Evolution of Neogene Mammals in Eurasia: Environmental Forcing and Biotic Interactions

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Keywords

ecometrics, computational methods, paleobiology, precipitation, community dynamics

Abstract

The relative weights of physical forcing and biotic interaction as drivers of evolutionary change have been debated in evolutionary theory. The recent finding that species, genera, clades, and chronofaunas all appear to exhibit a symmetrical pattern of waxing and waning lends support to the view that biotic interactions shape the history of life. Yet, there is similarly abundant evidence that these primary units of biological evolution arise and wane in coincidence with major climatic change. We review these patterns and the process-level explanations offered for them. We also propose a tentative synthesis, characterized by interdependence between physical forcing and biotic interactions. We suggest that species with evolutionary novelties arise predominantly in "species factories" that develop under harsh environmental conditions, under dominant physical forcing, whereas exceptionally mild environments give rise to "oases in the desert," characterized by strong competition and survival of relics.

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INTRODUCTION

The dualistic idea that evolutionary change is due on the one hand to the processes of life itself and on the other hand to the effects of its changing physical circumstances has deep roots in evolutionary theory. To Charles Darwin, the biotic component was clearly prevalent: "As far as I am able to judge, after long attending to the subject, the conditions of life appear to act in two ways; namely, the nature of the organism, and the nature of the conditions. The former seems to be much the more important" (Darwin 1859, p. 26). Most paleontologists of the nineteenth and early twentieth centuries would probably have agreed that both factors are involved, given that evolution was seen as increasingly perfect adaptation to external conditions, but the relative emphasis placed on the biotic versus the physical has varied. As it was for Darwin, the biotic side was dominant for neo-Lamarckist Edward Drinker Cope, despite differences in theoretical underpinnings. Cope's Law of the Unspecialized was based on the idea that because adaptation drives increasing specialization, evolving lineages become progressively susceptible to extinction. "Degeneracy is a fact of evolution . . . and its character is that of an extreme specialization, which has been, like an overperfection of structure, unfavorable to survival" (Cope 1896, p. 174).

The idea that biotic and environmental drivers of evolution should be somehow antagonistic is of much more recent origin. It is often tied in the literature to the enormously influential theoretical construct known as the Red Queen hypothesis, originally proposed by Leigh Van Valen (1973) and recently reviewed by Benton (2009) and Liow et al. (2011). The Red Queen hypothesis was originally offered as an explanation of a newly discovered empirical regularity, the Law of Constant Extinction, also known as Van Valen's law. This law, the empirical basis for which remains controversial (Liow et al. 2011), states that "all taxa for which data exist go extinct at a rate that is constant for a given group" (Van Valen 1973, abstr.), because "the probability of extinction of a taxon is . . . effectively independent of its age" (Van Valen 1973, p. 17). The Red Queen hypothesis states that this is the result of competition in a zero-sum situation: What one species gains, all others collectively lose. As a result, the effective environment of a species decays at a rate that is stochastically constant. Charles Darwin's famous simile of the wedges is an early version of the same idea (Van Valen 1973).

Van Valen's original concept of the Red Queen hypothesis has been widely misunderstood to apply only to competition under unchanging environmental conditions. For Van Valen, the competition clearly occurred within, and was influenced by, a framework of changing conditions:

> The [resource] landscape is changing continuously, at three levels. Species displace each other from areas of the adaptive surface. . . . Secondly, the distribution of [resources] within the landscape changes, as with climate change or (for herbivores) when the flora changes. Finally, the total amount of [resources] (or the amount in fact used) can change. . . . The first two kinds of change in the landscape lead to the Red Queen's Hypothesis, while the third is, without compensatory changes, inconsistent with it. (Van Valen 1973, p. 19)

There has been no shortage of later hypotheses relating evolutionary patterns to environmental change (e.g., Vrba 1985, 1992; Brett & Baird 1995). Barnosky reviewed the field and conveniently summarized the main hypotheses about environmental versus biotic forcing of evolutionary change (Barnosky 2001, table 1). He also proposed a development of the Red Queen theme particularly relevant for fossil-based research. In Barnosky's version, the Red Queen is paired with the Court Jester, who stands for the physical part of environmental change. Barnosky suggested that these causative factors have a scale-dependent inverse relationship: The Red Queen dominates at the low ends of spatial and temporal scales and the Court Jester at the high ends.

Quental & Marshall (2013) recently attempted to test the Red Queen hypothesis in Van Valen's (1973) original, broad sense. In a data set of Cenozoic fossil mammals, they found that clades showed a pattern of symmetric waxing from their origin and subsequent waning to their decline that suggested a decay of their effective environment as predicted by the Red Queen hypothesis. This result depended as much on declining origination as on increasing extinction, which recalls a theoretical treatment of extinction and origination developed by Van Valen (1985): He saw the process of deterioration as resulting from the filling up of available niche space under Red Queen competition. "It becomes progressively more difficult for most taxa to find a new way to exploit the less resistant parts of the environment around them. The biotic part of this environment is itself evolving for its own benefit. This produces a decline in the probability of origination" (Van Valen 1985, p. 136).

A recent trend in paleobiology has been the discovery of such patterns of waxing and waning at different levels of the biotic system, from the occupancy trajectories of individual species and genera (Jernvall & Fortelius 2004, Raia et al. 2006, Foote et al. 2007, Liow & Stenseth 2007) over the taxonomic diversity of entire clades (Quental & Marshall 2013) to the geographic range of chrono-faunas defined by taxonomic similarity (Eronen et al. 2009, Mirzaie Ataabadi et al. 2013). There are interesting echoes in this emerging view of much earlier evolutionary thinking, from Lyell and Darwin (Van Valen 1985) to Cope. In this article, we consider recently accumulated evidence on the climatic history and the evolution of the land mammal faunas of Eurasia from this simultaneously novel and traditional perspective, emphasizing quantitative and spatially explicit analyses.

NEOGENE MAMMALS AND ENVIRONMENTS OF EURASIA: THE ECOMETRIC APPROACH

The dense fossil record of Eurasian land mammals offers a particularly suitable empirical framework for addressing the causes of evolutionary change. It provides a record of actual change, potentially in great temporal or spatial detail but usually collapsed to coarser aggregates for simplicity or statistical power. An increasingly important and obviously useful direction of mammalian paleobiology has been interfacing fossil-based proxy data with results from paleoclimate modeling, a trend that not only is enabled by but also is driving the rapid augmentation of the use of large and complex data sets (see Brewer et al. 2012, Uhen et al. 2013) and increasingly complicated methods.

Mammalian fossils provide various kinds of proxy data such as climate variables (Janis et al. 2004; Eronen et al. 2010c,d; Polly 2010) and isotopes (e.g., West et al. 2006, Passey et al. 2009, Cerling et al. 2010). Through biostratigraphy, they provide a chronology of change to be used when other temporal data are either lacking or inferior in some way (Steininger 1999, Agustí et al. 2001, Wang et al. 2013). In response to the increased demand for quantitative proxy data, trait-based methods (Damuth 1982, Damuth et al. 1992, Fortelius & Hokkanen 2001, Fortelius et al. 2002) have become increasingly prominent in paleobiology, an approach that Eronen et al. (2010b) and Polly et al. (2011) have termed ecometrics. By trait-based ecometrics, we mean the study of traits that are functionally related to the organism's physical (e.g., climate) or biological (e.g., vegetation) environment. For the traits to be useful, they must be measurable from fossil remains and be relevant to important climatic and environmental factors (Eronen et al. 2010b). The effects of traits influence the success of individuals, which in turn influences the geographical distribution of populations and species. The cumulative effect of traits across species therefore feeds upward into the assembly and dissolution of ecological communities (Polly et al. 2011). The conclusions and models used should be taxon free, i.e., not dependent on the identities of the individual taxa but instead dependent only on their measured properties. That is, our conclusions should remain unchanged even if the names of taxa were deleted from our database.

HYPSODONTY

One of the best-understood ecometrics is the molar crown height of herbivorous large mammals, which has been shown to correlate with precipitation. The hypsodont crown is an adaptation to high rates of tooth wear (Janis & Fortelius 1988). Different diets vary in the amount of wear they produce: Species that eat abrasive or tough foods, or foods of poor nutritive quality, usually have high-crowned teeth. When hypsodonty is averaged across species in mammalian large herbivores, there is a strong geographical correlation with precipitation. The low-crowned species (e.g., *Capreolus*) live in more humid environments, whereas the high-crowned species (e.g., *Equus*) live in more arid conditions. Eronen et al. (2010b) used regression trees to quantify this relationship and found that 65.8% of the geographical variance in mean tooth crown height was explained by precipitation.

It is generally helpful and sometimes critically important to make a distinction between inherited and acquired traits. Particularly relevant for this review is the distinction between inherited dental traits with deep phylogenetic roots, such as the number of cusps or cutting edges; inherited traits with less deep roots, such as hypsodonty; and acquired traits, such as tooth wear patterns (Fortelius & Solounias 2000, Damuth & Janis 2011, Kaiser et al. 2013) or stable isotope ratios retrieved from dental tissues (Cerling et al. 2010, Uno et al. 2011). Only the latter are direct indicators of diet, whereas the former should be viewed more as setting the boundary conditions for the diets and habitats available to a particular species—that is, what is usually understood as a phylogenetic constraint (Raia et al. 2010). Although all are ultimately related to diet, we argue below that inherited traits have a much more direct relationship to climate than do acquired ones, and that they may even reflect (and estimate) climate better than they do diet (see the Hypsodonty sidebar).

For the fossil mammals of Eurasia, the trend of increasing emphasis on data analysis is closely tied to the advent and development of the NOW database (originally, Neogene of the Old World; since 2012, New and Old Worlds) (**http://www.helsinki.fi/science/now/**). This database is a public resource based on international collaboration that began in 1992 and launched its first web-based user interface in 1999 (for more information see Uhen et al. 2013). NOW grew out of an attempt to understand the paleoecological and stratigraphic relationships between Central Europe and the Eastern Mediterranean during the Miocene (Bernor et al. 1996), and its first product was a quantitative analysis of fossil mammal occurrence data that in addition to addressing diversity and taxonomy included analyses of body size and tooth shape that we would today describe as ecometrics. In the terrestrial Eurasian Neogene setting, other major data sources are the regional data sets compiled for the Potwar Plateau of Pakistan (e.g., Barry et al. 1995, 2002) and central Iberia (e.g., Daams et al. 1999a,b; van der Meulen et al. 2005; van Dam et al. 2006).

By generating quantitative, numerical estimates of climate variables, ecometrics has opened up the possibility to integrate fossil-based reconstructions with paleoclimate model output. A straightforward application is to match proxy values to model values, as was done in a study of the spatial expansion and contraction of the Pikermian chronofauna by Eronen et al. (2009). Other approaches involve integrating niche modeling and phylogeography with climate modeling to quantitatively examine the climate-distribution relationship in extinct organisms. So far, applications have mainly concerned Quaternary studies, and we do not review them here; see, for example, Lawing & Polly (2011), Nogués-Bravo & Rahbek (2011), Polly & Eronen (2011), and Bradshaw et al. (2012). Together, these approaches offer ways to integrate neoecology and paleontology for a full system view (see Polly et al. 2011, Fritz et al. 2013).

NARRATIVE: TOWARD A COHERENT HISTORY
OF THE EURASIAN NEOGENE

This section presents a very brief summary of our best understanding of "what really happened" to the environments and land mammal faunas of Eurasia during the Neogene. How this story feeds into our current understanding of evolutionary change in relation to environmental forcing and biotic interactions is discussed in the next section. The broad outlines of the Neogene environmental and faunal history of Eurasia have long been known, and quite detailed accounts have been published over the years (e.g., Kurtén 1972, Bernor 1983, Janis 1993, Agustí & Anton 2002), with no dramatic reinterpretation of the original patterns.

In the early and middle Miocene, large areas of the continent were forested until the global cooling at approximately 14 Ma prompted a trend toward drier and more open habitats, starting with the inner parts of the continent. This major and prolonged process caused alterations to the mammal fauna, progressing from Central Asia toward Western Europe during the late Miocene and culminating in a large turnover event in the Iberian Peninsula and Central Europe known as the Vallesian Crisis at approximately 10 Ma. This trend came to an end with an abrupt change seen in Europe at the Miocene–Pliocene boundary at approximately 5.3 Ma, when warm and humid conditions briefly returned (e.g., Kovar-Eder et al. 2006, 2008). Globally, the Pliocene was the last warm phase before the start of the large climate oscillations that led to development of continental ice sheets from 2.7 Ma onward (Zachos et al. 2001; Haywood et al. 2009, 2013).

Through decades of studies, this story has remained remarkably similar, although its details are far better understood today than they were a few decades ago. In particular, the advent of spatially resolved analyses using new and improved paleoclimate and paleodiet proxies (Fortelius et al. 2002, 2006a; Eronen et al. 2010c,d; Liu et al. 2012; see also the Hypsodonty sidebar) generated information that is more detailed, more explicit, and therefore more amenable to causal explanation than the broad generalizations available to earlier scholars.

Interestingly, progress in stratigraphy has been modest and largely concerned with local to regional schemes. At the subcontinental to continental scale, resolution has remained at about the same level for decades. Progress in computational biostratigraphy (seriation) (e.g., Ukkonen et al. 2005, Fortelius et al. 2006b, Puolamäki et al. 2006) has not dramatically improved resolution, although it offers some advantages over conventional approaches, especially ease of use and objectivity. It appears that current biostratigraphic schemes, such as the Mammal Neogene (MN) system (Mein 1989, de Bruijn et al. 1992), are already close to the limit of available resolution for spatial scales larger than the regional (Alroy et al. 1998, Fortelius et al. 2006a).

The Neogene history of Eurasia played out against a backdrop of global change that included increased seasonality and aridification and the spread of grasslands (see Strömberg 2011 for a recent review). The question of how grassland expansion impacted the trophic structure of mammal communities is currently a major emerging topic (Fortelius 2013) but has not yet produced matter enough for review. Here we focus on the climatic and evolutionary patterns of the story, with special emphasis on the spatial dynamics (see the Productivity and Harshness sidebar). For simplicity, we treat Eastern Asia separately from the rest of the continent. For context, we provide updated precipitation estimates (based on Eronen et al. 2010c,d) in **Figure 1** and the corresponding molar crown height information (hypsodonty) in **Supplemental Figure 1** (follow the **Supplemental Material link** in the online version of this article or at **http://www.annualreviews.org/**). In addition, we provide a summary of faunal dynamics in **Figure 2**. The latter shows the species-locality occurrence data (SPLOCs; see Fortelius & Hokkanen 2001 for details), summed to the family level for three areas (Western Europe; Eastern Europe and Central Asia; and Eastern Asia). As SPLOCs record the occurrence of a species through its range and therefore its abundance, these

PRODUCTIVITY AND HARSHNESS

The change from the tropical and subtropical conditions of the early Miocene to the cooler conditions of the later Neogene was connected to a general lowering of primary productivity. The net primary productivity (NPP) is limited in the terrestrial realm mainly by three interactive components: temperature, radiation, and water availability (Churkina & Running 1998, Nemani et al. 2003). In the tropical area neither water nor temperature limits the productivity, and in the extreme polar regions NPP is limited by radiation only. Outside these extremes, NPP is limited mainly by interactions of temperature and water availability. Lower productivity limits the availability of (easily) edible plant parts for herbivores and therefore leads to harsher overall conditions for them. One common response in herbivorous mammals to such harshness is increased dental durability (Janis & Fortelius 1988). Typically, increased dental durability means increased hypsodonty and occurs where NPP is low, in climates that are seasonally or permanently arid, cold, or both. Another, less commonly appreciated response is increased mean cutting efficiency of the dentition, which typically means the absence of forms without a sufficient battery of cutting edges (Liu et al. 2012).

figures depict the relative ecological dominance of mammalian families though time. In **Figure 2d** we also highlight the most important tectonic and climatic events through the Neogene, placed in their stratigraphic framework.

Europe and Central Asia

The early Miocene (23–15 Ma) was humid overall (1,000–1,500 mm/year) (Fortelius et al. 2002, Eronen et al. 2010d) (**Figure 1a**). Climate modeling studies have shown that the humid conditions were related to high CO_2 levels (700 ppm) and warm climate (3°C higher global surface temperature than today) (Henrot et al. 2010, Herold et al. 2011). There were drier regions in the Iberian Peninsula (500–700 mm/year), in the Eastern Europe/Eastern Mediterranean area (800 mm/year), and in central western China (600–800 mm/year). The early Miocene taxa indicating more arid conditions are primarily precociously mesodont and hypsodont ungulates of the *Hispanotherium* fauna, known in the early Miocene only from central Asia and Spain (Fortelius et al. 2002). Bruch et al. (2007, 2011) presented a detailed climatic reconstruction based on the paleobotanical record of the western Eurasian Neogene. According to these authors, precipitation in Europe during the early to middle Miocene was 800 to 1,500 mm/year. (These values are relatively close to today's, but the higher temperature and evapotranspiration during that time makes direct comparisons too complicated to attempt here.) The early Miocene was a time of weak seasonality and shallow temperature gradients (Utescher et al. 2000; Mosbrugger et al. 2005; Bruch et al. 2007, 2011), which is in line with the ecometric evidence from herbivore teeth (see Fortelius et al. 2002, Eronen et al. 2010c).

During the earliest Miocene, small to medium-sized ungulates were common and amphicyonids were the dominant carnivores in Europe. Most species of these families persisted from the late Oligocene and were adapted to soft vegetation browsing (Agustí & Anton 2002). Artiodactyls mainly included archaic forms such as Palaeomerycidae and Moschidae (see **Figure 2a**) in Western Europe. In Eastern Europe, the numerous families with restricted distributions included Entelodontidae, Leptomerycidae, Lophiomerycidae, and Sanitheridae (noted as other families in **Figure 2b**). In both Western and Eastern Europe, the relative proportion of rhinos was high (**Figure 2a,b**). During the early Miocene, cervids and suids dispersed widely in Eurasia. Perissodactyls were represented by midsized tapirs (*Protapirus*, *Paratapirus*, and
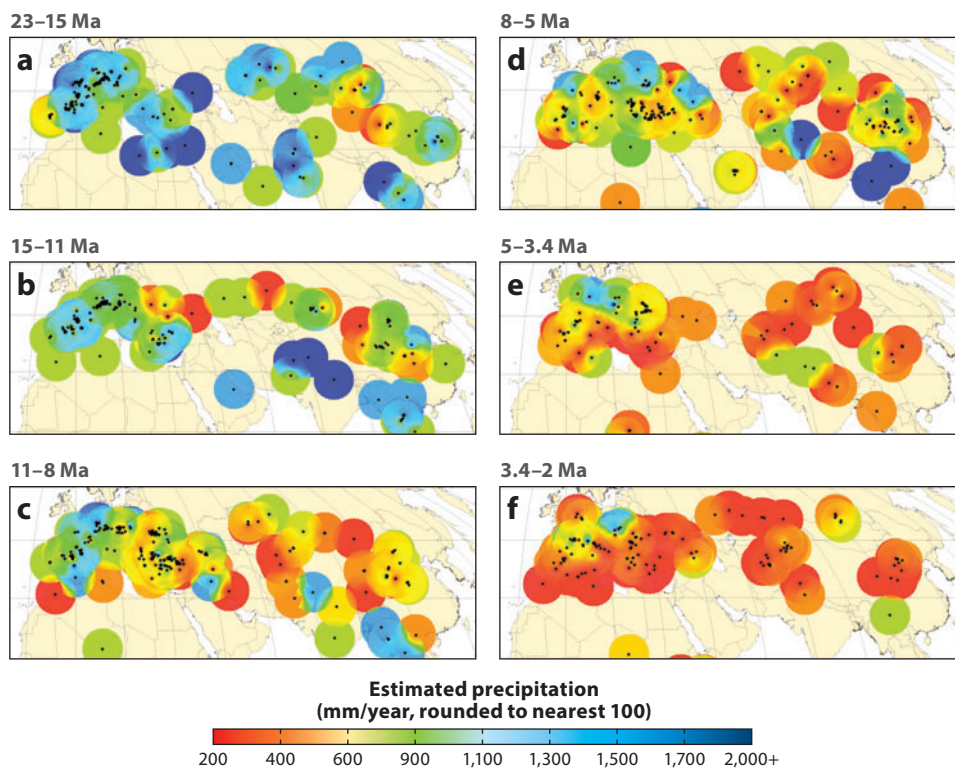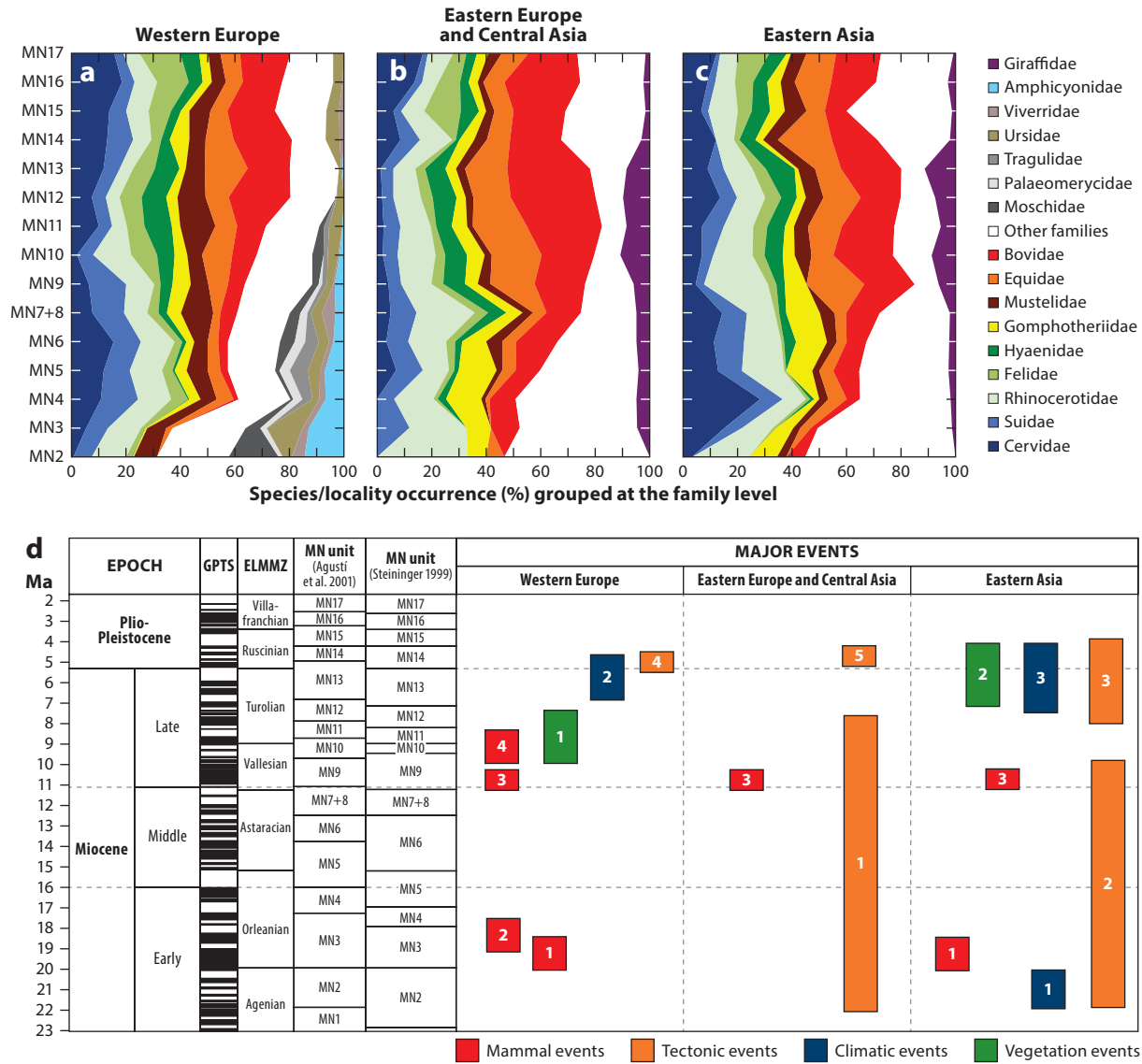
Figure 1

(*a*) Estimated precipitation values for the early Miocene (MN1–MN5, 23–15 Ma), (*b*) the middle Miocene
(MN6–MN7+8, 15–11 Ma), (*c*) the early late Miocene (MN9–MN11, 11–8 Ma), (*d*) the late late Miocene
(MN12–MN13, 8–5 Ma), (*e*) the early Pliocene (MN14–MN15, 5–3.4 Ma), and (*f*) the late Pliocene
(MN16–MN17, 3.4–2 Ma). All estimates are based on the method of Eronen et al. 2010b. The absolute
age boundaries of Mammal Neogene (MN) units are based on the conservative compromise correlation of
Steininger (1999), which is used in the NOW database and is the default correlation used in this review. For
an alternative correlation based on the Iberian record (Agustí et al. 2001), see **Figure 2d**.

Eotapirus), rhinos (*Protaceratherium*, *Menoceras*, and *Mesaceratherium*), and chalicothers (Agustí &
Anton 2002).

There is by now ample evidence that the western half of Eurasia experienced progressive
drying at the midlatitudes during the middle and late Miocene, with an associated development of
open-habitat-adapted mammalian fauna similar to the savanna fauna of present-day Africa, as first
noted by Othenio Abel (Bernor et al. 1996) (see the Productivity and Harshness sidebar). What
drove this development remains controversial, but the Tibetan uplift (Broccoli & Manabe 1992,
Kutzbach et al. 1993, An et al. 2001) and the shrinkage of the Paratethys Sea (or their combined
effects) (Ramstein et al. 1997, Fluteau et al. 1999, Zhang et al. 2007) are widely considered to have
been among the main physical causes of change (**Figure 2d**). Specifically, the strengthening of
the South Asian monsoon due to Tibetan uplift can also lead to summer drying of central Eurasia
and the Mediterranean (Kutzbach et al. 1993, Rodwell & Hoskins 1996) (**Figure 1d**).

The use of mean hypsodonty as a humidity proxy reveals a striking spatial pattern of changing
habitat distribution in Europe during the Neogene (Fortelius et al. 2002, 2006a; Eronen et al.
2010d). The first drying is seen during the early and early middle Miocene, as the appearance

Figure 2

Species-locality occurrence data for the Eurasian continent plotted at the family level through the Neogene for each Mammal Neogene (MN) unit. For a detailed description of the method, see Fortelius & Hokkanen 2001. The most important families (with more than 100 occurrences through the entire record) are shown as their own groups in the graph for each of the areas of interest. All other families (those with fewer than 100 occurrences through the whole record) are lumped into the "other families" group. (*a*) Western Europe, defined as all localities in Eurasia west of the 20°E longitude. (*b*) Eastern Europe and Central Asia, defined as all localities in Eurasia between 20°E and 70°E. (*c*) Eastern Asia, defined as all localities in Eurasia east of 70°E. (*d*) Stratigraphic framework in Eurasia, showing the Geomagnetic Polarity Time Scale (GPTS; following Gradstein et al. 2012) and European Land Mammal Mega-Zones (ELMMZ; Steininger 1999). We also show MN units using both the Agustí et al. (2001) and Steininger (1999) correlations. Shown in this framework are major events in the three areas of interest. Mammal events (*red bars*): 1, entry of Anchitherium; 2, entry of Gomphotherium; 3, entry of Hipparion; 4, Vallesian Crisis. Tectonic events (*orange bars*): 1, retreat of Paratethys Sea, 2, uplift of Southern and Central Tibetan Plateau; 3, uplift of Northern and Eastern Tibetan Plateau; 4, Messinian Salinity Crisis; 5, shrinking of Central Paratethys Sea. Climatic events (*blue bars*): 1, initiation of monsoon climate; 2, inception of Greenland ice sheet; 3, intensification of monsoon climate. Vegetation events (*green bars*): 1, appearance of deciduous forest; 2, expansion of C$_4$ plants.

and progressive strengthening of an east-west gradient between a drier and more seasonal East (600–1,000 mm/year) and a more humid and less seasonal West (800–1,500 mm/y) (Fortelius et al. 1996) (**Figure 1**). Progressive cooling eventually turned this into a north-south gradient from the latest Miocene onward (Fortelius et al. 2006a) (**Figure 1**).

In Western Europe, most of the middle Miocene mammal assemblages persisted from the early Miocene, and some of them (suids and cervids) even increased in number while early elements disappeared (**Figure 2a**). In Eastern Europe, rhinos, gomphotherids, and bovids became the dominant elements of the fauna (**Figure 2b**).

Eronen et al. (2009) defined a Pikermian chronofauna on the basis of taxonomic similarity to the locality of Pikermi and mapped its expansion and eventual contraction over 8 million years, from approximately 13 to 5 Ma. The Pikermian large mammal biome was characterized by the great diversity of felids, horses, rhinoceroses, antelopes, giraffes, and distant relatives of elephants and by the paucity of deer. The Pikermian chronofauna developed from a restricted area in the sub-Paratethyan province (essentially Persia and Anatolia) in the late middle Miocene at approximately 13 Ma, spread westward to reach its climax at 8 Ma, and then started to withdraw eastward to disappear at the Miocene–Pliocene boundary—that is, approximately 8 million years after its origination and 3 million years after its maximal spatial extent. Eronen et al. (2009) causally related the spatial expansion phase of the Pikermian chronofauna to the progressive strengthening of a high-pressure system over and to the south of the Paratethys Sea (see also Micheels et al. 2011). Its eventual decline and disappearance (at least from its original Eurasian range) was attributed to habitat fragmentation and partial reforestation in the latest Miocene.

In Western and Central Europe, the change from warm and wet to cooler and drier conditions was more abrupt than in the Pikermian core areas. At approximately 16 Ma, there were still tropical forests in Europe, supporting a high diversity of mammals including apes. This recently has been attributed to high atmospheric CO_2 content (560–700 ppm) and to a small East Antarctic ice sheet (Hamon et al. 2012). Also, the late Miocene (11–5 Ma) was warmer than the present (e.g., Pound et al. 2012). The warmth in the late Miocene has been mainly attributed to vegetation feedbacks (Dutton & Barron 1997; Micheels et al. 2007, 2009; Knorr et al. 2011) and to reduced gradients in sea surface temperature (LaRiviere et al. 2012).

At approximately 10 Ma, the Western Eurasian environments included both the old forest taxa (see **Figure 2a**, MN9; cervids and suids were still common) and new arrivals from the drier biomes developing in Asia and Eastern Europe (see **Figure 2b**, MN9; bovids and equids, among others, were becoming more common). This temporal edge effect resulted in high diversity of large mammals during the early Vallesian. According to Casanovas-Vilar et al. (2010), the mean standing diversity in large mammals in the Iberian Peninsula shows a gradual increase that started at approximately 13 Ma and culminated at 10 Ma, explained by a slightly positive balance between originations (including immigrants) and extinctions during the middle Miocene. The Vallesian diversity maximum at approximately 10 Ma (Agustí & Anton 2002) reflects this slow trickling of species into Iberia and adjacent regions of Western Europe from the Eastern Mediterranean, where the warm subtropical forests were able to maintain high species richness that contained immigrants as well as endemic relict forest taxa. The fossil mammal communities of Western Europe were especially rich in small large mammals (e.g., small suids, small cervids, mustelids, amphicyonids) of less than 30 kg in body mass, suggesting a productive, forested habitat (Franzen & Storch 1999, Agustí et al. 1999a).

The overall faunal similarity between Iberia and the Eastern Mediterranean was fairly low at 15 to 10 Ma, while similarity between Central Europe and Iberia was much higher. Between 10 and 9 Ma the similarity between Iberia and the Eastern Mediterranean suddenly increased (Casanovas-Vilar et al. 2010). This homogenization reflects the Vallesian Crisis at 9.7 Ma

(see **Figure 2d**), first described by Agustí & Moyà-Solà (1990). Increased seasonality—particularly, low winter temperatures (Mosbrugger et al. 2005)—spelled the end for the evergreen subtropical woodlands of Western Europe. The replacement of evergreen by deciduous forest had a dramatic effect on mammals that depended on year-round availability of browse, especially fruit (Agustí et al. 2003) (see the Productivity and Harshness sidebar). During this crisis the old forest-adapted taxa, such as nimravids, small suids, tapirs, and rhinos, were heavily affected; the hominoid *Dryopithecus* and the amphicyonids, among others, suffered extinction (**Figure 2a**) (see also Agustí et al. 1997, 2003). This could be seen as the completion of the process started during the early Vallesian: the eventual replacement of old forest taxa by new open-habitat-adapted immigrants that prior to the crisis had co-occurred with the forest taxa in superrich assemblages (a macroevolutionary edge effect).

An aspect of this shift toward open habitats was a change in community structure toward increased dominance of a smaller number of common species (Jernvall & Fortelius 2002). Taxonomically, this shift was accompanied by a gradual increase in the commonness of ungulates (see **Figure 2**). Initially, suids and rhinoceroses were the dominant families. Yet, open-adapted bovids and equids progressively came to dominate through adaptive radiation driven by increasing ecological specialization (Raia et al. 2011).

Whereas the Vallesian Crisis was an abrupt event in Western and Central Europe, there was no corresponding crisis in the Eastern Mediterranean (Fortelius et al. 1996, Koufos 2006). This pattern is expected under the scenario outlined above: The open biomes expanding in Eastern Europe and Asia did not undergo any corresponding abrupt change until much later, at the Miocene–Pliocene transition at 5 Ma, when the sudden return of more humid and forested conditions brought about a major turnover event (Eronen et al. 2009) (see also **Figure 2b**, change from MN13 to MN15). Climatic reconstructions for this period reveal a warm and dry climate in southwestern Spain, North Africa, and Sicily (Fauquette et al. 2006, Fortelius et al. 2006a), whereas the Black Sea region was comparatively more humid. Kostopoulos (2009) noted that the large mammal community in the Eastern Mediterranean was in constant flux, with a large number of migrants observed throughout the late Miocene.

The Pliocene epoch (5.3–2.7 Ma) was the last warm phase before the start of the Ice Age. There are excellent reviews on Pliocene climate (e.g., Salzmann et al. 2011); only a summary is given here. During the mid-Pliocene, the global mean temperature was 3°C warmer than present, and the warming was especially pronounced in the high latitudes, making the latitudinal climate gradient shallower than before (Haywood et al. 2009, Salzmann et al. 2011). Recent evidence suggests that the warming during this time was caused by increased atmospheric CO_2 content (e.g., Pagani et al. 2009). In Central Europe, evergreen and warm temperate mixed forests dominated; in southern parts, climates were drier (e.g., Agustí & Anton 2002, Salzmann et al. 2008). Surprisingly, despite abundant research on climate during the Pliocene, research on mammalian communities has been sadly neglected in recent decades, except for some interesting local and regional studies. Such studies will need to be synthesized to explore the broader patterns in mammalian evolution in the Pliocene.

Eastern Asia

The corresponding history of the eastern half of Asia is less well documented, but a coherent view is nonetheless beginning to emerge. The first areas to show aridification were in Central Asia (Fortelius et al. 2002, Eronen et al. 2010c); further to the east, there is evidence of a midlatitude dry belt from the early to early late Miocene (~400–800 mm/year) (see **Figure 1**), with increasing humidity in the later late Miocene (>800 mm/year) (Liu et al. 2009). The interpretation is that

Eastern Asian climate was dominated by the planetary system until the later late Miocene, when the regional monsoon system became dominant (Passey et al. 2009, Liu et al. 2009) due to the Tibetan uplift (An et al. 2001, Tang et al. 2011), particularly its northern and northeastern part (Tang et al. 2013). There is an interesting pattern of alternating conditions between the eastern and the western parts of the Eurasian continent from the middle Miocene onward, so that when one end is humid the other tends to be dry. Thus, in the late middle Miocene and early late Miocene (~13–8 Ma) China was more arid than Europe, whereas in the latest Miocene (8–5 Ma) the opposite was true. In the Pliocene the pattern was again reversed (Fortelius et al. 2002, Mirzaie Ataabadi et al. 2013).

This unrecognized reversed humidity trend in Eastern Asia compared with the rest of the planet was a longtime source of stratigraphic confusion. With the recognition that the younger faunas represent regionally more humid conditions (Fortelius et al. 2002), the relationships between time and environmental change became much clearer. A part of this revised interpretation is the surprising discovery that most of the classical *Hipparion* fauna (Red Clay) localities in China are younger than 8 Ma and some are even younger than 6 Ma, as summarized by Kaakinen et al. (2013) and Zhang et al. (2013). The Miocene–Pliocene transition in the Eastern Asian mammal faunas appears much less dramatic than in those from the western part of the continent, but data limitations preclude firm conclusions (**Figure 2c**).

The details of faunal history in Eastern Asia are difficult to discern because the data are still sparse. Nonetheless, the community structure and biodiversity seem to reflect environmental conditions much like in Europe, although the timing is offset due to the east-west climatic see-saw pattern described above. Thus, in the relatively arid context (400–800 mm/year) of the late middle and early late Miocene, the Chinese mammal fauna was relatively endemic, with several lineages of locally adapted taxa (including, e.g., several bovid and giraffid genera such as *Lantiantragus*, *Shaanxispira*, and *Schansitherium*) not known from the western part of the continent (Mirzaie Ataabadi et al. 2013). With increasing humidity (800–1200 mm/year) after 8 Ma, the fauna became markedly less endemic as species from the surrounding, increasingly arid areas spread into this suddenly attractive "oasis in the desert" (Fortelius & Zhang 2006) (see the Productivity and Harshness sidebar). As during the early Vallesian of Europe, up to the Vallesian Crisis, this generated highly diverse mammal communities with taxa of biogeographically diverse origins, a phenomenon similar to the familiar edge effect of ecology but at a macroevolutionary scale. And like in the Vallesian Crisis of Europe, the East Asian communities were eventually replaced by less diverse assemblages with species capable of existing under harsher conditions.

Mirzaie Ataabadi et al. (2013) computed additional chronofaunas on the basis of taxonomic similarity, analogous to the Pikermian chronofauna discussed above. They showed that during the middle to late Miocene, chronofaunas extended their range into Eastern Asia from the west. The so-called Tunggurian (middle Miocene) chronofauna can be seen as a late, eastern extension of the arid-adapted *Hispanotherium* fauna that first appeared in Iberia in the early Miocene. Similarly, the Baodean chronofauna can be seen as an eastern representation of the Pikermian chronofauna. Although the details are different, these chronofaunas, like the Pikermian one, clearly changed their spatial distribution in response to changing climate.

ENVIRONMENTAL FORCING AND BIOTIC INTERACTIONS: TOWARD A PROCESS-LEVEL UNDERSTANDING OF THE PATTERNS OBSERVED

Here we relate some of the patterns described in the above section to an emerging framework of causal processes. It is still premature to speak of an actual synthesis, but several of the pieces can be

seen as part of the same puzzle. Where feasible we point out conceptual links to earlier hypotheses and metaphors. The outline of a broad synthetic scenario of how environmental forcing and biotic interactions relate to evolutionary change is sketched in the next section.

Abundance Changes in Favored Species Drive Major Evolutionary Trends

Fortelius et al. (2002) introduced an ecometric approach to paleoprecipitation reconstruction based on hypsodonty (see the Hypsodonty sidebar). Jernvall & Fortelius (2002) observed that the change in mean hypsodonty, interpreted on paleoprecipitation maps of Eurasia as progressive aridification, was driven by the most common ungulates (species and genera) of each time interval. The process-level scenario is that as climate dries and open habitats spread, hypsodonty is required to access the spreading resource of open-habitat vegetation (see the Productivity and Harshness sidebar). It then becomes a favored trait, and hypsodont species increase in commonness (incidence) while brachydonts become less and less abundant. During the early Miocene, the dominant habitat was forest, and the most common species were brachydont forest forms; open-adapted species were rare and presumably confined to marginal habitats. As open habitats expanded, the tables turned, and open-adapted forms increased while forest forms decreased. The main driver of this signal was not trait evolution but the changed abundance and distribution of existing species.

Using a phylogenetic approach, Raia et al. (2011) showed that some hypsodont clades were speciating rapidly during this time; new species emerged that were shorter lived and less widespread than their parent species. Adaptive radiation into expanding, new resources was therefore also part of the change. Because the underlying habitat change itself was mainly driven by climate change, it follows that the change in community structure was also climatically driven, although it was inevitably mediated by biotic processes. This finding is consistent with the resource-use hypothesis of Vrba (1992; see also Cantalapiedra et al. 2012).

The scenario outlined above begs a puzzling question: How can it be that key functional traits of teeth, such as the crown height or the number of cutting edges of molar teeth, appear to reflect climate variables better than they reflect diet (Eronen et al. 2010d, Liu et al. 2012, Kaiser et al. 2013)? The function of teeth is, after all and undeniably, related directly to chewing food and only indirectly to temperature or rainfall. This seemingly counterintuitive observation might be explained by the theoretical construct known as Liem's paradox: Animals often avoid the foods to which they are structurally most obviously adapted (Robinson & Wilson 1998). When given free choice, animals typically prefer foods that are nutritious and easy to process. The structural adaptations instead reflect conditions when choice is not free and when survival may depend critically on mechanically highly demanding foods. The frequency and impact of events that require the ability to process demanding fallback foods have little to do with average or modal resource availability and very much to do with climate, especially climate variability and the frequency of harsh events. Under this model, these ecometrics really would be climate proxies first and diet proxies only indirectly. In keeping with this, highly hypsodont ungulate species have wider, not narrower, niches (Feranec & MacFadden 2006). This means that high-crowned molars were used to expand, rather than to change, the resource base (MacFadden et al. 1999) (see the Productivity and Harshness sidebar).

The idea of available versus preferred foods has recently been part of a lively exchange concerning the diet of fossil hominins, several of which turn out to have been consumers, directly or indirectly, of plants with C_4 photosynthesis, meaning mainly grasses and/or sedges (Cerling et al. 2011, Lee-Thorp et al. 2012). A tangential suggestion by Owen-Smith (2013) is that the critical requirement of hominization was the availability of medium-sized carcasses to scavenge and that this requirement was fulfilled uniquely in Africa, for reasons related to the occurrence there

of exceptionally nutritious and grazing-tolerant grasslands. Thus, in yet another permutation of the apparently immortal savanna theory of human evolution, the entire hominin radiation might indeed have been driven by the expansion of grasslands, either through primary or secondary consumption of this new resource (Fortelius 2013).

How Species Respond to Climate Change Depends on Their Body Size, Ecology, Behavior, and History

Body size has an obvious relation with space in that spatial patchiness has different implications for animals of different size. According to clustering of presence-absence information, small mammals, such as rodents and insectivores, form more coherent spatial distribution patterns than large mammals in the European fauna today (Heikinheimo et al. 2007). This finding could explain the result reported for Miocene rodents of the north-central Spanish Calatayud-Daroca Basin by van der Meulen et al. (2005). These authors showed that, under prevailing harsh conditions, the fossil rodent communities of the middle and early late Miocene of Spain were dominated by forms representing early stages of the ecological succession in the local ecosystems of the time. These so-called residents had predominantly continuous temporal distributions, whereas transients, often representing later successional stages, had discontinuous temporal presences.

Results by Casanovas-Vilar et al. (2010) suggest that the superficially similar diversity dynamics of small and large mammals may reflect processes at different geographic scales. In the large mammal fauna of Iberia, episodes of increased diversity coincide with periods of increased taxonomic similarity with other regions, suggesting that diversity increased when extra-Iberian species expanded their ranges into Iberia during favorable episodes. Although such a mechanism might explain the results of van der Meulen et al. (2005) discussed above, this relationship is in fact not observed for small mammals. The most likely explanation of the difference is the more limited dispersal potential of small mammals (Bowman et al. 2002), which is also suggested by the results of Heikinheimo et al. (2007). In line with this, van Dam et al. (2006) presented evidence for a 2.5-million-year periodicity of speciation and extinction events in rodent assemblages from central Iberia and related it to climatic forcing paced by eccentricity and obliquity cycles in Earth's orbit. There is thus growing independent evidence that small mammals respond to environmental change primarily by evolution in situ, whereas large mammals may also achieve niche tracking by shifting their ranges (Eronen & Rook 2004, Raia et al. 2012b).

For large mammals there is some information available on the relationship between in situ evolution and range shift. Badgley et al. (2008) showed that in the Siwaliks sequence, three main patterns emerge across the vegetation change documented in the stable isotope record between 8.5 and 6 Ma: Some lineages retained their dietary habits and perished, others altered their dietary habits somewhat to include components from the new vegetation and survived somewhat longer, and the few lineages that persisted showed continuous dietary change. In a single location, maximum adaptive change meant maximum survival.

In contrast, Raia et al. (2012b) showed, using data from the NOW database, that survival was longest in species that remained unchanged and instead tracked their preferred habitat spatially. The apparent contradiction is probably an illusion brought about by different perspectives: What locally appears as an extinction appears globally as a range shift, and what globally appears as reduced survival appears locally as successful adaptation with increased rate of change recognized as increased taxonomic turnover.

Needless to say, the distinction between stasis and change is to some extent a matter of resolution of the observational data. Eronen et al. (2010a) investigated the widespread and long-lived horse genus *Anchitherium* in an environmental setting derived from ecometrics (mean hypsodonty).

Using 3D morphometrics, they showed that samples from the more arid Iberia showed an evolutionary response of increased molar crown height, whereas the samples from the more humid region of Central Europe did not show any such response. Mesowear analysis showed evidence of more abrasive diets in the Iberian sample, supporting the view that a direct functional relationship was involved (Eronen et al. 2010a; see Fortelius & Solounias 2000 for a description of the method). This again points to Liem's paradox, as hypsodont species were shown to have diets more catholic than those of brachydonts (Feranec 2007). Such subtle responses not detectable by standard ordination techniques may be more common than has been realized; Damuth & Janis (2011) recently reviewed evidence for such changes in living ungulates.

The rate of change is by default expected to be faster in small mammals with short generations (Evans et al. 2012). But the rate of change is also sensitive to behavioral and life history traits and may in fact easily overrule the effect of body size (Okie et al. 2013). Liow et al. (2008) argued that sheltering (sleep-or-hide; SLOH) behaviors confer about double the temporal range, and thus about half the turnover rate, on species that display them. Their explanation was that SLOH behaviors, exemplified by nesting, burrowing, and hibernation, are far more common among the small mammals than the large and that such behaviors cause lower turnover by reducing the risk of extinction, an effect later shown by Liow et al. (2009) for the present-day mammal fauna. SLOH behaviors would thus be in a broad sense analogous to habitat tracking as a way of minimizing environmental stress. Because Liow et al. (2008) were only able to compare small mammals with large, and because only some small mammals (and a few large ones) show such behaviors, the implication is that removing only part of environmental stress from only part of the species results in a halving of the rate of evolution. Thus, well over half of the observed overall turnover would be attributable to environmental forcing.

Finally, Raia et al. (2011) showed that reduced temporal persistence and spatial coverage in Neogene bovids was associated with speciation driving an adaptive radiation. Raia et al. (2012a) argued that trend can be generalized to a pattern in which niche partitioning by ecological specialization also drives an increase in body size in the vast majority of lineages—the original sense of Cope's rule, as it appears in Cope's own writings (especially Cope 1887, 1896).

Over Their Entire Temporal Span, Species and Genera Show a Regular Pattern of Expansion Followed by Contraction

Although the inconclusive debate on coordinated stasis appears to be fading from the current literature and awareness, the general question of how taxon assemblages behave in relation to drivers of evolutionary change is very much alive. Just as for individual taxa, what drives the research and debate is the availability and analysis of large data sets. The possibility of creating computationally defined assemblages also enables more concrete and operationally constrained approaches (Raia et al. 2005, 2009; Eronen et al. 2009).

When the occurrence pattern of species and genera is observed over their entire temporal range, they are seen to exhibit a strongly unimodal trajectory, with little fluctuation between their first rise and ultimate drop to extinction. This pattern was originally reported for European Neogene mammals by Jernvall & Fortelius (2004) and has since been reproduced for other taxa and data sets by Foote (2007), Liow & Stenseth (2007), and Carotenuto et al. (2010), among others. The essence of the pattern of a unimodal commonness trajectory is not that species start rare, as they must, or that they typically decline in commonness as they near their extinction. It is remarkable that the strength of the pattern of lack of recovery from decline is (in land mammals) related to trophic level; herbivores, which are directly dependent on the vegetation, show stronger unimodality than carnivores, and omnivores show no significant unimodality at all

(Jernvall & Fortelius 2004, Raia et al. 2006). Unlike population and metapopulation fluctuations observed at ecological timescales, the metapopulations represented by evolving species and genera rarely exhibit more than a single peak during their entire existence.

Several explanations have been proposed for this pattern. Foote et al. (2007) suggested that the controls at geological timescales slowly cause niche space itself to expand and contract, whereas at ecological timescales species compete to fill the niche space in existence at that time. Liow & Stenseth (2007) speculated that interaction with an increasing number of predators, parasites, and/or competitors will eventually stop the expansion and that environmental changes will thereafter eventually cause decline and extinction of a species.

The explanation originally offered by Jernvall & Fortelius (2004) but removed from the published paper at the suggestion of concerned reviewers was that widespread and abundant species might for multiple reasons suffer an evolutionary slowdown and therefore be bypassed by fast-evolving, newly arisen species with properties more closely attuned to prevailing conditions. Under this model, the very success of a species would also contain the seed of its decline (Raia et al. 2012a, Raia & Fortelius 2013). This seed-of-decline hypothesis is close to Futuyma's (1987) ephemeral divergence model, which states that although continuous and rapid evolution often occurs in local populations, the mosaic of niches and adaptive optima of wide-ranging species prevents local evolutionary changes from spreading across the entire range. In the context of morphologically (and therefore ecometrically) based species and genera, this principle undoubtedly applies to both. And because species in families and orders are, on average, more similar to each other for most traits than to species from other higher taxa (the justification of phylogenetic correction), the cumulative effects of traits feed up higher in the taxonomic hierarchy.

Under a scenario of shifting and geographically differentiated resource bases, the seed-of-decline hypothesis implies that the populations of the future often come from productive environments that are about to become widespread. This idea is conceptually close to the majority rule of Vermeij & Dietl (2006), discussed in the concluding section of this article. Because of resistance to evolutionary change in widespread populations, the most successful populations will be especially at risk as their resource base escapes from their adaptive optimum. By the time the previously successful population has dwindled to a size at which its adaptability might increase, other populations from habitats that happened to anticipate the new environmental conditions will already have captured the newly emerged resources.

For evolving lineages, the seed-of-decline hypothesis predicts a mode of evolutionary change corresponding to the punctuated equilibria model of Eldredge & Gould (1972). A possibly related phenomenon is the blunderbuss pattern reported by Uyeda et al. (2011) for a wide range of data. Contrary to naive expectation, but in accordance with earlier discoveries presented by Estes & Arnold (2007), significant phenotypic divergence does not occur at timescales below 1–10 million years. The blunderbuss seems entirely compatible with the implications of unimodal commonness history of species and predicts that evolutionary change should follow a broadly punctuated-equilibria-like pattern.

An important methodological issue is that while an observation of a fossil is a reliable indicator of the presence of the taxon, nonobservation can be due either to true absence of the taxon or to nondetection of it. The rates of neither occupancy nor detection can be accurately separated in an extreme case when the fossil records are few, no additional assumptions are made, and no information about the sampling process (e.g., about the detection probability) is utilized (Liow 2013). However, the use of larger data sets and/or additional assumptions, such as knowledge of the temporal life spans of species or of similarity of detection probability across sites, makes it possible to reliably separate the effects of occupancy and detection. An example of such an approach is given by Puolamäki et al. (2006), who estimated occupancy and detection probabilities

by Bayesian modeling and used the additional assumptions that for each species there are unknown speciation and extinction dates and that the species should be absent before and after those dates.

The Neogene Land Mammal Faunas of Eurasia Form Distinct, Climate-Controlled Chronofaunas

Eronen et al. (2009) used a combination of ecometrics and similarity mapping to explore the 8-million-year history of the Pikermian (late Miocene) large mammal chronofauna of western Eurasia. Mirzaie Ataabadi et al. (2013) expanded this to other chronofaunas and showed that they also showed regular waxing and waning as well as evidence of climate-tracking spatial shifts. Liu et al. (2012) further showed that the Sansanian (middle Miocene) and Pikermian (late Miocene) chronofaunas occupied different regions of inferred climate space (humidity and temperature) not represented by any of today's major biomes. It therefore appears likely that chronofaunas in this sense represent faunas broadly adapted to resource use in particular paleobiomes and are therefore ultimately under climatic control. In this way, physical forcing of assemblage-level state shifts (inception and demise) could provide a mechanism for resetting the boundary conditions under which species and clades evolve to occupy and increasingly subdivide available niche space through adaptive evolution.

Quental & Marshall's (2013) recent finding that not only individual species and genera but entire mammalian clades exhibit a history of symmetrical waxing and waning over their existence suggests that the pattern may be a pervasive one in biotic systems observed at geological timescales. As discussed briefly in the introduction to this article, this pattern and the explanations offered for it recall some of the main strands of early evolutionary thinking (Lyell, Darwin, Cope). Whether physical forcing or biotic interactions are responsible for it may be a sterile question. As suggested above, the answer is likely to depend on the level at which the pattern is observed. Rather, and in the spirit of Van Valen (1973, 1985), we should ask how biotic interactions depend on physical forcing, resolved both temporally and spatially, over the entire history of the system. We tentatively develop this theme in the concluding section below.

SYNTHESIS: MACROSCALE SOURCE-SINK DYNAMICS

Much of the discussion in the previous section touches, in one way or another, on a classic and still controversial question in ecology: the relationship between productivity and biodiversity, or perhaps more properly the question of changing resource availability, changing resource use, and evolutionary change (reviewed in Mittelbach et al. 2007) (see the Productivity and Harshness sidebar). Some years ago addressing this question might have appeared intractable, but we feel that the new information reviewed above is sufficient for a preliminary attempt at synthesis. A recent study by Liu et al. (2012) offers a useful framework for such an attempt because it provides estimates of both temperature and precipitation from two dental ecometrics: hypsodonty and the count of lengthwise lophs on the molar crown. Of these, hypsodonty is a well-known proxy for rainfall while the number of cutting edges is a more general measure of dental capability (Fortelius 2003). As shown by Liu et al. (2012), they together explain more of both present-day rainfall (63%) and temperature (69%) than either of them does alone. Because humidity and temperature are the main determinants of primary productivity under a wide range of climatic conditions, a reasonable interpretation is that increased hypsodonty and increased lophedness somehow reflect complementary aspects of low primary productivity or dietary harshness, i.e., conditions that are generally or seasonally cold, dry, or both (see the Productivity and Harshness
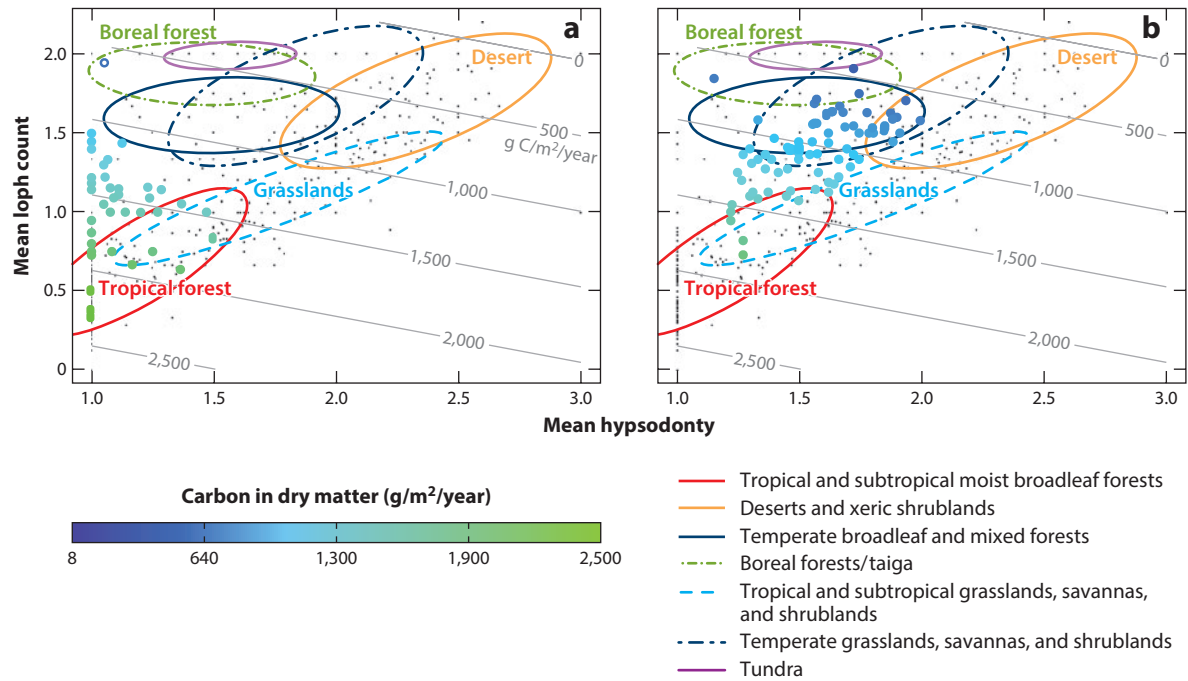
Figure 3

Bivariate plots (black points represent present-day data; colored points represent fossil data) of mean loph count versus mean hypsodonty for the (*a*) Sansan chronofauna and (*b*) Pikermi chronofauna and comparisons with known biomes. Based on Liu et al. 2012.

sidebar). This interpretation is supported by the fact that the two ecometrics together explain more of present-day primary productivity (73%) than they together explain of either rainfall or temperature.

Plotting ecometric temperature and humidity against each other reveals that approximately half of the 149 localities analyzed by Liu et al. (2012) of Europe's middle and late Miocene chronofaunas plot in what today is effectively empty biome space (**Figure 3**). Furthermore, the late Miocene localities are displaced toward the drier range compared with the middle Miocene ones. Two conclusions are evident from this. First, mammalian herbivores of the past were adapted to biomes, or climate regimes, that no longer exist. Second, the ecometric change from the middle to the late Miocene follows the known climate trend, indicating a shift toward drier conditions, closer to biome space occupied by major biomes of today.

The shift in biome space does not necessarily imply a geographic shift, but the following analysis reveals that they are associated with distinct continental-scale spatial dynamics of taxa and chronofaunas. Fortelius et al. (1996) suggested that the reason for the westward transgression of Pikermian forms during the late Miocene was the competitive superiority of the expanding forms, which evolved in eastern habitats that had only recently become available in western locations. Under a trend of sustained change toward drier conditions, species from the drier east are by default preadapted to conditions that will appear later in the wetter region, and they will be superior competitors there. For species from wetter regions the reverse is true: By default they will, after dispersal, face harsher conditions than before dispersal and will be weak competitors in their new environment. This simple asymmetry may give rise to the phenomenon called the "species factory" by Bernor et al. (1996): the generation of invasive biodiversity at the spatial

center of an expanding resource or habitat that cannot be exploited by species lacking some key adaptation or set of adaptations, typically associated with environments that are in some sense harsh (e.g., arid or cold). This is essentially a special case of the majority rule of Vermeij & Dietl (2006), which posits that the source of new or recovering populations is to be found primarily in productive and effectively large environments, and that "it is the conditions to which most individuals are exposed that overwhelmingly create the selective regime of the adaptations of the species" (Vermeij & Dietl 2006, p. 174).

At the hemispherical scale, evidence for a climate-driven species factory has recently been proposed by Eronen et al. (2012), on the basis of the finding that North America was significantly more arid than Eurasia from the middle Miocene to the Pliocene. During this interval, the flow of dispersal, which normally goes from the larger to the smaller continent, was reversed, and conspicuously successful North American invaders, such as hipparionine horses, camels, and canids, colonized the Old World. Similarly, the discovery of an early woolly rhinoceros, *Coelodonta thibetana*, from mid-Pliocene deposits in Tibet led Deng et al. (2011) to speculate that the rising Tibetan Plateau could have formed an early breeding ground for cold-adapted species.

A logical counterpart to the species factory is the oasis in the desert: The area that is milder than its surroundings under a global trend towards harsher conditions, such as the precrisis Vallesian of Western Europe (Casanovas-Vilar et al. 2010) or the latest Miocene of East Asia (Fortelius & Zhang 2006), will act as a refugium for less-harsh-adapted species. The naive expectation might be that in such a case a highly endemic relict community will be found, but that is not observed in either of these two cases. Instead, both in the precrisis Vallesian faunas of Spain and the monsoon-driven Red Clay faunas of China we see a highly diverse community that in addition to endemic or relict forms also includes immigrants from the adjacent, harsher world. This is the edge effect that, in modern ecology, identifies areas of high biodiversity where species from different habitats can mix. The highly productive mild centers would represent a suitable place to live for a variety of species, regardless of their primary structural adaptations, in keeping with Liem's paradox.

Thus, in the case of East Asia, the highest level of endemicity is found not during the late Miocene but during the preceding time interval, the earlier late Miocene (from 11 Ma to approximately 8 Ma), before the monsoon-driven humidity was established. Under a different climate scenario, that nucleus of harsh-adapted endemics could have turned into a species factory, but what actually occurred was that the endemics were largely lost in the highly cosmopolitan and diverse community that is preserved in the Red Clay sediments of the Chinese Loess Plateau (Fortelius & Zhang 2006).

Loss of diversity, including endemics, is expected when conditions turn harsher. Environmental forcing is a sufficient explanation for this outcome. Why endemics should be lost when conditions turn milder and diversity increases is harder to explain with reference to environmental forcing. In that case, a more likely reason is biotic interactions: The harsh-adapted endemics are unlikely to be strong competitors under milder conditions, and strong competition is a likely corollary of high diversity, as in today's tropics (Salisbury et al. 2012).

Under monotonous global change without significant reversals, as an oasis in the desert is a strong attractor for species around it but also a competitive environment where selection is likely to favor traits that will not be valuable in the surrounding world or in the world to come. It therefore acts as a macroevolutionary sink of species adapted to it. In contrast, a species factory is a macroevolutionary source, producing species for environments and resources of the immediate future. In that setting, biotic interactions are expected to be weaker, and environmental forcing is the main driver of evolution. Several and possibly all Neogene chronofaunas so far studied had their source in a species factory and their final refuge in an oasis in the desert (Mirzaie Ataabadi et al. 2013).

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This macroevolutionary source-sink model is entirely compatible with the idea that the evolution of dental functional traits such as hypsodonty or lophedness is related more to climatic extremes, which dictate the fallback foods during population bottlenecks, than to average foods. The prediction is that such traits will evolve mainly in the species factory setting, where environmental forcing is the main driver. The idea that resource availability (harshness) in relation to the spatial configuration of environmental conditions determines the relative importance of physical and biotic drivers of trait evolution is a restricted subset of the Red Queen hypothesis in its original formulation by Van Valen (1973)—less universal and perhaps more operational.

SUMMARY POINTS

1. Rather than ask whether biotic interactions or physical forcing is the main driver of evolutionary change, we need to study their interrelationships.

2. Quantification of the information from the fossil record is crucial for making that information available to modeling and interdisciplinary synthesis.

3. Resolving the information spatially as well as temporally is essential for understanding the patterns recorded in the fossil record.

4. Hypotheses about the causation of biotic change need to explicitly encompass underlying processes as well as the resulting patterns that are in fact observed.

FUTURE ISSUES

1. Can we use individual-based modeling to generate the pattern of symmetric waxing and waning of species, clades, and assemblages in a single experiment?

2. Proxy data so far are unable to resolve short-term (interannual to centennial) variability in deep time. Can we use paleoclimate modeling at different temporal scales to understand the roles of climate variability and extreme climate events as drivers of evolutionary change?

3. Similarly, the extent to which proxy data reflect extreme events rather than average conditions is (almost) unknowable from the record itself. Can modeling help?

4. Can we make use of climatic teleconnections to narrow down the number of explanatory hypotheses that arise from analysis of local data?

5. Can we understand changing resource use at multiple trophic levels? Will this limit the number of available explanations of ecosystem change in terms of top-down versus bottom-up forcing?

6. Can including animals in dynamic models of climate and vegetation answer questions about causal relationships of climate change, including the effect of herbivores on vegetation structure?

DISCLOSURE STATEMENT

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IUCN Red List of Threatened Species: Spatial Data Download. International Union for Conservation of Nature and Natural Resources (IUCN). **http://www.iucnredlist.org/technical-documents/spatial-data**

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Neogene Climate Evolution in Eurasia (NECLIME). **http://www.neclime.de/**

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WorldClim—Global Climate Data: Free Climate Data for Ecological Modeling and GIS. Museum of Vertebrate Zoology, University of California, Berkeley. **http://www.worldclim.org/**