There is no taxon-free lunch

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Abstract

Over the last few decades, the term "taxon-free" has been widely used in paleoecological literature to highlight reasoning via ecomorphological or other functional traits of organisms as opposed to reasoning via taxonomic affiliations and phylogenetic conservatism. In practice, however, "taxon-free" inferences are very rarely free from using taxonomic information and occasionally they are even using phylogenetic conservatism to infer environmental or ecological conditions of taxa in the past. While some publications acknowledge the mismatch between the semantics of the term and the practice, others highlight the lack of reliance on taxonomic information as an advantage of the methodology, even in practice that reliance is present in a masked form. Here I present a structured survey on the use of the term "taxon-free" in paleoecological literature with an emphasis on mammalian community paleoecology. Based on the results I advocate dropping the use of the term "taxon-free" to minimize the potential for misinterpretations and use the term "trait-based" approaches instead, or alternatively, "phylogeny-free" if absence of reliance on phylogenetic niche conservatism is to be highlighted.

Keywords: paleoecology, taxon-free, taxon-based, phylogenetic niche conservatism, evolutionary theory

Trait-based approaches in paleoecological reconstructions aim to capture the functional characteristics of past ecosystems by focusing on ecological traits that are directly linked to environmental conditions. This method allows for a generalised understanding of ecosystem structure and function, especially valuable in environments where taxonomic identification is difficult or where species present in the fossil record may not have modern analogues.

Trait-based approaches to paleoecology have been termed "taxon-free" to emphasize reasoning about ecology and environmental conditions via functional traits of organisms as opposed to their taxonomic affiliations (Orlóci and Stofella 1986; Wing 1988; Damuth 1992; Andrews and Hixson 2014; Barnosky et al. 2017). The term "taxon-free" in its broadest and most fundamental sense highlights freeing paleoecological reasoning from the assumption that species tend to conserve ecological requirements of their ancestors. Those trait-based approaches rely on persistence of biomechanical, physical, or chemical processes behind the function (Fortelius et al. 2021). In an idealized "taxon-free" scenario one could potentially sample a set of specimens from a fossil site without knowing species names or their affiliations to higher taxonomic groups, measure selected functional traits, compute statistics over the measurements and reason about the prevailing vegetation structure or climatic conditions. Or could one?

Before attempting to answer this question, let us consider the contexts in which the term "taxon-free" has been used in paleoecological literature with a focus on using traits to make an inference about local environmental conditions. To the best of my knowledge, the term emerged in paleobotanical literature in late 1980s (Orlóci and Stofella 1986; Wing 1988), followed by mammalian literature in early 1990s (Damuth 1992; Plummer and Bishop 1994; Viranta and Andrews 1995). More recently, the use of the term expanded to a broader range of organisms, reptiles, including marine organisms and plants (Lavorel et al. 2008; Smith et al. 2020; Mächler et al. 2021; Parker et al. 2023). Even if the term itself has not yet been in use, quantitative trait-based methods for characterization of organismal communities go back at least to the late 1970s (Andrews et al. 1979).

Table 1 summarizes different contexts in which the term "taxon-free" has been used in literature, focusing on mammals. While the primary use of the term has been to characterize the structure of organismal communities (Viranta and Andrews 1995; Mendoza et al. 2005; Soligo and Andrews 2005; Lavorel et al. 2008; Le Fur et al. 2009; Louys and Meijaard 2010; Polly et al. 2011; Hock 2018; Lintulaakso 2018; Smith et al. 2020; Parker et al. 2023; Wilson et al. 2024), some literature uses the term to characterize individual organisms in terms of their functional traits (Plummer and Bishop 1994; Palmqvist et al. 2002; Klein et al. 2010; Scott and Barr 2014; Barr 2018; Paine et al. 2019; Sambo 2020). In case of individual organisms, more often than not "taxon-free" is implicitly used as a synonym to "ecomorphological" when characterising organisms in terms of their ecology. Conceptual frameworks discussing methodological aspects of the approaches exist as well, most of them highlighting "taxon-free" approaches as methodologically superior to approaches drawing on taxonomic information (Eronen et al. 2010; Barnosky et al. 2017; Vermillion et al. 2018; Faith and Lyman 2019), while others are critical of the idea that ecomorphology is strictly taxon-free (Barr 2018).

In the context of analysing organismal communities, the term "taxon-free" is often used to highlight that functional trait distributions can be used to compare communities independent of taxonomic identities and even if they do not have species in common (Eronen et al. 2010; Vermillion et al. 2018). While this is theoretically possible, in practice analysis of this kind is rarely, if ever, free from taxonomic information and more recent literature sources often explicitly acknowledge that trait-based inferences are not taxon-independent (Klein et al. 2010; Polly et al. 2011; Barr 2018).

There are two main ways in which taxonomic or phylogenetic information is commonly used in "taxon-free" approaches. The first way is propagating morphological traits on the taxonomic basis. Often sufficient is to know morphological traits at the species or a higher taxonomic level. Once can then assume that all the individuals of the same species have the same traits and propagate those trait values through the lists of taxa at localities. For example, knowing that all the representatives of the genus *Equus* are hypsodont, studies would not need to inspect every specimen at every locality but instead would assign crown height to be "hypsodont" for all Equus that occur through the dataset (Fortelius et al. 2002; 2016). While not literally "taxon-free" this approach is theoretically legitimate as long as species identification is accurate. The second way is assigning functional traits on the basis of phylogenetic proximity. The difference from the first way is that in the first way taxa is exactly the same, while in the second way only the traits of a taxonomic relative are known.

For instance, traits that are in principle not directly observable in fossil specimens, such as arboreality, tropical guild or diet category can be assigned to fossil taxa assuming that phylogenetic relatives carry similar traits (Louys and Meijaard 2010) either only due to historical contingency due to common ancestry or also due to presence of phylogenetic niche conservatism. Phylogenetic niche conservatism refers to the tendency of closely related species to be more ecologically similar than would be expected based on their phylogenetic relationships (Losos 2008). While empirically such approaches can work, theoretically they are problematic, since phylogenetic similarities do not necessarily imply ecological similarities (Westoby et al. 1995; Losos 2008) when lineages evolve through time. And certainly, such approaches are not "taxon-free" and should not be labelled as such.

A different category of approaches do not use traits at all but rely on phylogenetic conservatism directly to infer ecological contexts (Birks 2005; Bobe 2011). Those approaches are out of the scope for current discussion.

The idea of functional trait ecology is that a direct functional relationship between a trait and an environmental factor exists and that there should be a causal relationship between environment and that trait through processes of natural selection or sorting. This is the core of what most authors mean by "taxon free", focusing on that relationship rather than species identity. We can only study the functional relationship directly in the present-day world where the species are different than they were in the past, but if we model the functional relationship in a trait-based way, we can make inferences on different communities composed of extinct species. Even traits that have evolved many times convergently, many of them still have a taxonomic scope, and functional traits are usually specific at least to a higher taxonomic group level. Thus, traits and taxonomy are inextricably linked.

While the use of taxonomic or even phylogenetic information is common in trait-based approaches, approaches that do not use taxonomic information, even if very rare, exist in the literature (Lavorel et al. 2008). Such approaches, however, are realistically only possible with small sample sizes. In addition, the community-level trait averages may be skewed towards traits carried by organisms of smaller body sizes (Žliobaitė and Lawing 2025).

Following the arguments above, I propose that approaches to paleoecological inferences from organismal community structure do not need to be taxon-free, but they better be phylogeny-free. That is, taxonomic information can be used to propagate traits through species lists for exactly matching species but inferring traits based on the nearest relatives should be avoided when possible.

Trait distribution within organismal communities carries predictive power about environmental conditions if the individuals included in the community have ecologically comparable ways of life. This corresponds to individuals belonging to the same adaptive zone or the same guild and sharing the same resource space. For instance, mammalian carnivore and herbivore communities occurring at the same locality do not directly compete for the same food resources and need to be treated separately when used for trait-based paleoecological inferences, while reptilian herbivores could be treated together with mammalian herbivores, since their edible resource space can at least partially overlap (Wilson and Parker 2023). One way or the other, to assemble ecologically meaningful communities for trait-based inferences for each fossil occurrence at a locality one needs to know at least: (1) which body part the specimen represents and (2) to which higher taxonomic group it belongs. Many putative taxon-free studies limit themselves to taxonomic groups where the independence of taxonomic affiliation is lost (e.g., teeth are uniquely a vertebrate trait, hair-covered integument is uniquely a mammalian trait). For instance, if one would like to make paleoecological inference from the limb proportions of carnivores, one needs to know which of the fossil specimens found at a site represent carnivores. The inevitable need for assigning to a higher-level taxonomic is the first reason why it is unrealistic for trait-based approaches to operate free from taxonomic information and unfair to claim so.

The potential for scalability and robustness of the analysis is the second reason why trait-based approaches to paleoecology in practice often to draw on taxonomic information. Researchers commonly identify functional traits at the species level (and sometimes even higher taxonomic levels) and propagate them to localities based on species occurrence data regardless whether the trait itself has been directly observed there (Liu et al. 2012; Polly and Head 2015; Oksanen et al. 2019; Faith and Lyman 2019; Parker et al. 2023). This way, dental traits, for instance, can be assigned even to fossil specimens that are represented only by limbs as long as the limbs are taxonomically identifiable. This common practice enables studies of large scope in space and time, but requires the explicit use of taxonomy to maximise sample sizes.

For these reasons trait-based approaches to paleoecology, even if they do not rely on phylogenetic niche conservatism, commonly rely on at least some taxonomic information, and, strictly speaking should not be labelled “taxon-free”. To prevent further confusion in the literature I propose dropping the term “taxon-free” and instead referring to those approaches as “trait-based” approaches.

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