Opinion

Diversity in time and space: wanted dead and alive

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Current patterns of biological diversity are influenced by both historical and present-day factors, yet research in ecology and evolution is largely split between paleontological and neontological studies. Responding to recent calls for integration, we provide a conceptual framework that capitalizes on data and methods from both disciplines to investigate fundamental processes. We highlight the opportunities arising from a combined approach with four examples: (i) which mechanisms generate spatial and temporal variation in diversity; (ii) how traits evolve; (iii) what determines the temporal dynamics of geographical ranges and ecological niches; and (iv) how species–environment and biotic interactions shape community structure. Our framework provides conceptual guidelines for combining paleontological and neontological perspectives to unravel the fundamental processes shaping life on Earth.

A split between disciplines

Present-day patterns of biological diversity are strongly influenced by mechanisms that have acted over past time periods and that underlie the appearance of new species, their evolution, and ultimately their extinction. Although neontological research (see Glossary) increasingly acknowledges past influences [1,2], these studies typically do not consider how assemblage structure, phylogenetic patterns, and trait variation of species in fossil communities might modify or support current understanding [3,4]. In contrast, paleontological research has focused on the ecology and evolution of prehistoric taxa and their communities and has often overlooked contemporary diversity patterns and newly developed methodologies to deduce processes from these patterns [5,6]. Originally, paleontology was an essential component of the 'Modern Synthesis' of evolutionary biology [7] and much neontological work goes back to macroevolutionary concepts developed by paleontologists [8,9]. Since the time of the Modern Synthesis, increasingly separate societies and specialist journals, growing numbers of researchers and publications, and differences in data sources have led to the current split between disciplines. It is increasingly recognized that researchers striving to understand the mechanisms underlying diversity need to formally reintegrate neontological and paleontological perspectives [3,4,6,10,11].

The challenge: common questions but separate data and approaches

Both neontological and paleontological researchers aim to understand the same fundamental processes that generate and maintain diversity in time and space, such as speciation and extinction [3,12]. Neontological studies usually try to infer the processes leading to contemporary patterns, such as the evolution of current trait variation [13], factors determining geographical ranges or ecological niches of species [14], or processes leading to regional differences in species richness [1]. Similarly, paleontologists try to establish links between the history of life and environmental change in both shallow and deep time; for example, by investigating evolutionary radiations [15],

Glossary

Biotic interactions: direct or indirect interactions between individuals of the same or different species; for example, competition, predation, parasitism, and mutualism.
Environmental filtering: the process by which properties of the (abiotic) environment exclude individuals or species with specific ecological, behavioral, or morphological traits from local assemblages.
Fundamental niche: all abiotic and biotic conditions where individuals of a species can persist and reproduce.
Lineage-through-time plot: a plot of the temporal accumulation of lineages, usually the log-transformed number of lineages in a phylogenetic tree against time.
Neontological research: studies on the ecology and evolution of present-day taxa, their communities, and their environments.
Paleoenvironmental proxies: any type of measurable entity that can be used to infer paleoenvironmental conditions; for example, plant fossil or pollen occurrences as a proxy for temperature and precipitation.
Paleontological research: studies on the ecology and evolution of prehistoric taxa, their communities, and their environments over short and long geological timescales ('shallow time' and 'deep time').
Realized niche: the abiotic and biotic conditions where individuals of a species occur, given real-world constraints by biotic interactions, limited dispersal ability, and the finite extent of realized environmental space.
Species distribution models (SDMs): statistical models that relate the geographical occurrence of species to the environmental conditions found at these points.
Trait lability: the degree to which trait values change within a lineage through time or between lineages.

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spatial turnover in taxa and traits [16,17], or large-scale temporal turnover of diversity and extinction dynamics [18,19].

Recent advances in both fields now provide an opportunity for the integration of neontological and paleontological perspectives [11,20]. For instance, considerable efforts have been made to adjust for possible biases in the paleontological record, which make well-sampled parts of this record comparable to data from living organisms [21]. The ongoing integration of ecological and evolutionary approaches in neontological research has paved the way for explicitly temporal perspectives [1,2,20,22]. Recent extensive compilations of species occurrences, traits, and environmental data in both fields, neontological [23,24] and paleontological [11,25], allow integrated investigations of many taxa, such as zooplankton, marine mollusks, vertebrates, and plants. Methods that incorporate disparate data sources are being developed [19,26,27]. Recent pioneering studies try to integrate contemporary and fossil data; for example, when studying trait evolution [28,29], extinction and diversification rates [19,30,31], or the stability of realized niches in the face of environmental change [32–34]. However, many open research questions remain that would benefit from better integration, such as inferring mechanisms underlying spatial patterns in diversity or evaluating the potential importance of abiotic versus biotic factors in structuring biological assemblages.

Here, we propose a framework to serve as a conceptual structure for analyses integrating neontological and paleontological perspectives. Rather than focusing on methodological implementation, we highlight the opportunities that arise from integrated approaches and give examples of how combined analyses of contemporary and fossil data can increase our understanding of fundamental ecological and evolutionary processes.

The framework

We propose a conceptual framework that profits from the different strengths of neontological and paleontological data sources and methods [19,35] to address key questions in ecology and evolution. The framework combines four types of data from both the neontological and the paleontological perspective into one joint structure: environment, species occurrences (or geographic ranges), trait information, and a phylogeny (Box 1). Neontological data document the contemporary environment, traits and interactions of extant species, and the evolutionary history of extant species is commonly reconstructed using molecular data (see Figure IA in Box 1). The fossil record provides paleoenvironmental conditions in time and space, past occurrences and trait values of extinct and extant species, and the appearance and disappearance of species in time (see Figure IB in Box 1). We propose that future studies integrate all of these data (see Figure IC,D in Box 1) to study the six fundamental processes that generate diversity patterns in time and space: species' interactions with the abiotic environment, biotic interactions, dispersal, trait evolution, speciation, and extinction. Environmental factors (here abiotic, such as climate and topography) constitute a major influence on the ecology and evolution of organisms and vary over time and space (see Figure IC in Box 1). This variation, together with biotic interactions and dispersal, determines species' geographical ranges. Following our framework, the processes underlying geographical range dynamics in time and space can be inferred from the combined data on environment and species occurrences (see Figure IC in Box 1). Geographical ranges and the processes shaping them in turn influence the other three key processes: trait evolution, speciation, and extinction. These processes are documented by the integrated neontological and paleontological trait data and phylogenies (see Figure ID in Box 1). Hence, our approach will encourage future studies to infer how patterns of extant and extinct diversity have been shaped by each of the six key processes.

In the following sections, we present examples showing how the integration of neontological and paleontological perspectives proposed here (Box 1) can be applied to investigate four key questions in ecology and evolution. The first three examples build on existing ideas and case studies that have implemented parts of our framework; the fourth develops a novel application of a neontological approach to fossil data. Our examples concentrate on the taxonomic level of species, but the framework can be adapted to investigate corresponding within-species processes and patterns as data become available. It is beyond the scope of this perspective to discuss the different ways of adjusting for biases or incorporating uncertainty [21,36], but we stress that these considerations are essential when applying our framework (see Concluding remarks).

Speciation, extinction, and interactions with the abiotic environment

Which environmental factors control variation in species richness across time and regions is a fundamental, open question in ecology and evolution [1,12]. Answering this question means considering at least three of the main processes identified above: species–environment interactions, speciation, and extinction. We explore the question with two interlinked examples. First, we consider changes in diversity over time by quantifying speciation and extinction rates, either globally for higher taxonomic groups or in one given region. We then extend this temporal approach to include an explicit spatial dimension, to infer how variation in environmental conditions has influenced speciation and extinction rates.

The first example concentrates on the temporal component of our framework; that is, the phylogeny of extant and extinct species (see Figure IA in Box 1). Neontological studies commonly use molecular phylogenies of extant species to generate lineage-through-time plots and estimate diversification rates [37,38], whereas paleontological research mainly employs diversity curves through time, which are generated from origination and extinction counts [18] (Figure 1A). Speciation and extinction events of extinct species and lineages cannot usually be captured in a phylogeny based only on extant taxa, but might be inferred from fossil occurrences (Figure 1A). For example, the global diversity of fossil whales declined from its peak in the late Miocene, whereas the lineage-through-time plot from the molecular phylogeny of extant species implies nearly constant, positive diversification rates during that

Box 1. A framework to integrate neontological and paleontological research

In our framework, we show how typical neontological and paleontological data on environment, species' occurrences, species' traits, and phylogeny can be integrated into a common quantitative structure (Figure I). Neontological and paleontological data usually differ in temporal and spatial scales [11,19]. The contemporary environment can be described at fine spatial resolution (e.g., remote sensing), whereas paleoenvironmental data are usually patchy (e.g., proxy estimates from pollen) or not spatially explicit (e.g., global isotope curves). The quality of occurrence data for extant species depends only on sampling effort, but data for fossil species are often averaged within time slices because their quality depends on both sampling effort and preservation [21]. Any type of trait can be recorded for extant species (morphology, diet, habitat use, behavior, physiological parameters), but only morphological traits can be directly measured for extinct species (although indirect inference is possible; e.g., for diet from isotope analyses) [69]. Molecular phylogenies can be reconstructed for extant taxa (Figure IA), whereas phylogenies of extinct taxa have to rely on morphological characters. Nevertheless, the fossil record offers an extensive temporal view of changing species diversity and co-occurrences (Figure IB), changing morphology, and changing environment. In our framework, we combine the strengths of both types of dataset (Figure IC,D). The framework has a spatial component with maps across time slices, including the present (species occurrences and environmental data) (Figure IC). The temporal component is given by phylogenies recording speciation, extinction, and traits for both extinct and extant species (Figure ID).

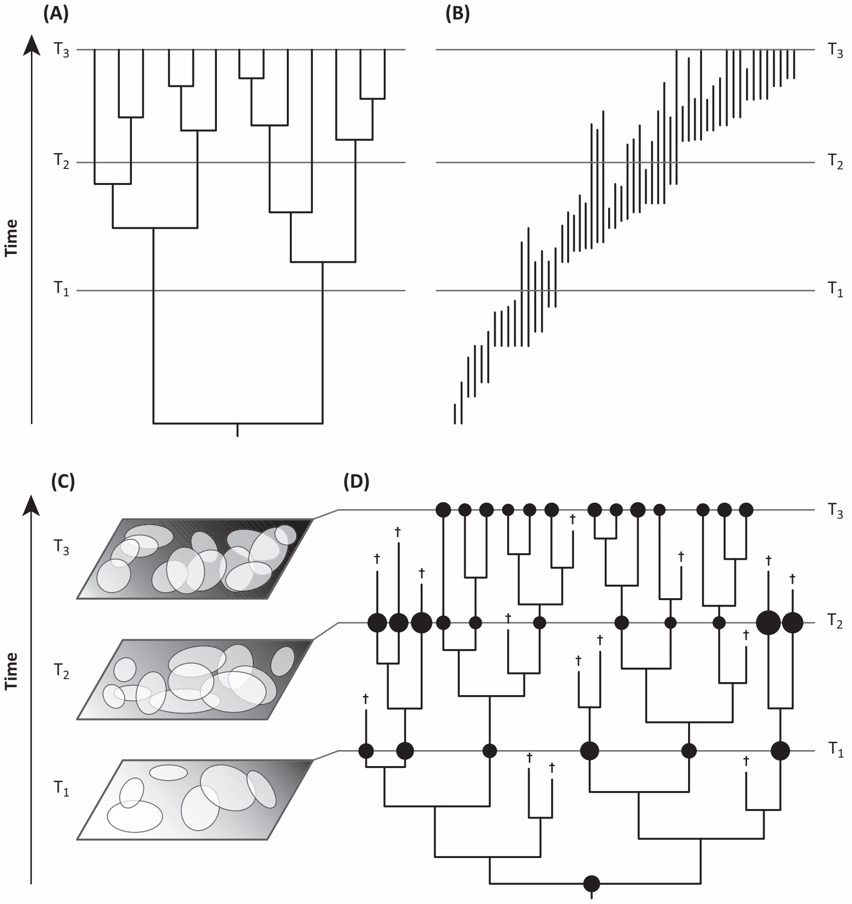

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Figure I. Framework integrating neontological and paleontological data for a hypothetical clade. A phylogeny **(A)** can be reconstructed for the extant species in the clade, usually with molecular information, and species occurrences and traits can be quantified directly. An ideal fossil record **(B)** affords species durations (shown as bars) for all extant and extinct lineages, as well as occurrences and trait information in time and space. Our framework **(C,D)** combines and profits from these data by documenting dynamics of species' geographical ranges along temporal and spatial environmental gradients (C) and the evolutionary history of the clade (D) with all extant and extinct lineages and their traits (circle size). The three time slices T_1–T_3 are identical in (A–D).

time [10]. Recently developed models might recover the diversification dynamics seen in fossils from the phylogeny of extant species, but capturing the signature of extinction, in particular, remains challenging [31,37,39]. The incorporation of extinct taxa into phylogenies of extant species [26,27] will provide a more robust measure of changes in the diversity of both extinct and extant lineages through time (Figure 1A).

Whereas such analyses of diversification rates quantify temporal dynamics, they generally lack an explicit spatial dimension. Neontological studies concerned with explaining spatial variation of species richness increasingly integrate evolutionary history or investigate the relationship of contemporary richness patterns with past environmental changes [40,41]. However, as in the temporal analyses above, extinct species are not usually considered. Paleontological studies often relate paleoenvironmental factors to diversity through time, but rarely in space ([42], but see [16,17]). A recent study on rodent diversification showed that the difference in fossil-species richness of two North

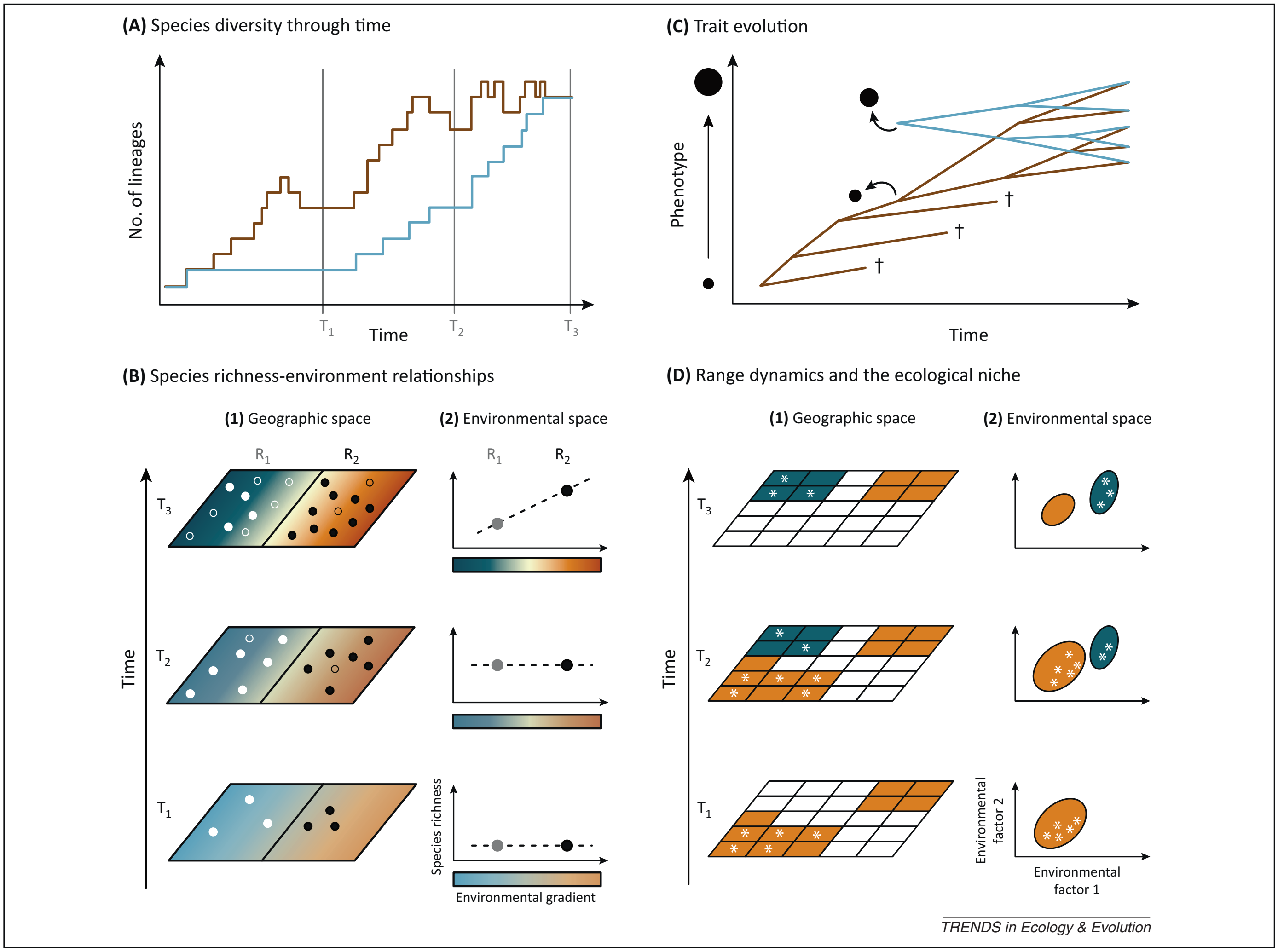

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Figure 1. Examples of the integration of neontological and paleontological data: species diversity through time **(A)**, species richness–environment relationships in time and space **(B)**, trait evolution **(C)**, and range dynamics and the ecological niche in time and space **(D)**. Time slices T_1–T_3 in each panel correspond to Figure I in Box 1. First, patterns of diversity through time (A), and speciation and extinction dynamics inferred from these, can be dramatically different when generated from a phylogeny reconstructed from the extant lineages (blue line, phylogeny in Figure IA in Box 1) or from a phylogeny including extant and extinct lineages of the same clade (brown line, phylogeny in Figure ID in Box 1). Second, relationships of speciation and extinction (B, 1) and of species richness (B, 2) with the environment (color gradient) through time (e.g., in two regions R_1 and R_2) can be inferred only with knowledge of extinctions from the fossil record. At each respective time slice, filled circles represent species alive at that time; species that have gone extinct before that time slice are indicated by open circles. In this example, equal speciation rates in the two regions and the increased extinction rate in region 1 drive the difference in diversity between the two regions (B, 2) and can be inferred only from the combined datasets (filled and empty symbols in B, 1). Third, the true dynamics of trait evolution (C, brown phylogeny with extant and extinct lineages) often cannot be captured in a phylogeny reconstructed from the extant lineages only (C, blue phylogeny). Phylogenies in (C) are displayed in trait space, with trait values plotted against time. Circles at the interior node indicate the true and reconstructed trait value for the most recent common ancestor of the five extant species in both phylogenies. Finally, the inclusion of past time slices allows documentation of temporal dynamics in both the geographical ranges of a given species (D, asterisks) and its association with different environmental conditions (colors). This temporal perspective leads to improved inference of the ecological niche as well as of key processes such as dispersal, extinction, and the formation and disappearance of no-analog climates: in our example, a species shifts from the orange to the blue environment that appears only after T_1 (D). If combined with phylogenetic information, this intraspecific example can also demonstrate a sister-species scenario, where speciation (appearance of a new species in the novel blue environment before T_2), extinction (loss of the species in the orange environment before T_3), and niche evolution of the lineage (compare T_1 and T_3 in D, 2) can be inferred.

American regions 5 million years ago had been caused by different underlying diversification histories [43]. Hence, we argue that the combination of neontological and paleontological approaches allows inference of the true speciation and extinction rates in different regions that have caused the spatial variation in species richness at different time slices up to the present day (Figure 1B). Our example relies only on spatial occurrences of species (see Figure IC in Box 1), although a phylogeny of extant and extinct species can be useful in differentiating dispersal effects between regions from true speciation and extinction events.

Further, the temporal perspective of the integrated analysis can illuminate the processes underlying dynamics in species richness–environment relationships (Figure 1B). The temporal and spatial variation in speciation and extinction can be combined with the contemporary and paleoenvironment; for example, the high contemporary tropical species richness of marine bivalves seems linked to higher tropical origination rates throughout the fossil record [44]. Future studies following the framework outlined here (Figure 1B) will be able to infer speciation and extinction rate dynamics in different regions or across environmental gradients.

Trait evolution

Explaining which factors influence the variation of species' traits in present-day or fossil taxa is a prominent challenge in (paleo-)ecology and evolutionary biology. The study of trait evolution provides insights into the evolutionary dynamics of species' attributes such as convergent evolution or the degree of trait lability [13], and recent studies increasingly link ecological and evolutionary approaches [22]. Much neontological research has used traits of extant species together with phylogenetic hypotheses to infer ancestral character states and the modes and rates of trait evolution [45]. The application of these approaches to a phylogeny reconstructed from extant species alone can be particularly misleading if extinction rates have been high and directional selection has acted, because then extant species provide an incomplete sample of phenotypic space for the evolution of the group as a whole (Figure 1C) [28,29]. For example, the estimated body mass of the most recent common ancestor of the Arctoidea (a suborder of carnivores) is 10–50 kg if estimated from extant taxa alone, but less than 5 kg incorporating fossil evidence [46].

Paleontological analyses often compare trait variation across higher taxa through time but lack a rigorous phylogenetic context; for example, when documenting the replacement of lineages in the fossil record [47,48]. Analyses of the rates of trait evolution have been conducted for only a few well-studied groups where traits can be readily reconstructed from fragmented fossil material [49,50]. Where available, fossil data can provide a more comprehensive sample of trait states throughout the evolutionary history of a clade, some of which might no longer be present in extant taxa (Figure 1C). In our framework, the integration of neontological and paleontological data and approaches improves inference of trait evolution and its impact on diversification (Figure 1C). The approach uses a combined phylogeny (see Figure ID in Box 1) [28], but it is not dependent on spatial-occurrence data. It is restricted to traits that can be measured in fossils and which have not been used in the reconstruction of the phylogenetic tree. Alternatively, trait measures from fossils can be placed as constraints on internal nodes of a phylogeny of extant taxa to improve the reconstruction of ancestral states and the evaluation of evolutionary models [29]. In summary, improved integration of contemporary and fossil data is crucial to understanding trait evolution.

Going further, evolutionary developmental research (evo-devo) offers opportunities for understanding the links between genes, developmental constraints, and phenotypic traits [51], and can be applied to investigate the functional ecology of adaptive radiations [52]. These ideas can be tested with the combination of contemporary data and a well-sampled fossil record. For example, developmental models of gene regulation in mammalian dentition can be compared with the phenotypic space occupied by fossils, such as for tooth-size proportions [53,54]. Future integrated studies could determine character independence and directional changes in developmental pathways for certain traits in both contemporary and fossil organisms [55].

Dispersal and species' interactions with the biotic and abiotic environment: geographical range dynamics and the ecological niche

Our third example addresses the question of how species–environment interactions, dispersal, and biotic interactions shape geographical ranges. The biological concept linking these processes to geographical range dynamics is the ecological niche [56,57]. Neontological research commonly describes the realized niche from observed species' occurrences and contemporary environmental conditions; for example, with species distribution models (SDMs) [14]. However, the quantification in SDMs might represent only a part of the fundamental ecological niche of a species due to dispersal limitations and biotic interactions, and because some abiotic conditions where a species could occur might not be present today (i.e., non-analogue climates) [57,58]. With advances in developing paleoenvironmental proxies and more sophisticated paleoclimatic simulation models, SDMs for the past are increasingly implemented [34], either directly with fossil-occurrence data [59–61] or by projecting current SDMs onto the paleoenvironment (hind-casting) [58,62]. Nevertheless, no strong paleontological perspective on the niche has been developed, although some studies of niche evolution and stability in shallow and deep time exist [32,61].

Even under the current neontological niche concept, the combination of neontological and paleontological data should result in better documentation of geographical range dynamics, provided the temporal data resolution is sufficient. This approach can provide insights into the processes influencing the niche in two ways (Figure 1D). First, the combination of a species' contemporary range and environmental conditions with fossil occurrences and paleoenvironmental data can allow more accurate quantification of the species' fundamental niche and its realization through time (Figure 1D) [62]. For example, the spotted hyena (*Crocuta crocuta*) was distributed widely in Europe during the late Pleistocene, but is now restricted to Africa; therefore, the niche of the species as inferred from combined Pleistocene and present occurrence data is much larger than that inferred from only the present data [33]. This combination of contemporary and past occurrence data into one SDM assumes that the fundamental niche did not change through time, but the realized niche did. Second, physiological experiments providing environmental limits for extant taxa allow approximations of the fundamental niche, another area where ecological and evolutionary approaches have recently been more integrated [63]. If the environmental conditions of fossil occurrences were outside the current physiological limits, a shift or contraction of the fundamental niche must have occurred [58]. These approaches can be applied to single species through time or to clades (Figure 1D). If combined with a phylogenetic hypothesis, researchers might even be able to evaluate the evolutionary rates of these changes [64]. The combination of neontological and paleontological perspectives on ecological niches and their evolution could lead to more realistic projections of species' future geographical ranges under anthropogenic climate and land-use change [4,58,64].

Species' interactions with the biotic and abiotic environment: phylogenetic assemblage structure

A rapidly growing field of community ecology integrates evolutionary approaches by evaluating the phylogenetic (and trait) structure of ecological communities or

Box 2. Analyzing temporal dynamics of phylogenetic assemblage structure

Investigations of phylogenetic structure and trait variation in ecological communities or assemblages aim to infer the relative influence of abiotic and biotic factors on assemblage composition, specifically the influence of environmental filtering through ecological traits versus biotic interactions such as competition [2,65]. The processes of dispersal, speciation, and extinction are assumed to act at larger spatial scales, forming the regional pool of species. To account for the non-independence of assemblages from the regional species pool, random draws from the pool are used to provide a null expectation of assemblage structure [65,70]. If species in the assemblage are more closely related than expected, the phylogenetic assemblage structure is clustered, probably as a consequence of environmental filtering of phylogenetically conserved traits (T_2 in Figure IA). Conversely, a pattern where species in the assemblage are spread more evenly across the phylogeny than expected (phylogenetic evenness) can suggest a signature of biotic interactions such as competitive exclusion (T_3 in Figure IA). Here, we propose to apply these tools across time because mechanisms inferred to influence contemporary assemblages can be different from those inferred for past assemblages (Figure I).

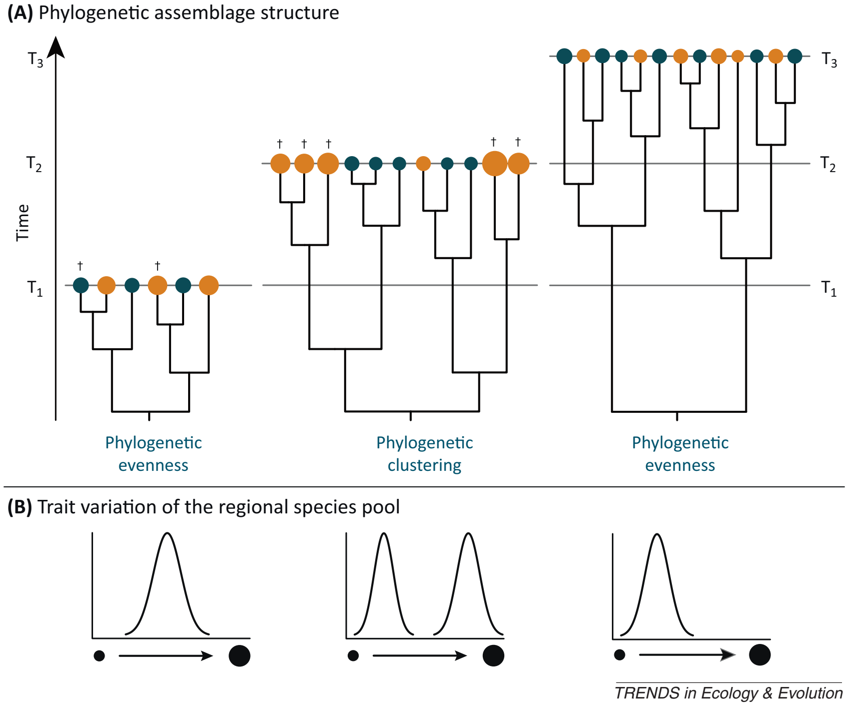

Figure I. Changes in assemblage structure through time: phylogenetic assemblage structure **(A)** and trait variation **(B)** of a hypothetical clade in the present (time slice T_3) and back in time (T_2 and T_1). Phylogenies in (A) correspond to the combined phylogeny (see Figure ID in Box 1), but show only the species living at each respective time slice, as well as their trait values (circle size). Crosses indicate lineages without living descendants in the following time slices (i.e., these lineages and all descendants become extinct before the next time slice). Phylogenetic patterns and trait values of the species in a given assemblage (blue) are compared with the regional species pool (including all species, blue and orange) within each time slice (A). When assemblage patterns and trait variation are then compared across contemporary and fossil assemblages, temporal changes of the processes structuring assemblages can be inferred. Specifically, biotic interactions (excluding close relatives) would be inferred from the phylogenetically even assemblage pattern today (A, T_3), but the phylogenetically clustered pattern and trait structure of the assemblage at T_2 suggest environmental filtering (the assemblage excludes species with large values from the pool at T_2, but also relative to the assemblage at T_1). In addition, the temporal changes in trait variation of the species pool (B) indicate extinction of the species with large values from the pool after T_2 (see Figure ID in Box 1), which deletes the signal of environmental filtering for the assemblage (no phylogenetic clustering at T_3 because only the lineages with small symbols survive in the pool).

assemblages (Box 2) [65]. The ultimate aim is to tease apart the relative importance of abiotic versus biotic factors in determining assemblage structure [2]. Paleontological studies have investigated this question typically without a phylogenetic framework and not at the assemblage level ([12], but see [50,66]). We argue that direct comparison of the phylogenetic structure and trait variation across fossil and extant assemblages can help in exploring the temporal dynamics of species–environment interactions and, possibly, biotic interactions (see Figure I in Box 2). Such comparisons can provide insights into when a given mechanism, such as environmental filtering, became important in structuring an assemblage (Box 2). If phylogenetic assemblage structure is consistent with environmental filtering through time, measurements of extant organisms might allow us to infer which functional traits a past environmental filter has acted on. These inferences require information on trait evolution and use the spatial and phylogenetic components of our framework (see Figure IC,D in Box 1). The investigation of phylogenetic and trait assemblage structure in the past will provide a completely new way of utilizing fossil assemblage information to infer the past and present effects of species–environment and biotic interactions. Describing and understanding these effects should be essential for predicting the susceptibility of ecological interaction networks to ongoing global change [4].

Concluding remarks

The examples above demonstrate that application of an integrative framework to key questions posed in (paleo-)ecology and evolutionary biology furthers our understanding of how the processes of species' interactions with the abiotic environment, biotic interactions, dispersal, trait evolution, speciation, and extinction act together to generate and maintain diversity. We recognize that some taxa might always be too poorly known to answer the key questions we have outlined. However, there are well-known groups that can be investigated in the field and in the fossil record with reasonable efforts. With these taxa, our framework can be explored if the three main challenges for its application can be overcome: to use existing data critically, to identify the often dispersed data sources and match them, and to generate phylogenies that include extant and extinct species. Critical use of existing data entails being aware of the limitations of neontological datasets [36] and the fossil record [21]. Factors that need to be considered when matching the different data sources include taxonomy and temporal and spatial resolution (Box 1), as well as the information science of connecting large and disparate databases [11]. Combined phylogenies, sometimes called 'total-evidence' phylogenies, can be generated using several methodologies. Advances in isolating and processing ancient DNA make it possible to build combined molecular phylogenies for extant and extinct species [67]. For deeper geological time, new phylogenetic methods are being developed for integrating morphological and molecular information from both extant and extinct species [26,27,68]. Communication and collaboration between the neontological and paleontological research communities is necessary to understand the potential and limitations of data from each discipline and to capitalize on new approaches and tools. Expanding collaborative efforts requires organizing joint workshops and sessions at scientific meetings, investing in building an integrated informatics infrastructure, fostering integrated research programs, and educating a new generation of students in both fields.

In conclusion, neontological and paleontological researchers address the same fundamental questions and can profit much from each other. Both disciplines are increasingly moving toward modeling processes instead of describing patterns [6,36]. Previous work has stressed common currencies that can be used to integrate the two perspectives, such as species traits [69] or the ecological niche [34,64]. Our framework extends these efforts to provide a more comprehensive vision of how neontological and paleontological data and approaches can be combined. Particularly in the face of ongoing anthropogenic land-use and climate change, it is vital to understand the processes underlying diversity. Our framework will serve as a guideline for integrated analyses and help to unravel the fundamental processes shaping temporal and spatial dynamics of life on Earth.

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