

Patterns of Herpetofaunal Species Richness Along Environmental Gradients in Kansas

ANDREW D. GEORGE, AMY M. HAMMESFAHR, MICHAEL W. BARNES, CHRISTINE C. REGA-BRODSKY, Department of Biology, Pittsburg State University, Pittsburg, Kansas 66762

ABSTRACT — *Species richness of most taxa follows a latitudinal gradient, reflecting broad-scale interactions between climate and topography. Yet the mechanisms explaining regional patterns of biodiversity remain poorly understood because environmental variables that affect species distributions are difficult to isolate. We used data from the Kansas Herpetofaunal Atlas (KHA) within an information-theoretic framework to evaluate relationships between herpetofauna species richness and variables representing topography and climate. We found that mean air temperature, total precipitation, and topographic variation best explained patterns of total herpetofauna species richness and reptile species richness. Amphibian species richness was related to annual temperature range and total precipitation, but models with only latitude and longitude were equally well-supported. Overall, we provide evidence that the diversity of amphibians and reptiles in Kansas is related to environmental factors that reflect ectotherm physiology and life-history characteristics. Our findings highlight the value of biological atlas projects for understanding regional patterns of biodiversity.*

INTRODUCTION

The latitudinal gradient in species richness remains one of the most persistent patterns in ecology (Hillebrand 2004; Wiens 2007). With some notable exceptions, most taxonomic groups are more diverse near the equator and less diverse near the poles (Wiens 2007; Mannion et al. 2014; Angielczyk et al. 2015). However, species richness is variable at regional scales, where latitude alone may be less important than underlying environmental gradients. Numerous hypotheses have been proposed to explain regional patterns of species richness, many of which are interrelated (Mannion et al. 2014). For example, species richness of amphibians and reptiles in North America increases with atmospheric energy and water availability (Currie 1991; Pyron and Wiens 2013). Other biotic factors, such as environmental heterogeneity and natural history, become more important at regional scales (Costa et al. 2007; Field et al. 2009; Moreno-Rueda and Pizarro 2009; Angielczyk et al. 2015). Statistical analyses linking species richness patterns to environmental gradients require adequate location-specific richness data and associated environmental covariates.

Biological atlas projects, broadly defined as spatially explicit datasets of species occurrence, are increasingly being used for applications in ecology and conservation biogeography (Robertson et al. 2010; Ochoa-Ochoa et al. 2014). The Kansas Herpetofaunal Atlas (KHA) is one of at least two dozen biological atlas projects that

document all known records of amphibians and reptiles from their respective states. KHA data originate from museum collections, literature records, and observations by both hobbyists and professional biologists. With >60,000 records from across the state, occurrence patterns of Kansas herpetofauna are relatively well documented (Taggart 2019).

Kansas is an ideal location for studying regional effects of environmental gradients on species richness patterns because climate factors (e.g., precipitation and air temperatures) vary widely across the state's diverse ecoregions (Chapman et al. 2001). We used county-level data from the KHA to assess spatial patterns of herpetofauna species richness within the state. Specifically, we compared hypotheses describing the relationships between species richness and 1) precipitation, 2) temperature, 3) topography, and 4) latitude and longitude.

Ectotherm physiology, behavior, and life history characteristics are closely linked to the thermal environment, impacting the suitable habitat ranges of species. Therefore, amphibians and reptiles are informative study organisms for understanding changes in biodiversity across environmental and climate gradients. Due to their life history and habitat requirements, we predicted that reptile species richness would be positively related to mean air temperature and that amphibian species richness would be positively related to both air temperature and annual precipitation (Qian 2010). We predicted

Table 1. Model-selection results for the best-supported models predicting herpetofaunal species richness in 105 Kansas counties. Candidate models included combinations of mean annual air temperature, mean annual precipitation, elevation, and topography. K = number of parameters in each model. ΔAIC_c = the difference in AIC_c values, w_i = model weight. The latitude-longitude models and null models are included for comparison with the best-supported models.

Response	Model	K	ΔAIC_c	w_i
Total Species Richness	Temperature + Precipitation + Topography	5	0.0	0.59
	Latitude + Longitude	4	25.2	0.00
	Null	2	44.6	0.00
Reptile Species Richness	Temperature + Precipitation + Topography	5	0.0	0.62
	Latitude + Longitude	4	26.3	0.00
	Null	2	46.1	0.00
Amphibian Species Richness	Temperature Range + Precipitation	4	0.0	0.24
	Latitude + Longitude	4	0.6	0.18
	Temperature + Precipitation	4	1.4	0.12
	Null	2	12.9	0.00

that overall species richness would more closely resemble the model for reptiles because there are more reptile species than amphibian species in Kansas.

METHODS

For each county in Kansas ($n = 105$), we used KHA occurrence records to calculate total species richness and species richness for both amphibians and reptiles. Species records that were considered accidental or questionable by KHA were omitted from the analysis. Species complexes were considered single species in richness calculations. We obtained 30-year averages of mean monthly air temperatures and total annual precipitation for each county from the Kansas State University climate database (Kansas State University 2019). The annual temperature range was calculated as the difference between mean temperatures for July and January. We used a 7.5-minute USGS digital elevation model (DEM) to calculate the mean elevation for each county. An index of topographic variation was calculated as the standard deviation of elevation in each county.

We used an information-theoretic framework to compare models representing a priori hypotheses about the relationships between herpetofaunal species richness and environmental gradients (Burnham and Anderson 2002). We fit generalized least squares (GLS) models with species richness as the response variable and all additive combinations of mean air temperature, temperature range, mean annual precipitation, elevation, and topography as predictor variables. We also fit models with only latitude and longitude as predictor variables, and null (intercept only) models. To reduce multicollinearity, correlated predictor variables ($r > 0.5$) were not included

in the same models. All models included an exponential correlation structure to account for spatial autocorrelation among species richness across counties. Akaike's Information Criterion for small sample sizes (AIC_c) and model weights were used to select the best-supported models for total species richness, species richness of amphibians, and species richness of reptiles (Burnham and Anderson 2002). Models within two ΔAIC_c of the top model were considered supported unless they added only uninformative parameters to the top model (Arnold 2010).

RESULTS

The KHA contained records for 98 species that met criteria for inclusion in our analysis, including eight species that were combined into four species complexes due to identification uncertainty. Total species richness ranged from 14 species in Thomas Co. to 68 species in Cherokee Co. Amphibian species richness ranged from 5 species in Decatur Co. to 22 species in Cherokee Co. Reptile species richness ranged from 8 species in Thomas Co. to 50 species in Crawford Co.

We found support for models that included climate, topography, and latitude and longitude as predictors of herpetofaunal species richness (Tables 1, 2). The best-supported models for both total species richness and reptile species richness included positive responses to mean air temperature, precipitation, and topographic variation. Amphibian species richness was best explained by models that included positive responses to air temperature and precipitation, and a negative response to air temperature range. For amphibians, latitude and longitude predicted species richness nearly as well as climate variables. Model-predicted species richness gener-

Table 2. Estimated coefficients for the best-supported models for herpetofaunal species richness in 105 Kansas counties. Temperature indicates mean air temperature (°C), precipitation indicates mean annual total precipitation (cm), and topography is the standard deviation of elevation.

Model	Parameter	Coefficient	Standard Error	Lower 95% CI	Upper 95% CI
Total Species Richness	Intercept	-232.27	30.05	-291.16	-173.38
	Temperature	4.28	0.57	3.16	5.41
	Precipitation	0.91	0.13	0.65	1.17
	Topography	0.35	0.07	0.22	0.48
Reptile Species Richness	Intercept	-203.85	24.52	-251.91	-155.79
	Temperature	3.73	0.47	2.81	4.64
	Precipitation	0.68	0.11	0.48	0.89
	Topography	0.30	0.06	0.19	0.41
Amphibian Species Richness					
Model 1	Intercept	29.40	7.78	14.14	44.65
	Temp Range	-0.56	0.16	-0.88	-0.24
	Precipitation	0.27	0.03	0.21	0.33
Model 2	Intercept	137.05	18.06	101.65	172.46
	Latitude	-1.18	0.31	-1.80	-0.57
	Longitude	0.83	0.14	0.56	1.10
Model 3	Intercept	-25.95	9.59	-44.74	-7.16
	Temperature	0.56	0.18	0.19	0.92
	Precipitation	0.19	0.04	0.11	0.28

ally increased from the northwest to southeast (Fig. 1). Residual maps indicated that several counties contain more or fewer reported species than predicted by the best-supported models.

DISCUSSION

Understanding the mechanisms underlying regional biodiversity patterns remains a central goal of biogeography and community ecology, and our results provide useful insight. We found relationships between environmental gradients and patterns of Kansas' herpetofauna species richness. For reptiles and combined herpetofauna, environmental gradients were better predictors of species richness than latitude and longitude. Environmental gradients also predicted amphibian species richness, although models with only latitude and longitude were equally well-supported. Latitude and longitude may serve as a proxy for predicting species richness in regions such as Kansas where environmental variables follow directional gradients.

Our findings are consistent with studies that found strong relationships between species richness and climate or productivity (Gaston 2000, Qian et al 2007). Air temperatures and water availability affect environmental energy and ecosystem productivity. Generally, ecosystems with greater environmental energy can gener-

ate higher biomass, which can in turn support minimum viable populations of more species (Gaston 2000, Buckley et al. 2008, Angielczyk et al. 2015). Populations of reptiles and amphibians may be further limited by local thermal conditions and water availability. The positive relationships we observed between species richness and mean air temperature may reflect constraints on ectotherm physiology, either during the growing season, winter, or both (Wiens 2007). Likewise, the positive relationships we observed between species richness and annual precipitation may reflect the fact that many of Kansas' reptiles and amphibians are limited by the availability of standing water. For example, southeast Kansas may support more species of amphibians and aquatic turtles because higher rainfall translates to a greater abundance and diversity of aquatic habitats. One of the best-supported amphibian models included a negative relationship between species richness and temperature range. Kansas counties that undergo seasonal temperature extremes may limit the persistence of amphibian species with narrow physiological limits (Buckley and Huey 2016). Relationships between species richness and climatic factors also reflect phylogenetic patterns of speciation, extinction, and shifts in

species distributions, although the scale of such processes is beyond the scope of our analysis (Mannion et al. 2014, Pyron and Wiens 2013).

Our residual plots indicated that the best-supported model predictions overestimated or underestimated species richness for several Kansas counties. The residuals likely represent one of two sources of potential error. First, type II errors may have resulted from under-sampled counties, in which the true number of species for a given county is higher than reported by the KHA. Models could be improved by increasing

future sampling efforts in these counties, or by basing models on quantitative species richness estimates rather than raw county records. The second source of error affecting model residuals likely arises from environmental variability that was not accounted for in our analysis. True species richness is dynamic and ultimately determined by interactions among complex environmental factors that affect organisms at multiple spatial and temporal scales. Depending on the objectives, future models could be refined by incorporating higher resolution species richness

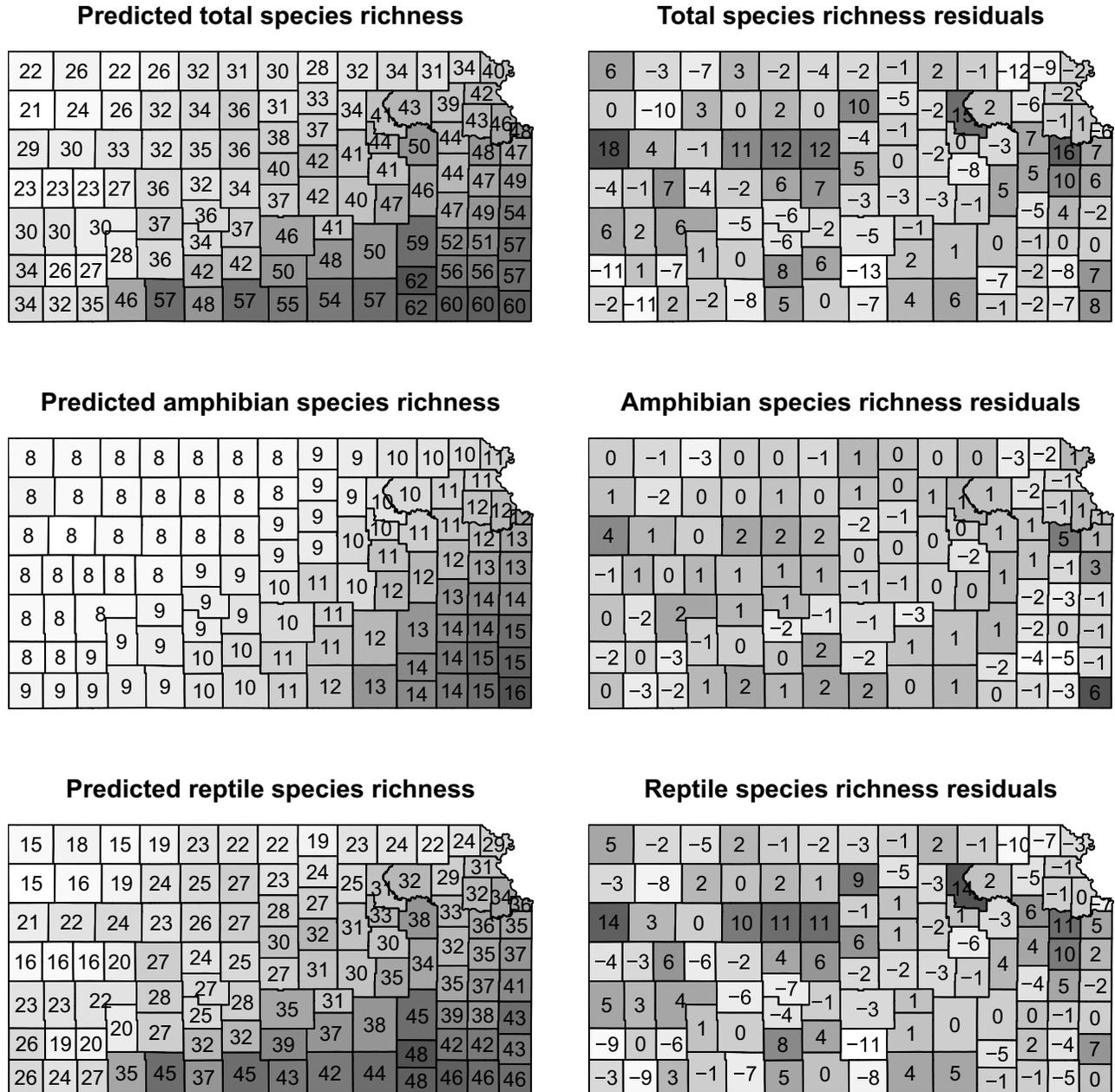


Figure 1. Predictions (left) and residuals (right) of the best-supported models of the relationships between environmental variables and total herpetofaunal species richness, amphibian species richness, and reptile species richness. Negative residuals indicate that documented species richness was lower than predicted species richness.

data and additional environmental covariates.

In addition to describing patterns of herpetofauna species richness in Kansas, we demonstrate a novel application of data from biological atlas projects. The KHA is one of a growing number of spatially explicit datasets based on both museum collections and observations from citizen scientists (Robertson et al. 2010). Because data could be linked to county-level environmental data, we were able to elucidate relationships between herpetofaunal species richness and environmental gradients at a finer scale than many previous studies of biodiversity patterns. Understanding factors that affect the distribution of species richness at the state-level can help identify locations with high biodiversity, and ultimately inform conservation efforts. Continued improvements in data quality and accessibility of biological atlas projects will permit their continued use in biogeography and conservation.

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