in several species on small islands (Richardson et al. 2014; Cheek et al. 2022). In particular, several other Lesser Antillean species display patterns of within-island microgeographic structure including other anoles (Stenson et al. 2002; Jung et al. 2024; McGreevy et al. 2024), *Setophaga plumbea* warblers (Daniel et al. 2023), and *Eleutherodactylus* whistling frogs (Yuan et al. 2022; Myers et al. 2024). In particular, our *A.*

pogus results contrast with previous work that found IBD in *A. gingivinus* co-distributed on the island of St. Martin (Jung et al. 2024). It is possible that this difference could arise from greater dispersal propensity (i.e. stronger gene flow) in *A. pogus* compared to *A. gingivinus*. To our knowledge, the relative dispersal capabilities for these species have not yet been characterized. Alternatively, the contrasting spatial genetic patterns between *A. gingivinus* and *A. pogus* may reflect their different recent demographic histories. Notably, we recovered a signal of rapid recent population growth in *A. pogus* that coincides with population decline in *A. gingivinus* (Fig 3A).

Rapid population growth following a bottleneck can result in little to no population structure (Slatkin and Hudson 1991; Slatkin 1993; Milà et al. 2000; Tolley et al. 2005). Following population expansion, gene flow and genetic drift are predicted to be in disequilibrium. Indeed, our observed relationship between genetic and geographic distance is consistent with disequilibrium between gene flow and genetic drift in which gene flow predominates (Fig 3B). Furthermore, we observed a strong potential demographic bottleneck in *A. pogus* beginning during the last Pleistocene glacial period and persisting until ~3000 years ago when the population began to expand (Fig 3A). By contrast, *A. gingivinus* has experienced a dramatic population decline beginning around ~3000 years ago that followed a rapid population expansion exiting the Last Glacial Maximum (LGM). Because population declines often reduce local genetic variation (Frankham 1996), they may heighten rather than lessen population structure by increasing the effect of drift (Young et al. 1996; Alcaide et al. 2009). Thus, population structure in *A. gingivinus* may be reflective of either structure that has accumulated since the LGM or a result of elevated drift during recent population decline. In any case, our data

353 suggest that accounting for recent demographic histories is likely important for contextualizing
354 extant genomic structuring at a fine geographic scale.

355 Although, we did not observe genetic structure in either the nuclear or mitochondrial
356 genomic datasets for *A. pogus*, we found that landscape features did predict differences in
357 relative abundances in this species across St. Martin (Fig 1). Our findings that canopy cover best
358 predicted the local abundance of *A. pogus* supports previously reported natural history
359 observations (Lazell 1972; Schwartz and Henderson 1991; Powell et al. 2005) and available
360 survey data (Jesse et al. 2018). On other Lesser Antillean islands with two anole species (i.e., St.
361 Kitts and Grenada), competition suppresses local abundance beyond what would be predicted by
362 bioenergetic models (Buckley and Roughgarden 2005). Thus, the high abundance of *A.*
363 *gingivinus* in open canopy habitats (Lazell 1972; Schwartz and Henderson 1991; Eaton et al.
364 2002; Powell et al. 2005) likely further suppresses the population of *A. pogus* that would
365 otherwise occur. Unfortunately, we could not directly assess the influence of competition on *A.*
366 *pogus* abundances because we lacked survey data for *A. gingivinus* but our results suggest that
367 further investigations of competition between the species may be fruitful.

368 Like abundances, other ecological features may also respond more rapidly than genetic
369 structure to environmental variation following major demographic events. For example,
370 epigenetics (Wogan et al. 2020), microbiomes (Yuan et al. 2015; Couch and Epps 2022), and
371 morphology (Malhotra and Thorpe 1991; Yuan et al. 2023), can exhibit microgeographic
372 variation despite a lack of concordant genomic structure. Indeed, *A. gingivinus* displays variation
373 in dorsal coloration in response to environment that is not predicted by background population
374 structure (Yuan et al. 2023; Jung et al. 2024). Whether this phenomenon is shared in *A. pogus*
375 has not been formally tested. Expanding our view of these phenotypes are likely to be fruitful

avenues of research for understanding landscape ecology following major demographic expansions or contractions.

Demographic response to the Anthropocene

Our demographic models indicated that *A. pogus* and *A. gingivinus* do not follow the same population trends. Both species showed population declines during the last glacial period, perhaps due to shared environmental pressures. However, only *A. gingivinus* experienced demographic expansion following the LGM. This pattern is somewhat unexpected given that total land area of St. Martin was larger during the last glacial period and subsequently shrunk throughout the Holocene. Island area effects would generally predict that carrying capacity should be higher for larger islands (Connor et al. 2000); however, other factors such as habitat suitability and competitive interactions may have greater impacts on carrying capacity than simply island size. Because we lack systematic abundance data for *A. gingivinus* and historical habitat data is limited, we cannot assess current or past habitat suitability for this species to compare with that of *A. pogus*. With respect to competition, however, fossil evidence suggests a dramatic increase in relative *A. gingivinus* abundance on Anguilla coincident with the extinction of predatory *Leiocephalus* lizards approximately 9 thousand years ago (Kemp and Hadly 2016). Thus, population expansion in *A. gingivinus* may be due to shifts in the overall community composition during the early Holocene.

More recently, we infered a decline in *A. gingivinus* and a population expansion in *A. pogus* following human arrival on St. Martin an estimated 5,000 years before present (Napolitano et al. 2019). *Anolis gingivinus* is thought to be better adapted to human commensal living (Powell et al. 2005) and deforestation throughout the Holocene, particularly acute

following European arrival (Boldingh 1909; Watts 1993), would have increased their preferred open canopy area (Lazell 1972; Eaton et al. 2002). Correspondingly, we predicted that *A. gingivinus* should have expanded and *A. pogus* contracted during the human-occupied period. Yet, we recovered the opposite pattern. Recent work has highlighted that tolerance for urbanization does not necessarily mean species are insulated from population declines (Moran et al. 2024; Petrenko et al. 2024). Our study provides further evidence that human activity can have counterintuitive effects on species including leading to declines despite their apparent ability to inhabit urban environments.

With respect to the divergence in the demographic responses of *A. gingivinus* and *A. pogus* to a shared history, one explanation is that ecological partitioning impacted how each species responded to changes in habitat distribution or overall community structure (Pacala and Roughgarden 1982). An alternative explanation is that interspecific competition with *A. gingivinus* drove population trends in *A. pogus*. Evidence for competition between Lesser Antillean anoles is strong and comes from both observational, modeling, and experimental data (Pacala and Roughgarden 1982, 1985; Losos 1990). Further, there is evidence that competition between *A. pogus* and *A. gingivinus* is the strongest among Lesser Antillean anole communities because they have undergone less niche partitioning. Lesser Antillean anoles exhibit strong body size partitioning on islands with two species, but this pattern is weakest on St. Martin (Losos 1990) and experiments have shown that the fitness consequences of competition between *A. pogus* and *A. gingivinus* exceeds that of other Lesser Antillean anole species pairs (Pacala and Roughgarden 1982, 1985).

We found similar recent demographic histories for *A. gingivinus* on Anguilla (where *A. pogus* is absent) and those on St. Martin (where *A. pogus* is present), suggesting that *A. gingivinus*

422 populations are responding to broader patterns influencing the region rather than responding
423 directly to *A. pogus* (Fig 3A). Previous work by Schall (1992) posited that coexistence between
424 *A. gingivinus* and *A. pogus* may be mediated by *Plasmodium* infection rates. Originally, this
425 hypothesis was supported by greater susceptibility to *Plasmodium* parasites in *A. gingivinus* and
426 greater densities of *A. pogus* in habitats with higher parasite pressure. As anole infecting
427 *Plasmodium* have largely disappeared from St. Martin (Perkins 2001), *A. pogus* should have
428 recently declined if this hypothesis was true. Yet, we observe the opposite pattern of increasing
429 *A. pogus* and decreasing *A. gingivinus* despite the decline of *Plasmodium*.Thus, we argue the
430 countervailing population trends in *A. pogus* are likely due to increased competition due to the
431 expansion of *A. gingivinus* in the early Holocene and the subsequent decline of *A. gingivinus*
432 following human arrival in the region.
433
434 *Relevance to Conservation*
435 Widespread deforestation for agriculture during the colonial period (Boldingh 1909;
436 Watts 1993) does not appear to have had a major impact on demographic trends in *A. pogus*.
437 Furthermore, the genomic signatures of population expansion into the present are supported by
438 the limited available census data (Schwartz and Henderson 1991; Powell 2006). In addition to
439 population demographic growth, overall genomic diversity appears to be strong and estimated
440 inbreeding is extremely low. Thus, it appears that the population of *A. pogus* on St. Martin is
441 both demographically expanding and exhibits low genome-wide inbreeding. Overall, our data
442 support the recent reclassification of *A. pogus* from Vulnerable to Near Threatened on the IUCN
443 Red List (Powell et al. 2020). Our study, along with the IUCN reclassification, indicates that *A.*
444 *pogus* does not require the heightened level of protection it is currently afforded. This case study

highlights the value in conducting studies of species assumed to be of conservation concern based on limited empirical data. When conservation resources are scare, they may be better served on other species. We note, however, that the long-term population stability of *A. pogus* is more likely if forested habitats are preserved given that the species occurs at lower abundances in degraded habitat including urban environments. Conservation of forested habitats should produce positive outcomes beyond *A. pogus* as deforestation appears to have broad negative impacts on many of St. Martin's other native species (Jesse et al. 2018).

Conclusion

All together, we present evidence that *A. pogus* consists of a panmictic island-wide population that is demographically expanding and does not show signs of reduced genetic diversity or high levels of inbreeding that might be expected from a bottleneck. (Fig 2, 3B). The lack of population structure was in contrast to the co-distributed *A. gingivinus* (Jung et al. 2024). We posit that this difference is likely due to different recent demographic histories in which *A. gingivinus* has declined despite being more urban-adapted and *A. pogus* has expanded, perhaps due to its declining competitor (Fig 3A). Furthermore, we show that the landscape of human activity can sometimes be less important than major historical demographic events for determining extant population structure and demography. In particular, we highlight the value in considering species interactions in relation to anthropogenic stressors.

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Data Availability

Raw sequence data are accessioned in SRA (PRJNA1278788). All other data are accessioned in Dryad and code in Zenodo (DOI:10.5061/dryad.59zw3r2mg).

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731

Figure Captions

Fig 1 (A) Boxplots of importance for each variable (%decrease in MSE) in our full RF models. Minimum, mean, and maximum null values are also shown. Variables are colored by importance assessment: green – important, yellow – marginally important, and orange – not important. (B) Predicted abundance across the landscape of St. Martin based on important variable (canopy cover + elevation + urbanization) RF model. Abundance survey plots are shown as magenta points. (C) Predicted abundance across St. Martin based on GLM.

Fig 2 Above: PCA and MDS plots generated from WGS data for *A. pogus* sampled throughout the island of St. Martin. Individuals are labeled by collecting locality which corresponds to the map below. Below: dated mitogenome phylogeny of *A. pogus* on the island of St. Martin. Tips are connected to sampling locality on a canopy cover map of St. Martin. Nodes with a posterior probability above 0.98 are denoted by grey circles.

Fig 3 (A) Inferred demographic history from ngsPSMC for *A. pogus* and *A. gingivinus*. For *A. gingivinus* overall demographic patterns are consistent between Anguilla and St. Martin. Events of potential interest (European arrival, human arrival, and the LGM) are denoted. (B) Relationship between genetic and geographic distance including the 95% confidence interval as determined by *graph4lg* for *A. pogus* on St. Martin. Geographic distance is shown in meters.

Tables

Table 1 MMRR models of correlations between either (I) genomic or (II) mitogenomic distance with geographic and environmental distances. Environmental variables tested are canopy cover, elevation, urbanization, mean annual temperature (BIO1), and isothermality (BIO4). For each model, individual coefficients and P-values for each predictor variables are shown.

I. Genomic		
	Coeff	*P*
Geographic	-0.073	0.602
Canopy Cover	-0.037	0.468
Elevation	-0.060	0.650
Urbanization	0.149	0.114
Annual Temperature	-0.069	0.662
Isothermality	0.107	0.412
II. Mitogenomic		
	Coeff	*P*
Geographic	-0.031	0.807
Canopy Cover	0.035	0.353
Elevation	-0.024	0.686
Urbanization	0.014	0.831
Annual Temperature	-0.048	0.699
Isothermality	0.027	0.746