VOL. 164, NO. 5 THE AMERICAN NATURALIST NOVEMBER 2004

Maintenance of Trophic Structure in Fossil Mammal Communities: Site Occupancy and Taxon Resilience

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Submitted July 25, 2003; Accepted July 8, 2004;
Electronically published September 23, 2004

ABSTRACT: Commonness of organisms typically fluctuates through time, and understanding such fluctuations has long been an important part of ecological research. Studies at paleontological timescales provide a perspective on how changes in population size might affect community structure over millions of years. To overcome the obstacle that population size parameters such as abundance are difficult to detect in the fossil record, we here used fossil locality coverage to approximate changes in site occupancy in the Neogene of Europe over the course of 20 million years. Our aim was to examine whether the trophic structure of mammalian communities is maintained through time despite continuing environmental change. Ecomorphological grouping of fossils indicates that herbivore genera have low taxon resilience in that each genus has predominantly only one locality coverage peak before disappearance. Despite this continuous replacement of the most prevalent herbivore genera, the herbivore trophic group as a whole remains the largest and maintains a roughly constant share of locality coverage throughout the Neogene. The successive herbivore genera, however, show increasing adaptations to harshening environments, indicating shifting properties of niches while the overall trophic structure is conserved. Carnivores, dependent on primary productivity for food indirectly through their prey, show moderate lack of resilience. In contrast, in omnivores changes in locality coverage are close to random fluctuations.

Keywords: trophic structure, macroevolution, primary consumers, population size, ecomorphology, herbivory.

To depict and understand the dynamics in ecological communities, one needs to know about community structure. Knowledge about which taxa are present, how abundant they are, and what kind of interactions they have are all data that most ecologists would attempt to obtain first. However, if we want to reconstruct communities of extinct organisms, we are almost immediately in trouble just trying to compile these basic data. Diversity, or richness, is perhaps the most commonly estimated and investigated aspect of extinct ecosystems. Fossils also potentially provide a wealth of paleoecological data that can be used to infer aspects of trophic structure such as body size, diet, and habitat use. Abundance, although it is difficult to estimate from fossil material, has also long been part of the macroevolutionary theory. Among others, Simpson (1944, pp. 65–74), Wright (1945), and Eldredge and Gould (1972) have argued about the role of population size in terms of how number of individuals and geographic range may influence speciation rates and the rise of local adaptations. The basic problem with paleontological data is that sampling over the landscape is typically not evenly distributed in time or space. Of the sampled fossil localities, relatively few preserve relative abundance information, and except for certain marine assemblages (Kidwell 2001; Todd et al. 2002), there are not enough locality abundance data for large-scale analyses of evolutionary dynamics. An exception for terrestrial communities is the study by Barnosky et al. (2003), who investigated changes in mammalian abundance at individual localities during the middle Miocene warming event in the Rocky Mountains of the United States.

A general impetus for estimating abundance in the fossil record, when considering current research traditions, is a need for data that link macroevolutionary "taxon counting" to the population ecology focus on "taxon interactions." Our immediate stimulus for this study stems from paleoecological work on Eurasian herbivorous mammals during the Miocene epoch in the past 25 million years. The overall pattern of evolutionary changes in paleoecological indicators, most notably in dental morphology, is diagnostic of the increasing seasonality and drier environ-

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Am. Nat. 2004. Vol. 164, pp. 614–624.

ments of the Miocene (Broccoli and Manabe 1997), but this change is almost entirely limited to taxa that are inferred to have been abundant (Fortelius et al. 2002; Jernvall and Fortelius 2002). This suggests that common taxa reflect environmental changes better than do rare taxa, presumably by being more successful in exploiting the prevalent resources.

Our aim in this article is to examine whether the trophic structure of mammalian communities is maintained through time despite a changing environment and corresponding changes in the ecomorphology of taxa. We first test the hypothesis that the most common mammalian taxa should differ from random fluctuations of inferred abundance in response to environmental changes. This question basically addresses whether, and how well, the niches of the most common taxa are maintained through time. Operationally, we measure fluctuations through time by tabulating whether commonness rebounds from a decline. We call this tendency for recovery over paleontological time "taxon resilience." While obviously functioning at a different timescale, the concept of taxon resilience seems in line with usage of the term "resilience" in ecology to denote how fast a population recovers from a perturbation (Pimm 1991; Gunderson 2000). Our second hypothesis concerns the role of trophic level in determining the taxon resilience and overall commonness of these fossil mammals. Based on present-day ecosystems, our hypothesis is that primary consumers should attain the highest abundance, a fundamental relationship still poorly known at paleontological timescales.

Because of the absence of fossil locality level abundance information for large data sets consisting of many localities over large geographic areas, we have used locality coverage, or the proportion of the total number of localities that are occupied, to approximate relative abundance (Fortelius et al. 2002; Jernvall and Fortelius 2002). Locality coverage is thus basically the same as site occupancy used in ecology, with the obvious difference that here sampling has at least one more step: the taphonomic filter with extensive time averaging between the living community and documented site occupancy. Occupancy and local abundance are linked in a wide range of living taxa and over a wide range of spatial scales; an increase or decrease in abundance is reflected in a corresponding increase or decrease in the number of occupied sites (Brown 1984; Hanski et al. 1993; Gaston 1996; Lawton 1999; Gaston et al. 2000). Furthermore, this intraspecies relationship between abundance and occupancy is also found among species, and thus taxa that are found from many sites tend to be common and those that are found from a few sites are rare.

In order to provide a relatively stable temporal cline of environmental change without significant extinction events, we included Miocene to Pliocene localities encompassing 24 to 2 million years ago. Moreover, because we were interested in estimating temporal changes in locality coverage of individual mammalian lineages apart from regionally heterogeneous changes in environment, we limited the analysis to western European localities up to 20°E longitude. These localities have been previously shown to represent a relatively synchronous and uniform environmental context (Fortelius et al. 1996, 2002). The localities (fig. 1) form an east-west belt, limited in the north by lack of preserved or exposed localities because of Pleistocene glaciations and in the south by the Mediterranean Sea. We used upper cheek tooth morphology to identify three trophic categories—carnivores, omnivores, and herbivores—among all large mammals (orders Artiodactyla, Carnivora, Perissodactyla, Primates, and Proboscidea). For a consistent measure of commonness among diverse taxonomic groups and through time, we performed the analyses at the genus level.

Material and Methods

Data

We used a data set of 421 localities from the Neogene Old World (NOW) database of Eurasian Neogene fossil mammals (http://www.helsinki.fi/science/now/). For a more conservative measure of locality coverage within each time interval, we grouped localities that are within one degree of geographic separation from each other, as described previously (Jernvall and Fortelius 2002). Of the resulting 252 localities, seven to 30 occur in each time interval. Mammal Neogene (MN) units 1 and 17 of the European mammal chronology (Mein 1989; Steininger et al. 1996; Alroy et al. 1998) were used to identify genera whose first and last presence was within the study period. The enclosed MN units 2 to 16 cover the interval 22.8 to 2.6 million years ago (fig. 1), and the durations of individual MN units range from 0.5 to 2.8 million years, thus producing a variable degree of time averaging. While time units of even duration will ultimately be desirable, European mammal chronology currently provides only MN unit resolution for the majority of fossil mammal localities throughout the Neogene. Furthermore, as we show below, locality coverage measures of commonness should be relatively insensitive to differences in time averaging.

We analyzed only large mammal genera (orders Artiodactyla, Carnivora, Perissodactyla, Primates, and Proboscidea) of long duration, excluding the small mammals (orders Insectivora, Chiroptera, Rodentia, and Lagomorpha) that might cause major taphonomic biases. Body-size-related biases should not affect the commonness curves for individual genera because, within each genus, size remained largely constant through time, even though there is an overall tendency for genera with larger body size through time. Of 288 genera in the data set, 78 were present in at least three consecutive MN units inside the studied time bracket, allowing the tabulation of the number of times that a recovery in commonness is observed before disappearance. One hundred seventy-nine genera had MN durations of one or two. To test the possible effect of genera evolving into other genera, we also analyzed a subset of 45 genera lacking putative descendants and also a subset of 23 immigrant genera lacking both putative ancestors and descendants within the study area and period (based on Rössner and Heissig 1999 and references therein and on region of first occurrence in the database itself). For a robust measure of resilience, we placed more emphasis on the periods of continuous presence of each genus because temporal gaps in presence can be due either to true local extinction and recolonization events or to a decline of commonness below the "sampling horizon" (when the taxon is so rare that it is not detected). Of the 78 long-lived genera, 22 had additional ("lazarus") occurrences, all less than three MN units long.

With upper cheek tooth crown types (Jernvall et al. 1996; Jernvall and Fortelius 2002), we classified genera into three trophic groups. Crown types with three cusps (e.g., R2100) indicate carnivory, and crown types with additional cusps (teeth with the hypocone; Hunter and Jernvall 1995) indicate strict herbivory or omnivory depending on whether well-developed shearing crests were (e.g., L2220) or were not (e.g., R2200) present (Hunter and Jernvall 1995; Jernvall et al. 1996). We also make use of tooth crown height, which becomes high, or hypsodont, in many herbivores during the Miocene (Fortelius et al. 2002; Jernvall and Fortelius 2002).

Estimating Site Occupancy: Locality Coverage

For our analysis we assume a positive abundance-occupancy correlation, regardless of the existence of underlying biological causes behind this correlation (see Wright 1991; Hanski et al. 1993; Hartley 1998; Gaston et al. 2000; Harte et al. 2001). Of course, even if locality abundance would vary (to a limit) randomly and have no correlation with site occupancy, abundance calculated for the whole region would still be expected to be higher for taxa found in many localities than for taxa found in a

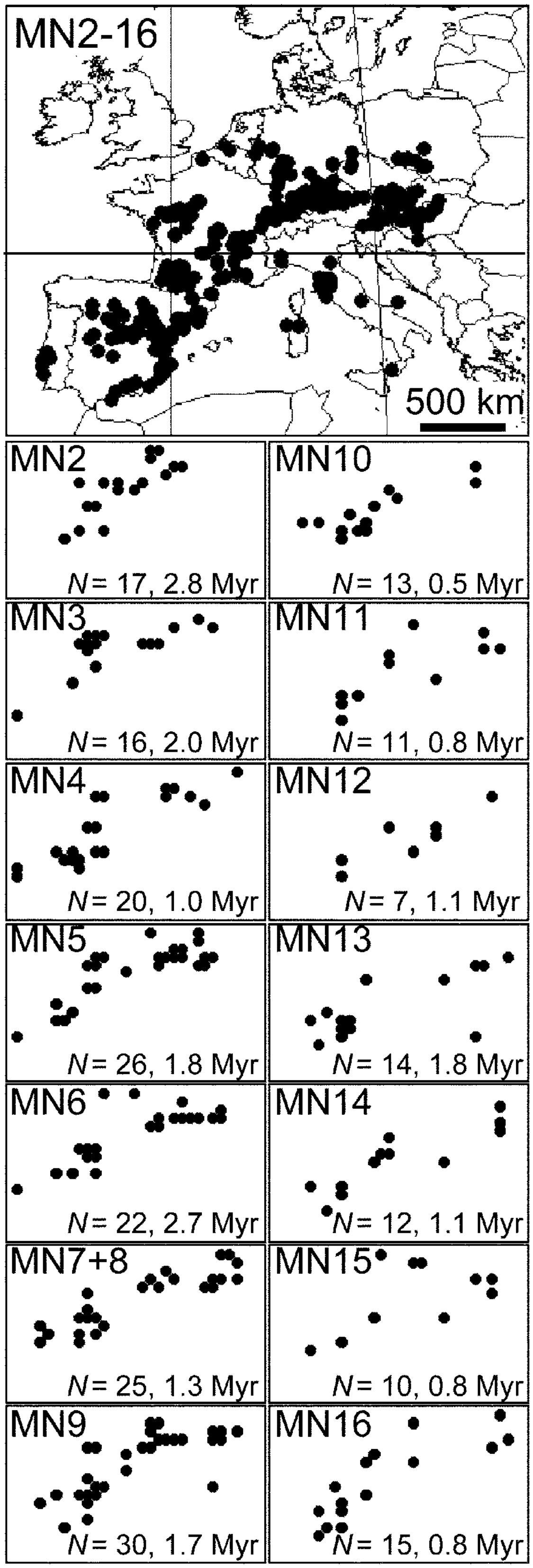


Figure 1: Geographic distribution of the 252 fossil localities. The localities are divided into 14 time intervals from MN 2 (the oldest) to MN 16 covering 22.8 to 2.6 million years (lower panels at a smaller scale than the top panel). Each MN unit has seven to 30 localities, with weaker sampling in the late Miocene. The number of localities tends to be greater in longer MN units ($r_s = 0.54$, $P = .051$).

single or a few localities. In reality it is likely that there is only a rough correspondence between locality coverage and actual site occupancy, but this is to be expected with practically all measures used for the fossil record. Even fossil species richness estimations are biased by the relative ease that some fossil taxa can be identified (such as bovids due to their horn cores) compared to more cryptic groups (such as horses), but performing the analyses at the genus level largely resolves this problem.

Unlike ecological time averaging, in which, for example, species composition of mature rainforest trees is a time-averaged sample of the successional history of the forest, paleontological time averaging can group localities and organisms that do not belong to the same temporal community. While time averaging is unavoidable in most paleontological data, and is often even desirable in order to increase sampling, it can be hypothesized to affect measures such as species richness. Indeed, the NOW data have been shown to have the typical positive correlation between time averaging and number of species and localities (Fortelius et al. 1996; Fortelius and Hokkanen 2001). However, all else being equal, time averaging should not affect locality coverage and abundance estimates because it is calculated as a proportion of all the localities (fig. 2). On the other hand, as Lyons (2003) has pointed out, time averaging can inflate geographic range estimates (fig. 2). Range inflation can be expected to be an issue in our data because we are estimating population size changes over millions of years when mammals can shift their geographic ranges even seasonally. Shifts in geographic ranges in the fossil record have received considerable research attention in connection to speciation, extinction risk, and climatic change (see, e.g., Davis and Shaw 2001; Jablonski and Roy 2003; Lyons 2003). We will therefore also examine links between locality coverage and geographic range and test for the effects of time averaging. However, we are not placing too much confidence in the geographic range estimates because of the nonuniform distribution of the sampling (fig. 1) and because of the lack of applicable paleogeographic maps showing areas as they existed in the past. In particular, many of the coordinates of the early

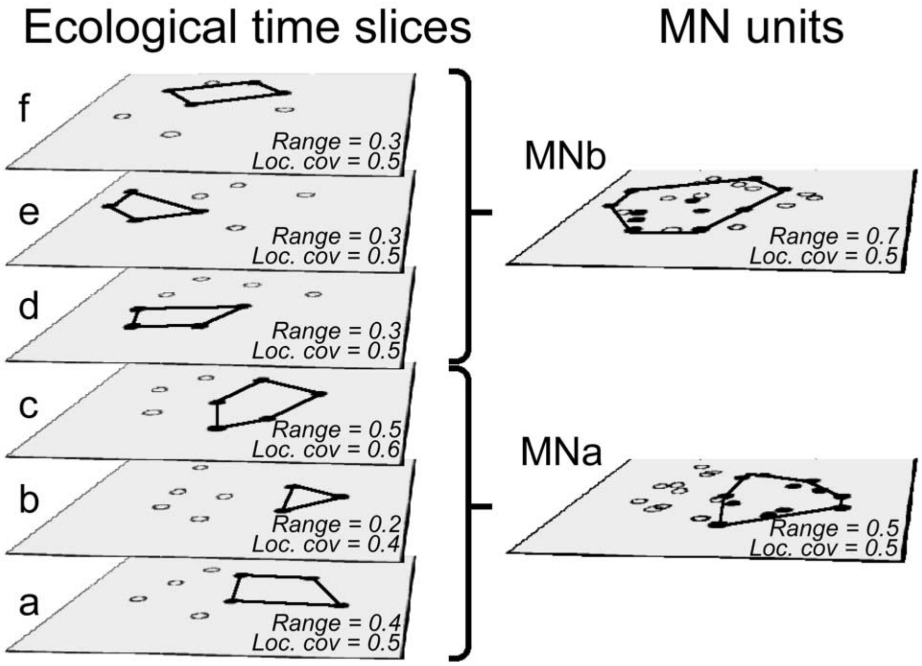


Figure 2: A simple diagram of how time averaging affects locality coverage and geographic range differently. A temporary decline in site occurrence (occupied sites in black) in ecological time slice *b* results in a drop of both range and locality coverage that is below the temporal resolution of MN unit *a*. The following increase in range in *c* is picked up in the MNa range because geographic ranges are summed up over time slices while locality coverages are averages. For example, in the ecological time slices *d–f*, site occupancy and range remain constant while the population shifts its range. This inflates the calculated geographic range for MNb while locality coverage remains unchanged. Range inflation makes it ambiguous to determine whether broad geographic range with small locality coverage is due to taxa being rare with wide distribution or with narrow distribution that has moved. In general, when MN units do not contain the same number of ecological time slices causing variable time averaging, locality coverages can be expected to provide better estimates of site occupancy than geographic ranges.

Miocene localities, when the latest major uplifting of Alps was still under way, are likely to have been shifted.

Analyses

We used the ratio of occupied localities to all localities to calculate locality coverage within each time interval for the 78 genera that were present in at least three consecutive MN units. Additionally, we tested whether the locality coverage for the 179 short-lived genera peaked at the same value as for the 78 longer-lived genera. We calculated the geographic range for the 78 genera for each MN unit both in degrees (separately for latitude and longitude) and as greater circular distance, which is the distance (km) of two localities that are farthest apart from each other. These geographic range measures were used as proportions of the total range of all localities in each MN unit (fig. 1). Time averaging was tested by calculating whether relative change in MN duration correlated with relative change in locality coverage or geographic range (from log-transformed data). For these calculations, we excluded the appearance and disappearance of genera as well as single locality occurrences.

Resilience was measured as the number of recoveries after a decline in locality coverage. For example, locality coverages of unimodal genera peak once (e.g., *Anchitherium*, *Pliopithecus*, *Palaeomeryx*) with no recovery, while bimodal genera peak twice with one recovery (e.g., *Micromeryx*, *Semigenetta*, *Xenohyous*). We used a randomization test to obtain the probabilities that the observed number of recoveries result from random fluctuations through time. This kind of analysis takes into account the fact that probability of unimodality declines with the length of the random walk, but we also analyzed the resilience separately for genera with different durations. For each genus, we randomly reshuffled the temporal order of its MN units 1,000 times and calculated the number of recoveries for each randomization. We tabulated how many times the observed, or smaller, number of recoveries occurred in the randomizations. For the analyses, we calculated fluctuations at the resolution of 1%; thus taxa were tabulated as experiencing a recovery even if the increase in locality coverage was only 0.01. Because such small changes in locality coverage may spuriously exaggerate the number of recoveries, we also performed the analyses after rounding changes in locality coverage to the nearest 5%.

To examine whether trophic level affects average and maximum locality coverage of genera, we randomized the locality coverage assignments 1,000 times. From the random probability distributions we calculated the frequency of the observed or higher locality coverages for herbivores and omnivores and the observed or lower locality coverages for carnivores (which, as predators, are expected to have low abundances). We also tested the effect of using rank-order locality coverages (calculated for each MN unit), which further increased the significance of the differences among trophic groups. Yet another possible bias in paleontological data is the taphonomically caused overrepresentation of large-bodied mammals (Damuth 1982), while in present-day ecosystems, all else being equal, we would expect larger-bodied mammals to be less abundant (Damuth 1981). Because large mammals are typically herbivores, we tested the possibility that preservation artifacts resulting from body size differences among trophic groups affect the results by excluding taxa of more than 2 m head and body length (25 genera, 20 of them herbivores). Note that this also tested for the bias that smaller-bodied taxa, with shorter generation times, might be overrepresented in the localities (Vermeij and Herbert 2004).

We calculated the correlation between genus locality coverage and relative species origination within each genus (origination divided by species richness) with first occurrences of genera, when origination is always 1, and without first occurrences of genera. All analyses were performed using Panorama 3 (http://www.provue.com).

Results and Discussion

Locality Coverage, Range, and Time Averaging

Compared to the shorter-lived genera, the 78 studied genera that were present in at least three consecutive MN units also had higher locality coverages in each MN unit. The average maximum locality coverage was 0.27 for the 78 studied genera, while it was 0.13 for the 179 genera with MN durations of 1 or 2. Only 7% of the short-lived genera had locality coverages higher than the average for the 78 studied genera (0.27), indicating that the 78 genera constitute the most successful mammalian taxa in terms of both peak locality coverage and longevity. Indeed, while short-lived genera are taxonomically rich, their inclusion would add only an average of 35% to the total locality coverage (number of genera present in each locality).

While we used locality coverage to approximate site occupancy and abundance, it is to be expected that the proportion of the total number of localities that are occupied also correlates with overall geographic range. Locality coverage correlates with the maximum span of relative geographic range (greater circular distance, Spearman rank correlation, $r_s = 0.66$, $P < .001$; fig. 3) as well as geographic range along longitude ($r_s = 0.62$, $P < .001$) and latitude ($r_s = 0.66$, $P < .001$). Next we tested whether time averaging might affect locality coverage or geographic range. There is a weak positive correlation between change in MN unit duration and change in geographic range ($r_s = 0.25$, $P < .001$) and no discernible correlation be-

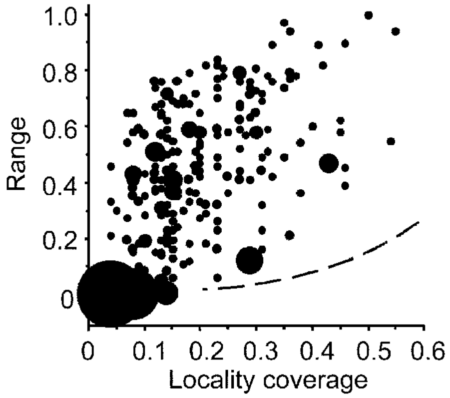


Figure 3: Locality coverage and relative geographic range (greatest circular distance) for all occurrences of the 78 genera. Correlation including single locality occurrences, when range is always 0, is $r_s = 0.66$, $P < .001$; excluding single occurrences, it is $r_s = 0.39$, $P < .001$. Taxa can have apparently broad geographic ranges either because they had a wide distribution or because their narrow distribution moved during the time unit (fig. 2). The dashed curve is the minimum possible geographic range, which depends on the spatial clustering of the localities (fig. 1).

tween change in MN duration and locality coverage ($r_s = -0.02$, $P = .754$). As predicted (fig. 2), this suggests that some of the scatter in locality coverage and geographic range correlation (fig. 3) is due to the susceptibility of geographic range to range inflation with increasing time averaging (fig. 2). Note that because we have only limited knowledge about temporal distribution of sites within MN units, the effect of time averaging on geographic ranges could be greater. We take these patterns as support for the robustness of locality coverage as a site occupancy proxy through time even if sampling intensity varies.

Taxon Resilience

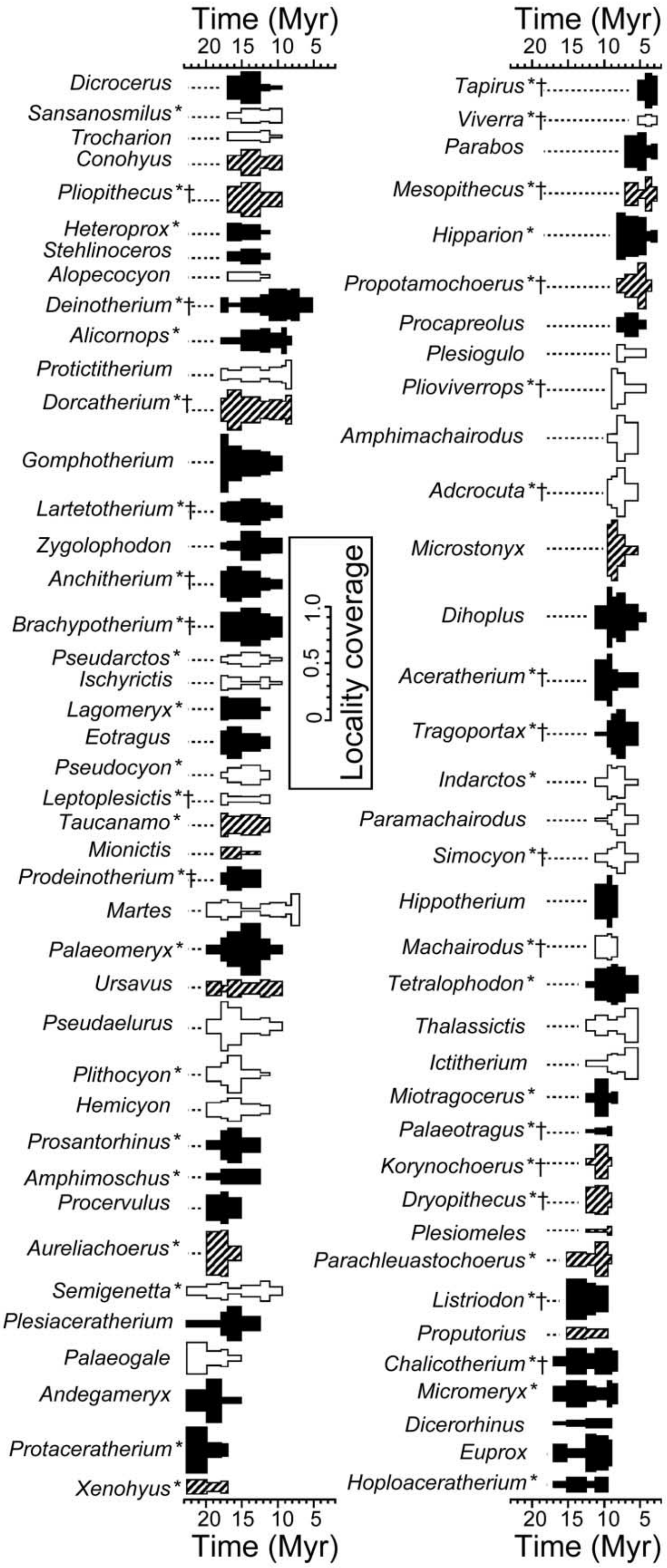
Based on initial visual inspection of the commonness profiles through time (fig. 4), genera typically have only a single locality coverage peak. Furthermore, most (84%) of these unimodal genera attain their maximum locality coverage well within their temporal range. Locality coverage of a genus thus typically increases from an initial value, peaking close to the middle of the temporal range, and then begins to decline. Of the 19 genera that have their locality coverage maxima in their first or last MN unit, 13 (68%) peak in their first MN unit. Many of these initial peak genera, such as *Gomphotherium*, *Listriodon*, and *Plioviverrops*, are known immigrants to the region and may represent relatively abrupt immigration events (fig. 4).

In order to compare fluctuations in commonness through time, we calculated for each genus the number of times that relative locality coverage increased after a decline. Based on tabulations of all changes in relative locality coverage, regardless of their magnitude, 58% of genera are unimodal, lacking a single recovery (fig. 4). This contrasts with the average of 33% unimodality obtained from 1,000 random walk simulations of the genera. The observed average number of recoveries is 0.51 ($P < .001$, obtained from the random walk simulations; table 1). Because the magnitude of changes in commonness can differ among taxa and through time (fig. 4), we also analyzed resilience using only larger, more robust changes in locality coverage. For example, if changes in locality coverages are rounded to the nearest 5%, 72% of the genera show no recovery, and the average number of recoveries drops to 0.31 ($P < .001$). Moreover, while up to four recoveries might be expected because of fluctuating commonness during the life span of genera with the longest durations, the maximum number of recoveries actually observed in the data is only two. The pattern of results remained unchanged for the 45 genera lacking putative descendants and the 23 genera lacking both putative ancestors and descendants within the study area (table 1). Similarly, inclusion of lazarus occurrences increases the number of recoveries but not up to the levels obtained from the random walk simulations (table 1).

Trophic Level, Resilience, and Locality Coverage

We next examined whether ecological differences among genera affect their resilience. Ecomorphological crown type classification of cheek teeth was used to identify carnivorous, herbivorous, and omnivorous dietary specializations regardless of taxonomic affiliation (Jernvall et al. 1996). The omnivore class in this tabulation consists of mammals whose diet ranges from animals to soft plant parts and includes members from taxonomic groups like bears, pigs, and primates. Carnivores and herbivores, on the other hand, are specialized to eat animals or fibrous plant parts, respectively. The average numbers of recoveries for carnivores, omnivores, and herbivores are 0.64 ($P = .007$), 0.69 ($P = .788$), and 0.35 ($P < .001$), respectively, suggesting that omnivore locality coverage is the most similar to and herbivore locality coverage the least similar to the random walk simulations (table 1). The subsets of the 45 genera lacking putative descendants and the 23 genera lacking additionally putative ancestors show similar differences among trophic groups. The same applies to analysis after inclusion of lazarus occurrences (table 1).

Because herbivorous mammals seem to be largely responsible for the overall bias toward lack of random fluctuations in locality coverage, we also investigated whether any specific group of herbivores was responsible for the pattern. In essence, almost all herbivores regardless of size



Time (Myr)
20 15 10 5
Dicrocerus
Sansanosmilus*
Trocharion
Conohyus
Pliopithecus*†
Heteroprox*
Stehlinoceros
Alopecocyon
Deinotherium*†
Alicornops*
Protictitherium
Dorcatherium*†
Gomphotherium
Lartetotherium*†
Zygolophodon
Anchitherium*†
Brachypotherium*†
Pseudarctos*
Ischyrictis
Lagomeryx*
Eotragus
Pseudocyon*
Leptoplesictis*†
Taucanamo*
Mionictis
Prodeinotherium*†
Martes
Palaeomeryx*
Ursavus
Pseudaelurus
Plithocyon*
Hemicyon
Prosantorhinus*
Amphimoschus*
Procervulus
Aureliachoerus*
Semigenetta*
Plesiaceratherium
Palaeogale
Andegameryx
Protaceratherium*
Xenohyus*
20 15 10 5
Time (Myr)
Locality coverage
0 0.5 1.0
Time (Myr)
20 15 10 5
Tapirus*†
Viverra*†
Parabos
Mesopithecus*†
Hipparion*
Propotamochoerus*†
Procapreolus
Plesiogulo
Plioviverrops*†
Amphimachairodus
Adcrocuta*†
Microstonyx
Dihoplus
Aceratherium*†
Tragoportax*†
Indarctos*
Paramachairodus
Simocyon*†
Hippotherium
Machairodus*†
Tetralophodon*
Thalassictis
Ictitherium
Miotragocerus*
Palaeotragus*†
Korynochoerus*†
Dryopithecus*†
Plesiomeles
Parachleuastochoerus*
Listriodon*†
Proputorius
Chalicotherium*†
Micromeryx*
Dicerorhinus
Euprox
Hoploaceratherium*
20 15 10 5
Time (Myr)

Table 1: Average resilience (number of recoveries) in locality coverage for all 78 genera and two subsets

	All 78 genera			Subset of 45 genera lacking putative descendants			Subset of 23 genera also lacking putative ancestors		
	Resilience	*N*	*P*	Resilience	*N*	*P*	Resilience	*N*	*P*
Without lazarus taxa:									
All genera	.51	78	<.001	.47	45	<.001	.39	23	<.001
Carnivore	.64	25	.007	.42	12	.008	.33	6	.175
Omnivore	.69	16	.788	.70	10	.764	.67	6	.549
Herbivore	.35	37	<.001	.39	23	<.001	.27	11	<.001
With lazarus taxa:									
All genera	.90	78	<.001	.84	45	<.001	.96	23	.016
Carnivore	.92	25	.008	.75	12	.018	.83	6	.153
Omnivore	1.00	16	.938	.90	10	.891	1.00	6	.756
Herbivore	.84	37	<.001	.87	23	<.001	1.00	11	.006

Note: The probabilities are from 1,000 random walk simulations.

show a relative dearth of recovery (fig. 4; table 1), manifested in the number of recoveries calculated separately for the herbivore members of the orders Artiodactyla (0.24, $P < .001$), Perissodactyla (0.40, $P < .001$), and Proboscidea (0.60, $P = .018$). While the random walk simulations take into account the decline in probability of unimodality with increasing number of MN units, we also analyzed the resilience separately for genera with different durations. Herbivores have low resilience all the way to genera with longevity of six MN units (fig. 5*A*). Of the 37 herbivore genera, only *Dorcatherium* and *Deinotherium* have longer MN durations (seven and nine), and their resilience does not differ significantly from the random walk simulations (fig. 5*B*). The remaining 35 herbivore genera make up 45% of the studied 78 genera, and thus the general pattern of low resilience in the data is explained by the genus richness of the herbivore trophic category. Furthermore, herbivores, as primary consumers, have the highest locality coverage compared to omnivores and carnivores, which have the lowest locality coverage (table 2), a pattern concordant with present-day ecosystems (Elton 1927; Robinson and Redford 1986; Fryxell et al. 1999). While carnivores have the lowest locality coverage, their genus richness is greater than that of omnivores (25 compared to 16). The high locality coverage of herbivores is therefore unlikely to be an artifact of high richness increasing their likelihood of being sampled. Rather, if there is a bias, it is the intrinsically high locality coverage of herbivores that has probably increased their sampled genus richness. Additionally, herbivores retained the highest locality coverage after removal of large-bodied genera, which are mostly herbivores, suggesting that preservation artifacts favoring large fossils are not responsible for the pattern of results (table 2). Together the high locality coverage, low taxon resilience, and high genus richness of the herbivore trophic group indicate that for any given MN unit, genera with the highest locality coverages are most likely going to be herbivores. The identity of those genera is, however, almost always different from one MN unit to another. These patterns suggest a remarkable stability for the overall trophic structure for at least 20 million years (fig. 6). This trophic stability was maintained even though the exact properties of the herbivore niches, as judged from the increase in shearing ability and crown height of their cheek teeth (fig. 6; Jernvall et al. 1996; Jernvall and Fortelius 2002), seem to have been tracking the continuing spread of seasonal and arid environments (Broccoli and Manabe 1997). If the trophic structure is maintained but the details of the niches as well as the identity of the most common taxa change continuously, how fast are these changes?

Compared to that of herbivores, omnivore locality coverage shows the most frequent fluctuation through time, with one locality coverage peak in an average of 3.7 million years; carnivore genera are intermediate, with one locality coverage peak in an average of 4.8 million years. In contrast, herbivores, which have one locality coverage peak in

Figure 4: Changes through time in relative locality coverage of the 78 long-lived genera analyzed, arranged in the order of appearance. Genera are grouped into carnivorous (*white*, $N = 25$), omnivorous (*hatched*, $N = 16$), and herbivorous (*black*, $N = 37$) ecomorphological groups based on upper cheek tooth crown types. Asterisks denote a subset of 45 genera lacking putative descendants, and daggers denote a subset of 23 genera lacking both putative ancestors and descendants within the study area and period. For example, *Prodeinotherium*, while implicated in the ancestry of *Deinotherium*, lacks here putative descendants because *Deinotherium* appears first outside the study area.

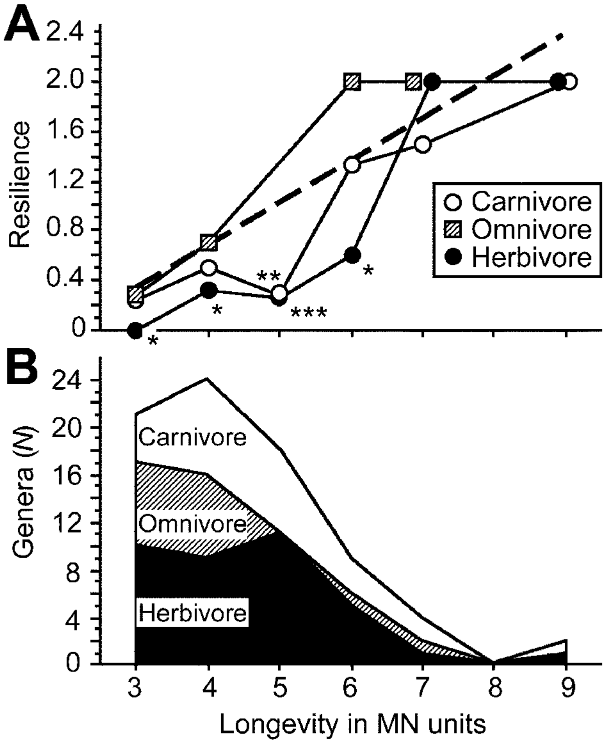


Figure 5: Distribution of average resilience as a function of longevity of genera (*A*). With increasing longevity, resilience increases, but all herbivores have low resilience compared to the random walk expectation (*dashed line*), excluding the two longest MN durations. However, the great majority of genera have MN durations less than six units long, and only two herbivore genera have longer MN durations (*B*). Note how carnivore resilience tends to be slightly below while omnivore resilience is slightly above the random walk expectation. Significant departures from random walk simulations are marked with asterisks in *A*. These *P* values for the herbivores with MN duration 3, 4, 5, and 6 are 0.00 ($N = 10$, $P = .016$), 0.33 ($N = 9$, $P = .049$), 0.27 ($N = 11$, $P < .001$), and 0.60 ($N = 5$, $P = .006$), respectively. The carnivore resilience with MN duration 5 is 0.29 ($N = 7$, $P = .001$).

an average of 5.7 million years, show few increases or decreases in their relatively high locality coverage. While these patterns may seem reminiscent of population fluctuations at ecological timescales, the similarity is almost certainly superficial. Even the shortest possible rebounds in the data, 0.5 million years, are still too long for direct comparisons between ecological and paleontological data. However, our results may indicate the existence of long-term population-level fluctuations that, considering the differences among trophic groups, may have some connection to processes at ecological timescales. Two recurrent explanations for the positive abundance-occupancy link in ecological literature are that abundant resource availability or broader resource use and tolerance of taxa tend to promote populations to be both locally abundant and present in many sites (Brown 1984; Hanski et al. 1993; Gaston et al. 1997). In our analyses the most common taxa are herbivores, and while we have not estimated the degree of specialization within trophic groups, in each MN unit the ecomorphology of the most common herbivores reflects the concurrently prevailing environmental conditions (fig. 6; Jernvall and Fortelius 2002). We therefore suggest that changes in locality coverage over millions of years may indeed reflect changes in the availability of resources as experienced by members of individual trophic groups. To the extent that these changes are mirrored in local abundance, these data are in agreement with resource availability as one explanation for the abundance-occupancy link.

It is noteworthy that while we calculated these results at the genus level, they are likely to reflect at least partly population-level processes because increasing locality coverage in the data does not correlate with increased speciation rates ($r_s = -0.03$, $P = .57$; excluding first occurrences of genera: $r_s = 0.10$, $P = .10$). Thus, common genera tend to consist of relatively few wide-ranging species. This may partly explain why of the 78 genera, 45 lacked putative descendants altogether, suggesting limited phylogenetic continuity from one common genus to another. Despite this discontinuity, trophic structure is preserved over time such that the herbivore group, for example, always has the highest genus richness and commonness (fig. 6). This raises the question of where all the common genera come from. Apart from immigration we hypothesize that common genera mostly derive from speciation and adaptive evolution leading to increased locality coverage in originally rare genera. Thus, while the rare taxa contribute relatively little to the biomass and ecosystem function, some of the rare taxa may be "evolutionary keystone species" by giving rise to the taxa that

Table 2: Average and maximum locality coverage averages for different trophic groups

	N	Average locality coverage	*P*	Maximum locality coverage	*P*
All 78 genera:					
Carnivore	25	.14	.007	.24	.062
Omnivore	16	.17	.620	.26	.767
Herbivore	37	.19	.024	.30	.049
Large-bodied genera excluded:[a]					
Carnivore	21	.13	.034	.23	.167
Omnivore	15	.16	.466	.24	.789
Herbivore	17	.18	.039	.28	.151

Note: The probabilities are obtained from 1,000 randomizations.

[a] A subset of 53 genera that excludes those genera with larger than 2 m head and body length.

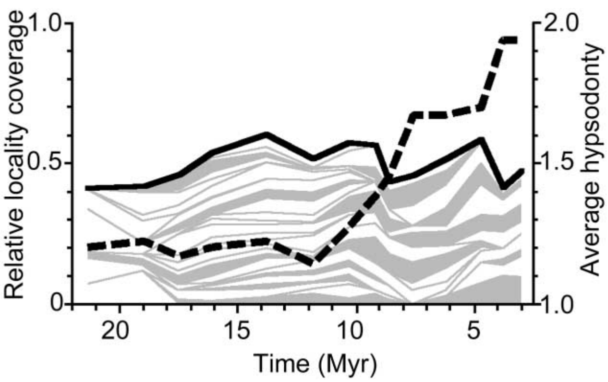


Figure 6: Despite continuous replacement of herbivore genera (*white and gray spindles*), the herbivore trophic group as a whole maintains roughly constant share of locality coverage through the 20-million-year study period (*black line*). On average, half of the genera are herbivores in each locality. At the same time ecomorphological features of the herbivore group change, such as the replacement of genera with low crowned teeth (*white spindles*) with genera with hypsodont teeth (*gray spindles*), indicating gradual harshening of environments. This is also visible in the figure as an increase in average hypsodonty of genera (*hatched line*) resulting from both relative increase of genera with hypsodont teeth and increase in the degree of hypsodonty. Adding short-lived genera or lazarus occurrences does not change the relative share of herbivores. Figure plotted using the 37 long-lived herbivore genera contained within the studied time bracket and eight additional long-lived genera that span beyond the time bracket.

will later become abundant and thus maintain the trophic structure. Because our analysis spanned 20 million years without major extinction episodes, it remains to be tested how trophic structure is reassembled after mass extinctions, when most rare taxa are lost. Furthermore, it remains to be tested with specimen-level data how speciation rates in fossil mammals change with increasing locality coverage.

Conclusions

Why do most herbivores have unimodal commonness distributions over evolutionary time? In the Miocene of Europe, the overall environmental trend has been reconstructed as a shift toward progressively drier, more seasonal conditions (Broccoli and Manabe 1997), widely implicated in having strongly influenced the evolution of mammalian faunas (Bernor et al. 1996; Fortelius et al. 2002). Most notably, changes in herbivore tooth morphology reflecting the relative aridification of environments and the decline in quality of available foods have previously been shown to be almost entirely limited to common genera (Jernvall and Fortelius 2002). Therefore, a substantial increase in commonness is most likely among those herbivorous mammals that have been best able to use the most abundant and widespread resources and habitats. However, as the availability of abundant plant foods changed through the Neogene, the common herbivore genera seem to have been unable to evolve with the changing resources, instead suffering monotonic decrease in locality coverage. Despite this continuous replacement of herbivore genera, the herbivore trophic group as a whole maintains the largest and roughly constant share of locality coverage through time. We interpret this to indicate a tendency for overall conservation of trophic structure despite shifting properties of niches. Carnivores, dependent on primary productivity for food through their prey, still reflect this change in resources moderately while omnivores appear to have been most indifferent to environmental changes.

Acknowledgments

We thank J. Alroy, J. Eronen, M. Foote, A. Gentry, I. Hanski, A. Kangas, G. Rössner, I. Salazar-Ciudad, J. van Dam, J. van der Made, L. Werdelin, P. C. Wright, and especially K. Roy and anonymous reviewers for comments on this work, which was supported by the Academy of Finland.

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Associate Editor: Jonathan B. Losos