Systemic racism alters wildlife genetic diversity

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Abstract: Humans are the defining feature of urban ecosystems. In the United States, systemic racism has had lasting effects on the structure of cities, specifically due to government-mandated "redlining" policies that produced racially segregated neighborhoods that persist today. However, it is not known whether varying habitat structure and natural resource availability associated with racial segregation affects the demographics and evolution of urban wildlife populations. We repurposed public nuclear genetic data from 7,698 individuals from 39 terrestrial vertebrate species sampled in 268 urban locations and found patterns of reduced genetic diversity due to low population sizes and decreased connectivity in neighborhoods with fewer white residents. This suggests that systemic racism alters the demography of urban wildlife populations in ways that limit population sizes and negatively affects their chances of persistence. Limited capacity to support large, well-connected wildlife populations reduces access to nature and builds on existing environmental inequities shouldered by predominantly non-white neighborhoods.

Introduction

Historic and ongoing systemic racism and racial segregation have played a prominent role in the development and structure of cities in the United States (1, 2). One of the most direct causes of racial segregation was the government-sponsored practice of *redlining*, which graded neighborhoods based on desirability and systematically excluded racial and ethnic minorities—namely Black Americans—from homeownership in better-ranked neighborhoods. During the suburb boom in the 1950s, discriminatory redlining policies and practices related to lending, insurance, zoning, and public housing collectively encouraged white Americans to move into new suburban communities and simultaneously pushed Black Americans and other racial and ethnic minorities to reside towards urban cores (2). Lower-ranking redlined neighborhoods subsequently received less public investment and typically became densely populated, had more industrial infrastructure, and less green space (reviewed in 1, 2). Racial segregation and spatial isolation were often reinforced by physical barriers such as highways, railroad tracks, and sometimes walls (2). These practices, although outlawed in the Fair Housing Act of 1968, created a socially-structured urban geography associated with socioeconomic and environmental inequality that persists in American cities today (2, 3).

Ecological and evolutionary effects of systemic racism

Accumulating knowledge of the effects of systemic racism on the structure of urban environments now allows us to explore its effects on the ecology and evolution of urban wildlife. In a comprehensive review, Schell et al. (1) showed that socioeconomic decision-making and racial inequality have created environmental conditions that can alter the distribution and demography of wildlife in cities in ways that should cause evolutionary change (1, 4). However, these ideas have received little empirical attention. Residential racial segregation creates disparities in natural resource availability, land use, pollution, and habitat connectivity, such that neighborhoods that historically excluded minorities tend to be better wildlife habitat (1). This means that local environmental carrying capacities in cities are likely predicted by the racial makeup of neighborhoods. In general, larger, more connected populations have better chances of persisting because they are less strongly affected by genetic drift and have higher genetic diversity. Cities are now the primary place where people interact with and benefit from nature (5), and their design is becoming increasingly important for the conservation of native biodiversity (6). Managing wildlife for conservation and human well-being requires a comprehensive understanding of eco-evolutionary processes in cities, and this extends to identifying the ways that human social patterns shape evolution in urban wildlife.

We test the hypothesis that systemic racism produces urban environments that alter population demography and thus evolutionary change in city-dwelling populations of amphibians, birds, mammals, and reptiles across the continental United States. It is now clear that urbanization and human land use generally affect the genetic composition of wildlife populations when compared to populations in more natural environments, although directions of effect can vary (7–9). How ecological and evolutionary processes shape genetic diversity within cities is less well understood. We predicted that levels of genetic diversity and connectivity among urban wildlife populations would vary with the racial composition of neighborhoods, increasing in predominantly white, less environmentally disturbed areas. The effect of systemic racism on ecological and evolutionary change in urban wildlife will be likely mediated by differential resource distribution and habitat degradation (1). We explored this idea by testing the effects of the racial composition of neighborhoods on genetic diversity alone, and while statistically controlling for habitat degradation measured by the Human Footprint Index (10). Our prediction here is that general patterns of environmental degradation captured by the racial composition of neighborhoods will have generally detectable effects on genetic diversity across species, although these effects are unlikely to be strong because other features of urbanization will also affect genetic diversity—often in species-specific ways. Explaining all effects of urbanization on genetic diversity is beyond the scope of this paper and likely not possible to do in a way that is generalizable across species (9, 11).

Residential segregation has also contributed to the present marked wealth disparities across racial groups in the United States (12, 13). The ecological effects of wealth on wildlife can be notable. Wealth, or the “luxury effect”, alters habitat quality, population dynamics, and the species composition of urban wildlife communities. However, the strength of the luxury effect varies regionally and across taxa (1, 14, 15). Additionally, the greatest disparities in urban forest cover across the racial mosaic appear on public, rather than private land, reflecting the effect of biased municipal investment in communities rather than the effects of individual wealth (3). For these reasons the environmental effects of structural racism cannot be captured by neighborhood wealth alone, and here we focus on habitat disturbance more generally.

Quantifying genetic diversity in terrestrial vertebrates

We tested our hypothesis by building a database of georeferenced publicly archived, raw, neutral microsatellite data sets (Fig. 1; Methods; 9). We aggregated 7,698 individual genotypes from 8 amphibian, 14 bird, 15 mammal, and 3 reptile species native to North America. Genetic diversity measured with microsatellites is strongly correlated to genome-wide diversity ($R^2 = 0.83$; 16). Due to a lack of suitable archived SNP data, we focused on microsatellite data sets only, and conducted a systematic search for data in online data repositories in R (17) using a list of terrestrial vertebrate species native to North America (Methods). By repurposing raw data, we were able to consistently calculate our chosen metrics of genetic composition and environmental variation across the entire dataset. For each sample site, we calculated the effective population size of the parental generation using a linkage disequilibrium method (18), gene diversity (19), standardized allelic richness, and genetic divergence using site-specific F_{ST} (20). The effective population size is an estimate of the strength of genetic drift a site experiences. Gene diversity and allelic richness are two measures of genetic diversity, and site-specific F_{ST} was our estimate of relative genetic differentiation among sites. We excluded sites not located within US Census-designated urban areas (21).

We calculated the percentage of residents identifying as white in census blocks located within 0.5, 1, and 5 km of each sample site in our dataset using demographic data from the 2010 US Census (22). We present results from 0.5 km buffers here, but note results were consistent across all scales (Fig. S1). We chose this metric of segregation because white Americans are the most racially separated demographic. According to the 2010 Census, the average white American lives in a predominantly white neighborhood, while other racial groups typically live in more diverse neighborhoods (23). Because the goal of redlining policies was to maintain homogenous, predominantly white communities (2), the proportion of white residents in a neighborhood should broadly capture variation in environmental heterogeneity regardless of regional histories that have shaped the racial composition of neighborhoods in different ways. To test whether the well-established relationship between neighborhood racial composition and habitat disturbance held for our sample sites, we quantified disturbance at each site with the Human Footprint Index (10). The Human Footprint Index measures human-caused habitat transformation from the most wild to the most disturbed. It provides a broad index of habitat degradation by incorporating human population density, roads, railways, access to navigable rivers, built-up areas, land cover, and nighttime lights. The percentage of white residents in a neighborhood was negatively correlated with the Human Footprint Index at our sample sites (Pearson's r = -0.52; 95% confidence interval: -0.60 – -0.43), demonstrating that in our dataset, predominately non-white neighborhoods were located in more disturbed environments.

We tested the relationship between the racial composition of people and the genetic composition of species at sample sites using Bayesian hierarchical models (generalized linear mixed models; 24)(24). We controlled for variation across taxonomic class and species using a random effect structure with random intercepts for species nested in class, and allowed slopes to vary with species (Methods). Here, random slope and intercept models estimate the effect of racial composition on each species, and the distribution of species-specific parameter estimates shrink towards an overall mean, or the effect size across all species. This is a feature of hierarchical models that is highlighted in a multi-species context. Shrinkage allows levels of a random effect to inform each other, yielding more robust estimates of effect size, at the same time detecting general effects across species that may be difficult to detect in single-species analyses (25). Moran's I tests detected no residual spatial autocorrelation in the models, indicating that our models captured spatial variation in genetic diversity well. This suggests there was no detectable spatial structure in model residuals caused by spatial variation in environments or regional histories. The whiteness of a neighborhood captures the environmental variation we are interested in here well.

Effects of racial segregation on genetic variation

We detected consistent relationships between the genetic composition of wildlife and the racial composition of neighborhoods (Fig. 2). Species tended to have larger effective population sizes, higher genetic diversity, and were less genetically differentiated in neighborhoods with higher proportions of white residents (Fig. 2; Table 1; SI Figs. S1-S2). Random effects accounting for species-specific effects captured most of the variation in the model, thus it is clear that species-specific effects of environments are important. In general, our results suggest that demographic and evolutionary processes in urban wildlife vary within US cities in ways that make population persistence in minority neighborhoods more difficult.

We then explored whether the effects of neighborhood racial composition might be mediated by habitat degradation. To test this idea, we fit separate models relating the Human Footprint Index alone, and both the Human Footprint Index and the racial composition of neighborhoods together, to our measures of genetic composition. We used adjusted R^2 values to determine whether models including both racial composition and the Human Footprint Index explained more variation than either covariate alone. The Human Footprint Index was negatively related to genetic diversity, effective population size, and connectivity (Table 1). As expected, the amount of variation explained by racial composition and human disturbance was low across all models (Table S1). For all genetic metrics, the proportion of variance explained by models including both racial composition and the Human Footprint Index was similar to the variation explained using only one of these covariates (Table 1). These results suggest that segregation drives the unequal distribution of resources across neighborhoods within cities, creating landscape heterogeneity that shapes demography and genetic diversity in urban wildlife.

Our results suggest that neighborhoods that are largely non-white support smaller, more fragmented, less genetically diverse wildlife populations. Source-sink dynamics could potentially create this pattern, because wildlife from natural and less disturbed sites further from city centers have limited access to urban cores (1). Notably, the effects of racial composition and habitat degradation on genetic composition were consistent across taxa and cities. Previous multispecies work along urban-rural gradients suggests that mammal populations were generally negatively affected by increasing human disturbance, but responses in birds were species-specific with both increases and decreases in diversity detected (9), and no effects were detected across amphibians (11). When considering habitat variation within US cities, it appears urban wildlife populations, regardless of taxa or location, tend to be larger and harbor higher genetic diversity in the less disturbed habitat patches of predominantly white neighborhoods.

Urban evolutionary ecology research is only beginning to more deeply explore the effects of spatial heterogeneity within cities generated by human social processes (1, 4). In our dataset, 87% of sites were located in predominantly white neighborhoods (>50% residents identifying as white). If we are to fully consider environmental heterogeneity within and across cities to understand the spectrum of ways humans affect their environments, more informed, comprehensive sampling of urban habitat is needed. Research in urban evolutionary ecology will become an increasingly important resource for decision-makers and city planners to make cities sustainable habitats for wildlife while meeting human needs (4). Environmental crises like climate change and biodiversity loss disproportionately affect non-white communities (1). Achieving environmental equity, and ultimately cities that support humans and wildlife alike will require engagement and solutions from a diverse research community. Yet, racial diversity is enduringly low in ecology and evolution (26, 27), fostering blind spots that hold back progress in research that intersects with environmental justice (28).

We have shown that the well-described environmental patterns associated with historic and ongoing racial segregation in US cities (1, 2) have caused parallel patterns in wildlife demography detectable with genetic data. It is clear that systemic racism is altering the demography of urban wildlife populations on a national scale in ways that can shape the evolutionary processes acting on them and the probability of long-term persistence in cities. These results are concerning because urban biodiversity is important for human mental and physical well-being (29), and disparities in access to nature build on existing health-related environmental disamenities in predominantly non-white neighborhoods (1, 30). Equitably distributing and increasing the amount and connectivity of natural habitat in cities can therefore benefit human well-being while simultaneously helping build resilience in urban wildlife.

Methods

Data compilation

To create the database of genetic metrics, we performed 3 systematic searches of online data repositories between 2018 and 2020 using the DataONE interface for R (31) with the keywords “str”, “microsat*”, single tandem*”, “short tandem*”, and species name (e.g. “*Alces alces*”). DataONE is a network of public data repositories, such as Dryad. We used existing datasets described in (9, 11) where detailed methods for dataset assembly can be found. We augmented this dataset in February 2019 with data from reptiles, and in November 2020 with additional mammal data using the same inclusion criteria. In brief we retained datasets with neutral microsatellite datasets sampled from native species located in North America where study design would not influence genetic diversity (e.g., island or managed populations). We retrieved 68 total search results for reptiles, 28 of which were duplicates. In total 11 datasets met our inclusion criteria. For additional mammal data we obtained 37 search results, of which 10 were duplicates and 8 were added to our database. We measured effective population sizes, allelic richness, gene diversity, and population-specific F_{ST} for each sample site from raw microsatellite datasets. We the estimated effective population size of the parental generation using the linkage disequilibrium method in Neestimator (18). We were unable to estimate effective population size when sampling error overwhelmed signals of genetic drift, as is the case when too few individuals were sampled or populations were extremely large. We calculated allelic richness and gene diversity using the hierfstat (32) and adegenet packages in R (33). Allelic richness is sensitive to the number of sampled individuals, thus we standardized this measure to the minimum sample size across the entire dataset (5 individuals; 34). Gene diversity (19) is a heterozygosity metric that is minimally affected by sample size variation (35). Finally, population-specific F_{ST} (20) is a relative measure of genetic differentiation that estimates how far populations have diverged from a common ancestor in a sample. We computed this metric with the hierfstat package, and note that it can only be computed when at least 2 populations were sampled per dataset.

Because this study focuses on the effects of human demographics within cities, we excluded non-urban sites from this analysis based on whether they were located within the boundaries of census-designated urban areas (21). Data from 43 studies were ultimately included, and the final dataset consisted of 380 sites across all taxa (Tables 1, S2). Of these, we were able to estimate gene diversity and allelic richness at all sites, site-specific F_{ST} at 373 sites, and effective population size at 285 sites. The datasets included a site-level measure of the Human Footprint Index (10) from previous analyses (9, 11). We then obtained demographic data from the United States Census Bureau through the IPUMS National Historical Geographic Information System (22). Demographic data is from census blocks, the smallest census geographic unit. For each site, we measured the percent of residents identifying as white within 3 buffer sizes: 0.5, 1, and 5 km. Note sample sizes differed across these scales when sites were not located near populated blocks within the designated buffer size (e.g., gene diversity $n_{0.5km}$ = 268 sites; n_{1km} = 283 sites, n_{5km} = 296 sites).

Statistical analysis

All analyses were conducted in R version 3.6.3 (17). To test for the effects of residential racial segregation (% white residents in neighborhood) on the genetic diversity of wild populations we used Bayesian linear mixed models implemented in the brms package (24). We log-transformed effective population size, and scaled and centered all variables prior to analysis.

Our modelling strategy incorporated a random effect structure to account for variation across taxonomic class and species. We included random intercepts for species nested in class, allowing slopes to vary within species. Random slope models provide more conservative parameter estimates due to shrinkage, where the distribution of group-level effects are drawn towards the overall mean effect (25). Shrinkage to the overall effect is strongest for groups with fewer observations, allowing them to borrow strength from better sampled-groups. In this way, knowledge is shared across grouping levels of a random factor because we assume they are drawn from a common statistical population—whereas in fixed-effect only models, groups are assumed to be independent. The benefits of shrinkage in random slopes and intercept models are especially salient from a macrogenetics perspective. Species- or city-specific analyses often yield varying results (e.g., 36), but when analyzing raw data aggregated across broader spatial or taxonomic contexts, random slope and intercept models can provide better estimates of general effects.

We treated previous results from a different dataset showing the effect of the Human Footprint Index on mammal gene diversity, allelic richness, effective population size, and population-specific F_{ST} (9) as suitable priors given the negative correlation between the percentage of white residents in a neighborhood and the Human Footprint Index. We assigned slightly informative normally distributed priors with mean 0.5 and 0.25 standard deviation for allelic richness, gene diversity, and effective population size. For site-specific F_{ST} we assigned priors with mean -0.5 ± 0.25 SD. We ran all models with 4 chains and minimum 3000 iterations. We tested for spatial autocorrelation in model residuals with Moran's *I* tests in the package adespatial. Here, spatially autocorrelated residuals would indicate the presence of residual dependencies in genetic composition potentially due to population structure (for example isolation by distance patterns) or spatial structure induced by the environment not captured by model predictors (such as effects specific to cities or regions, or broader gradients in city structure). We used marginal and conditional R^2 to see the amount of variation explained by fixed, and fixed and random effects respectively (Table S1; 37). Next, we used the same modeling approach to test for the effects of Human Footprint Index alone, and the joint effects of racial segregation and the Human Footprint Index on genetic composition in another series of models. Finally, to compare explanatory ability between univariate models and models including both racial composition and Human Footprint Index, we used adjusted R^2 values. Adjusted R^2 for Bayesian models calculates the amount of variation explained using leave-one-out cross validation taking into account model complexity. If models including both covariates explain more variation than models with either covariate, this suggests that the effect of neighborhood racial composition and environmental disturbance on genetic composition are to some extent independent. If the opposite is true, it is more likely that racial composition affects genetic composition due to its correlation with environmental disturbance.

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Author contributions: C.S. and C.J.G. conceived of and designed the study. C.S. performed the analyses with input from C.J.G. and wrote the first draft of the manuscript. C.S. and C.J.G edited subsequent manuscript drafts.

Data availability: All data are open source; synthesized data will be made available upon acceptance.

Table 1. Effects of racial segregation and environmental disturbance (the Human Footprint Index) on genetic composition. Coefficient estimates are given with 95% credible intervals. Adjusted R^2 (R^2_{Adj}) is an estimate of variation explained taking into account model complexity. Moran's *I* index of spatial autocorrelation ranges between -1 and 1 with 0 indicating no autocorrelation; *p*-values are given for permutation tests on model residuals.

Variable	**Covariate**	**Coefficient (95% CI)**	**R^2_{Adj}**	**Moran's *I* (*p*)**
allelic richness	Racial segregation (% white residents)	0.13 (0.02, 0.25)	0.43	-0.01 (0.68)
n = 268 sites	Human Footprint Index	-0.12 (-0.25, 0.01)	0.43	0.02 (0.80)
	both	--	0.43	-0.02 (0.82)
gene diversity	Racial segregation (% white residents)	0.11 (0.01, 0.21)	0.84	-0.00 (0.46)
n = 268 sites	Human Footprint Index	-0.13 (-0.24, -0.04)	0.83	-0.01 (0.31)
	both	--	0.84	-0.01 (0.55)
effective population size	Racial segregation (% white residents)	0.14 (-0.01, 0.30)	0.24	-0.02 (0.73)
n = 202 sites	Human Footprint Index	-0.14 (-0.31, 0.03)	0.25	-0.02 (0.77)
	both	--	0.24	-0.02 (0.81)
F_{ST}	Racial segregation (% white residents)	-0.21 (-0.39, -0.05)	0.49	-0.02 (0.67)
n = 264 sites	Human Footprint Index	0.24 (0.03, 0.49)	0.43	-0.02 (0.67)
	both	--	0.48	-0.02 (0.78)

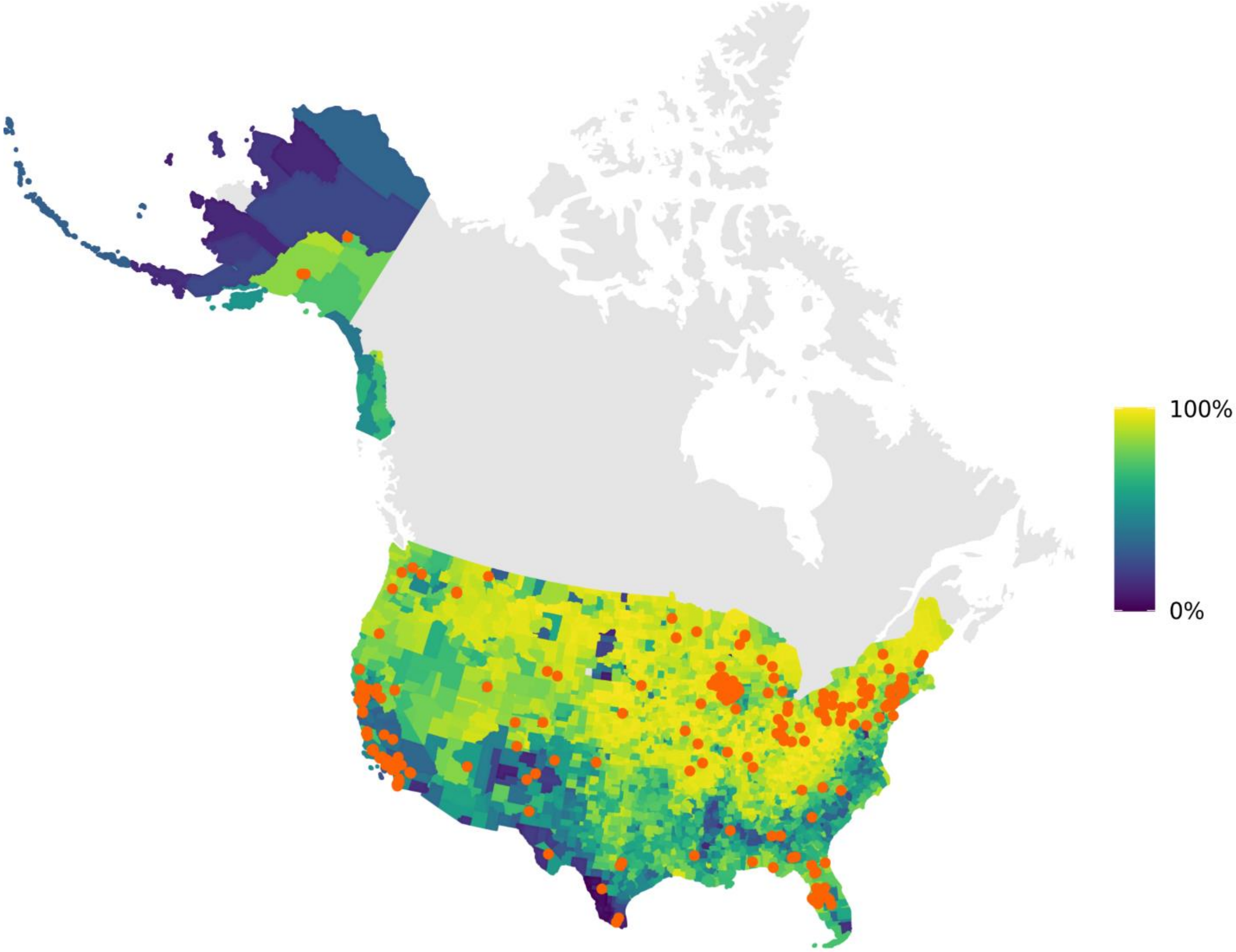


Figure 1. Map of 268 sample sites for 39 species of amphibian, bird, mammal, and reptile located in urban areas in the continental United States (points). Racial composition, measured by the proportion of the population identifying as white according to 2010 US census data, is depicted at the county level.

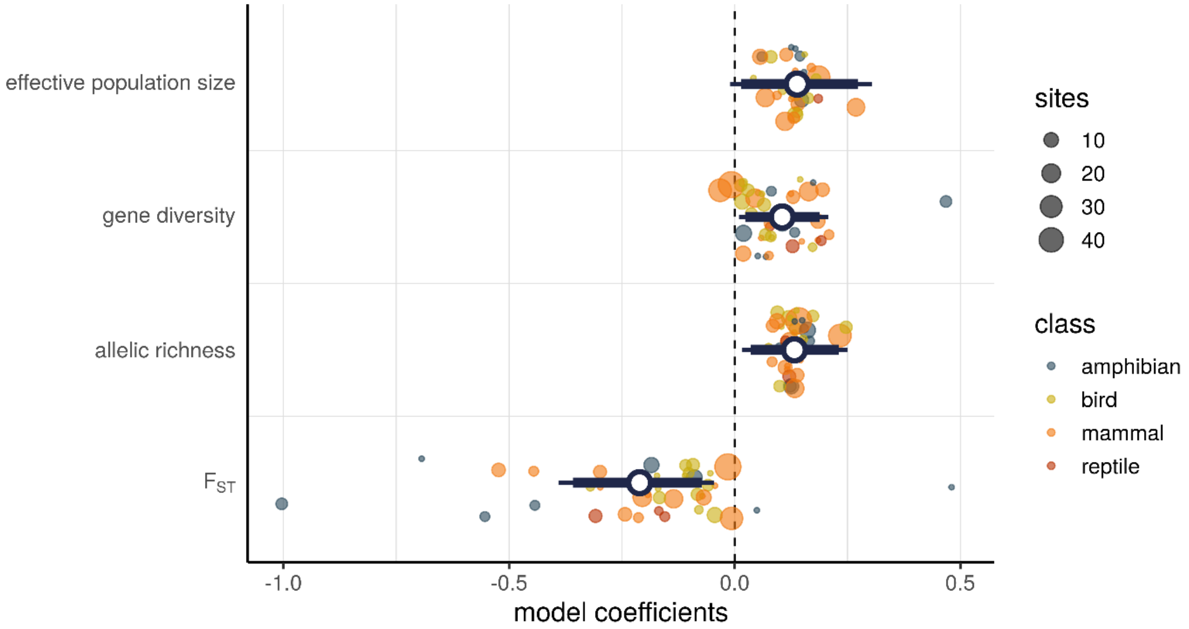


Figure 2. Bayesian GLMM coefficients for the effect of racial segregation, measured as percent of white residents in a neighborhood, on genetic composition. Coefficient estimates (open circles) are shown with 90% (bold lines) and 95% (narrow lines) credible intervals. Species-specific slope estimates are shown by filled circles where the diameter is proportional to sample size (number of sites), and color corresponds to taxonomic class.

Supplementary Information

Contents:

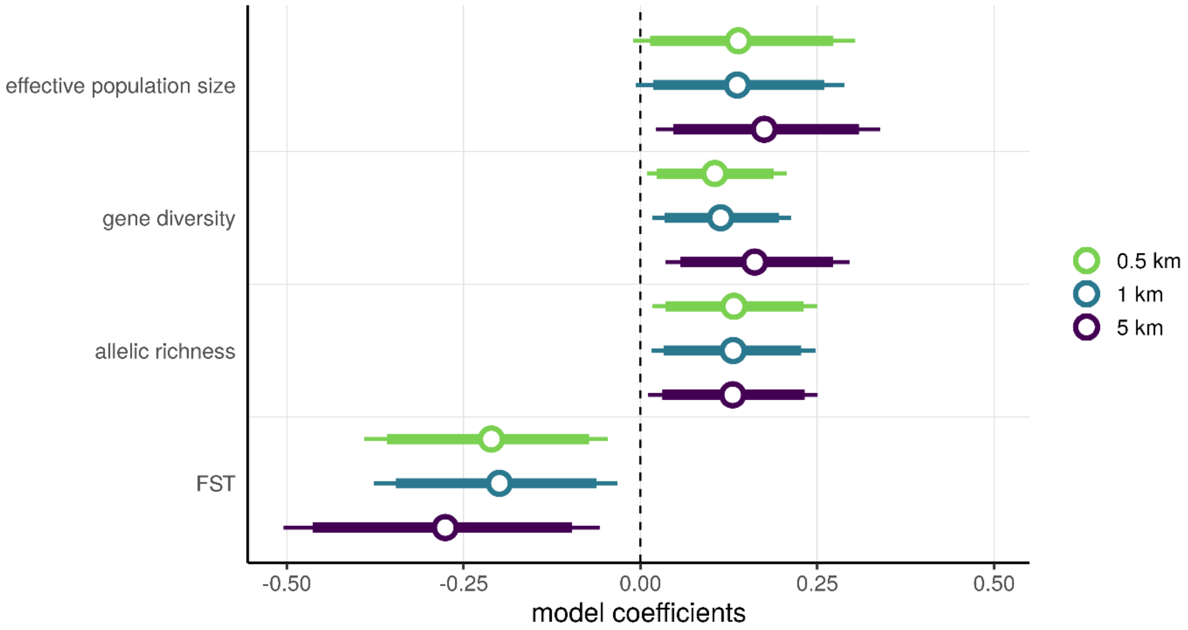
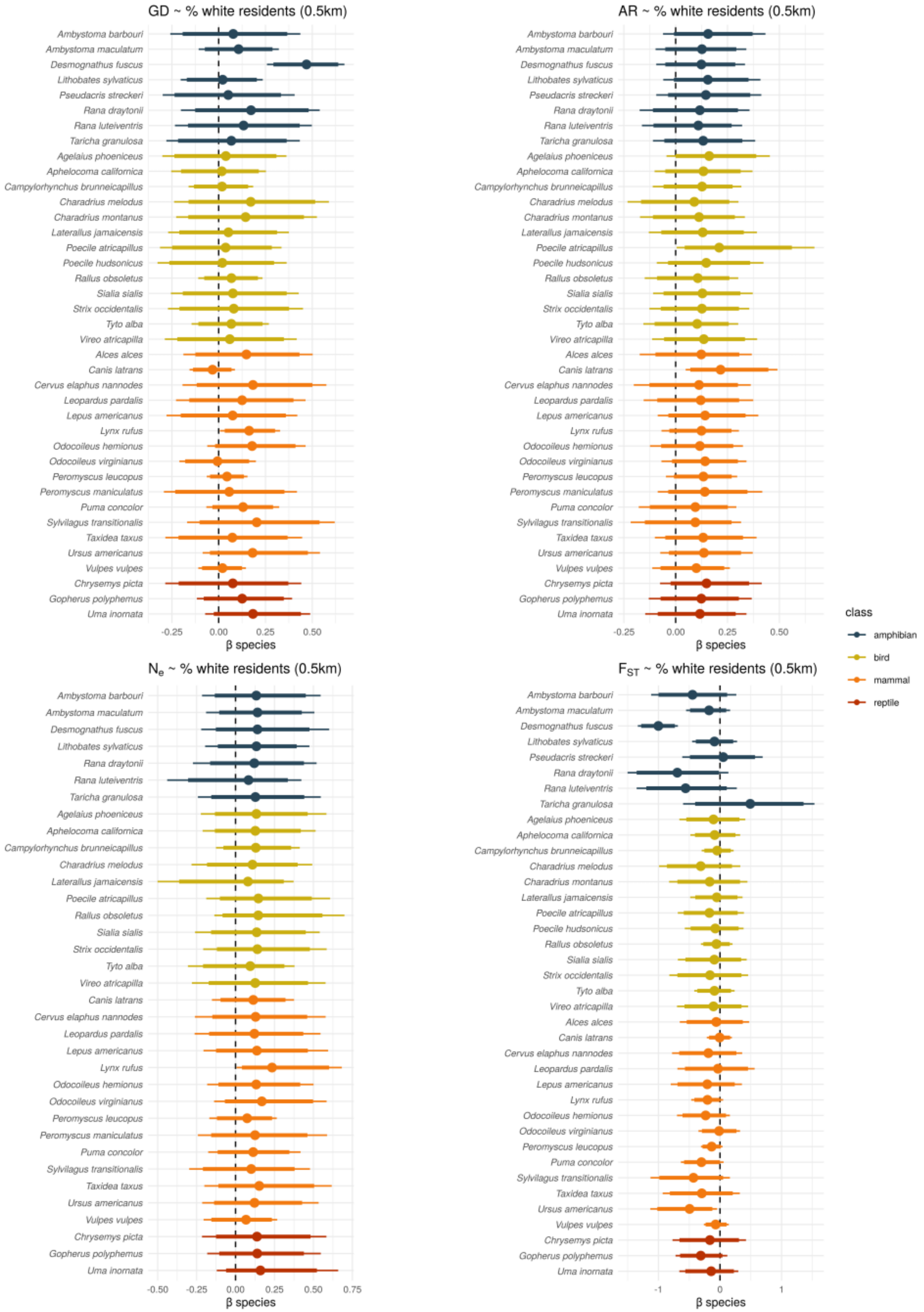


Figure S1.

Model results for the percent of residents identifying as white within 0.5 (main text), 1, and 5 km of a sample site. Coefficient estimates (open circles) are given with 90% (narrow lines) and 95% (thick lines) credible intervals. Effects of neighborhood racial composition are similar across all tested scales.



GD ~ % white residents (0.5km)
AR ~ % white residents (0.5km)
N_e ~ % white residents (0.5km)
F_{ST} ~ % white residents (0.5km)
Ambystoma barbouri
Ambystoma maculatum
Desmognathus fuscus
Lithobates sylvaticus
Pseudacris streckeri
Rana draytonii
Rana luteiventris
Taricha granulosa
Agelaius phoeniceus
Aphelocoma californica
Campylorhynchus brunneicapillus
Charadrius melodus
Charadrius montanus
Laterallus jamaicensis
Poecile atricapillus
Poecile hudsonicus
Rallus obsoletus
Sialia sialis
Strix occidentalis
Tyto alba
Vireo atricapilla
Alces alces
Canis latrans
Cervus elaphus nannodes
Leopardus pardalis
Lepus americanus
Lynx rufus
Odocoileus hemionus
Odocoileus virginianus
Peromyscus leucopus
Peromyscus maniculatus
Puma concolor
Sylvilagus transitionalis
Taxidea taxus
Ursus americanus
Vulpes vulpes
Chrysemys picta
Gopherus polyphemus
Uma inornata
-0.25
0.00
0.25
0.50
-0.50
0.75
-1
0
1
β species
class
amphibian
bird
mammal
reptile

Figure S2. Plots of species-specific effect sizes for regressions shown in the main text (% of white residents within 0.5 km of a site). Slope estimates (points) are shown with 90% (bold lines) and 95% (narrow lines) credible intervals.

Table S1.

Amount of variation in genetic composition explained by fixed and random effects, shown for models including either racial segregation (neighborhood racial composition), the Human Footprint Index, or both, as covariates. Marginal R^2 (R^2_m) is the proportion of variation explained by fixed effects, and conditional R^2 (R^2_c) is that explained by fixed and random effects.

Variable	**Covariate**	**R^2_m; R^2_c**
allelic richness	Racial segregation (% white residents, 0.5 km)	0.02; 0.46
n = 268 sites	Human Footprint Index	0.02; 0.46
	both	0.03; 0.47
gene diversity	Racial segregation (% white residents, 0.5 km)	0.01; 0.88
n = 268 sites	Human Footprint Index	0.02; 0.88
	both	0.02; 0.89
effective population size	Racial segregation (% white residents, 0.5 km)	0.02; 0.34
n = 202 sites	Human Footprint Index	0.02; 0.36
	both	0.04; 0.37
F_{ST}	Racial segregation (% white residents, 0.5 km)	0.04; 0.68
n = 264 sites	Human Footprint Index	0.05; 0.68
	both	0.06; 0.70

Table S2. Data summary for analyses presented in the main text. List of classes, species, and the number of populations sampled within each species. Number of individuals are summed across all populations; loci is the mean number of loci used across studies. Species medians and ranges are given for allelic richness and effective population size (N_e), and means and standard deviations are given for gene diversity and population-specific F_{ST}.

Class	Species (sites)	Individuals	Loci	Allelic richness	Gene diversity	N_e	F_{ST}
amphibian	*Ambystoma barbouri (3)*	63	11	4.90 (4.75-8.09)	0.69 (0.03)	49.20 (35.50-94.90)	0.21 (0.03)
amphibian	*Ambystoma maculatum (11)*	311	13.36	4.24 (3.65-4.46)	0.68 (0.02)	118.10 (29.70-1983.20)	0.04 (0.03)
amphibian	*Desmognathus fuscus (5)*	140	5	2.44 (1.64-3.94)	0.39 (0.19)	142.70	0.40 (0.29)
amphibian	*Lithobates sylvaticus (13)*	279	14.31	5.97 (5.79-6.41)	0.80 (0.03)	86.30 (43.60-352.10)	0.03 (0.02)
amphibian	*Pseudacris streckeri (1)*	18	14	5.90	0.82	NA	-0.09
amphibian	*Rana draytonii (1)*	10	15	2.53	0.41	13.90	0.39
amphibian	*Rana luteiventris (3)*	46	8	2.72 (2.57-3.94)	0.49 (0.12)	6.50 (5.60-12.50)	0.27 (0.17)
amphibian	*Taricha granulosa (1)*	20	6	4.65	0.77	38.70	-0.39
bird	*Agelaius phoeniceus (5)*	196	10	6.51 (6.50-6.67)	0.86 (0.01)	67.9	0.01 (0.01)
bird	*Aphelocoma californica (6)*	111	13	4.81 (4.64-5.04)	0.70 (0.03)	49.20 (12.60-178.50)	0.03 (0.02)
bird	*Campylorhynchus brunneicapillus (11)*	347	15	5.24 (4.65-5.44)	0.61 (0.04)	19.20 (12.30-83.50)	0.05 (0.02)
bird	*Charadrius melodus (2)*	93	8	1.92 (1.78-2.07)	0.33 (0.10)	23.95 (12.50-35.40)	0.12 (0.28)
bird	*Charadrius montanus (1)*	15	14	2.81	0.47	NA	0.03
bird	*Laterallus jamaicensis (1)*	123	15	4.35	0.71	1027.20	0.00
bird	*Poecile atricapillus (7)*	122	11	5.08 (3.85-22.64)	0.62 (0.11)	101.65 (27.40-779.00)	0.08 (0.07)
bird	*Poecile hudsonicus (2)*	69	6	5.98 (5.97-60.00)	0.84 (0.00)	NA	0.01 (0.00)
bird	*Rallus obsoletus (5)*	71	9	2.72 (2.63-2.80)	0.47 (0.01)	7.10 (2.30-78.40)	0.03 (0.02)
bird	*Sialia sialis (4)*	73	12	4.51 (4.43-4.78)	0.7 (0.02)	69.40 (63.40-72.20)	0.00 (0.02)
bird	*Strix occidentalis (1)*	39	10	4.23	0.73	139	0.02
bird	*Tyto alba (7)*	173	20	3.19 (3.13-3.29)	0.5 (0.01)	131.55 (25.60-320.80)	0.02 (0.02)
bird	*Vireo atricapilla (1)*	34	9	5.03	0.77	35.90	0.01
mammal	*Alces alces (1)*	40	10	2.84	0.51	NA	0.01
mammal	*Canis latrans (33)*	260	9.97	5.80 (4.86-13.7)	0.76 (0.03)	19.50 (2.90-332.70)	0.02 (0.03)
mammal	*Cervus elaphus nannodes (1)*	21	20	2.03	0.39	40.00	0.08
mammal	*Dipodomys ingens (1)*	66	14	7.17	0.90	29.90	0.01

mammal	*Leopardus pardalis (1)*	28	10	2.98	0.58	8.40	-0.02
mammal	*Lepus americanus (3)*	142	8	5.17 (5.00-5.46)	0.73 (0.01)	66.85 (58.70-75.00)	0.07 (0.04)
mammal	*Lynx rufus (20)*	943	13.75	4.28 (3.18-4.94)	0.71 (0.06)	98.10 (10.40-1749.50)	0.07 (0.05)
mammal	*Odocoileus hemionus (9)*	245	10.56	3.77 (3.16-3.98)	0.63 (0.04)	53.30 (1.10-557.00)	0.07 (0.03)
mammal	*Odocoileus virginianus (47)*	1582	14	5.56 (5.14-5.74)	0.81 (0.01)	168.70 (22.40-199577.50)	0.01 (0.01)
mammal	*Peromyscus leucopus (19)*	338	15.05	5.55 (4.67-6.88)	0.8 (0.03)	24.60 (8.10-221.30)	0.08 (0.03)
mammal	*Peromyscus maniculatus (1)*	31	10	5.38	0.80	15.10	NA
mammal	*Puma concolor (7)*	397	35.71	2.59 (1.97-3.09)	0.43 (0.07)	19.10 (1.90-84.30)	0.24 (0.13)
mammal	*Sylvilagus transitionalis (3)*	157	10	2.53 (1.87-2.63)	0.42 (0.09)	17.70 (3.60-31.80)	0.15 (0.14)
mammal	*Taxidea taxus (2)*	346	12	4.58 (3.91-5.25)	0.76 (0.07)	229.30 (81.50-377.10)	0.14 (NA)
mammal	*Ursus americanus (8)*	129	15	4.89 (3.59-7.15)	0.72 (0.07)	17.50 (3.60-207.80)	0.13 (0.09)
mammal	*Vulpes vulpes (11)*	364	13	3.83 (2.97-4.03)	0.63 (0.04)	14.00 (2.20-39.10)	0.10 (0.07)
reptile	*Chrysemys picta (2)*	56	11	5.81 (5.80-5.83)	0.75 (0.02)	107.70 (45.00-170.40)	0.04 (0.00)
reptile	*Gopherus polyphemus (7)*	234	20	3.77 (3.61-4.31)	0.62 (0.03)	57.35 (27.20-202.90)	0.16 (0.05)
reptile	*Uma inornata (3)*	64	11	3.64 (3.62-3.65)	0.58 (0.05)	95.00 (11.70-178.30)	0.00 (0.03)

Table S3. References for newly acquired raw microsatellite datasets. References for other mammal and bird datasets can be found in (1), and for amphibians in (2).

Class	Species	Search date	References
reptile	*Chrysemys picta*	Feb-19	(3, 4)
reptile	*Gopherus polyphemus*	Feb-19	(5–10)
reptile	*Uma inornata*	Feb-19	(11, 12)
mammal	*Cynomys leucurus*	Nov-20	(13, 14)
mammal	*Dipodomys ingens*	Nov-20	(15, 16)
mammal	*Myotis lucifugus*	Nov-20	(17, 18)
mammal	*Myotis septentrionalis*	Nov-20	(17, 18)
mammal	*Myotis thysanodes*	Nov-20	(17, 18)
mammal	*Canis latrans*	Nov-20	(19–22)
mammal	*Martes americana*	Nov-20	(23, 24)
mammal	*Taxidea taxus*	Nov-20	(25, 26)
mammal	*Vulpes vulpes*	Nov-20	(27, 28)

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Table S4. Raw search results for reptile and additional mammal datasets performed in February 2019 and November 2020, respectively. Reason for exclusion is NA if study met inclusion criteria.

Class	Search Date	Reason for exclusion	URL
reptile	February2019	outside North America	http://dx.doi.org/10.5061/dryad.6r7qn?ver=2017-07-19T10:01:44.901-04:00
reptile	February2019	duplicate	http://dx.doi.org/10.5061/dryad.6r7qn?ver=2017-08-16T11:46:06.333-04:00
reptile	February2019	outside North America	http://dx.doi.org/10.5061/dryad.pp6bm/9?ver=2015-07-24T12:53:55.745-04:00
reptile	February2019	duplicate	http://dx.doi.org/10.5061/dryad.pp6bm/13?ver=2015-06-03T17:09:06.080-04:00
reptile	February2019	duplicate	http://dx.doi.org/10.5061/dryad.pp6bm/10?ver=2015-06-03T17:05:53.305-04:00
reptile	February2019	duplicate	http://dx.doi.org/10.5061/dryad.pp6bm/11?ver=2015-06-03T17:06:56.070-04:00
reptile	February2019	outside North America	http://dx.doi.org/10.5061/dryad.4gb62?ver=2016-04-05T20:17:58.764-04:00
reptile	February2019	outside North America	http://dx.doi.org/10.5061/dryad.1tv72?ver=2017-02-13T11:11:53.277-05:00
reptile	February2019	duplicate	http://dx.doi.org/10.5061/dryad.1tv72?ver=2017-03-10T11:14:04.837-05:00
reptile	February2019	outside North America	http://dx.doi.org/10.5061/dryad.32h8t/1?ver=2015-10-01T17:00:02.499-04:00
reptile	February2019	outside North America	http://dx.doi.org/10.5061/dryad.3780c/1?ver=2016-05-06T14:07:01.196-04:00
reptile	February2019	duplicate	http://dx.doi.org/10.5061/dryad.1tv72/1?ver=2017-03-10T11:14:09.117-05:00
reptile	February2019	NA	https://doi.org/10.5061/dryad.cc6r3?ver=2017-11-08T08:18:53.221-05:00
reptile	February2019	duplicate	https://doi.org/10.5061/dryad.cc6r3/1?ver=2017-11-08T08:18:55.630-05:00
reptile	February2019	NA	http://dx.doi.org/10.5061/dryad.30t5b/1?ver=2015-11-19T12:07:35.851-05:00
reptile	February2019	SNP	http://dx.doi.org/10.5061/dryad.8br5c?ver=2016-11-29T11:42:36.904-05:00
reptile	February2019	duplicate	http://dx.doi.org/10.5061/dryad.30t5b?ver=2016-03-03T10:39:21.500-05:00
reptile	February2019	island	http://dx.doi.org/10.5061/dryad.6c7p5/1?ver=2016-11-23T11:51:06.881-05:00
reptile	February2019	duplicate	http://dx.doi.org/10.5061/dryad.6c7p5?ver=2016-11-23T11:50:57.890-05:00
reptile	February2019	marine species	http://dx.doi.org/10.5061/dryad.q1kf0/2?ver=2014-10-14T14:13:13.498-04:00
reptile	February2019	duplicate	http://dx.doi.org/10.5061/dryad.q1kf0/1?ver=2014-10-14T14:13:12.459-04:00
reptile	February2019	marine species	http://dx.doi.org/10.5061/dryad.7dk0m36r/1?ver=2013-05-16T02:30:08.080-04:00
reptile	February2019	outside North America	https://doi.org/10.5061/dryad.7db01?ver=2018-05-22T14:04:14.702+00:00
reptile	February2019	duplicate	http://dx.doi.org/10.5061/dryad.q1kf0?ver=2014-10-14T14:13:12.507-04:00
reptile	February2019	duplicate	https://doi.org/10.5061/dryad.7db01/2?ver=2018-04-23T16:35:58.186+00:00
reptile	February2019	duplicate	https://doi.org/10.5061/dryad.7db01/3?ver=2018-04-23T16:35:58.616+00:00
reptile	February2019	outside North America	http://dx.doi.org/10.5061/dryad.mb2sf?ver=2014-04-09T16:58:42.922-04:00

reptile	February2019	outside North America	https://doi.org/10.5061/dryad.d3kk74r?ver=2018-08-13T13:06:33.980+00:00
reptile	February2019	outside North America	http://dx.doi.org/10.5061/dryad.t5952?ver=2012-10-02T11:02:41.091-04:00
reptile	February2019	outside North America	http://dx.doi.org/10.5061/dryad.6k2qm/1?ver=2015-04-16T12:43:02.465-04:00
reptile	February2019	outside North America	http://dx.doi.org/10.5061/dryad.048kf?ver=2016-08-31T17:30:53.860-04:00
reptile	February2019	NA	http://dx.doi.org/10.5061/dryad.77rf2/2?ver=2014-06-06T17:18:52.451-04:00
reptile	February2019	duplicate	http://dx.doi.org/10.5061/dryad.77rf2/1?ver=2014-06-06T17:18:45.299-04:00
reptile	February2019	NA	http://dx.doi.org/10.5061/dryad.t0j7s/1?ver=2013-05-21T10:58:46.161-04:00
reptile	February2019	wrong taxa	http://dx.doi.org/10.5061/dryad.rb7h0/3?ver=2016-06-16T11:55:54.677-04:00
reptile	February2019	duplicate	http://dx.doi.org/10.5061/dryad.rb7h0/2?ver=2016-06-16T11:55:51.774-04:00
reptile	February2019	genetic restoration	http://dx.doi.org/10.5061/dryad.ps736/1?ver=2013-07-11T12:11:02.666-04:00
reptile	February2019	SNP	http://dx.doi.org/10.5061/dryad.p6m94/4?ver=2016-06-08T09:53:41.409-04:00
reptile	February2019	duplicate	http://dx.doi.org/10.5061/dryad.p6m94/5?ver=2016-06-08T09:53:47.011-04:00
reptile	February2019	SNP	https://doi.org/10.5061/dryad.k7k4m/3?ver=2018-05-03T12:50:08.216+00:00
reptile	February2019	NA	http://dx.doi.org/10.5061/dryad.50070?ver=2014-02-11T10:57:33.277-05:00
reptile	February2019	SNP	http://dx.doi.org/10.5061/dryad.19gp1?ver=2017-01-26T10:46:46.236-05:00
reptile	February2019	wrong taxa	http://dx.doi.org/10.5061/dryad.j7260?ver=2014-02-14T15:12:14.172-05:00
reptile	February2019	wrong taxa	http://dx.doi.org/10.5061/dryad.c62gg/1?ver=2013-12-18T15:34:27.101-05:00
reptile	February2019	duplicate	http://dx.doi.org/10.5061/dryad.c62gg/2?ver=2013-12-18T15:35:14.414-05:00
reptile	February2019	duplicate	http://dx.doi.org/10.5061/dryad.c62gg/3?ver=2013-12-18T15:35:58.876-05:00
reptile	February2019	hybrid zone	http://dx.doi.org/10.5061/dryad.14811?ver=2016-11-17T10:31:59.918-05:00
reptile	February2019	wrong taxa	http://dx.doi.org/10.5061/dryad.6mt23?ver=2015-06-03T09:35:09.158-04:00
reptile	February2019	NA	http://dx.doi.org/10.5061/dryad.v22n5/1?ver=2014-07-29T02:30:04.181-04:00
reptile	February2019	no coordinates	http://dx.doi.org/10.5061/dryad.s6f76?ver=2016-05-18T16:29:09.831-04:00
reptile	February2019	outside North America	http://dx.doi.org/10.5061/dryad.ct849?ver=2016-01-04T11:46:03.357-05:00
reptile	February2019	outside North America	http://dx.doi.org/10.5061/dryad.rq430/1?ver=2014-02-04T02:30:10.986-05:00
reptile	February2019	duplicate	http://dx.doi.org/10.5061/dryad.rq430?ver=2014-02-04T02:30:11.019-05:00
reptile	February2019	outside North America	http://dx.doi.org/10.5061/dryad.6697t?ver=2017-08-10T14:53:05.430-04:00
reptile	February2019	duplicate	http://dx.doi.org/10.5061/dryad.ct849/1?ver=2015-11-25T09:18:46.004-05:00
reptile	February2019	non-neutral	http://dx.doi.org/10.5061/dryad.7ck13/5?ver=2017-04-13T10:58:03.807-04:00
reptile	February2019	duplicate	http://dx.doi.org/10.5061/dryad.7ck13/6?ver=2017-04-13T10:58:09.420-04:00
reptile	February2019	no microsatellite data	http://dx.doi.org/10.5061/dryad.40c7c/2?ver=2016-08-02T16:54:46.211-04:00

reptile	February2019	duplicate	http://dx.doi.org/10.5061/dryad.40c7c/1?ver=2016-08-02T16:54:44.683-04:00
reptile	February2019	NA	http://dx.doi.org/10.5061/dryad.nk064/1?ver=2017-07-28T10:33:28.805-04:00
reptile	February2019	NA	https://doi.org/10.5061/dryad.31bc37q?ver=2018-08-06T12:14:39.063+00:00
reptile	February2019	duplicate	http://dx.doi.org/10.5061/dryad.7ck13?ver=2017-06-27T23:15:03.209-04:00
reptile	February2019	duplicate	http://dx.doi.org/10.5061/dryad.nk064/2?ver=2017-07-28T10:33:31.619-04:00
reptile	February2019	duplicate	https://doi.org/10.5061/dryad.31bc37q/1?ver=2018-07-30T21:50:40.332+00:00
reptile	February2019	NA	http://dx.doi.org/10.5061/dryad.54bm8/2?ver=2015-03-31T21:34:30.861-04:00
reptile	February2019	duplicate	http://dx.doi.org/10.5061/dryad.40c7c?ver=2017-05-15T20:31:23.849-04:00
reptile	February2019	mtDNA	http://dx.doi.org/10.5061/dryad.4hs71t6t?ver=2012-06-26T10:59:57.747-04:00
reptile	February2019	duplicate	http://dx.doi.org/10.5061/dryad.nk064?ver=2017-08-24T08:15:25.367-04:00
reptile	February2019	wrong taxa	http://dx.doi.org/10.5061/dryad.3c212?ver=2016-03-18T15:59:30.598-04:00
reptile	February2019	NA	https://doi.org/10.5061/dryad.8rb35rj?ver=2018-07-24T18:11:49.412+00:00
reptile	February2019	parentage analysis	https://doi.org/10.5061/dryad.121sk?ver=2017-10-26T13:32:16.379-04:00
reptile	February2019	duplicate	https://doi.org/10.5061/dryad.121sk/1?ver=2017-10-26T13:32:18.977-04:00
reptile	February2019	marine species	https://doi.org/10.5061/dryad.q2kf0?ver=2018-01-29T09:54:13.769-05:00
reptile	February2019	NA	http://dx.doi.org/10.5061/dryad.p5c04?ver=2016-08-31T17:27:54.752-04:00
reptile	February2019	duplicate	http://dx.doi.org/10.5061/dryad.p5c04/1?ver=2017-01-06T15:45:11.178-05:00
mammal	November 2020	NA	https://datadryad.org/stash/dataset/doi:10.5061/dryad.jn365c2
mammal	November 2020	already included	https://datadryad.org/stash/dataset/doi:10.5061/dryad.qn4kq
mammal	November 2020	NA	https://datadryad.org/stash/dataset/doi:10.5061/dryad.5jh21k3
mammal	November 2020	outside North America	https://datadryad.org/stash/dataset/doi:10.5061/dryad.dk73qp7
mammal	November 2020	outside North America	https://datadryad.org/stash/dataset/doi:10.5061/dryad.nvx0k6dqm
mammal	November 2020	outside North America	https://datadryad.org/stash/dataset/doi:10.5061/dryad.th71ss0
mammal	November 2020	already included	https://datadryad.org/stash/dataset/doi:10.5061/dryad.s04h8
mammal	November 2020	NA	https://datadryad.org/stash/dataset/doi:10.5061/dryad.h9b3d30
mammal	November 2020	already included	https://datadryad.org/stash/dataset/doi:10.5061/dryad.h7n25
mammal	November 2020	duplicate	https://datadryad.org/stash/dataset/doi:10.5061/dryad.h9b3d30
mammal	November 2020	samples not from populations	https://datadryad.org/stash/dataset/doi:10.5061/dryad.9nb07pr
mammal	November 2020	duplicate	https://datadryad.org/stash/dataset/doi:10.5061/dryad.5b2k6
mammal	November 2020	data too sparse	https://datadryad.org/stash/dataset/doi:10.5061/dryad.t77f1p4
mammal	November 2020	NA	https://datadryad.org/stash/dataset/doi:10.5061/dryad.j76c4k4

mammal	November 2020	outside North America	https://datadryad.org/stash/dataset/doi:10.5061/dryad.xwdbrv195
mammal	November 2020	NA	https://datadryad.org/stash/dataset/doi:10.5061/dryad.c0282c8
mammal	November 2020	outside North America	https://datadryad.org/stash/dataset/doi:10.5061/dryad.17r39p2
mammal	November 2020	already included	https://datadryad.org/stash/dataset/doi:10.5061/dryad.p2ngf1vp0
mammal	November 2020	duplicate	https://datadryad.org/stash/dataset/doi:10.5061/dryad.qn4kq
mammal	November 2020	NA	https://datadryad.org/stash/dataset/doi:10.5061/dryad.5k8q374
mammal	November 2020	already included	https://datadryad.org/stash/dataset/doi:10.5061/dryad.8ff46
mammal	November 2020	already included	https://datadryad.org/stash/dataset/doi:10.5061/dryad.bj7r3
mammal	November 2020	outside North America	https://datadryad.org/stash/dataset/doi:10.5061/dryad.vr61ks2
mammal	November 2020	outside North America	https://datadryad.org/stash/dataset/doi:10.5061/dryad.dv41ns1ts
mammal	November 2020	outside North America	https://datadryad.org/stash/dataset/doi:10.5061/dryad.54p37
mammal	November 2020	NA	https://datadryad.org/stash/dataset/doi:10.5061/dryad.46c39p1
mammal	November 2020	already included	https://datadryad.org/stash/dataset/doi:10.5061/dryad.f81c5
mammal	November 2020	SNP	https://datadryad.org/stash/dataset/doi:10.5061/dryad.gb5mkkwkw
mammal	November 2020	duplicate	https://datadryad.org/stash/dataset/doi:10.5061/dryad.qn4kq
mammal	November 2020	data too sparse	https://datadryad.org/stash/dataset/doi:10.5061/dryad.m58q16m
mammal	November 2020	non-neutral	https://datadryad.org/stash/dataset/doi:10.5061/dryad.rr4xgxd55
mammal	November 2020	NA	https://datadryad.org/stash/dataset/doi:10.5061/dryad.cj3v894
mammal	November 2020	outside North America	https://datadryad.org/stash/dataset/doi:10.5061/dryad.c6t0470
mammal	November 2020	non-urban populations	https://datadryad.org/stash/dataset/doi:10.5061/dryad.8931zcrmb
mammal	November 2020	outside North America	https://datadryad.org/stash/dataset/doi:10.5061/dryad.43j74d0
mammal	November 2020	non-urban populations	https://datadryad.org/stash/dataset/doi:10.5061/dryad.7k2g187
mammal	November 2020	already included	https://datadryad.org/stash/dataset/doi:10.5061/dryad.n8v973b