

Paleoenvironmental Reconstruction from Faunal Remains: Ecological Basics and Analytical Assumptions

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Abstract Paleozoologists have long used taxa represented by ancient faunal remains to reconstruct paleoenvironments. Those ancient environments were the selective contexts in which hominin biological and cultural evolution took place. Knowing about those particularistic selective environments and how organisms responded to them is increasingly seen as critically important to identifying both how biota will respond to future (to some degree anthropogenically driven) environmental change, and biological conservation and management applications that will ensure sustainability of ecological resources and services. Reconstructing paleoenvironments requires knowledge of species' ecological tolerances, geographic ranges, habitats, environments, and niches. It also requires assumptions that extant species had the same ecological tolerances in the past as they do today and that changes in taxonomic composition or abundances reflect environmental change rather than sampling or taphonomic factors. Greater knowledge of ecological processes as well as increased analytical sophistication in paleozoology is providing increasingly rigorous and detailed insights to paleoenvironments.

Keywords Ecological tolerances · Paleoclimate · Paleoenvironmental reconstruction · Paleozoology · Taxonomic identification · Zooarchaeology

Science can only help us if we use it to show how the present is a product of the past, and to remind us that we are now shaping the future. It is the privilege of the paleoecologist to reconstruct a [temporal ecological] continuum so convincing that the lesson will be heeded.... It may well be that [paleoecological] findings will, in the end, mean far more to the future of mankind than [we] now suspect. (Sears 1964, p. 5)

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Introduction

It has become increasingly apparent in the past three decades that the paleozoological record, whether paleontological or zooarchaeological, comprises an archive of experimental results concerning how biota respond to environmental change (Dietl et al. 2015; Sandweiss and Kelley 2012, respectively). As such, that record is being consulted more and more often as conservation biologists and others seek to predict the future biological health of planet Earth. The hope is that learning how past biotas responded to environmental change will provide insight to how future (to some degree anthropogenically driven) environmental change might be mediated such that ecological goods and services are not significantly impacted (e.g., Dietl and Flessa 2009; Lyman and Cannon 2004; Wolverton and Lyman 2012). As custodians of a large portion of the paleozoological record, archaeologists have, I believe, a moral and ethical responsibility to not only protect but to utilize that record for humankind's benefit. How might it be so utilized?

Zooarchaeologists and paleontologists have long known about the insights to paleoecology that might be gained by close study of ancient faunal (and floral) remains (for some history, see Grayson 1981; Lundelius 1998; Semken 1983). Over the years they have summarized some of the necessary analytical assumptions and critically evaluated several of them (e.g., Churcher and Wilson 1990; Graham and Mead 1987; Graham and Semken 1987; Grayson 1981; Semken and Graham 1987). Today we have a much more intimate understanding of ecological principles, the limitations of paleoecological analyses of ancient faunas, and how to sometimes overcome those limitations (e.g., Andrews 2006; Domínguez-Rodrigo and Musiba 2010; Fernández-Jalvo et al. 2011). In addition, there are now numerous efforts to forecast changes in biota that may occur as a result of future (anthropogenically driven) climatic change (e.g., Hijmans and Graham 2006; Parmesan 2006). That large and growing body of literature contains several nuanced discussions of the limitations of using biological data as proxies for environmental variables that are directly pertinent to using zooarchaeological remains to reconstruct or “hindcast,” the modelers say, paleoenvironments (e.g., Belyea 2007; Birks et al. 2010; Huntley 2012; Nógues-Bravo 2009). Therefore, the time is ripe for an up-to-date synthesis. It is my purpose here to provide just such a synthesis in the hope that it will foster greater use of the paleozoological record for purposes of future conservation biology.

In particular, I do two things in this paper. First, I outline some basic theoretical ecology that underpins paleoenvironmental reconstruction based on taxonomically identified faunal remains. The development of ecology as a field of inquiry influenced the development of paleoenvironmental reconstruction because the former was the source of several key interpretive concepts embedded within the latter (Terry 2009; Wilkinson 2012). Once the ecological basics have been introduced, I describe and critically evaluate analytical assumptions that underpin paleoenvironmental reconstructions based on taxonomically identified faunal remains. I consider just those assumptions and limitations that result from analytical dependence on taxonomic identifications of faunal remains, highlighting

weaknesses of the assumptions and analytical hurdles that must be cleared and identifying means to contend with them.

I do not explore analyses used to reconstruct past environments based on stable isotopes of faunal remains (e.g., Lee-Thorpe 2008; Munoz et al. 2014), tooth structure (e.g., Fortelius et al. 2006), dental attrition (e.g., Caporale and Ungar 2016; Faith 2011; Rivals et al. 2007), dental pathologies (e.g., Byerly 2007), and the like. Nor do I delve into the assumptions and processes of paleoenvironmental reconstruction based on taxon-free analytical methods (e.g., Andrews and Hixson 2014; Damuth 1992). Omission of particular fields of inquiry is not meant to imply other data and methods are unimportant, only that they are not the focus of this discussion. I do not here delve deeply into the diverse analytical methods that have been used over the years to decipher the paleoenvironmental meaning of taxonomically identified animal remains. For introductory overviews of analytical methods, see Andrews (1996), Graham and Semken (1987), Reed (2013), and Reed et al. (2013).

I largely ignore the influence of particular taphonomic processes that skew paleoenvironmental signals of collections of faunal remains, only mentioning generic outcomes of accumulation and preservation of remains when consideration of them is essential. Detailed coverage of taphonomy alone would require expanding the length of the discussion considerably (e.g., Behrensmeyer 1991; Behrensmeyer et al. 2007; Fernández-Jalvo et al. 2011; Lyman 1994; Turvey and Cooper 2009). Similarly, I do not spend significant time on issues attending the quantification of faunal remains; that topic has been covered in detail elsewhere (e.g., Grayson 1984; Lyman 2008b). Here I presume the favored unit of quantification for measuring, say, taxonomic abundances is not a significant issue, yet acknowledge that it is in fact contentious (e.g., Domínguez-Rodrigo 2012; Giovas 2009; Lyman 2008b; Nikita 2014; Thomas and Mannino in press; Turvey and Blackburn 2011).

Even though the assumptions underpinning paleoenvironmental reconstructions based on zooarchaeological remains have been previously outlined (e.g., Findley 1964; Harris 1963a; Lundelius 1964; Redding 1978; Yalden 2001), none of these earlier discussions identified all key assumptions, nor were those assumptions critically evaluated from a modern ecological or taphonomic perspective. The underpinning assumptions were spelled out explicitly several times in the 1960s and 1970s during a florescence of interest in paleoecological research by paleontologists and the formalization of analytical methods and assumptions (Gifford 1981; Lundelius 1998; Rainger 1997; Semken 1983; Terry 2009). The assumptions are, however, seldom mentioned in recent literature. To review them from a modern perspective is, then, to guard against researchers becoming complacent and resulting “ignorance creep” (Jackson 2012), or the loss of cognizance of critical assumptions and knowledge.

My interest is particularly on mammal remains because they tend, on average, to be much more ubiquitous and abundant in archaeological deposits than remains of fish, birds, reptiles, and mollusks. My remarks, however, pertain to all taxonomically identified vertebrates, and invertebrates and plants as well. Throughout I use the term *assemblage* to label an aggregate of faunal remains that are thought to be

temporally associated or similar in calendric age. I use *paleozoologist* as a generic term for both zooarchaeologists and paleontologists who study animal remains. Given my training and research experiences, much of what I know concerns North America, hence the somewhat geographic-centric literature cited. When introducing the analytical assumptions that underpin interpretation of paleozoological remains in environmental terms, I cite numerous references for two reasons. First, the number of citations is positively and directly (if imperfectly) related to the perceived analytical importance of the particular assumptions. And second, the dates of publication of the references cited reveals something of the history of a particular assumption, such as when it was explicitly (originally?) acknowledged. I am a firm believer in that knowing where we came from intellectually helps us understand why we are now where we are intellectually.

Ecological Basics

Biologists and ecologists have since the middle of the 18th century observed that each particular species of organism is not ubiquitous but instead has a somewhat unique geographic distribution that is more or less limited (Brown and Lomolino 1998). Environmental variables that limit a species' distribution were initially obscure. Eventually, inductive pattern recognition prompted questions. Was there an impassable barrier between two equally habitable areas of which only one was occupied by a species? Was there too much (or too little) rainfall in unoccupied areas for a particular plant to survive? Did the flora in an area not include plant species eaten by a particular animal species and hence that animal was not present there, or was there another species of animal that out-competed (and thus displaced) the absent species? And so on. As is often the case in natural history endeavors, familiarity with the phenomena under study eventually began to reveal patterns that seemed to have explanatory potential. Figuring out why organisms had the distributions they did eventually become a, if not *the*, foundational basis for paleoenvironmental reconstruction.

Ecological Tolerances

Early in the 20th century ecologist Shelford (1913, 1931) proposed what is today sometimes referred to as “Shelford’s law of tolerance.” Shelford noted that ecological factors influence the presence, absence, and abundance of animals (and plants), and these factors operate according to Liebig’s law of minimum. Liebig’s law holds that the ecological variable necessary to an organism’s occurrence that is least abundant in an area will limit the organism’s abundance in that area; other necessary resources may be significantly more abundant than necessary, but the least available resource will be the limiting one. Shelford indicated that if a critical variable was too abundant, it too could limit an organism’s abundance. This *law of toleration* as Shelford referred to it is typically modeled as shown in Figure 1.

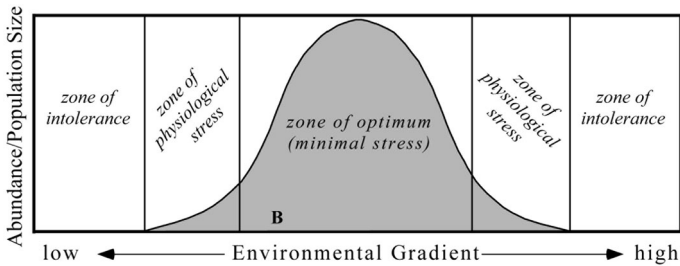


Fig. 1 Ecological tolerance curve. Any environmental variable can be plotted on the horizontal axis; the gray shaded area represents the population distribution for one species. When interpreting the presence or abundance of a species in a prehistoric assemblage, the analyst assumes the individuals represented fall near the middle of the tolerance curve

In theory, any ecological variable can be plotted on the x-axis for any species. Typical x-axis variables include temperature, precipitation, frost-free days, biomass of food sources, frequency of competitors, frequency of predators, or any of a plethora of other variables that an organism requires or with which it may have to contend. Today the filled-in graph is often referred to as an organism's niche (Lynch and Gabriel 1987; Pianka 1978) (see discussion of the niche concept below), but Figure 1 is also a model of how environmental variables influence an organism's presence/absence and abundance across an environmental gradient (e.g., cool to warm temperature). The values of an environmental variable at the extremes of the tolerance curve are sometimes referred to as *limiting factors* (e.g., King and Graham 1981; Raup and Stanley 1971). Whether or not values of any given environmental variable on the x-axis are known for a particular taxon is another matter. Those values are difficult to know given that any organism, plant or animal, must adapt simultaneously to a plethora of (but typically not all) environmental variables (Kearney and Porter 2009; Sexton et al. 2009; Wisz et al. 2013).

There are several subsidiary principles of the law of tolerance (after Odum 1971). The environmental variable controlling the abundance of a taxon in one area may not be the same variable that is controlling that taxon's abundance in another area. A species may have a wide range of tolerance for one environmental variable but a narrow range for another variable. Species with wide tolerance ranges (referred to as *eurytopic*) for most or all environmental variables tend to have larger geographic distributions than those with narrow tolerances (referred to as *stenotopic*) for many variables. Fourth, environmental variables may interact through the physiology of a species such that, say, if conditions of one environmental variable are suboptimal for that species, tolerances may be suboptimal with respect to other variables as well. One or several environmental variables may be more important than others with respect to limiting where a species can live. And finally, environmental factors are most likely to be limiting during a species' reproductive season.

And if the preceding did not make the job difficult enough, the particular environmental factors influencing the prehistoric presence/absence or abundances of a taxon must be identified (inferred or assumed) by the paleozoologist (Harris 1985).

How to determine those parameters is beyond my scope here, but as indicated below, several modern modeling techniques seem to hold great promise.

The breadth of the *tolerance curve* is the total response of all individuals of a species over an environmental gradient (Lynch and Gabriel 1987). Within a population of a species, each individual organism's unique genotype results in a slightly different location and breadth of tolerance curve along the environmental gradient than other individuals, recognizing that each unique phenotype has a more or less unique adaptation because it is a result of interaction between the environment and the genotype (Fig. 2). The tolerance curve for a population (or all populations) of a species is, then, a composite (not an average or mode) of the particular tolerances of individuals (Lynch and Gabriel 1987), much like a summed probability distribution of multiple radiocarbon dates (Fig. 2). Intraspecific variability is masked, creating a potential interpretive pitfall when it comes to paleoenvironmental reconstruction (McCain et al. 2016). Our reconstructions are founded on the overall tolerances of all individuals making up a species. We interpret the presence of a species in a prehistoric assemblage as indicating environmental conditions for that species' tolerance curve, even though the individuals represented in the assemblage of paleozoological remains could be ones with tolerances in some limited portion of the curve (Walker 1978). Anderson (1968) suggests this possible pitfall can be avoided by considering all species in an assemblage. If all imply the same environment, one can have greater confidence in the validity of a reconstruction because it is unlikely that all individuals, or species, were living atypically. A multispecies (or multiple independent lines of evidence) solution is a common approach when we are faced with potential interpretive pitfalls.

Environments and Niches

The *environment* is “the sum total of all physical and biological factors impinging on a particular organismic unit” (Pianka 1978, p. 2). Physical factors include such abiotic things as weather, climate, geology, solar radiation, and the like; biotic factors include species and abundances of plants and animals present. The environment is the context in which an organism lives, with which it interacts, and

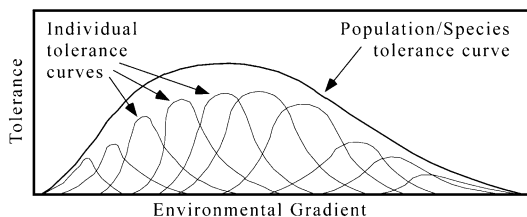


Fig. 2 A model of how tolerances of individual organisms of a species produce a fundamental niche or a species-level tolerance curve, here labeled “Population fitness” (see Fig. 1). When interpreting the presence or abundance of a species in a prehistoric assemblage, the analyst assumes the individuals represented fall near the middle of the tolerance curve. This figure reveals that those individuals might not

to which it may adapt. The environment is hyperdimensional; it consists of all those variables external to the organism. It is complex and multiscalar, varying along both spatial (e.g., geography or location, area or size) and temporal scales (e.g., daily vs. seasonally vs. annually). Part of the biotic environment of concern to an individual organism is individuals of its own species (conspecific mates) as well as of other species (e.g., prey, competitors, predators). With respect to paleoenvironmental reconstruction in archaeology, the term environment is usually restricted to the natural environment—climate, weather, flora, fauna, topography, geography, geology, etc., and their types, frequencies, amplitudes, distributions in geographic space and time (or structure), and the like; people tend to be excluded as part of the environment. The paleoenvironment is the natural context of the prehistoric site or culture under study at the time the site was occupied or when the represented culture existed. Given how the term is used by paleozoologists who reconstruct paleoenvironments, a (paleo)*habitat* is a description of a kind of a spatiotemporally bounded place where an organism lived; vegetation is often the emphasized environmental variable but not to the exclusion of climate (e.g., temperature extremes, annual precipitation).

It is today generally agreed that three categories of variables influence the distribution of a particular species. Referred to as the BAM model, these variables are the distribution of biotic factors (B) required by the species and those with which the species might compete, and to which the species might fall prey or be otherwise susceptible (e.g., pathogens); the abiotic factors (A) such as climate and elevation to which the species must adapt; and the mobility (M) or dispersal capabilities of the species, including its vagility (Soberón 2007; Soberón and Peterson 2005). The included variables are important to keep in mind because if the ecological tolerances of organisms are poorly known, the geographic distributions of species can be used to approximate those tolerances (see discussion of *Assumption 3*, below). Similar reasoning has permeated much of modern ecological modeling and the niche concept.

Following Hutchinson's (1957) classic conceptualization, an organism's *niche* is conceived as a multidimensional hypervolume of environmental conditions and resources defining the requirements for a species to exist (e.g., Colwell and Rangel 2009; Soberón 2007; but see Holt 2009). A species' *fundamental niche* concerns the particular combination of environmental variables in which that species can occur; the species' *realized niche* incorporates the effects of biological factors (e.g., competitors) that preclude that species' occurrence such that it only occurs in a portion of its fundamental niche (Graham 2005; Jackson and Overpeck 2000; Kearney and Porter 2004; Williams and Jackson 2007). The former concerns where a species *could* occur, whereas the latter concerns where a species *actually does* occur, thus a species' realized niche tends to be geographically smaller than its fundamental niche. This distinction of fundamental and realized niches is critically important in light of the recent work in ecological modeling.

With greater computer power combined with modeling expertise and growing concerns over being able to predict how future anthropogenically driven climatic change may influence biota (Dawson et al. 2011), numerous researchers have constructed ecological niche models (Morin and Lechowicz 2008; Qiao et al. 2015;

Soberón and Nakamura 2009), species distribution models (Austin 2007; Elith and Leathwick 2009), and bioclimatic envelope models (Araújo and Peterson 2012; Polly and Eronen 2011). Archaeologists have recently discussed the potential of such models for the study of human prehistory (Franklin et al. 2015), but it must be noted that biologists continue to identify weaknesses in these models (Heads 2015). Coarsely put (Peterson and Soberón 2012), the models incorporate as many environmental variables as possible into a species' ecological tolerance model (Fig. 1) in order to predict where that species might survive on a changing environmental landscape (e.g., Mota-Vargas and Rojas-Soto 2016). These models are now being tested with paleobiological data for which environmental parameters are known (e.g., Dietl et al. 2015; McGuire and Davis 2014; Rowe and Terry 2014; Terry et al. 2011). Much of this work so far has involved searches for correlations and stops short of identifying causal linkages between a species' presence/absence and an environmental variable (Belyea 2007; Hampe 2004; Kearney and Porter 2004, 2009; Qiao et al. 2015; Sexton et al. 2009; Varela et al. 2011), thereby revealing a major weakness in the models. Nevertheless, insofar as these models provide ecological tolerance-like information on species, they could be of major use to paleozoologists interested in reconstructing paleoenvironments (Svenning et al. 2011; Varela et al. 2011). The model in Figure 3 captures the essence of conceptualizing a species' niche and also how climatic change over time results in changes in the fauna of an area.

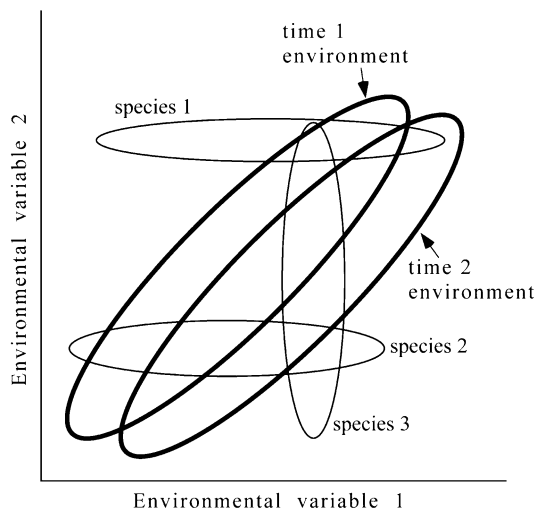


Fig. 3 A conceptual model of species' niches and the co-occurrence of two or more species and why species assemblages change over time as a result of environmental change. Two different environments (*bold ovals*) exist at two different times. The fundamental niches (ecological tolerances) of three species (*nonbold ovals*) are shown and do not change from time 1 to time 2. Co-occurrences of species can occur when their fundamental niches overlap with one another and with the environment at a particular time. Thus species 1 and 3 co-occur at time 1 without species 2, and species 2 and 3 co-occur at time 2 without species 1. Species 1 and 2 cannot co-occur because their fundamental niches do not overlap (redrawn after Williams and Jackson 2007)

It has become increasingly clear since Hutchinson's (1957) influential conceptualization that a species' niche may be static over long temporal periods or it may evolve (see review and references in Holt 2009). This makes modeling a modern niche difficult, particularly if that niche model is used to reconstruct paleoenvironments. Further, as indicated in Figure 3, what Quaternary paleozoologists in particular refer to as *disharmonious* or *non-analog faunas* (Graham 2005) occurred with some regularity in the past. These faunas are made up of species that are stratigraphically and temporally associated (e.g., Semken et al. 2010) and are inferred to represent biological communities of species that were in the past biogeographically *sympatric* or coexisted but today are *allopatric* or do not co-occur in an area or habitat. Such faunas were recognized by paleozoologist Hibbard (1955, 1958, 1960), who came to understand that they did not represent stratigraphically mixed or time-averaged remains from different climatic eras (Zeuner [1936] mentioned the co-occurrence of “tropical” and “temperate” species but his discussion seems to have had little impact on the discipline). Multiple records of non-analog faunas quickly lead to the realization that past climates were at least sometimes more seasonally equable than modern climates (e.g., Graham and Mead 1987). Summer temperatures were cooler, allowing northern species to occupy more southern latitudes than at present, and winter temperatures were warmer, allowing southern species to live north of their modern range.

Non-analog is the preferred label rather than disharmonious because the fact that the species occurred together suggests there was no ecological disharmony (Semken 1988); “no-analog” has been used to label floras without modern analogs and is conceived differently than non-analog faunas (Graham 2005). Importantly, non-analog faunas also reinforced among ecologists the shift from conceiving a biological community as made up of functionally interdependent species—a sort of superorganism kind of entity (Clements 1936; Clements and Shelford 1939)—to a set of organisms that were functionally and ecologically independent of one another. Under the former model, communities shift as a whole, in a kind of expanding and contracting accordion-like manner such that the composition of the communities does not change (e.g., Martin 1958). The alternative thesis, referred to as the *individualistic hypothesis* using the term coined by ecologist Gleason (1926), is preferred today and explains why non-analog communities are found in the past. In short, each individual species has unique ecological tolerances and is ecologically independent (more or less) of all other species with which it might come in contact and interact. Thus it is not surprising that unique climatic regimes in the past would produce unique faunal communities.

Without explicit recognition that they were labeling a concept similar to non-analog faunas, botanists proposed the term *novel ecosystem* (Chapin and Starfield 1997) when considering the effects of modern, anthropogenically driven global warming on arctic plant communities. Paleobotanists had acknowledged that Pleistocene plant communities were often novel in species composition relative to modern communities (e.g., Davis 1976, 1981). Conservationists quickly picked up on the concept of novel ecosystems (e.g., Hobbs et al. 2009, 2014; Williams and Jackson 2007) but have seldom acknowledged Hibbard's (1960) seminal insight. An important aspect of non-analog faunas and novel ecosystems is implied in Figure 3.

In short, species may exist under environmental conditions that do not exist today but did exist in the past and may exist in the future (Jackson and Overpeck 2000; Williams and Jackson 2007). This of course renders modeling species-specific bioclimatic envelopes, niches, and distributions tenuous when only modern data for a species are used. However, as our knowledge of critical variables making up a species' niche increases, models should become more accurate and thus of value to those seeking to reconstruct past environments.

What to Do When Environment Changes

What happens when the environment changes, say, summer temperatures get warmer than the temperature to which an organism is adapted? The taxon represented by the tolerance curve (Fig. 1) has three options (Gauthreaux 1980; Gienapp et al. 2008; Lister 1997). It can relocate, that is, geographically track favorable conditions to which it is adapted (e.g., Guilday and Parmalee 1972). Alternatively, the local population can die out in the area where the temperature has risen (e.g., Grayson and Delpech 2005). Or the local population can adapt; in this case, a population may alter its behaviors (e.g., Varner et al. 2016) or it may evolve as a result of natural selection such that the geographic range of the species does not shift (e.g., Faith et al. 2016). Environmental change is, of course, a driving force of evolutionary change. Paleozoologist Vrba (1985, 1992) used that truism to develop the *turnover pulse hypothesis* that provides explanations for species evolution, extinction, and biogeographic range shifts. Independent tests of the hypothesis with animal fossils have shown it to be a viable explanation of faunal turnover (Faith and Behrensmeier 2013).

If winter temperature minima decrease or increase a degree or two in a particular area, we have essentially relocated the position on the tolerance graph we are considering. Consider point “B” on the x-axis of Figure 1. Point “B” represents the drop in winter temperature from the optimal value corresponding to the peak in the population curve. The bell-shaped curve in the horizontal position of point “B” is low, indicating fewer individuals because that lower temperature is not the most optimal one. The implication is that a species can respond to environmental change by altering the frequency of individuals, increasing when environments get better, decreasing when environments become more stressful and less optimal. Yet organisms can increase or decrease in abundance for unclear reasons, perhaps even for nonenvironmental ones.

Top-Down or Bottom-Up Ecology

Through much of the early history of ecology the preference was to conceive of the composition and structure of an animal community as strongly influenced by available resources, particularly vegetation (e.g., Elton 1927). The abundance or availability of resources at the lowest level or tier of the trophic pyramid (Fig. 4) was believed to influence abundances (and kinds) of organisms at higher levels

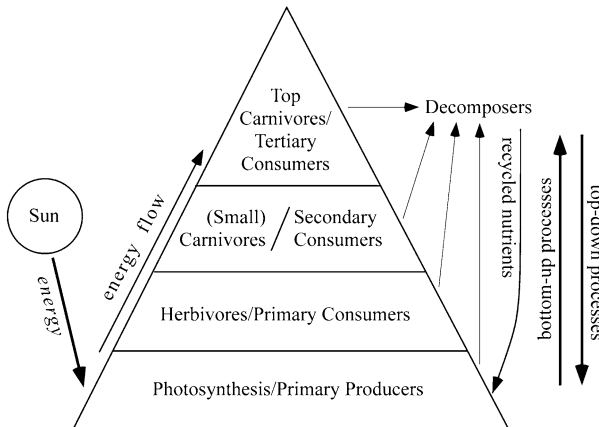


Fig. 4 A model of the trophic pyramid including the flow of energy and recycling of nutrients through decomposition at all levels of the pyramid. Bottom-up processes work from the sun (climate) upwards in the direction of energy flow; top-down processes involve changes at high levels (e.g., an increase in tertiary consumers) such that lower levels are influenced

(Leroux and Loreau 2015). The preference for these *bottom-up ecological models* (Hunter and Price 1992) began to change in the second half of the 20th century when it was suggested that predators (e.g., carnivorous mammals) could, by their abundances, influence the abundance of herbivores, which in turn influenced the abundance of vegetation (e.g., Estes 1996; Hairston et al. 1960). These *top-down models* resulted in the notions of *keystone species* (e.g., Mills et al. 1993; Simberloff 1998) and *trophic cascade effects* (e.g., Paine 1980). A keystone species is one that has a large effect on an ecosystem relative to its abundance. Trophic cascades are triggered by (keystone) species occupying middle or high levels in the trophic pyramid that, when they increase or decrease in abundance, alter ecosystem structure and nutrient cycling. Keystone species are sometimes carnivores (e.g., Estes 1996) and sometimes herbivores (Owen-Smith 1988; see for example Knapp et al. [1999] and Mack and Thompson [1982] on North American bison [*Bison bison*] as a keystone species). The ultimate keystone species today is humans as reflected in the concept of the Anthropocene (e.g., Ruddiman 2013); modern manifestations of top-down cascade effects in archaeology are found in models of prey depression used by zooarchaeologists (e.g., Broughton and Cannon 2010; Lupo 2007). Recent ecological research indicates both bottom-up and top-down processes typically operate, and at times one, the other, or neither is dominant (Hanley and La Pierre 2015).

The distinction of bottom-up and top-down ecological processes is relevant to paleoenvironmental reconstruction for two reasons. First, much of the literature concerning paleoenvironmental reconstruction suggests that plant remains are a better source of information on ancient climates because the distributions and abundances of animals are more strongly influenced by their habitats or the flora in which they live than by climatic variables such as temperature or precipitation (e.g., Andrews 1996; Avery 1982, 1990, 2007; Bökönyi 1982; Chaline 1977; Churcher

and Wilson 1990; Faunmap Working Group 1996; Flannery 1967; Grayson 1977; Huntley 2012; King and Graham 1981; Reed et al. 2013; Tchernov 1975; White 2008; Woodcock 1992). Vegetation, it is argued, is strongly and relatively directly influenced by climate. Climate change influences types and abundances of vegetation that in turn influence types and abundances of herbivores that feed on it. The appropriate analytical protocol should, it is therefore reasoned, involve reconstruction of past vegetation on the basis of the fauna and then reconstruction of past climate based on the (reconstructed) flora. This recommendation is at least partially a reflection of a bottom-up model of ecosystem structuring.

This model is still generally followed by researchers who attempt to build paleohabitat or paleoclimate models (e.g., Avery 1990; Reed et al. 2013), but it also has been shown that the middle step may not be necessary. Because some species of animals are sometimes strongly influenced directly by climate (Birch 1957; Heisler et al. 2014 [and references therein]), one can sometimes reason from animals directly to climate once a climatic envelope for each species is determined (e.g., Polly and Eronen 2011).

The second reason to be aware of the distinction between bottom-up and top-down ecological processes is that the latter include anthropogenic processes, both modern industrial ones and prehistoric ones. The significance of this observation is that those interested in reconstructing paleoenvironments must not confuse top-down (e.g., anthropogenic) driven change from bottom-up (e.g., climatic) driven change in paleofaunas. Zooarchaeologists recognized this potentiality when they worried about the “cultural filter” (Reed 1963; Reed and Braidwood 1960), a label for human behavioral processes thought to jeopardize (if not completely invalidate) any attempt to reconstruct paleoenvironments from zooarchaeological remains (e.g., Daly 1969; Holbrook 1975, 1982a, b; Reed 1963). But though the “cultural filter” is indeed a potential problem, it is no more of a problem than any taphonomic process that results in a collection of faunal remains that, because of biased accumulation or preservation or both, provides an inaccurate environmental signal (Semken 1983; Semken and Graham 1987). Despite the fact that we are much more taphonomically sophisticated today than even a couple of decades ago, the decipherment of which changes in prehistoric faunas reflect environmental (bottom-up) changes and which represent shifts in human behaviors or other top-down processes remains a significant challenge (Gandiwa 2013; Parmesan 2006; Pierce et al. 2012).

Discussion

Standard meteorological data derived from conventional weather stations concern macroclimate (patterns $>1000 \text{ km}^2$) or mesoclimate ($1\text{--}1000 \text{ km}^2$) (Birks et al. 2010; Coope 1986; Graham and Semken 1987; Huntley 2012). If habitats occupied by species are conceived in very general terms (e.g., woodland, grassland), the resulting reconstructions will be of similar resolution (Andrews et al. 1979; Evans et al. 1981; Gustafson 1972; Kingston 2007; Wilson 1973). The construction of ecological niche models, species distribution models, and bioclimatic envelope models mentioned above seems to hold great promise for providing interval-scale

resolution in paleoenvironmental reconstructions. Paleozoologists have built species-specific bioclimatic envelope models (Polly and Eronen 2011) and other models that provide high-resolution reconstructions (e.g., Hernández-Fernández 2001; Hernández-Fernández and Peláez-Campones 2005; Sénégas and Thackeray 2008; Thackeray 1987; Thackeray and Reynolds 1997).

What is hoped for is a high-resolution reconstruction such as one that reveals, for example, an annual 7–10 cm increase in precipitation and a concomitant decrease in temperature of 2–3 °C (e.g., Bañuls-Cardona et al. 2012). In the absence of detailed knowledge about the environmental variables that define a species' ecological tolerances (the horizontal axis in Fig. 1), one of three analytical alternatives is called for. One is to consider the geographic distribution of a species (e.g., Graham 1976; Johnson 1960; Lundelius 1967, 1976; Rymer 1978; Slaughter 1967; Tchernov 1975; Yalden 2001). From a northern hemisphere viewpoint, if the species is today found only in high latitudes to the north of the site of recovery, the species must be relatively cold adapted; if it is today found only in low latitudes to the south of the site of recovery, the species must be relatively warm adapted.

Another alternative is to consider the kind of vegetation or habitat in which the species is found today (e.g., Andrews et al. 1979). Is it in boreal forests, grasslands, savannas or steppes, open woodlands, parklands? The result is often a relatively low-resolution reconstruction of a past environment (e.g., Czaplewski et al. 1999; Schubert 2003). The third alternative is to examine one or more morphological or metric attributes of the bones and to interpret those attributes as ecologically sensitive (e.g., Gould 1969). This alternative has been referred to as *ecometrics* (Eronen et al. 2010; Polly et al. 2011) and *ecomorphology* (Reed et al. 2013), though the labels refer to different techniques. This alternative is not a focus of the following discussion, but I mention it where appropriate. In short, the basic method involves identifying a dental or skeletal trait that co-varies with one or more environmental variables and then assuming the correlation between the two holds in the past (e.g., Jass et al. 2015).

Species also may respond to environmental change according to eco-geographical rules (Mayr 1970). These include Bergmann's rule—"races from cooler climates in species of warm-blooded vertebrates tend to be larger than races of the same species living in warmer climates" (Mayr 1970, p. 197)—and Allen's rule—"in warm-blooded animals protruding body parts like tail and ears are shorter in cooler than in warmer climates" (Mayr 1970, p. 199). The traditional explanation concerns retention and loss of metabolic heat. The larger the body, the smaller the ratio of surface area to volume (Bergmann's rule). The longer the appendage (forelimb, hindlimb, ear), the greater the surface area (Allen's rule). In warm climates, smaller bodies will have relatively larger surface areas and greater loss of (unnecessary) metabolic body heat. There are many discussions about the validity of and exceptions to these rules (e.g., Alhajeri and Stepan 2016; Huston and Wolverton 2011; McNab 2010; Millien et al. 2006; Yom-Tov and Geffen 2011). Nevertheless, study of *chronoclines*—a character gradient (e.g., increasing size) expressed within a taxon over time (Simpson 1943)—has provided insight to paleoenvironments by assuming the cline is the result of the operation of an

ecological principle such as Bergmann's rule (e.g., Klein 1986; Purdue 1989; Semken 1983; Wolverson et al. 2007).

My major concerns here are assumptions that are required by analytical techniques applied to the particular taxa identified in an assemblage of ancient faunal remains, their abundances, or both. Many analytical methods in use today depend on taxonomic identifications, yet the assumptions necessary for analysis and interpretation are seldom explicitly acknowledged in the recent literature (e.g., Bañuls-Cardona et al. 2014; Emery and Thornton 2014; Gómez Cano et al. 2014; López-García et al. 2015a, b; Matthews et al. 2011; Socha 2014), and the fear of becoming complacent and ignorance creep (Jackson 2012) are sufficient reason to review them, particularly from a taphonomically, analytically, and ecologically up-to-date perspective.

Operating Assumptions

Assumptions necessary to interpreting taxonomically identified faunal remains in terms of their paleoenvironmental implications are stated rather eclectically in the paleozoological literature. Typically, as preludes to analysis, paleozoologists describe (but do not evaluate) one or two of the assumptions and interpretive bases underpinning paleoenvironmental reconstruction. There are several incomplete lists of these assumptions compiled by biologists (Findley and Jones 1962; Harris 1963b) working with paleontological and zooarchaeological vertebrate remains (Findley 1964; Harris 1963a; Lundelius 1964). The assumptions described below are a compilation of these, plus a couple additional ones. In the following I identify each assumption, discuss its strengths and weaknesses, and identify relevant ecological principles. Analytical means to overcome or circumvent weaknesses are described.

Assumption 1

The key assumption to interpreting vertebrate faunal remains, or the remains of any organism, plant or animal, in terms of their paleoenvironmental implications, is that the identified species, if it exists today, had the same ecological tolerances in the past that it has today (Andrews 1995; Avery 1982; Brown 1908; Cleland 1966; Coope 1986; Craig 1961; Dalquest 1965; Evans 1978; Frazier 1977; Grayson 1976, 1981; Guilday 1971; Hibbard 1955; Hibbard et al. 1965; Hokr 1951; Holbrook 1975, 1980; Holbrook and Mackey 1976; Lawrence 1971; Lozek 1986; Lundelius 1964, 1983; Miller 1937; Odum 1971; Patton 1963; Polly and Eronen 2011; Redding 1978; Romer 1961; Rymer 1978; Schultz 1967, 1969; Semken 1966; Taylor 1965; Tiffney 2008; Walker 1978; Zeuner 1961). The ecological tolerances of extant species are assumed to have not evolved or changed over time (Belyea 2007; Chaline 1977; Cheatum and Allen 1964; Findley 1964; Johnson 1960; Levinson 1985; Scott 1963; Yalden 2001). This has been referred to as “taxonomic uniformitarianism” (Bottjer et al. 1995), “physiological uniformitarianism” (Tiffney 2008), and simply as the principle of uniformitarianism (Ager 1979; Behrensmeyer et al. 2007; Birks et al. 2010; Gifford 1981; Graham and Semken

1987; Guthrie 1968a; Johnson 1960; Kingston 2007; McCown 1961; Rymer 1978; Scott 1963; Wilson 1968). The uniformitarian principle is typically and coarsely glossed as *the present is the key to the past* (Gould 1965, 1987; Rudwick 1971; Simpson 1970). Lawrence (1971, p. 602) refers to this assumption (critically) as “transferred ecology” because it “limits our ability to see how the ecology of the past was different from that of today” (Behrensmeyer et al. 2007, pp. 13–14).

Many researchers acknowledge that this key assumption could be invalid. Because of the likelihood that species have evolved, analysts often consider more than one species in analysis to reduce the possibility of error resulting from evolutionary change in the tolerances of one or a few species (Avery 1988; Bobe and Eck 2001; Dalquest 1965; Dorf 1959; Grayson 1981; Guilday 1962; Johnson 1960; Lundelius 1964; Redding 1978; Romer 1961; Semken 1966; Walker 1978; Wells 1978; Winkler and Gose 2003; Zeuner 1961). The use of multiple taxa is seen as a better means of reconstructing past environments than using one or a couple taxa, but few who mention this analytical protocol indicate why one should place greater trust in multiple taxa than in a single one. The reasoning is straightforward. It is unlikely that every one of the multiple taxa consulted will have evolved in precisely the same way to changing environments. It is improbable that all cold-adapted taxa will have (or obtain through mutation or breeding) the necessary alleles that result in their all becoming adapted to warmer climates. Increasing the improbability that all involved species evolved in like manner, it is likely that the plethora of selective processes will not be the same for all considered species given what we know of ecological tolerances, and thus only some of the species will ultimately become adapted; some will alter their distributions and others will be locally extirpated. Nevertheless, any paleoenvironmental reconstruction based on mammalian remains, for example, should be corroborated as rigorously as possible by consultation of independent data such as plant, insect, avian, and molluscan remains.

That evolutionary change and altered adaptations or ecophenotypic adjustments present a not insignificant analytical challenge is found in the observation that the chronologically older the faunal collection examined, the more tenuous the key assumption becomes (Craig 1961; Guilday 1962; Guthrie 1968a; D. Reed 2007; Romer 1961; Scott 1963; Smith 1919). The tenuousness becomes greater because with greater age the greater the probability that evolutionary change in a species’ tolerances has occurred (Guthrie 1968a; Lundelius 1964, 1985; Walker 1978). Because of the possibility of evolutionary change in adaptations and ecological tolerances, environmental reconstructions are said by some to be imperfect or tenuous (Avery 2007; Walker 1978). Another way to think about paleoenvironmental reconstructions is not that they are imperfect but rather that they are of low resolution, or ordinal scale rather than ratio scale (Birks et al. 2010).

In the absence of specific information on the ecological tolerances of species, some analysts have determined the habitats preferentially occupied by the species represented in a collection and then developed a variety of metrics that might be loosely categorized as habitat metrics or indices (e.g., Andrews et al. 1979; Evans et al. 1981; Fernández-Jalvo et al. 1998; Hernández-Fernández and Peláez-Campomanes 2005; López-García et al. 2014; Matthews et al. 2005; D. Reed 2007;

K. Reed 2008; Su and Harrison 2007). These approaches appear analytically elegant because they result in paleoenvironmental reconstructions such as tropical forest, or steppe/savanna, or open woodland, or grassland. Do not be misled by the mathematics involved (Belyea 2007); paleohabitat reconstructions are ordinal scale. In addition, terms such as woodland or savanna are subject to variable interpretations because they generally encompass a wide variety of habitats. The vagueness of these terms may be accepted by some because of the low environmental resolution of the fossil data (Kingston 2007). A weakness of habitat index techniques is that the architects seldom describe in sufficiently detailed guidelines how to assign values to the variables that make up the metrics that distinguish habitats (D. Reed 2007). That is, it is unclear how we determine whether species A should be considered 20% desert, 25% grassland, 25% brushy grassland, and 30% open forest or woodland, or some other combination of values. Emery and Thornton (2012, 2014) provide instructions for their *habitat fidelity analysis* technique that likely approximate the manner in which other analysts have constructed their habitat indices.

Habitat metrics rest on a slightly modified version of the first assumption—that the habitat preferences of an extant species were the same in the past as they are today. Once a grassland species 70% of the time and a steppe species 30% of the time, always a grassland species 70% of the time and a steppe species 30% of the time. So far as I have been able to determine, this first key assumption does not appear in any habitat metric study.

A growing body of research suggests that the key assumption of no shift having occurred in a species' ecological tolerances over time, known as *niche conservatism*, is true for at least some taxa (e.g., DeSantis et al. 2012; DiMichele et al. 2004; Martínez-Meyer et al. 2004; Wake et al. 2009; Wiens et al. 2010), but not always (e.g., Cerling et al. 2015). We must however not overlook the fact that some species may have evolved and their ecological tolerances shifted. Robust tests of apparent cases of niche conservatism are still under development (Nógués-Bravo 2009). Thus we must be careful to not over interpret data suggestive of niche conservatism (Peterson 2011) or to presume that paleoenvironmental reconstructions are interval scale. Best analytical practice in paleoenvironmental reconstruction is to consult as many independent lines of evidence as possible. Convergence of those varied kinds of evidence toward the same reconstruction would suggest not only a correct reconstruction but also niche conservatism among the monitored species.

Assumption 2

Extinct species are assumed to have had ecological tolerances similar to those of their closest living relative (Allan 1948; Andrews 1996; Avery 1982; Bobe and Eck 2001; Dorf 1959; Findley 1964; George 1958; Gidley and Gazin 1938; Guilday 1971; Guthrie 1982; Harris 1985; Hibbard 1944, 1958, 1960, 1963; Kingston 2007; D. Reed 2007; K. Reed 2013; Rhodes 1984; Romer 1961; Schultz 1967, 1969; Semken 1966; Simpson 1953; Stephens 1960; Wing et al. 1992; Woodcock 1992; Woodring 1951; Zeuner 1936, 1961). This assumption is sometimes referred to as

“taxonomic uniformitarianism” (Reed et al. 2013) or “taxonomic analogy” (Bobe and Eck 2001). Choosing its closest living relative as an appropriate ecological analog for an extinct species assumes the two species, because they are members of the same genus, family, or clade, not only share lots of genes but also have the same or similar ecological tolerances. The more distant the genetic relationship between the extinct and extant (modern analog) taxon, the more tenuous the assumption becomes because as genetic relationship grows distant, the greater the chance that similarity in ecological tolerances decreases (Jehl 1966; Reed et al. 2013).

Some early paleontologists bemoaned the fact that we can never know the ecological tolerances of extinct taxa, and because of that they argued extinct taxa are of limited analytical value when reconstructing past environments (e.g., Ager 1979; Andrews 1990, 1995; Dalquest 1965; Hester 1964; Hokr 1951; Ladd 1959; Levinson 1985; Lundelius 1972, 1974, 1976, 1985; Simpson 1947; Tchernov 1975). Combined with a lack of trust in the validity of using an extant relative as an ecological analog, it might seem that extinct taxa provide minimal insight to past environments. That extinct species had particular ecological tolerances just as extant species do is undeniable. To learn something about the ecological tolerances of an extinct species, analysts have traditionally suggested three alternatives. One involves the assumption that similar phenotypic features signify similar adaptations, such as the familiar one of browsers versus grazers (Bobe and Eck 2001; Damuth and Janis 2011; Evans 1978; Gould 1969; Lundelius 1964; Simpson 1953; Yalden 2001). In other words, basic functional morphology holds that similar morphological traits denote similar ecological characteristics (Herm 1972; Lundelius 1964; Nelson and Semken 1970; Semken 1966; Tiffney 2008; Wells 1978; Whittington 1964; Wing et al. 1992; Zeuner 1936, 1961).

The second alternative to assuming that an extinct taxon and its closest living relative have similar ecological tolerances is to consult the ecological tolerances of extant taxa that are stratigraphically and temporally associated with the extinct taxon (e.g., Case 1936; Cheatum and Allen 1964; Harris 1985; Miller 1937; Romer 1961; Simpson 1947; Wells 1978). Co-occurrence of the two (extinct and extant) suggests they had similar ecological tolerances (e.g., Hughes 2009; Walker 1978). This analytical strategy rests on the first assumption, that extant taxa have not changed their ecological tolerances. But using the same strategy of close study of all associated extant taxa, it has been shown that occasionally the first assumption is false for some extant taxa (e.g., Mead and Spaulding 1995; Owen et al. 2000); their ecological tolerances have evolved. The thus far seldom-used third alternative involves computer-based models of past climates used to estimate the climatic parameters to which an extinct species was adapted (e.g., McDonald and Bryson 2010).

Any of the three alternatives to Assumption 2 may suggest a particular extinct taxon had different ecological tolerances and habitat preferences than its closest living relative (Lundelius 1985; Miller 1937). For example, the western North American extinct noble marten (*Martes americana nobilis*) was originally thought to have ecological tolerances similar to the extant conspecific pine/American marten (*M. a. caurina*). Study of extant fauna stratigraphically associated with the noble

marten shows that its ecological tolerances were in fact unique among members of this species (Hughes 2009; Lyman 2011).

Fortunately, today we have several additional means to determine the ecological tolerances of extinct taxa. These include techniques I explicitly did not set out to discuss but that should be mentioned. As noted above, study of the ecomorphology of extinct taxa involves assuming that particular (functional) skeletal traits of a species signify adaptation to a particular kind of habitat such as open grassland or closed forest (e.g., Faith et al. 2012; Plummer et al. 2008). In addition, studies of tooth wear, both at micro- and mesoscales, suggest the habitats to which a species was adapted and thus the kind of habitat present at the time the teeth were accumulated and deposited (e.g., Faith 2011; Pinto-Llona 2013; Rivals et al. 2011). And finally, study of the stable isotopes in faunal remains reveals details of the habitats and environments in which animals lived (e.g., Cerling et al. 2015; Eastham et al. 2016). Thus these additional techniques can be used not only to gain insight to the ecological tolerances of extinct taxa, they can be used as somewhat independent lines of evidence to strengthen (or cast doubt on) inferences of paleoenvironments based on the three traditional alternatives.

Assumption 3

It is assumed each species has a set of ecological tolerances more or less unique from all other species (Avery 2007; Cheatum and Allen 1964; Cleland 1966; Evans 1978; Guilday 1962; Harris 1963a; Lundelius 1964; Moine et al. 2002), and we know those tolerances sufficiently well for every species to predict with near certainty where, in terms of habitats and climates, a particular species will occur (Evans 1978; Findley 1964; Harris 1963a, 1985; Kingston 2007; Redding 1978; Rhodes 1984; Romer 1961; Woodcock 1992; Yalden 2001). There can be more than one species of a genus in a fauna but they need to occupy different niches so as to avoid interspecific competition. Thus, some authors believe that multiple related species in a collection means environmental variety (Simpson 1936), or multiple microhabitats blended to reveal regional environment (Semken 1966; Wilson 1973), or multiple genotypes signifying multiple tolerance levels (Walker 1978).

Some researchers suggest we know very little about the ecological tolerances of many extant taxa (Anderson 1968; Andrews 1995; Avery 1988; Calaby 1971; Cheatum and Allen 1964; Guilday 1962; Harris 1963a; Huntley 2012; Lundelius 1967, 1985; McCown 1961; Taylor 1965; Wells 1978). As noted earlier, an analytical alternative when details of ecological tolerances and limiting factors of extant taxa are poorly known is to consult the modern distribution of each particular taxon as a low-resolution clue to their ecological tolerances (see Assumption 10 below). It has been argued, however, that inferring a prehistoric biome—a kind of combination of kinds of plants and animals found over large and multiple areas as a result of similar climatic regimes (Moncrieff et al. 2016; Whittaker 1975) (Fig. 5)—on this basis may be subject to error (Mares and Willig 1994), though it has been shown that such is not necessarily the case (Andrews 2006; Le Fur et al. 2011). If known, the biome rather than the specific habitat(s) in which a species commonly occurs is used as a low-resolution indication of the paleoenvironment (e.g., Gidley

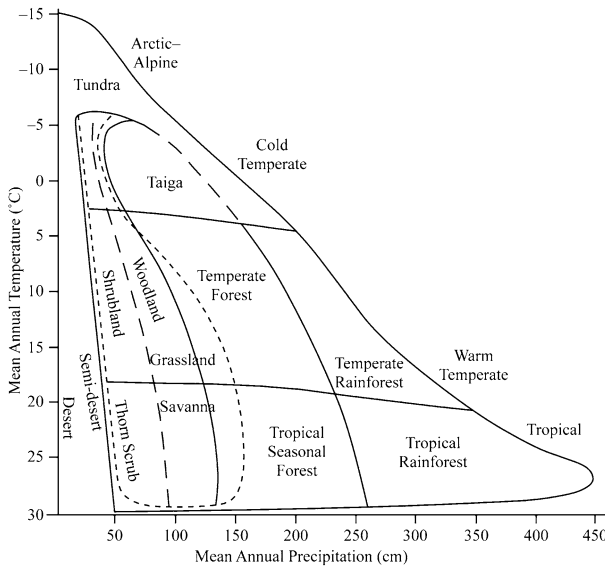


Fig. 5 A model of world biome types in relation to mean annual precipitation and mean annual temperature. Boundaries between biome types are approximate. The fine *dashed line* encloses a range of environments in which either grassland or one of the woody-plant dominated biomes may be the prevailing vegetation (redrawn after Whittaker 1975)

and Gazin 1938; Gustafson 1972; Hughes 2009). Ranges of multiple taxa are thought to give greater resolution because each taxon is conceived as ecologically independent of all others and thus each provides an independent indication of biome (Moine et al. 2002).

Any time the geographic range of a taxon is used as a proxy for the ecological tolerances of an organism, the analyst assumes that the organism’s distribution is controlled by its ecological tolerances (Lundelius 1983). Some suggest that a species’ geographic range may not be a good proxy for ecological tolerances (Dalquest 1965; Evans 1978; Guilday 1971; Guthrie 1968a; Lundelius 1983; Moine et al. 2002; Smith 1957; Walker 1978; Woodcock 1992). The major reason is that a species’ range represents its realized niche rather than its fundamental niche. Yet use of a species’ geographic range is not unusual (Birks et al. 2010; Churcher and Wilson 1990; Escarguel et al. 2011; Gidley and Gazin 1938; Guilday 1971; Hoffmann and Jones 1970; Slaughter 1967). It is, for instance, something of an ecological truism that taxa with large ranges tend to have wider (less restrictive) ecological tolerances than taxa with small ranges (Cheatum and Allen 1964; Lundelius 1964). The presumption is that a correlation between the distribution of a species and some environmental/climatic variable represents a causal relationship (Birks et al. 2010; Lundelius 1983), although some indicate the causal mechanisms producing the relationship need not be known in order to use the correlation as an interpretive algorithm (Avery 2007; Lawrence 1971; see also Kearney and Porter 2009; Polly and Eronen 2011). Gifford (1981) is a rare exception and argues it is

critically important to seek causal relationships between ecological variables when it comes to deciphering paleoecologies. I agree.

Much that we know about biogeographic ranges is descriptive (Avery 1982; Kearney and Porter 2009; Lavergne et al. 2010; Redding 1978; Scott 1963); causal relationships between distributions and environmental variables are unknown (see overviews by Holt 2003; Louthan et al. 2015). Further, published surveys and distribution maps for species are not always thorough or accurate, respectively (e.g., Grayson et al. 1996). As a result, the paleozoologist may need to trap animals around the archaeological site to determine the local environment and the animal species present (e.g., Grayson 1983; Holbrook 1975; Walker 1982).

Assumption 4

The natural or autochthonous occurrence of a taxon in an assemblage is assumed to indicate the existence of a set of local environmental conditions under which that taxon could exist at the time of its occurrence (Harris 1963a; Lundelius 1964; Moine et al. 2002; Redding 1978; Tchernov 1982). This assumption is here distinguished from Assumption 1 because analysts sometimes interpret the absence of a taxon from an assemblage as indicative of the presence of environmental conditions that are outside the absent taxon's ecological tolerances (Harris 1963a; Walker 1978).

Although some analysts have interpreted the absence of a taxon in the manner indicated, they were aware of the taphonomic pitfalls of doing so. Simpson (1937) early on pointed out that the absence of remains of a taxon did not necessarily mean that that taxon was not present in the area. A few years later White (1954) noted that to accept the notion that the absence of a taxon from a paleozoological assemblage signified the absence of that taxon from a prehistoric fauna was problematic. One should instead, White (1954) reasoned, consider (1) if a missing taxon was present in areas near the site under investigation or only in remote areas; (2) if the missing taxon was present in geologically earlier, later, or both kinds of deposits; (3) the abundance of the missing taxon when it was found, because taxa that were rare but present on the ancient landscape might not often be found in the paleozoological record; (4) whether remains of taxonomically related taxa were present; (5) whether the depositional conditions were favorable to preservation of the remains of the missing taxon; (6) the thoroughness with which the deposits supposedly lacking the remains of the missing taxon had been examined; and (7) whether or not the local climate at the time the missing taxon's remains might have been deposited was conducive to the occupancy of the area by the missing taxon. These all were then, and are still today, important things to consider.

Other analysts have subsequently made the point that the absence of evidence of a taxon is not necessarily evidence of that taxon's absence (e.g., Erynck 1999; Grayson 1981, 1983; Guthrie 1968b; Lyman 2008a). The remains of a taxon may not be in an assemblage because the taxon was not in the area at the time the remains comprising the assemblage under study were accumulated and deposited. This is of course necessary to know if the absence of a taxon is to serve as the basis for inferring this taxon's requisite environmental conditions were not present (an ill-advised inference, as we will see). The taxon may, however, have been present in

the area at the time but its remains were not accumulated and deposited in site sediments (e.g., Grayson 1981). Alternatively, the remains were accumulated and deposited but were not preserved. Or, if they were accumulated and deposited and preserved, perhaps they were not found given recovery methods such as screens with large mesh (e.g., Lyman 2012b). Analytical techniques to determine when the absence of remains of a species can be taken as evidence that the species was in fact absent have been discussed (Burnham 2008; Lyman 1995; Nowak et al. 2000), but these techniques have not been generally adopted by archaeologists perhaps because they rest on tenuous assumptions of their own. Paleontologists, on the other hand, often use similar techniques to determine what they refer to as *first appearance dates* (FADs) and *last appearance dates* (LADs) of fossil species. These techniques incorporate statistical estimates of chronological distributions based on both observed stratigraphic ranges and measures of data quality (e.g., number of specimens, sampling intensity) (Barry et al. 2002).

We currently lack robust techniques for the determination of which possible reason for the absence of remains of a taxon applies in any given case. Thus it has been suggested that analysis must be asymmetrical (Ervynck 1999; Grayson 1981, 1983; Lyman 2008a); analysis should be based only on taxa that are present in an assemblage (but see Pinto et al. [2016] for a recent exception). Finally, recalling Assumption 3, the analyst should not overlook the fact that we still do not know in detail the biogeographic histories or even the modern ranges of many species, the latter indicating that it is unlikely we know much about the ecological reasons why a taxon might be absent from the general location of a site.

A final comment about Assumption 4 concerns its seeming dependence on a more deeply implicit assumption—the presence of a taxon’s remains is indicative of the local environment at the time of accumulation and deposition because they are (assumed to be) of local, not extralocal or extratemporal, origin. This is a taphonomic issue and is addressed in more detail under Assumptions 5 and 7.

Assumption 5

Changes in faunal composition (species represented, species abundances) are assumed to reflect changes in environmental conditions (Avery 1990, 2007; Evans 1978; Graham 1985a; Graham and Semken 1987; Grayson 1976, 1977, 1979; Harris 1963a; Lawrence 1971; Tchernov 1968). Although the point had been made earlier, Grayson (1981, 1983) highlighted that the taxa in an assemblage could be treated as attributes of a fauna—their presence in an assemblage is the subject of study—or as variables—their frequencies relative to one another are the subject of study. Because the latter provides more information, it is more powerful analytically; changes in relative abundances of taxa are more sensitive to small-scale environmental flux than the presence–absence of taxa (Graham and Semken 1987). But to blindly believe taxonomic abundances are universally better than presence–absence data (particularly noting that one should not place great interpretive weight on the absence of taxa, as documented under Assumption 4) ignores all the well-known problems of determining those abundances (Grayson 1984; Lundelius 1964; Lyman 2008b; McCown 1961). Some analysts have taken

those problems to be so great that they recommend against using the abundances of remains as a proxy for abundances on the landscape (e.g., Holbrook 1975; Redding 1978). Fortunately, we have learned taxonomic abundances are best quantified, if quantified at all, as NISP, MNI, or biomass depending on their taphonomic histories and depositional contexts (e.g., Badgley 1986; Guilday 1969; Terry 2009; Thomas and Mannino in press).

Once taxonomic abundances have been determined, the next issue concerns deciphering what shifts in those abundances signify. Although he did not deny the influence of climate on a species' abundance, Darwin (1859) suggested the amount of food available for a species was the limiting variable, and some modern researchers agree and add the abundance of food is controlled by climate (White 2008). This is a bottom-up perspective. But there are several possible reasons for changes in faunal composition and taxonomic abundances other than food availability or climate (Avery 1982; Belyea 2007; Grayson 1979; Guilday 1969; Guthrie 1968b; McCown 1961). The appearance or disappearance of a competitor (Belyea 2007; Guilday 1971), cyclical or random flux in abundance (Guthrie 1968b), ecological succession (Avery 1982), historical contingency (Fukami 2015; Svenning et al. 2015), or other processes may cause flux in taxonomic abundances on the landscape.

The frequently expressed worry concerns the possibility that shifts in taxonomic abundances resulted from change in the mechanism of bone accumulation or preservation that had nothing to do with environmental change (Behrensmeier and Hook 1992; Behrensmeier et al. 2007; Guilday 1962; McCown 1961; Redding 1978; Turvey and Cooper 2009). For instance, Grayson (1981) demonstrated Assumption 5 is not necessarily true by finding varied abundances of rodent remains in collections of modern pellets egested by different species of owl. This does not mean all changes in the taxonomic composition of faunal assemblages or the abundances of taxa in those assemblages are suspect. A host of *fidelity studies* suggest that at least some times abundances of taxa in collections of faunal remains accurately reflect the environmental context in which those remains have been accumulated (e.g., Cutler et al. 1999; Hadly 1999; Lyman 2012c; Lyman and Lyman 2003; Miller 2011; Miller et al. 2014; Terry 2010a, b; Western and Behrensmeier 2009).

How does one know if a particular prehistoric assemblage of faunal remains accurately reflects the paleoenvironmental conditions within which that assemblage was accumulated and deposited? How do we know if the prehistoric fauna is a representative sample of the actual fauna on the landscape at the time the former was formed? In short, we do not know and cannot know these things. Detailed taphonomic analyses are the usual suggested means of estimating the confidence that should be placed in the environmental fidelity of a prehistoric faunal collection (e.g., Andrews 1990; Domínguez-Rodrigo and Musiba 2010; Terry 2009; Wing et al. 1992). This suggestion presumes that we can decipher taphonomic data sufficiently well to analytically distinguish taphonomic or other nonenvironmental causes of faunal change from environmental causes. Only recently has our taphonomic knowledge become sufficient that we can sometimes (not always) analytically contend with various biases. Some of the more interesting studies along

these lines have used large datasets to simulate the effects of impoverished samples and of mixed samples on interpretations (e.g., Le Fur et al. 2011); the former often provide fairly accurate signals, whereas the latter do not (Andrews 2006; contra Mares and Willig 1994).

But what does one do when faced with, say, a set of assemblages that reveal change in taxa represented or fluctuations in taxonomic abundances over time? One approach is to compare only assemblages that are isotaphonomic, those assemblages that have been subjected to the same taphonomic processes and biasing agents (Behrensmeyer 1988, 1991; Behrensmeyer and Hook 1992; Wilson 2001). This vetting of data is meant to eliminate variability that is the result of taphonomic processes and retain variability that is the result of environmental change (e.g., Alemseged et al. 2007). That might sometimes be more reasonable than attempting to strip away the taphonomic overprint (e.g., Lawrence 1968, 1971). An alternative method is to plot taphonomic data such as frequencies of carnivore gnawing against changes in presence/absence of species or fluctuations in taxonomic abundances (e.g., Faith 2013). If the two correlate, the seeming paleoenvironmental signal may instead be a sign of taphonomic history.

Regardless of our skills to decipher taphonomic data, multiple lines of independent evidence of paleoenvironments should be consulted. Thus one might compare the paleoenvironmental implications of large mammals to those of small mammals on the assumption that it is unlikely that the two categories of remains underwent similar taphonomic histories. Or one might compare the paleoenvironmental signal provided by mammal remains with that provided by mollusk remains, palynological analysis, and geomorphology and sedimentology. If all lines of evidence suggest the same paleoenvironmental conditions, then because it is unlikely that all these kinds of evidence were skewed so as to provide the same false paleoenvironmental signal, the analyst can have confidence in the results.

Assumption 6

If interpretations depend on the taxonomic identifications of remains, one must assume faunal remains have been correctly identified to taxon (Avery 2007; Behrensmeyer et al. 2007; Bell et al. 2010; Calaby 1971; Coope 1986; Findley 1964; Gustafson 1972; Harris 1963a; Rhodes 1984; Stewart 2005; Walker 1978; Woodcock 1992; Zeuner 1961). Identification to subspecies typically is impossible, but identification to the species level is often though not always possible (Graham and Semken 1987). Finer taxonomic distinction typically means greater resolution because of narrower ecological tolerances (Avery 2007; Findley 1964). Subspecies have smaller geographic ranges than the species to which they belong, implying narrower ecological tolerances of the former; species have smaller geographic distributions than the genus to which they belong, implying narrower ecological tolerances; and so on. Identifications to the genus level may be useful for paleoecological inferences though it is likely that resolution will be coarse relative to inferences based on species-level identifications (George 2012). And while taxonomic identification is now facilitated by study of ancient DNA (e.g., Orlando and Cooper 2014; Rull 2012), this method is destructive, it may be cost prohibitive,

and it depends on the preservational condition of the remains. The standard, typically used taxonomic identification procedure is of concern here. Given the critical nature of accurate taxonomic identifications, there is surprisingly little discussion of this fundamental analytical step in the zooarchaeological literature (but see Brothwell and Jones 1978; Driver 1992, 2011; Gobalet 2001; Lawrence 1973; Lyman 2002, 2010a; Rea 1986; Wolverton 2013). It is therefore worthwhile to consider the usual identification protocol involving skeletal anatomy.

Simpson (1942) referred to the identification procedure as the “comparative method”—hence the oft-applied label of “comparative collection” to a natural history collection of skeletons of known taxonomic identity—and noted that it required the assumption that the bones and teeth of different taxa have characteristic forms that consistently distinguish those taxa. The paleozoologist makes a taxonomic identification by placing two homologous bones—one the modern specimen of known taxonomy, the other the prehistoric taxonomically unknown—next to one another and visually comparing the two (Simpson 1942). Given the assumption that each taxon’s bones have characteristic forms that reflect taxonomically distinct genotypes (Tiffney 2008), if the two bones look alike, the unknown is “identified” as the same taxon as the known. If the bones look different, the prehistoric unknown is “identified” as being from a taxon other than the modern known with which it is being compared (e.g., Bell et al. 2010)

Perhaps the greatest hurdle to taxonomic identification is that extant species tend to be defined based on attributes that do not preserve in the paleontological record (Avery 2007). Because of this, the “paleozoologist must establish osteological criteria that are species specific” (Graham and Semken 1987, p. 3; see also Cheatum and Allen 1964). Describing those criteria in publications is important because they are sometimes “not statistically significant, not applicable beyond local regions, or not agreed upon by specialists” (Graham and Semken 1987, p. 3). If the supposed taxonomically diagnostic criteria are not described, published identifications cannot be independently evaluated (Semken and Graham 1987). Examples of published morphometric criteria are not unusual in the paleontological literature (see Schultz [2010] for a recent example) but are rare in the zooarchaeological literature except when a particular paleoecologically significant taxon is the focus of analysis (e.g., Grayson 1977; Lyman 2012a).

Some researchers note that identifying the remains of small-bodied mammals such as insectivores and rodents is difficult and often restricted to cranial and dental remains. Recent advances in identifying dental remains of the genus *Microtus*, a taxon with numerous species and widespread across North America and also found in the Old World, not only demonstrate this but underscore how difficult it is to identify even dental remains of some rodent groups (compare Semken and Wallace [2002] with McGuire [2011]). Postcranial remains of this taxon are typically not studied because they cannot often be identified to genus let alone species.

As anyone who has worked with a large collection of remains that includes numerous taxa of similar morphometry knows, the identification process is infrequently simple. Walker (1978, p. 259) summarized the issue well: “The [taxonomic] level to which a fossil can be identified often depends on the part which is fossilized and our technical capacity for recording details of morphology....

Practically every attribute of a potential or actual fossil of a species has some variance; exactness of match will be greatest where there are several attributes on which to base comparisons, each of which has small variance.”

In other words, one must be cognizant of intrataxonomic variability and intertaxonomic variability, have knowledge of which morphometric attributes or features of each skeletal element are taxonomically diagnostic, and have a feel for how similar skeletal specimens must be to confidently identify them as from the same taxon. To learn these things requires long hours of study of comparative collections of skeletons of known taxonomy (Bell et al. 2010; Findley 1964; Lyman 2010a). As if that were not enough of a hurdle to this analytical step, nearly constant revision of the biological taxonomy (which populations should be lumped into one species, which species should be placed in one genus, etc.) exacerbates the difficulty (Avery 2007; Lundelius 1985).

Although there are several detailed studies of the taxonomically diagnostic osteological criteria that distinguish certain taxa that are difficult to distinguish (e.g., Balkwill and Cumbaa 1992; Castaños et al. 2014; Emslie 1982; Grayson 1977; Hargrave and Emslie 1979; Jacobson 2003, 2004; Monchot and Gendron 2010), such studies are also rare. The significance of not publishing the bases of a taxonomic identification increases as the significance of an interpretation of that identification increases. If the identification is not explicitly well justified, then there is minimal support for a paleoenvironmental (or any other) interpretation of that identification. It is for this reason that some individuals argue that particularly important identifications must be well documented in publications (e.g., Calaby 1971; Lyman 2002; Wolverson 2013). Posting the morphometric criteria used to make taxonomic identifications as part of the supplementary online material for a published study is now possible for many journals and this possibility should be exploited!

Assumption 7

Particularly if taxonomic abundances are the target of analysis, one must assume there are minimal sample size effects and minimal taphonomic skewing of the sample(s) under study (Harris 1963a; Lundelius 1964; Redding 1978). Taking these two things in order, the pernicious effects of sample size on such measures as taxonomic richness, evenness, and heterogeneity have been well documented (Grayson 1984; Lyman 2008b). Paleozoologists have long worried about sample adequacy (e.g., Gamble 1978; Gould 1969; Guilday 1962; Guthrie 1968b; Morlan 1984), and Simpson (1937) was among the first to worry explicitly and propose a solution. He suggested “Probably the best criterion of the adequacy of a collection as a sample of the preserved fossils is that of repetition. When collecting begins to pile up mainly or only duplicates, it probably has achieved sampling adequacy for the local deposit, but as long as many species remain very rare in collections, it probably has not” (Simpson 1937, p. 68). He was largely concerned with basing conclusions on a sample that was representative of what was in a stratum, and that what was in the stratum was representative of the fauna on the landscape. The former concerns sample size and the latter concerns taphonomy.

Sampling theory indicates that the greater the heterogeneity in the population being sampled, the larger a sample must be to correctly estimate population parameters such as richness, evenness, and heterogeneity. Any suggestion of a universally adequate sample size (e.g., Casanova-Vilar and Agusti 2007; Daams et al. 1999; García-Alix et al. 2008) is ill advised. Paleozoologists have suggested several ways to assess sample adequacy. One individual used the trophic pyramid (Fig. 4) as a model to compare against a faunal assemblage. Wolff (1975; see also Gamble 1978; Wells 1978) argued that small herbivores should be more abundant than small carnivores and that large herbivores should be less abundant than small herbivores but more abundant than large carnivores. He plotted abundances of faunal remains in these categories to determine if his assemblages met the prediction, presuming that when his samples met the prediction, they were representative of the prehistoric community. Wolff (1975) also plotted the cumulative volume of sediment excavated on the horizontal axis against cumulative taxonomic richness of his samples on the vertical axis. He argued that when the taxonomic richness curve leveled off, he had accumulated a total sample that was representative of what was in the stratum sampled. Following Wolff's second technique (1975), Lyman and Ames (2004, 2007) suggested constructing a cumulative curve with sample size measured as NISP increasing on the horizontal axis and taxonomic richness, evenness, heterogeneity, or other variable of interest on the vertical axis (e.g., Travouillon et al. 2007). Once the curve levels off and remains stable over successively added samples (producing a cumulatively larger total sample), the analyst can argue that based on the notion of sampling to redundancy (Simpson's repetitiveness), the total sample is representative in terms of the variable of interest. Other paleozoologists have independently come to similar conclusions (Jamniczky et al. 2003, 2008).

If sampling to redundancy is not possible and samples compared are of quite different sizes, a rarefaction analysis can be undertaken (Tipper 1979). This procedure probabilistically reduces all large samples to the smallest of the samples under study. Rarefaction assumes statistical independence of the quantitative units (NISP, or MNI, or something else) being rarified, specifically that each tally of "1" represents a different individual, which is unlikely for NISP in vertebrate collections (Grayson 1984; Lyman 2008b). This has not, however, dissuaded some from performing rarefaction of NISP values (e.g., Blois et al. 2010; Lyman 2014). This seems reasonable if interpretations are of coarse resolution, such as "species A increased in abundance relative to species B" rather than of the sort "species A became twice as abundant as species B."

Throughout the 20th century, paleontologists worried about the taphonomic histories of the prehistoric faunal assemblages they studied and how those histories might skew or obscure a paleoecological signal (e.g., Cheatum and Allen 1964; Dodson 1973; George 1958; Gidley and Gazin 1938; Guilday 1962, 1969; Guthrie 1968a, 1968b; Harris 1963a; Lawrence 1968, 1971; Lundelius 1964; McCown 1961; Simpson 1953; White 1953, 1956; Wilson 1968; Wolff 1973). One of the best-known considerations of this is Shotwell's (1955) effort to distinguish taxa that were members of the proximal (geographically local relative to the paleozoological deposit) community from those taxa that had been transported into the location of

the fossil collection and thus represented what he called the distal (distant, nonlocal) community(s). Although some analysts recommended the use of Shotwell's technique (e.g., Raup and Stanley 1971) and some used it (e.g., Estes and Berberian 1970), subsequent consideration of that technique showed it to be flawed (Dodson 1973; Grayson 1978; Wolff 1973). Shotwell's method was dependent on sample size. Further, although it was meant to measure skeletal completeness of represented carcasses, it ignored frequencies of each of the particular skeletal elements (mandibles, humeri, tibiae, etc.). Recently developed measures have addressed precisely this deficiency (Mannion and Upchurch 2010).

Assumption 8

It is often assumed that small-bodied taxa such as most rodents and insectivores are better ecological indicators than large-bodied taxa (Andrews 1990; Avery 1988, 1990, 2007; Bate 1937; Calaby 1971; Churcher and Wilson 1990; Evans 1978; Falk and Semken 1998; Graham 1976, 1981, 1985b, 1991; Guthrie 1968b, 1982; Harris 1985; Hibbard 1955; Jaeger and Wesselman 1976; Mares and Willig 1994; McCown 1961; Morlan 1984; Redding 1978; D. Reed 2007; Semken 1966; Smith 1957; Stephens 1960; Yalden 2001). This assumption is exemplified in (and likely gained a lot of traction from) a statement authored by five individuals (Hibbard et al. 1965, p. 515), who, at the time, were the North American leaders in paleoenvironmental reconstruction based on paleozoological remains: “Smaller mammals, with a narrower range of habitat and individual home range than the larger carnivores or herbivores, are influenced more by the microclimate in which they live than by regional climatic change (Burt 1958). Hence it is reasonable and a justification of uniformitarian interpretations that the ecological conclusions drawn from rodents and insectivores are similar to those drawn from the associated lower vertebrates, mollusks, and plants.”

Interestingly, the threshold of how small is small is seldom specified, even though Brothwell and Jones (1978) noted early on that it was unclear how small a “small mammal” was. Avery (1988, 1990, 2007) indicates “micromammals” are of ≤ 150 g body mass but provides no warrant for that threshold. The usual definitive criterion is taxonomic; rodents and insectivores are considered to be small bodied, which of course overlooks the fact that some rodents such as North American beaver (*Castor canadensis*) are not particularly small, having an adult average body weight of 20–22 kg.

Assumption 8 is usually warranted by one or more presumed properties of a small-bodied animal: small-bodied taxa are less able to migrate from an environmentally unfavorable area to a favorable one (recall the options an organism has in the face of environmental change) (Churcher and Wilson 1990; Falk and Semken 1998; Graham 1976, 1981, 1985b; Graham and Semken 1987; Harris 1985; Smith 1957); small-bodied taxa generally have relatively narrow environmental tolerances and are adapted to local (as opposed to regional) environments (Avery 2007; Bate 1937; Chaline 1977; Falk and Semken 1998; Graham 1985b; Graham and Semken 1987; Guthrie 1968b; Harris 1963a, 1985; Holbrook 1975; Jaeger and Wesselman 1976; Morlan 1984; Redding 1978; Stephens 1960); small-bodied taxa

have relatively small home ranges (Falk and Semken 1998; Guthrie 1968b; Smith 1957); remains of small-bodied taxa are abundant in some contexts (Avery 1990, 2007; Graham 1976, 1985b; Guilday 1971); remains of small-bodied taxa are easy to identify (Graham 1976, 1985b; Graham and Semken 1987; but see Morlan 1984); small-bodied taxa are unlikely to have served as food resources for humans and thus have not been transported far from their habitat of origin by human hunters (Avery 2007; Holbrook 1975, 1977, 1982a; Holbrook and Mackey 1976; Olsen 1982; D. Reed 2007).

Occasionally it is noted that this assumption does not hold universally or across all taxa at all times and places. Guilday (1967), White (1953, 1956), and Evans (1978) point out that ecological tolerances are wide for some taxa and narrow for others, regardless of body size; thus, before accepting Assumption 8 at face value, the analyst must know the ecological tolerances of the taxa under study in some detail. Only in some cases are small mammals better for reconstructing paleoenvironments, and this is so only when the small mammals in an assemblage have narrow tolerances relative to the large mammals in the assemblage (Lang and Harris 1984). In addition, small-bodied species tend to adapt to microenvironmental variables such as whether a hillside is north- or south-facing, whereas large-bodied species tend to be more influenced by larger-scale variables such as vegetation zones or biomes (Andrews 1990; Churcher and Wilson 1990; Wilson 1973). For this reason Guilday (1967, p. 124) observed, “Small mammals, because of their size and smaller home ranges, can survive in microhabitats barred to larger forms. They are not so drastically affected by a given climatic change as a large mammal. An environmental change, say from a park-savanna to steppe, would eliminate the large browsing forms from the fauna but would have less effect upon herbivorous rodents.”

Stegner (2015) recently reiterated this point when she noted that local edaphic conditions create microhabitats that may buffer the influences of regional climatic shifts on small mammals. In fact, some paleozoologists have long observed that large animals may well be more susceptible to climate change than small mammals. Many such observations derive from the fact that at the end of the Pleistocene many more large-bodied than small-bodied mammals went extinct, probably because the former have slower reproductive rates than the latter (e.g., Guilday 1967; Grayson 1991; Koch and Barnosky 2006). Biologists have recently noted that the responses of living mammals to climate change tend to be mediated by body size and behavioral patterns (e.g., nocturnal or diurnal) such that large-bodied species respond more often than small-bodied species, perhaps because microhabitat variability may provide sufficient areas for the latter but insufficient area for the former (McCain and King 2014). It seems then that although it is often assumed that small-bodied species are better indicators of environmental change than large-bodied species, this assumption may not be true. Knowing the ecological tolerances of the species represented in a paleozoological assemblage would seem to be the best means of evaluating the validity of Assumption 8.

Assumption 9

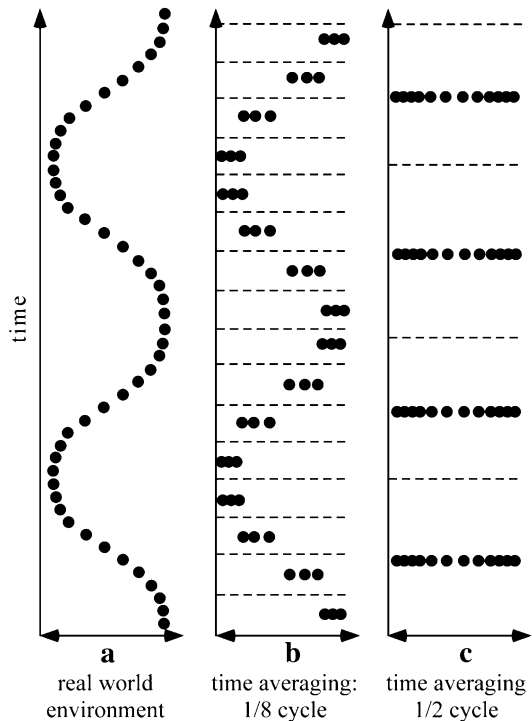
It is assumed that the temporal resolution of faunal assemblages under study is sufficient to monitor the magnitude and rate of change in the environmental variable of interest (habitat composition or structure, temperature, effective moisture, etc.) (Behrensmeyer et al. 2007; Birks et al. 2010; Graham and Semken 1987; Lundelius 1985; Morlan 1984; Wells 1978). The requisite degree of chronological resolution is dictated by two aspects of reconstruction. First, we need tight chronological control of assemblages so that they can be placed in their correct temporal order (Behrensmeyer et al. 2007; Wells 1978), compared, and correlated (Lundelius 1985). Concluding there was environmental stasis or change demands we know the age and the duration of periods represented by the faunal assemblages. The necessity for temporal correlation concerns two distinct scales. At the coarser scale, tight chronological control may facilitate recognizing if one assemblage in a comparison of two is in some important way not temporally the same as the other (same or different period, different duration of formation) (Blaauw 2012). At the finer scale, when basing a reconstruction on multiple species, one must be sure that the remains of those species are contemporaries (Lundelius 1964; Semken et al. 2010; Stegner 2015). Stratigraphically (or analytically) mixed assemblages can mute or alter the paleoenvironmental signal (e.g., Grayson 1981; Lundelius 1964; Redding 1978; Rhodes 1984).

The second temporal aspect of reconstruction concerns the desired scale and resolution of one's paleoenvironmental reconstruction (Behrensmeyer et al. 2007). This issue has been touched on earlier, but it warrants acknowledgment here that finer temporal resolution will tend to provide finer resolution in one's reconstruction. That is, the temporal scale of assemblages of ancient remains may be different than the ecological scale of interest (Avery 2007). This is the increasingly acknowledged distinction between ecological time and paleoecological time (e.g., Peterson 1977; Roy et al. 1996; Turvey and Cooper 2009). The latter is signified in paleobiology as *time averaging* (Behrensmeyer 1982; Behrensmeyer et al. 2007).

Time averaging does *not* refer to some duration of accumulation of faunal remains that produces a statistical average representation of multiple faunal communities (Behrensmeyer et al. 2007). Rather the concept refers to the creation of an assemblage of faunal remains that represents temporally (or perhaps spatially) unrelated communities. Schematic models of time averaging are shown in Figures 6 and 7. In light of column b in Figure 6, Avery (1990) was on the mark when she observed that each paleozoological sample in effect provides evidence of paleoenvironmental conditions during the total period of its accumulation and shorter-term fluctuations will not be reflected. Column c in Figure 6 and also Figure 7 is what concerns those worried about time averaging—the muting or skewing of the paleoenvironmental signal. Importantly, the uniquely long temporal perspective provided by a temporal sequence of paleozoological assemblages more than compensates for the temporally coarse resolution of individual assemblages relative to modern ecological environments (Roy et al. 1996).

North American paleozoologists have long recognized that collections of prehistoric animal remains are not necessarily equivalent to an ecological unit

Fig. 6 One model of time averaging (see also Fig. 7). In all three columns, *each dot* represents an environmental indicator such as the presence or relative abundance of an animal species during one temporal increment such as a year or a decade: **a**, the environment (e.g., climate) shifts causing the environmental indicator to shift over time; **b**, time averaging resulting from stratigraphic lumping of three temporal increments per stratum, or 1/8 of a complete environmental cycle; note that a paleoenvironmental signal would still be present but with muted temporal resolution; **c**, time averaging resulting from stratigraphic lumping of 12 temporal increments per stratum, or 1/2 of the complete environmental cycle; note that the paleoenvironmental signal is completely muted (redrawn after Hopley and Maslin 2010)



such as a biological community having a limited spatiotemporal distribution (Tedford 1970). That this is so is reflected by the concepts of *local fauna* and *faunule*. The former was defined by Hibbard (1958, p. 3) as “an association of identifiable remains of animal life of the same age which have been collected from a restricted geographic area.” *Faunules* are the parts of a local fauna that can be stratigraphically and/or archaeologically distinguished (Graham 1981; Graham and Semken 1987; Walker 1982). These terms appear only occasionally in the North American zooarchaeological literature (e.g., Graham 1981; Walker 1982; Wilson 1974). Although local faunas typically comprise multiple temporally (and perhaps spatially) unique communities, and each faunule represents a temporal duration of some length that may exceed the existence of an ecological-time community, each local fauna is thought to provide a fairly accurate reflection of local (not micro) ecology (Semken 1966).

Often the term *time averaging* refers to an assemblage of animal (or plant) remains that represents a span of time longer than the ecological or climatic event of interest (Roy et al. 1996). If an episode of environmental change spanned a century, for example, and the faunal assemblage under study accumulated during those 100 years plus the 200 years before the episode and the 200 years after the episode, that assemblage would represent a time-averaged collection. The ecological signal of interest would be muted or undetectable (Fig. 6, column c). This does not mean all time-averaged assemblages are analytically worthless (as shown in column b of

Fig. 7 Another model of time averaging (see also Fig. 6). Two distinct habitats, each with individuals (*dots*) of a distinct species restricted to that habitat, are separated by an ecotone. The ecotone is in one position at T3 (time 3), a different position at T2 (time 2), and another position in T1 (time 1); assume that its location at any one time is a function of prevailing climate and its different locations signify different climates. If remains of each individual organism are deposited where the organism is shown to be living at T1, T2, or T3, the fossil assemblage in the bottom polygon will result. Study of that fossil assemblage will not reveal the shifting location of the ecotone nor suggest that different climatic conditions existed during the period when the fossils were deposited (redrawn after Behrensmeier et al. 2007)

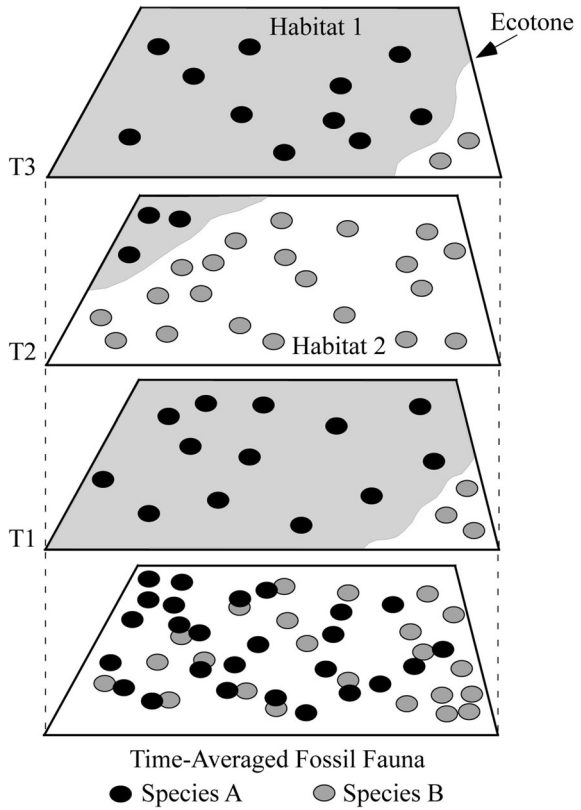


Fig. 6) (e.g., Kidwell and Tomasovych 2013; Kowalewski 1996; Olszewski 1999). For one thing, time averaging mutes idiosyncratic (day-to-day weather) and seasonal fluctuation, things that may not be of interest. Attempts to analytically monitor time averaging have thus far focused on climatic events of multithousand-year durations (Hopley and Maslin 2010).

In archaeology, results of time-averaging processes are often labeled with the term *palimpsest* (Binford 1981). Su and Harrison (2007) mention that a time-averaged fauna could represent an ecological palimpsest (Fig. 7). Some archaeologists have discussed the related concept of *time perspectivism* (Bailey 2007; Holdaway and Wandsnider 2008). This concept rests on the notion of archaeological assemblages that are palimpsests or temporally coarse-grained (low resolution) with respect to the human behavior(s) of interest. Many assemblages of artifacts have been interpreted using models and explanatory theories that concern human behaviors or cultural processes that span relatively limited amounts of (ethnographic) time relative to the amount of (archaeological) time over which an assemblage accumulated (Holdaway and Wandsnider 2008). Time perspectivism refers to aligning the temporal scale (duration) of the event or process of interest with the scale and temporal resolution of the archaeological assemblage(s) under investigation. Along identical lines, paleozoologists note that ecological theories

based only on living communities may not explain ancient ones, and thus will need to be modified to account for the latter in order to produce more comprehensive theories (Wing et al. 1992).

Concern over how the temporal scale and resolution of a paleoecological event or process could be aligned with the scale and resolution of a paleobiological assemblage is precisely what led paleontologists to develop the concept of time averaging (Behrensmeyer 1982; Peterson 1977). They have come to recognize that whether an assemblage of faunal remains should be considered time-averaged depends not just on the formational history of the assemblage(s) of remains under study but also on the scale and resolution of the environmental variable in the research question being asked. Alignment of the two is critical to valid analysis. Simulations mentioned earlier that used modern faunas with known habitat affiliations found that the paleoenvironmental signal is not always obscured or muted by time averaging (Andrews 2006; Le Fur et al. 2011). Although important, these simulations do not encourage conceptualizing appropriate temporal scales and resolutions, nor do they mean all time-averaged faunal assemblages will provide accurate paleoenvironmental signals of some desired scale and resolution.

Because fossil samples are often small (total NISP per assemblage), some paleozoologists lump assemblages of the same or nearly the same age to achieve sample sizes that are sufficiently large to foster confidence that analytical results are not a function of nonrepresentative samples (e.g., Bobe and Eck 2001). Some research shows that such analytical time and space averaging may produce a rather different paleozoological signal than the original, nonlumped assemblages (Lyman 2003, 2010b). Deciding which of the two signals is the correct one requires independent evidence of paleoenvironmental change that correlates with one or the other of the two paleozoological signals. This brings us back to the assumption that led us to this point—that the paleozoological record is of sufficient temporal resolution to align with those independent paleoenvironmental data.

Assumption 10

It is assumed an ecotone (a transition area between two habitats or biomes; e.g., Fig. 7) or community edge is the best place to detect environmental change (Avery 1982; King and Graham 1981; Louthan et al. 2015; Rosvold et al. 2013; Semken 1980; Taylor 1965; Tchernov 1975; Woodcock 1992). This in turn seems to presume that at least some species are found in only one or a few kinds of habitat or biome (it is recognized some species are tightly adapted to habitat edges); outside of that area species are beyond their ecological tolerances (Fig. 1). If winters are colder or summers are warmer by a degree or two, or if there are a few centimeters more (or less) of annual precipitation, either stress becomes too great and the species becomes locally extirpated or stress is reduced and the species increases in abundance, potentially leading to changes in species composition that may be detected in the paleozoological record. The converse of this is equally important. If the paleoenvironment of the fossil site is within the “minimal stress zone” of the tolerance curve for a species whose remains are represented, a drop in winter temperatures of a couple degrees or the addition of a few centimeters of

precipitation each year likely will not have a noticeable impact on the species of concern because it is well within its optimal tolerance range, in which case environmental changes may not be apparent in the faunal record.

A version of this assumption appears regularly in the biological literature and is referred to as the *central–marginal hypothesis* (e.g., Eckert et al. 2008; Guo 2014). Originally, and as implied by Figures 1 and 2, it was thought a species would display an abundance or frequency distribution such that few individuals occur near range boundaries and numerous individuals occur near the center of the species' range (e.g., Erasmus et al. 2002; Swihart et al. 2003) (Fig. 8a). However, it has become increasingly clear that this presumed geographic frequency distribution is idealized and that reality often tends to be more complex (Eckert et al. 2008; Guo 2014; Ries et al. 2004), with more or less isolated populations varying in size and density (Guo et al. 2005) (Fig. 8b). Both the size and isolation of those populations may or may not increase as one moves from the center of the species' range to the range margin. Study of numerous modern communities has shown that the sensitivity of a species to climatic change relates to its range size, niche breadth (specialized or generalized) (Thuiller et al. 2005), and the environmental gradients within the species' range (Guo et al. 2005; Holt and Keitt 2005). Thus, although the boundary of a species' range will suggest the species' niche edges and limits of its ecological tolerances, the relationship may be less than perfect.

Rhoades (1978) nearly 40 years ago scolded North American archaeologists who simplistically borrowed the ecotone concept and the related notion of *edge effect*. His point was that the latter rested on the former and an essentialist or typological notion of communities as relatively immutable. In his view, where archaeologists had gone wrong was to conceive ecotones as transitions between communities or habitats that supposedly contained plants and animals

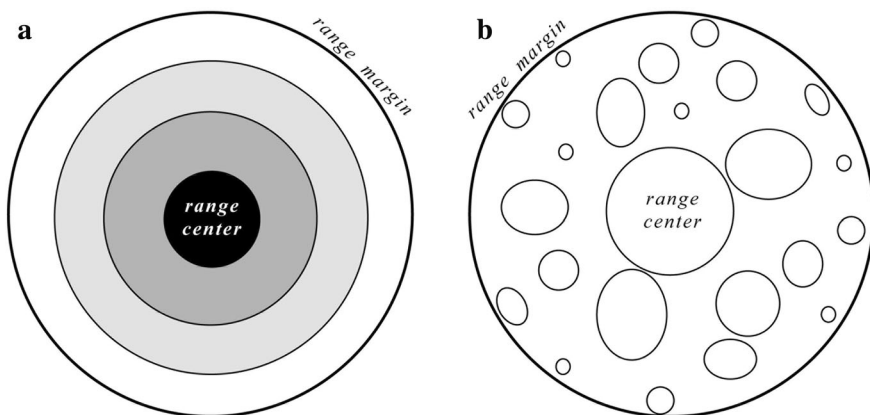


Fig. 8 Models of the distribution of a species: a, idealized distribution showing population density decline from range center to range margin; b, individuals are discontinuously distributed from range center where many individuals occur to successively smaller more or less isolated populations toward range margin (redrawn after Guo 2014)

representative of the adjacent communities and also organisms unique to the ecotone; thus ecotones were thought to have more diverse taxa in greater frequencies than individual community centers (=edge effect) (after Odum 1971). Rhoades pointed out that, in fact, this essentialist, typological ontology was then being replaced by a model of communities not as discrete entities but rather as more or less gradual continua from one to the other (e.g., Whittaker 1975). The replacement was sped along by mounting evidence for Gleason's (1926) individualistic hypothesis. This is not to say that one cannot sometimes detect distinct boundaries to at least plant communities (Whittaker 1975), but rather that the real world is more complex than one or the other simplistic model implies.

What does all of this have to do with reconstructing paleoenvironments on the basis of paleozoological remains? In short, Assumption 10 seems to rest on one or both of the models represented in Figure 8. Both of those rest on the model of ecological tolerances in Figure 1 with the margins of those tolerances for a particular species corresponding to the margins of that species' geographic range, and the center of that species' range corresponding to the optimal tolerance zone. In other words the horizontal axis of Figure 1 represents not only gradients of environmental variables but also a corresponding geographic (latitude, longitude) gradient. Such a correspondence may, however, not exist. And that is the point of modern studies of the center–margin hypothesis.

Assumption 10 is seldom mentioned in the paleozoological literature. It is unlikely that it is seldom mentioned because of the center–margin hypothesis. Rather it is likely infrequently mentioned because locations of prehistoric range edges (such as might have existed at the time the fossil assemblage under study was accumulated and deposited) are not always known. Knowing if a site that has produced remains of a particular species was near the edge of that species' range at the time the remains were deposited is also difficult to know. I say “difficult” rather than “impossible” because as our knowledge grows regarding the prehistoric distribution of particular species, so too does our knowledge of the locations of the boundaries of a species' range at particular times in the past. In North America, the development of the FAUNMAP database in 1994 (Graham and Lundelius 1994) and its evolution into the FAUNMAP II database (Graham 2005) are a prime North American example of our increasing knowledge. Alternatively, to approximate the prehistoric location of a range edge, the researcher can examine the modern distribution of a species that is of analytical interest and presume that the modern edge of the range approximates the tolerance limits for that taxon. Or consider only more obvious range edges based on nonfaunal data, such as those between terrestrial and aquatic habitats (e.g., lakeshore, riverbank). Whatever analytical path the researcher takes, if it involves Assumption 10, the researcher should be cognizant of the center–margin hypothesis and the key aspect of this hypothesis that there may be only a weak or no correspondence of the models in Figures 1 and 8 for the species under consideration.

Discussion and Conclusion

Paleoenvironmental reconstruction based on ancient animal remains has become more common among zooarchaeologists than it previously has been. It should continue to increase in frequency for three reasons. First, the zooarchaeological record (and the paleozoological record, too) is finite. That record should be used to the fullest extent possible. I do not mean we should rush out into the field and excavate every deposit that contains animal remains but that zooarchaeological collections be studied for what they reveal about ancient human behaviors and also for what they suggest about ancient environments and climates. Archaeologists are well aware of the critical role of the natural environment as the selective context for the last ~3–5 million years of hominin biological and cultural evolution (e.g., Bobe et al. 2007; Kintigh et al. 2014). Knowing what that environment was like is important to understanding humankind's cultural and biological history.

The second reason paleoenvironmental reconstruction based on faunal remains should become more commonplace rests on the fact that zooarchaeology should increasingly have an applied aspect to it (e.g., Wolverton et al. 2016). Conservation paleobiology is now a hot topic (Dietl et al. 2015); using paleobiological data from pre-hominin times (>5,000,000 years ago) to understand how past environmental change influenced organisms in order to better predict how future environmental change might impact organisms is becoming fairly common. Paleozoological (including zooarchaeological) data are beginning to be used to test bioclimatic envelope, ecological niche, and species distribution models, all built by neocologists, biologists, and conservation biologists. But those data also need to be used to inform conservation biology by increasing our understanding of how and why particular species responded in particular ways to environmental change. Such findings can then inform identification of the most appropriate conservation applications aimed at sustained ecological goods and services. Not only would development of the applied aspect of zooarchaeology seem to be ethically mandatory, it could provide additional sources of funding for study of existing collections. Finally, zooarchaeological data, unlike paleontological data, often reflect human influence on environments and faunas, and this could be quite valuable in an applied or conservation setting (Wolverton et al. 2016).

The zooarchaeological record in the Old World extends back in time several million years and clearly spans major shifts in environments and climates. The New World archaeological record extends back only ~14,000 years, but zooarchaeological remains dating to the Pleistocene–Holocene transition suggest major environmental changes occurred at that time (e.g., Driver 1988, 2001; Johnson 1986, 1987; Morlan 1984; Walker 1982). Similarly, remains from Holocene deposits suggest there were major environmental shifts throughout this epoch (e.g., Falk and Semken 1990; Schmitt and Lupo 2012; Semken 1980). How faunas in an area throughout the period of human occupancy responded to humans is, however, still only patchily known. It is my hope that this paper might facilitate growth in paleoenvironmental reconstruction based on zooarchaeological remains, what can be considered a wide-open field of inquiry.

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