# The contrasting controls on the occurrence of fossils in marine and nonmarine systems

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*ABSTRACT - Stratigraphy is the first-order control on the fossil record. The formation of sedimentary basins dominates this control over large spatial (> 100 km) and long temporal scales (> 10 myr), with sequence-stratigraphic architecture becoming dominant over shorter time scales as low as 10 kyr. Numerical modeling of siliciclastic shallow-marine and nonmarine settings provides a framework for predictions about the structure of the fossil record. Despite the nearly limitless range of possible stratigraphic architectures, these simplify into three main contexts: slow relative rise in sea level, rapid relative rise in sea level, and relative fall in sea level. Each produces characteristic stratigraphic changes in the structure of the fossil record. For example, clusters of first and last occurrences in marine systems are expected at subaerial unconformities, nondepositional surfaces (such as downlap surfaces), flooding surfaces, and surfaces of forced regression, whereas such clusters are expected only at subaerial unconformities in nonmarine systems. Similarly, community composition will change predictably in marine and nonmarine systems, reflecting the distribution of species along ecological gradients in water depth and elevation. Numerous field studies demonstrate that these effects are pervasive. Any paleontological study that is grounded in where fossils occur must therefore consider these effects before making any interpretations of biological processes. Several studies are highlighted that demonstrate how to isolate the stratigraphic controls on fossil occurrences and reach well-grounded interpretations of mass extinctions, ecosystem changes, morphological evolution, and phylogenetic history. Areas of promising avenues of research are presented, including the role of stratigraphic architecture over long time scales (> 10s-100s myr), the development of models specific to shallow-water carbonates, and field-based studies of the role of nonmarine alluvial and lacustrine stratigraphic architecture.*

## INTRODUCTION

That the fossil record is incomplete is perhaps the most fundamental and long-known observation that paleontologists have made. It shapes nearly every interpretation made from the fossil record, and it is presented almost immediately in paleontology textbooks (e.g., Raup & Stanley, 1978; Prothero, 2013; Stanley & Luczaj, 2015). The topic is often introduced with a statement about how rare fossilization is and how few individuals become fossils, and it is typically followed by a discussion of taphonomy and the specific mechanisms of fossilization. All of this is true, but it misses the larger issue that with few exceptions the fossil record is embedded in the stratigraphic record. The first-order control on the fossil record does not lie in the various mechanisms of fossilization, but on the accumulation of a stratigraphic record. As a result, knowing how the stratigraphic record is constructed is crucial not just for recognizing the limits of the fossil record, but also for knowing what can be gained from it. This is the domain of stratigraphic paleobiology: incorporating our knowledge of how the stratigraphic record is constructed into our paleobiological interpretations.

Stratigraphic paleobiology is rooted in numerical and conceptual models, whose predictions have been demonstrated in a substantial array of field studies (see reviews in Patzkowsky & Holland, 2012, and Holland & Loughney, 2021). Central to stratigraphic paleobiology is the recognition that the fossil record is not simply the history of life's evolution and ecology, but that it is equally the record of how the sedimentary record has been built. It includes the recognition that stratigraphic processes are not biases or artifacts that arise in special situations, but that they are an inherent part of the entire fossil record. Although these processes impose limits on temporal and spatial resolution, they also open avenues for addressing deep-time biological questions in a way that is honest to the nature of the fossil record.

This review will focus on one aspect of stratigraphic paleobiology, where fossils occur in stratigraphic columns, with a particular emphasis on advances in the past decade. The occurrence of fossils, especially first and last occurrences, is central to numerous topics in paleontology, including biostratigraphy, community analysis, divergence times, as well as the dynamics of extinctions, recoveries, biotic invasions, and diversifications. Understanding the controls on fossil occurrences is crucial to making any inferences about biological history and processes.

This review begins with a discussion of how the sedimentary record is assembled and how that affects the distribution of fossils. This is followed with a description of three important sequence-stratigraphic contexts, using numerical models of marine and nonmarine systems to form predictions about the structure of the fossil record. Case studies are presented to show how these model predictions are validated and how they can be used to interpret biological events and processes. The review concludes with a consideration of how the principles of stratigraphic paleobiology should guide the study of

mass extinctions, community paleoecology, phylogenetic models, and morphological evolution. Promising areas of future research in stratigraphic paleobiology are described.

## ASSEMBLING THE SEDIMENTARY RECORD

### Sedimentary basins

At the coarsest scales, the fossil record is controlled by where sediments accumulate in sedimentary basins (Holland, 2016). Two astounding statistics frame this concept. First, only 16% of modern terrestrial land area lies within a sedimentary basin, that is, where a long-term stratigraphic record is accumulating (Nyberg & Howell, 2015). Second, only 28% of modern coastlines are depositional (Nyberg & Howell, 2016). Although sediment can be observed over perhaps the majority of Earth's surface, even if only in patches, sediment is incorporated into the stratigraphic record over a far smaller proportion. Extended into deep time, these statistics are eye-opening in that not only are large portions of Earth's biota unlikely to be preserved in any window of geological time, but also that where the fossil record is assembled will be strongly correlated spatially and temporally because of plate-tectonic processes.

Unless sediment is buried deeply under more sediment, it is likely to be eroded and carried farther from its source. Such deep burial cannot be accomplished solely by depositing more and more sediment, which would simply build a mound that would enhance its own erosion. Deep burial requires accommodation space, which is created through tectonic subsidence and eustatic rise. Because eustatic rise tends to be cancelled by eustatic fall, a stratigraphic record that persists into deep time depends primarily on tectonic subsidence, that is, the formation of a sedimentary basin (Allen & Allen, 2005). Moreover, the amount of subsidence in basins commonly exceeds several thousand meters, compared with the roughly 200 m of variation in eustatic sea level: tectonic subsidence is necessary to preserve a thick stratigraphic record.

Tectonic subsidence is distinguished from the isostatic subsidence that results from the weight of sediments and water. Although sediment deposition creates some subsidence, it is only a fraction (at most about 2/3) of the thickness of sediments, such that sediment deposition alone cannot create a long-lasting sedimentary record. Tectonic subsidence is generated by a variety of processes, with the four most important being: 1) lithospheric extension and stretching such as at rifts and pull-apart basins, 2) cooling such as along passive margins and in cratonic basins, 3) loading and flexure, such as in foreland basins, and 4) dynamic topography produced by mantle downwelling (Allen & Allen, 2005).

Sedimentary basins differ markedly in duration and spatial extent and therefore the area over which biota could potentially be incorporated into the fossil record (Holland, 2016). For example, cratonic basins and passive margins have durations that can span a couple hundred million years, whereas rifts and foreland basins typically last fewer than 50 m.y. Similarly, passive margins and foreland basins can exceed several thousand km in length, whereas cratonic basins tend to be smaller than 700 km, and individual rift basins are commonly less than 200 km long and 50 km wide (although the length of rift systems can exceed thousands of km).

Sedimentary basins comprise the basic building blocks in which the fossil record is assembled. Of particular importance are how the largest scale biotic units - provinces and biomes - intersect with sedimentary basins and how that has changed over time. As the location of provinces and biomes changes, they may be fully or partly encompassed by sedimentary basins, or not at all. An additional consideration is modern outcrop area, driven by the structural evolution of a region following deposition, which controls how the record of sedimentary basins can be sampled.

This structure to the fossil record has important implications for inferences of the original geographic ranges of fossil species. Simply put, geographic ranges in the fossil record will be systematically less than the original ranges of species. How much less will depend on the overlap of biomes and provinces with sedimentary basins, the sedimentary environments in which species lived and how those are distributed through the sedimentary basin, as well as how the sedimentary basin has been exposed by subsequent patterns of structural uplift. Although this list might seem daunting, the structure of the fossil record can be used advantageously for the study of geographic range. For example, long-lived and large basins such as passive margins and cratonic basins provide better measures of range size and its changes through time than smaller or shorter-lived basins.

Finally, it is important to consider that sedimentary basins are not random samples of environments on the Earth's surface. For example, only 40% of the area of modern terrestrial basins falls within a non-arid climate, one hospitable for diverse life (Nyberg & Howell, 2015). Similarly, except for extensional basin systems such as rifts, most nonmarine basins that are likely to be preserved into deep time record low elevations from 0 to 500 m above sea level (Holland et al., 2023). Given that biodiversity today tends to reach a maximum at elevations of 1000-1500 m above sea level and that many modern biodiversity hotspots are in mountainous regions, the nonmarine fossil record will consist primarily of low-elevation biotas, and many clades could be expected to lack fossils from their early history (Holland et al., 2023).

### Sequence-stratigraphic architecture

Within sedimentary basins, the accumulation of sediment is governed by sequence-stratigraphic processes, that is, the interplay of accommodation (driven by tectonic subsidence and eustasy) and sediment supply (controlled by climate and source area). Although a full review of sequence-stratigraphic principles is beyond the scope of this review, a short introduction helps to establish the framework through which the stratigraphic record is interpreted. For detailed explanations, see Van Wagoner et al. (1990) for a short, clear, but somewhat dated introduction to sequence-stratigraphic principles, and Catuneanu (2006) for a more recent and exhaustive coverage.

Sequence stratigraphy describes how sediment accumulates in response to changes in the rates of accommodation and sediment flux. Accommodation is the sum of tectonically driven subsidence and eustatic
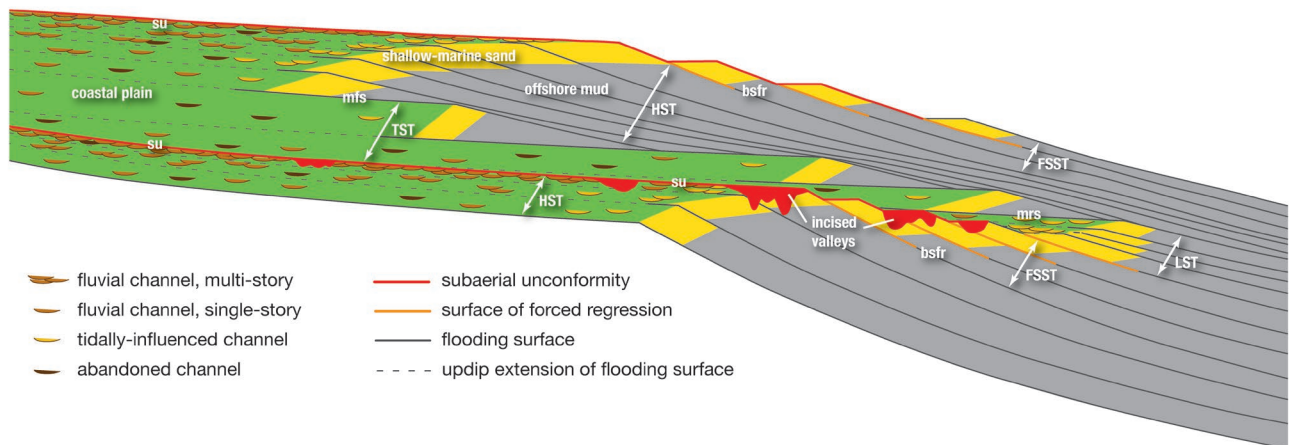
Fig. 1 - Schematic cross-section along a dip-line through a sedimentary basin, showing principal surfaces and systems tracts of a depositional sequence (following the framework of Hunt & Tucker, 1992). LST: lowstand systems tract. TST: transgressive systems tract. HST: highstand systems tract. FSST: falling-stage systems tract. su: subaerial unconformity. bsfr: basal surface of forced regression. mrs: maximum regressive surface. mfs: maximum regressive surface.

sea-level change (lake level in some nonmarine settings), and accommodation is also sometimes called relative sea level. Sequence stratigraphy generates predictions about the spatial distribution of hiatuses, sedimentation rates, and sedimentary environments through time, and these are a pervasive control for how the fossil record is structured over time scales of tens of thousands to tens of millions of years. Changes in the rates of accommodation and sediment flux produce changes in stacking patterns, which give rise to systems tracts and surfaces (Figs 1, 2). Importantly, these cause sedimentary environments as well as zones of non-deposition to systematically shift laterally.

Stepping through one cycle of relative sea-level change illustrates the main aspects of sequence-stratigraphic architecture. Starting with the initial rise in relative sea level, accommodation is produced at a rate that is less than sedimentation rate at the shoreline. The shore therefore follows a seaward and upward trajectory and undergoes normal progradation (Neal & Abreu, 2009). If there are higher-order changes in sediment supply or accommodation, a progradational to aggradational stacking of these higher-order sequences (or parasequences) results, in which these units stack seawards and upwards, but progressively more upwards than seawards through time. This interval of strata is known as the lowstand systems tract (LST). In nonmarine areas, the relatively slow rate of accommodation favors the formation of a low-accommodation systems tract (LAST) in which channel facies dominate over floodplain facies, and in which channel deposits tend to be multistory and multilateral (Fig. 2).

As the rise in relative sea level accelerates, it eventually exceeds the rate of sedimentation at the shoreline, causing the shoreline to transgress with an upward and landward trajectory (Neal & Abreu, 2009). If higher-order sequences or parasequences are present, this produces a retrogradational stacking pattern in which depositional units are stacked landward and upwards (Van Wagoner et al., 1990). This body of strata is called the transgressive

systems tract (TST), and the maximum regressive surface (formerly called the transgressive surface) marks the contact between the LST and TST (Van Wagoner et al., 1990). In nonmarine areas, rapid rates of accommodation favor the formation of high-accommodation systems tracts (HAST) comprising thick floodplain deposits and isolated, single-story channel deposits (Fig. 2).

As the rise in relative sea level slows, it again becomes less than the rate of sedimentation at the shoreline. This drives a return to normal progradation, a regressing shoreline with a seaward and upward shoreline trajectory, and an aggradational to progradational stacking pattern (Neal & Abreu, 2009), in which the progradational trend becomes stronger through time. These strata are known as the highstand systems tract (HST), and the contact of the HST on the TST contact is called the maximum flooding surface (Van Wagoner et al., 1990). In nonmarine areas, a return to low-accommodation systems tracts is favored.

When relative sea level begins to fall, the loss of accommodation drives a forced regression of the shoreline as it moves seawards and downwards (Neal & Abreu, 2009). On wave-dominated shelves, this shoreface trajectory produces one or more erosion surfaces called surfaces of forced regression that record abrupt shallowing, typically with offshore facies overlain by upper shoreface facies (Hunt & Tucker, 1992). Strata deposited during the relative fall in sea level are known as the falling-stage systems tract (FSST). The lowest surface of forced regression is called the basal surface of forced regression, and it separates the underlying HST from the FSST.

On land, a relative fall in sea level causes rivers to incise. This creates valleys that initiate at the terminal highstand shoreline, and these valleys deepen and grow landwards and seawards through time (Blum & Törnqvist, 2000). What were interfluves between rivers before sea level began to fall become starved of sediment, favoring the formation of well-drained mature paleosols. These paleosols also extend seaward

## Accommodation / Sediment flux

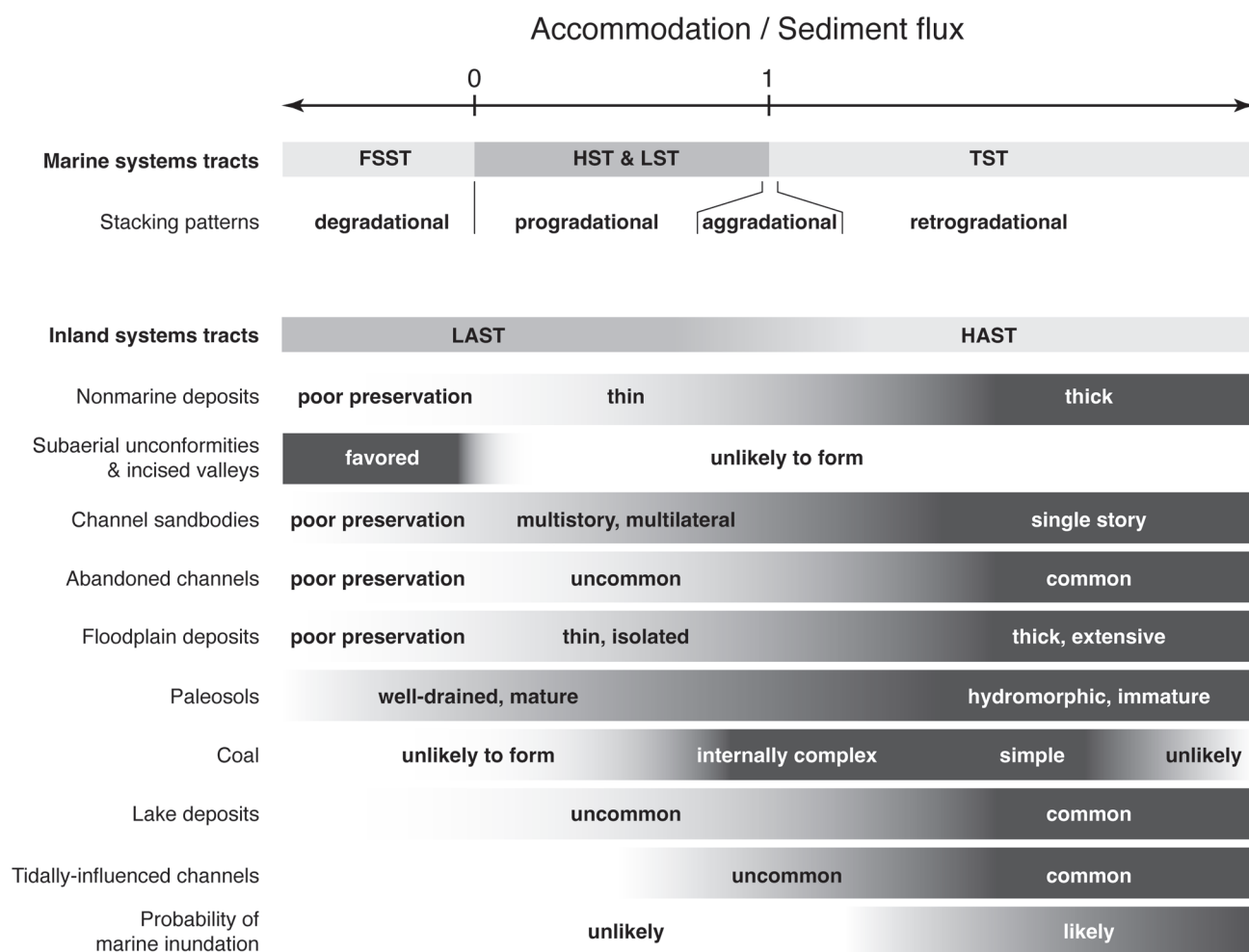| | 0 | | 1 | |
|---|---|---|---|---|
| **Marine systems tracts** | FSST | HST & LST | | TST |
| Stacking patterns | **degradational** | **progradational** | **aggradational** | **retrogradational** |
| | | | | |
| **Inland systems tracts** | LAST | | HAST | |
| Nonmarine deposits | **poor preservation** | thin | | **thick** |
| Subaerial unconformities & incised valleys | **favored** | | unlikely to form | |
| Channel sandbodies | **poor preservation** | **multistory, multilateral** | | single story |
| Abandoned channels | **poor preservation** | uncommon | | **common** |
| Floodplain deposits | **poor preservation** | thin, isolated | | **thick, extensive** |
| Paleosols | **well-drained, mature** | | hydromorphic, immature | |
| Coal | **unlikely to form** | internally complex | simple | unlikely |
| Lake deposits | uncommon | | **common** | |
| Tidally-influenced channels | | uncommon | | **common** |
| Probability of marine inundation | unlikely | | **likely** | |

Fig. 2 - Characteristics of marine and inland systems tracts and their relationships to the ratio of accommodation and sediment flux. Adapted from Holland & Loughney (2021) and based partly on Catuneanu (2006). LST: lowstand systems tract. TST: transgressive systems tract. HST: highstand systems tract. FSST: falling-stage systems tract. LAST: low-accommodation systems tract. HAST: high-accommodation systems tract.

along the interfluves onto what were originally marine sediments, now exposed by the sea-level fall. The incision from rivers and these interfluve paleosols constitute the subaerial unconformity. Because fluvial deposition can occur within the valley, forming terraces as the river continues to incise, the subaerial unconformity can be a composite surface (Blum & Törnqvist, 2000). As sea level continues to fall, the valley lengthens and exposure on the interfluve expands seaward. As a result, the subaerial unconformity caps or truncates the falling-stage systems tract and possibly underlying strata, depending on the depth of incision. In carbonate systems, the subaerial unconformity is manifested by paleosols and karst features. In the most widely used sequence-stratigraphic frameworks, the subaerial unconformity and surfaces that correlate with it are called the sequence boundary (Van Wagoner et al., 1990; Hunt & Tucker, 1992), although other frameworks may place the sequence boundary at other surfaces (Catuneanu et al., 2009), including the maximum regressive surface (Embry & Johannessen, 1992), maximum flooding surface (Galloway, 1989), and the basal surface of forced regression (Posamentier & Allen, 1989). Stratigraphic units bounded by subaerial unconformities and their correlative surfaces are called

depositional sequences. In contrast, stratigraphic units bounded by flooding surfaces are called parasequences.

## SEQUENCE-STRATIGRAPHIC OCCURRENCE OF FOSSILS: BUILDING NUMERICAL MODELS

Because sequence-stratigraphic architecture creates predictable and repeatable patterns in the locations of hiatuses and sedimentary environments, it controls the times and locations where individual species leave a fossil record. Because sequence-stratigraphic architecture is commonly complex, the stratigraphic origins of patterns of fossil occurrence can easily go unnoticed. As a result, patterns of fossil occurrence have commonly been treated as simple records of when species were extant.

For example, consider a cluster of last occurrences of species. Such a cluster is typically regarded as an extinction pulse (e.g., Yin et al., 2007; Harper et al., 2014; Tobin, 2017). However, such a cluster could also be formed by a subaerial unconformity, a flooding surface, a surface of forced regression, or a condensed section (Bayer & McGhee, 1985; Bambach & Gilinsky, 1988; Armentrout, 1991; Holland, 1995). Compounding matters,

the cluster might have a "common cause" in that a sea-level rise might elevate extinction rates as well as generate a flooding surface that also causes last occurrences to cluster (Peters & Foote, 2001). Without other data, it is difficult or even impossible to uniquely interpret such a cluster and to rule out alternatives. To distinguish these possibilities, and to understand the controls on fossil occurrences more generally, it is essential to use numerical models. Such models have played an important role in establishing the principles of stratigraphic paleobiology, and field data have corroborated these model predictions.

Three steps are needed to simulate the stratigraphic occurrence of fossils within sequence-stratigraphic architecture: simulate the stratigraphic record of a sedimentary basin or of stratigraphic columns, simulate the evolution and ecology of species, and combine those two to simulate the stratigraphic occurrence of those fossil species (Holland, 1995, 2000, 2020, 2022; Holland & Patzkowsky, 2002, 2015).

*Simulating basins and stratigraphic columns*

Models for simulating stratigraphy follow a similar approach (e.g., Read et al., 1986; Flemings & Jordan, 1989; Steckler, 1999; Watney et al., 1999; Hutton & Syvitski, 2008; Holland, 2022a). First, accommodation space is generated at each time step through a combination of eustasy and tectonic subsidence. Next, sediment is deposited in this accommodation space, and this is accomplished through a wide variety of rules. Some models also incorporate isostatic subsidence from this sediment load.

The rules of sedimentation vary widely, including depth-dependent sedimentation rates (e.g., Read et al.,

1986), diffusion from a sediment source (Flemings & Jordan, 1989), geometric rules (e.g., Steckler, 1999; Holland, 2020), or rules based on the physics of sediment transport (e.g., Hutton & Syvitski, 2008). Although one might intuitively prefer a process-based model, these necessarily have numerous parameters and finding reasonable values for them is often difficult (Koerschner & Read, 1989; Elrick & Read, 1991; Bornholdt et al., 1999). Exploring their large parameter spaces may be difficult or practically impossible (Peters, 1991). Moreover, these models can display a sensitive dependence on initial conditions (Slingerland, 1990), and they are prone to the problem of equifinality in which multiple combinations of parameter values generate the same outcome (Watney et al., 1999). Models that employ simpler rules (e.g., diffusion or geometric models) can provide realistic results even though their parameters may not mimic the process of deposition.

Stratigraphic models commonly produce a history of water depth or elevation through time across a sedimentary basin or through a stratigraphic column. Some also generate histories of sediment properties such as lithology, grain size, porosity, etc. Where models generate sedimentary basins, it is often possible to extract stratigraphic columns from them.

Two stratigraphic models are employed in this paper. For the marine realm, the process-based Sedflux model (Hutton & Syvitski, 2008) is used, owing to its realistic architectures (Fig. 3). Sedflux is specifically a siliciclastic model, but the principles derived from it can be applied to shallow-marine carbonate systems that share similar architectures, such as parasequences, parasequences sets, unconformitities, etc. For the nonmarine realm, the
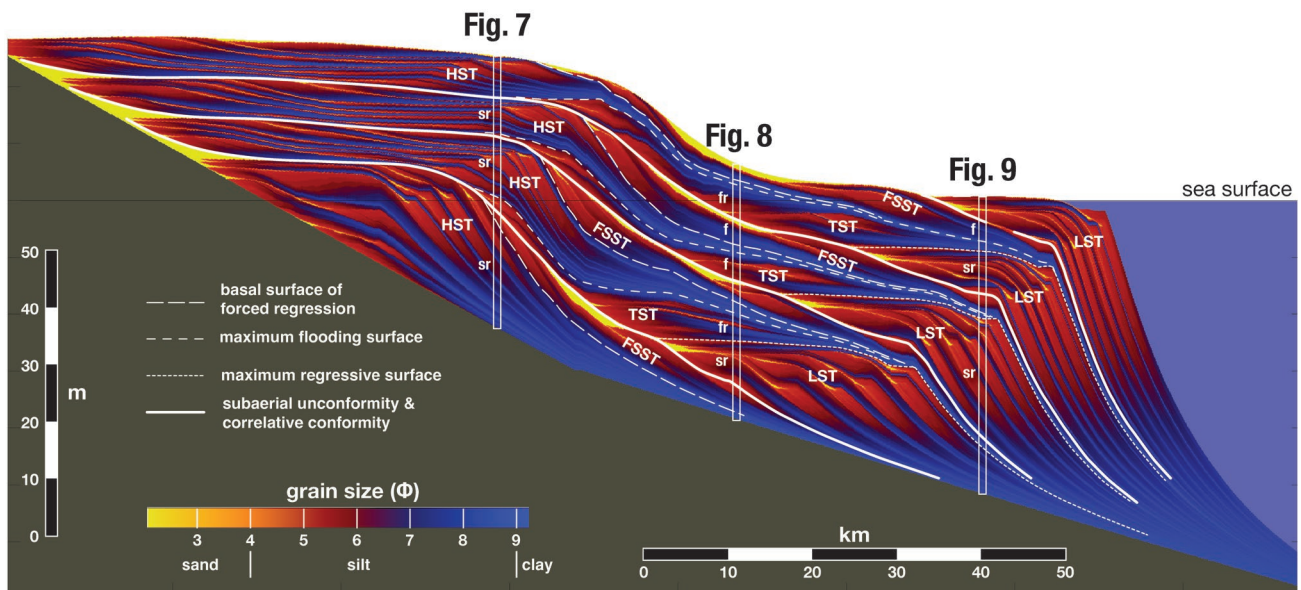


Fig. 3 - Model run of Sedflux (Hutton & Syvitski, 2008) used in this paper. The basin simulates a passive margin, with subsidence rates increasing towards the right, away from the sediment source at the left edge of the model. Three depositional sequences are shown, produced by eustatic cycles with a period of 3.0 m.y. and generated by a 30 m sea-level cycle, with superimposed 5-m cycles with a period of 50 k.y. Systems tracts and surfaces are indicated, as are the locations of three stratigraphic columns where the fossil record is simulated. The left column (Fig. 7) is designed to be dominated by highstand systems tracts (HST), the middle column (Fig. 8) primarily records transgressive (TST) and falling-stage (FSST) systems tracts, and the right column (Fig. 9) highlights the lowstand systems tract (LST). Representative intervals corresponding to slow relative rise in sea level (sr), fast relative rise (fr), and relative fall in sea level (f) are indicated to the left of the three columns.
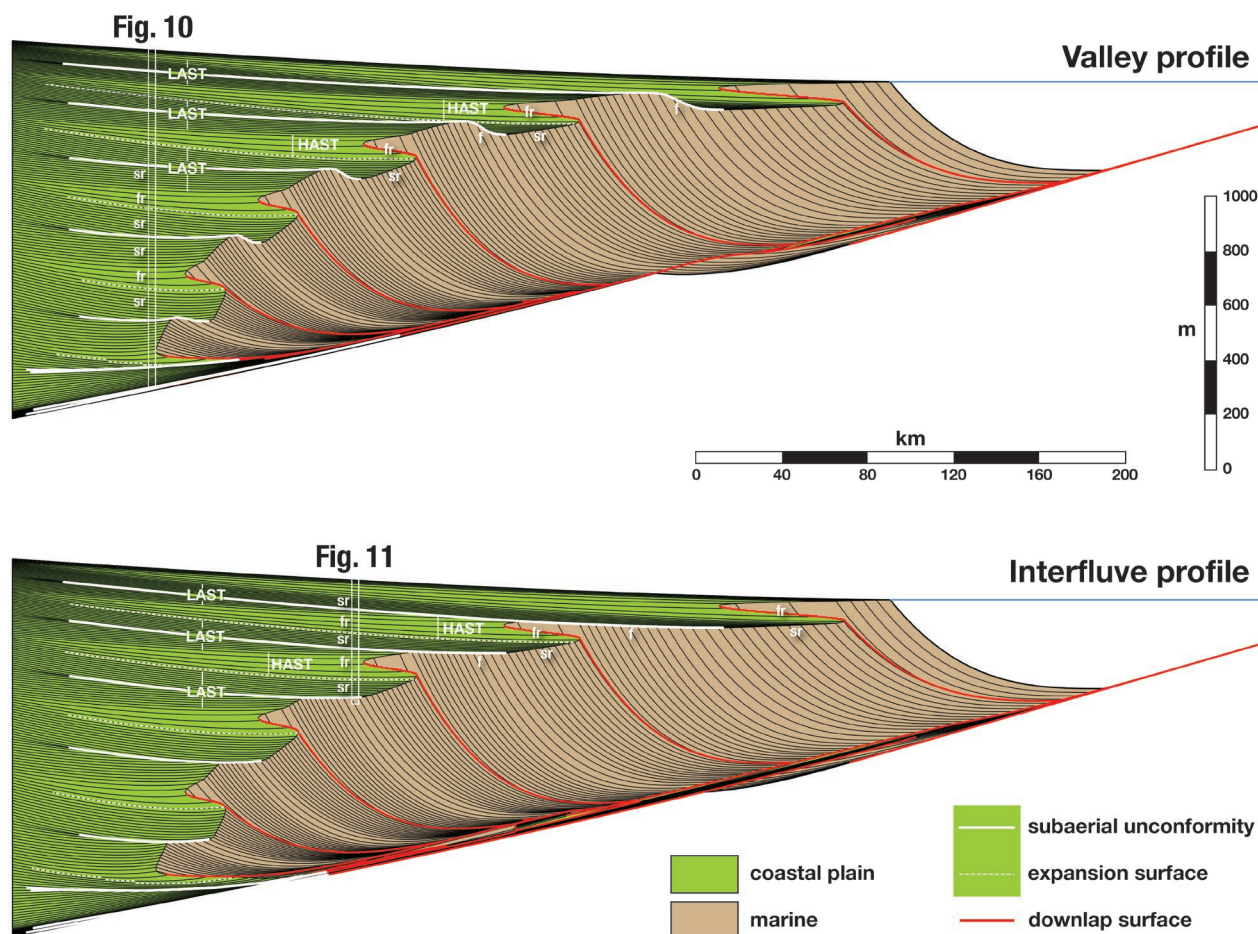
Fig. 4 - Model run of strataR (Holland, 2022b) used in this paper. The model generates a 21 myr history of a foreland basin, in which subsidence rates decrease to the right away from the sediment source at the left edge of the basin. After an initial period of low subsidence, subsidence rates greatly increase as the foreland basin is initiated and decline over time; sedimentation rates increase through time. Superimposed are seven eustatic cycles, each 3 m.y. long with a peak-to-peak amplitude of 80 m. The locations of two stratigraphic columns where the fossil record is simulated are indicated. The column shown in Figure 10 is from a depositionally updip area where valleys are formed during eustatic falls; the column shown in Figure 1 is from a depositionally downdip area on an interfluve during eustatic falls. Representative intervals corresponding to slow relative rise in sea level (sr), fast relative rise (fr), and relative fall in sea level (f) are indicated. HAST: high-accommodation systems tract. LAST: low-accommodation systems tract.

geometric strataR model (Holland, 2022b) is used for its ability to simulate the systems tracts characteristic of fluvial strata (Fig. 4). strataR is an extension of the model used by Holland (2022a), and it allows for any spatial pattern of subsidence, as well as temporally variable subsidence and sediment flux, in addition to changes in eustatic sea level or lake level. See Hutton & Syvitski (2008) for detailed descriptions of the mechanics of Sedflux; see the Supplementary Online Material 1 (SOM1) and Holland (2022a, b) for a description of strataR. Source code for running the Sedflux and strataR simulations used in this paper are included in the SOM2.

*Simulating species*

Species are generated first by simulating their origination and extinction, which is handled through a random-branching model in which each species may go extinct at each time step, speciate to form a new species, or persist unchanged (Raup, 1985). The probability of extinction is typically held constant through time at a rate based on a Phanerozoic average (time-homogeneous rate

of 0.25 per lineage million years; Raup, 1991), but it can also be varied to simulate a mass extinction (i.e., time-inhomogeneous; Holland & Patzkowsky, 2015; Holland, 2020). The probabilities of speciation and extinction are commonly set equal such that diversity is not forced to rise or fall through time, although it may vary stochastically owing to these two probabilities (Raup, 1985). The probability of speciation can also be diversity-dependent, such that the probability of speciation declines as a species carrying capacity is approached (Holland, 2020).

The ecology of species is simulated using Gaussian species-response curves (Gauch & Whittaker, 1976; ter Braak & Looman, 1986; Holland, 1995) that describe the probability of species occurring as a function of water depth for marine species or elevation for nonmarine species (Fig. 5). This relationship is used because decades of studies in modern and ancient ecosystems have repeatedly shown that these topography-correlated gradients in community composition are the dominant descriptor of the distribution of species. The ubiquity of this pattern is reviewed by Patzkowsky & Holland (2012)
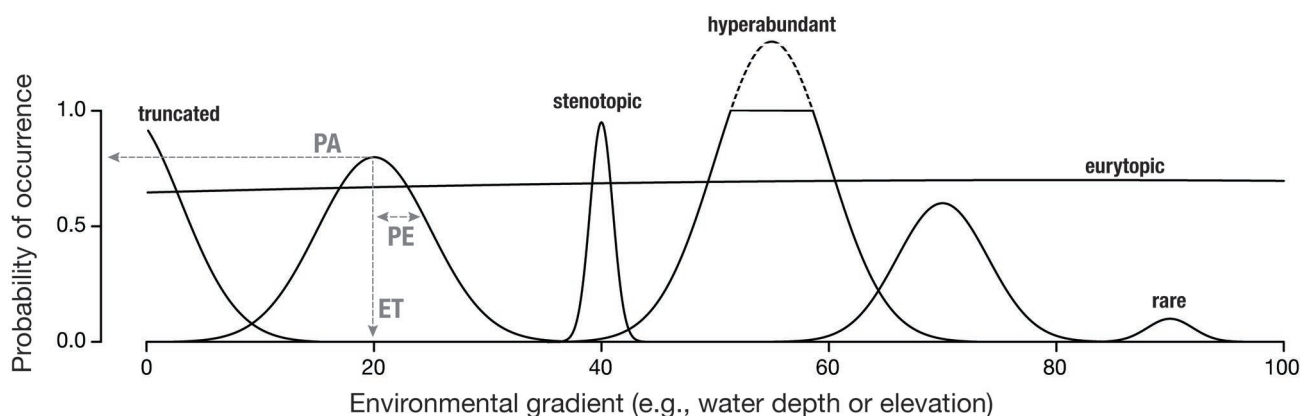
Fig. 5 - Species response curves showing how the probability of occurrence of a species varies with position along an environmental gradient, such as water depth for marine species or elevation for nonmarine species. Seven example curves are shown to illustrate some of the variation in species ecologies that can be be generated. PA: peak abundance. PE: preferred environment. ET: environmental tolerance.

for marine systems and by Holland & Loughney (2021) for nonmarine systems.

Three parameters describe a species response curve. Preferred environment (PE) describes the water depth (for marine species) or elevation (for nonmarine species) where that species is most likely to be encountered. Peak abundance (PA) is the probability that a species will occur in a bed deposited at a value corresponding to a species' PE. Environmental tolerance (ET) is the standard deviation of these Gaussian response curves, and it reflects the tendency for species to be found at elevations or water depths other than PE. Nonmarine species have an additional parameter called affinity, which describes the tendency of a species to be preserved in channel versus floodplain deposits. This can be used to simulate differential taphonomy, given the control of floodplain and channel facies on fossil preservation (Behrensmeyer & Hook, 1992).

Upon its origination, each species is given randomly generated values of the three parameters that describe these response curves. Nonmarine species are also given a randomly generated value of affinity. These values stay constant over the lifespan of a species; that is, species display niche conservatism. These values span a broad range and combinations of possibilities of depth/elevation preference, degree of stenotopy/eurytopy, and degree of abundance/rarity (Fig. 5).

*Simulating species occurrences*

From a stratigraphic column and a suite of species, fossil occurrences can be generated (Holland, 1995). Starting at the base of the column and proceeding upward at a specified sampling interval, the elevation or water depth recorded in the stratigraphic column is obtained, along with the age of that horizon. For every species extant at that time, its probability of occurrence is calculated from its response curve (i.e., PE, ET, PA) and the elevation or water depth for that horizon. For nonmarine species, the probability of occurrence is also based on whether that horizon is a channel or floodplain deposit, plus the affinity value for the species. The probability of occurrence can also be modified based on the concentration of fossils at that horizon (Nawrot et al., 2018).

After the probability of occurrence is obtained, a random number from a uniform distribution on {0,

1} is generated. If the random number is less than the probability of occurrence for a species, the species is recorded as occurring at that horizon. This procedure continues for every species extant at that horizon, and subsequently for every other sampling horizon. The result is a list of every species occurring at every horizon.

From these occurrences, the first (lowest, FAD) and last (highest, LAD) occurrence of every species can be determined. From the FADs, range offset can be calculated as the difference in age between the first occurrence and the time of origination. Range offset can be similarly calculated for LADs and the time of extinction.

## CONTROLS ON THE STRATIGRAPHIC DISTRIBUTION OF FOSSIL OCCURRENCES

Intuition, simple reasoning, and stratigraphic models have established the principal controls on the occurrence of marine and nonmarine fossils. These establish the basis for our understanding of first and last occurrences as well as range offset (Jaanusson, 1976; Signor & Lipps, 1982; Holland & Patzkowsky, 1999, 2002; Holland, 2022a). Seven main sets of factors are the dominant controls on fossil occurrences.

*Origination and extinction*

In a perfect world, a species would be expected to be preserved everywhere during the time it was extant and only when it was extant (i.e., no reworking). As such, the ultimate controls on first and last occurrences are the times of origination and extinction. In such a world, diachrony and range offset would be zero. Although this is clearly unrealistic, some studies tacitly assume it to be true, such as when last occurrences are taken to indicate the time of extinction. A principal effect of the remaining six factors is that first and last occurrences will rarely coincide with times of origination and extinction. As such, diachrony and range offset are rarely zero.

*Unconformities*

Unconformities intuitively truncate fossil ranges, generating clusters of first and last occurrences (Bambach & Gilinsky, 1988). For example, any species that became

extinct while an unconformity was being developed at some location cannot occur higher than that unconformity, barring reworking. Similarly, species that originated or emigrated into a sedimentary basin as an unconformity was forming at some location cannot occur below that surface. Clusters of first and last occurrences of species at unconformities are common, so much so that they have been used as evidence of unconformities in some biostratigraphic methods such as graphic correlation (Shaw, 1964).

*Sedimentation rate*

Variations in sedimentation rate can also cause first and last occurrences to be stratigraphically concentrated where sediment accumulation rates are slower (e.g., at horizons of stratigraphic condensation; Hohman, 2021). Conversely, first and last occurrences are expected to be more stratigraphically dispersed where sediment accumulation rates are higher than average. The amount of concentration or dispersal of first and last occurrences should be proportional to the difference in sediment accumulation rates. Clustering of first and last occurrences at condensed sections is commonly reported in the biostratigraphic literature (e.g., Armentrout & Clement, 1991).

*Biomes and provinces*

Fossil occurrences at any location are controlled by the occurrence of species within large-scale biogeographic units (biomes and provinces). These partly reflect ecological controls on species distribution, such as temperature and moisture for biomes, and temperature and carbonate-siliciclastic preferences for provinces. They also reflect limitations on species dispersal caused by species characteristics, environmental boundaries, or simply distance. The geographic boundaries of biomes and provinces can change over geological time, changing where and when species occur. As a result, regional first or last occurrences can be controlled by these biogeographic shifts, such that the regional last occurrence of a species may predate its global last occurrence.

Changes in the distribution of water masses, for example, play an important role in the diachrony of marine plankton (e.g., Spencer-Cervato et al., 1994; Westermann, 2001; Lam et al., 2022) as well as benthic marine biotas (e.g., Patzkowsky & Holland, 1993). On land, temperature and moisture are the dominant factors, and large-scale biogeographic shifts are possible on relatively short time scales, such as during episodes of climate change (10's k.y.; Jackson & Overpeck, 2000). The geographic expansion of a species early in its history and its contraction late in its history is likely a principal cause of the changing frequency or occupancy of a species over its history (Foote, 2007b; Liow & Stenseth, 2007).

*Sampling intensity and probability of occurrence*

Sampling intensity coupled with the probability of occurrence of a species also intuitively control the occurrence of fossils, their first and last occurrences, and apparent biodiversity (Sheehan et al., 1991; Harper et al., 2019; Capel et al., 2022). Because most species have a probability of occurrence at any horizon that is less than one, and because sampling effort is limited, a species is unlikely to be preserved continuously between its time of origination and extinction, or between its invasion and extirpation in a sedimentary basin (Strauss & Sadler, 1989). This not only creates gaps in the occurrence of species, but also causes last occurrences to predate times of extinction and first occurrences to follow times of origination (Paul, 1982; McKinney, 1986). The magnitude of this mismatch is directly tied to a species' intrinsic abundance (probability of occurrence) and a paleontologist's sampling intensity (Paul, 1982; Signor & Lipps, 1982; Paul, 2005). Increased sampling intensity can decrease this mismatch, but the abundance of a species ultimately limits how continuously it may be encountered within its range. The probability of occurrence varies by orders of magnitude among taxa, reflecting not only their ecology but also their taphonomy (Holland et al., 2001; Regan et al., 2022).

Recognition of this reciprocal relationship between species abundance and sampling intensity came to the forefront during early studies of the K-Pg mass extinction, when paleontologists noted that last occurrences in boundary sections did not all cluster at the mass-extinction horizon (Signor & Lipps, 1982). Last occurrences were said to be "backwardly smeared" below that horizon (Foote, 2007a), and this pattern became widely known as the Signor-Lipps Effect. First occurrences can show the opposite pattern of forward (upward) smearing (Jaanusson, 1976), now called the Jaanusson Effect.

The reciprocal relationship between species abundance and sampling intensity is one source of differing estimates of the age of last occurrences (or first occurrences), called diachrony (Shaw, 1964). Similarly, it is also one source of range offset, the difference in age between first occurrences and time of origination, and last occurrences and times of extinction (Holland & Patzkowsky, 2002).

Bioclastic accumulations (shell/bone beds) are horizons where fossils are more abundant than in surrounding strata (Kidwell, 1984, 1986, 1991a, b; Kidwell & Bosence, 1991; Tomašových et al., 2006). These can create clusters of first and last occurrences, as well as favor the occurrence of normally rare species (Crampton et al., 2006; Egenhoff & Maletz, 2007; Dominici & Zuschin, 2016; Nawrot et al., 2018; Fürsich et al., 2021). They do so by raising the probability of occurrence of species, such that typically uncommon species have their first occurrences pulled downward to the bioclastic accumulation, with their last occurrences pulled upwards to the bioclastic accumulation. For rare species, this boost to their probability of occurrence may cause the shell/bone bed to mark their only occurrence, such that bioclastic accumulations are expected to contain an elevated number of singleton species. This is also true for Konservat-Lagerstätten, where exceptional preservation may provide the only occurrence of some species (Allison, 1988; Briggs, 2014). Through taphonomic feedback, where the accumulation of shells promotes the colonization of species that prefer hard substrates (Kidwell & Jablonski, 1983), shell beds can raise the probability of preservation of hardparts through the buffering effects of shells (Tomašových & Schlögl, 2008), and they can also selectively raise the probability of preservation of certain species (e.g., Fürsich et al., 1991). Many types of bioclastic accumulations occur in specific

sequence-stratigraphic settings, including marine onlap, downlap, and toplap surfaces (Kidwell, 1991a; Abbott, 1997; Kidwell & Holland, 2002; Fürsich et al., 2016; Garciá-Ramos & Zuschin, 2019; Rodriguez et al., 2022).

*Ecology, taphonomy, and facies*

The distribution of fossil occurrences is strongly governed by facies coupled with ecological and taphonomic controls on the probability of occurrence of species. For marine species, their ecology is dominantly tied to environmental gradients correlated with water depth and secondarily to other factors such as substrate consistency, disturbance, etc. (see review in Patzkowsky & Holland, 2012, also Brown & Larina, 2019). This correlation takes on special significance because water depth changes systematically and predictably with sequence-stratigraphic architecture, discussed at length below. As a result, the probability of occurrence of species also varies systematically and predictably. The same is true for nonmarine species relative to elevation, where it is the correlation of temperature, moisture, and stream gradients with elevation that drives species distributions (see review in Holland & Loughney, 2021). Correlations of species' taphonomy with water depth or elevation can also contribute to these relationships.

These relationships can drive a variety of patterns. For example, the species composition of communities will gradually change where facies change gradually, such as in intervals of net upward deepening or shallowing (Fig. 6; Holland, 1995). Abrupt facies changes (e.g., change across a surface) similarly drive abrupt changes in community composition as well as generate clusters of first and last occurrences. In nonmarine settings, progressive upsection change in the ratio of channel to floodplain deposits will similarly drive changes in community composition, owing to the taphonomic differences of the two facies (Behrensmeyer & Hook, 1992; Holland & Loughney, 2021). Repeated cycles of facies change create recurrent biotas, communities and species that repeatedly occur and disappear from the stratigraphic record (Fig. 6; Brett, 1995; Holland, 1995; Brett et al., 2016). Longer-term facies change unrelated to water depth can also produce recurrent faunas, such as carbonate-siliciclastic or temperature reversals (Patzkowsky & Holland, 1993) and cyclic shifts in water masses (e.g., Goldman et al., 1999; Sheets et al., 2016).

Because patterns of facies change are often complicated, and because biotas are often more sensitive indicators of environments than are lithofacies (Brett, 1998; Holland et al., 2001), the connection between patterns of species distribution and stratigraphic architecture may not be immediately apparent. Moreover, this is exacerbated if paleontologists do not have the background to recognize sedimentological facies. As a result, these effects on the occurrence of fossils are likely underreported and substantially underappreciated (e.g., Harper et al., 2014; Tobin, 2017).

*Post-depositional processes*

First and last occurrences can be affected by post-depositional movement of fossil remains through burrowing, erosional reworking, burrowing, downhole caving. Burrowing may move fossils upwards or downwards, typically on the range 10-20 cm, except
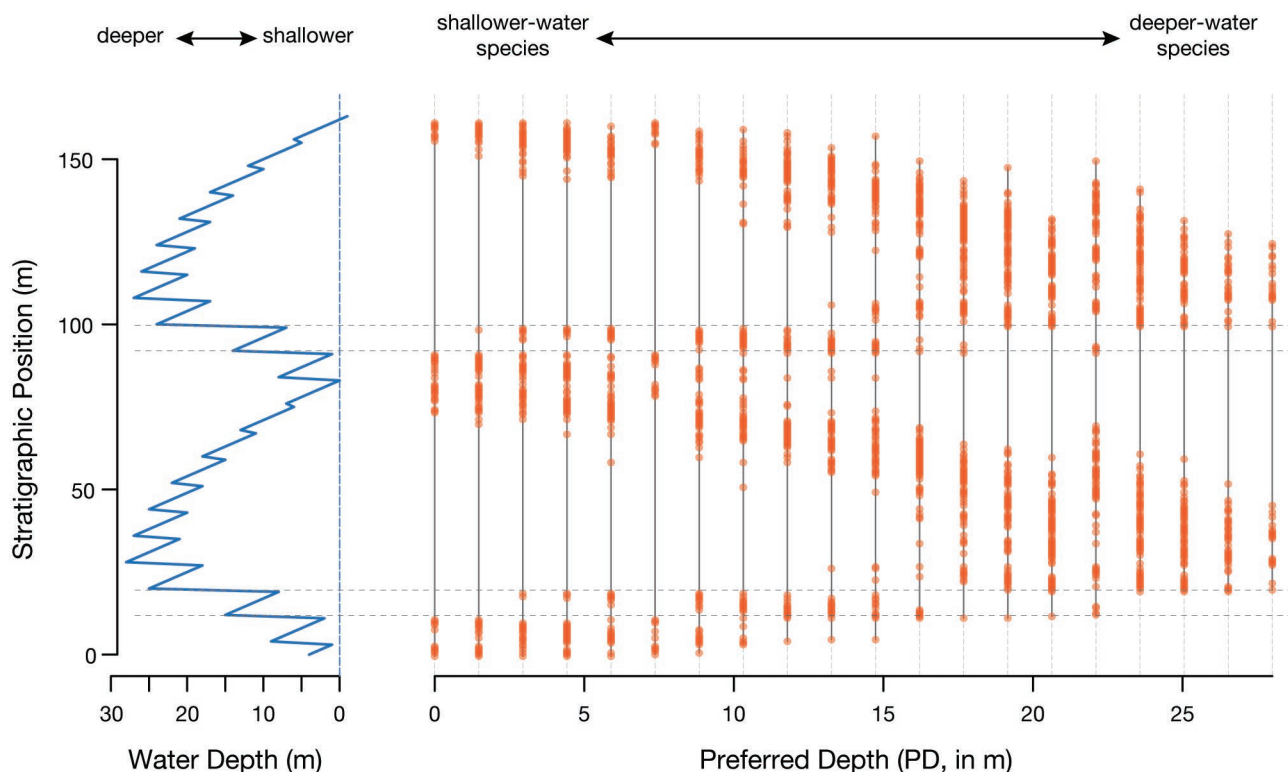


Fig. 6 - A simple model of fossil occurrences showing the interplay between changing water depths and the preferred depth (PD) of species. Note the upward changes in the occurrence of relatively shallow-water and deeper-water species. Repeated changes in water depth give rise to recurrent faunas. Abrupt changes in water depth (dashed lines) generate clusters of local last occurrences of species.

for deep burrows such as those of calianassid shrimp, which may be as deep as 2 m (Kidwell & Flessa, 1996). Erosional reworking causes fossils to be redeposited in beds higher than those in which they were originally buried. Such reworking will tend to have a greater effect on last occurrences than first occurrences, since only one occurrence of a fossil needs to be moved upwards to raise the last occurrence, whereas shifting the position of the first occurrence requires all occurrences of a species at a particular stratigraphic level to be displaced upwards. In drilling operations, caving of the sidewall can cause fossils to be transported downward and therefore has a much greater effect on first occurrences than last occurrences. This problem is so pervasive that industry biostratigraphers commonly focus only on the highest occurrences of species (e.g., Boomer et al., 2021).

*Implications*

As a result of all these factors, it becomes apparent that fossil occurrences are strongly controlled by stratigraphic architecture, including their first and last occurrences. Consequently, diachrony and range offset will rarely be zero. For diachrony and range offset to be zero, an imposing set of requirements must be true: there are no unconformities, no condensed sections, the probability of occurrence of species or the sampling intensity must be quite high, species ecology or preservation has no relationship with water depth (or elevation, for nonmarine taxa) or water depth/elevation does not vary through the stratigraphic column, bioclastic accumulations are not present, and post-depositional movement of fossils is absent. As such, it can be generally concluded that first occurrences are generally not times of origination, and last occurrences seldom record the time of extinction.

## SIMULATIONS OF THREE ESSENTIAL STRATIGRAPHIC CONTEXTS

Forward modeling demonstrates how these factors come together, and field studies bear out the predictions of these models. These models also contrast how marine and nonmarine systems differentially express the same underlying geological drivers. Although an extraordinarily wide range of simulations of the fossil record under different stratigraphic scenarios could be generated, including ones that attempt to mimic the stratigraphy of specific field examples, such an approach is a difficult way to gain intuition for the principles controlling fossil occurrences. Moreover, simulations typically capture three simple cases that can be used to understand how the fossil record will be shaped under a wide range of circumstances (Holland, 2022a). These include: 1) slow relative rise in sea level (e.g., HST, LST, normal regression, LAST), 2) rapid relative rise in sea level (TST, flooding surfaces, HAST), and 3) relative fall in sea level (FSST, surfaces of forced regression, subaerial unconformities). These cases are encompassed in two model runs, one of Sedflux (Fig. 3) and one of strataR (Fig. 4). From these, three representative columns are extracted from the Sedflux run (Figs 7-9) and two from the strataR run (Figs 10, 11). Field evidence that bears on the predictions of these models is presented following the discussion of these simulations.

*Slow relative rise in sea level*

Under a slow relative rise in sea level, where the rate of sedimentation exceeds the rate of accommodation at the shore, the coastal plain progrades as the shoreline regresses (sr intervals in Figs 3, 4). In nonmarine areas, this will be recorded as a simple upward increase in elevation caused
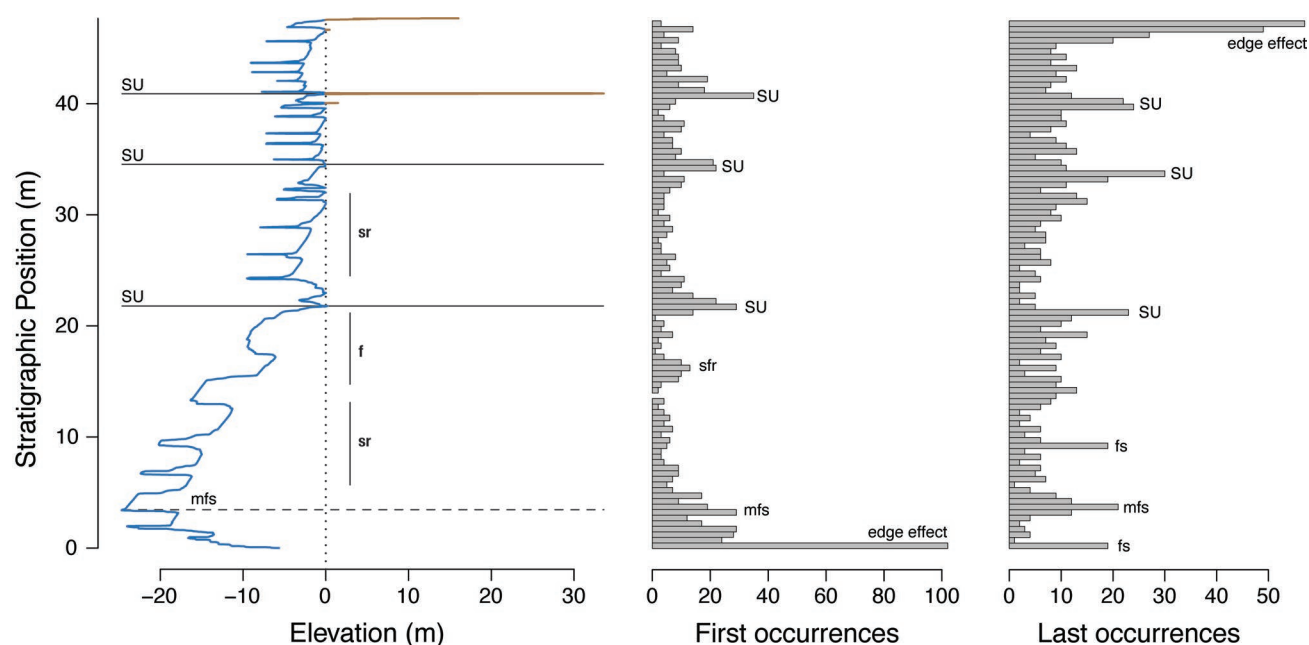


Fig. 7 - Stratigraphic column from an updip position in the Sedflux model run shown in Fig. 3, showing changes in elevation and numbers of first and last occurrences of marine species. Strata in this updip setting are dominated by highstand systems tracts, particularly so in the upper half of the column. In this updip setting, clusters of first and last occurrences form primarily at subaerial unconformities (SU). Lower in the section, they also form at surfaces of forced regression (sfr), maximum flooding surfaces (mfs), and other major flooding surfaces (fs). Clusters of first occurrences at the base of the column and last occurrences at the top of the column are edge effects of the beginning and end of the simulation. Representative intervals of slow relative rise in sea level (sr) and relative fall in sea level (f) are indicated.
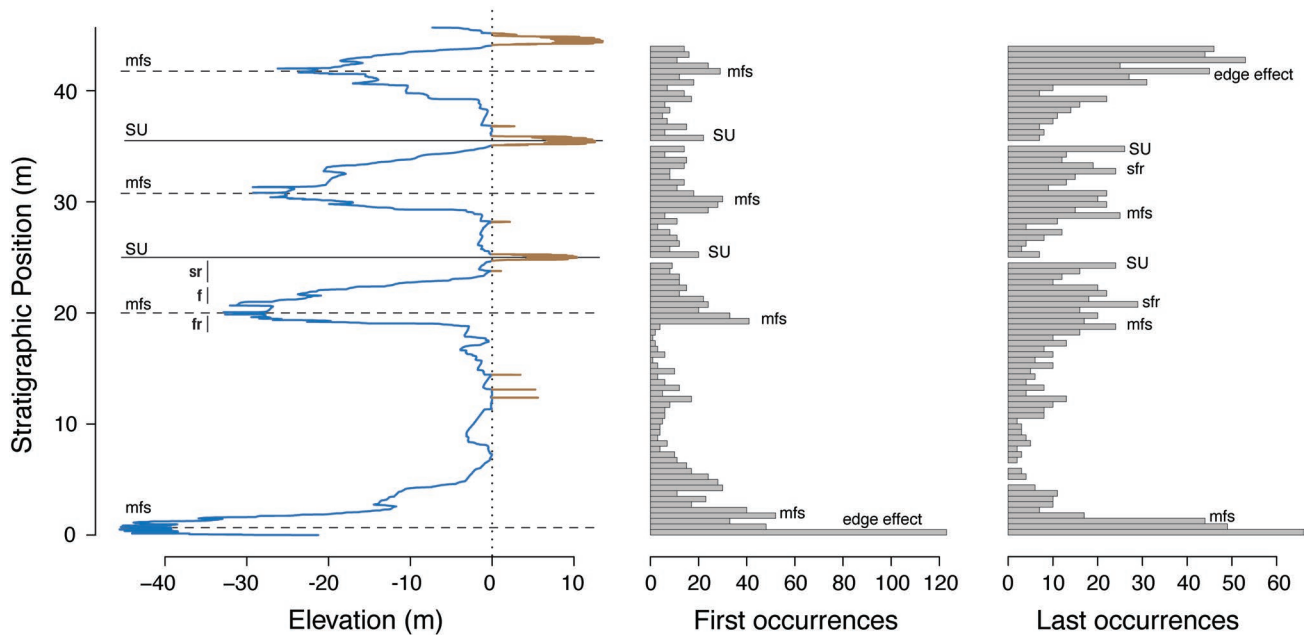
Fig. 8 - Stratigraphic column from a mid-dip position in the Sedflux model run shown in Fig. 3, showing changes in elevation and numbers of first and last occurrences of marine species. Strata in this column are dominated by those of the transgressive and falling-stage systems tracts, although highstand and lowstand systems tracts are also present. Blue portions of the elevation curve correspond to marine conditions; brown portions represent nonmarine conditions. In this mid-dip setting, clusters of first and last occurrences form at a variety of surfaces, including subaerial unconformities (SU), surfaces of forced regression (sfr), and maximum flooding surfaces (mfs). Clusters of first occurrences at the base of the column and last occurrences at the top of the column are edge effects of the beginning and end of the simulation. Representative intervals corresponding to slow relative rise in sea level (sr), fast relative rise (fr), and relative fall in sea level (f) are indicated.

by lengthening of fluvial equilibrium profile (Holbrook et al., 2006; Holland & Loughney, 2021). Because the low angle of the shoreline trajectory allows much of the sediment supplied to the basin to escape the coastal plain to the marine realm, nonmarine rates of aggradation tend to be low and form a low-accommodation systems tract (Fig. 4; Martinsen et al., 1999; Holland, 2022a).

In marine areas, a slow relative rise in sea level will produce a simple upward shallowing if no higher order (i.e., shorter duration) cyclicity is present, such as in the main body of most parasequences (Van Wagoner et al., 1990). Where higher-order cyclicity is present, a slow relative rise in sea level produces a progradational set of parasequences or high-frequency sequences (Figs 1, 3; Van Wagoner et al., 1990). Such conditions characterize the LST and HST.

A slow relative rise in sea level therefore generates progressive community change at any given location from lower-elevation to higher-elevation biotas in nonmarine systems, and a change from deeper-water biotas to shallower-water biotas in marine systems (Fig. 6). Unless species have nearly identical species-response curves (PE and ET especially) such that their probabilities of occurrence are highly correlated, the upwards turnover in species composition will be gradual and lack abrupt changes in community composition. Moreover, if diversity structure (richness, evenness, etc.) varied along the ecological gradient, it will also change stratigraphically in a predictable way.

This gradual turnover produces a steady low level of first and last occurrences in marine and nonmarine systems (sr intervals in Figs 7, 9, 10). Increasing the probability

of occurrence of species (e.g., by increasing PA or ET) or increasing sampling effort will raise this background level of first and last occurrences. The numbers of first and last occurrences through a stratigraphic column can also reflect diversity gradients tied to elevation or water depth. For example, if diversity increases from offshore to onshore, upward shallowing will be accompanied by an upwards increase in the number of first occurrences.

Although marine bioclastic accumulations tied to sequence-stratigraphic architecture are not expected in a column that records a slow relative rise in sea level (Kidwell, 1991a), other types of bioclastic accumulations (e.g., storm beds) could generate smaller clusters of first and last occurrences. In nonmarine areas, differences in preservation between channel and floodplain deposits may also cause clusters of first and last occurrences. For example, the upward decrease in aggradation rate as the coastal plain progrades is expected to favor channel-belt deposits over floodplain deposits (Bridge & Leeder, 1979). As a result, this would produce upward increases in the numbers of first and last occurrences of species preferentially preserved in channels. Similarly, this would produce upward decreases of first and last occurrences of species favored in floodplain deposits. Likewise, autogenic clustering of channel belts could also generate clusters of first and last occurrences.

One special case of a slow relative rise in sea level would be expected to produce clusters of first and last occurrences, and intuitively so. Where progradation causes nonmarine deposits to overlie marine deposits, forming a within-trend normal regressive surface (Catuneanu, 2006), a cluster of last occurrences of marine species and first
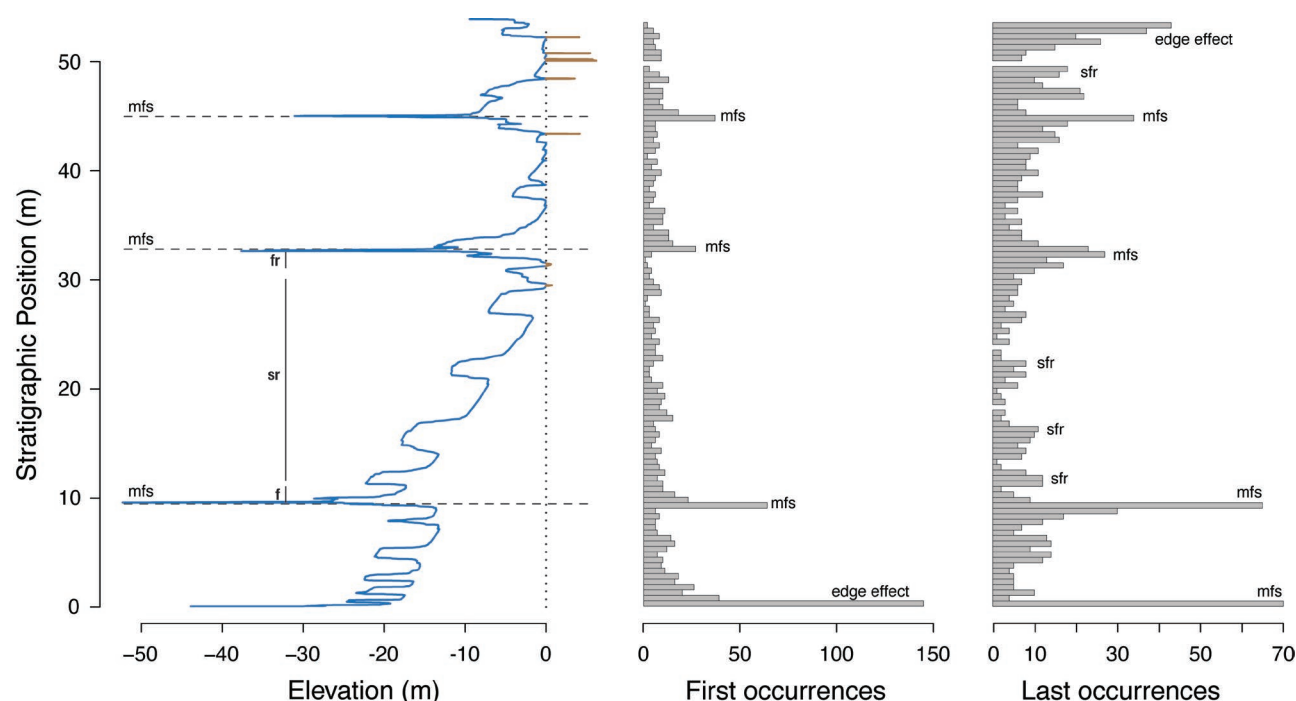
Fig. 9 - Stratigraphic column from a downdip position in the Sedflux model run shown in Fig. 3, showing changes in elevation and numbers of first and last occurrences of marine species. Strata in this column are dominated by those of lowstand systems tracts, although other systems tracts are also present. Blue portions of the elevation curve correspond to marine conditions; brown portions represent nonmarine conditions. In this downdip setting, clusters of first and last occurrences occur mainly at maximum flooding surfaces (mfs) and surfaces of forced regression (sfr). Clusters of first occurrences at the base of the column and last occurrences at the top of the column are edge effects of the beginning and end of the simulation. Representative intervals corresponding to slow relative rise in sea level (sr), fast relative rise (fr), and relative fall in sea level (f) are indicated.

occurrences of nonmarine species will result. The marine cluster will be dominated by shallow-water species as well as eurytopes, and the nonmarine cluster will be dominated by low-elevation species plus eurytopes. Low values of peak abundance and low sampling intensities will reduce the magnitude of these clusters and cause them to be more diffuse, much as the Signor-Lipps effects blur the record of mass extinctions. These effects of peak abundance and sampling intensity apply for any cluster of first or last occurrences, regardless of how they are generated.

*Fast relative rise in sea level*

During a fast relative rise in sea level, where the rate of sedimentation at the shore is less than the rate of accommodation, the coastal plain retreats as the shore transgresses (Figs 1, 4). Because the shoreline trajectory is landwards and upwards (Neal & Abreu, 2009), substantial aggradation of the coastal plain results (Holland & Loughney, 2021), forming a high-accommodation systems tract (fr intervals in Fig. 4). If the base of this HAST is sharp, it is known as an expansion surface (Martinsen et al., 1999); otherwise, it is known as an expansion zone.

In marine areas, a fast relative rise in sea level will generate an upward-deepening trend if no higher-order cyclicity is present. Where higher-order cyclicity is present, it will produce a retrogradational set of parasequences or high-frequency sequences as found in the TST (Fig. 3; Van Wagoner et al., 1990). In siliciclastic systems, trapping of sediment on the coastal plain during a fast relative rise in sea level commonly starves the

marine shelf of sediment (Holland, 2020), creating a hiatal downlap surface instead of a deepening-upward interval (e.g., red surfaces in Fig. 4; Van Wagoner et al., 1990). Flooding surfaces that bound parasequences are examples of these hiatal surfaces. Erosion during transgressive shoreface retreat can likewise create a hiatal surface called a transgressive ravinement surface (Swift, 1968; Cattaneo & Steel, 2003; Catuneanu, 2006; Zecchin et al., 2019). Carbonate systems also commonly experience sediment starvation during a fast relative rise in sea level that produces a flooding surface, although the mechanisms of this starvation remain unclear (Read et al., 1986; Tipper, 1997).

The formation of hiatal flooding surfaces in marine systems contrasts sharply with nonmarine systems, which undergo significant aggradation during rapid relative rise in sea level, recording an upward decrease in elevation (Holland, 2022a). As a result, patterns of fossil occurrences in nonmarine and marine systems differ substantially under conditions of fast relative rise in sea level, far more so than in the case of a slow relative rise.

In nonmarine areas, a fast relative rise in sea level will generate progressive community change passing upwards from higher-elevation communities to lower-elevation (i.e., closer to shore) communities as the shoreline transgresses. Because aggradation rates are rapid within the HAST, elevated numbers of first and last occurrences are produced over a broad interval corresponding to the expansion zone (the vertical transition from a LAST to

a HAST), rather than limited to a surface (Figs 10, 11). First occurrences in these zones will be dominated by relatively lower-elevation species, and last occurrences by relatively higher-elevation species. Like the case of a slow relative rise, the numbers of first and last occurrences will be controlled by the probability of occurrence of species, sampling effort, and elevation-correlated diversity gradients. The numbers of first and last occurrence are also controlled by the rate of transgression, with greater rates of transgression increasing the pace of community change, thereby raising the numbers of first and last occurrences. For example, compare the substantial numbers of first and last occurrences related to the major transgression accompanying the initiation of a foreland basin (meters 50-100 in Fig. 10) to the greatly reduced numbers of first occurrences higher in the column corresponding to smaller eustatic changes (e.g., meters 400 and 700 in Fig. 10). Finally, the pace of community change and numbers of first and last occurrences will also be controlled by background rates of accommodation. For example, greater numbers of first and last occurrences are produced where background rates of accommodation are low (e.g., meters 900, 1100, and 1250 in Fig. 10) than when background rates are high (e.g., meters 400 and 700 in Fig. 10).

In contrast, a fast relative rise in marine systems will create distinct horizons of abrupt community change at flooding surfaces, accompanied by elevated numbers of first and last occurrences (fr intervals Figs 8, 9). The magnitude of community change and the numbers of first and last occurrence will directly reflect the amount of water depth change across the flooding surface. For example, flooding surfaces in the TST generally encompass much greater change in water depth than the comparatively weak flooding surfaces of the LST and HST; consequently, flooding surfaces in the TST often display dramatic abrupt changes in communities as well as substantial numbers of first and last occurrences. Because the TST typically contains a series of major flooding surfaces, starting with the maximum regressive surface and culminating with the maximum flooding surface, the TST can contain multiple surfaces of abrupt community change.

Because marine areas are commonly starved of sediment during the TST, stratigraphic condensation can greatly compress the thickness of the TST (Figs 8, 9), further elevating the numbers of first and last occurrences. Although bioclastic horizons are not included in models like Sedflux, sediment starvation (and sediment bypass) in the TST and at flooding surfaces can generate bioclastic horizons (Kidwell, 1991a). These raise the probability of occurrence of species, allowing normally rare species to occur and raising the numbers of first and last occurrence. In addition, because such bioclastic horizons provide substrates for species that prefer hard substrates, they allow for the development of communities not found elsewhere (Kidwell & Jablonski, 1983).
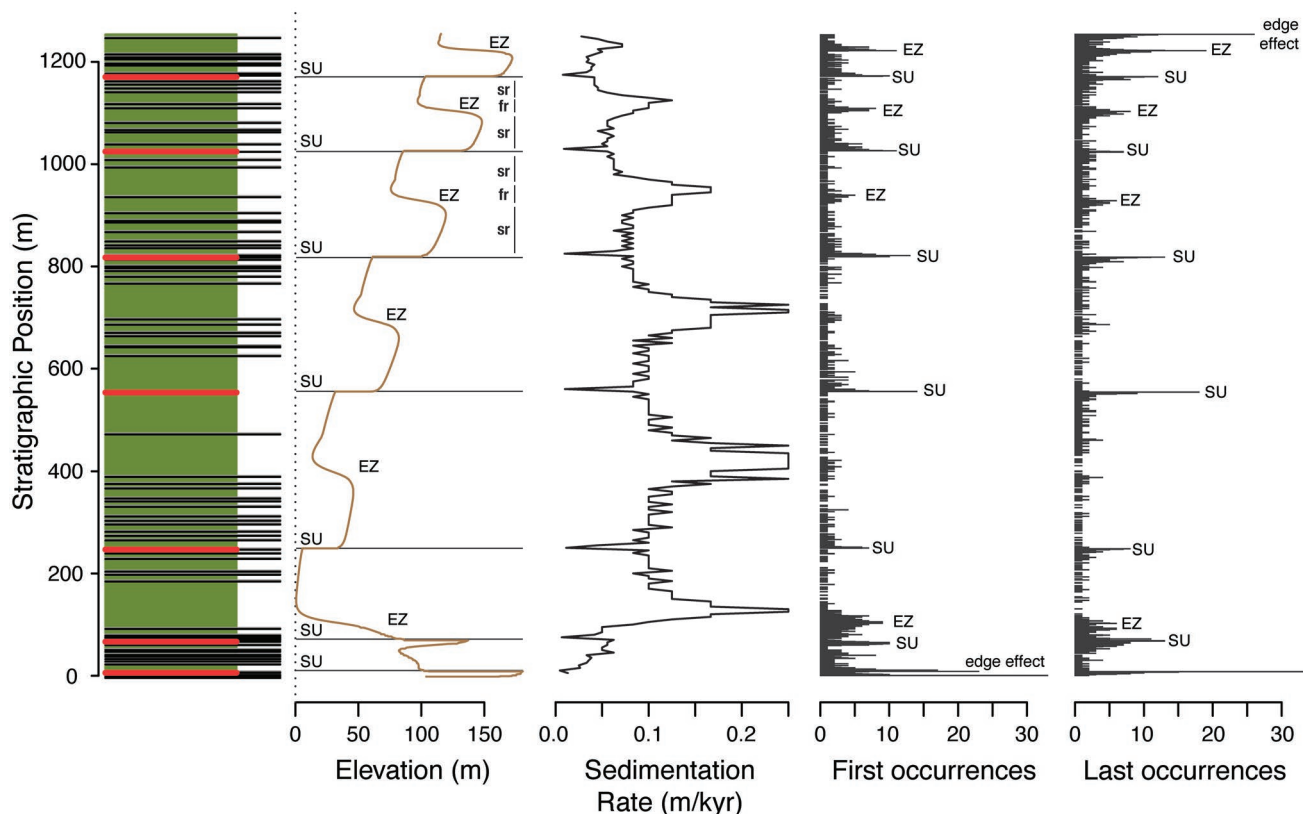


Fig. 10 - Stratigraphic column from an updip position in the strataR model run shown in Fig. 4, showing elevation, sedimentation rate, and numbers of first and last occurrences. In the stratigraphic column, green corresponds to floodplain facies, black to fluvial channels, and red to hiatal surfaces. Throughout the column, clusters of first and last occurrences of nonmarine species occur at subaerial unconformities (SU) and expansion zones (EZ; terminology of Martinsen et al., 1999). Clusters of first occurrences at the base of the column and last occurrences at the top of the column are edge effects of the beginning and end of the simulation. Representative intervals corresponding to slow relative rise and (sr) fast relative rise (fr) in sea level are indicated.

*Relative fall in sea level*

When sea level undergoes a relative fall, the shore is forced to move seawards and downwards. In most cases, this forces rivers to incise at the terminal highstand shoreline. Over time, the incision widens, propagates seawards with the regressing shore, and advances landward through headward erosion of knickpoints in rivers courses (white surfaces in Fig. 4, top; Blum & Törnqvist, 2002; Martin et al., 2011). Areas between rivers become perched topographically above these deepening valleys. These interfluves are thus starved of sediment and become areas in which well-drained mature paleosols tend to form (white surfaces in Fig. 4, bottom; Kraus, 1999; McCarthy & Plint, 2013). Terraces that form adjacent to the incising channel systems also become sites of paleosol formation (Blum et al., 2013). Although some sediment accumulates temporarily within the river during incision, most is flushed seaward into the marine system as the river continues to incise into its own deposits (Blum et al., 2013). This combination of incision along rivers and paleosol development on interfluves constitutes the subaerial unconformity. Note that although nonmarine sequence-stratigraphic models typically place the sequence boundary at the base of the LAST (e.g., Martinsen et al., 1999; Catuneanu, 2006), modeling predicts that the subaerial unconformity will commonly lie within the LAST, except where the unconformity overlies marine deposits (Fig. 4).

In marine areas, a relative fall in sea level generates rapid to abrupt upward shallowing (Figs 1, 3), where the regression of the shore caused by sea-level fall is amplified by the increased delivery of sediment to the shelf. On wave-dominated shelves, the seaward- and downward-translating marine profile triggers erosion in the lower shoreface, forming a surface of forced regression at which offshore deposits are abruptly overlain by upper shoreface deposits (Hunt & Tucker, 1992; Catuneanu, 2006). Where higher-order cyclicity is present, a series of seaward and downward-stepping surfaces of forced regression will form, typically separated by normal regressive shallow-

upward deposits. These constitute the falling-stage systems tract (FSST).

Although models like strataR are currently not able to simulate sediment deposition within progressively deepening valleys, conceptual and physical models suggest that these early valley fills will be floored by erosive contacts (Martin et al., 2011; Blum et al., 2013). Moreover, falling sea level and forced regression of the shoreline implies that the elevation recorded in these deposits will be greater than those of the preceding highstand. Because accommodation rates are low, the deposits should have the channel-dominated characteristics of a LAST (Blum et al., 2013). Collectively, these suggest that these early valley fill deposits will record an abrupt transition to higher-elevation communities dominated by species likely to be preserved in channels.

In the absence of such early valley fill deposits, the subaerial unconformity is expected to display abrupt community change owing to the hiatus (Figs 10, 11). In addition, model results suggest that the deposits above the subaerial unconformity will record higher-elevation habitats than deposits below the unconformity, and this will also add to the change in community composition across the surface (Figs 10, 11). As a result of the hiatus and the elevation change, elevated numbers of first and last occurrences are expected at subaerial unconformities. The number of first and last occurrences will increase with species origination and extinction rates, the duration of the hiatus, and the amount of elevation change across the surface. Where the subaerial unconformity overlies marine deposits, there will intuitively be a cluster of nonmarine first occurrences (Fig. 11) as well as a cluster of marine last occurrences.

It is important to recognize that the hiatus in the valley and the hiatus on the interfluve span different intervals of time. Erosion in the valley creates a degradational vacuity (Wheeler, 1964) that removes older deposits, but these remain intact on the interfluve. Conversely, sedimentation resumes in the valley immediately after sea level begins to rise, whereas sedimentation cannot resume on the
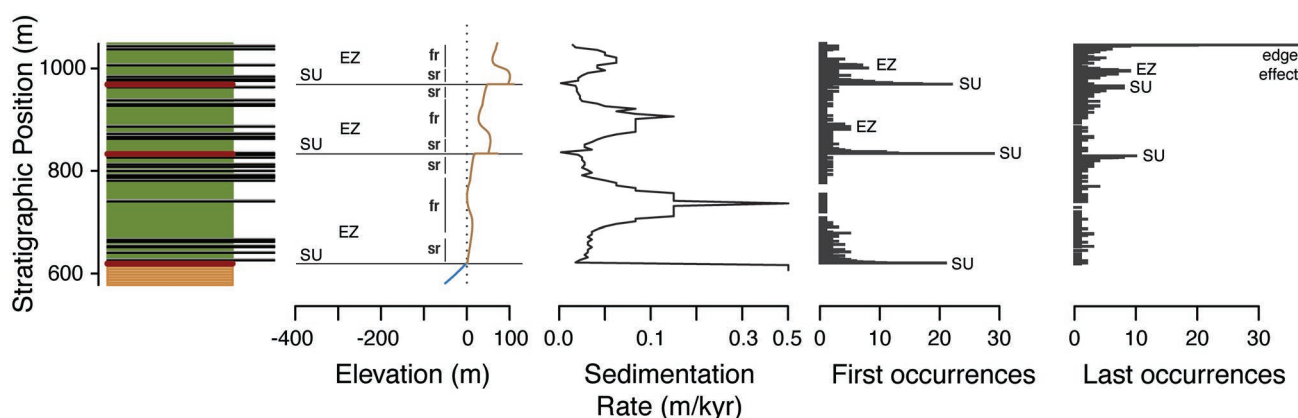


Fig. 11 - Stratigraphic column from a downdip position in the strataR model run shown in Fig. 4, showing elevation, sedimentation rate, and numbers of first and last occurrences. In the stratigraphic column, brown corresponds to marine facies, green to floodplain facies, black to fluvial channels, and red to hiatal surfaces. Throughout the column, clusters of first and last occurrences of nonmarine species occur at subaerial unconformities (SU) and expansion zones (EZ; terminology of Martinsen et al., 1999). The cluster of first occurrences at the base of nonmarine interval occurs at the within-trend normal regressive surface (Catuneanu, 2006) and intuitively marks the first interval in which nonmarine species could occur, barring out-of-habitat transport into marine areas, which can be important in areas with sediment gravity flows (Dominici & Zuschin, 2005). Representative intervals corresponding to slow relative rise and (sr) fast relative rise (fr) in sea level are indicated.

interfluve until after the valleys have filled. As such, the hiatus in the valley spans an older but partly overlapping interval of time compared with the interfluve.

In marine areas where a surface of forced regression does not form (e.g., on fluvially or tidally dominated shelves, and possibly some carbonate platforms), the FSST will be characterized by rapid but gradational upward change from relatively deeper-water communities to relatively shallower-water communities. Clusters or zones of elevated first and last occurrences could be expected where the shallowing is particularly rapid (f intervals in Figs 7, 8). Where a surface of forced regression does form, community change will reflect abrupt shallowing, producing a cluster of first occurrences of shallower-water species and a cluster of last occurrences of deeper-water species.

Owing to sediment bypass at surfaces of forced regression, bioclastic accumulations may be expected (Kidwell, 1991a). Like those that form in intervals of rapid relative rise in sea level, these favor the occurrence of normally rare species, as well as species that prefer shelly substrates, and therefore can increase the numbers of first and last occurrences.

*Field evidence versus these model predictions*

For marine setting, numerous field studies support these model predictions. For example, progressive upsection change in benthic invertebrate communities has long been reported and recognized as reflecting changes in water depth and correlated environmental variables (e.g., Ziegler, 1965; Ludvigsen, 1978; Boucot, 1981; Brett, 1998; Benvenuti et al., 2007; Balseiro et al., 2011; Olóriz et al., 2012; Slattery et al., 2018, and many others). This pattern of depth-correlated community change is so pervasive that it is also visible at higher taxonomic levels (Mitchell et al., 2014; Zuschin et al., 2017). Marine vertebrates similarly show a relationship to water depth, likely because their ecology was tied to benthic habitats or because they tended to inhabit certain water depths (Peters et al., 2009; McMullen et al., 2014; Dominici et al., 2018a, 2018b). Depth-correlated taphonomic processes also contribute to these patterns (Brett & Baird, 1986; Tomašových & Zuschin, 2009; Scarponi et al., 2013, 2017; Tomašových et al., 2017; Ritter et al., 2019).

Ordination is now widely seen as a powerful tool for detecting and describing such community change (Clapham, 2011; Huntley, 2011). Comparison of ordination axis scores with sedimentologically defined facies establishes the relationship of community change to changes in water depth and other environmental variables (Patzkowsky & Holland, 2012). Detrended correspondence analysis and nonmetric multidimensional scaling have both proven their utility (e.g., Patzkowsky, 1995; Holland et al., 2001; Scarponi & Kowalewski, 2004; Holland & Patzkowsky, 2007; Tomašových & Siblik, 2007; Zuschin et al., 2011; Ayoub-Hannaa et al., 2013; Amorosi et al., 2014; Dominici & Zuschin, 2016; Danise & Holland, 2017; Rossi et al., 2018; Dominici et al., 2019, 2020). In Quaternary and Holocene deposits, where many species are extant, ordination of fossil communities can be used to place precise estimates of water depth through a stratigraphic column, along with error estimates (Zong & Horton, 1998; Horton et al., 1999; Wittmer et al., 2014).

Field studies have also demonstrated that recurrent faunas arise from repeated and hierarchical sedimentary cycles driven by changes in relative sea level (Miller, 1993; Holland, 1995; Nagy et al., 2001; Hendy & Kamp, 2004, 2007; Zuschin et al., 2017; Abdelhady et al., 2020). The resilience of benthic marine communities in the face of repeated sea-level changes is evidence of long-lasting niche stability of species (Brett & Baird, 1995; Bonelli & Patzkowsky, 2011; Holland & Zaffos, 2011; Kowalewski et al., 2015; Brett et al., 2016). Repeated sedimentary cycles also produces patterns of iterative morphological change within species whose morphology varies clinally with water depth (McGhee et al., 1991; Hannisdal, 2006, 2007; Webber & Hunda, 2007).

In addition, major flooding surfaces commonly display the expected clusters of first and last occurrences. These are well-documented for benthic marine invertebrates (e.g., Dockery, 1986; Sundberg, 1996). Abrupt community changes for benthic marine invertebrates also commonly occur at major flooding surfaces (Abbott & Carter, 1997; Smith et al., 2001, 2006; Botquelen et al., 2006; Rossi et al., 2018). Because nektic species commonly have ecologies that are tied to benthic habitats and communities, and because pelagic species are commonly stratified by water depth, they can also display clusters of first and last occurrences at major flooding surfaces, as well as abrupt changes in community composition. For example, these have been documented for conodonts (Jarochowska et al., 2016), foraminifera (Armentrout, 1987, 1991, 1996; Armentrout & Clement, 1991; Armentrout et al., 1991), graptolites (Goldman et al., 1999; Egenhoff & Maletz, 2007), and ammonites (McGhee et al., 1991; Sandoval et al., 2001).

Clusters of first and last occurrences at unconformities are likewise widely reported from the fossil record, not only for benthic marine species (Gaskell, 1991), but also for pelagic and nektic groups such as foraminifera (Armentrout & Clement, 1991), ammonites (Sandoval et al., 2001), conodonts (Jarochowska et al., 2018), and graptolites (Goldman et al., 1999). Deep-sea unconformities similarly produce clusters of first and last occurrences (MacLeod & Keller, 1991). More broadly, unconformities are widely reported to record abrupt community changes, especially of benthic marine invertebrates (Abbott & Carter, 1997; Dominici & Kowalke, 2007; Hendy & Kamp, 2007; Zuschin et al., 2011; Carlucci & Westrop, 2015).

Although the ability of stratigraphic architecture to generate clusters of last occurrences is well-established, where such clusters are observed in association with mass extinctions, they are commonly taken uncritically as support of a rapid extinction (see reviews in Holland & Patzkowsky, 2015; Holland, 2020). In most cases, these clusters coincide with major flooding surfaces, commonly combined with a subaerial unconformity. Given this association, the most parsimonious explanation is that these clusters are stratigraphically generated, and that the extinction occurred over a longer period than a face-value reading of the fossil record would suggest. Still unresolved is the possibility of common cause (Peters & Foote, 2001), specifically that originations and extinctions might be driven by the same processes that drive relative sea-level change.

Field support for the predictions of modeling in nonmarine systems lags far behind that of marine systems. In part, this reflects the recency of the nonmarine modeling (Holland & Loughney, 2021; Holland, 2022a). Moreover, it reflects the difficulty of gradient analysis in nonmarine systems and the difficulty of demonstrating that ecological gradients are correlated with elevation. In marine systems, facies are commonly correlated with water depth; for example, facies models are commonly illustrated with a cross section or block diagram showing facies variations along an onshore–offshore axis. In contrast, nonmarine facies do not vary strongly with elevation, except for tidal influence on river systems. Without such an external lithofacies-based control, it will be difficult to establish that nonmarine biotas are elevation correlated, even if such correlations are common today (Holland & Loughney, 2021). In addition, although evidence so far is limited, the probabilities of occurrence for nonmarine species may be so low (Regan et al., 2022) that sampling effects dominate, weakening the ability to detect clusters of first and last occurrence. Testing numerical models for nonmarine systems with field data is a promising area for future studies.

RANGE OFFSET

One pattern that becomes clear from these model results is how seldom a first or last occurrence coincides with the time of origination or extinction and that the discrepancy is commonly on the scale of tens to hundreds of thousands of years (Holland & Patzkowsky, 2002). This has long been clear to biostratigraphers but is often lost in paleobiological studies where last occurrences and extinctions are often equated, especially in mass extinction studies (e.g., Harper et al., 2014; Tobin, 2017).

Although range offset and diachrony are related, they have a crucial distinction. Because range offset requires knowing the time of extinction, it can be measured only in simulations. Diachrony, however, can be measured from fossil data as it compares only last occurrences. The hope is that diachrony approximates range offset, although it will generally underestimate range offset by some unknowable amount.

Modeling studies indicate that for marine species, median values of range offset are commonly several hundreds of thousands of years up to a few million years (Holland & Patzkowsky, 2002). Range offset increases with the duration of hiatuses at subaerial unconformities, rapid and large facies change, persistent monotonic trends in water depth, and lower values of depth tolerance and peak abundance of species.

Several studies have measured diachrony, and even for biostratigraphically important taxa such as marine microplankton, values of diachrony are consistent with simulated values of range offset. For example, calcareous nannofossils, diatoms, planktonic foraminifera, and radiolarians from the Neogene have average standard deviations of first and last occurrences ranging from 0.30 m.y. to 0.88 m.y. (Spencer-Cervato et al., 1994). For some species, these standard deviations approach 2.5 m.y., with diachrony greater for cosmopolitan rather than endemic species. Only 42% of first or last occurrences occur at nearly synchronous levels, defined by magnetic reversal events. Even within a single ocean basin, 28 of 39 biostratigraphic events (first or last occurrences) of radiolaria had a minimum diachrony of 0.15 m.y. (Moore et al., 1993). Latitudinal migration, rather than preservation, is commonly attributed as the cause of this diachrony (but see Aubry & Van Couvering, 2005). Some diachrony has been attributed to miscorrelation of magnetic reversals and to the presence of undetected unconformities (Berggren et al., 1995; Aubry et al., 2000; Aubry & Van Couvering, 2005). Even so, not all diachrony of marine microplankton can be dismissed, and similar estimates are widely reported (e.g., Johnson & Nigrini, 1985; Wei, 1993; Schneider et al., 1997; Kučera, 1998; Kučera & Kennett, 2000; Chaisson & D'Hondt, 2000; Raffi, 2002; Sinha & Singh, 2008), but see Belka et al. (1997) for a case where diachrony is apparently minimal. One recent study stated that "diachroneity rules the mid-latitudes" (Lam et al., 2022) and another that "many, if not most species first and last occurrences are at least to some degree diachronous" (Lazarus, 2011).

Estimates of diachrony for macrofossils are less common, but they are again consistent with model-based estimates of range offset. North America mammal species have an average interregional diachrony of 1.4 m.y. (Alroy, 1998). Of Cretaceous ammonoids in western North America, 18% of species have demonstrably diachronous first or last occurrences (Monnet et al., 2015). Ample opportunity remains for documenting diachrony among taxa and understanding its causes. Quantitative biostratigraphic methods such as graphic correlation (e.g., Dowsett, 1989; Wei, 1993; Gouwy et al., 2016), unitary associations (e.g., Monnet et al., 2015), and constrained optimization (e.g., Sadler et al., 2011; Wang et al., 2014) all show promise.

IMPLICATIONS FOR STUDIES OF BIOTIC EVENTS

Stratigraphic architecture is a pervasive control on the fossil record. Any interpretation of the fossil record must explicitly recognize how and to what degree the pattern of fossil occurrences reflects stratigraphic processes as opposed to ones that directly reflect biological processes, such as mass extinction and ecosystem change. To be sure, incorporating the stratigraphic framework into the design and interpretation of a paleobiological study creates complications, but many studies provide successful examples of how this can be done. Here, I highlight four sets of studies that demonstrate the range of solutions.

*Mass extinction*

Mass extinction studies have some of the greatest potential for applying the concepts of stratigraphic paleobiology (Holland & Patzkowsky, 2015; Holland, 2020). For example, the Late Ordovician mass extinction is commonly regarded as a two-pulsed extinction based on a face-value reading of last occurrences (Sheehan, 2001; Harper et al., 2014), but the pattern of fossil occurrences is also consistent with a single long period of elevated

extinction, with two stratigraphically generated clusters of last occurrences (Holland & Patzkowsky, 2015; Zimmt et al., 2021).

The earlier of these clusters principally includes nektic and planktic species, especially graptolites, and it coincides with an abrupt decrease in water depth caused by glacioeustatic fall (Harper et al., 2014). This is significant because graptolites were stratified by water depth (Mitchell et al., 2007; Sheets et al., 2016), raising the prospect that the abrupt disappearance of graptolites seen at many localities is the result of their local facies-related disappearance caused by abrupt shallowing. This interpretation is supported by the presence in younger strata at some localities of many of graptolite species thought to have gone extinct (Mitchell et al., 2007).

Disentangling the history of mass extinction from sequence-stratigraphic architecture is difficult in situations like this, but Sheets et al. (2016) devised a novel approach. Using a global occurrence database of Late Ordovician graptolites, the authors constructed a Bayesian model of species occurrences in a shallow-water site and a deep-water site, and then used that to calculate the posterior probability for whether each species lived in an epipelagic (shallower) or mesopelagic (deeper) water mass. The authors then used the $^{143}$Nd/$^{144}$Nd ratio as a proxy for global sea level. From this, they could separate the local faunal changes related to water depth from the mass extinction signal. Notably, what they found was that the turnover was not a single abrupt event as a literal reading of last occurrences would suggest. Community changes began several million years before the pulse of last occurrences, supporting the argument that the Late Ordovician mass extinction was prolonged.

Similarly, the Permo-Triassic extinction is commonly regarded as rapid, largely because it is manifested by one or more pulses of last occurrences in boundary sections (e.g., Hongfu et al., 2001; Algeo et al., 2007; Farabegoli et al., 2007). These pulses are all associated with obvious flooding surfaces in the authors' measured sections, some of which may also be subaerial unconformities. That at least some of the last occurrences are stratigraphically controlled is confirmed by the recurrence of some species 14-22 m above the Permo-Triassic boundary (Farabegoli et al., 2007). Moreover, most studies focus on a few measured sections or even only one, making it difficult to understand which stratigraphic patterns represent extinction and which reflect local changes in water depth. By using constrained optimization to correlate a series of columns along a dip-oriented transect, Wang et al. (2014) showed that conditions were deteriorating 1.2 myr before the peak of the Permo-Triassic extinction. Moreover, exposures from India spanning the boundary demonstrate the upsection loss of species owing to deepening rather than extinction (Brookfield et al., 2003), underscoring that last occurrences are not equivalent to times of extinction.

Such stratigraphic-paleobiologic approaches support the hypothesis that nearly all mass extinctions were substantially longer than a literal reading of the fossil record would suggest (Holland & Patzkowsky, 2015). It is important to underscore that the reality of mass extinctions is not in question (but see Smith et al., 2001, 2006), only how to interpret the pattern of fossil occurrences in stratigraphic sections. The question facing all future studies in mass-extinction boundary sections is not whether stratigraphic architecture affects the pattern of fossil occurrences, as it assuredly does, but how to distinguish stratigraphic origins underlying fossil occurrences from the extinction event.

*Community paleoecology*

Of all the areas of stratigraphic paleobiology, the analysis of community ecology has received the greatest attention. These include studies that document the variation in community composition with water depth and other variables, those that demonstrate how ordination techniques can be used to quantify this variation, and those that use these relationships and the stratigraphic variation in communities to understand community change through time. One particularly remarkable set of studies involves Pleistocene and Holocene communities from Italy (Scarponi & Kowalewski, 2004, 2007; Scarponi et al., 2013, 2017; Amorosi et al., 2014; Wittmer et al., 2014; Huntley & Scarponi, 2015; Kowalewski et al., 2015; Nawrot et al., 2018; Rossi et al., 2018). These studies span a wide range of taxa, including mollusks, ostracods, and foraminifera, as well as mollusk-hosted predatory and parasitic traces.

These studies are built from a series of cores (10 cm diameter) along depositional strike and depositional dip, which allows the authors describe regional variability in facies and community composition. From these cores, counts of abundance of species are used in ordinations of community composition. Taking advantage of the young age of these strata, the authors compare the ordination scores of species to modern data on the depth distribution of these species, which reveals that water depth explains 82% of the variance in DCA axis 1 sample scores (Scarponi & Kowalewski, 2004, 2007). This allows them to confidently use axis 1 scores to quantify water depth trends within a core. They also demonstrate that axis two is related to salinity, which varies among systems tracts and position along depositional dip.

This basic characterization allows samples to be compared through time to understand community changes during Quaternary sea-level fluctuations, and it reveals differences in species turnover among systems tracts (Scarponi & Kowalewski, 2007). By incorporating $^{14}$C-calibrated amino acid racemization dates, the authors demonstrate progressive decreases in temporal resolution, frequency of depositional events, and net accumulation rates through a TST towards the maximum flooding surface, followed by a subsequent reversal of all three trends in the following HST, confirming long-suspected patterns about the fossil record. From this, the authors extended a quantitative bathymetric model for transgressive-regressive cycles deeper into the Quaternary, demonstrating the robustness of using mollusk communities for reconstructing water depth histories (Wittmer et al., 2014). The baseline of molluscan responses to substantial Quaternary sea-level changes shows that modern anthropogenic changes in community composition far exceed anything experienced in the Quaternary, despite the magnitude of Quaternary sea-level changes (Kowalewski et al., 2015). By imposing an artificial mass extinction, the authors convincingly demonstrate how a literal reading of the fossil record would

give a misleading impression of the tempo of the mass extinction, owing to stratigraphically generated clusters of last occurrences (Nawrot et al., 2018). Finally, these authors were also able to confirm sequence-stratigraphic predictions about how the quality and temporal resolution of the fossil record varies with bathymetry. Specifically, the offshore decrease in sedimentation rates increases the time bioclasts are subject to taphonomic degradation, driving an offshore decline in the quality and temporal resolution of the fossil record (Scarponi et al. 2013). Such onshore-offshore variations in temporal resolution are particularly significant in that they can generate spurious stratigraphic patterns in alpha and beta diversity (Kidwell & Tomašových, 2013).

By taking advantage of data not available in deep time, such as depth preferences of species and amino-acid racemization, these authors tested an astonishing array of hypotheses about the fossil and stratigraphic records. Their methods and the patterns they found have been applicable elsewhere in Italy (Amorosi et al., 2014; Rossi et al., 2018). More broadly, they suggest that the implications of these studies are likely applicable to many other siliciclastic marine depositional systems (Scarponi et al., 2017).

*Phylogenetic models*

Divergence times play an important role as a prior for Bayesian phylogenetic models, which often span tens to hundreds of millions of years. Over these time scales, first occurrences of species and higher taxa are controlled primarily by the intersection of biogeography and the spatial distribution of sampled sedimentary basins, that is, whether species lived where a sedimentary record was accumulating. Sequence-stratigraphic controls often play a secondary role at these time scales. In these studies, the primary goal becomes to characterize how fossil recovery varies with time, geography, and environment, which is used to set informative priors on the Bayesian models (Donoghue & Yang, 2016; Wright et al., 2022).

Several studies exemplify this approach. In a study of carnivoramporphan mammals of North America and Eurasia, Wagner & Marcot (2013) calculated lognormal rates of fossil recovery by binning their data by continent and stage, and by using lepidosauromorphs as an ecological/taphonomic control group. Notably, they found that these variable rates performed substantially better than a single rate, underscoring the importance of not assuming constant preservation through time and among different geographic regions. Similarly, in a study of early jawless vertebrates that are restricted to shallow-water environments, Sansom et al. (2015) constrained divergence times by modeling preservation potential as a function of rock outcrop area and sea level. By doing so, they could show that ghost clades are better explained by allowing preservation potential to vary through time. Although their approach does not specifically address geographic variation like Wagner & Marcot (2013), simply assessing temporal variation in preservation probability produces superior results compared with assuming a constant probability of preservation. This underscores an important point: although the list of what controls first or last occurrences is long, any effort at allowing preservation rates to vary in an analysis is better than assuming constant

preservation. Similarly, Hopkins (2014) estimated the affinity of trilobite genera for latitudinal bands, carbonate vs. siliciclastic substrates, and water depth, and these could also be used to set priors on phylogenetic models.

*Morphometrics*

Reconstructing patterns of morphological evolution also benefits from a stratigraphic-paleobiologic approach because patterns of evolution depend not only on fossil occurrences, but also on the morphologic variation of species along ecological gradients (e.g., Cisne et al., 1982; Bayer & McGhee, 1985; Ludvigsen et al., 1986). Because water depth changes through time, stratigraphic changes in water depth combined with the correlation of species morphologies with depth can mimic evolutionary patterns. As such, methods are needed to distinguish environmental variation in morphology from evolutionary change.

Two studies demonstrate effective strategies. In a study of the Ordovician trilobite *Flexicalymene*, Webber & Hunda (2007) used ordination scores from whole-fauna community studies as a proxy for water depth, against which they compared landmark-based morphometric measurements. They found that a substantial portion of the shape change, particularly related to eye position, was correlated with water depth. By doing so, it becomes possible to distinguish evolutionary variation from clinal variation. Hannisdal (2007) applied Bayesian inversion to recover the evolutionary signal from a Miocene benthic foraminifer, using sample age and depositional environment as priors. As uncertainty in both was included, this allowed uncertainty estimates on the recovered evolutionary trajectory. In addition, this approach also produced estimates and uncertainties for preferred depth, depth tolerance, and peak abundance, as well as preferred grain size and grain size tolerance.

## RESEARCH OPPORTUNITIES IN STRATIGRAPHIC PALEOBIOLOGY

The stratigraphic paleobiology of shallow marine systems is now well-established through numerical models and numerous case studies. The integration of carbonate stratigraphic models has lagged that of siliciclastics, and that is a promising area of research, as some carbonate systems can have substantially different architectures and fossil distributions than siliciclastic systems (Goldhammer et al., 1993; Holland & Patzkowsky, 2009). Methods of describing stratigraphic architecture are well-established, as are the ordination methods used for detecting ecological gradients and determining whether they are correlated with water depth. These can be used to create confidence intervals on range endpoints that account for variations in water depth and other gradients such as substrate consistency (Holland, 2003; Wang & Marshall, 2016). They can also be used to quantify sampling probabilities (Hannisdal, 2007) and distinguish clinal variation (Webber & Hunda, 2007). They can be used for creating sampling frameworks for studying community change (Holland & Patzkowsky, 2007; Patzkowsky & Holland, 2007), quantifying niche stability (Holland & Zaffos, 2011), for simulating and analyzing the fossil record of mass extinctions (Nawrot et al., 2018; Zimmt et al., 2021), and

evaluating the ecological response to climate change, sea-level change, and anthropogenic impacts on community structure (Kowalewski et al., 2015; Dominici & Danise, 2022). The solid footing for the stratigraphic paleobiology of shallow marine systems makes it a fertile area for other novel applications.

In contrast, the stratigraphic paleobiology of nonmarine systems is in its earliest stages (Rogers & Kidwell, 2000, 2007; Eberth et al., 2001; DiMichele & Gastaldo, 2008; Gastaldo & Demko, 2011; Loughney & Badgley, 2017, 2020; Holland & Loughney, 2021; Holland, 2022a). There is ample study of taphonomy on which to build, particularly in fluvial systems (e.g., Bown & Kraus, 1981; Behrensmeyer, 1987, 1988, 1991; Badgley & Behrensmeyer, 1995; Rogers & Kidwell, 2000, 2007; Gastaldo et al., 2005; Loughney et al., 2011). For alluvial (river/floodplain) systems, a framework for systems tracts and surfaces is well-established (Martinsen et al., 1999; Catuneanu, 2006; Holland & Loughney, 2021), as is the relationship of sequence-stratigraphic architecture to the preservation of bone (Rogers & Kidwell, 2000, 2007) and plants (Gastaldo & Demko, 2011). More recently, the development of strataR (see SOM1; Holland, 2022b) provides a means for simulating the basin architecture, stratigraphic columns, and fossil occurrences in the nonmarine portions of sedimentary basins. Numerous possibilities exist here for simulating the wide range of conditions in nonmarine settings and their implications for the fossil record, particularly among different basin types. In addition, there is a great need for a process-based basin-scale stratigraphic model that couples alluvial and marine systems, which would allow another means of testing the predictions of the geometric model strataR.

Many other aspects of the stratigraphic paleobiology of nonmarine systems are promising areas of future work. Lacustrine systems are nearly unexplored territory, and the recent development of lacustrine sequence-stratigraphic models that avoid the misapplication of marine-based models provide a promising basis (Gearon et al., 2022). Although modern ecological studies demonstrate the ubiquity of elevation-correlated ecological gradients in fluvial systems and depth-correlated ecological gradients in lacustrine systems, these are poorly documented in the rock record. In large part, this is because elevation is not clearly reflected in alluvial facies, whereas water depth is the principal gradient in shallow-marine facies models. One strategy for recognizing these gradients is to sample perpendicular to shore for a constrained time interval, since elevation would be expected to gradually increase with distance from the shore. In my experience with several student theses in a variety of nonmarine settings, a substantial challenge to the stratigraphic paleobiology of alluvial settings is the generally low probability of occurrence of fossils - including bone, plant, and mollusks - relative to marine invertebrates (Regan et al., 2022). Advances in nonmarine stratigraphic paleobiology may require methods that are designed to work with rare fossils.

At the largest scale, that of basins and the globe, substantial work is needed to understand the paleobiological implications of basin formation, filling, and cessation, and how that governs the structure of the fossil record at these large scales. The realization of how little terrestrial area is depositional and how few coastlines are depositional (Nyberg & Howell, 2015, 2016) is sobering for thinking not just about how little modern biodiversity is likely to be preserved into deep time, but how that diversity is structured. For example, most nonmarine basins preserve elevations of 0-500 m above sea level, except for extensional and some foreland basins, which can preserve elevations up to 3500 m (Holland et al., 2023). Because different types of sedimentary basins will form at different times during a Wilson Cycle of supercontinent and breakup, nonmarine diversity maxima will be systematically preserved in only parts of the geological record (Holland, 2016). Far more can be done with understanding how preservation varies among environments and continents through geological time, and its implications for the interpretation of the fossil record (e.g., Wagner & Marcot, 2013; Sansom et al., 2015).

In closing, the underlying stratigraphic structure to the fossil record must be considered to correctly interpret ancient biotic events. This is what distinguishes stratigraphic paleobiology. A stratigraphic paleobiologist recognizes that the fossil record is not just the history of life, it is equally the history of sedimentation. These stratigraphic processes are not a bias that distorts a typically faithful fossil record, they are an intrinsic and pervasive part of the fossil record. The history of sedimentation is the starting point for interpreting the fossil record.

## SUPPLEMENTARY ONLINE MATERIAL

Supplementary data of this work are available on the BSPI website at: https://www.paleoitalia.it/bollettino-spi/bspi-vol-621/

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