



DEPARTMENT OF BIOLOGICAL AND
ENVIRONMENTAL SCIENCES

ESTIMATING HISTORIC RANGES OF EXTINCT SCAVENGING BIRDS IN NORTH AMERICA DURING THE LATE PLEISTOCENE

USING CO-OCCURRENCE DATA FROM THE FOSSIL RECORD

Melissa Miranda

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Supervisor: Dr. Søren Faurby, Department of Biological and Environmental Sciences

Examiner: Dr. Bengt Oxelman, Department of Biological and Environmental Sciences

Index

Abstract	3
Introduction	4
Background	4
<i>Importance of extant scavenging birds</i>	4
<i>Co-extinction of mammalian megafauna and scavenging birds in the North America during the Late Pleistocene</i>	4
Estimating historic ranges of extinct fauna based on co-occurrence data in the fossil record.....	5
<i>Co-occurrence data in estimating historic ranges</i>	5
<i>Reconstructing geographic range-size using fossil data</i>	6
<i>Using present-natural diversity of North American mammals as a dependent variable</i>	7
<i>Data collection, organization and manipulation to conduct range analysis</i>	7
Aim	7
Hypotheses	7
Material and Methods	8
Study species	8
Fossil site localities and co-occurrence data	8
Rasterization	9
Estimating Historic Ranges	9
General Linear Model	11
Autocorrelated Linear Model	12
Spatial Autoregressive Model	13
Results	13
Fossil sites and number of co-occurrence species	14
Estimated Ranges	15
Present-Natural Mammal Diversity.....	18
General Linear Model	19
<i>GLM using Mammalian co-occurrence data</i>	19
<i>GLM using Avian co-occurrence data</i>	19
Autocorrelated General Linear Models	20
Spatial Autoregressive Models.....	20
<i>SAR using mammalian co-occurrence data</i>	21
<i>R-squared and Akaike Information Criterion</i>	21
<i>SAR using avian co-occurrence data</i>	21
<i>R-squared and Akaike Information Criterion</i>	21
<i>Comparing both models</i>	22

Discussion.....	22
Correlation between estimated ranges and present-natural mammal diversity	22
<i>R-squared and auto-generated correlation</i>	22
Spatial autocorrelation.....	23
Using multivariate datasets to more accurately reconstruct historic range estimates	24
Differences in Estimated Ranges using Avian and Mammal Co-occurrence Data	24
Limitations.....	25
<i>Working with few fossil sites</i>	25
<i>Working with a low number of species in co-occurrence data</i>	25
<i>Incompleteness of the fossil-record</i>	25
<i>Incomplete Biodiversity Databases</i>	25
Synonyms	26
Benefits of using rasters	27
Implications for studying Co-extinction Events.....	28
Conclusion.....	28
References	30
Text References (APA 7th edition – Journal of Zoology Style)	30
Appendix 1 – Popular Science Summary.....	34
<i>Why did so many scavenging birds go extinct?</i>	34
<i>Estimating the historic ranges of extinct scavengers</i>	34
<i>Does their historic range correlation with the range of their mammalian prey?</i>	34
<i>Why is this important?</i>	34
Appendix 2 – List of co-occurrence species	35
Appendix 3 – Fossil site references	37

Abstract

The aim of my study was to estimate and compare the historic range of nine scavenging birds from North America that went jointly extinct with their mammalian megafaunal prey in the Late Pleistocene. Although the severity and timing of their co-extinction are strongly correlated, there has been little analytical support in providing estimates for the possible geographic distribution of scavenging birds prior to the extinction event. To build an estimate of their historic range, I utilized rasters depicting the range of the mammal and bird species that co-occurred alongside the scavengers at different fossil sites. Using co-occurrence data to reconstruct the historic distributions of extinct scavenging birds was the selected approach because many extinct scavengers are known from very few fossil sites. Results showed that the estimated range size for extinct scavengers, based on avian co-occurrence data, was generally larger than the range estimates using mammal data. To measure the relationship between the distribution of scavengers and their prey, I compared the estimated ranges to the present-natural range of North American mammals using linear and spatial autoregressive models. The analysis revealed that both estimated ranges, using avian or mammalian co-occurrence data, were significantly positively correlated with and are significant predictors of present-natural mammalian diversity, but estimates based on mammals exhibited a stronger effect size and are thus a better predictor of present-natural mammalian diversity compared to using avian species. The results of this study determined a significant relationship between the extinct scavengers estimated distributions and present-natural mammalian diversity, providing biogeographic corroboration in support of the theorized co-extinction event in which the decline in mammalian prey was the causal link affecting scavenging bird declines. Future studies could employ similar methods and further test the procedure of using co-occurrence data from the fossil record to approximate the distribution of data-limited extinct species.

Keywords: Scavenging birds, Vultures, Co-occurrence Data, Range Estimates, Spatial Autoregressive Models, Co-extinction

Introduction

Background

Importance of extant scavenging birds

Scavenging birds are among the most threatened groups of birds throughout the globe, with 57% of vulture species worldwide listed on the IUCN Red List as being threatened with extinction (IUCN, 2023). In many ecosystems, vultures are considered keystone species that play an extremely important ecological role by disposing of carcasses quickly and efficiently, ensuring a clean and safer environment for humans, livestock, and wildlife (Markandya et al., 2008). A recent study that focused solely on Turkey vultures and the ecosystem services they provide, estimated that, as a species with a population of 13 million, they cumulatively removed over 1,000 tons of organic material every year, totaling a value of over 700 million USD every year (Graña Grilli et al., 2019).

Carnivores are necessary for maintaining ecosystem health and thriving biodiversity levels, but a reduction in prey abundance and diversity has in many circumstances been a leading contributor to carnivore extinctions (Ripple et al., 2014). Scavenging birds are an especially sensitive group of carnivores because they depend on megafaunal species through highly intimate commensalism interactions, such as when vultures feed on carrion, and are particularly vulnerable to co-extinction events (Pires and Guimarães, 2012). The ongoing megafaunal declines worldwide are likely to trigger another wave of co-extinctions in the Anthropocene, solely due to the extremely wide range of ecological interactions and functional roles mammalian megafauna provide, such as carrion prey for scavenging birds (Moleón et al., 2020). Meaning it's very likely that if the megafauna in Africa were to go extinct, so would the remaining scavenging bird species that live in Africa. The loss of African vultures would pose a major threat to the stability of ecosystems and may ultimately result in the rise of increased pathogenic bacteria and the transmission of viral diseases at the wildlife-human-livestock interface (Van den Heever et al., 2021).

Co-extinction of mammalian megafauna and scavenging birds in the North America during the Late Pleistocene

Scavenging birds and the megafauna they consumed were both highly diverse groups of animals throughout the Americas prior to the mass extinction they experienced in the Late Pleistocene/Early Holocene. Prior to the mass extinction event, there existed 12 known scavenging birds in North America, 9 of which went extinct towards the end of the last Ice Age, leaving only 3 currently extant species that remain in North America. An analysis of the Late Pleistocene extinction of continental birds and prey showed that avian extinctions are strongly correlated with mammalian megafaunal extinctions with respect to severity and timing, but questions remain regarding the geographic distribution of scavengers prior to the co-extinction event (Tyrberg, 2008). This gap in available information about the historic distribution of extinct scavenging birds in North America provides an opportunity to test the method of building estimated ranges based on co-occurrence data, as well as contribute to the biogeographic knowledge of these extinct scavenging species, which has been largely unknown.

At the end of the Pleistocene, there was a 72% reduction in the diversity of mammalian megafauna in North America. (Emslie, 1987). The loss of megafauna led to a wave of avian extinctions, with vultures being among the species that were most severely affected, especially in North America (Tyrberg, 2008). The reduction in mammalian prey coincides with the extinction of many North American vultures, including *Neogyps errans*, *Breagyps clarki*, and *Neophrontops americanus* (Emslie, 1987). The coextinction of mammalian megafauna and scavenging birds during the Late Pleistocene does not seem to be coincidental. Rather, many researchers have suggested that the decrease in large terrestrial mammal diversity during the Late Pleistocene is

directly responsible for the impoverishment and reduction of vulture fauna and diversity during that time period (Fox-Dobbs et al., 2006).

Some species of scavenging birds, such as the California Condor, *Gymnogyps californianus*, survived the co-extinction event but suffered severe range contractions (Fox-Dobbs et al., 2006). The fossil record shows that the California condor's historic range was from coast to coast and throughout North America, but following the extinction of mammalian megafauna in North America, the California condor withdrew to the California coast, where it could feed on the carrion of stranded marine megafauna such as beached whales. (Fox-Dobbs et al., 2006). This knowledge of their feeding habits has been deduced from radiocarbon and stable isotope data that suggests inland California condor populations were highly dependent upon the carrion of terrestrial continental megafauna as their main source of sustenance (Emslie, 1987). For the remaining species of vultures from the Late Pleistocene, their paleoecology and feeding behaviors were determined using morphological analysis (Hertel, 1994).

By continuing to study the geographic distribution of both extinct scavenging birds and mammalian megafauna in North America during the Late Pleistocene, my project can contribute to better understanding how the extinction of megafauna impacted scavenging bird populations in the past and be better able to assess the threat that future declines in prey species pose to extant scavenging birds today. Using co-occurrence data from the fossil record, we can estimate the historic ranges of extinct fauna and reconstruct their geographic range size. The resulting knowledge can be of critical importance for maintaining biodiversity and informing conservation strategies.

Estimating historic ranges of extinct fauna based on co-occurrence data in the fossil record

Co-occurrence data in estimating historic ranges

By examining the geographic locations where fossils of a particular species have been found, scientists can make inferences about where that species lived in the past. Fossil data holds information about the past distribution of extinct species but suffers from vastly incomplete sampling. In situations where the species being studied has only been recorded at a few fossil locations, co-occurrence data can help answer questions about the species distribution and geographic range. The use of co-occurrence data from the fossil record to infer historic geographical ranges of extinct animals is an existing technique in paleontology, and the methods for this approach were developed and outlined in 2015 by Soren Faurby and Jens-Christian Svenning (Faurby and Svenning, 2015).

I estimated the historic range of the extinct scavenging birds based on the species they co-occurred with at individual fossil sites. Co-occurrence data refers to this list of other species whose fossils were found alongside the extinct scavenging birds of North America. Collection records show that fossils from a variety of different organisms co-occur alongside scavenging bird species, including invertebrates, fish, fungi, plants, reptiles, amphibians, mammals, and birds, but for the scope of this study, we only used mammal species and bird species that were listed in the co-occurrence data.

The reason I chose this method is because it allows us to estimate the probable distribution of data-limited species that are known from a few or even a single fossil site, which is crucial for this project because the extinct scavengers we aim to map are only known from a small number of dig sites. The reasoning behind this approach is that if all species are constrained by the same ecological criteria, the distribution of extant species should provide information about whether a region's climate is suitable for the species whose distribution we are attempting to estimate (Faurby and Svenning 2015). We made the inference that the presence of species whose fossils

were found alongside those of extinct scavenging birds at any of the excavation sites, in a specific area indicates the probability of the occurrence of extinct scavengers in that location.

To accomplish estimating the geographic range of each extinct scavenging bird, I utilized the rasterized distribution of each mammal and bird species included in the co-occurrence list. Using rasters that depict the geographic range of these species, I attempted to model the historic ranges of extinct scavenging birds in North America. The computational aspect of my study was accomplished using various packages in R. Rasters are spatially explicit grids where each cell is representative of a pixel on a surface. Each pixel represents a geographic location. Rasters can be applied to represent continuous phenomena such as temperature, precipitation, and species diversity. In the case of our study, the rasters depict the range distribution of different species.

In the case of extinct scavengers discovered at a single fossil site, we designated all grid cells containing at least 50% of the co-occurring species from the fossil site as the extinct species' most likely estimated range. When estimating the range of extinct species found at several fossil sites, we calculated the probability of their occurrence in each grid cell by finding the fossil site that was geographically closest to each cell in the grid; this ensured that our estimated ranges for the extinct species were independent of how many fossil sites the species was found at.

Reconstructing geographic range-size using fossil data

A relatively simple, straight-forward, and common method for measuring the home ranges of extant species has been to construct minimum convex polygons around locations where species occur to define the minimum area that encloses all of the localities (Lyons and Smith, 2010). In the case of extinct scavenging birds of North America, many species are known from less than three collection localities, in some cases only one or two localities, making the minimum convex polygon method immaterial to what this study is hoping to accomplish. Because sample size is variable amongst the species in question, using this method would certainly underestimate the true geographic range size simply due to the incompleteness of the fossil record. If an extinct species is known from just one locality, you can assume that not every area where the species occurred was sampled. This is problematic in estimating historic ranges for data-limited extinct species because species with fewer localities will have smaller ranges on average than those with more localities. Therefore, species that are better sampled will have larger expected ranges than species that receive less sampling. Although the minimum convex polygon method is defensible in the sense that it does not exceed in extrapolating more information than that which the data points from the fossil collection localities provide, the method simply takes the geographic sites as data points and uses this information to provide a minimum estimate of the known range size for a species.

This study is conducted with the understanding that the fossil record is incomplete and that preservation potential relies on a variety of factors. It's been suggested that species with more extensive ranges could have higher preservation potentials because they exist in multiple different habitat types, giving them more opportunities to be preserved (Lyons and Smith, 2010). Similarly, certain traits that are positively correlated with increased geographic range size could also contribute to increased preservation potential, for example, a larger body size being associated with species that have larger range sizes. (Madin and Lyons, 2005) It may be more likely for larger-bodied animals with more robust skeletal elements to be preserved in the fossil record. Their size and sturdiness make it more likely they will be recovered and properly identified. These claims were confirmed in a study that examined the traits of extant taxa and found that the fossil record favors the fossilization of species with a more extensive geographic range and larger body sizes in both mammals and marine mollusks (Valentine et al., 2006).

Using present-natural diversity of North American mammals as a dependent variable

It is difficult to say with certainty whether the resulting estimated ranges this study produces are accurate or not, merely due to the fact that we are dealing with extinct species that are known from very few fossil localities. We used two different datasets to model this approach, which resulted in two separate and different estimated ranges. We can logically conclude that both can't be simultaneously accurate. Although I am confident in my attempt to estimate the ranges of these extinct species using the co-occurrence method as outlined by Faurby & Svenning, the estimates are essentially best-guess estimates based on the co-occurrence information we have at hand, but the accuracy of these estimates cannot be definitively proved or denied.

Unlike extant species, whose ranges can be accepted or refuted, we needed another method for quantifying how likely our estimated ranges are to be accurate. To statistically measure if our estimated ranges are likely accurate, we compared the estimated ranges of the extinct scavenging birds to the present-natural distribution of their primary prey source, North American mammals, and measured the correlation and significance between the abundance and distribution of both animal groups. The present-natural range refers to what the estimated range of extinct and extant species would be if there had been no influence by modern humans on their current distribution (Peterken, 1977).

Data collection, organization and manipulation to conduct range analysis

For this study, I created an inventory of fossil site locations where extinct scavenging bird species from North America have been found. The site localities and coordinates were taken from incomplete databases and various scientific sources that also included mammal and avian co-occurrence data. Deliverables for this study include a summary of the co-occurrence data and geographical visual representations of estimated ranges based on co-occurrence data using aves and mammals. This represents the first attempt to summarize fossil data specifically for extinct scavenging birds from North America and estimate their historical range based on this co-occurrence data.

Aim

The goal of my study is to estimate the historic ranges of extinct scavenging birds in North America using co-occurrence data from the fossil record.

The main research questions I aim to answer are:

1. What are the estimated historic ranges of extinct scavenging birds in North America using avian and mammalian co-occurrence data?
2. How does the estimated range of extinct scavenging birds based on avian co-occurrence data compare to their range that is estimated using mammalian co-occurrence data? I
3. Is there a statistical relationship between the estimated ranges of extinct scavenging birds in North America and present-natural mammalian diversity?

To answer my main research questions, I first need to answer: What other avian species did the extinct scavenging birds of North America co-occur with? What mammal species did they co-occur with?

Hypotheses

I hypothesized that the estimated ranges of extinct scavenging birds would be similar in size and extent using either avian or mammalian co-occurrence data. I also hypothesized that we would see a strong correlation between present-natural mammalian diversity in North America and the diversity of extinct scavenging birds across the continent based on their estimated geographic distribution.

Material and Methods

Study species

List of extinct scavenging bird species from North America

The list of extinct scavenging bird species to investigate for this study was decided based on information from an unpublished database on extinct birds provided by my supervisor, as well as Elton traits, a published database about the foraging behavior of the world's extant mammals and birds (Wilman et al. 2014). The nine species of extinct scavenging birds in this study were selected based on where they lived as well as the percentage of what they consumed by means of scavenging. For this study, only extinct scavengers from continental North America were selected. For the scope of this project, North America was defined as continental Canada, the United States, and Mexico, excluding the Caribbean islands and Central America. Elton traits provided foraging information such as the percentage of an animal's diet attained by scavenging. Using the information about closely related extant scavenging birds from Elton traits, we can assume that the extinct species of vultures in our study were also scavenging to the same extent. All nine species of extinct scavengers in this study are considered obligate scavengers, meaning 100% of what they consumed was by means of scavenging. Scientific literature describing the fossil finds of these nine species also confirmed the details of their dietary consumption and foraging strategies from inferred information based on morphological data. data.

Note on *Coragyps occidentalis*: Up until 2022, *Coragyps occidentalis* had only been known from the USA and Mexico, until it was revealed in a scientific paper last year that a fossil for this species had been found in Peru (Ericson 2022). For the sake of a larger sample size, *Coragyps occidentalis* was still included in the scope of our study, although we now know their estimated range extends outside of North America. This species is an example of how being found at different fossil sites could directly impact the estimated range based on the co-occurrence method.

Fossil site localities and co-occurrence data

Dig site locations that contain fossils of the extinct scavengers were compiled using information from the Paleobiology Data Base (PBDB) and other published literature entries from scientific journals found online. To create spatial models that represent the estimated historic ranges of extinct scavenging birds in North America, the fossil co-occurrence approach as outlined by Faurby & Svenning was utilized (Faurby and Svenning, 2015). For this approach, we needed to gather information on fossil occurrence localities as well as the bird and mammal species that also occurred at these fossil sites alongside our extinct scavenging bird species of interest.

Information for all fossil sites was obtained and aggregated into an Excel file, including coordinates, name of the site, site location (state, country), source, number of mammal species found at each site, and number of bird species found at each site. Some dig sites contained fossils of multiple extinct scavenging birds. For each unique fossil site, a list of species names, including genus and epithet, of all the mammals and birds that co-occurred at that site was compiled in Excel. The nine extinct scavengers were found across 29 different and unique terrestrial sites. Island sites were not included in this study due to endemic island species and marine fauna potentially causing noise in the data. The fossil sites are listed in Table 2. The Irvington site is listed but was excluded from our study because there was no avian co-occurrence data found for this site. In total, 357 species of birds and mammals were included in the co-occurrence data and thus in our estimation of historic ranges for the extinct scavenging birds. 189 of those species were birds, and 168 were mammals; all species names are provided in the supplementary information in Appendix 2.

The bulk of the work for this project was conducted using R and R Studio. This method section will outline step-by-step the processes that were taken to accomplish the goal of our study.

Rasterization

Rasters depicting the geographic range for all 357 co-occurrence species in this study needed to be located or created for use in building our range estimates of the extinct scavenging birds. Our first attempt to locate rasters for the avian co-occurrence species was in a folder that contained over 200,000 files of geographic range maps for extant birds that were currently being used by one of my supervisor's PhD students. Less than 20% of the avian species in our study had rasters contained in that folder, so a further search was conducted to locate shapefiles depicting the geographic range for each species so that we could then transform the shapefiles into rasters. A folder containing 40,000 files from Bird Life International was searched to locate shapefiles that depict the range of the remaining avian co-occurrence species in our study, and 80% of the birds in our co-occurrence list were found to have shapefiles in that folder that we could transform into rasters. Of the remaining 20% of bird species that did not have rasters or shapefiles that could be located, the majority of those species are extinct, so there is not yet an estimated historic range for them. For the 80% of bird co-occurrence species that did have shapefiles, we transformed these shapefiles into rasters to be used in our study.

Four different packages were employed in R to help with rasterization, including *raster*, *fasterize*, *sp*, and *sf*. After reading in a source raster and a shapefile of one of the co-occurrence species, I transformed the shapefile into the projection of our source raster. The source raster can be any raster that has the projection and extent you want your shapefiles to match. Using the *spatial* line's function, I created an object that was the outline of the shapefile polygon, and then the *fasterize* function created a raster of all cells that exist inside the polygon shape. All NAs in the raster were changed to zero before saving the raster for further use. This process was repeated for all avian co-occurrence species that needed their shapefile transformed to a raster. The PHYLACINE Database provided rasters depicting the geographic distribution of 95% of the mammalian co-occurrence species in our study. Once all the rasters for the co-occurrence species were attained or created, the process to build our estimates for the historic range of extinct scavenging birds in North America could begin.

Estimating Historic Ranges

Site by site

Twenty-nine fossil sites were included in this study. For each fossil site, two rasters were created. The first raster was the sum of all bird co-occurrence species found at that fossil site and the second raster was the sum of all mammal co-occurrence species found at that site. The steps for summing up avian and mammalian species are the same. The first step is to stack all the rasters of the bird or mammal species that were present at that fossil site. The second step is to sum all the rasters in that stack.

Plotting the resulting raster will give you a general understanding of where the greatest abundance of bird species occurred. The next step is to attain a raster map with only the cells where the majority of bird or mammal species found at that fossil site occurred. Dividing the sum by the total number of bird or mammal species that occurred at that site allows us to attain an average and assigns a value to each cell in the raster. Now that each cell has a value, we are interested in a map that only includes raster cells where over 50% of the co-occurrence bird species found at this fossil site are present. To accomplish this, we could make the raster binary by assigning all cells that have a value equal to or greater than 0.5 a value of one and assigning all cells that have a value less than 0.5 a value of zero, so that we are left with only the cells that contain over 50% of species for that site. This process is repeated for the mammal co-occurrence

species of this fossil site, so that two rasters are created from the co-occurrence data for this fossil site. This process of creating two rasters, one using avian co-occurrence species and one using mammalian co-occurrence species, is repeated for all fossil sites.

Species level estimates

For every fossil site, two range estimates were produced, one based on bird co-occurrence data and the other on mammal co-occurrence data. This is accomplished by essentially conducting the same process at the species level. Two range estimates for each species of extinct scavenging bird were built, one based on bird co-occurrence data and the other using mammal co-occurrence data.

To ensure that the size of the estimated ranges for each species of extinct scavenging bird is independent of how many fossil sites they were found at, additional steps were taken and are outlined below. Taking these steps ensured that species found at more fossil sites do not necessarily have an increased size of their estimated range but rather an increased precision of the estimates. For this step, four packages were utilized: the raster, sf, sp, and geosphere packages.

To estimate the historic range of a species, I first extracted the coordinates for each cell in the raster, transformed them to latitude and longitude, and calculated the distance from the fossil sites to each cell using the great-circle distance method to find the minimum distance from the fossil sites to each cell. The coordinates obtained were from the center of each cell in the raster. After extracting the coordinates, I created a matrix of these coordinates and then converted the matrix into a spatial points object so that I could apply the same coordinate reference system to this spatial points object as the raster object, and then further transformed the coordinates into a geographic coordinate system in latitude and longitude. Latitude and longitude for all fossil sites were defined using the 'distHaversine' function to create a vector of the distances from each cell in the raster to each of the fossil sites that species was found at. I then combined the multiple distance vectors into one matrix, in which each row corresponds to the same cell in the raster and each column corresponds to one of the fossil sites, and the values that make up the matrix correspond to the distance of that cell to each fossil site. Using the 'apply' function, R calculated the minimum distance for each row in the matrix.

After attaining the minimum distance of each cell to the fossil site, I created an empty raster that is the same size and shape as the raster depicting the estimated range of extinct scavenging birds that was built using either avian or mammal co-occurrence data, and I set the values of all cells in the new empty raster to zero. I created minimum distance raster objects, one for each of the fossil sites that species was found at, and assigned the value 1 to all cells that have a minimum distance to that fossil site. By multiplying the fossil site's minimum distance raster by the original raster for that site, I created a new raster object where cells that are closest to the fossil site have the original value from the original raster, and all other cells have a value of zero. By adding together and plotting the three new raster objects, I created a raster that only contains cells that have a minimum distance to one of the three fossil sites. By repeating this process for each of the extinct scavenging birds, I attained the estimated historic range for each extinct scavenger using avian and mammal co-occurrence data.

To summarize what I accomplished using the minimum-distance method, by assigning the value 1 to all cells that have a minimum distance to a given fossil site, I essentially created a binary mask where the cells closest to the fossil site have a value of 1 and all other cells have a value of 0. I then used this binary mask to subset the original raster so that only the cells closest to the fossil site were retained. By multiplying this subset raster by the original raster value at the fossil site, I effectively assigned the original raster value to the cells closest to the fossil site and set all other cells to 0. This created a new raster object where cells that are closest to that site have the original value from the original raster, and all other cells have a value of 0.

This approach helps make estimated ranges more accurate by ensuring that the range is not biased towards species found at more fossil sites. Instead, it assigns values to cells based on their proximity to the fossil site, making the estimated range more accurate for species that were found at fewer fossil sites. By calculating the minimum distance using the great-circle distance method, this approach accounts for the curvature of the Earth and obtains more accurate distance estimates. Overall, this step helps to create a more objective and unbiased estimate of the extinct species' range size.

It should be noted that not all sites were included in the estimation of extinct scavenging birds historic ranges. As previously mentioned, island sites were excluded from this study, and if there were two mainland sites that were geographically close to one another and had very similar co-occurrence species, then the site with a larger set of co-occurrence data was selected to be included in the estimate of historic ranges and the other fossil site was excluded.

For presentation purposes, the shape of North American states was projected on top of the raster, and fossil sites where each species was found were added to better visually compare the estimated range size of each extinct species using mammal vs. bird co-occurrence data. The estimated ranges for each species using mammal vs. bird co-occurrence data can be seen in Table 3.

To statistically compare the two methods of using either mammal or bird co-occurrence data, I summed the estimated ranges of extinct scavenging birds using mammal co-occurrence data and summed the estimated ranges of extinct scavenging birds using bird co-occurrence data so as to see where in North America extinct scavengers were estimated to be most abundant. The estimated abundance of extinct scavenging birds in North America using either mammal or bird co-occurrence data can be seen in Table 4.

Present-natural mammal diversity

To statistically measure the relationship between the estimated diversity of extinct scavenging birds and the diversity of their mammalian prey, I compared the summed estimated ranges of the nine extinct scavenging birds to the present-natural distribution of North American mammals so as to determine the correlation and significance between the diversity and distribution of both animal groups. The present-natural range of North American mammals refers to what the estimated range of extinct and extant mammal species would be if there had been no influence by modern humans on their current distribution (Peterken, 1977). Figure 1 depicts the present-natural range for terrestrial North American mammals from the Late Pleistocene that weighed over 10 kg. The rasters depicting the present-natural range for these mammals were obtained from the Phylacine Database.

General Linear Model

I performed two linear regression analyses to investigate the relationship between the diversity of extinct scavenging birds and present-natural mammal diversity. The relationship between the two variables is depicted in the scatterplots in Figure 2. I adjusted the resolution of the rasters representing the estimated range of extinct scavengers using the 'projection' and 'aggregate' functions. This allowed for proper alignment and matching of the resolution with the present-natural mammal diversity raster. The 'projection' function was used to ensure that the predictor data was in the same projection as the response variable data. By applying the 'projection' function, the predictor data is transformed to match the coordinate system and spatial reference of the response variable data. The use of the 'projection' function helps to achieve spatial consistency and alignment between the predictor and response variable data by transforming them into a shared coordinate system, or projection. This step allowed for proper alignment of the datasets. Then, I utilized the 'aggregate' function to match the resolution of the target raster,

which in this case was the present-natural mammal diversity raster. Since the 'aggregate' function only works with integers, I needed to perform some intermediate steps. To achieve the desired resolution, I used the 'disaggregate' function to resample the projected raster into a different raster. This new raster served as a basis for further adjustments. Then, I employed the 'projectRaster' function to project the raster into the equal-area cylindrical projection. This step ensured consistency in the spatial framework. Next, I rescaled the raster using the 'resample' function with the 'bilinear' method. This rescaling process helped align the raster with the desired resolution. Finally, I applied the 'aggregate' function to the raster, matching it to the resolution of our present-natural mammal diversity data. By implementing these steps, the raster resolution was effectively adjusted, enabling smoother and faster operation of the general linear model.

When running the general linear model, it was expected that there would be spatial autocorrelation in the data, but GLMS does not generally account for it. Spatial auto-correlation occurs when two raster cells that are close to each other in space have similar values. With range data, it is expected that the mammalian diversity values of two neighboring cells will be more similar to each other than to cells further away, on average. Further along in this study, a spatial autoregressive model was run to account for the spatial autocorrelation in our data, but firstly, a general linear model was fit to our present-mammal diversity data to see if there was a correlation with our predictor variable, extinct scavenging bird diversity.

To run a general linear model, the first step was to transform the raster data into a data frame format. For this, I extracted the coordinates, raster cell centroids, using the 'coordinates' function. Next, I extracted the corresponding values from both rasters using the 'values' function. Then put the coordinates and the values from both rasters together into one data frame. I then removed all cells that do not have any values assigned to them by utilizing the 'complete cases' function to remove all rows from the data frame that contain NA to only extract rows with complete data.

I further scaled the values for both the response and the predictor variables to be centered at 0 using the 'scale' function. I scaled the parameters so that all predictors are scaled to have a mean of zero and a standard deviation of one, so that each standard deviation in the x axis corresponds to one standard deviation in the y axis. The reason for scaling is so that the effect sizes of the models are comparable to each other. In general, scaling is good practice for understanding and comparing effect sizes. Scaling the parameters before running the SAR analysis may have resulted in coefficient values greater than 1. In that case, the AIC value is used to determine the best fit among the models.

By plotting the final values of the predictor, extinct scavenger diversity, against the response variable, present-natural mammal diversity, a first impression of the variable's relationship was attained. This relationship is depicted in Figure 2, using mammal and bird co-occurrence data.

Autocorrelated Linear Model

By plotting the residuals of both of the previously run general linear models, a degree of spatial autocorrelation was attained. To accomplish this, I utilized the 'correlog' function from the 'ncf' library to calculate the spatial autocorrelation. The function takes the coordinates and residuals from the linear model and additional parameters such as 'increment', which defines the distance intervals for autocorrelation; 'latlon=T', which indicates the coordinates are in latitude and longitude; and 'resamp,'" which specifies the bootstrap resamples for significance testing. For this model, the increment and resamp values were both set to 100. The figure below, Fig. 3, depicts two plots showing the correlation between the residuals of each model at different distances.

Spatial Autoregressive Model

The initial general linear models did not consider spatial autocorrelation. To examine the relationship between the predictor variables and the response variable while also accounting for spatial autocorrelation, a spatial autoregressive model (SAR) was utilized. Two SARR models were utilized, with the response variable being mammal diversity and the explanatory variable being the abundance of extinct scavenging birds based on their estimated range size using either mammal or bird co-occurrence data. The goal was to determine whether the diversity of extinct scavenging birds based either on their estimated ranges using mammal or bird co-occurrence data provides a more accurate predictor for predicting present-natural mammalian diversity in North America.

Finding the best neighborhood

To address spatial autocorrelation, a spatial weight matrix was incorporated into the models. The selection of the best neighborhood structure was crucial to obtaining accurate estimates of model parameters. The choice of the spatial weight matrix was based on the "best neighborhood model" to avoid overfitting or underfitting the model (Breiman, 1996). Different definitions and thresholds of "neighborhood" were examined, and over 40 neighborhood models with varying values and distances were evaluated using the Akaike Information Criterion (AIC). The model with the lowest AIC was chosen as the best neighborhood model.

The AIC serves as a trade-off measure between model goodness of fit and complexity while accounting for a small sample size. It is important to select an appropriate neighborhood size and structure to capture spatial dependence without overcomplicating the model. If the neighborhood is too small, spatial dependence may be overlooked, resulting in biased estimates. Conversely, an excessively large neighborhood can lead to an overly complex model that may not generalize well.

By applying the best neighborhood model and plotting the results of the spatial autoregressive (SAR) analysis, the integration of spatial autocorrelation into the model can be observed such as in Figure 4. The resulting effect size, R-squared, and AIC values from the SAR models allow for comparison and determination of the predictor variable with the highest correlation to present-natural mammalian diversity.

Results

Table 1. Nine extinct scavenging birds (n=9) from North America. The letters in the fossil sites column correspond with the fossil site listed in Table 2.

Species name	Order	Family	Fossil sites	Fossil site locations
<i>Neogyps errans</i>	Accipitriformes	<i>Accipitridae</i>	(n=3) B,D,E	California
<i>Neophrontops americanus</i>	Accipitriformes	<i>Accipitridae</i>	(n=6)B,D,E,F,U,bb	California, New Mexico, Wyoming
<i>Breagyps clarki</i>	Cathartiformes	<i>Cathartidae</i>	(n=3)D,R,V	California, Mexico, New Mexico
<i>Gymnogyps amplus</i>	Cathartiformes	<i>Cathartidae</i>	(n=13)B,C,D,G,H,I,J,N,O,Q,S,U,W	California, Florida, New Mexico, Mexico
<i>Coragyps occidentalis</i>	Cathartiformes	<i>Cathartidae</i>	(n=11)C,D,E,H,O,P,S,U,V,Y,Z	California, Florida, New Mexico, Mexico, Texas
<i>Aiolornis incredibilis</i>	Cathartiformes	<i>Teratornithidae</i>	(n=2)A,T	California, Nevada
<i>Cathartornis gracilis</i>	Cathartiformes	<i>Teratornithidae</i>	(n=1)D	California

<i>Terratornis merriami</i>	Cathartiformes	<i>Teratornithidae</i>	(n=10)B,D,E,J,M, Q,K,L,N,aa	California, Florida, Utah
<i>Teratornis woodburnensis</i>	Cathartiformes	<i>Teratornithidae</i>	(n=1)X	Oregon

Seven of the nine species included in this study belong to the Order Cathartiformes, New World Vultures, while the other two belong to the Order Accipitriformes, which is an Order of birds that includes many diurnal birds of prey, including hawks, old-world vultures, eagles, and kites. The nine species of extinct scavenging birds and the last name of the person who described them, as well as the year they were discovered, are listed here: *Neogyps errans* Miller 1916, *Neophrontops americanus* Miller 1916, *Breagyps clarki* Miller 1910, *Gymnogyps amplus* Miller 1911, *Aiolornis incredibilis* Howard 1952, *Cathartornis gracilis* Miller 1910, *Teratornis merriami* Miller 1909, *Teratornis woodburnensis* Campbell & Stanger 2022, and *Coragyps occidentalis* Miller 1909. The nine species are also listed in Table 1, above, with additional information about the fossil sites they have been found at.

Fossil sites and number of co-occurrence species

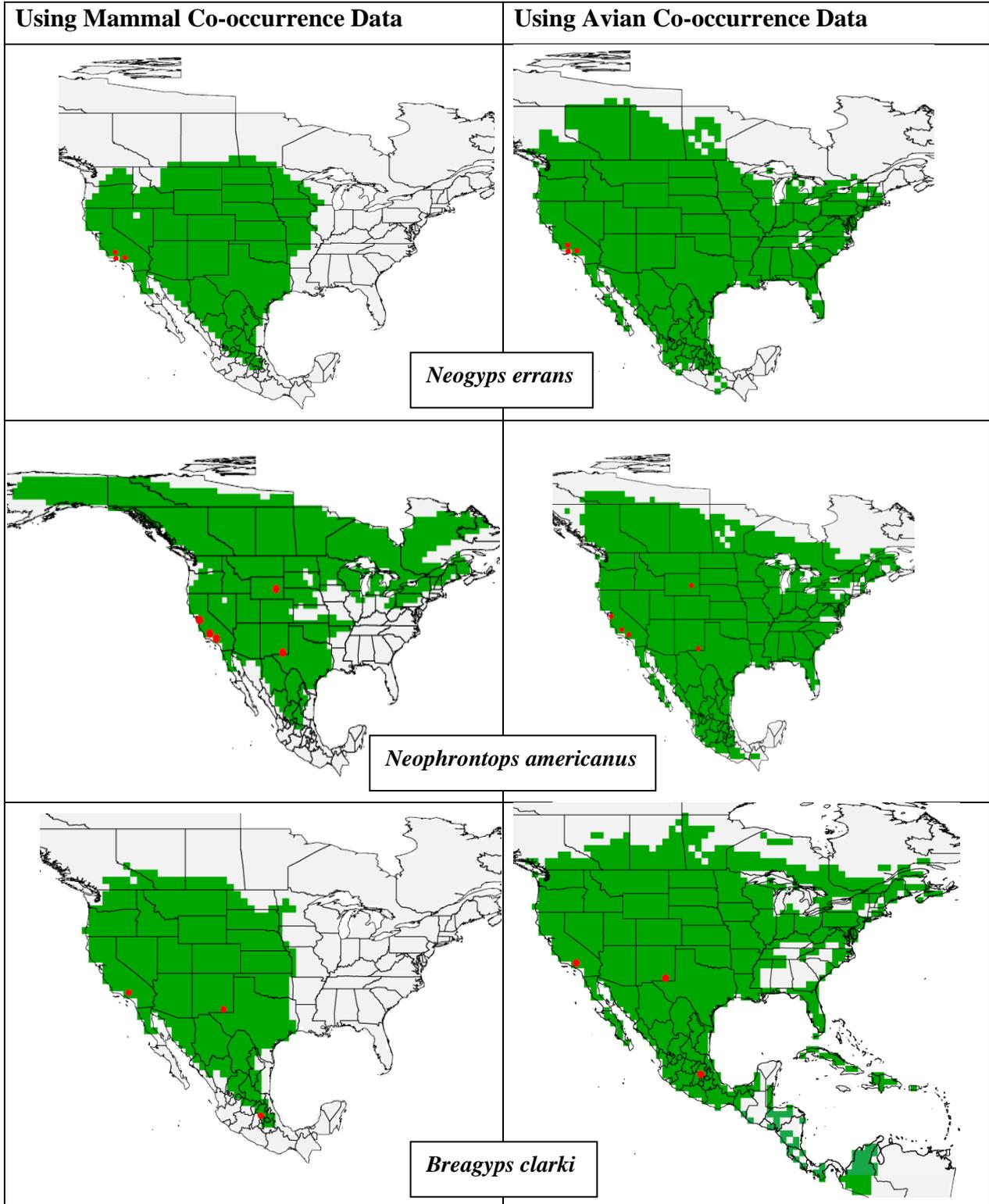
Table 2. Fossil sites (n=29) where extinct scavenging bird remains have been collected in North America. Site 4 is listed but grey because it was not included in our study due to lack of co-occurrence data. Aves and Mammals columns states how many bird and mammal species co-occurred at that site.

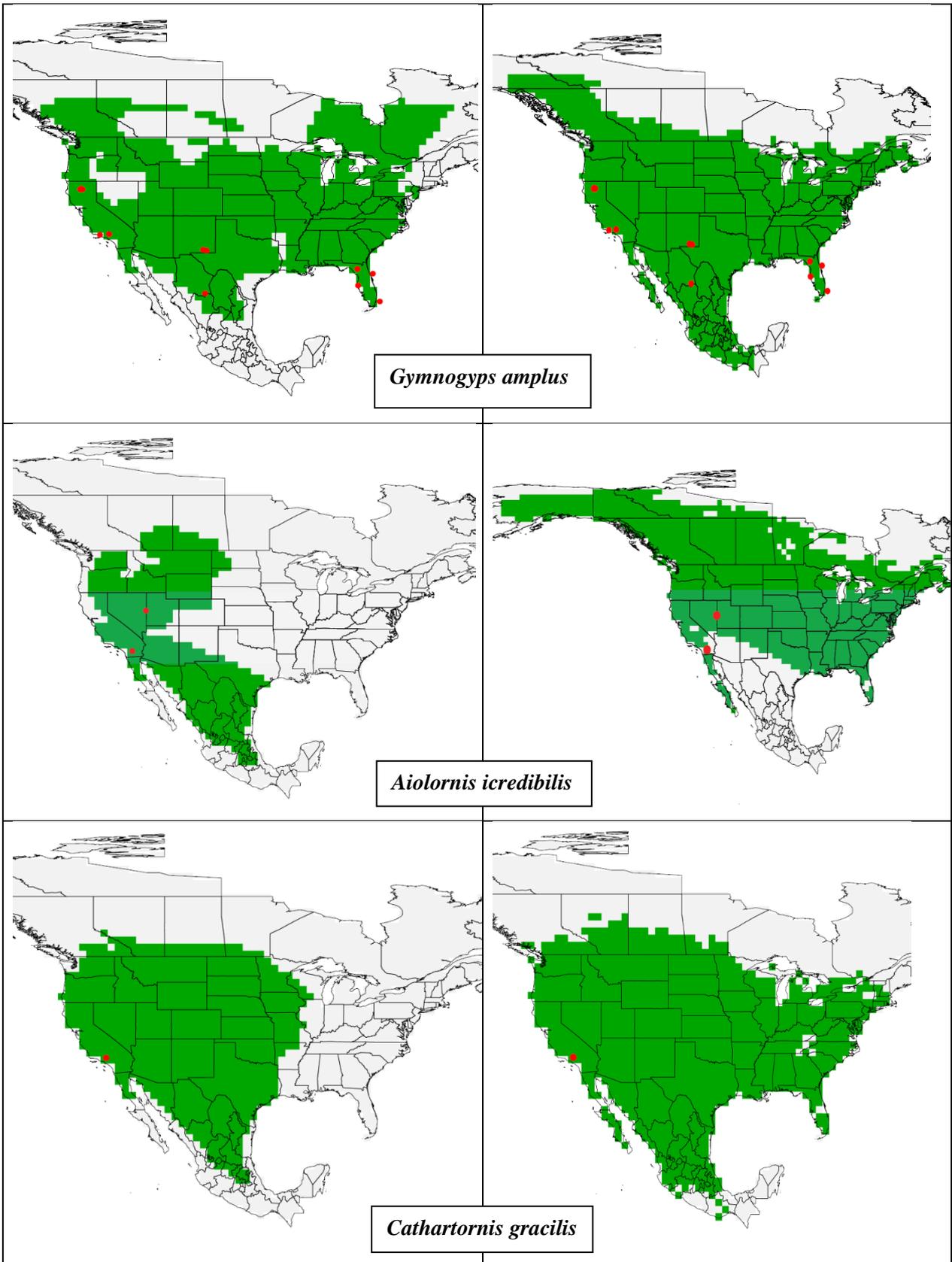
Site	Site Name	Location	Coordinates (Lat, Long)	Aves	Mammals
A	Murrieta Sandstone	California	33.4° N, -116.2° W	1	18
B	Carpinteria Asphalt Pit	California	34.4° N, -119.5° W	7	3
C	Carpinteria Tar Pits	California	34.4° N, -119.5° W	35	9
D	La Brea Tar Pits	California	34.5° N, -118.2° W	66	44
E	McKittrick Asphalt Pit	California	35.3° N, -119.6° W	41	15
F	Irvington	California	37.5° N, -121.7° W	0	8
G	Stone Man Cave	California	40.8° N, -122.0° W	3	2
H	Potter Creek Cave	California	40.8° N, -122.3° W	11	31
I	Samwel Cave No.1	California	40.9° N, -122.2° W	8	7
J	Cutler Hammock	Florida	25.8° N, -79.6° W	33	42
K	Bradenton	Florida	27.5° N, -82.5° W	6	4
L	Manatee County	Florida	27.7° N, -80.8° W	3	6
M	Leisey Shell Pit	Florida	27.7° N, -82.3° W	15	13
N	Seminole Field	Florida	27.8° N, -82.7° W	37	25
O	Reddick 1A	Florida	29.3° N, -80.6° W	42	43
P	Haile XIB	Florida	29.8° N, -81.9° W	58	25
Q	Ichetucknee River	Florida	29.9° N, -82.8° W	42	8
R	LACM	Mexico D.F.	19.9° N, -99.1° W	6	4
S	Jimenez Cave	Chihuahua, Mexico	26.8° N, -104.5° W	14	19
T	Smith Creek Cave	Nevada	39.25 N, -114.1 W	26	1
U	Dark Canyon Cave	New Mexico	32.3° N, -104.3° W	22	5
V	Dry Cave	New Mexico	32.4° N, -104.5° W	9	24
W	Burnet Cave	New Mexico	32.4° N, -104.8° W	15	28
X	Woodburn Bog	Oregon	45.15° N, -122.5° W	3	4
Y	Hall's Cave	Texas	30.08° N, -99.3° W	1	39
Z	Friesenhan Cave	Texas	28.9° N, -97.9° W	3	31

aa	Crystal Ball Cave	Utah	39.5° N, -114.0° W	19	42
bb	Little Box Elder Cave	Wyoming	42.8° N, -105.7° W	56	17

Estimated Ranges

Table 3. Estimated ranges for nine extinct scavenging birds from North America using mammal and bird co-occurrence data. Red dots depict fossil sites.





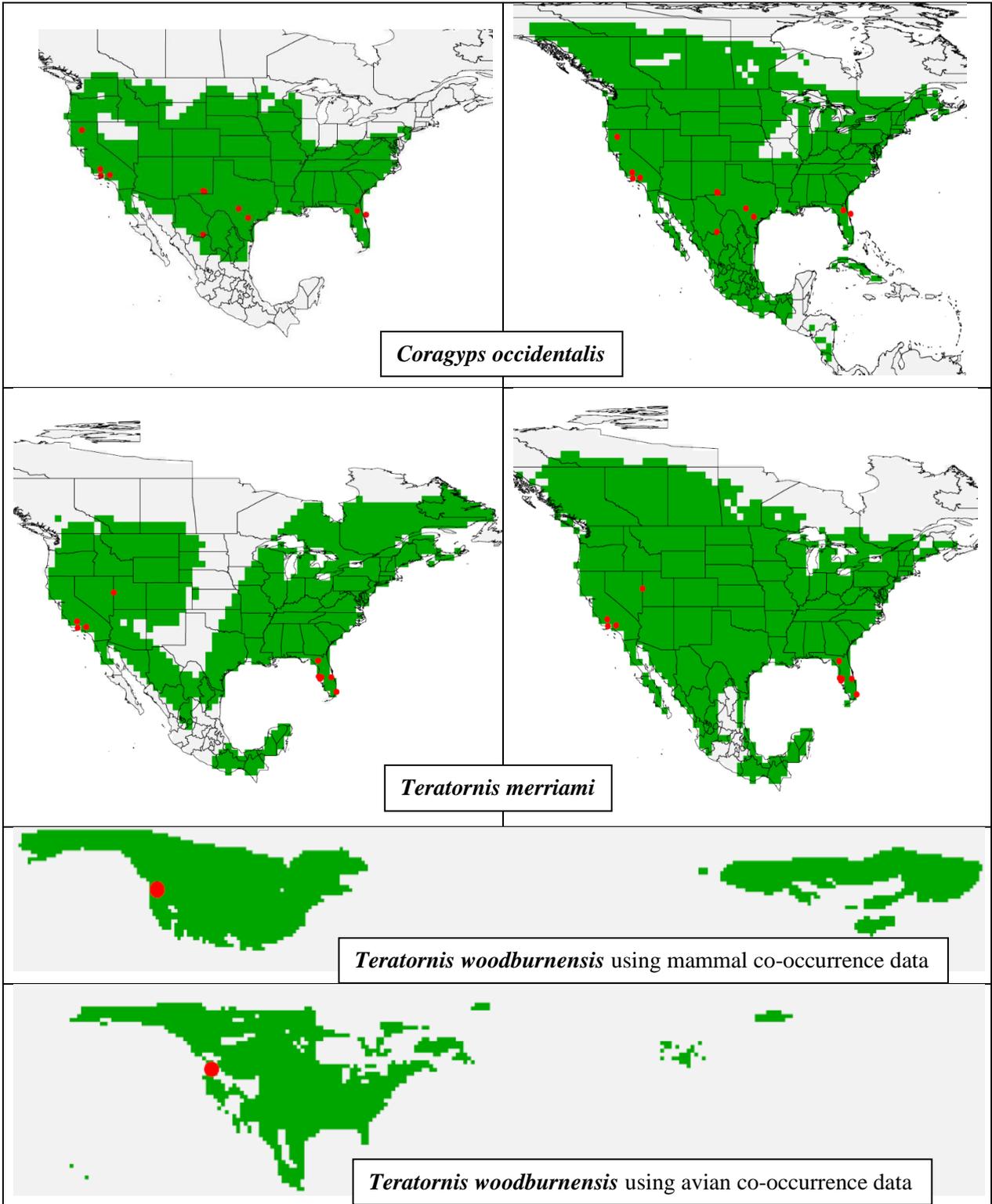
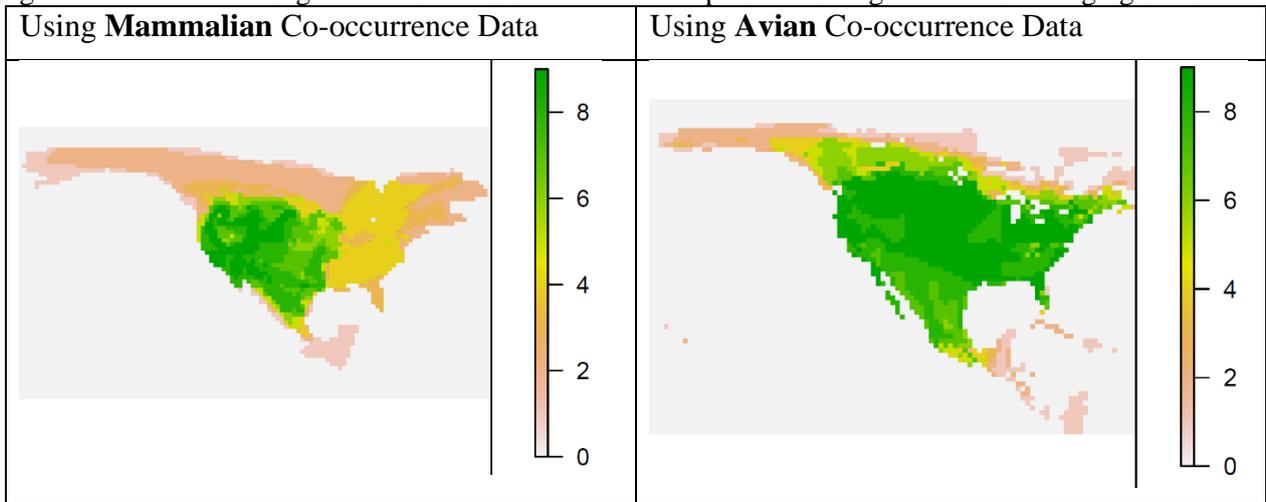


Table 4. Estimated abundance and distribution of extinct scavenging birds in North America (n=9). Summing all nine rasters, the color bar represents how many scavengers are estimated to be present in a given cell. The darkest green cells are associated with the presence of eight extinct scavenging birds.



Present-Natural Mammal Diversity

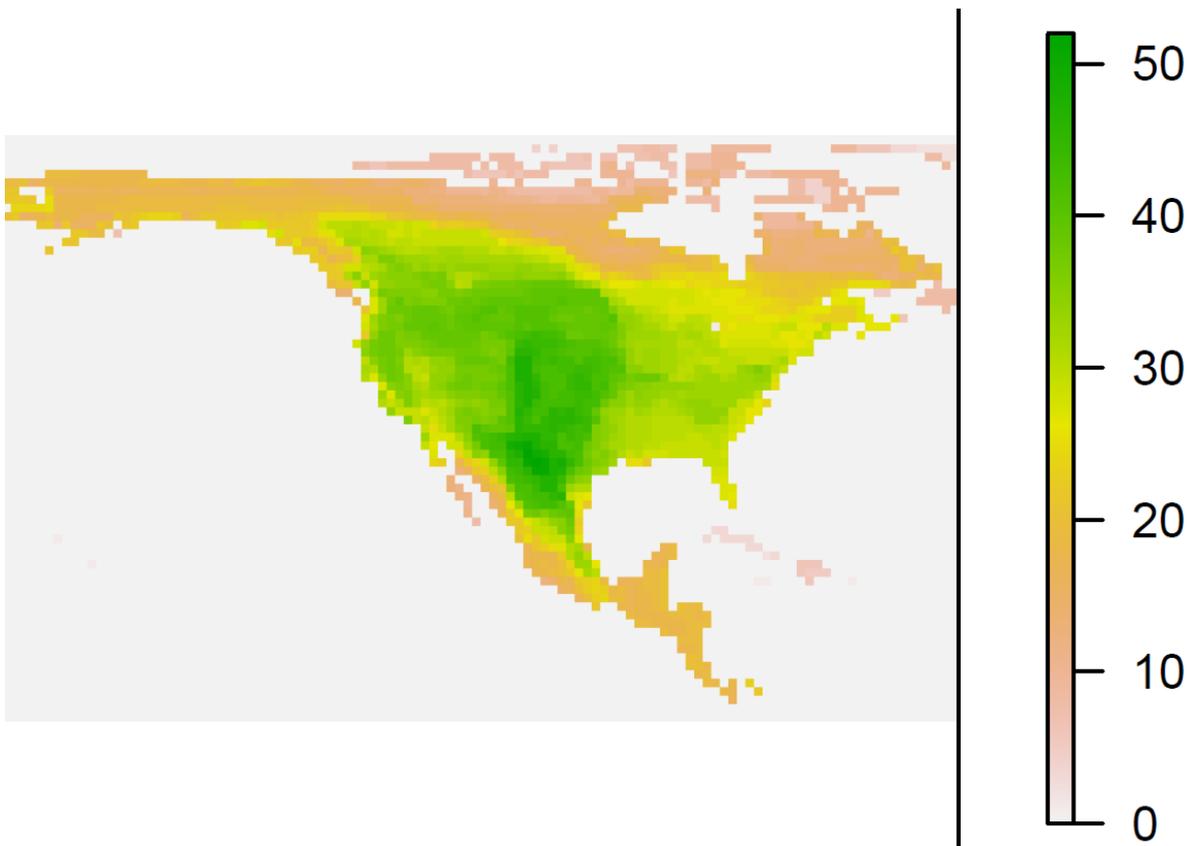


Figure 1. Present-natural diversity of terrestrial North American mammals from the Late Pleistocene that weigh/weighed >10kg (n=616). Regions with the high abundance of mammals(>40 species) are colored in green. The cells with the highest presence of mammals are the darkest green (n=51).

General Linear Model

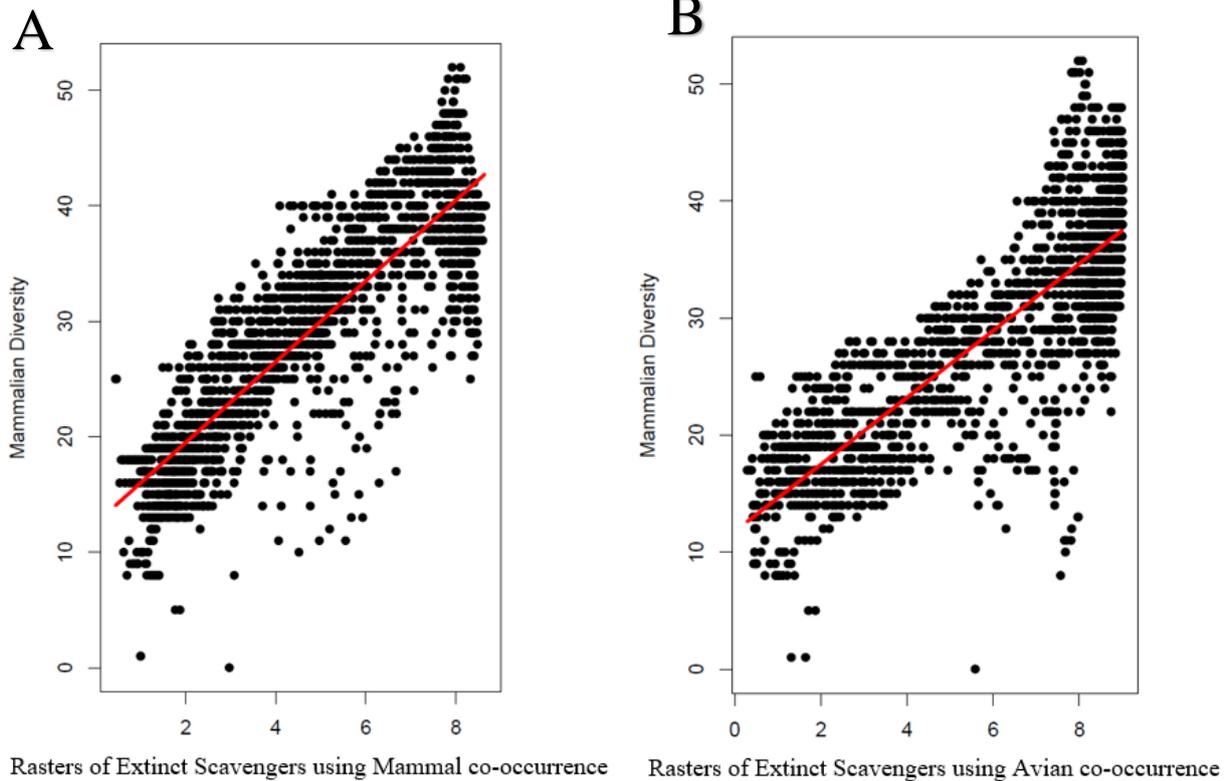


Figure 2. Linear regression analysis with the predictor variable as abundance of extinct scavenging birds based on their estimated range using either mammal co-occurrence data, A, or avian co-occurrence data, B, correlated with the response variable, present-natural mammal diversity in North America. Using mammal data (coefficient: 0.8654, R-squared = 0.7334, $p < 2e-16$) produced an estimate of extinct scavenger diversity that is more strongly correlated with present natural mammal diversity, than using bird data (coefficient: 0.8223, R-squared = 0.676, $p < 2.2e-16$) by general linear models with a fitted regression line.

GLM using Mammalian co-occurrence data

The estimate for the coefficient is 0.8564 (standard error: 0.01, $p < 2e-16$) indicating that scavenging bird diversity using mammal co-occurrence data has a significant positive effect on present-natural mammal diversity. meaning that as the abundance of scavengers increases, mammal diversity also increases. In other words, as more scavengers are estimated to exist in a given location, the mammalian diversity in that location will also increase. The R-squared value of 0.7334 indicates that the predictor variable explains about 73.3% of the variation in the response variable. The minimum residual is -2.38005, the maximum residual is 1.37259, and the residual standard error is 0.5164, which represents the average amount of deviation between the predicted values and the actual values of mammal diversity. The general linear model suggests a strong positive relationship between estimated scavenging bird diversity based on mammal co-occurrence data and present-natural mammal diversity, and thus estimating the range of extinct scavengers based on mammalian co-occurrence data is a significant predictor of present-natural mammalian diversity.

GLM using Avian co-occurrence data

The estimate for the coefficient is 0.8223 (standard error: 0.01, $p < 2.2e16$) indicating a significant relationship between the predictor and response variable. Although the results are significant, the coefficient in this model has a lower value than that of the model using mammal co-occurrence data, suggesting that using mammal data produces an estimated range of extinct scavenging birds that is a better predictor of present-natural mammalian diversity. The residual standard error is 0.5692, and the R-squared value of 0.676 indicates that 67.6% of the variance of present-natural

mammal diversity can be explained by the predictor variable. The residuals show some deviation from normality, with a minimum value of -2.90592 and a maximum value of 1.82562.

Autocorrelated General Linear Models

This plot is used to identify the presence of spatial autocorrelation in our model, which is a violation of the assumptions of linear regression. At distances less than 2000 km, there is an extremely high degree of spatial autocorrelation. The presence of spatial autocorrelation is common for spatial data and is the reason we need to account for autocorrelation in our model. The high correlation at greater distances could potentially arise from sampling bias. Anything over 6000km in our data can be disregarded as inaccurate because that exceeds the extent of North America and at such large distances there may be fewer data points for the model to choose from, and the few data points that there are could be close to each other, artificially inflating the autocorrelation at larger distances.

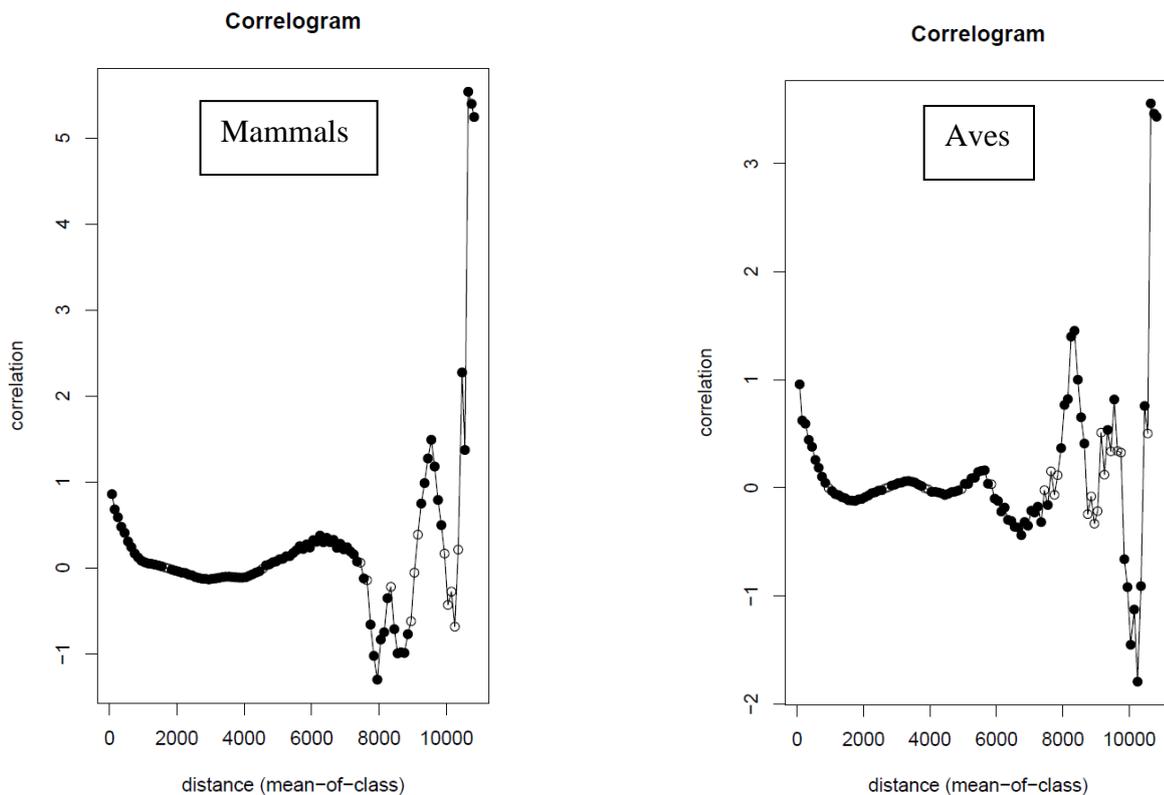


Figure 3. Estimating the degree of spatial autocorrelation for each GLM model. The left plot, is a correlelogram for the model using mammal co-occurrence data, and the right is the correlelogram for the model using avian co-occurrence data. Both models show a degree of spatial auto-correlation for distances <2000km.

Spatial Autoregressive Models

The correlograms in Figure 4 depict how the SAR models practically eliminate the effects of spatial autocorrelation in our data, so that only distances very close together still show a slight degree of autocorrelation, and distances from 100km to 7000km hover around the value zero, indicating spatial autocorrelation has been fully integrated into our models. As with the general linear model, anything over 7000km can be disregarded as inaccurate, noisy data because at such large distances, the low number of data points creates an inflated autocorrelation at larger distances.

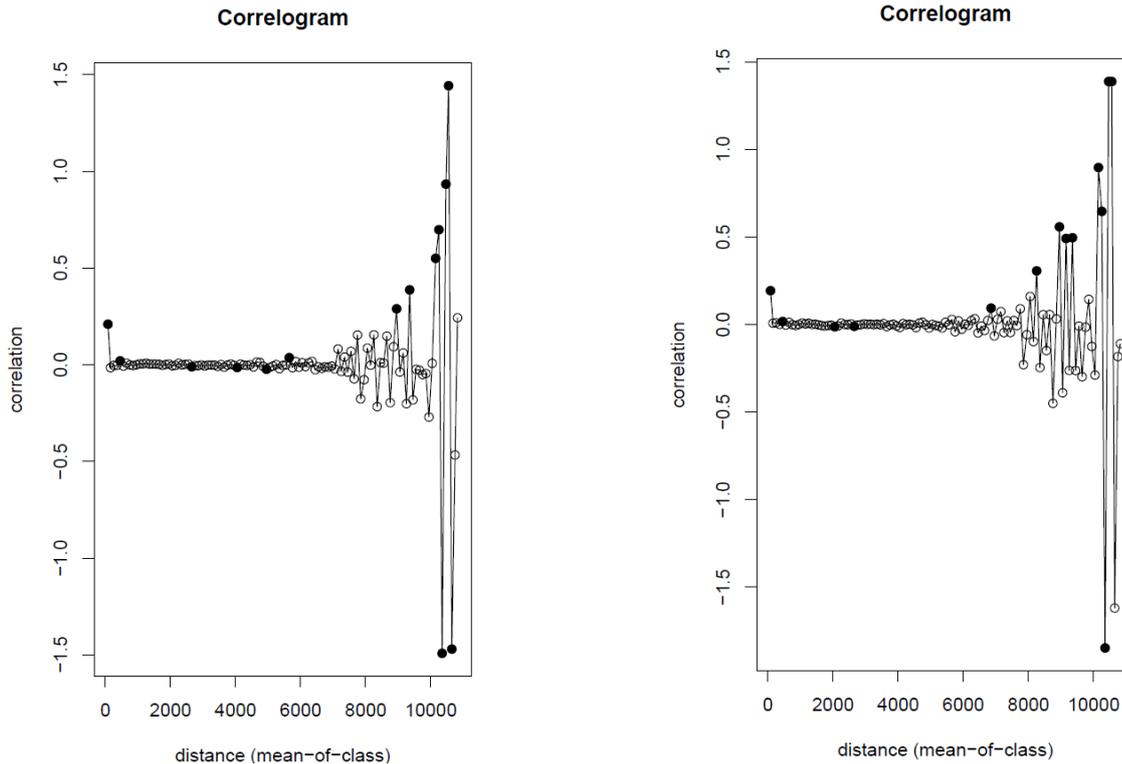


Figure 4. Estimating the degree of spatial autocorrelation for each SAR model. The left plot, is a correlogram for the model using mammalian co-occurrence data, and the left is the correlogram for the model using avian co-occurrence data. Both models show a slight degree of spatial auto-correlation for distances <100km. Distances from 101km to 7000km hover around zero for both models, indicating spatial auto-correlation was accounted for in the data and fully integrated into the SAR models.

SAR using mammalian co-occurrence data

The coefficient for the estimated range of extinct scavenging birds in North America using mammalian co-occurrence data is 1.04379 (standard error: 0.058, $p < 2.22e-16$). For all models, cells that are associated with the presence of more extinct scavengers or higher scavenging bird diversity are also associated with an increase in present-natural mammalian diversity.

R-squared and Akaike Information Criterion

The Nagelkerke pseudo-R-squared value is a measure of the goodness of fit of the model. This value is based on the difference between the log-likelihood of the full model and a null model with no predictors. For this model, the Nagelkerke pseudo-R-squared is 0.9536, indicating that the model explains a large proportion of the variation in the dependent variable. The Akaike Information Criterion (AIC) is a measure of the trade-off between the goodness of fit of the model and the complexity of the model. The AIC for this SAR model is -457.27, and the AIC for a simple linear regression model without spatial autocorrelation is 3030.5. The lower AIC value for the SAR best neighbor model suggests that it provides a better balance of fit and complexity than the general linear model.

SAR using avian co-occurrence data

The coefficient for the estimated range of extinct scavenging birds in North America using avian co-occurrence data is 0.762186 (standard error: 0.0551, $p < 2e-16$) indicating that this coefficient is highly significant.

R-squared and Akaike Information Criterion

The Nagelkerke pseudo-R-squared for this model is 0.94688. The AIC for this model is -173.68, and the AIC for a simple linear regression model without spatial autocorrelation is 3181. The

lower AIC value for the SAR model suggests that it provides a better balance of fit and complexity than the general linear model.

Comparing both models

Table 4. Summary of four model results. Intercepts reported with standard error in parentheses.

Model	Coefficient	P-value	R-squared	AIC	Intercept
SAR - MAM	1.044	< 2e-16	0.953	-457.27	-0.107 (se = 0.108)
SAR - AVES	0.762	< 2e-16	0.947	-173.68	-0.101(se = 0.093)
GLM - MAM	0.856	< 2e-16	0.733	3030.5	3.1e-16(se = 0.016)
GLM - AVES	0.822	< 2.22e-16	0.676	3181	-1.023(se = 0.013)

Scavenging bird diversity based on either mammal or bird co-occurrence data are both significant predictors of present-natural mammalian diversity. The effect size of the estimated range using mammalian co-occurrence, 1.04379, is higher than the effect size of the estimated range using avian co-occurrence, 0.762.

The Nagelkerke pseudo-R-squared values of 0.9536 and 0.94688 for the mammal and avian models, respectively, indicate that the model using mammal co-occurrence data provides a better fit than the model using avian co-occurrence data. The AIC values of -457.27 and -173.68 for the mammal and bird models, respectively, indicate that the model using mammal co-occurrence data provides a better balance of fit and complexity than the model using bird co-occurrence data.

Table 4 provides a summary of our results. Both estimated ranges of extinct scavenging birds built using either mammal or bird data provide estimated scavenger diversity that is a significant predictor of present-natural mammalian diversity, but the model using mammal data has a stronger effect size. The SAR models confirmed that spatial autocorrelation is present in the data, and based on the AIC values, we can conclude that the SAR models provide a better fit than the GLM models that did not account for spatial autocorrelation. Overall, my analysis suggests that the estimated range of extinct scavenging birds using mammal co-occurrence data provides an estimated scavenging bird diversity that is a better predictor of present-natural mammalian diversity than the model based on avian co-occurrence data.

Discussion

Correlation between estimated ranges and present-natural mammal diversity

R-squared and auto-generated correlation

The results of this study revealed that the estimated range of extinct scavenging birds based on mammal co-occurrence data was more strongly correlated to present-natural mammal diversity. This is a result we expected simply based on the fact that the species listed in the mammal co-occurrence data are also included in the list of species used to determine present-natural mammal diversity. Using mammal co-occurrence data to estimate the range size of the extinct scavengers resulted in a larger effect size than when using avian co-occurrence data, but that's partly due to the fact that many of the same species were included in both of the variables that we statistically compared to one another, resulting in some automatically generated correlation that was expected. Likewise, we also expected that using avian co-occurrence data to estimate the ranges of extinct scavengers would result in a lower effect size because calculating with bird species created an estimate that was completely independent from the species that were included in building the present-natural mammalian distribution, meaning there wasn't an auto-generated correlation between those two variables. It is therefore hard to determine if the large effect size is stronger simply because the variables are autocorrelated, or if estimating the ranges of scavenging

birds using mammal co-occurrence data truly produces more accurate predictors of present-natural mammal diversity.

The normal scope of effect size when computing SAR models is for the values to fall within the range of -1 to 1, which is a measure of the association between variables. To reiterate our results, the SAR model using mammal data produced a coefficient value of 1.04379, which is a larger effect size than the SAR model using avian data, which produced a coefficient value of 0.762. The model produced a coefficient value greater than one for two reasons: the data was scaled prior to running the analysis and also because count numbers are way less treatable as continuous numbers when they are small. Although these effects are not necessarily deterministic in causing coefficient values greater than one, in this case they generated so much noise in our data that it happened to cause a coefficient value higher than one. Scaling the parameters so that all predictors are scaled to have a mean of zero and a standard deviation of one is an important step to take so that effect size is comparable amongst the two SAR models, but in this case also produced a coefficient that was greater than the value of one. Referring back to Figure 1, the scales on the x and y axes do not grow at the same intervals. The highest number of scavengers found at a given cell in the raster is 8, while the highest number of mammals found at a given cell is 51. When count numbers are as low as they are, as in the case with scavengers, they are less treatable as continuous than when count numbers get higher, as in the case with mammal diversity, which can be treated as essentially continuous.

The extremely high R-square values that our model produces could be a function of a strong neighborhood effect. In other words, the high R-squared values could be attributed to the fact that the response variable, present-natural mammal diversity, is strongly influenced by the values of its neighboring observations. The extremely high R-squared values of 0.953 and 0.947 are representative of the combined effect of the predictor and the neighborhood. The presence of a strong neighborhood effect implies that the values of mammal diversity in a particular area are closely related to the values in neighboring areas, leading to high R-squared values for both models. So, even though the results produced extremely high R-squared values for both models, this does not, by definition, mean that the predictors are important. Both r-squared values are so high that we cannot extrapolate much meaning from the R-squared values of these models. Rather, by comparing AIC values, we can gain an understanding of which model estimates the strongest predictor, which in our case is the model that used mammal co-occurrence data.

Spatial autocorrelation

Spatial autocorrelation (SAC) is the phenomenon where observations that are geographically close to each other tend to be more similar than observations that are farther apart (Overmars et al., 2003). In other words, there is a spatial dependence between observations.

Spatial autocorrelation is an important consideration in spatial data analysis because it violates the independence assumption that underlies most traditional statistical techniques. Conventional methods such as general linear regressions assume data to be statistically independent, but with range studies, species distribution data tends to be dependent, meaning cells that are closer in distance to each other are expected to be more or less similar to one another than a randomly associated pair of observations would be. If spatial autocorrelation exists in the data and one were to use a traditional statistical method that assumes independence and an identical distribution, you run the risk of biased parameter estimates, incorrect p-values, low model fit, and encountering type 1 errors (false positives), which result in falsely rejecting the null hypothesis of no effect (Dorman et al., 2007).

To account for spatial autocorrelation in our model, we used spatial error autoregressive models (SAR) which consider the relationship between error values in one area and associated errors in

another corresponding area (Saputro et al., 2019). In this type of model, the errors in one area are correlated with the errors in adjacent or nearby areas, which are captured through a spatial weight matrix. This weight matrix specifies how much the errors in one location are influenced by the errors in neighboring locations. By incorporating this spatial dependency structure into the model, the SAR model can account for the spatial autocorrelation in the data and provide more accurate parameter estimates, standard errors, and p-values compared to traditional statistical techniques such as general linear models.

SAR models are thus important in spatial data analysis because they account for the spatial autocorrelation in the data, which is critical for obtaining accurate parameter estimates and making reliable statistical inferences. To detect if spatial autocorrelation was present in the data, an autocorrelated regression model for both range estimates, using mammalian and avian co-occurrence data, was performed. The resulting plots revealed there is spatial autocorrelation in the data, which was expected, and in the following step of conducting the spatial autoregressive models, the resulting lambda values and large difference in AIC between the SAR model and GLM without spatial autocorrelation confirmed that spatial autocorrelation was present in the data, which is exactly why it is important to account for autocorrelation in our model.

Using multivariate datasets to more accurately reconstruct historic range estimates

For the scope of this study, I aimed to estimate the historic ranges of extinct scavenging birds solely based on the ranges of the other birds and mammals each scavenging species was found to co-occur with at the different fossil sites. This simpler project design did not account for the biotic or abiotic factors that govern species diversity in real-world scenarios. Traditionally, when ecologists are estimating the home range, diversity, and abundance of living organisms, their models often include biotic and abiotic variables to account for the complex interactions that influence the distribution patterns of species diversity (Solórazano et al., 2019). Generally speaking, abiotic factors that can influence species diversity and range size include plate tectonics, oxygen availability, changes in sea level, temperature, rainfall, and light availability (Solórazano et al., 2019). Biotic factors can include prey availability, competition among predators, and vegetation coverage. Being that this study did not take into account biotic or abiotic factors, I can recommend to future students or researchers interested in exploring this topic more in depth that they include biotic and abiotic factors into the study design and models. Biotic and abiotic factors that particularly influenced the Late Pleistocene, a period marked by the last Ice Age, include but are not limited to the disappearance of mammoth steppe, once the most extensive biome on earth; a vast reduction in ice sheets; a shift in temperature and climatic conditions; quantifiable shifts in vegetation and fire regimes; and the decline of species due to the loss of certain functional groups, such as scavenging birds, which all lead to the rearrangement of trophic and ecological interactions amongst species as well as changes in biogeochemistry (Toth et al., 2019).

Differences in Estimated Ranges using Avian and Mammal Co-occurrence Data

In this study, using avian co-occurrence data to estimate the range of the extinct scavenging birds of North America consistently produced larger range maps than when using mammalian co-occurrence data. The avian species included in our co-occurrence data tended to have much larger ranges compared to the mammals included in our co-occurrence data. This fact is the probable cause for the difference in range size when comparing the estimates made using aves and mammal co-occurrence data.

Limitations

Working with few fossil sites

Using great-circle distance and convex-hull methods, researchers at Cambridge University were able to accurately reconstruct the geographic range size of various species that lived during the Rancholabrean period using only a few fossil occurrence sites. Numbers as low as five fossil collection localities were used to reliably reconstruct the species ranges (Darroch 2018). Granted, the study did only focus on and test fossil data of currently extant species with known range sizes so that they could measure the accuracy of their methods. Yet they went on to state that range dynamics and extinction patterns from 'the relatively recent past' could be reliably reconstructed using a few localities. With many of the extinct scavenging species in my study being found at just a few fossil sites, including two species that are known only from one fossil site each, it is both thought provoking and contestable whether these few fossil sites are sufficient to accurately estimate the historic range of these extinct species that I studied.

Working with a low number of species in co-occurrence data

The accuracy of our model predictions improves as we have larger datasets for estimating historic ranges based on co-occurrence data. However, in some cases, the estimation of extinct scavenger ranges was biased and likely unreliable due to low species counts in the co-occurrence data from fossil sites. Specifically, the species *Teratornis woodburnensis* had a very limited number of co-occurring species in its range estimation. These co-occurrence species, such as the migratory pintail *Anas acuta*, the muskrat *Ondatra zibethicus*, and the elk *Cervus canadensis*, are widely distributed in the northern hemisphere. Consequently, the low number of co-occurring species and their global distribution led to an estimated range for *T. woodburnensis* that exceeded the bounds of North America, making it likely unreliable and inaccurate.

Incompleteness of the fossil-record

In the case of our study, we are operating under the fact that the fossil record is incomplete. Paleontologists have gathered sufficient information to understand the many factors and variety of reasons that contribute to the fossil record being incomplete. Paleontologists may overlook existing fossils due to available sampling techniques not detecting all fossil that are present at a site (Holland 2000). Organisms may have been uncommon in the wild, and as a result, their fossils are also uncommon. In terms of preservation potential, only the hard sections of organisms are often retained, and a lot of these fossil parts can be lost due to breakage, abrasion, and dissolution. Organisms that only inhabit particular habitats can result in the discovery of their fossils only in particular facies, or rock formations made from sediment deposited in those ecosystems. If sediments did not accumulate where the organism once lived it is unlikely the organisms fossil would be preserved. Likewise, erosion could subsequently removed rocks or sediments in which fossils are preserved, exposing them to the elements and possibly eliminating the likelihood of well-preserved fossil specimens. Many fossils of the 9 extinct scavenging birds in this study were found over 100 years ago and no other traces of these animals have since been discovered. If additional fossils for these species were found, their ranges could be re-estimated to provide more accurate historic distributions.

Incomplete Biodiversity Databases

Integrating the variety of numerous biodiversity information sources into a more complete database is critical to supporting more efficient and effective conservation efforts and environmental management strategies to protect global biodiversity. A tremendous amount of information regarding global biodiversity is already in collections and repositories around the world. However, digitization has not yet been achieved for the majority of this information (Shanmughavel 2007). A study conducted by researchers from various Natural History Museums

around the world found that globally, biodiversity databases are in the initial stages of data compilation, and those that are available and accessible to the public primarily focus on extant species or recently extinct organisms (Ball-Demerow et al. 2019). There is much opportunity to fully integrate the scope of biodiversity knowledge that is currently available across the globe, and across a variety of disciplines, taxonomic nomenclatures, and geopolitical boundaries but efforts must be made to compile and consolidate information from the diverse set of resources currently available, including biological databases and scientific publications (Heberling 2021). Biodiversity informatics infrastructure must be built from a holistic approach that is inclusive of both historical observations and contemporary environmental aspects so as to fully encapsulate the complexity of all life on Earth (Hardisty 2013). Moving away from the idea that biodiversity databases as just a collection of taxon names, to more of a holistic approach inclusive of a wide variety of biodiversity facets, from genes to whole ecosystem processes, scientists will be better able to comprehend, quantify and forecast how changes in biodiversity within community structure can affect ecosystem functioning. The field of biodiversity informatics has seen such attempts to integrate and publish previously disconnected data sources including the current efforts such as the Global Biodiversity Information Facility also known as GBIF, and iNaturalist.

In relation to the scope of this study, only limited efforts have been made to date to identify, consolidate and share available fossil data on extinct birds, with PBDB and 'Recently Extinct Species' being the most comprehensive databases. Searching for fossil localities from incomplete databases required additional efforts such as reviewing scientific literature available online and compiling information from various resources such as partial databases and publications in scientific journals. My experience of having to cross reference multiple databases and various resources only solidifies my support for fully integrating biodiversity knowledge into one easily accessible and easy to navigate comprehensive source.

Synonyms

Synonyms in taxonomy pose a significant challenge, especially when studying extinct species that already have limited data. Taxonomy relies on a standardized naming system that reflects evolutionary relationships. However, historical variations in naming by different scientists have led to numerous synonyms for the same species.

For extinct species, this challenge is intensified due to limited available information, making it difficult to differentiate between synonyms and valid species names. This can result in confusion and errors during data analysis, as researchers may unknowingly combine data from multiple species under a single name.

The International Commission on Zoological Nomenclature (ICZN) maintains a standardized list of approved species names to address this issue. However, there are cases where uncommon synonyms are widely recognized and may be considered alternative or conserved names by the ICZN (Dubois, 2011).

This creates difficulties for researchers, as they may need to search for data under multiple names to compile a comprehensive dataset. Additionally, the use of different names for the same species in different studies hinders result comparison and synthesis.

To address synonyms within the scope of the study, the Paleobiology Database (PBDB) combines synonyms under the most accepted taxonomic name, making it seamless to search for a species of interest within the database. Scientific sources beyond PBDB were searched using known synonyms to ensure that all fossil sites where these species of extinct scavenging birds have been recorded are included in the study. Fossil sites with coordinates and scientific sources confirming the presence of these species were incorporated into the study.

Breagyps clarki Miller 1910 has three synonyms: *Sarcorhamphus clarki* Miller 1910, *Vultur clarki* Lambrecht 1933, and *Breagyps clarkii* Miller 1910.

Gymnogyps amplus Miller 1911 has one synonym: *Gymnogyps californianus amplus* Miller 1911.

Aiolornis incredibilis Howard 1952 has one synonym: *Teratornis incredibilis* Howard 1952.

Teratornis merriami Miller 1909 has one synonym: *Pleistogyps rex* Miller 1910.

Coragyps occidentalis Miller 1909 has 3 synonyms: *Coragyps atratus occidentalis* Miller 1909, *Catharista occidentalis* Miller 1909; and *Coragyps shastensis* Miller 1911.

The bird and mammal species in the co-occurrence data were directly taken from various sources and compiled into a list. Raster files were then identified based on these species' names. With over 350 species in the study, the majority of which had raster files, I did not systematically check if every species without a raster file had a synonym. I assumed that the absence of a raster file was due to data deficiency for those extinct species without an estimated range map, rather than the possibility of them having a synonym. Most of the species without an associated raster file are extinct species that do not have estimated ranges because there is no known estimated range for that extinct species currently.

During the process of rasterizing shapefiles, I coincidentally discovered that a few species in the co-occurrence list were listed under synonyms. I adjusted their names to their currently recognized taxonomic names and found raster files for them after making the adjustment. If I were to redo the study, I would take the time to systematically check the non-scavenging birds and mammals in the co-occurrence data to ensure that their synonyms were not used instead of their currently recognized names.

The number of non-scavenging birds and mammals included in the study is relatively large compared to the excluded species without range maps, so we can assume that their exclusion did not significantly impact the study's results.

Benefits of using rasters

Using rasters for this study provided several benefits:

1. **Spatial Analysis:** Rasters allow for efficient spatial analysis and modeling. By converting shapefiles to rasters, we can perform various analytical operations such as overlaying different layers, calculating proximity, conducting spatial autocorrelation analysis, and generating distribution models. Raster data structures are particularly useful for continuous phenomena like species abundance.
2. **Data Integration:** Rasters provide a standardized format for integrating data from multiple sources. By converting shapefiles to rasters, we can combine different spatial datasets into a single, consistent format. This integration allows for easy data manipulation and analysis. Although the scope of this study did not include non-spatial data, another benefit of using raster-based data is that it can be combined with other raster layers or used in conjunction with non-spatial data for comprehensive analysis.
3. **Efficient Storage and Processing:** Rasters are often more space-efficient than shapefiles, especially for large and continuous datasets. Rasters store data in a grid format, where each cell contains a single value. This grid structure enables efficient storage and processing, making it easier to handle and analyze large datasets. Additionally, many software tools are optimized for raster-based analysis, enabling faster processing times.

Implications for studying Co-extinction Events

In my study, I tested the method of estimate the ranges of data-limited species using co-occurrence data from a small number of fossil sites. This approach can be applied in future studies to estimate the distributions of other extinct animals that are known from only a few fossil sites.

Previously, it was suggested that the decline in mammalian prey was responsible for the extinction of scavenging birds in North America, but there was limited evidence regarding the geographic extent of these scavengers prior to the extinction event. The results of this study establish a significant relationship between the estimated distributions of the extinct scavengers and the present-natural mammalian diversity, providing biogeographic evidence that supports the theory of co-extinction, in which the decline of scavenging birds was directly caused by the reduction in their mammalian prey.

The co-extinction of scavenging birds and mammalian megafauna in North America likely led to significant changes in community assemblages, including the loss of top-down control and shifts in ecosystem dynamics (Toth et al., 2019). By estimating the historic range of extinct scavenging birds and understanding their distribution, we can gain insights into the impact of their absence on ecosystems where they no longer exist. The extinction of nine scavenging bird species in North America during the Late Pleistocene likely had detrimental effects on other species and the overall ecosystem. This information about their historic range and distribution can contribute to our understanding of how the loss of megafauna affected scavenging bird populations and can inform conservation strategies for extant scavenging birds today.

Studying the co-extinction of mammalian megafauna and scavenging birds in North America during the Late Pleistocene also has implications for modern conservation efforts. Scavenging birds, especially vultures, play a crucial ecological role in rapidly and efficiently disposing of carcasses, thus maintaining a clean and safe environment for humans, livestock, and wildlife (DeVault et al., 2016). Extant scavenging birds and megafauna are vital for ecosystem health and biodiversity, making them focal points for conservation strategies due to their size and ecological significance.

When keystone species like scavenging birds are lost, it disrupts biotic interactions within the ecosystem, leading to direct and indirect ecological impacts that affect ecosystem health and dynamics (Beschta and Ripple, 2009). These impacts include loss of pest control, nutrient cycling, and ecosystem engineering, which can result in a decline in biodiversity and overall degradation of ecosystem health (Ripple et al., 2015). Protecting scavenging bird populations and preserving the ecosystem services they provide will not only benefit humanity but also support vulnerable communities at risk of economic instability and disease spillover into their communities (Van den Heever et al., 2021).

Conclusion

This study aimed to test the use of co-occurrence data to estimate the ranges of data-limited species known from only a few fossil sites. Specifically, I estimated the historic range of nine extinct scavenging birds from North America using this method. The approach of using co-occurrence data can also be applied in future studies to estimate the distribution of other extinct animals with limited fossil evidence.

Previous hypotheses have suggested that the decline in mammalian megafauna directly contributed to the reduction in scavenging bird diversity. By comparing the estimated ranges of scavenging birds using avian or mammalian co-occurrence data and analyzing their statistical

relationship with present-natural mammalian diversity, valuable insights into the biogeographic distribution of scavenging birds before the Late Pleistocene mass extinction were obtained.

Notably, range maps estimated from avian co-occurrence data were generally larger than those from mammal co-occurrence data, likely due to the wider distribution and larger home ranges of birds compared to mammals. Autocorrelated linear models revealed spatial autocorrelation in the data, prompting the use of spatial autoregressive models with an optimized neighborhood structure to improve the accuracy of the effect size estimation.

The results of our generalized linear models (GLM) and spatial autoregressive (SAR) models indicated that both avian and mammalian co-occurrence data were significant predictors of present-natural mammalian diversity. However, range estimates based on mammalian co-occurrence data had a stronger effect size, suggesting that it is a better predictor of present-natural mammalian diversity compared to avian co-occurrence data.

These findings provide geographic evidence supporting the theory of co-extinction, which posits that the decline of scavenging birds in North America was directly linked to the reduction in their mammalian prey. Understanding the historic range and distribution of extinct scavengers contributes to our knowledge of the ecological impacts of megafauna extinction and can inform conservation strategies for extant scavenging birds.

Preserving scavenging bird populations is crucial for maintaining ecosystem health and biodiversity. These birds play essential roles in carcass disposal and biotic interactions within ecosystems. Therefore, conservation efforts focused on scavenging birds have broader implications for ecosystem stability, human well-being, and the preservation of vulnerable communities.

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Appendix 1 – Popular Science Summary

Fossil data gives new insight into the historic range size of North Americas largest extinct birds

With a wingspan of 5 meters, the largest flight-capable bird to ever have existed on the continent of North America is a species called *Teratornis incredibilis*, sometimes also called the Giant Condor. At the end of the last Ice-Age, the Giant Condor along with 8 other species of scavenging birds from North America went extinct. The historic range of these nine species has long been a mystery, but utilizing the fossil co-occurrence method has provided new insight into their estimated historic range size, and what implications that poses for the still living scavenging birds around the globe.

Many extinct scavengers whose ranges were estimated in this study are known from less than 3 fossil sites, in some cases only 1 or 2 locations! How do you estimate the historic range of an animal that is known from such few fossil sites you ask? Using fossil co-occurrence data! By gathering a list of all the other mammals and bird fossils found alongside the extinct scavenging bird of interest and using the range size of all the animals in that co-occurrence list, we can infer the historic range of the extinct scavenging birds themselves.

Why did so many scavenging birds go extinct?

At the end of the last Ice Age, there was a 72% reduction in mammalian species in North America. Lots of megafauna like mammoths, saber tooth tigers, and giant sloths went extinct. This led to a wave of bird extinctions, vultures being the most severely affected. The drastic decrease in prey availability led to populations of starving and impoverished scavengers, eventually resulting in their extinction as a species. Past studies suggest a strong correlation between the extinction of scavengers and their mammalian prey in terms of severity and timing, yet questions remained regarding the geographic range of the scavengers prior to the co-extinction event. Thus, the aim of this study was to contribute to this gap in biogeographical information by estimating the historic range of extinct scavenging birds using co-occurrence data.

Estimating the historic ranges of extinct scavengers

Using images that depict the range of all the co-occurrence species I worked with a computer software called program R and went site by site, and species by species until I had the result of two estimated ranges for each species, one based on bird co-occurrence data, and one based on mammal co-occurrence data. Estimate range size of all 9 species were consistently geographically larger when using avian data over mammal data.

Does their historic range correlation with the range of their mammalian prey?

The results of statistical analysis suggested a positive relationship between scavenging diversity and prey diversity, but that using mammalian co-occurrence data to estimate the range of extinct scavenging birds provides an estimated diversity of scavengers that is more strongly correlated with diversity of their mammalian prey.

Why is this important?

Scavenging birds are keystone species because of the extremely important ecological service they provide of efficiently disposing of carcasses. Their presence helps slow the spread of diseases and keeps ecosystems healthy. Unfortunately, they are amongst the most threatened group of birds in the world, with 57% of vulture species worldwide being threatened with extinction. Protecting living mammalian megafauna and scavenging birds is critical for maintaining ecosystem health, and by providing geographic information about the historic range of extinct scavengers we can better convey the effects of the co-extinction event between these two groups and hopefully urge stakeholders to take stronger actions to protect wildlife for future generations.

Appendix 2 – List of co-occurrence species

In total, 357 unique species of birds and mammals were included in the co-occurrence data.

189 avian species included in co-occurrence data:

<i>Accipiter cooperii</i>	<i>Buteo regalis</i>	<i>Gallinago gallinago</i>	<i>Pipilo chlorurus</i>
<i>Accipiter gentilis</i>	<i>Buteo swainsoni</i>	<i>Gallinula chloropus</i>	<i>Pipilo erythrophthalmus</i>
<i>Accipiter striatus</i>	<i>Calamospiza melanocorys</i>	<i>Gavia immer</i>	<i>Pipilo maculatus</i>
<i>Actitis macularius</i>	<i>Calidris melanotos</i>	<i>Geococcyx californianus</i>	<i>Platalea ajaja</i>
<i>Aechmophorus occidentalis</i>	<i>Callipepla californica</i>	<i>Geothlypis trichas</i>	<i>Pluvialis squatarola</i>
<i>Aegolius acadicus</i>	<i>Caracara cheriway</i>	<i>Glaucidium gnoma</i>	<i>Podiceps auritus</i>
<i>Aegolius funereus</i>	<i>Cardinalis cardinalis</i>	<i>Grus americana</i>	<i>Podiceps nigricollis</i>
<i>Agelaius phoeniceus</i>	<i>Cardinalis cardinalis</i>	<i>Gymnogyps californianus</i>	<i>Podilymbus podiceps</i>
<i>Aix sponsa</i>	<i>Cathartes aura</i>	<i>Haemorrhous mexicanus</i>	<i>Porzana carolina</i>
<i>Ammodramus savannarum</i>	<i>Centrocercus urophasianus</i>	<i>Haliaeetus leucocephalus</i>	<i>Quiscalus major</i>
<i>Amphispiza bilineata</i>	<i>Chamaea fasciata</i>	<i>Jabiru mycteria</i>	<i>Quiscalus quiscula</i>
<i>Anas acuta</i>	<i>Charadrius montanus</i>	<i>Lagopus leucura</i>	<i>Rallus elegans</i>
<i>Anas carolinensis</i>	<i>Charadrius vociferus</i>	<i>Lanius ludovicianus</i>	<i>Rallus limicola</i>
<i>Anas crecca</i>	<i>Chordeiles minor</i>	<i>Laterallus exilis</i>	<i>Rallus longirostris</i>
<i>Anas fulvigula</i>	<i>Circus cyaneus</i>	<i>Leucosticte arctoa</i>	<i>Recurvirostra americana</i>
<i>Anas platyrhynchos</i>	<i>Circus hudsonius</i>	<i>Limnodromus griseus</i>	<i>Salpinctes obsoletus</i>
<i>Anas rubripes</i>	<i>Cistothorus platensis</i>	<i>Limnodromus scolopaceus</i>	<i>Scolopax minor</i>
<i>Anhinga anhinga</i>	<i>Clangula hyemalis</i>	<i>Lophodytes cucullatus</i>	<i>Sialia mexicana</i>
<i>Anser albifrons</i>	<i>Coccyzus americanus</i>	<i>Loxia curvirostra</i>	<i>Sitta canadensis</i>
<i>Anser caerulescens</i>	<i>Colaptes auratus</i>	<i>Mareca americana</i>	<i>Sitta pygmaea</i>
<i>Anser rossii</i>	<i>Colinus virginianus</i>	<i>Mareca strepera</i>	<i>Spatula clypeata</i>
<i>Aphelocoma californica</i>	<i>Coragyps atratus</i>	<i>Megascops asio</i>	<i>Spatula cyanoptera</i>
<i>Aphelocoma coerulescens</i>	<i>Corvus brachyrhynchos</i>	<i>Melanerpes carolinus</i>	<i>Spatula discors</i>
<i>Aquila chrysaetos</i>	<i>Corvus caurinus</i>	<i>Melanerpes erythrocephalus</i>	<i>Spinus pinus</i>
<i>Aramus guarauna</i>	<i>Corvus corax</i>	<i>Melanerpes lewis</i>	<i>Spinus tristis</i>
<i>Ardea alba</i>	<i>Corvus cryptoleucus</i>	<i>Melanitta perspicillata</i>	<i>Spiza americana</i>
<i>Ardea herodias</i>	<i>Corvus ossifragus</i>	<i>Meleagris gallopavo</i>	<i>Spizella passerina</i>
<i>Asio flammeus</i>	<i>Coturnicops noveboracensis</i>	<i>Melospiza fusca</i>	<i>Strix varia</i>
<i>Asio otus</i>	<i>Cyanocitta cristata</i>	<i>Mergus merganser</i>	<i>Sturnella magna</i>
<i>Athene cunicularia</i>	<i>Cyanocitta stelleri</i>	<i>Milvago chimachima</i>	<i>Sturnella neglecta</i>
<i>Aythya affinis</i>	<i>Cygnus buccinator</i>	<i>Mimus polyglottos</i>	<i>Surnia ulula</i>
<i>Aythya americana</i>	<i>Cygnus columbianus</i>	<i>Molothrus ater</i>	<i>Toxostoma rufum</i>
<i>Aythya collaris</i>	<i>Dendragapus fuliginosus</i>	<i>Mycteria americana</i>	<i>Tringa flavipes</i>
<i>Aythya marila</i>	<i>Dendragapus obscurus</i>	<i>Nucifraga columbiana</i>	<i>Tringa melanoleuca</i>
<i>Aythya valisineria</i>	<i>Ectopistes migratorius</i>	<i>Numenius americanus</i>	<i>Troglodytes aedon</i>
<i>Bombycilla cedrorum</i>	<i>Egretta caerulea</i>	<i>Numenius borealis</i>	<i>Turdus migratorius</i>
<i>Bonasa umbellus</i>	<i>Egretta thula</i>	<i>Nyctanassa violacea</i>	<i>Tympanuchus cupido</i>
<i>Botaurus lentiginosus</i>	<i>Egretta tricolor</i>	<i>Nycticorax nycticorax</i>	<i>Tympanuchus pallidicinctus</i>
<i>Branta canadensis</i>	<i>Elanus leucurus</i>	<i>Oreortyx pictus</i>	<i>Tympanuchus phasianellus</i>
<i>Branta hutchinsii</i>	<i>Eremophila alpestris</i>	<i>Oreoscoptes montanus</i>	<i>Tyrannus tyrannus</i>
<i>Bubo scandiacus</i>	<i>Eudocimus albus</i>	<i>Oxyura jamaicensis</i>	<i>Tyto alba</i>
<i>Bubo virginianus</i>	<i>Falco columbarius</i>	<i>Pandion haliaetus</i>	<i>Vireo griseus</i>
<i>Bucephala albeola</i>	<i>Falco mexicanus</i>	<i>Passerella iliaca</i>	<i>Xanthocephalus</i>
<i>Buteo jamaicensis</i>	<i>Falco peregrinus</i>	<i>Patagioenas fasciata</i>	<i>xanthocephalus</i>
<i>Buteo lagopus</i>	<i>Falco rusticolus</i>	<i>Petrochelidon pyrrhonota</i>	<i>Zenaida macroura</i>
<i>Buteo lineatus</i>	<i>Falco sparverius</i>	<i>Phalaenoptilus nuttallii</i>	<i>Zonotrichia albicollis</i>
<i>Buteo nitidus</i>	<i>Fulica americana</i>	<i>Phoenicopterus ruber</i>	
<i>Buteo platypterus</i>	<i>Gallinago delicata</i>	<i>Pica pica</i>	

168 mammalian species included in co-occurrence data:

<i>Alces alces</i>	<i>Geomys pinetis</i>	<i>Neomonachus tropicalis</i>	<i>Procyon lotor</i>
<i>Ammospermophilus leucurus</i>	<i>Glaucomys volans</i>	<i>Neotamias dorsalis</i>	<i>Puma concolor</i>
<i>Antilocapra americana</i>	<i>Glyptotherium cylindricum</i>	<i>Neotamias senex</i>	<i>Reithrodontomys humulis</i>
<i>Antrozous pallidus</i>	<i>Gulo gulo</i>	<i>Neotoma albigula</i>	<i>Reithrodontomys megalotis</i>
<i>Aplodontia rufa</i>	<i>Hemiauchenia</i>	<i>Neotoma cinerea</i>	<i>Reithrodontomys montanus</i>
<i>Arborimus longicaudus</i>	<i>macrocephala</i>	<i>Neotoma floridana</i>	<i>Scalopus aquaticus</i>
<i>Arctodus simus</i>	<i>Holmesina septentrionalis</i>	<i>Neotoma fuscipes</i>	<i>Scapanus latimanus</i>
<i>Azlanolagus agilis</i>	<i>Homotherium serum</i>	<i>Neotoma lepida</i>	<i>Sciurus carolinensis</i>
<i>Baiomys taylori</i>	<i>Lasiurus borealis</i>	<i>Neotoma mexicana</i>	<i>Sciurus griseus</i>
<i>Bassariscus astutus</i>	<i>Lasiurus cinereus</i>	<i>Neotoma micropus</i>	<i>Sciurus niger</i>
<i>Blarina carolinensis</i>	<i>Lasiurus intermedius</i>	<i>Neovison vison</i>	<i>Sigmodon hispidus</i>
<i>Bootherium bombifrons</i>	<i>Lemmiscus curtatus</i>	<i>Nothrotheriops shastensis</i>	<i>Smilodon fatalis</i>
<i>Brachylagus idahoensis</i>	<i>Leopardus pardalis</i>	<i>Notiosorex crawfordi</i>	<i>Sorex hoyi</i>
<i>Brachyprotoma obtusata</i>	<i>Lepus alleni</i>	<i>Nycticeius humeralis</i>	<i>Sorex longirostris</i>
<i>Callospermophilus lateralis</i>	<i>Lepus americanus</i>	<i>Ochotona princeps</i>	<i>Sorex monticolus</i>
<i>Camelops hesternus</i>	<i>Lepus californicus</i>	<i>Ochrotomys nuttalli</i>	<i>Sorex ornatus</i>
<i>Canis dirus</i>	<i>Lepus townsendii</i>	<i>Odocoileus hemionus</i>	<i>Sorex trowbridgii</i>
<i>Canis latrans</i>	<i>Lontra canadensis</i>	<i>Odocoileus virginianus</i>	<i>Spilogale putorius</i>
<i>Canis lupus</i>	<i>Lynx rufus</i>	<i>Ondatra zibethicus</i>	<i>Sylvilagus audubonii</i>
<i>Capromeryx minor</i>	<i>Mammuth americanum</i>	<i>Onychomys leucogaster</i>	<i>Sylvilagus bachmani</i>
<i>Castor canadensis</i>	<i>Mammuthus columbi</i>	<i>Onychomys torridus</i>	<i>Sylvilagus floridanus</i>
<i>Cervus canadensis</i>	<i>Mammuthus primigenius</i>	<i>Oreamnos americanus</i>	<i>Sylvilagus nuttallii</i>
<i>Cervus elaphus</i>	<i>Marmota flaviventris</i>	<i>Oryzomys palustris</i>	<i>Sylvilagus palustris</i>
<i>Chaetodipus formosus</i>	<i>Martes americana</i>	<i>Otospermophilus beecheyi</i>	<i>Synaptomys cooperi</i>
<i>Chaetodipus hispidus</i>	<i>Megalonyx jeffersonii</i>	<i>Otospermophilus</i>	<i>Tadarida brasiliensis</i>
<i>Conepatus leuconotus</i>	<i>Mephitis mephitis</i>	<i>variegatus</i>	<i>Tamias striatus</i>
<i>Cratogeomys castanops</i>	<i>Microdipodops</i>	<i>Ovis canadensis</i>	<i>Tamiasciurus hudsonicus</i>
<i>Cryptotis parva</i>	<i>megacephalus</i>	<i>Palaeolama mirifica</i>	<i>Tapirus veroensis</i>
<i>Cynomys gunnisoni</i>	<i>Microtus californicus</i>	<i>Panthera atrox</i>	<i>Taxidea taxus</i>
<i>Cynomys ludovicianus</i>	<i>Microtus longicaudus</i>	<i>Panthera leo</i>	<i>Thomomys bottae</i>
<i>Dasypus bellus</i>	<i>Microtus mexicanus</i>	<i>Panthera onca</i>	<i>Thomomys monticola</i>
<i>Dasypus novemcinctus</i>	<i>Microtus montanus</i>	<i>Paramylodon harlani</i>	<i>Thomomys umbrinus</i>
<i>Desmodus stocki</i>	<i>Microtus ochrogaster</i>	<i>Perognathus inornatus</i>	<i>Tremarctos floridanus</i>
<i>Didelphis virginiana</i>	<i>Microtus pennsylvanicus</i>	<i>Peromyscus boylii</i>	<i>Urocyon cinereoargenteus</i>
<i>Dipodomys agilis</i>	<i>Microtus pinetorum</i>	<i>Peromyscus californicus</i>	<i>Urocyon cinereoargenteus</i>
<i>Dipodomys elator</i>	<i>Mustela frenata</i>	<i>Peromyscus crinitus</i>	<i>Ursus americanus</i>
<i>Dipodomys microps</i>	<i>Mustela nigripes</i>	<i>Peromyscus gossypinus</i>	<i>Ursus arctos</i>
<i>Dipodomys nelsoni</i>	<i>Mylohyus nasutus</i>	<i>Peromyscus maniculatus</i>	<i>Vulpes macrotis</i>
<i>Dipodomys simulans</i>	<i>Myotis austroriparius</i>	<i>Peromyscus polionotus</i>	<i>Vulpes velox</i>
<i>Dipodomys stephensi</i>	<i>Myotis velifer</i>	<i>Peromyscus truei</i>	<i>Vulpes vulpes</i>
<i>Eptesicus fuscus</i>	<i>Navahoceros fricki</i>	<i>Pipistrellus subflavus</i>	<i>Zapus hudsonius</i>
<i>Erethizon dorsatum</i>	<i>Neochoerus aesopi</i>	<i>Platygonus compressus</i>	
<i>Euceratherium collinum</i>	<i>Neofiber alleni</i>	<i>Podomys floridanus</i>	

Appendix 3 – Fossil site references

Fossil sites where extinct scavenging birds from North America have been found:

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