1 Introduction

Stratigraphic paleobiology uses the principles of sequence and event stratigraphy to interpret patterns in the fossil record (Patzkowsky and Holland 2012). Its principles have been developed mostly for marine systems, in which the occurrence of fossils is controlled primarily by two factors (Holland 1995, 2000). The first is the distribution of species along a water-depth gradient, the primary source of ecological variation at regional scales in both modern and ancient systems. The second is sequence-stratigraphic architecture, which describes how facies change vertically and laterally (therefore, how the water-depth gradient is sampled through time), how sedimentation rates vary, and where unconformities lie.

An understanding of these two factors reveals that patterns of fossil occurrence cannot be taken at face value as straightforward records of evolution and ecological change. Moreover, stratigraphic paleobiology represents a shift away from a long tradition of viewing the fossil record as being biased to, instead, thinking of it as having a predictable and interpretable structure (Holland 2017). Recognizing this structure improves our interpretations of patterns in the fossil record and allows us to understand how ecosystems change over time (Dominici and Kowalke 2007; Holland and Patzkowsky 2007; Patzkowsky and Holland 2007; Zuschin et al. 2007; Danise et al. 2019). This recognition makes it possible to differentiate between the time of origination and first occurrence in a stratigraphic column (or the time of extinction and last occurrence; Holland and Patzkowsky 2002), and to identify true patterns of morphological change through time (Webber and Hunda 2007). It enables an understanding of the true timing and tempo of turnover (Smith et al. 2001; Holland and Patzkowsky 2015; Nawrot et al. 2018), and how to best use fossil data for calibrating phylogenies (Holland 2016). The vast majority of these studies have focused on marine systems. Far less is understood about the stratigraphic paleobiology of nonmarine settings, which differ in their stratigraphic architecture and ecological gradients.

In this Element, we develop the principles of stratigraphic paleobiology for nonmarine systems, and, based on them, we present eight broad sets of hypotheses of expected patterns in the nonmarine fossil record. Our hypotheses build on studies in modern ecology, basin analysis, sequence stratigraphy, and, especially, taphonomy (e.g., Behrensmeyer 1982, 1988; Badgley 1986; Gastaldo 1988, 1992; Rogers 1993; Badgley and Behrensmeyer 1995; Aslan and Behrensmeyer 1996; Behrensmeyer et al. 2000; Wing 2005; Rogers and Kidwell 2007). Other processes, such as climate change, biotic interchange, extinction, and so on, also create patterns in the fossil record, and we do not minimize their importance. What we want to emphasize is that the fossil record reflects not only these climatological and biological processes but also the

effects of stratigraphic architecture, and that these must be separated if we are to reconstruct the history of life.

In some cases, we provide examples from the fossil record that bear on these hypotheses, although our aim is not to provide a comprehensive review. In other cases, data bearing on these hypotheses may not currently exist, and collecting data to test these hypotheses is a promising avenue of future research.

We focus primarily on fluvial and lacustrine systems because they hold the majority of the nonmarine fossil record. Insights from fossil occurrences in these systems may promote similar investigations of the more limited nonmarine fossil record from eolian, volcanic, karst, and glacial systems, all of which operate under differing sets of stratigraphic processes.

2 The Nonmarine Stratigraphic Record

Most nonmarine biotas will not be preserved because they do not occur within sedimentary basins. The vast majority (84%) of nonmarine areas today are uplands, that is, they lie outside of and provide sediment to basins (Nyberg and Howell 2015; equivalent to the "extrabasinal" of Pfefferkorn 1980). Although it is true that many of these areas do currently have young (Plio–Pleistocene) sediments, often with a fossil record, most of these would be considered doomed sediments that have little prospect of long-term preservation (Holland 2016). Only the 16% of nonmarine areas that lie within basins have any prospect of preserving a fossil record. It is a sobering thought that large swaths of North America, eastern South America, southern Africa, and much of northern Asia will leave no permanent fossil record, including the many modern biodiversity hotspots in mountainous areas and other regions that lie outside of sedimentary basins (Myers et al. 2000; Rahbek et al. 2019).

The majority (49%) of continental basins today are intracratonic. Owing to how Nyberg and Howell (2015) classified basins, many of these areas could be considered the distal extensions of foreland basins (Fig. 1), such as in Argentina, northwestern India, parts of China, and the region surrounding Kazakhstan. Extensional basins (7%; Fig. 2), passive-margin basins (10%; Fig. 3), and proximal parts of foreland basins (29%; Fig. 1) represent most of the remaining basin types. Forearc basins (1%) and strike-slip basins (4%) constitute only a minor portion of areas lying within basins. The proportions of these basin types will vary over the 400-Myr Wilson Cycle of supercontinent assembly and breakup, which principally affects the relative proportions of extensional, passive-margin, intracratonic, and foreland basins (Holland 2016). Moreover, these basins differ in their
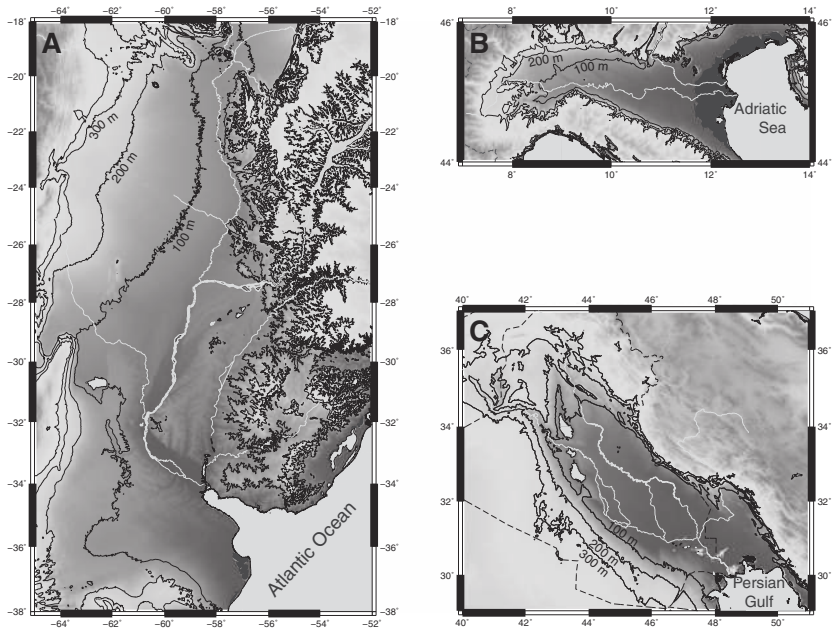
Figure 1 Relief maps of present-day foreland basins. A: Andean foreland basins of Argentina, Uruguay, Paraguay, and Bolivia. B: Po Basin of Italy. C: Persian Gulf foreland basin of Kuwait, Iraq, and Iran. Contour intervals are 100 m; contours for higher elevations outside the sedimentary basins are not shown. Map prepared with GMT (Generic Mapping Tools), using data from the National Geophysical Data Center ETOPO1 1 arc-minute global relief model (Amante 2009).

survival into the deep geologic record, with extensional, passive-margin, intracratonic, and foreland basins being more likely to survive than those associated with collisional continental margins, such as forearc basins (Sadler 2009).

These basin types differ greatly in their subsidence rates, longevity, and size (Angevine et al. 1990; Allen and Allen 2005), as well as their preservation potential (Sadler 2009). Accordingly, they differ markedly in the volume of nonmarine strata they contain and, therefore, in their contribution to the nonmarine fossil record. Foreland basins and extensional basins have fast subsidence rates, yet are relatively short-lived (Holland 2016). In contrast, passive-margin and intracratonic basins have slower subsidence rates, particularly where sediment is introduced into the basin, but they exist almost an order of magnitude longer and are far larger than foreland and rift basins (Angevine et al. 1990; Allen and Allen 2005). Finally, although forearc and backarc basins can contain substantial nonmarine records, their position along convergent margins greatly reduces their survivorship into deep time (Sadler 2009).
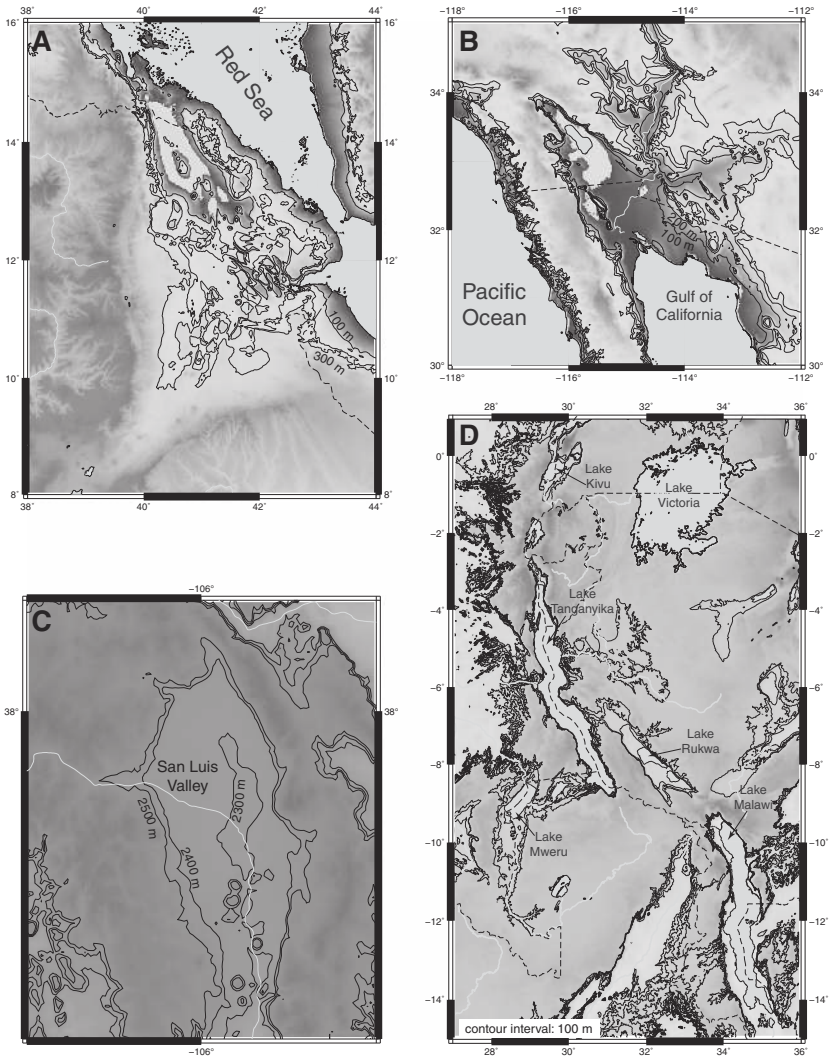
Figure 2 Relief maps of present-day coastal (A, B) and inland (C, D) extensional basins. A: Red Sea and adjacent Ethiopia. B: Gulf of California, with adjacent Mexico and California. C: San Luis Valley, part of the Rio Grande Rift System in southern Colorado, USA. D: Rift basins of East Africa. Contour intervals are 100 m; contours for higher elevations outside the sedimentary basins are not shown. Map prepared with GMT, using data from the National Geophysical Data Center ETOPO1 1 arc-minute global relief model (Amante 2009).

To understand the effects of stratigraphic architecture on the nonmarine fossil record, the starting point should be basins that are most likely to survive into deep geologic time, that contain the greatest volume of nonmarine sediments

Figure 3 Relief map of the present-day passive margin on east coast of USA.
Contour intervals are 100 m; contours for elevations outside the sedimentary
basins (above 200 m) are not shown. Map prepared with GMT, using data from
the National Geophysical Data Center ETOPO1 1 arc-minute global relief
model (Amante 2009).

(foreland, including both pro-foreland/peripheral and retro-foreland/retroarc),
and that are the largest and have the longest subsidence histories (passive-
margin and intracratonic). Although percentages of basin types vary over
geologic time, focusing on just four basin types (extensional, passive-margin,

intracratonic, and foreland basins) would encompass almost 95% of modern land area lying within basins (Nyberg and Howell 2015). Subsequent work may be able to apply principles we present here to the remaining basin types.

3 Nonmarine Ecological Gradients

Species are distributed along environmental gradients in both the modern and the ancient past. In nonmarine systems, important environmental controls on species distributions include temperature (e.g., annual mean and range), pre-cipitation (e.g., annual mean and range), soil moisture, productivity (nutrient availability, biomass), insolation, evapotranspiration, and substrate. Temperature and precipitation are fundamentally important not only for defin-ing biomes (Olson et al. 2001), but also because they are frequently correlated with elevation. These relationships have been well studied in modern plants, and Alexander von Humboldt and Aimé Bonpland (1805) were among the first to document changes in plant communities with elevational changes in tem-perature and precipitation. Species richness also varies with elevation, peaking at mid-elevations (commonly around 1000–1500 m), even when richness is standardized for area (e.g., von Humboldt and Bonpland 1805; Whittaker 1960; Rahbek 1995; Grytnes and Vetaas 2002).

The quantification of ecological gradients was pioneered by Robert Whittaker (1956, 1960, 1970), who evaluated changes in plant community composition in relation to moisture, temperature, elevation, and bedrock. Numerous multivariate analytical methods were subsequently developed for characterizing ecological gradients, particularly by terrestrial plant ecologists (Jongman et al. 1995). Some of these techniques include various forms of ordination, such as nonmetric multidimensional scaling (NMS), detrended correspondence analysis (DCA), canonical correspondence analysis (CCA), detrended canonical correspondence analysis (DCCA), as well as cluster analysis.

The distribution of species along environmental gradients reflects spatial variations in physical and chemical conditions, as well as species interactions. Three types of gradients are recognized: resource, direct, and indirect gradients. Resource gradients are caused by spatial variations in the resources required by organisms, such as nutrients, food, or water (Austin et al. 1984). Direct gradi-ents are generated by environmental variables that are not consumed by organ-isms but that are important controls on growth and physiology, such as moisture and temperature. Indirect gradients are formed by environmental variables that do not directly affect organisms but are linked to other environmental factors that do (e.g., water depth, elevation). Because many indirect gradients reflect the combination of several resource and direct gradients whose effects are difficult

to isolate, indirect gradients are also known as complex gradients (Whittaker 1960). In this way, elevation in nonmarine systems is a proxy for a wide suite of covarying direct and resource gradients, even though elevation itself does not control the occurrence of species. Water depth in marine systems functions in the same way: water depth does not control the distribution of marine species, but it is a first-order descriptor of where species occur because it summarizes many of the factors that do control where species live.

Plants, invertebrates, and vertebrates in nonmarine systems are arrayed primarily along gradients in temperature and moisture, and these gradients are typically correlated with elevation over regional scales. Although many early studies of plant gradients (e.g., Whittaker 1956, 1960) focused on mountainous areas where elevation spanned thousands of meters, it is essential to consider the smaller elevation range spanned within sedimentary basins. Nonmarine portions of sedimentary basins have a characteristic topographic form consisting of a gently dipping plain, which may be a coastal plain in coastal basins (those that adjoin an ocean), or an alluvial plain in inland basins (those lacking a connection to the ocean). For a broad suite of basins, including those that comprise the majority of the nonmarine stratigraphic record, these alluvial and coastal plains characteristically have low relief, with a total elevation range of 200–300 m (Figs. 1–3).

3.1 Ecological Gradients on Modern Coastal and Alluvial Plains

Ecologists have widely found gradients in species composition correlated with elevation but controlled by temperature and moisture on coastal and alluvial plains, even with their modest spans of elevation. Although anthropogenic effects on modern alluvial systems can be severe (Gibling 2018), most ecological studies have attempted to use areas less impacted by human activity. Moreover, although species distributions today may be altered by human activity, it is reasonable to assume that species distributions in the past were also tied in some way to temperature and precipitation.

In coastal areas, environmental and ecological gradients are correlated with elevation and distance from the shore. For example, in the western Gulf Coastal Plain of Texas, ordination of the species composition of longleaf pine forests reveals a complex gradient reflecting the joint importance of moisture, soil texture, phosphorous, and nitrogen (Harcombe et al. 1993). On the coastal plain of North Carolina, ordination of forest vegetation demonstrates that the most important source of variation is a complex gradient reflecting moisture, physiography, stream order, and elevation (Wyant et al. 1991; Rheinhardt et al. 1998; Rheinhardt et al. 2013). Ordination of coastal plant communities in South

Africa also indicates the overriding importance of temperature and precipitation in species composition (Morgenthal et al. 2006). In inland areas, environmental and ecological gradients are correlated with elevation. The species composition of plants in the bottomland forests of the lower alluvial plain of the Mississippi River reflects flood tolerance, which is tied to floodplain slope and elevation (Dale et al. 2007). Ordination indicates that the composition of Oregon plant communities is controlled by moisture and temperature, and that these covary with elevation, a pattern that is true statewide as well as in coastal areas (Ohmann and Spies 1998). Even in arid coastal settings, such as Saudi Arabia, plant species are distributed primarily on a gradient of rainfall and elevation (Al-Aklabi et al. 2016).

Unsurprisingly, the distribution of terrestrial invertebrates and vertebrates parallels that of plants and shows similar relationships to elevation. This similarity partly reflects the way that animals are controlled by many of the same physical and chemical gradients that affect plants, but it also reflects the importance of plant–animal interactions, such as herbivory and habitat structure. For example, ordination of Scandinavian beetle communities indicates that temperature and other climatic factors are the dominant controls on their distribution (Heino and Alahuhta 2015), although this study includes areas not in sedimentary basins. Ecological diversity and species density of North American mammals are predicted by annual minimum and maximum temperature, mean annual actual evapotranspiration, relief, and elevation (Badgley and Fox 2000). These trends are most pronounced in coastal areas where the effects of increasing continentality with elevation are evident. Vertebrates of northern Australia are distributed along a gradient of rainfall and soil type, which is correlated with distance from the coast (Woinarksi et al. 1999). Some mammal species of Western Australia have distributions strongly related to distance from the coast, with others occurring more broadly (Gibson and McKenzie 2009). A perusal of field guides of many terrestrial animal groups on any coastal plain reveals a similar pattern in which some species have ranges tightly restricted to the coast, the lower coastal plain, or the upper coastal plain, often reflecting the position of the water table. Some species are more eurytopic, with a wider distribution among environments.

Possibly more surprising, aquatic animals of coastal plains are also distributed along similar gradients correlated with elevation and distance from the coast. For these aquatic species, the gradients are controlled by the upstream increase in stream gradient. For example, aquatic macroinvertebrates of the Virginia coastal plain are distributed primarily along a gradient from coastal, tidally influenced areas to nontidal, inland areas (Dail et al. 2013). This pattern

is also true for macroinvertebrates on the coastal plain of North and South Carolina (Maxted et al. 2000). Unionid bivalves in the Flint River of Georgia are distributed primarily on a gradient from slack-water streams with fine sediment bottoms to shaded riffles with coarser sediment, corresponding with decreasing stream order and distance from the coast (Gagnon et al. 2006). The composition of fish communities in the Savannah River (Meffe and Sheldon 1988) and other streams of South Carolina (Paller 1994) varies along a gradient from slower-flowing, high-order streams closer to the coast to faster-flowing, low-order streams farther from the coast. Similar spatial variations are also seen in fish from eastern Costa Rica, where salinity plays a strong role in coastal areas (Winemiller and Leslie 1992).

Coastal gradients in physical and chemical properties and their effects on the distribution of species are well shown in the southeastern USA, where a wide range of data are available (Fig. 4). On a visible satellite image, the fall line that separates coastal-plain strata from upland (that is, outside of the sedimentary basin) rocks (Fig. 4, C) is marked by an abrupt change in vegetation (Fig. 4, A, G, H). Complex patterns in vegetation are also present in upland or extrabasinal areas, but as these areas have no prospect of leaving a long-term stratigraphic record, this discussion focuses only on patterns in the coastal plain. The gentle decrease in elevation towards the coast is apparent on a relief map (Figs. 3, 4, B). Although the north–south variation in ecosystems (Fig. 4, G) and bioclimates (Fig. 4, F) is partly due to latitudinal climate variation, the orientation of these ecosystem and bioclimate boundaries parallel to the Atlantic coast demonstrates the influence of the coastal-plain elevation gradient. The sources of these ecological differences are gradients in rainfall (Fig. 4, D) and temperature (Fig. 4, E) that are correlated with elevation on the coastal plain. In particular, areas closer to the coast tend to receive more rainfall than areas farther from the coast. Maximum summertime temperatures as well as mean annual temperature variations also tend to be higher inland than on the coast, owing to the buffering effects provided by the ocean. Variations in plant communities and moisture are reflected in distributions of animals. For example, birds show greater diversity in coastal areas (Fig. 4, I). At a finer scale (Fig. 4, J–L), the types of wetland habitats also vary with elevation and distance from the coast, with estuarine–marine wetlands limited to tidal areas and freshwater emergent areas just inland of the coast. Other sources of variation in community composition are also present. For example, even within areas of similar elevation, ecosystems and forest types vary with microclimate, soil type, bedrock, and human land use (Fig. 4; Edwards et al. 2013).

Elevation and distance from the coast are complex gradients (Whittaker 1956): they describe the distribution of species, but they do not directly
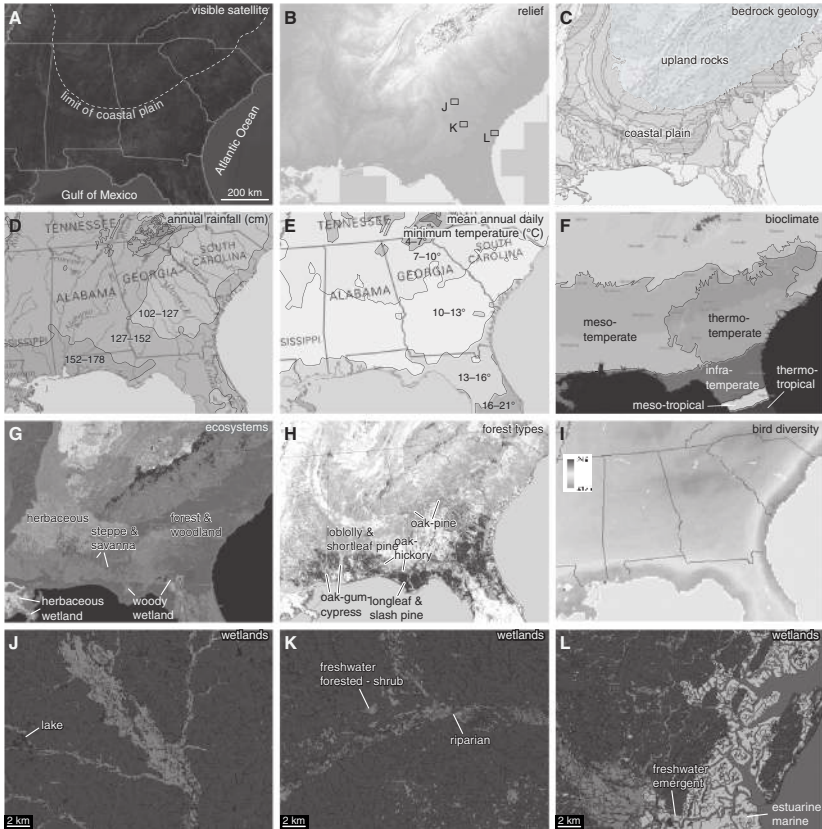
Figure 4 Elevation-related gradients on the modern coastal plain of the
southeastern USA. Locations of detailed maps J, K, and L are indicated on
B. Image sources: A–G: U.S. National Map; H: U.S. Forest Service, Forest
Types; I: BiodiversityMapping.org; J–L: U.S. Fish and Wildlife Service,
Wetlands.

control the distribution of species. These complex gradients are controlled
by direct and resource gradients that affect species distribution: these are
predominantly temperature and precipitation, but also soil type, soil mois-
ture, stream gradient, and for animals, food sources. Because of the
covariation of environmental factors with a complex gradient, it is often
difficult to identify which environmental factor or factors are the most
important. This is true in the Recent, and even more so in ancient systems.
Even so, the distribution of species along a complex gradient can be
described and used, even if the specific underlying causes for that distri-
bution remain unknown.