The paleobiologic implications of modern nonmarine ecological gradients

Steven M. Holland[1] (ID), Cade J. Orchard[1] and Katharine M. Loughney[2] (ID)

[1]Department of Geology, University of Georgia, Athens, Georgia 30602-2501, U.S.A.
[2]Department of Earth and Environmental Sciences and Watershed Studies Institute, Murray State University, Murray, Kentucky 42071, U.S.A.

Non-technical Summary

Over geologic time, shorelines build seaward and retreat landward, causing the elevation of coastal areas to change. Sediments deposited in rivers record these changes in elevation and distance to the coast, and organisms living in these environments may be preserved as fossils. If species vary among these environments, this variation might be preserved in the fossil record, yet paleontologists have seldom documented this phenomenon. This absence raises the question of how commonly species distributions are related to elevation and distance to the coast. Here, we investigate the distributions of many plants, invertebrates, and vertebrates along the coastal plain of the southeastern United States, compiled from a community-sourced public database. Statistical evaluation shows that many coastal communities vary primarily with elevation and distance to the coast and to a lesser degree with latitude. Several poorly documented groups display no detectable pattern of geographic variation, but it is unclear whether this is a true lack of variation or a lack of adequate data. The widespread occurrence of this pattern suggests that it is present in the fossil record yet has gone largely unnoticed.

Abstract

In modern nonmarine settings, previous studies have demonstrated the importance of elevation-correlated ecological gradients, but such studies tend to focus on relatively small areas and only one higher taxon. Here, we analyze Global Biodiversity Information Facility occurrence records from a wide variety of taxa across the southeastern U.S. coastal plain. Many taxa display ecological gradients (gradients in proportional or relative abundance) correlated with elevation, distance to the coast, and latitude. These gradients tend to be steepest within a few tens of kilometers near the coast and at elevations less than 25 m. Some taxa, notably terrestrial mammals, do not display gradients correlated with elevation and distance to the coast. The small sample sizes of these groups and their heterogeneous sampling raise concerns about whether sufficient data exist. Coupled with previous studies of these ecological gradients, their common presence over distances of tens to hundreds of kilometers and elevations of tens to hundreds of meters suggests they are likely important in the nonmarine fossil record. Because elevation and distance to the coast change predictably with cycles of accommodation and sediment flux, these ecological gradients are predicted to occur in the nonmarine stratigraphic record, especially through intervals that record transgression or regression. Such gradients will affect the local composition of species associations and occurrences, even in the absence of regional species origination, immigration, and extinction and of regional change in the structure of ecological gradients. The ordination of taxon counts in stratigraphically limited samples has great potential for establishing their existence.

PALEOBIOLOGY | **Paleontological** SOCIETY
A PUBLICATION OF THE

CAMBRIDGE UNIVERSITY PRESS

Introduction

In modern settings, the distribution of plants and several types of animals is well known to vary with elevation (e.g., von Humboldt and Bonpland 1805; Whittaker 1956, 1960, 1970; Ohmann and Spies 1998), and elevation–diversity gradients are an area of active ecological study (e.g., Rahbek et al. 2019; van Els et al. 2021). Such variation with elevation is of particular interest for the nonmarine fossil record, because elevation changes predictably with shoreline transgression and regression (Holland and Loughney 2021; Holland 2022). Because of this, the composition of fossil communities will display stratigraphic changes, even though there may be no sedimentological manifestation of such changes, which complicates interpretations of biotic events in the past. The extent and form of such elevation-correlated variations in community composition are crucial for understanding the circumstances under which elevation-correlated changes are likely to present in the stratigraphic record.

Here, we analyze modern distributions of various plants and animals (Table 1) on the southeastern coast of the United States, a passive margin sedimentary basin, using occurrence

Table 1. Numbers of unique species, 0.2° grid cells, and species occurrences in Global Biodiversity Information Facility (GBIF) datasets analyzed in this study. Small-bodied mammals are non-volant clades dominated by species generally less than 3 kg and include Rodentia, Soricomorpha, Didelphimorphia, Cingulata, and Lagomorpha; this excludes the Carnivora, Artiodactyla, and Perissodactyla, as well as the Chiroptera, which might be expected to have larger ranges owing to their ability to fly.

Taxon	Species	Grid cells	Occurrences
Fungi and lichens	2932	382	38,055
Plantae	5542	558	217,687
Bryophytes	338	301	8542
Lycopodiopsida	12	66	358
Polypodiopsida	101	418	7271
Pinopsida	36	284	4280
Liliopsida	1287	542	41,860
Magnoliopsida	3185	559	151,474
Bivalvia	149	383	10,141
Gastropoda	331	380	6907
Arthropoda	8882	563	256,912
Insecta	7679	546	224,877
Fishes	367	540	73,003
Amphibia	107	507	41,170
Reptilia	116	545	53,266
Aves	528	562	15,881,022
Anseriformes	53	555	744,395
Birds of prey	25	566	1,103,695
Charadriiformes	106	544	1,862,305
Passeriformes	211	561	8,048,955
Pelecaniformes	21	560	1,416,293
Aves, summer	397	559	2,810,844
Aves, winter	427	561	4,778,109
Mammalia	120	438	39,082
Mammalia, terrestrial	80	423	19,715
Mammalia, small bodied	43	344	13,559

records in the Global Biodiversity Information Facility (GBIF 2023). We compare ordinations of occurrences to elevation, distance to the coast, and latitude to evaluate the strength and form of controls on community composition. We discuss what these results imply for the nature of the nonmarine fossil record, specifically that we predict that these gradients will be expressed in the nonmarine fossil record, especially in intervals of transgression and regression. Moreover, local changes in community composition resulting from the changing sampling of these gradients might be misinterpreted as reflecting regional species origination, immigration, and extinction or as perturbations to the structure of regional ecological gradients.

Background

The fact that biotas vary with elevation is a well-documented principle of ecology and biogeography. One of the earliest descriptions of this pattern was by Alexander von Humboldt and Aimé Bonpland (1805), who documented the elevational ranges of tropical vegetation in the equatorial Andes Mountains of Ecuador (Moret et al. 2019). Robert Whittaker led a resurgence of gradient ecology with similar studies of the Great Smoky Mountains in Tennessee (Whittaker 1956) and the Siskiyou Mountains of Oregon (Whittaker 1960). Numerous similar studies followed, illustrating the general pattern while showing that the underlying controls are dominated by precipitation, temperature, and other factors such as slope aspect and bedrock geology (Ohmann and Spies 1998). These studies led to analytical tools for identifying and characterizing ecological gradients in plant communities. Ordination became one of the most valuable tools, and a wide range of methods were developed, including polar ordination, correspondence analysis, detrended correspondence analysis (DCA), and nonmetric multidimensional scaling (NMS; Jongman et al. 1995; McCune and Grace 2002; Borcard et al. 2018). As a result, elevation-correlated gradients have been widely documented in plants, fish, and invertebrates (see review in Holland and Loughney 2021). Moreover, the extensive recent study of elevation diversity gradients underscores the underlying fact that species have elevational ranges and that those ranges are mainly controlled by temperature and precipitation.

Many of these studies span large elevational ranges of several thousand meters. In contrast, sedimentary basins typically have elevational ranges of 1000 m or lower, particularly in basin types with strong preservation potential (Holland et al. 2023). For coastal sedimentary basins, the elevation range is typically 200–300 m. Although such small elevation spans might cause one to question whether elevational differences in species composition can be detected, several ordination studies of plants, fish, and invertebrates show that they can (e.g., Gagnon et al. 2006; Dale et al. 2007; Drucker et al. 2008; Dail et al. 2013; Goncalves et al. 2020; Yin and Yan 2020). Even so, such studies typically focus on one or a few higher taxa, such as trees or fishes. This raises the question of how pervasive elevation-correlated gradients are among various taxa within a region. Moreover, it raises the question of whether community change is continuous along the span of elevations or is focused within particular spans of elevation. For example, one might expect that most community change in a coastal sedimentary basin might occur at low elevations near the coast (elevations of a few tens of meters above sea level or distances of a few tens of kilometers from the coast), owing to the presence of an ocean, with limited ecological change at greater distances from the coast (Holland and Loughney 2021). In particular, oceans buffer temperature fluctuations and provide a source of moisture for precipitation, thereby influencing coastal microclimates.

Methods

Here, we focus on the variation in community composition for a wide variety of higher taxonomic groups (Table 1) in the southeastern United States (Fig. 1) using occurrence data from GBIF (see Supplementary Data for download parameters, data files, and R source code). Two aspects of the study area make it ideal for this study, the first being that the biota is well documented. Second, the shore is oriented at a high angle to latitude, which allows latitudinal changes to be separated from changes with elevation or distance to the coast in a way that would not be possible, for example, on the U.S. Gulf Coast. Specifically, we assess whether the species composition of communities varies with
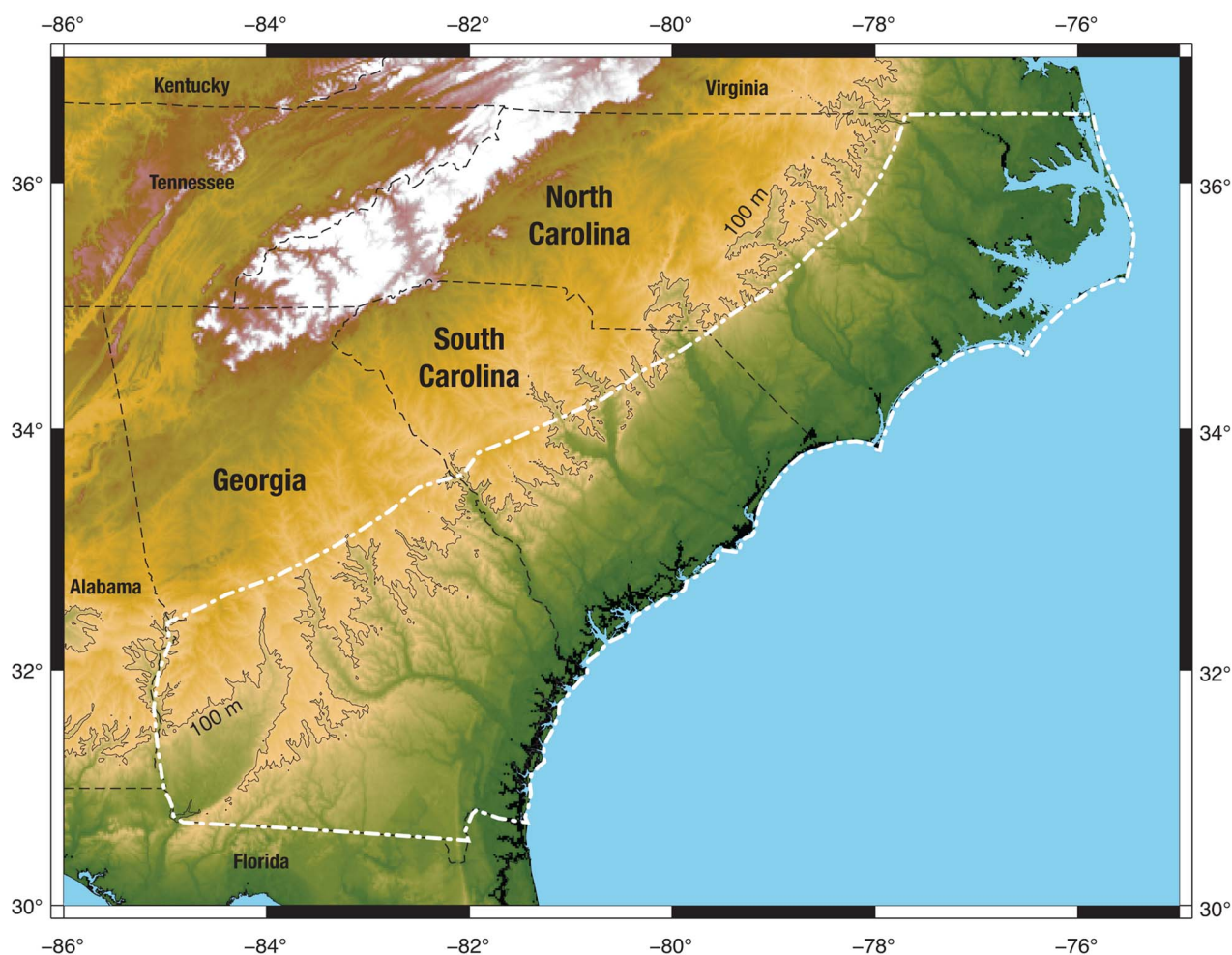
Figure 1. Relief map of the southeastern United States; dashed line encloses the study area. The northwestern limit of this study area is defined as the landward edge of the passive margin basin, where Cretaceous and Cenozoic sedimentary rocks abut and onlap primarily Paleozoic igneous and metamorphic rocks. The seaward limit is defined by a path connecting the barrier islands and beaches; estuaries are therefore included in the study area. Map generated with Generic Mapping Tools (GMT; http://www.soest.hawaii.edu/gmt; Wessel and Smith 1998).

elevation and distance to the coast. All analyses were performed in R v. 4.1.0 (R Core Team 2023).

Occurrence data were downloaded for a wide variety of taxonomic groups. Some will likely leave a fossil record (e.g., mammals and magnoliopsids). Others are unlikely to leave a fossil record (e.g., fungi and lichens), yet might provide food for those that could leave a fossil record. The datasets vary widely in their number of species, occurrences, and latitude–longitude grid cells (Table 1). For example, occurrences of birds equal those of nearly all other taxa combined, largely because GBIF draws from iNaturalist data supplied by amateurs such as birders, but also because there are many bird species. Subsets of some higher taxa are analyzed to determine whether particular taxonomic subsets are the main source of relationships with elevation, distance to the shore, and latitude. The amount of data commonly limits the ability to subset data in this way. For birds, we also analyzed summer months (June–August) and winter months (January–March) separately to remove the effects of migratory species.

We bin the species occurrences into 0.2° latitude and longitude grid cells to analyze these occurrence data. This bin size provides a compromise between high spatial resolution and sufficient species occurrences within each grid cell for analysis, although no

fixed cutoff in species occurrences was used. This binning produces a count of the number of reports of each species within each grid cell. Because grid cells can differ substantially in the number of species occurrences, and because the relative abundance of species is of interest, we perform a percent transformation, which converts the abundance of each species in each grid cell to a percentage of all species occurrences in that grid cell. To prevent the ordinations from being dominated by a few highly abundant species, we follow with a percent maximum transformation, which expresses all percentages for a given species as a fraction of the highest percentage observed for that species. As a result, the values for every species range from 1.0 in the grid cell in which it is most abundant to 0.0, in which the species is absent. Both transformations are standard in gradient ecology (Jongman et al. 1995; McCune and Grace 2002; Borcard et al. 2018), because they dampen the effects of outliers, specifically unusually large samples and unusually abundant species.

To summarize the variation in the species composition among these grid cells, we use nonmetric multidimensional scaling (NMS, also called NMDS and MDS) of these doubly transformed binned occurrence data. NMS is a widely adopted method in ecological gradient analysis, because it can recover ecological

gradients with little distortion (Minchin 1987; Patzkowsky and Holland 2012). Specifically, we use the metaMDS method in the vegan package of R, which performs an NMS ordination, followed by a principal components analysis, which rotates the NMS ordination such that NMS axis 1 explains the greatest source of variation in the data, followed by axis 2, and so on. We employ a three-dimensional NMS ordination with 100 restarts to avoid settling on a local minimum.

Although elevation and distance to the coast are highly correlated (Spearman's $r_s = 0.94$, Pearson's $r = 0.90$), the relationship of community composition to each is measured. The relationship between elevation and distance to the coast weakens inland (Fig. 2), partly because of the increasing topographic relief inland and partly because the elevation of the landward edge of the basin increases southward. We also visually assess the form of these relationships, whether the community change is even along the elevation span or concentrated along specific elevation spans, particularly near the coast. For comparison, we also assess whether community composition varies with latitude within the study area's limited span (~6.5°). Because we are interested in broad relationships that could be preserved in the fossil record, we do not evaluate spatial autocorrelation.

The elevation of the centroid of each grid cell and its distance to the coast are calculated using the geodata package in R. From this, we calculate the correlation of the NMS axes with elevation, distance to the coast, and latitude. Because elevation is typically correlated most highly with NMS axis 1, we prepared maps of the variation in NMS axis 1 scores across the region. All plots are included in the Supplementary Material, but only representative plots are shown in the text, owing to space considerations.

Results

The structure of these taxonomic communities is commonly correlated with elevation (Table 2) and distance from the coast (Table 3). Although some datasets are nested and therefore not independent, in 7 of the 26 datasets, elevation explains more than 25% of the variance in community composition as captured by the three-dimensional NMS ordinations (Table 2). These datasets include gastropods, fishes, birds (and several subsets of
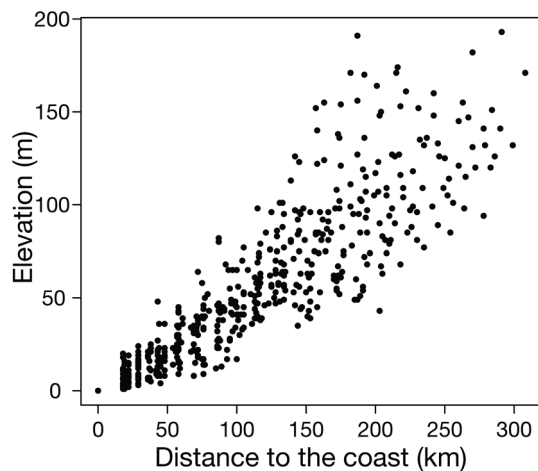

Figure 2. A plot of the elevation of the 0.2° grid cells used in this study versus their distance to the coast. Elevation and distance from the coast are measured at the centroids of the grid cells.

Table 2. The proportion of variance in nonmetric multidimensional scaling (NMS) ordination explained by elevation (r^2). All values shown are statistically significant at 0.05 with a Bonferroni correction (see Supplementary Data); dashes indicate values that are not statistically significant. Values of r^2 greater than 0.25 are indicated with boldface; values between 0.1 and 0.25 are italicized.

Taxon	NMS 1–3	NMS 1	NMS 2	NMS 3
Fungi and lichens	0.037	—	—	—
Plantae	*0.155*	*0.147*	—	—
Bryophytes	—	—	—	—
Lycopodiopsida	—	—	—	—
Polypodiopsida	—	—	—	—
Pinopsida	*0.132*	—	0.091	—
Liliopsida	—	—	—	—
Magnoliopsida	*0.186*	0.064	0.051	0.072
Bivalvia	*0.237*	*0.199*	—	—
Gastropoda	**0.261**	*0.129*	*0.132*	—
Arthropoda	*0.191*	*0.165*	—	—
Insecta	0.077	0.047	—	—
Fishes	**0.478**	**0.430**	0.047	—
Amphibia	0.071	—	—	0.047
Reptilia	*0.199*	—	*0.175*	—
Aves	**0.258**	*0.202*	0.046	—
Anseriformes	*0.204*	*0.187*	—	—
Birds of prey	**0.251**	*0.190*	0.050	—
Charadriiformes	**0.391**	**0.330**	0.057	—
Passeriformes	*0.203*	0.025	0.097	0.081
Pelecaniformes	**0.356**	*0.101*	**0.255**	—
Aves, summer	*0.238*	*0.192*	0.039	—
Aves, winter	*0.247*	*0.218*	0.030	—
Mammalia	**0.281**	*0.226*	—	0.044
Mammalia, terrestrial	0.035	—	—	—
Mammalia, small bodied	0.052	0.047	—	—

birds), and mammals. In an additional 10 of the datasets, elevation explains 10–25% of the variance in community composition (Plantae, Pinopsida, Magnoliopsida, Bivalvia, Arthropoda, Reptilia, Anseriformes, Passeriformes, summer Aves, and winter Aves). Most of the remaining nine datasets have small sample sizes (e.g., fungi and lichens, bryophytes, lycopods, ferns, terrestrial mammals, and small-bodied mammals).

The explained variance for distance from the coast exceeds 25% for 11 datasets and is between 10–25% for 6 datasets. In addition to gastropods, fishes, birds, and mammals, these include bivalves and reptiles. In most cases, the explained variance is greater for distance from the coast than for elevation. This partly results from the weakening correlation inland between elevation and distance from the coast (Fig. 2). Coastal areas more uniformly lie at low elevations in the study area, whereas relief increases inland (Fig. 1), such that interfluves are substantially higher than valley floors.

The variation in community composition is most correlated with NMS axis 1, indicating that it is correlated with the

Table 3. The proportion of variance in nonmetric multidimensional scaling (NMS) ordination explained by the distance to the coast (r^2). All values shown are statistically significant at 0.05 with a Bonferroni correction (see Supplementary Data); dashes indicate values that are not statistically significant. Values of r^2 greater than 0.25 are indicated with boldface; values between 0.1 and 0.25 are italicized.

Taxon	NMS 1–3	NMS 1	NMS 2	NMS 3
Fungi and lichens	—	—	—	—
Plantae	*0.168*	*0.166*	—	—
Bryophytes	—	—	—	—
Lycopodiopsida	—	—	—	—
Polypodiopsida	0.041	—	—	—
Pinopsida	0.099	—	0.073	—
Liliopsida	0.038	—	—	—
Magnoliopsida	*0.223*	0.092	0.044	0.087
Bivalvia	**0.360**	**0.324**	—	—
Gastropoda	**0.334**	*0.178*	*0.156*	—
Arthropoda	*0.240*	*0.205*	0.025	—
Insecta	*0.100*	0.068	—	—
Fishes	**0.547**	**0.481**	0.060	—
Amphibia	0.061	—	—	0.046
Reptilia	**0.250**	—	*0.196*	0.040
Aves	**0.312**	*0.219*	0.055	0.039
Anseriformes	*0.207*	*0.194*	—	—
Birds of prey	**0.262**	*0.200*	0.059	—
Charadriiformes	**0.467**	**0.350**	*0.101*	—
Passeriformes	*0.232*	0.032	0.081	*0.119*
Pelecaniformes	**0.386**	0.086	**0.300**	—
Aves, summer	**0.255**	*0.199*	0.056	—
Aves, winter	**0.279**	*0.221*	0.054	—
Mammalia	**0.373**	**0.292**	—	0.063
Mammalia, terrestrial	0.052	—	—	—
Mammalia, small bodied	0.076	0.070	—	—

ordination axis capturing the most important source of variation (Tables 2, 3). Of the datasets with strong correlations, elevation is more strongly correlated with NMS axis 2 for gastropods (but only slightly so) and Pelecaniformes (herons, ibises, spoonbills, and pelicans). Only for the magnoliopsids is the correlation strongest with NMS axis 3, but the correlations are similar across all three NMS axes. Similar relations hold for distance from the coast, which is most commonly correlated with NMS axis 1. For reptiles (lizards, snakes, turtles, and crocodilians) and Pelecaniformes (pelicans, ibises, spoonbills, herons, and bitterns), elevation is most strongly correlated with NMS axis 2; for Amphibia and Passeriformes (perching birds), elevation is most highly correlated with NMS axis 3.

Plots of NMS axis 1 versus elevation and distance from the coast illustrate the form of the correlations (Figs. 3, 4). Four main patterns in community composition emerge: steep coastal change, gentle inland change, decreasing inland variance, and an absence of inland change.

Many groups show pronounced changes in NMS axis 1 scores in the coastal zone, in the 0–25 m elevation range (Fig. 3), and at distances of 0–50 km from the coast (Fig. 4). Fishes, birds, and several subgroups of birds illustrate this pattern well. For several groups, such as arthropods, amphibians, and mammals, the change in NMS axis 1 scores is limited to a tight zone adjacent to the coast at elevations near sea level.

Several groups display gradual changes in NMS axis 1 scores inland of the coastal zone. For some groups (fishes, bivalves, and arthropods), the scatter around this trend is relatively small, but some groups display the trend of increasing NMS axis 1 scores inland but with substantial scatter (e.g., Plantae and Magnoliopsida).

Birds and several of their subgroups display a pattern of an inland decrease in the scatter of NMS axis 1 scores, rather than a linear inland trend in NMS axis 1 scores (Figs 3, 4). For example, this trend of decreasing inland variance is present in the Anseriformes (ducks, geese, and swans), birds of prey (eagles, hawks, and falcons), Charadriiformes (shorebirds), and Pelecaniformes. The inland decrease in variance is more evident with elevation (Fig. 3) than with distance to the coast (Fig. 4).

Maps of NMS axis 1 scores provide another way to visualize the pattern of community change (Fig. 5). Abrupt coastal change is apparent for birds and fishes and less so for arthropods. Latitudinal variation is also visible for fishes, arthropods, liliopsids, and several other taxa (Table 4, Supplementary Material). For 18 of the 26 datasets, the explained variance by latitude exceeds 25%; for another 6 datasets, the explained variance is 10–25%. The explained variance is <10% for the remaining two datasets. In other words, latitude explains a statistically nonzero proportion of the variance in community composition for every dataset. Even so, latitude is less commonly the strongest source of variation in each dataset (i.e., it is infrequently correlated with NMS axis 1), but its effects are commonly spread over several ordination axes rather than being expressed on a single NMS axis. For four taxa (liliopsids, bivalves, insects, and small-bodied mammals), latitude explains >25% of the variance in NMS axis 1. For five other taxa, the explained variance is 10–25%, and for the remaining 17 taxa, the explained variance is either statistically nonsignificant or less than 10%. More commonly, latitude correlates more strongly with NMS axis 2 and even more with NMS axis 3.

Subanalyses of larger taxonomic groups help assess whether particular subtaxa (or seasons in the case of birds) drive the patterns seen with elevation and distance to the coast. For Plantae, the variation with elevation and distance to the coast appears to be driven primarily by the magnoliopsids, with all other subgroups displaying weak correlations (non-bold, non-italicized values in Tables 2 and 3) or ones that are not statistically distinguishable from zero (dashes in Tables 2 and 3). Sample sizes are small for many of these groups with weak or no correlations with elevation or distance to the coast, whereas magnoliopsids alone represent nearly 70% of the plant occurrences. Small sample sizes greatly inhibit the ability to dissect patterns of taxa less frequently recorded in the GBIF data.

For birds, the strong relationships with elevation and distance to the coast are reflected in three major subtaxa, including birds of prey, Charadriiformes (shorebirds), and Pelecaniformes (pelicans, ibises, spoonbills, herons, and bitterns). Correlations are strong but somewhat weaker for the Anseriformes (ducks, geese, and swans) and Passeriformes (perching birds), although these are still stronger correlations than what is seen in most other taxa.
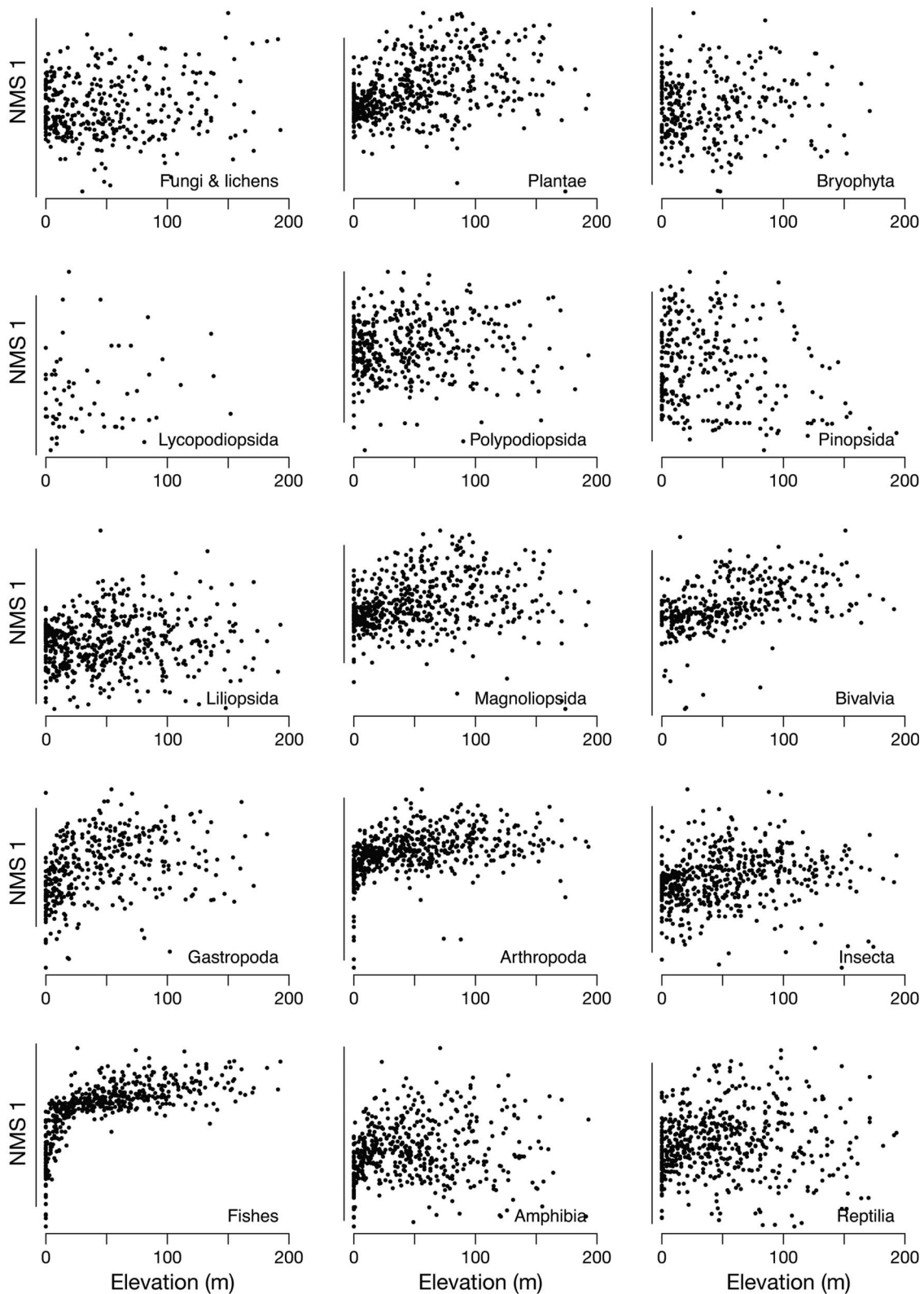
Figure 3. Scatter plots of the relationship of nonmetric multidimensional scaling (NMS) axis 1 scores to elevation for 27 taxonomic groups; points correspond to 0.2° grid cells.

Because the West Atlantic Flyway is a major migration path for many birds, we evaluated whether the correlations remain when the migration seasons (March–May and September–November) are excluded. For the summer months (June–August) and the winter months (January–March), the correlations are great for distance to the coast (>25% explained variance) and slightly
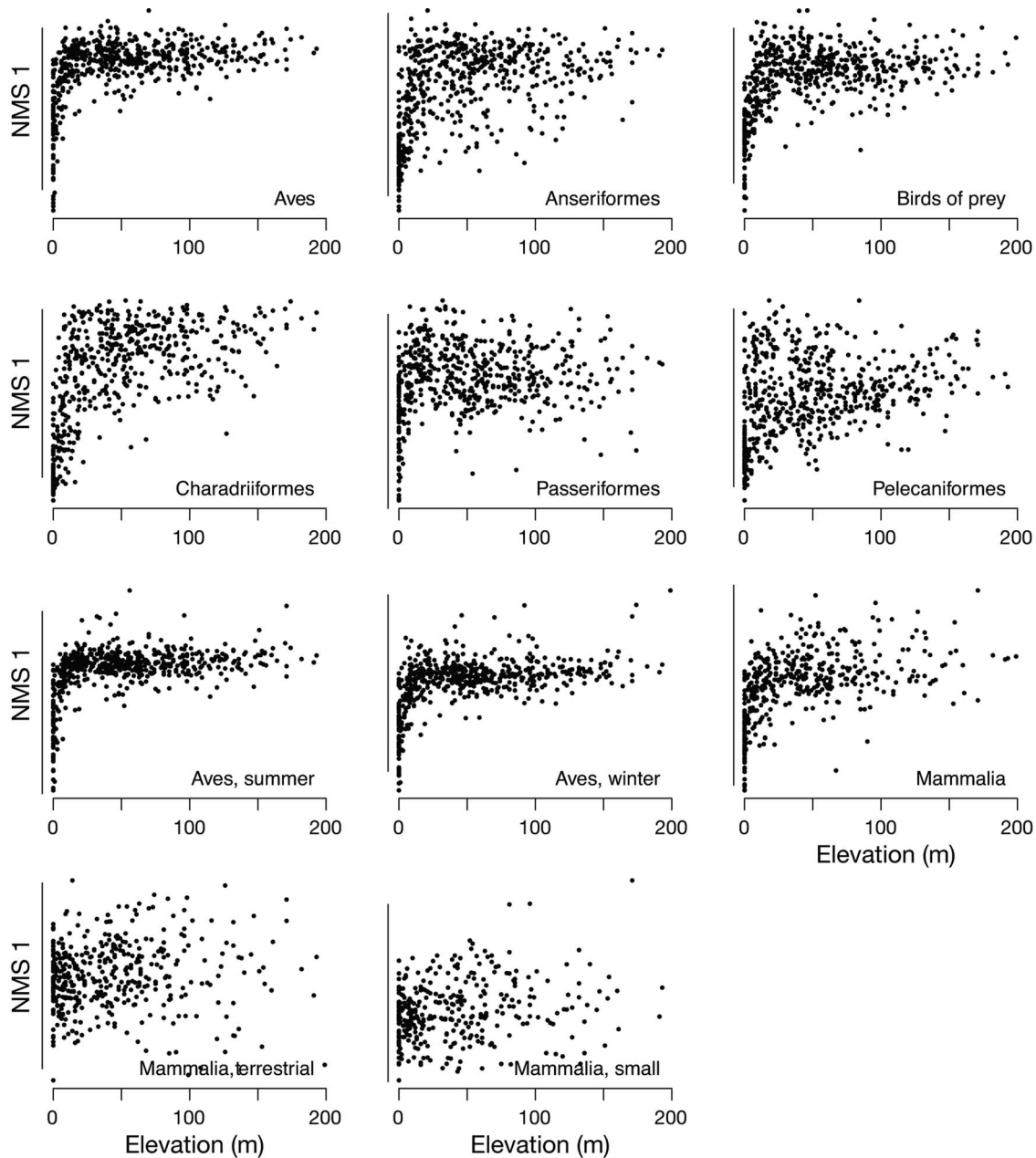
Figure 3. Continued.

weaker (20–25% explained variance) for elevation, indicating that the strong gradient in bird communities is not driven primarily by coast-hugging migrants.

Mammals display a weak relationship with elevation and distance to the coast, primarily manifested by an abrupt change in NMS axis 1 scores near the coast. This change is produced by the occurrence of cetaceans (whales, dolphins, and porpoises), sirenians (manatees), and phocids (earless seals) in coastal estuaries. Removing them removes any signal of a gradient (Figs. 3, 4, Tables 3, 4), but it also reduces the amount of data by nearly one-half. Because non-volant small-bodied mammals (i.e., <3 kg) have smaller ranges than large-bodied mammals, they might be more likely to show a gradient in species composition, although home range of individuals does not necessarily reflect the geographic range of a species. A test using a subset of mammals that includes

the Rodentia (mice, rats, squirrels, and beavers), Soricomorpha (shrews and moles), Didelphimorphia (opossums), Cingulata (armadillos), and Lagomorpha (hares and rabbits) showed no evidence of a gradient in species composition, although the dataset is the seventh smallest of the 26 datasets.

Discussion

Ubiquity and Strength of the Elevation Gradient

These results confirm the existence of gradients in species composition in many taxa correlated with elevation and distance from the coast. They provide a more objective basis for changes that are often visible even from a simple drive to the coast, where the types of plants visibly change, especially in the region closest to the coast. Similar anecdotal evidence of gradients is also shown
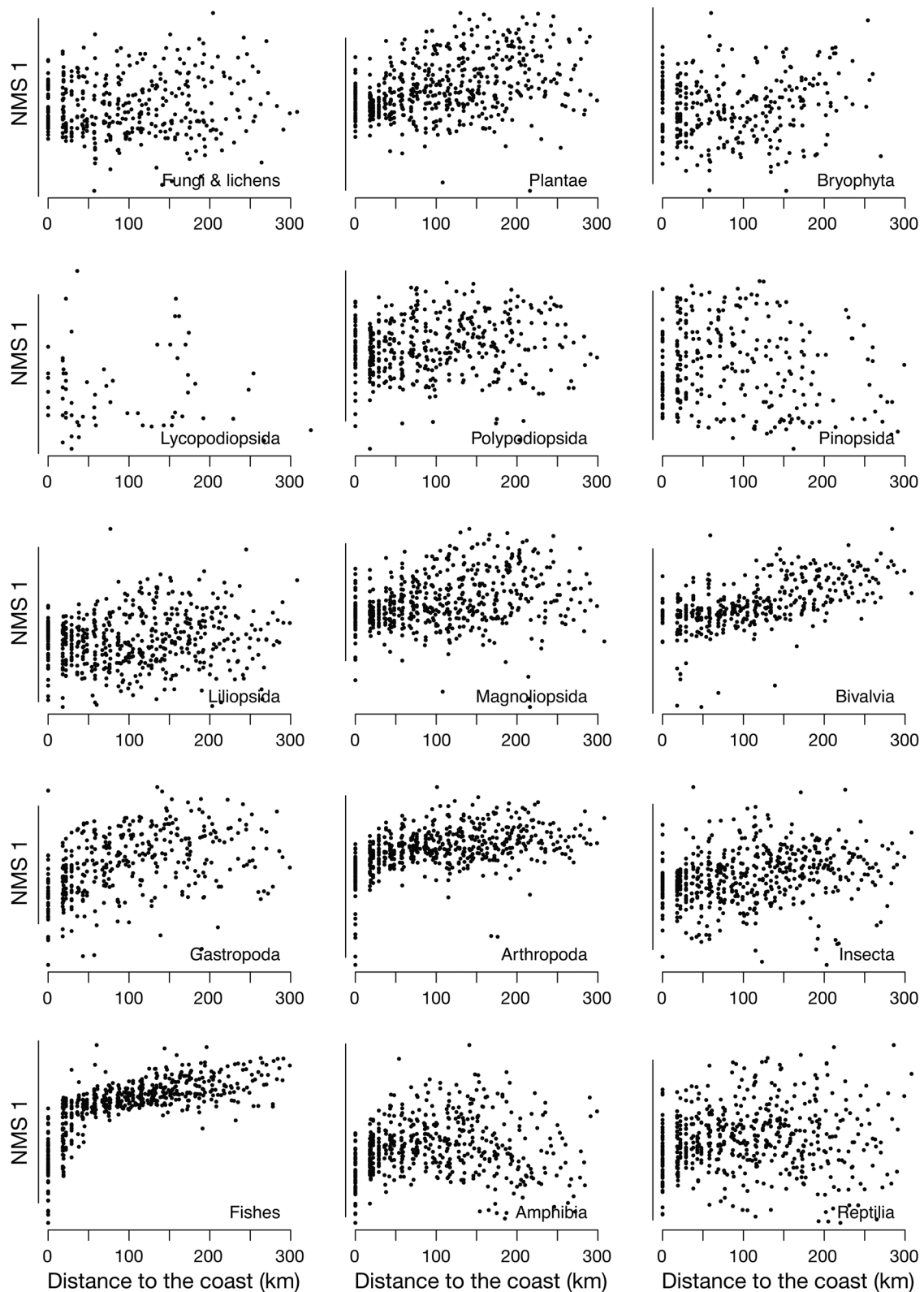
Figure 4. Scatter plots of the relationship of nonmetric multidimensional scaling (NMS) axis 1 scores to distance from the coast for 27 taxonomic groups; points correspond to 0.2° grid cells.

by the range maps of many plants and animals included in field guides, where some species are confined to coastal areas or various inland belts. Such distributions are documented in the study area for many species, including trees (Brown and Kirkman 1990), insects (Beaton 2007), amphibians (Dorcas and Gibbons 2008; Mitchell and Gibbons 2010), reptiles (Gibbons and Dorcas
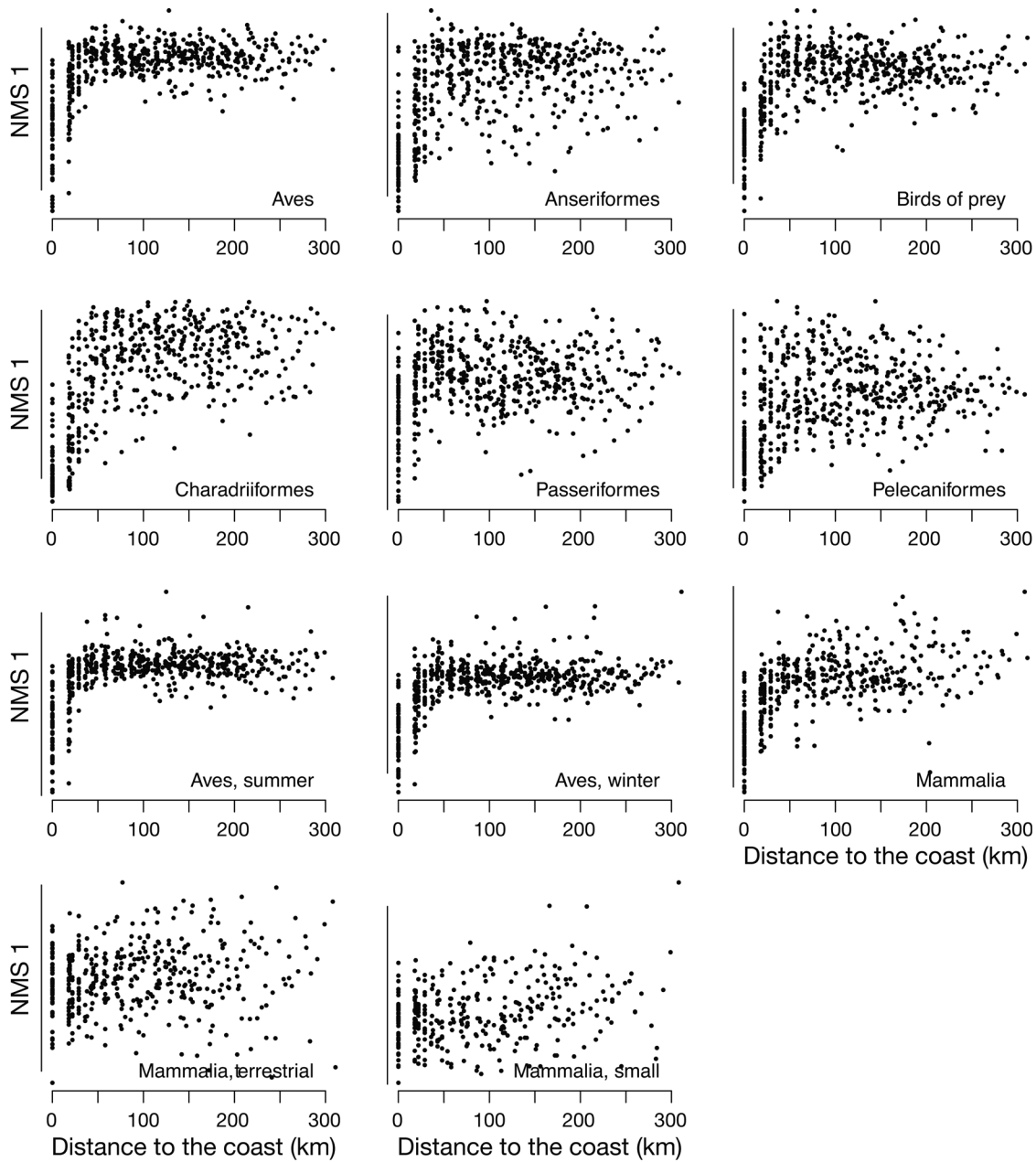
Figure 4. Continued.

2005; Buhlmann et al. 2008; Gibbons et al. 2009), and birds (Alderfer and Dunn 2021). Such maps also underscore the other sources of geographic variation in species occurrences, including latitude and river basins. Many factors such as soil type, bedrock, drainage, and disturbance are also important sources of variation in where species occur in the region (Edwards et al. 2013). We want to underscore that although we document the occurrence of ecological gradients correlated with elevation and distance to the coast, we fully acknowledge the importance of many other factors that control species distribution and communities' species composition. Moreover, elevation and distance to the coast are proxies for a wide suite of variables that directly affect species composition.

Numerous gradient analyses of communities in coastal plain settings worldwide have demonstrated widespread variation in community composition with elevation. Plants and fishes have been particularly well studied, likely due in part to the ease of obtaining quantitative data on abundance. Gradients in species composition correlated with elevation are well documented for trees (e.g., Gemborys and Hodgkins 1971; Marks and Harcombe 1981; Ahmad et al. 2024) and herbs (e.g., Drewa et al. 2002; Vieira et al. 2015; Fanfarillo et al. 2020). In both cases, the direct control of plant distributions is dominated by soil moisture, commonly correlated with elevation. Microtopographical variations can influence soil moisture, such as in lateral proximity to a river or stream, leading to small-scale variations in the species composition of plant communities (e.g., Titus 1990). Elevation-correlated variations in plants are documented in a wide variety of habitats, including rainforests (Drucker et al. 2008), mangroves (Yin and Yan 2020), temperate forests (Dale et al. 2007), arid settings
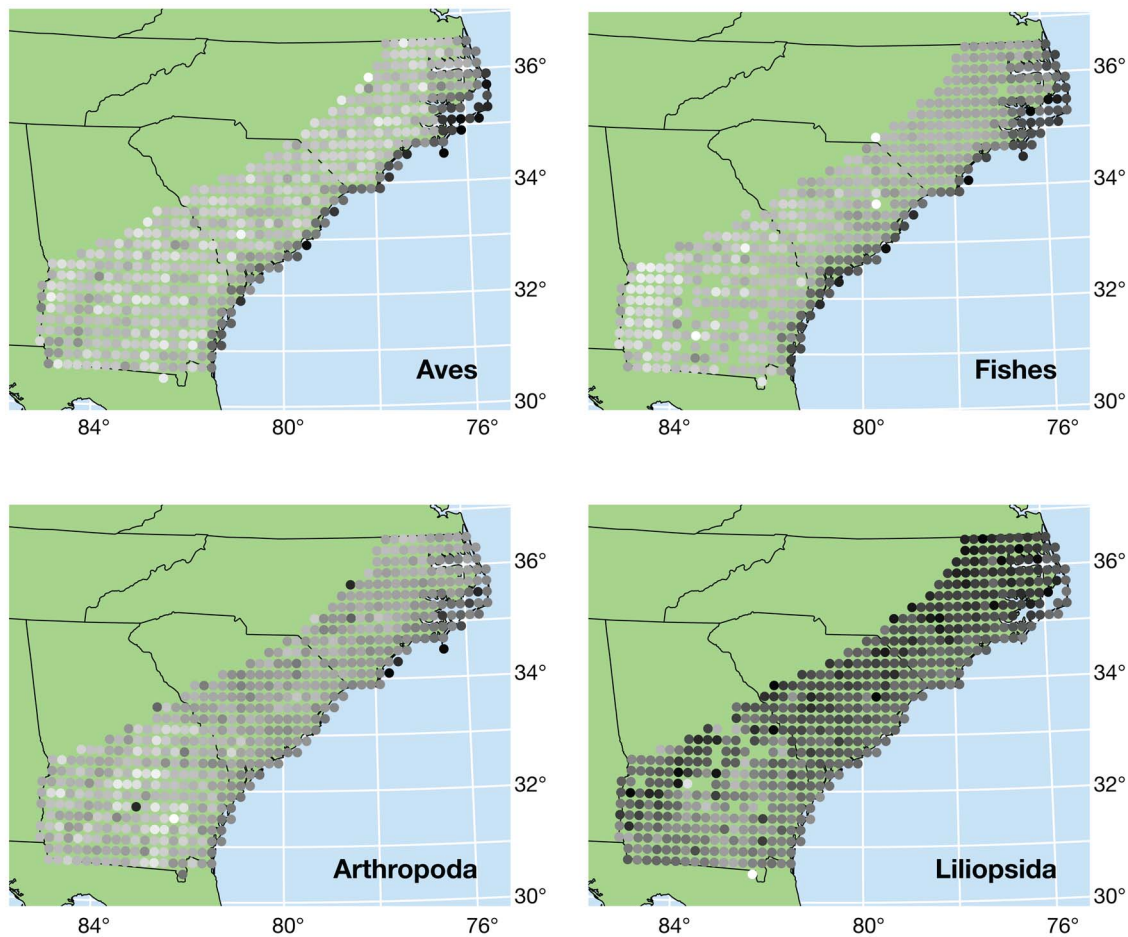
Figure 5. Representative maps of nonmetric multidimensional scaling (NMS) axis 1 scores for the 0.2° grid cells. Relative NMS scores are indicated with grayscale, from black (most negative score) to white (most positive score). Maps for all taxa are included in the Supplementary Material.

(Abd El-Ghani and El-Sawaf 2005), and inland (non-coastal) basin meadows (Castelli et al. 2000).

Fishes commonly display variation in the composition of species communities along river courses, which are necessarily correlated with elevation (e.g., Meffe and Sheldon 1988; Paller 1994; Lorion et al. 2011; Goncalves et al. 2020). Such gradients are driven by changes in stream gradient, as well as saltwater mixing in near-coastal settings (Winemiller and Leslie 1992). The distribution of unionid bivalves can also vary along river courses (Gagnon et al. 2006), as can the distribution of macroinvertebrates more generally (Maxted et al. 2000; Dail et al. 2013). In terrestrial settings, variation with elevation has also been documented for beetles (Heino and Alahuhta 2015), mammals (Gibson and McKenzie 2009), and vertebrates in general (Woinarski 1999). Although not all species are distributed along gradients correlated with elevation or distance to the coast, many species are distributed along these gradients in a wide variety of settings.

In this study, the amount of explained variance is in a range typical of ecological datasets, where the species composition of samples is influenced by many factors (McCune and Grace 2002). In particular, values greater than 25% constitute a substantial source of the variance in community composition (McCune and Grace 2002). By comparison, in ordinations of Ordovician benthic communities in which ordination axis 1 is correlated with water depth, axis 1 represents 17–30% of the variance in

community composition (Holland and Patzkowsky 2007). The importance of bathymetric variation in community composition is now well appreciated for marine studies in the fossil record (Scarponi and Kowalewski 2004; Patzkowsky and Holland 2012; Wittmer et al. 2014; Holland 2023). The existence of similarly strong values for nonmarine settings suggests that the effects of the elevation gradient should be considered for the nonmarine fossil record.

Causes

Despite the correlation of community composition with elevation and distance to the coast, it must be emphasized that these factors do not directly control species occurrences. Moreover, species lack the means to sense and respond directly to elevation or distance to the coast. As such, these correlations arise because there are physical and chemical factors of direct importance to species that are correlated with elevation and distance to the coast, much as is true with the bathymetric gradient in marine communities (Holland 2000; Patzkowsky and Holland 2012). Moreover, biotic interactions, especially in the cases of food selectivity for herbivores or carnivores, can control the distribution of species along biotic gradients. For example, the change in communities of Charadriiformes (shorebirds) and Pelecaniformes (pelicans, ibises, spoonbills, herons, and bitterns) near the coast likely

Table 4. The proportion of variance in nonmetric multidimensional scaling (NMS) ordination explained by latitude (r^2). All values shown are statistically significant at 0.05 with a Bonferroni correction (see Supplementary Data); dashes indicate values that are not statistically significant. Values of r^2 greater than 0.25 are indicated with boldface; values between 0.1 and 0.25 are italicized.

Taxon	NMS 1–3	NMS 1	NMS 2	NMS 3
Fungi and lichens	0.068	—	—	0.050
Plantae	**0.431**	*0.107*	0.072	**0.252**
Bryophytes	*0.106*	—	—	0.087
Lycopodiopsida	**0.264**	—	—	—
Polypodiopsida	*0.114*	—	—	*0.102*
Pinopsida	*0.158*	0.083	—	0.075
Liliopsida	**0.397**	**0.387**	—	—
Magnoliopsida	**0.301**	*0.134*	*0.153*	—
Bivalvia	**0.577**	**0.511**	0.058	—
Gastropoda	**0.357**	—	**0.280**	0.044
Arthropoda	**0.497**	*0.121*	*0.244*	*0.132*
Insecta	**0.334**	**0.313**	—	—
Fishes	**0.504**	*0.120*	0.052	**0.331**
Amphibia	**0.274**	—	**0.273**	—
Reptilia	**0.399**	—	0.060	**0.329**
Aves	*0.163*	—	—	*0.149*
Anseriformes	*0.202*	—	0.029	*0.150*
Birds of prey	**0.251**	0.096	—	*0.153*
Charadriiformes	*0.161*	0.038	*0.100*	—
Passeriformes	0.041	—	—	—
Pelecaniformes	**0.543**	*0.186*	**0.357**	—
Aves, summer	**0.303**	—	*0.114*	*0.169*
Aves, winter	**0.318**	—	0.036	**0.274**
Mammalia	**0.316**	—	—	**0.272**
Mammalia, terrestrial	**0.272**	0.059	*0.179*	0.035
Mammalia, small bodied	**0.340**	**0.286**	—	0.043

reflects their food sources in the coastal zone as well as the much greater area of wetlands. In addition, it is important to consider the distribution of taxa likely to leave a fossil record (vascular plants, shelled mollusks, and vertebrates with robust skeletons), but also the distribution of potential food sources with lesser potential for fossilization (e.g., fungi, non-vascular plants, insects, and vertebrates with fragile skeletons). These gradients with elevation and distance to the coast arise for several reasons.

For plants, moisture and temperature are the dominant controls on species distribution that are correlated with elevation and distance to the coast (Whittaker 1956, 1960, 1970). In the southeastern United States, precipitation tends to be higher near the coast, as the ocean is a source of moisture (Holland and Loughney 2021), and this is true more generally (Bradley 2015). The ocean also buffers temperatures near the coast, dampening swings to extremely high temperatures in the summer and extremely low temperatures in the winter. Plants are particularly sensitive to extreme fluctuations in temperature (e.g., Hatfield and Prueger 2015). In near-

coastal settings, groundwater salinity and salt spray can significantly affect plants for distances up to tens of kilometers from the coast (Griffiths 2006; Du and Hesp 2020).

Where local relief is substantial, such as in inland areas of the southeastern United States, local elevation gradients may be orthogonal to rivers and, therefore, parallel to the coast. This is likely one reason that the amount of explained variance differs for elevation and distance to the coast (Tables 2, 3). In these regions, areas adjacent to rivers may have wet soils with plant communities more similar to those of coastal areas, unlike higher-elevation interfluves at the same distance from the coast (Edwards et al. 2013; see also Gastaldo and Demko 2011). Even so, floodplain plant communities of the southeastern United States vary downstream in their community composition (Rheinhardt et al. 1998). These inland variations in soil moisture between river and interfluve settings and their consequent effects on plants may also be a source of variation in terrestrial invertebrate and vertebrate community composition.

For aquatic organisms, such as gastropods, bivalves, and fishes, the increasing gradient (slope) of streams inland substantially affects species distributions (Maxted et al. 2000; Gagnon et al. 2006; Dail et al. 2013). For example, the species composition of fish communities varies from inland low-order streams with steeper channel gradients and higher velocities to coastal high-order streams with flatter channel gradients and lower velocities (Meffe and Sheldon 1988; Paller 1994). In near-coastal areas, the intrusion of salt water and the increase in salinity have a pronounced effect, given the substantial metabolic effects of salinity (Cañedo-Argüelles et al. 2018).

Some taxa analyzed in this study display either weak gradients with elevation and distance to the coast or none at all. For some, the gradient may be weak or absent, such as for terrestrial mammals, many of which are ubiquitous and eurytopic (white-tailed deer, raccoon, opossum, etc.). In many cases, though, the relatively few reports in the GBIF database support there being insufficient data to detect any gradients. For example, there are fewer than 10,000 species occurrences of bryophytes, lycopods, ferns, and conifers, none of which have a detectable gradient. Low numbers of occurrences mean that few latitude–longitude grid cells have occurrences, and many of those grid cells that do have occurrences will not have a representative sampling of what occurs within that area.

Birds and mammals provide an interesting contrast in sample coverage. Birds have more than 15,000,000 species occurrences within the study area, whereas mammals have only 39,000 occurrences, over half of which are marine mammals occurring within estuaries. Much of the GBIF bird data comes from amateur birders, who have enthusiastically documented species occurrences that experts subsequently verify. For example, a sampling of several widespread bird species shows that they are reported from nearly all grid cells: American robin (97.7%), tufted titmouse (96.2%), northern cardinal (97.9%), and American crow (98.3%). In comparison, similarly common, eurytopic, widespread, and easily observable mammals are reported far less frequently: white-tailed deer (57.1%), raccoon (34.0%), opossum (27.7%), gray squirrel (39.9%), and eastern cottontail (27.4%). Nocturnal mammals are even more underreported: coyote (16.2%) and bobcat (15.2%). The striped skunk is curiously far underreported (2.1%). Similar underreporting in other groups raises the question of whether gradients in those groups truly do not exist or that insufficient data exist. In that sense, the observations reported here are asymmetric: detecting an ecological gradient is meaningful, but its absence may not be.

Application

Many physical, chemical, and biological processes control the species composition of nonmarine communities. Here, we focus on the correlation of species distributions with elevation and distance to the coast, because these variables vary systematically and predictably in the stratigraphic record. As a result, the composition of ancient communities will vary stratigraphically in ways likely to be misinterpreted as ecosystem changes rather than as a reflection of stratigraphic processes. Understanding these relationships can inform better models and interpretations of the nonmarine fossil record, much like it does for marine systems.

Elevation and distance to the coast in marine-connected basins change predictably with variations in the rate of accommodation (tectonic subsidence, plus eustasy in marine-connected basins) and sediment flux (Holland 2022). For example, in the case of no sea-level rise, sediment flux is typically sufficient for the sedimentation rate to exceed the accommodation rate at the shore, causing the shore to regress (move seaward). As a result, the distance to the shore increases everywhere in the nonmarine part of the basin. Because the fluvial profile is anchored at its updip end at the edge of the basin and because rivers tend toward a graded profile, extending the fluvial profile will also cause elevation to increase everywhere along the fluvial profile, even though the position of sea level has not changed (progradation in Holland and Loughney 2021: fig. 6). In short, elevation and distance to the shore are not only empirically correlated in the modern environment but also causally connected through geomorphic processes. The same relationships hold in fully nonmarine inland basins, where there is a lacustrine shore instead of a marine shore or an axial river system instead of an ocean or lake.

Changes in sea level also change the elevations of every point along the fluvial profile through time. Although sea-level rise would be expected to cause a decrease in elevation everywhere along the fluvial profile, its actual effects depend on what happens to the position of the shoreline. For modest rates of sea-level rise, sediment flux is typically sufficient to cause the shoreline to regress, increasing the distance to shore. However, although the increasing distance to the coast raises the fluvial profile, promoting an increase in elevation, the rising sea level promotes a decrease in elevation (progradation plus aggradation; Holland and Loughney 2021). The net effect is for elevation to increase near the shore but for elevation to decrease inland near the depositionally updip edge of the sedimentary basin.

At some greater rate of sea-level rise, sediment flux is balanced such that the shoreline is laterally fixed—it neither regresses nor transgresses. In such unusual cases, the distance to the shore does not change. Elevation will, however, decrease due to the rise in sea level (aggradation; Holland and Loughney 2021). At even greater rates of sea-level rise, sediment flux is insufficient to fill the available accommodation, and the shoreline transgresses, which decreases the distance to the shore and lowers the elevation everywhere on land (retrogradation; Holland and Loughney 2021).

Sea-level fall is the simplest case, because it extends and lowers the fluvial profile (degradation; Holland and Loughney 2021). This causes the distance to the shore to increase everywhere on land; similarly, it causes elevation to increase everywhere on land. Note that because elevation is measured relative to sea level, changes in lake level or the elevation of an axial river do not trigger analogous changes in elevation.

These cases occur in a predictable cycle during relative sea-level changes, causing elevation and distance to the shore to change predictably (Holland 2022). This commonly produces progressive increases or decreases in elevation and distance to the coast at any particular location. Across subaerial unconformities, elevation and distance to the coast can change abruptly. Because the composition of nonmarine communities is correlated with elevation and distance to the coast, it will necessarily change stratigraphically simply by the lateral movement of the elevation gradient, even if the underlying ecological structure and taxonomic composition of the gradient are static. As such, trends in community composition and abrupt changes in community composition at subaerial unconformities cannot be read as direct evidence of ecosystem perturbations by external forcing such as climate change. By ecosystem perturbations, we mean changes in the presence and distribution of species along ecological gradients that cause the structure of the ecological gradient to change. Although such perturbations to ecological gradients can create stratigraphic trends and abrupt changes in fossil assemblages, changes in fossil communities will also arise whenever the elevation gradient is lengthened or shortened by progradation and retrogradation of the fluvial profile, such as through regression and transgression. To isolate the ecological changes resulting from a perturbation of the region-wide ecosystem, one must factor out the stratigraphic changes in fossil communities driven by the correlation with elevation and distance to the coast. It is important to underscore that elevation and distance to the coast do not need to directly control the species composition of nonmarine communities; they only need to be correlated for their effects to be manifested in the stratigraphic record.

More complex is the possibility that the same factors that cause progradation and retrogradation of the fluvial system might also perturb the structure of the elevation gradient itself. For example, global warming might promote sea-level rise sufficiently to drive transgression, and it might also change the very structure of ecological gradients, such as through species origination, immigration, or extirpation, or by changing the distributions of species relative to elevation. This complex case is known as the common-cause hypothesis, and although such interactions are difficult to test, there is some evidence for the common-cause hypothesis in marine systems (Peters 2005).

The correlation with elevation and distance to the coast in modern systems suggests that the degree to which the effects of the elevation gradient are expressed will vary among taxa and with geographic position in the nonmarine system. For example, some modern taxa display strong correlations with elevation and distance to the coast, and others (e.g., mammals) do not, although this must be balanced by the concerns over sample size and having sufficient data to detect a gradient. For many modern taxa, the change in community composition is strongest within a few tens of kilometers of a marine coast, suggesting that the lowest and most distal parts of fluvial profiles have the greatest potential for elevation-related changes in species composition.

Detection in the Fossil Record

Terrestrial paleoecologists have long been aware of the potential for environmental gradients in the species composition of communities, knowledge founded on long-standing observations of gradients in modern settings dating back to Humboldt and Bonpland's classic 1805 study of Andean vegetation. Gradient ecology gained renewed vigor in the 1960s and 1970s with a series

of monographs on the distribution of plant communities by Robert Whittaker (1956, 1960, 1970). Paleobotanists have long considered the role of ecological gradients in the origination and diversification of higher taxa (e.g., Axelrod 1952, 1966; Cridland and Morris 1963; DiMichele and Aronson 1992; DiMichele et al. 2017, 2020) and the composition of ecological communities (e.g., Pfefferkorn and Thomson 1982; Johnson et al. 2003). Moreover, paleobotanists have recognized that the generally poor preservation of plants in well-drained soils typical of topographically high areas might obscure the recognition of elevation-correlated gradients (Gastaldo and Demko 2011). Paleobotanists have commonly tended to focus on relatively short (hundreds of meters) ecological gradients (e.g., DiMichele et al. 1991; Davies-Vollum and Wing 1998; Wing et al. 2012), such as elevation changes with distance from a river channel rather than relatively long (tens to hundreds of kilometers) gradients, such as distance from the coast (but see DiMichele and Aronson 1992). This is partly because shorter gradients are easier to sample, but it is also because it is simpler to relate samples to sedimentological criteria associated with a gradient expressed over short distances rather than long ones (S. Wing personal communication, 2024).

Similarly, vertebrate paleontologists have recognized the importance of identifying basin margin (upland) settings, owing to their potential for the origin and diversification of taxa (Gunnell et al. 1992; Gunnell and Bartels 2001). Vertebrate paleontologists have likewise recognized the role of elevation-correlated differences in the biogeography and species composition of fossil communities (Lehman 1987; Brinkman et al. 1998; Hornung et al. 2023) and the general scarcity of upland faunas (e.g., Gingerich 1989). Not all agree on the importance of these gradients, such as for dinosaurs (e.g., Vavrek and Larsson 2010).

Detecting ecological gradients is essential for interpreting the fossil record. Ordination is a particularly powerful tool for detecting, characterizing, and quantifying ecological gradients in the fossil record (Jongman et al. 1995; McCune and Grace 2002; Borcard et al. 2018). Notably, many of these methods were pioneered and widely applied by modern terrestrial ecologists, particularly botanists. Ordination has been successfully applied in many paleontological studies, both nonmarine (DiMichele et al. 1991, 2007; DiMichele and Aronson 1992; Davies-Vollum and Wing 1998; Wing et al. 2012; Barbacka et al. 2016; Cullen and Evans 2016) and marine (Scarponi and Kowalewski 2004; Patzkowsky and Holland 2012; Wittmer et al. 2014; Holland 2023).

The approach of ordination is to conduct a series of taxonomic counts, preferably based on a stratigraphically constrained sample, such as a bonebed or a bedding plane. Taxa are identified to the lowest possible taxonomic level, although species-level identifications are not required (Ludvigsen et al. 1986). These counts are used to create a data matrix with columns of taxa and rows of samples, which is standardized through data transformations to mitigate the effects of differing sample sizes and species abundances (e.g., Holland and Patzkowsky 2007). The result is ordinated with a method not prone to severe distortions of the ecological gradient, such as NMS or DCA (Patzkowsky and Holland 2012). The ordination scores of samples can be compared with other aspects that describe the samples, such as lateral position within a sedimentary basin, type of deposit, stratigraphic position, and so on, to assess the influences on the ordination axes. Species scores thus allow one to interpret the position of species along those ecological gradients.

An example using the data of Cullen and Evans (2016) of Campanian bonebeds from Alberta demonstrates the approach of detecting a gradient correlated with distance to the coast. A reanalysis of their data using NMS displays the primary ecological gradients well (Fig. 6). NMS axis 1 is correlated with position landward and seaward, with coastal (transitional) samples occupying an intermediate position between marine and coastal plain samples (Fig. 6A). Although the pattern is weaker, upper coastal plain samples are typically more different from the transitional samples than lower coastal plain samples are. Coding the species by higher taxon allows one to see the distribution of taxa along this gradient. The marine samples are dominated by sharks and marine reptiles (Fig. 6B). Various bony fish occur in positions typical of marine, transitional, and coastal plain settings,
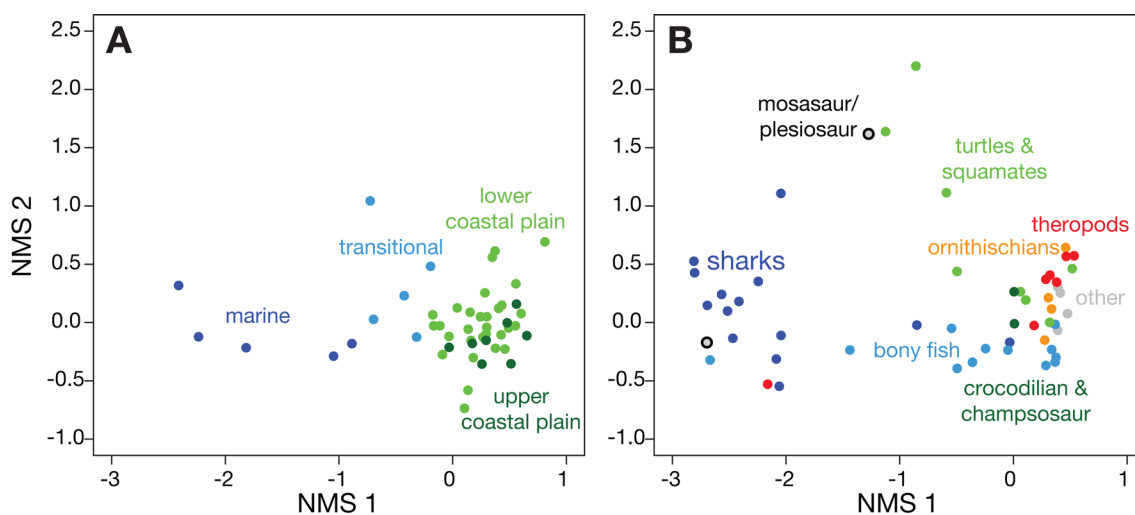

Figure 6. Nonmetric multidimensional scaling (NMS) ordination of bonebeds from Campanian strata of Alberta; data from Cullen and Evans (2016). **A,** Sample scores coded by depositional setting, indicating a seaward (left) to landward (right) gradient on NMS axis 1. **B,** Taxon scores show the sorting of taxa along the seaward to landward gradient.

presumably reflecting their salinity tolerances. Turtles and squamates are most common in transitional to lower coastal plain environments, whereas dinosaurs typically occur in inland samples.

More studies like this are needed, and the data may already exist. For example, one question is whether shorter and steeper elevation profiles such as along some active margins would show a different pattern from the long, gentle-elevation profiles on the passive margin studied here. Although ordination can be performed on presence/absence data instead of counts, counts can better reveal ecological gradients. This is especially true where the gradient is characterized by changes in relative abundance more than by the loss and addition of species. For example, consider a simple ecological gradient represented by three species that are present everywhere along the gradient but with varying probabilities of collection ([Fig. 7](#)). If the gradient is sampled at five positions, and if the probabilities of occurrence scale with the abundance of the species, the relative abundance of the species will change systematically along the gradient. Ordination would readily be able to detect such a gradient. If presence/absence data were used instead, all three species would likely be preserved along the gradient, given that their probabilities of occurrence are relatively high, and no gradient in species composition would be evident (cf. Rahel [1990](#)).
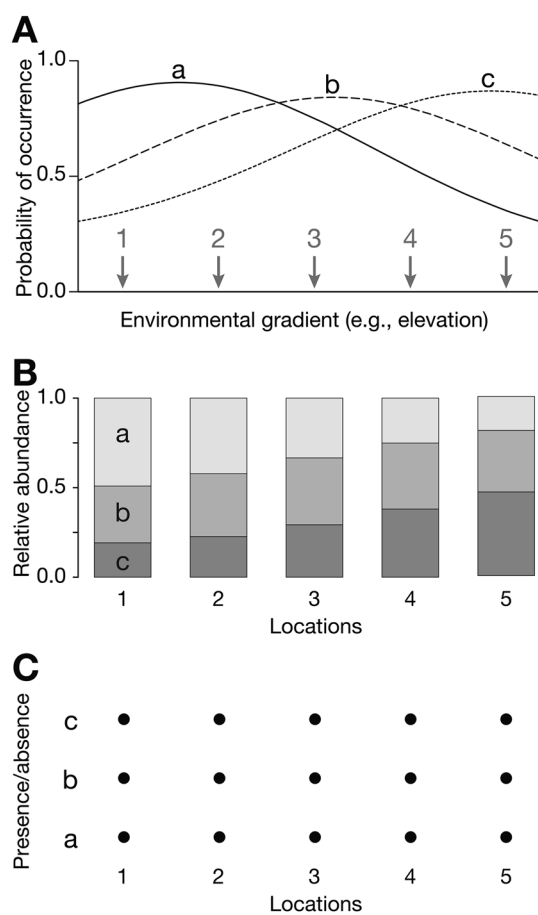

Figure 7. A, Schematic illustration of a simple environmental gradient of three species (a–c). Although numerical data on the abundance of the species **(B)** would show the progressive change in dominance from species a to species c along the gradient, presence–absence data **(C)** likely would not, as all species are abundant enough to occur everywhere along the gradient.

Conclusion

1. Analysis of species occurrences in the southeastern United States recorded in the GBIF database reveals the common occurrence of gradients in species composition correlated with elevation and distance from the coast. Many taxa show substantially stronger changes in species composition near the coast than inland.

2. Several taxa also display correlations with latitude. Although latitude is a stronger overall predictor of species composition in these data, its effects are typically expressed over multiple ordination axes rather than one. As a result, the primary ordination axis is more commonly correlated with elevation and distance to the coast. Regardless, species composition is commonly strongly related to elevation, distance to the coast, and latitude.

3. Because elevation and distance to the coast will change systematically and predictably in response to cycles of accommodation and sediment flux, these gradients are likely to generate stratigraphic changes in the species composition of fossil communities. These changes will generally be gradual, but they can be abrupt across subaerial unconformities. It may be challenging to distinguish local changes in the taxonomic composition of fossil assemblages that result simply from the lateral shifting of these regional gradients during progradation and retrogradation of the coastal plain from other causes, such as changes in the regional species pool or perturbations of the organization of species along environmental gradients (e.g., those caused by climate change).

4. Ordination is an effective means for detecting these gradients in the nonmarine fossil record. An important goal will be to understand the strength of these gradients in structuring the nonmarine fossil record compared with the ecological changes that result from perturbations such as climate change (e.g., DiMichele et al. [2020](#)).

Literature Cited

Abd El-Ghani, M., and N. El-Sawaf. 2005. The coastal roadside vegetation and environmental gradients in the arid lands of Egypt. *Community Ecology* **6**:143–154.

Ahmad, A., A. Saeed, A. B. Gulshan, S. Wali, F. Hadi, S. Ullah, Fazlullah, A. A. Sher, M. Rizwan, and M. Rafiq. 2024. Prediction of soil seed bank of piedmont and alluvial environments of Dera Ghazi Khan, Punjab, Pakistan. *Brazilian Journal of Biology* **84**:1–8.

Alderfer, J., and J. L. Dunn, eds. 2021. *Complete birds of North America*, 3rd ed. National Geographic, Washington, D.C.

Axelrod, D. I. 1952. A theory of angiosperm evolution. *Evolution* **6**:29–60.

Axelrod, D. I. 1966. Origin of deciduous and evergreen habitats in temperate forests. *Evolution* **20**:1–15.

Barbacka, M., M. E. Popa, J. Mitka, E. Bodor, Z. Püspöki, and R. W. McIntosh. 2016. A quantitative approach for identifying plant ecogroups in the Romanian Early Jurassic terrestrial vegetation. *Palaeogeography, Palaeoclimatology, Palaeoecology* **446**:44–54.

Beaton, G. 2007. *Dragonflies and damselflies of Georgia and the Southeast*. University of Georgia Press, Athens.

Borcard, D., F. Gillet, and P. Legendre. 2018. *Numerical ecology with R*. Springer, New York.

Bradley, R. S. 2015. *Paleoclimatology: reconstructing climates of the Quaternary*, 3rd ed. Academic Press, Oxford.

Brinkman, D. B., M. J. Ryan, and D. A. Eberth. 1998. The paleogeographic and stratigraphic distribution of ceratopsids (Ornithischia) in the upper Judith River Group of western Canada. *Palaios* 13:160–169.

Brown, C. L., and L. K. Kirkman. 1990. *Trees of Georgia and adjacent states*. Timber Press, Portland, Ore.

Buhlmann, K., T. Tuberville, and W. Gibbons. 2008. *Turtles of the Southeast*. University of Georgia Press, Athens.

Cañedo-Argüelles, M., B. Kefford, and R. Schäfer. 2018. Salt in freshwaters: causes, effects and prospects—introduction to the theme issue. *Philosophical Transactions of the Royal Society B* 374:20180002.

Castelli, R. M., J. C. Chambers, and R. J. Tausch. 2000. Soil-plant relations along a soil-water gradient in Great Basin riparian meadows. *Wetlands* 20:251–266.

Cridland, A. A., and J. E. Morris. 1963. *Taeniopteris*, *Walchia*, and *Dichophyllum* in the Pennsylvanian system in Kansas. *University of Kansas Science Bulletin* 44:71–85.

Cullen, T. M. and D. C. Evans. 2016. Palaeoenvironmental drivers of vertebrate community composition in the Belly River Group (Campanian) of Alberta, Canada, with implications for dinosaur biogeography. *BMC Ecology* 16:52.

Dail, M., J. Hill, and R. Miller. 2013. *The Virginia coastal plain macroinvertebrate index*. Technical Bulletin WQA/2013-002. Virginia Department of Environmental Quality, Richmond.

Dale, E. E., S. Ware, and B. Waitman. 2007. Ordination and classification of bottomland forests in the lower Mississippi alluvial plain. *Castanea* 72:105–115.

Davies-Vollum, S. K., and S. L. Wing. 1998. Sedimentological, taphonomic, and climatic aspects of Eocene swamp deposits (Willwood Formation, Bighorn Basin, Wyoming). *Palaios* 13:28–40.

DiMichele, W. A., and R. B. Aronson. 1992. The Pennsylvanian–Permian vegetational transition: terrestrial analogue to the onshore–offshore hypothesis. *Evolution* 46:807–824.

DiMichele, W. A., T. L. Phillips, and G. E. McBrinn. 1991. Quantitative analysis and paleoecology of the Secor Coal and roof-shale floras (Middle Pennsylvanian, Oklahoma). *Palaios* 6:390–409.

DiMichele, W. A., H. J. Falcon-Lang, W. John Nelson, S. D. Elrick, and P. R. Ames. 2007. Ecological gradients within a Pennsylvanian mire forest. *Geology* 35:415–418.

DiMichele, W. A., S. D. Elrick, and W. J. Nelson. 2017. Vegetation zonation in a swamp forest, Middle Pennsylvanian, Illinois Basin, U.S.A., indicates niche differentiation in a wetland plant community. *Palaeogeography, Palaeoclimatology, Palaeoecology* 487:71–92.

DiMichele, W. A., A. R. Bashforth, H. J. Falcon-Lang, and S. G. Lucas. 2020. Uplands, lowlands, and climate: taphonomic megabiases and the apparent rise of a xeromorphic, drought-tolerant flora during the Pennsylvanian–Permian transition. *Palaeogeography, Palaeoclimatology, Palaeoecology* 559:109965.

Dorcas, M., and W. Gibbons. 2008. *Frogs and toads of the Southeast*. University of Georgia Press, Athens.

Drewa, P. B., W. J. Platt, and E. B. Moser. 2002. Community structure along elevation gradients in headwater regions of longleaf pine savannas. *Plant Ecology* 160:61–78.

Drucker, D. P., F. R. C. Costa, and W. E. Magnusson. 2008. How wide is the riparian zone of small streams in tropical forests? A test with terrestrial herbs. *Journal of Tropical Ecology* 24:65–74.

Du, J., and P. A. Hesp. 2020. Salt spray distribution and its impact on vegetation zonation on coastal dunes: a review. *Estuaries and Coasts* 43:1885–1907.

Edwards, L., J. Ambrose, and L. K. Kirkman. 2013. *The natural communities of Georgia*. University of Georgia Press, Athens.

Fanfarillo, E., S. Petit, F. Dessaint, L. Rosati, and G. Abbate. 2020. Species composition, richness, and diversity of weed communities of winter arable land in relation to geo-environmental factors: a gradient analysis in mainland Italy. *Botany* 98:381–392.

Gagnon, P., W. Michener, M. Freeman, and J. B. Box. 2006. Unionid habitat and assemblage composition in coastal plain tributaries of Flint River (Georgia). *Southeastern Naturalist* 5:31–52.

Gastaldo, R. A., and T. M. Demko. 2011. The relationship between continental landscape evolution and the plant-fossil record: long term hydrologic controls on preservation. Pp. 249–285 *in* P. A. Allison and D. J. Bottjer, eds. *Taphonomy: processes and bias through time*. Springer, Dordrecht.

Gemborys, S. R., and E. J. Hodgkins. 1971. Forests of small stream bottoms in the coastal plain of southwestern Alabama. *Ecology* 52:70–84.

Gibbons, W., and M. Dorcas. 2005. *Snakes of the Southeast*. University of Georgia Press, Athens.

Gibbons, W., J. Greene, and T. Mills. 2009. *Lizards and crocodilians of the Southeast*. University of Georgia Press, Athens.

Gibson, L., and N. McKenzie. 2009. Environmental associations of small ground-dwelling mammals in the Pilbara region, Western Australia. *Records of the Western Australian Museum* 78(Suppl.):91–122.

Gingerich, P. D. 1989. New earliest Wasatchian mammalian fauna from the Eocene of northwestern Wyoming: composition and diversity in a rarely sampled high-floodplain assemblage. *University of Michigan Papers on Paleontology* 28:1–97.

[GBIF] Global Biodiversity Information Facility. 2023. What Is GBIF? https://www.gbif.org/what-is-gbif, accessed 23 August 2023.

Goncalves, C. S., R. D. Holt, M. C. Christman, and L. Casatti. 2020. Environmental and spatial effects on coastal stream fishes in the Atlantic rain forest. *Biotropica* 52:139–150.

Griffiths, M. E. 2006. Salt spray and edaphic factors maintain dwarf stature and community composition in coastal sandplain heathlands. *Plant Ecology* 186:69–86.

Gunnell, G. F., and W. S. Bartels. 2001. Basin margins, biodiversity, evolutionary innovation, and the origin of new taxa. Pp. 403–432 *in* G. F. Gunnell, ed. *Eocene biodiversity: unusual occurrences and rarely sampled habitats*. Kluwer Academic/Plenum, New York.

Gunnell, G. F., W. S. Bartels, P. D. Gingerich, and V. Torres. 1992. Wapiti Valley faunas: early and middle Eocene fossil vertebrates from the North Fork of the Shoshone River, Park County, Wyoming. *Contributions from the University of Michigan Museum of Paleontology* 28:247–287.

Hatfield, J. L., and J. H. Prueger. 2015. Temperature extremes: effect on plant growth and development. *Weather and Climate Extremes* 10:4–10.

Heino, J., and J. Alahuhta. 2015. Elements of regional beetle faunas: faunal variation and compositional breakpoints along climate, land cover and geographical gradients. *Journal of Animal Ecology* 84:427–441.

Holland, S. M. 2000. The quality of the fossil record: a sequence stratigraphic perspective. Pp. 148–168 *in* D. H. Erwin and S. L. Wing, eds. *Deep time: Paleobiology's perspective*. Paleontological Society, Lawrence, Kans.

Holland, S. M. 2022. The structure of the nonmarine fossil record: predictions from a coupled stratigraphic–paleoecological model of a coastal basin. *Paleobiology* 48:372–396.

Holland, S. M. 2023. The contrasting controls on the occurrence of fossils in marine and nonmarine systems. *Bollettino della Società Paleontologica Italiana* 62:1–25.

Holland, S. M., and K. M. Loughney. 2021. *The stratigraphic paleobiology of nonmarine systems*. Elements of Paleontology. Cambridge University Press, Cambridge.

Holland, S. M., and M. E. Patzkowsky. 2007. Gradient ecology of a biotic invasion: biofacies of the type Cincinnatian Series (Upper Ordovician), Cincinnati, Ohio region, USA. *Palaios* 22:392–407.

Holland, S. M., K. M. Loughney, and M. Cone. 2023. Preferential preservation of low-elevation biotas in the nonmarine fossil record. *Geology* 51:111–114.

Hornung, J. J., S. Sachs, and A. H. Schwermann. 2023. The first record of sauropod dinosaurs from a palaeotopographical upland environment and its implications for megaherbivorous dinosaur faunal turnover in the Early Cretaceous of northwestern Europe. *Geologie und Paläontologie in Westfalen* 97:3–36.

Johnson, K. R., M. L. Reynolds, K. W. Werth, and J. R. Thomasson. 2003. Overview of the Late Cretaceous, early Paleocene, and early Eocene megafloras of the Denver Basin, Colorado. *Rocky Mountain Geology* 38:101–120.

Jongman, R. H. G., C. J. F. Ter Braak, and O. F. R. Van Tongeren, eds. 1995. *Data analysis in community and landscape ecology.* Cambridge University Press, Cambridge.

Lehman, T. M. 1987. Late Maastrichtian paleoenvironments and dinosaur biogeography in the Western Interior of North America. *Palaeogeography, Palaeoclimatology, Palaeoecology* 60:189–217.

Lorion, C. M., B. P. Kennedy, and J. H. Braatne. 2011. Altitudinal gradients in stream fish diversity and the prevalence of diadromy in the Sixaola River basin, Costa Rica. *Environmental Biology of Fishes* 91:487–499.

Ludvigsen, R., S. R. Westrop, B. R. Pratt, P. A. Tuffnell, and G. A. Young. 1986. Dual biostratigraphy: zones and biofacies. *Geoscience Canada* 13:139–154.

Marks, P., and P. Harcombe. 1981. Forest vegetation of the Big Thicket, southeast Texas. *Ecological Monographs* 51:287–305.

Maxted, J., M. Barbour, J. Gerritsen, V. Poretti, N. Primrose, A. Silvia, D. Penrose, and R. Renfrow. 2000. Assessment framework for mid-Atlantic coastal plain streams using benthic macroinvertebrates. *Journal of the North American Benthological Society* 19:128–144.

McCune, B., and J. B. Grace. 2002. *Analysis of ecological communities.* MJM Software Design, Gleneden Beach, Ore.

Meffe, G. K., and A. L. Sheldon. 1988. The influence of habitat structure on fish assemblage composition in southeastern blackwater streams. *American Midland Naturalist* 120:225–240.

Minchin, P. R. 1987. An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio* 69:89–107.

Mitchell, J., and W. Gibbons. 2010. *Salamanders of the Southeast.* University of Georgia Press, Athens.

Moret, P., P. Muriel, R. Jaramillo, and O. Dangles. 2019. Humboldt's Tableau Physique revisited. *Proceedings of the National Academy of Sciences USA* 116:12889–12894.

Ohmann, J. L., and T. A. Spies. 1998. Regional gradient analysis and spatial pattern of woody plant communities in Oregon forests. *Ecological Monographs* 68:151–182.

Paller, M. H. 1994. Relationships between fish assemblage structure and stream order in South Carolina coastal plain streams. *Transactions of the American Fisheries Society* 123:150–161.

Patzkowsky, M. E., and S. M. Holland. 2012. *Stratigraphic paleobiology.* University of Chicago Press, Chicago.

Peters, S. E. 2005. Geologic constraints on the macroevolutionary history of marine animals. *Proceedings of the National Academy of Sciences USA* 102:12326–12331.

Pfefferkorn, H. W., and M. C. Thomson. 1982. Changes in dominance patterns in upper Carboniferous plant-fossil assemblages. *Geology* 10:641–644.

Rahbek, C., M. K. Borregaard, R. K. Colwell, B. Dalsgaard, B. G. Holt, N. Morueta-Holme, D. Nogues-Bravo, R. J. Whittaker, and J. Fjeldså. 2019. Humboldt's enigma: what causes global patterns of mountain biodiversity. *Science* 365:1108–1113.

Rahel, F. J. 1990. The hierarchical nature of community persistence: a problem of scale. *American Naturalist* 136:328–344.

R Core Team. 2023. *R: a language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org.

Rheinhardt, R. D., M. C. Rheinhardt, M. M. Brinson, and K. Faser. 1998. Forested wetlands of low order streams in the inner coastal plain of North Carolina, USA. *Wetlands* 18:365–378.

Scarponi, D., and M. Kowalewski. 2004. Stratigraphic paleoecology: bathymetric signatures and sequence overprint of mollusk associations from upper Quaternary sequences of the Po Plain, Italy. *Geology* 32:989–992.

Titus, J. H. 1990. Microtopography and woody plant regeneration in a hardwood floodplain swamp in Florida. *Bulletin of the Torrey Botanical Club* 117:429–437.

van Els, P., L. Herrera-Alsina, A. L. Pigot, and R. S. Etienne. 2021. Evolutionary dynamics of the elevational diversity gradient in passerine birds. *Nature Ecology and Evolution* 5:1259–1265.

Vavrek, M. J., and H. C. E. Larsson. 2010. Low beta diversity of Maastrichtian dinosaurs of North America. *Proceedings of the National Academy of Sciences USA* 107:8265–8268.

Vieira, L. T. A., R. T. Polisel, N. M. Ivanauskas, G. J. Shepherd, J. L. Waechter, K. Yamamoto, and F. R. Martins. 2015. Geographical patterns of terrestrial herbs: a new component in planning the conservation of the Brazilian Atlantic Forest. *Biodiversity and Conservation* 24:2181–2198.

von Humboldt, A., and A. Bonpland. 1805. *Essai sur la géographie des plantes.* Levrault, Schoell, and Company, Paris.

Wessel, P., and W. H. F. Smith. 1998. New, improved version of Generic Mapping Tools released. *EOS, Transactions of the American Geophysical Union* 79:579.

Whittaker, R. 1956. Vegetation of the Great Smoky Mountains. *Ecological Monographs* 26:1–80.

Whittaker, R. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* 30:279–338.

Whittaker, R. 1970. *Communities and ecosystems.* MacMillan, New York.

Winemiller, K. O., and M. A. Leslie. 1992. Fish assemblages across a complex, tropical freshwater/marine ecotone. *Environmental Biology of Fishes* 34:29–50.

Wing, S. L., C. A. Strömberg, L. J. Hickey, F. Tiver, B. Willis, R. J. Burnham, and A. K. Behrensmeyer. 2012. Floral and environmental gradients on a Late Cretaceous landscape. *Ecological Monographs* 82:23–47.

Wittmer, J. M., T. A. Dexter, D. Scarponi, A. Amorosi, and M. Kowalewski. 2014. Quantitative bathymetric models for Late Quaternary transgressive–regressive cycles of the Po Plain, Italy. *Journal of Geology* 122:649–670.

Woinarski, J., A. Fisher, and D. Milne. 1999. Distribution patterns of vertebrates in relation to an extensive rainfall gradient and variation in soil texture in the tropical savannas of the Northern Territory, Australia. *Journal of Tropical Ecology* 15:381–398.

Yin, Y., and Z. Yan. 2020. Variations of soil bacterial diversity and metabolic function with tidal flat elevation gradient in an artificial mangrove wetland. *Science of the Total Environment* 718:137385.