PALEOECOLOGY

Ecological stasis on geological time scales

Communities and functional structure persist for millions of years in a mammal fauna

By **Peter D. Roopnarine** *and*
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The rise and decline of organismal lineages dominate our view of life's history. Less appreciated is the persistence of ecological communities for tens of millions of years (*1*). On p. 300 of this issue, Blanco *et al.* (*2*), analyzing a series of mammalian faunas spanning the past 21 million years of the Iberian Peninsula, demonstrate increasing persistence of functional systems over time and the decoupling of those systems from species composition and duration. This study adds to a growing body of evidence that community structure is fundamentally important to ecosystem persistence (*3*).

The Blanco *et al.* study spans a time of dynamic environmental changes. Mild climates of the middle Miocene contributed to the expansion of forest habitats on the peninsula and the immigration of Eurasian faunas (*4*), followed by a transition to more seasonal climates and the expansion of grasslands (*5*). The authors defined 169 communities with an average duration of 0.1 million years. Species within each community were aggregated into functional units according to body size, diet, and locomotion. Applying a network-based approach, they identified taxonomic and functional modules shared across communities based on significantly co-occurring species or functional traits, respectively. Durations of taxonomic modules were brief—0.9 million years on average. Functional modules, however, were more persistent, having a mean span of 2.8 million years. Three long-lived communities, identified on the basis of shared faunal modules and called "functional faunas," subdivide the data temporally.

These successive faunas lasted 2.58 million, 4.66 million, and 9.37 million years, respectively, representing associations of functional traits that persisted against backdrops of high species turnover. Species turnover occurred only within each fauna's functional structure. The authors interpret this as structure excluding new species on the basis of their functional traits. The transition between functional faunas was in each case associated with major climatic shifts, extinction, and the introduction of new species with functional traits more suited to the new climatic conditions. Extinction rates were not increased during transitions, and species extinctions were more dependent on collapsing functional structures. Furthermore, the transitions between faunas were abrupt. There were no transient or intermediate faunas to suggest that new faunas were reorganizations of their predecessors rather than replacements.

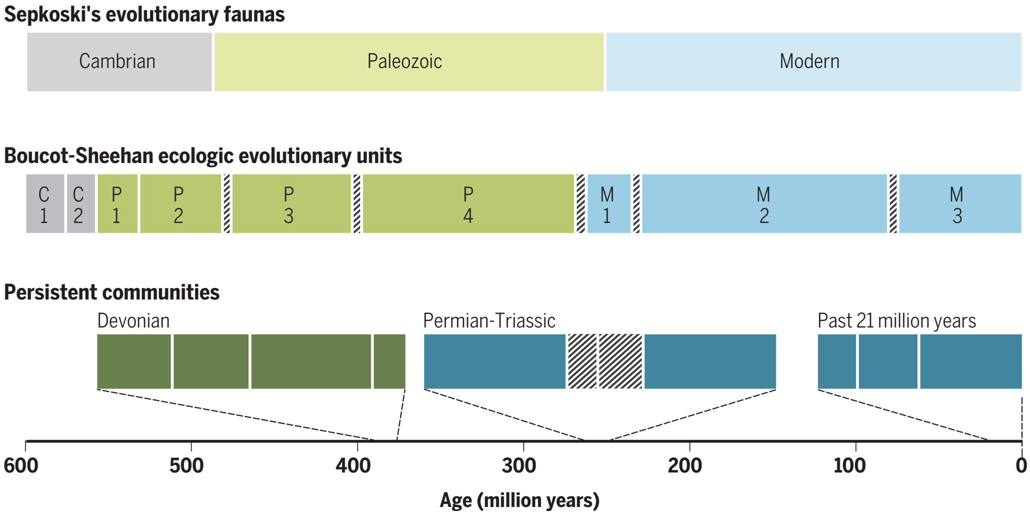
Blanco *et al.* bolster ideas that the addition of new species to a system, and the extinction of species during crises, are dictated by existing functional structures (*6*). Indeed, it has been suggested that system dynamics act as agents of selection on species within a system (*7*). Although transitional faunas were absent in the Iberian series, the transition between persistent end-Permian and Middle Triassic terrestrial communities in the Karoo Basin of South Africa was marked by several short-lived communities (*6*). Models of those systems suggest that they would have been unstable and easily replaced by alternatively structured systems, which they were by the Middle Triassic. Their geological transience, however, corresponds to tens of millennia, suggesting that functionally "inferior" systems can persist for considerable intervals on ecological time scales.

Species' functional properties both affect and are affected by the network in which they are embedded. Species' evolution may therefore be constrained by the systems to which they belong. System persistence itself is likely the result of diffuse coevolutionary interactions (*8*) that developed over long, abiotically stable intervals. Differential persistence between systems is based on functional diversity (*2*), functional redundancy, and the configuration of interactions among functions (*6*). Features determining the processes and feedbacks of a system may ultimately subject systems to selection (*9*), from which patterns of persistence emerge.

The shortest-lived types of persistent systems are those based on unchanging

Intervals of static ecological associations at multiple scales

Persistent communities can be seen at multiple taxonomic and temporal scales: Devonian (*9*), Permian-Triassic (*6*), and the past 21 million years (Blanco *et al.*). Times for persistent communities are not to scale. Vertical bars show transitions between communities, and patterned intervals are post–mass extinction transitional systems.



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taxonomic composition (*10*). A hierarchy emerges, however, when definitions are broadened to include ecological traits and processes (see the figure). The largest are Sepkoski's marine evolutionary faunas (*11*), followed by the ecologic evolutionary units of Boucot and Sheehan (*1*, *12*, *13*). Regardless of the hierarchical level at which a system is defined, common features exist across multiple scales when systems are defined functionally and ecologically: Systems last longer than species (*12*, *13*), and species turnover is more rapid and often decoupled from system persistence. The end of a system is marked by species extinction, which is often associated with external abiotic drivers (*1*). Transitions between systems are abrupt relative to typical system duration, marked either by the absence of structurally intermediate systems, as shown by Blanco *et al.*, or by new systems of short duration (*6*).

> **"Systems last longer than species, and species turnover is more rapid and often decoupled from system persistence."**

Thus, persistent paleoecological systems warrant examination beyond genealogical dynamics, but documentation and analysis using the fossil record are challenging, leaving outstanding questions. How do persistent systems arise, why do they eventually fail (*6*), and why are some more persistent than others (*8*)? Addressing these questions from a systems-based perspective is key to understanding processes of community assembly and persistence that exist across hierarchical, temporal, geographical, and spatial scales. ■

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GENOMICS

The gut microbiomes of 180 species

Animal microbiomes are a treasure trove of previously unknown bacteria and genes

By **Abigail L. Lind** *and* **Katherine S. Pollard**

Microbial life is ubiquitous in most environments on Earth, including in the gastrointestinal tract of animals. The composition of these collections of microbes, called the microbiota, can differ dramatically between individuals and species. Across the animal tree of life, these microbiotas contain a broad array of microbial diversity. Animal gut microbiota composition is more similar when hosts share diet or genetic ancestry, especially in mammals; the correlation of microbiota composition with genetic ancestry is weaker in fish, reptiles, birds, and invertebrates (*1*–*4*). In many cases, gut microbes contribute to key host processes, including metabolizing specialized dietary compounds (*5*). On page 264 of this issue, Levin *et al.* (*6*) interrogate the microbes that inhabit the animal gut by sequencing fecal samples from ~180 wild and captive species across the animal tree of life. Most of the bacterial species and genes they found have not been described before.

This massive compendium includes 406 samples from mammals, reptiles, birds, fish, and some invertebrates collected at six different sites globally, with the highest sampling in Israel and Uganda. The animals span a variety of feeding patterns and behavioral traits, although they are predominantly terrestrial vertebrates. The key contribution of Levin *et al.* is the use of whole-metagenome sequencing, as opposed to the single-gene amplicon sequencing that has yielded much of our current understanding of animal gut microbiome (microbial genomes) composition across diverse groups (*5*). Whole-metagenome sequencing differs from amplicon sequencing in that it involves sequencing all of the DNA present in a sample rather than selecting for a specific piece, as in the case of the 16*S* ribosomal RNA gene in amplicon sequencing. One major advantage of the whole-metagenome approach is that whole or partial genomes, called metagenome-assembled genomes (MAGs), can be reconstructed by sorting and piecing together the sequencing reads themselves, a process called binning and assembling. Increasingly large numbers of MAGs are being generated from environmental, human, animal, and plant sources, which has revolutionized our understanding of the function, ecology, and evolution of host-associated and environmental microbiotas (*7*, *8*).

Levin *et al.* find that most of the reads they sequence from animal microbiomes cannot be mapped to existing reference databases, highlighting the unexplored diversity of animal microbiomes. They use their sequencing reads to assemble more than 5000 MAGs from 1209 bacterial species, of which 75% are uncharacterized. This unexplored microbial diversity in animals stands in contrast to the well-studied human microbiome, which is much better represented by reference databases. The animal microbiota species are distributed across the bacterial tree of life, with the highest enrichment in undescribed species coming from Verrucomicrobia, a phylum found in water, soil, and human intestines but with relatively few cultivated species. Aligning the original sequencing reads back to the MAGs increases the amount of the sequencing library that can be assigned to bacterial genomes from 7 to 21% of reads. That most of the sequences remain unassigned is expected because MAGs do not capture all genomes in a sample. Specifically, they often miss lower-abundance taxa, mobile genetic elements, and organisms with large or complex genomes, including most microbial eukaryotes.

Using these assembled genomes, Levin *et al.* recapitulate findings first noted with amplicon sequencing, including that herbivore microbiomes are more diverse than carnivore microbiomes. By examining the gene content of their MAGs, the authors find that the genetic pathways encoded by the microbiomes of different groups of animals differ based on host diet, body size, and other traits. In a compelling proof-of-concept experiment to demonstrate that new bacterial functions can be discovered in animal microbiomes, the authors experimentally validated bacterial toxin–metabolizing proteases found in the MAGs from carrion-eating griffon vul-

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