

地点覆盖度、集合群落、地质时期动物群：连接古生物学和现代种群生物学的概念

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摘要: 在古生物群落中新近出现的地点覆盖度或发生率的概念,以及对生物集合种群的空间动态学的深入了解,使古生物学和现代生物学的联系更加紧密。集合群落的概念以及地质时期动物群的古生物学认识显示,将古生物学和生态学结合在一起是大有希望的。评述了目前对这些概念的理解,并以欧亚大陆大型食草动物群落的发育作为范例,介绍了运用这些理论来研究化石记录的方法。研究表明,化石记录中种群覆盖度的研究可以在以化石为基础的进化研究和以现存有机体为基础的进化研究之间架起一座桥梁。地点覆盖度最大的类群,像现代生态学中发生率最大的类群一样,往往是地理分布最广泛、在当地最丰富的类群。

关键词: 欧亚大陆,大哺乳动物化石,地点覆盖度,集合群落,地质时期动物群

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LOCALITY COVERAGE, METACOMMUNITIES AND CHRONOFAUNA: CONCEPTS THAT CONNECT PALEOBIOLOGY TO MODERN POPULATION BIOLOGY

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Abstract The emerging idea of locality coverage, or incidence, in the paleontological community and progress in the understanding of the spatial dynamics of metapopulations biology are bringing the paleobiology and present-day biology closer together. The concept of metacommunities and the paleontological notion of chronofauna show much promise for synthesis of paleontology and ecology. Here I review the present understanding of these concepts. I show how these can be used to investigate the paleontological record, using the development of Eurasian large herbivorous mammal communities as a case study.

Key words Eurasia, large fossil mammals, locality coverage, metacommunities, chronofauna

1 Introduction

Recent developments in geosciences have made it possible to focus on understanding ecological patterns in deep time. The most important of these are; increased temporal control resulting from integrative stratigraphical work, the development of a detailed global stratigraphic framework from the deep sea sediments and its attendant isotope-based paleotemperature curve

(e. g., Flower and Kennett, 1994; Hilgen et al., 1995; Shackleton et al., 1995; Rea et al., 1998; Zachos et al., 2001), the development of increasingly sophisticated paleogeographic reconstructions (e. g., Rögl, 1998; Dercourt et al., 2000; Popov et al., 2004, 2006), increasingly reliable methods to extract climatic proxy data from fossils and sediments (see Liang et al., 2003; Micheels et al., 2003; Uhl et al., 2003 for recent multiproxy comparisons), increasingly sophisticated paleoclimatological applications of atmospheric general circulation models (e. g., Kutzbach et al., 1993; Ruddiman, 1997; Ramstein et al., 1997; Fluteau et al., 1999; Haywood et al., 2000, 2002; Haywood and Valdes, 2004; Steppuhn et al., 2006), and lately the development of large, accessible compilations and databases of fossil organisms such as the Paleobiology Database (<http://www.paleodb.org/>), MioMap (<http://www.ucmp.berkeley.edu/miomap/>) and NOW (<http://www.helsinki.fi/science/now>).

These have made it possible to investigate patterns and processes that are more familiar from contemporary biological literature. The increased amount of paleobiological research focusing on community assembly and dynamics (e. g., Jernvall and Fortelius, 2002; McGill et al., 2005; van der Meulen et al., 2005; van Dam et al., 2006), local, regional and continental environmental change (e. g., Barnosky, 2001; Fortelius et al., 2002; Barnosky et al., 2003; Eronen and Rook, 2004; Eronen, 2006; Fortelius and Zhang, 2006; Koufos, 2006; van Dam et al., 2006) and climatic patterns and teleconnections in deep time (e. g., Ramstein et al., 1997; Ruddiman, 1997; Fluteau et al., 1999; Kutzbach and Behling, 2004; Steppuhn et al., 2006) is remarkable. These together with recent developments in the field of metapopulation biology are opening new ways to investigate and understand paleontological data.

2 Emerging view

2.1 Metacommunity thinking and paleobiology

The emerging research into metacommunity structure and evolution (Leibold and Miller, 2004; Holyoak et al., 2005) shows much promise for synthesis of paleontology and ecology. The concept of metacommunity has developed as a consequence of observations that patterns of distribution, abundance and interaction of species can vary depending on the scale of observation (Levin, 1992; Rosenzweig, 1995; Chase and Leibold, 2002). Leibold et al. (2004), based on Wilson (1992), define a metacommunity as a set of local communities that are linked by the dispersal of multiple potentially interacting species. A metacommunity is a regional representation of continental patterns (e. g., MacArthur, 1972), based on the local metapopulation dynamics of sets of localities.

The metacommunity, regarded as the species pool from which local communities are drawn, is arguably (because of temporal and spatial averaging) the best match for the “communities” or “chronofaunas” (Olson, 1952, see below) sampled in fossil material, and therefore connects patterns observed at evolutionary time scales and those observed in present-day ecosystems. Question is whether spatial units at the subprovince level, typically resolvable in good-quality fossil data (e. g., Fortelius et al., 2002), show evidence of coherence and environmental control in present-day data. Recent results (Heikinheimo et al., in press) support the interpretation that spatially and structurally distinct assemblages seen in the mammalian fossil record (Bernor et al., 1979, 1996; Bernor, 1983, 1984) reflect ecologically distinct biogeographical units (e. g., paleobiomes), bounded by environmental conditions.

Olson (1952) introduced the term chronofauna to capture the persistence and continuity of structure of evolving animal complex. The purpose of chronofauna, to interpret “the movement of a complex of interacting vertebrate populations through time under the influence of changing environmental conditions” (Olson, 1952:181), is quite similar to the definitions of metacommunity (see Leibold and Miller, 2004). According to Olson, “the scope of such fauna is limited

by the particular ecological system of which it is a part" (Olson, 1952:181).

According to Olson, "major changes in equilibrium of the system . . . might have resulted from immigration tended to be reduced by the partial ecological and geographical isolation provided by the environment and by the internal balance of the complex" (Olson, 1952:181). Heikinheimo et al. (in press) demonstrate that modern mammalian taxa in Europe show distinct clustering that seems to be ultimately controlled by climate and geographical features. These clusters seem like regional metacommunities, and thus hold great promise for use in paleoecological studies and bridging the gap between modern ecology and paleoecology.

2.2 Commonness and metapopulation biology

In recent years there has also been a strong resurgence of biological-paleontological synthesis in the rapidly growing field of "evo-devo" (Raff, 1996; Hall, 2004). This has led to new ideas about how we think about the development of environments and species in deep time.

One of these ideas is the concept of commonness, or incidence in paleontological context. It has been suggested that relatively small number of species with wide locality coverage are paleoecologically informative irrespective of the rest of the species (Jernvall and Fortelius, 2002). As they showed, the taxa with high locality coverage reflect the overall dynamics of the communities and evolutionary trends better than the taxa with low locality coverage. This commonness effect has been defined and used in many ways in ecology.

Commonness is not straightforward measure of richness or abundance. It has some time-averaging built-in, because of the nature of the fossil record (see Jernvall and Fortelius, 2004). Commonness is related to site occupancy within a community, as used in metapopulation ecology (e. g., Hanski, 1982, 1999). Hanski (1982; Hanski and Gyllenberg, 1993) used the terms "core" and "satellite" species to define different species. The core species are "regionally common and locally abundant and relatively well-spaced in niche space" (Hanski, 1982), while the satellite species characterized by attributes opposite of those of core species (Hanski, 1982). He defends the defining of core and satellite species by arguing that "if the core-satellite hypothesis is upheld, one may proceed by restricting the application of the equilibrium theory to the core species, and employing appropriate non-equilibrium models for the satellite species" (Hanski, 1982:218). Brown (1984) points out that specialists with narrow tolerances should be more efficient in exploiting more limited resources and hence should have more restricted distributions but higher local abundance than generalists. He goes further by pointing out that species that have restricted distributions are more often rare, while more widespread species have higher population densities (Brown, 1984). It is likely that locally rare species represent the tails of the spatial distributions of species that are more common in other regions (Brown, 1984). The commonness measure is usually done at community level, while those described above are defined for more local assemblages. The recent development of the metacommunity concept (Leibold et al., 2004) expands the ideas of metapopulation theory (Hanski, 1982, 1999; Hanski and Gyllenberg, 1993) to metacommunities (see Hanski and Gaggiotti, 2004; Holyoak et al., 2005). From metapopulation theory (Hanski, 1999; Hanski and Gaggiotti, 2004) it might be expected that the species with the regionally highest incidence largely correspond to the core species of local populations, and thus that a metacommunity made up of core species should be a more stable and distinctly bounded unit than a metacommunity that includes rare (satellite) species. Based on these observations, it seems that regional abundance and range of distribution seem to be well correlated.

3 Eurasian Neogene herbivorous mammals as a case study

3.1 Eurasian scale trends

As a case study in this context, the environmental history of Eurasia serves as an example.

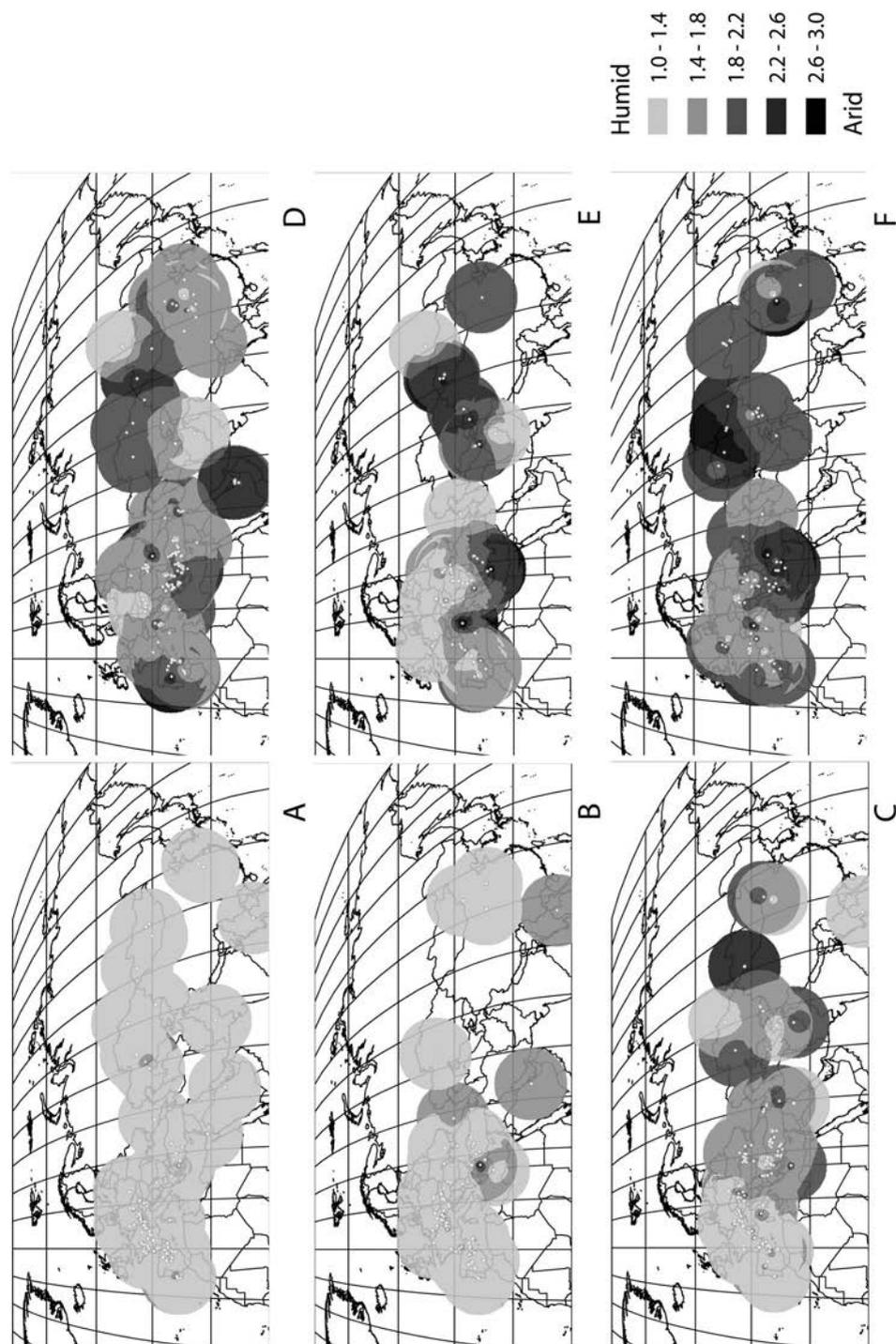


Fig. 1 Eurasian scale maps of fossil herbivore tooth crown height

Legend shows the ordinated mean tooth crown height value of the localities; low tooth crown height is related to more humid conditions and higher tooth crown height is indicative of more arid conditions; maps are modified from Eronen, 2006; the mapping method is the same as described in Fortelius et al., 2002 and in Eronen, 2006

A. Early Miocene; B. Middle Miocene; C. early Late Miocene; D. late Late Miocene; E. Early Pliocene; F. Late Pliocene

According to evidence from large mammals, there is a trend from humid Middle Miocene (Fortelius et al., 2002, 2006; Eronen and Rook, 2004) towards drier conditions during the Late Miocene in western Eurasia (Fig. 1A-F). In early Late Miocene (11-10 Ma ago) there are still wide humid areas in Europe (Fig. 1C). These assemblages were dominated by genera that were adapted to the closed and humid habitats. The mammals with high locality coverage within this timeslice were still descendants of the Early Miocene taxa that were adapted to more humid environments. In Central Asia the fossil mammal assemblages showed tendency towards more open and arid habitats (Fortelius et al., 2002; Eronen, 2006) (Fig. 1C & D).

Mammals are not strictly confined to certain habitats, but they are only able to flourish in certain habitats. For example, the taxa with high locality coverage in Europe during earlier part of Miocene were adapted to humid environments typical to Early and Middle Miocene. They were present in drier habitats in Eastern Europe, but they did not have high locality coverage there.

During the Late Miocene (10-8 Ma) times the arid conditions spread westwards in Europe (Fortelius et al., 2002, 2006; Eronen and Rook, 2004). With the new large biome developing, a new type of mammalian taxa developed with it. As the biome spread through the central part of the Eurasian continent, so did the associated taxa, which consequently had high locality coverage within this timeslice (Eronen, 2006).

In latest Late Miocene (8-5 Ma) there is continued drying in Europe (Fortelius et al., 2002, 2006; Eronen and Rook, 2004) (Fig. 1D). Especially the south Europe is very dry, and the humid conditions are prevalent only in the Pannonian Basin (Fortelius et al., 2002, 2006; Eronen and Rook, 2004). The genera with high locality coverage in Central Asia and Europe were more adapted to open and arid habitats, while the genera with low locality coverage were those that were adapted to humid and closed habitats (Eronen, 2006).

The taxon pool from which the common mammals come, forms in the largest biomes. They might have high locality coverage in restricted biomes in the beginning, but still low locality coverage at regional scale. When the biomes spread so does the locality coverage of the dominant taxa of the biome. Leibold (1998) argues that species co-existence is most likely among species with the most similar responses to environmental factors when both local and regional biotas are at equilibrium. In terms of metacommunities (sensu Leibold et al., 2004), local communities are viewed as heterogenous in some factors and the outcome of the local species interactions depends on aspects of the abiotic environment (Leibold et al., 2004). If different species can only inhabit exclusive habitat types, the resulting metacommunity can be broken down into two independent ones, but when individual species can inhabit multiple habitat types, there is a variety of outcomes that reflect how species interact at larger spatial scales (Leibold et al., 2004). Because of the time-averaging, we usually cannot differentiate between these two possibilities in fossil material.

3.2 East Asia

In contrast to rest of Eurasia, late Late Miocene of East Asia shows a striking difference to early Late Miocene time (Fig. 1D). There is a wide area of humid conditions in the whole eastern part of Asia, especially in North China (Fortelius et al., 2002; Eronen, 2006). Fortelius et al. (2002) described this as the effect of monsoon and Fortelius and Zhang (2006) describe the faunal development in North China in more detail. This development towards humid conditions in the latest Miocene during a time when Western and Central Eurasia was already experiencing drier conditions clearly resulted in an influx of species from the surrounding areas. These immigrants were of several kinds and came from different directions. Perhaps the most interesting group consists of archaic forest forms, such as anchitherine horses. Another important group of immigrants is the deer, especially the genus *Cervavitus*, a northern or western immigrant, which becomes very common in the latest Miocene (Baodean). These assemblages showing adaptation to the humid and closed habitats had low or very low locality coverage in other re-

gions in Eurasia. In this monsoon-affected region in China their locality coverage was much higher than elsewhere. Nevertheless, this type of biome was restricted, and these forms did not survive elsewhere. With the end of the humid period in the Pliocene, they disappeared also from China.

4 Conclusions

It appears that the study of locality coverage in the fossil record may provide a much-needed bridge between evolutionary studies based on fossils and evolutionary studies based on living organisms. Locality coverage is similar to the concept of incidence as used in metapopulation ecology and appears to behave similarly in many ways. It is thus likely that the taxa with highest locality coverage, like those with the highest incidence, tend to be the most geographically widespread and the locally most abundant, although lack of abundance data and sampling problems make this difficult to demonstrate in the fossil material. Taxa with high and low locality coverage also appear analogous to the core and satellite species of the core-satellite model of metapopulation ecology at least in that taxa with high locality coverage (core) show greater temporal persistence and resistance to environmental perturbations than taxa with low locality coverage (satellite). This has also close connections to the developing metacommunity theory.

Metacommunity theory provides a potential link to fossil-based studies at evolutionary time scales, where the main data consist of presence or absence of taxa at specific locations during intervals measured in hundreds of thousands or millions of years. It remains to be seen whether these similarities could offer a common ground for evolutionary studies based on fossils and living populations, respectively.

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