

Species occupancy and its course in the past: macroecological patterns in extinct communities

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ABSTRACT

Questions: What is the shape of occupancy trajectories in fossil organisms? And what is the effect of occupancy on species survival?

Data studied: Occupancy and its course through time for a species in extinct large mammal communities from Italy.

Search method: We tested if occupancy (the proportion of fossil sites representing a given paleocommunity where a species is present) patterns in extinct communities match a bimodal distribution as in living communities. Then we regressed occupancy on species duration to estimate its effect on long-term survival. We built a null model of random occupancy trajectories and compared it to real data.

Conclusions: The occupancy–frequency distribution in extinct communities is either bimodal or right skewed. We found a positive relationship between high occupancy and species survival. We found peaked occupancy trajectories to be the norm for hoofed mammals at least.

Keywords: Galerian, large mammals, macroecology, occupancy, Villafranchian.

INTRODUCTION

Animal communities exhibit patterns in their assembly, taxonomic composition and species' attributes, such as body size, abundance and commonness (Hanski, 1982; Brown, 1995; Weiher and Keddy, 1999; Gaston and Blackburn, 2000). The field of macroecology focuses on these patterns. However, few studies of macroecological patterns in extinct communities have been conducted. Unfortunately, the vagaries of fossil records discourage their use in macroecological studies. However, Kidwell and Flessa (1995) demonstrated that there are good arguments for their use. They emphasized that for some groups (e.g. large mammals, molluscs) the potential for preservation is high enough that fossil assemblages are very good representations of the once-living community. Moreover, it is not only the taxonomic compositions of assemblages that are reliable. Often, in a given fossil or death assemblage, species rank order in abundance is not statistically different from that in the live community

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from which it originates (Kidwell and Flessa, 1995; Hadly, 1999). Due to their large size (which translates into a very high preservation potential), commonness and relatively young age, large-bodied Quaternary mammals provide a model system for ecological studies. For instance, they were investigated for body size distribution (Legendre, 1986), intrasexual competition (Van Valkenburgh and Sacco, 2002), guild evolution (Turner, 1990), sensitivity to climate changes (Vrba, 1995), faunal dynamics (Webb and Barnosky, 1989) and macroevolutionary patterns (Turner and Anton, 1998) to name just a few exemplar studies. Here, macroecological patterns in Ice Age communities of large-bodied mammals in Italy are documented. Italy has an exceptionally rich and continuous record of Quaternary mammals. This abundance of information makes paleoecological reconstruction more robust, thus allowing evaluation of macroecological patterns in extinct communities.

Occupancy patterns in macroecology

Species differ in their ability to settle across landscapes. These differences result in specific patterns in the frequency distribution of species abundance, range size and body size that are common across taxa (Brown, 1995; Rosenzweig, 1995; Gaston and Blackburn, 2000). For instance, the shape of the occupancy frequency distribution (where occupancy is the proportion of sites where a species is actually found, within a given sampling area) has received much attention by macroecologists (Gotelli and Simberloff, 1987; Collins and Glenn, 1997; McGeogh and Gaston, 2002). McGeogh and Gaston (2002) pointed out that occupancy distribution is scale-sensitive. At the local geographical scale, occupancy is bimodal in agreement with Raunkiaer's law – that is, most species are either very common or very rare. Thus, an occupancy–frequency plot of species in a given area provides a distribution with the smallest and largest occupancy classes having the highest number of species (Raunkiaer, 1934; Gotelli and Simberloff, 1987; Collins and Glenn, 1997). At larger (e.g. continental) geographical scales, occupancy is unimodal and right-skewed (i.e. most species are found in just a few sampled sites). The reason for these patterns is still a matter of controversy (McGeogh and Gaston, 2002), yet their shape is of great interest from an evolutionary point of view. This is because many studies show a beneficial effect of geographical range size [i.e. the total area occupied by a species over the Earth's surface (Gaston, 2003)] on long-term species survival via reduced extinction risk in times of higher perturbation (Cardillo and Bromham, 2001; Cardillo *et al.*, 2003). The greater the geographical range size, the greater the chance that at least one refugium area will be available during a species' darkest hour (Stewart and Lister, 2001). The refugium will then serve as a source area for future recolonizations (Hewitt, 2004).

Although occupancy is not the geographical area occupied by a species, Gaston and Blackburn (2000) and Gaston (2003) found a close relationship between local occupancy and geographic range size (Gaston and Blackburn, 2000, pp. 105–106). Therefore, occupancy is a good proxy for geographic range size when its effect on local species survival is the focus of attention.

Geographic range size changes from a species' birth to extinction (Miller, 1997; Gaston, 1998; Webb and Gaston, 2000; Roy *et al.*, 2001; Ricklefs and Bermingham, 2002) even if remarkable examples of constant range size have been reported (Jablonski, 1987). The trajectory assumed by geographic range size as a species ages has then been reported as flat, monotonically increasing or peaked. Webb and Gaston (2000) examined the relationship between age and the size of geographical ranges for bird species whose age was estimated through molecular analyses. They found that geographic range size commonly expands early during a species' existence and then contracts to extinction – that is, it follows a peaked trajectory.

Here we analyse the occupancy of Italian Ice Age large mammals from a triple perspective. We computed occupancy–frequency distribution. Then we scrutinized the effect, if any, of occupancy on species survival in Italy. Finally, we studied the shape of the occupancy–time curve.

The extinct communities

The study of extinct communities (PCOMs) is a difficult task because of the scarcity of fossil remains and the differential preservation probability among organisms. In spite of these limitations, some macroecological patterns have indeed been tested with them (Alroy, 2000). Here we used PCOMs for the same purpose. A PCOM represents the large mammal community living in peninsular Italy at a given period during the Quaternary. Successive PCOMs replaced each other in time during the Quaternary. PCOMs were obtained by performing a bootstrapped cluster analysis on the presence/absence matrix of fossil large mammal species per local assemblage of the Italian Quaternary epoch. A local assemblage is the list of species present at a given fossil site at a given stratigraphic interval. Statistically discrete clusters have been ordered in time with reference to absolute dating of the local assemblages they include. These discrete clusters have been given the name of PCOMs [for a thorough discussion on PCOMs and on the methodology to obtain them, see Raia (2003) and Raia *et al.* (2005, in press)].

PCOMs show some long-standing ecological patterns typical of living communities (Raia, 2003, and see below). This is critical if they are to be used in palaeoecological investigations. Ideally, any conglomerate of local assemblages could represent a PCOM, just as a collection of species lists coming from a number of sampling districts represents the living ecological community at some geographically larger scale. The greatest difference is in the very different impact of sampling biases (taphonomy vs. ecological sampling). Furthermore, PCOMs are not a snapshot of the living community because local assemblages are not perfectly synchronous. Despite these caveats, we argue that PCOMs can safely be used to examine macroecological patterns. We specifically test this statement by analysing PCOMs for their obedience to Raunkiaer's law.

Although we calculated occupancy as it is calculated in ecological studies, we wish to highlight that the interpretation using fossil data may be different. In fact, the presence of species at local assemblages is influenced by taphonomic processes, sampling and species abundance of the living community (Hadly, 1999; Hadly and Mauer, 2001). Both the taphonomic sorting of remains and sampling are influenced to some extent by abundance (i.e. negative factors potentially leading to species absence in the fossil assemblage are mitigated if it was abundant). Therefore, we expect our measure of occupancy to be somehow controlled by abundance. This is not a problem, as occupancy and abundance are tightly correlated in living species (Gaston and Blackburn, 2000).

MATERIALS AND METHODS

Our data set includes 73 fossil sites (local assemblages) distributed across the Italian peninsula. They range in age from 3.2 to 0.3 Mya, and are distributed across nine PCOMs ordered in time as follows: Triversa (2 local assemblages), Montopoli (5 local assemblages), Upper Valdarno (14 local assemblages), Val di Chiana (5 local assemblages), Pirro (5 local assemblages), Galerian 1 (6 local assemblages), Galerian 2 (5 local assemblages), Galerian 3

Table 1. Framework of PCOMs of the Italian peninsula from the Late Pliocene to the Late Pleistocene

PCOMs	Biochronological age	No. of local assemblages included	Absolute age
Aurelian	Early Aurelian	22	300 Kya
Galerian 3		8	
Galerian 2	Galerian	5	1 Mya to 300 Kya
Galerian 1		6	
Pirro	Upper Villafranchian	6	2 Mya to 1 Mya
Val da Chiana		5	
Upper Valdarno		14	
Montopoli	Middle Villafranchian	5	2.6 Mya to 2 Mya

(8 local assemblages), Aurelian (22 local assemblages) (see Table 1). A total of 89 species have been included. The Triversa PCOM was excluded from the analyses because of the scarcity of local assemblages it includes and the discontinuity of the fossil record intervening between it and the successive (Montopoli) PCOM. The exclusion of Triversa PCOM decreases species diversity to 85, distributed across 71 local assemblages. The taxonomic groups included in the analysis were the orders proboscideans, artiodactyls and perissodactyls, and the families canids, felids, hyaenids and ursids. Species whose reconstructed body size was smaller than 5 kg were excluded unless they belonged to one of the above groups. Similarly, species with predicted body sizes greater than 5 kg were excluded if they belonged to groups not included here. Details and data on body size reconstructions can be found in Raia (2003).

The occupancy of a species was quantified as the proportion of local assemblages where it is present within a single PCOM. For instance, consider a species occurring at Pirro PCOM. Now, suppose it occurs at three Pirro local assemblages. As Pirro PCOM comprises six local assemblages, that species' occupancy will be 0.5. As PCOMs are compositionally stable by definition and include almost all contemporary fossil assemblages located over the Italian peninsula, our measure of occupancy is inherently geographic in nature.

We investigated occupancy–frequency distributions across PCOMs to determine if patterns are bimodal, unimodal, or neither. The occurrence of bimodality should be taken as evidence that PCOMs replicate living communities, in terms of the structure of species occupancy at least.

The relationship between occupancy and species survival was analysed by regressing the occupancy of each species against the number of consecutive PCOMs it survived. The occupancy of a species was calculated within a PCOM. For this, for any species lasting more than one PCOM, we took the mean occupancy value. A species that was absent in PCOM *X* intervening between two PCOMs where it was present was assumed to be present in PCOM *X* (range-through correction). In the case of a range-through, occupancy was assumed to be the mean between the bracketing values. Only 8.4 occurrences in our data are range-through (17/201). Therefore, we argue that applying range-through correction does not alter our results. The number of PCOMs in which a species occurred is indicative of its ability to survive changing environmental conditions. We considered the latter a better measure of

species survival – in a given place – than raw species duration. Species duration is very difficult to calculate because it requires absolute dating. Furthermore, it suffers greatly from the small chance of fossilization for rare species [Signor-Lipps effect (Signor and Lipps, 1982)]. In particular, we tested for the correlation among the number of PCOMs occupied and: (1) arithmetic mean of species occupancy, (2) geometric mean of species occupancy and (3) maximum occupancy. Geometric mean is used because it is highly relevant in extinction dynamics. Simons (2002) underlined that in a bet-hedging context, minimum values are more important than mean values because catastrophic minima could wipe out a species. Therefore, he suggested using the geometric mean, which is more sensitive to minimum values. Extending our results to larger geographical scales depends on the strength of the relationship between local occupancy and geographical range size (Gaston and Blackburn, 2000).

We computed changes in the occupancy of Quaternary large mammals from the Italian peninsula over time. Only species that appeared and vanished within the time boundaries of our data set were considered. Species occurring at only one PCOM were excluded. Occurrences corresponding to a range-through were similarly excluded. For each species, we plotted occupancy per PCOM. Because PCOMs are ordered in time, the course of species occupancy through PCOMs is its course through time. We were interested in the shape of the occupancy trajectory. We concentrated on the frequency of peaked trajectories in particular. We considered ‘peaked’ any trajectory whose occupancy maximum does not coincide with either the first or the last occupancy values but is higher than both. In addition, either the first or the last value should be the lowest in occupancy (see Fig. 1). Based on these criteria, we regard as ‘peaked’ any trajectory that increases after a species’ appearance and reaches its maximum prior to the species’ demise.

We compared the frequency of peaked trajectories in our data with a null model of random occupancy over time. Indeed, for trajectories three PCOMs long, the expected frequency of peaked trajectories is easily calculated. It is the probability of occupancy rising from the first to the second PCOM and then decreasing again. As occupancy can simply increase or decrease, this probability is 0.25 (0.5×0.5). For longer trajectories, we built the null model as follows. First, a species at a hypothetical PCOM was randomly given an occupancy value between 0 and 1 (zero excluded). This was repeated for a run of n occupancy values to simulate the occurrence of the species in n consecutive PCOMs. Next, we computed the trajectory type. In our data set, there are species occupying 4, 5 and even 6 consecutive PCOMs. Therefore, for each run we computed trajectory type after 4, 5 and 6 steps (each step represents a hypothetical PCOM consecutively occupied). We performed 1000 runs. Then, we counted peaked trajectories appearing in runs 4, 5 and 6 hypothetical PCOMs long. Finally, we compared these counts with real data.

Indeed, this procedure treats occupancy values in a single course as independent from each other. Yet, occupancy is probably autocorrelated in time. Allowing for this autocorrelation requires preliminary information on how much occupancy can change between successive PCOMs. Unfortunately, this information is not available. In theory, we could calculate it from the data, yet this is somewhat tautological and does not account for singletons (species that lived in a single PCOM). Notwithstanding, we stressed the effect of autocorrelation imposing some limits to occupancy variation. We repeated the ‘independent occupancies’ experiments above forcing occupancy in a certain PCOM to be the previous value $\pm 20\%$, $\pm 50\%$ or $\pm 80\%$ that value. Overall, we obtained four peakedness frequency estimates (three from ‘autocorrelated’ and one from ‘independent occupancies’ models).

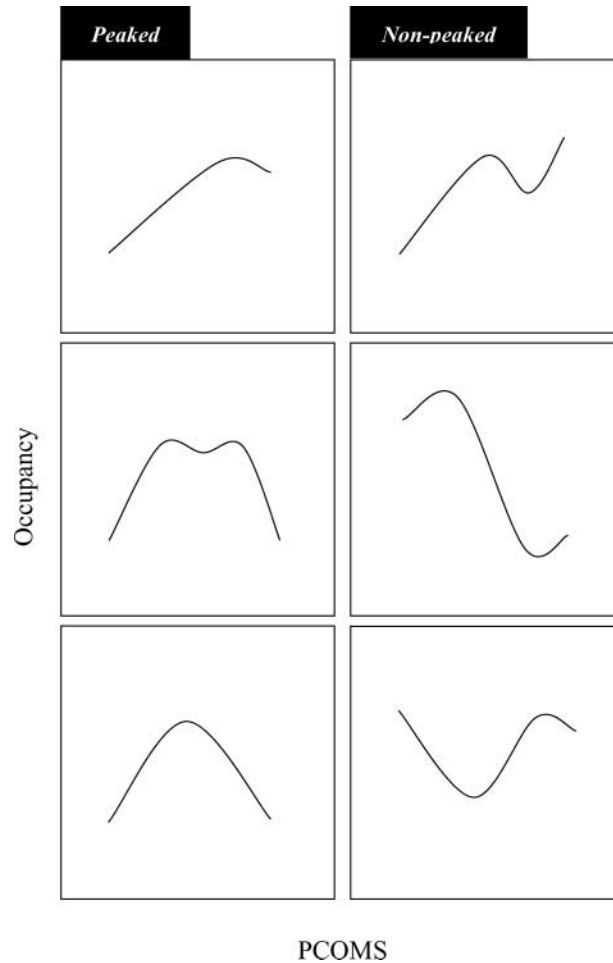


Fig. 1. Explanatory depiction of peaked trajectories of occupancy through time. We considered to be ‘peaked’ only those trajectories that rose after a species’ appearance and reached their maximum prior to the species’ demise.

The statistical comparison with the real data was based on the most conservative of these estimates.

We paid special attention to species surviving for more than two PCOMs because those that survived two or less could not be investigated for the occurrence of a peaked trajectory. Since our measure of occupancy is greatly influenced by abundance, nearly extinct species should only rarely show high occupancy. Similarly, if species are not very abundant at their infancy, they probably won’t be recorded at high occupancy. A species which is rare early in its life could even pass undetected. In the latter case, a true peaked trajectory could appear to be declining because it is truncated at the left. These observations indicate that peaked trajectories are probably underrepresented in our data. We did not attempt to correct for this *a priori*. Yet, we take these facts into consideration in discussing some specific differences that emerged between carnivores and herbivores.

RESULTS

Occupancy–frequency distributions at the PCOM level are mainly right-skewed (Fig. 2). In some cases (U Valdarno, V di Chiana, Pirro and Galerian 1 PCOMs), the occupancy–frequency distribution is bimodal. For instance, at U Valdarno, nine species have occupancy of 9 or more, ten species have occupancy of 0–2, and only eight species lie in the 3–8 occupancy interval. The Pirro and Galerian 1 PCOMs show similar patterns. The case for V Chiana is less clear. All other PCOMs present a clearly unimodal right-skewed distribution (Fig. 2). Maximum occupancy is significantly correlated with the number of consecutive PCOMs occupied in time (Pearson product–moment correlation: $r = 0.501$; $P < 0.001$) and the same holds true for arithmetic mean occupancy ($r = 0.242$; $P = 0.026$) but not for geometric mean occupancy ($r = 0.185$; $P = 0.091$). Occupancy is uneven across orders (one-way ANOVA, $F_3 = 2.990$; $P = 0.036$). Carnivores have the lowest absolute occupancy (arithmetic mean occupancy: carnivores, 0.25; artiodactyls, 0.37; perissodactyls, 0.33; proboscideans, 0.47).

Interestingly, species that belong to anagenetic series had, on occasion, very high occupancy. For instance, species belonging to the axis-like deer genus *Pseudodama* [or *Euraxis* (see Di Stefano and Petronio, 2002)] replaced each other quickly in time, but reached very high occupancy (see Fig. 3). If we accept that *Pseudodama* is a chronospecies (which is indeed undisputed), we should count *Pseudodama lyra*, *P. nestii* and *P. eurygonos* as a single species in computing occupancy–time relationships. If *Pseudodama* is excluded, occupancy–survival relationships become much stronger. The adjustment for chronospecies is difficult to apply because most cases are controversial. Yet, this emphasizes that the positive influence of occupancy on species survival is probably stronger than we found.

Twenty-seven species could be evaluated for the occupancy trajectory (see Fig. 4). In 16 of 27 (59.2%) species, the occupancy value was the lowest just before extinction. This suggests a negative effect of low occupancy on species survival. Nineteen of them were species surviving for at least three consecutive PCOMs. For the latter, we could examine the shape of the occupancy–time relationships. Twelve of these 19 (63.1%) species show a peaked trajectory. Altogether, some 26–32% peaked trajectories are expected by chance, depending on the random model and trajectory length. In the ‘autocorrelated occupancy’ model, the trajectories appear very insensitive to their own length (Table 2).

Peaked trajectories do occur more often than expected by our null models (Table 2). The trajectory types are unevenly distributed across ecological groups. Herbivores have far more peaked trajectories (10 of 11 cases with at least three consecutive data points, 90.9%) than carnivores (2/8, 25%). Five out of the six 3-PCOMs long trajectories and the sole 4-PCOMs long trajectory not showing a peaked shape belong to carnivores. The only carnivores showing a peaked function are the coyote-like *Canis arnensis* (6 PCOMs, see Fig. 4) and the wolf ancestor *Canis etruscus* (4 PCOMs, Fig. 4). The results indicate that herbivores and not carnivores show a clear tendency to follow peaked trajectories.

DISCUSSION

The results of this study show a striking similarity between living communities and PCOMs with respect to occupancy–frequency distributions. They tend to be either bimodal or right skewed in agreement with Raunkiaer’s law. It is well known that megaherbivores are more common in fossil deposits than expected by their size. This is because the preservation of

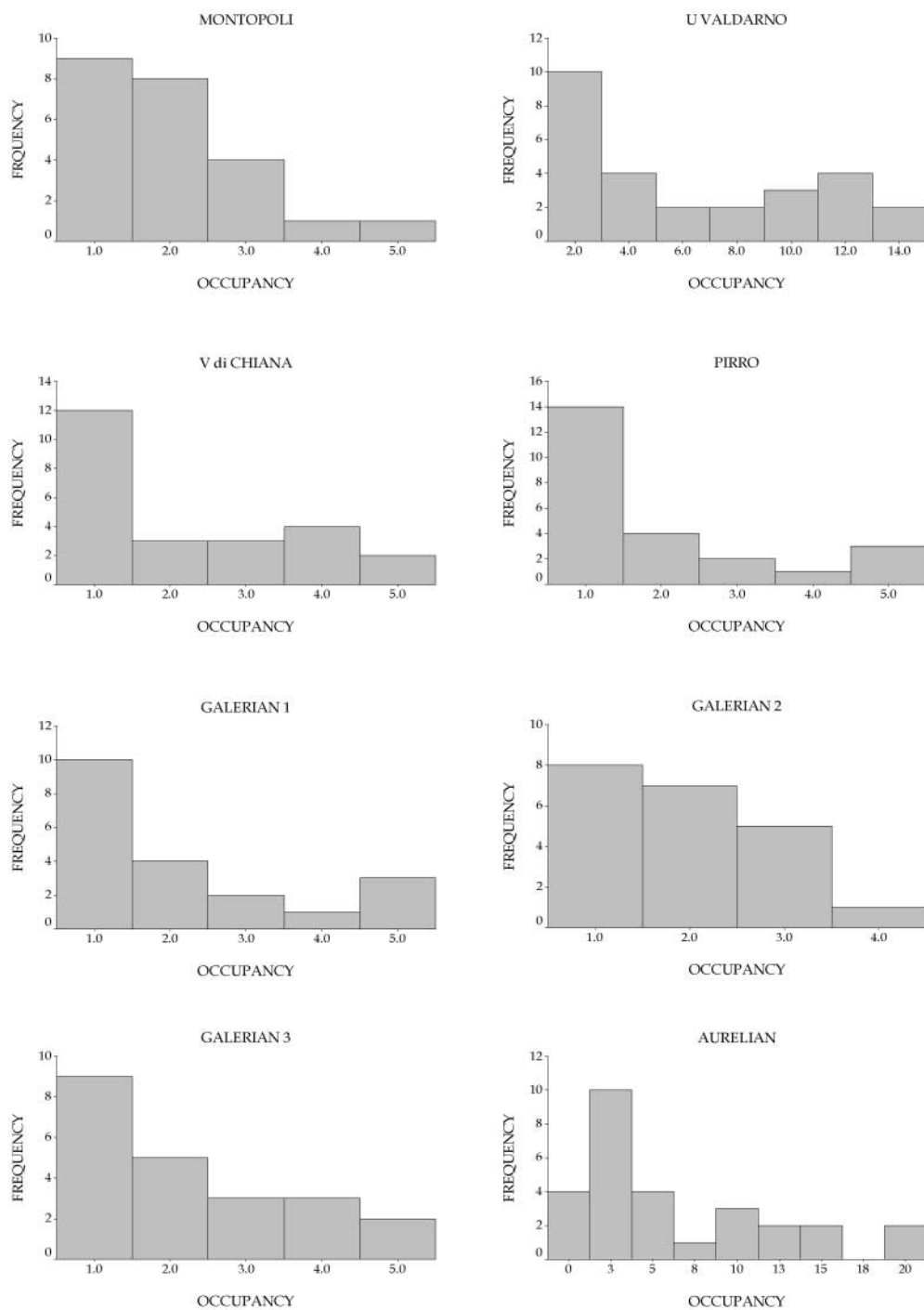


Fig. 2. Occupancy–frequency distribution in PCOMs.

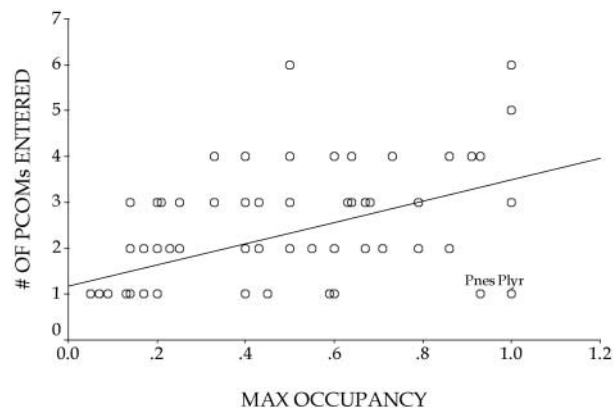


Fig. 3. The relationship between species survival over successive PCOMs and maximum occupancy. Pnes = *Pseudodama nestii*; Plyr = *Pseudodama lyra*.

their bones is more likely by virtue of their large size (Damuth, 1982). If megaherbivores are more common at 'bimodal' PCOMs, then bimodality could be a side-effect of the artificially high megaherbivores occupancy. However, the only true megaherbivore present at 'bimodal' PCOMs is the mammoth *Mammuthus meridionalis*. Conversely, non-bimodal PCOMs yield very large rhinos and bovids (such as *Bison priscus*, *Hemibos galerianus* and *Bos primigenius*) other than proboscideans, which almost certainly were megaherbivores by common standards [e.g. 1000 kg according to Owen-Smith (1990)]. Therefore, we do not think that bimodality is a result of the presence of megaherbivores.

Bimodality shows no correlation with species diversity, or the number of local assemblages included in a PCOM. Indeed, the most diverse and local assemblage-rich PCOMs are either bimodal (Upper Val d'Arno PCOM, c. 2 Mya) or unimodal (Aurelian, some 0.3 Mya). The occurrence of bimodality is not random in time. Non-bimodal PCOMs occurred mostly during the Middle to Late Pleistocene. Middle to Late Pleistocene PCOMs underwent the most intense climate cooling, related to the harshest phase of Quaternary glaciations. There were intense fluctuations in temperatures during this time (Imbrie *et al.*, 1993). Barnosky (2001) contended that Ice Age mammals should be equipped to withstand more than one Milankovitch cycle, as the mammalian average species duration far exceeds the 100,000 years the typical Ice Age cycle lasts. Barnosky envisioned range shifts as a typical mechanism to reduce extinctions in the face of climatic change. Many studies on the dispersal of Ice Age large mammals point out the use of southern refugia as a way to avoid the harsh conditions at northern latitudes for many species (Koenigswald and Werdelin, 1992).

Arguably, a species does not maintain constant levels of abundance (and therefore occupancy) throughout its lifetime, either because it is forced to disperse or runs into climatically less/more favourable conditions. Hanski (Hanski, 1982; Hanski and Gyllenberg, 1993) pointed out that species within communities occur as either core (abundant) or satellite (rare). We suggest that the core-satellite hypothesis structure was altered by intense climatic changes during the last 1 million years. The core species status could have been constantly changing during the increasingly cold and unstable Galerian-Aurelian period. It is easy to imagine how such ephemeral core-status could transform a bimodal function into right-skewed by declining the right-hand, 'core' peak in bimodal distributions. Consistent with

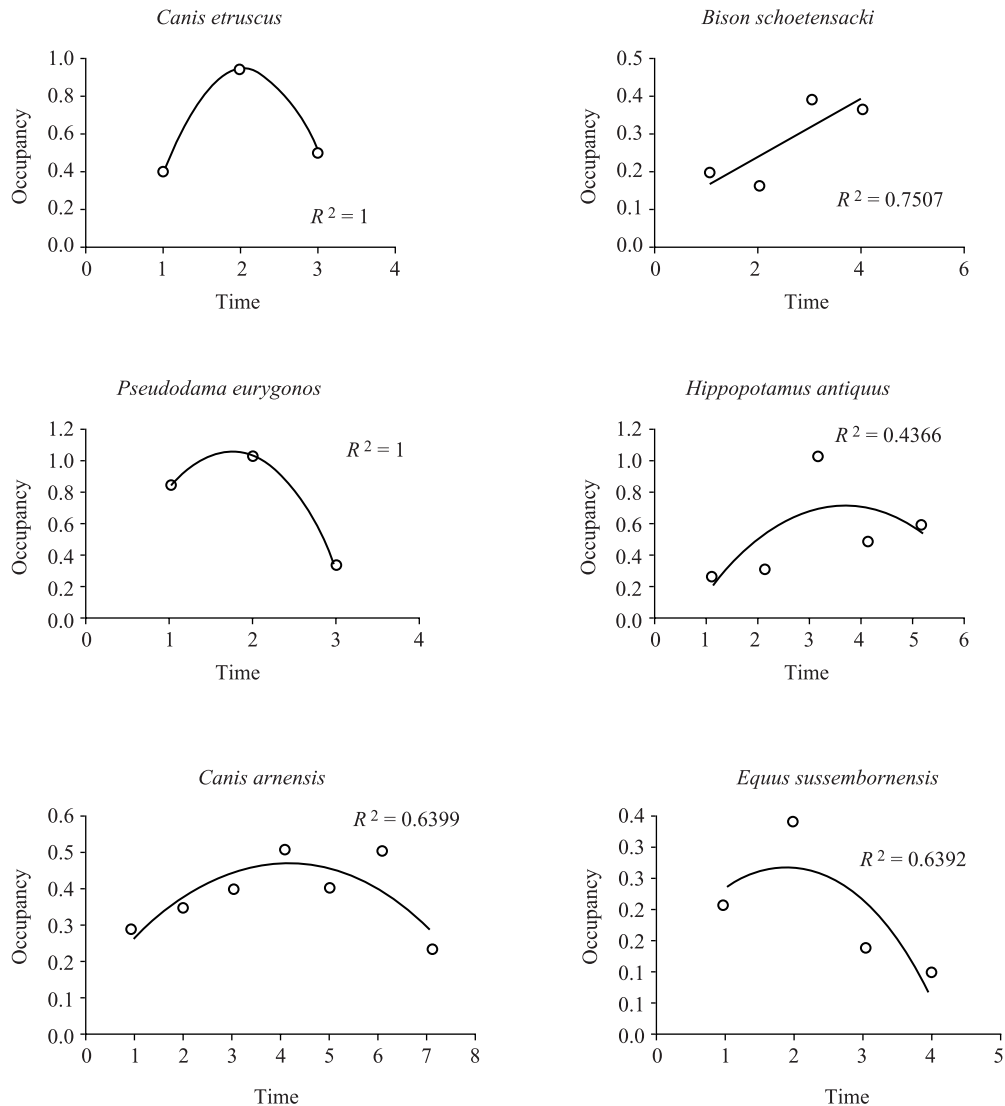


Fig. 4. Occupancy trajectory to extinction for some representative Ice Age mammals from Italy.

our interpretation, broad population level changes in abundance have been reported for mid-Pleistocene mammals of the Porcupine Cave (Barnosky, 2004; Barnosky *et al.*, 2004).

High-occupancy species are likely to survive longer for two reasons. The first is bet-hedging. Species that are low in abundance will be more vulnerable to catastrophic accidents. The second reason has to do with Brown's (1984) generalism hypothesis. If high occupancy is a side-effect of generalism, then a high-occupancy species has the same virtues as a generalist species. It can tolerate a greater range of environmental conditions and therefore survive longer. Bet-hedging is related to the geometric mean occupancy. We found the latter was the only measure of occupancy that showed no significant relationship with

Table 2. Occurrence of peaked trajectories in the real data and in a simulated sample of 1000 random occupancy trajectories

Length of the trajectory	No. of peaked simulations (out of 1000)				No. of peaked trajectories	Total no. of trajectories	<i>P</i> of occurrence of peaked trajectories
	‘Independent occupancies’ model	‘Autocorrelated occupancies’ model					
		80%	50%	20%			
6 PCOM	259	262	278	301	2	2	0.067
5 PCOM	304	274	283	294	1	1	0.304
4 PCOM	324	263	288	295	4	5	0.037
3 PCOM	250*	—	—	—	5	11	0.080

Note: The probability *P* has been calculated from the binomial distribution. The percentage of peaked trajectories appearing in the simulation is assumed to be the fraction of peaked trajectories expected in the real data.

* Based on probability calculus.

local survival. This suggests the generalism hypothesis (Brown, 1984; Hadly and Mauer, 2001) may be more compelling here.

A point should be made clear about chronospecies. Walsh (1995) demonstrated mathematically that the addition of new genes to the species pool requires large populations. Population size – that is, abundance – is positively correlated with occupancy (Brown, 1984; Brown and Maurer, 1987; Rosenzweig, 1991; Hanski *et al.*, 1993; Holt, 1997; Gaston and Blackburn, 2000; Harte *et al.*, 2001). Therefore, in keeping with Walsh (1995), we argue species having high occupancy could transform more rapidly than others. As far as this (phenotypic) variation is prompted by genetic novelties, high occupancy may favour both local survival and chronospecies formation while reducing the strength of the occupancy–survival relationship!

It is unsurprising that only rarely is occupancy still rising prior to extinction. First, it is trivial that mammals often become rare before going extinct (Brashares, 2002). Furthermore, species on the brink of extinction seemingly hang on for a while either by becoming locally abundant but regionally uncommon, or becoming locally rare but widespread (Johnson, 1998). Given that peaked functions do occur more often than expected at random, we argue this study indicates the peaked-trajectory is the mode among hoofed mammals, as it is for birds (Webb and Gaston, 2000). A peaked trajectory does suggest a progressive adaptation of species to their environment. This fine-tuning is likely to unbalance species survival when the environmental setting changes too much. This explanation of peakedness is consistent with the taxon cycle hypothesis (Ricklefs and Cox, 1972). Herbivores show peaked trajectories more often than carnivores. In theory, as carnivores were less common, their true first occurrence could pass undetected because of rarity. If a peaked trajectory is the norm for them as with herbivores, their first recorded occurrence should then correspond to a phase of rising occupancy. Therefore, the difference in occupancy between carnivores and herbivores at the (recorded) first appearances should be lower than the average difference. Indeed, the difference in occupancy at first occurrence between carnivores and herbivores is 0.181. This falls well within the average occupancy difference (0.155; 95% confidence interval = 0.058–0.252). The difference in occupancy course between carnivores and herbivores appears not

to be a by-product of taphonomic processes and is therefore real. Unfortunately, our data are not suitable to investigate this further.

CONCLUSIONS

Extinct communities conform to the rules for occupancy patterns that were established for living ones. For instance, to our knowledge, this is the first time bimodality in species occupancy has been specifically tested for in fossil faunas. Furthermore, this means that PCOMs could be safely used to study occupancy patterns for them.

Occupancy has a positive effect on species survival, at least at our scale of investigation. For herbivores at least, occupancy is typically low at a species' birth. Then it rises to a peak and decreases until the species' demise. Carnivores do not show any consistent pattern.

For some mammals, we found occupancy was still rising just before extinction. Often, the latter were cases of species anagenetically transforming into new species (chronospecies). This suggests a positive effect of abundance on morphological transformation.

The study of macroecological patterns in extinct communities is still new in most regards. Here we demonstrate that some macroecological 'rules' are detectable in extinct communities. Since macroecological patterns can be detected in extinct communities, we hope this study will encourage other paleoecologists and evolutionary ecologists to embark on this kind of research.

ACKNOWLEDGEMENTS

We are indebted to Tony Barnosky, Kate Lyons and an anonymous reviewer whose important suggestions and careful review greatly improved the manuscript. Kate Lyons helped us also with the English.

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