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Turnover pulse or Red Queen? Evidence from the large mammal communities during the Plio-Pleistocene of Italy

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Abstract

This study investigates the effect of climate changes (during the Ice Ages) on the evolution of Plio-Pleistocene large land mammal communities of the Italian peninsula. We recognized paleocommunities by using both the classic, biochronologic approach and with a special type of cluster analysis able to recognize a statistically discrete number of paleocommunities. These approaches ensure the potential for including rare species, dilute taphonomic biases, and give stronger emphasis on the conjoint occurrence of species. Irrespective of the way we partitioned the fossil record, our results are consistent with the prediction that climate changes affected Turnover Rates (TRs). We found out that only cold shifts in climate were effective in influencing communities' turnover. Phylogenetic and ecologic inheritance from Pliocene (warmer) climate probably made large mammal communities by far more sensitive to cold than to warm shifts in global temperature.

Eventually, we discuss various potential flaws affecting studies on TRs. Those flaws depend on the phylogenetic, geographic and body-size level of investigation. The existence of these restrictions makes studies on turnover hardly comparable with each other.

Keywords: Community evolution; Large mammals; Turnover; Italy; Plio-Pleistocene

1. Theoretical framework

Some authors emphasize that major global climatic and tectonic changes drove communities' compositional changes through their extensive effect on the origination–extinction dynamics. That is to say, communities undergo periods of compositional revolution in coincidence with the greatest changes in climate. Hence, rates of taxonomic changes during these 'revolutions' should be distinctively higher than in periods of relatively more constant climate (Vrba, 1985a,b, 1987, 1992, 1993, 1995a,b; Janis, 1989, 1993; Turner and Anton, 1998; Prothero, 1999; Van Valkenburgh, 1999; MacFadden, 2000; Bobet and Eck, 2001). On the other hand, other authors

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postulated that biological interactions shape communities at an almost constant rate (Van Valen, 1973; Alroy, 1994, 1996, 1998, 2000). Critical to the latter is that rates of change in the origination–extinction dynamic (namely, turnover rates, TRs) should be decoupled from climate changes.

Vrba (1985a,b, 1987, 1992, 1993, 1995a,b) found a strong correlation between phases of climatic deterioration during the past 2.5 My and both FOs (first occurrences, including speciation plus immigration) and LOs (last occurrences, including extinction plus local disappearances) in African Bovidae. In keeping with the theory of punctuated equilibria (Eldredge and Gould, 1972; Eldredge, 1995; Gould, 2002), she argued that major faunal turnovers occur in brief periods (pulses). The pulses coincide with the largest climatic oscillations and/or tectonic events. Barry et al. (1995) examined faunal turnovers in the Neogene Siwaliks mammals finding some correlations with climatic changes but not to local or global events. Turner and Anton (1998) demonstrated Old-World machairodonts did evolve according to turnover pulses and Bobet and Eck (2001) confirmed Vrba's hypothesis about turnover pulses in African bovids. Nevertheless, Vrba's Turnover-Pulse hypothesis was strongly opposed by Alroy (1996, 1998, 2000), Behrensmeyer et al. (1997) and McKee (2001). The latter authors argued repeatedly that biological interactions are the main source of community evolution, in keeping with Van Valen's Red Queen hypothesis (Van Valen, 1973). Behrensmeyer et al. (1997) criticized Vrba's conclusions arguing that turnover dynamics of Plio-Pliostecene of Africa (particularly in the Turkana Basin) did not have short pulses being, instead, diluted in time. Prothero (1999) argued that no obvious turnover responses were present over the entire Cenozoic among land Mammals in North America. He specifically avoided to include in his analysis immigrational turnovers considering they can "...complicate the picture of in situ change". In fact, the analysis of the entire Cenozoic in North America could lead to different conclusions because of the very big temporal and geographic scale (Barnosky, 2001; see below). It is important to emphasize here that we intend the terms "communities evolution" as the compositional change communities undergo because of immigrations/extinctions dynamics. It does not necessarily implicates a true "phyletic evolution". However, one can argue that during strong climatic/environmental changes major habitat fragmentation can cause greater allopatry within populations. Under this scenario an increase in the speciation rate is indeed expected (even if this is not uniquely expected under a cause/effect dynamic!).

Indeed, it is possible that statistical treatment of data confounds the results of many studies. Different data treatments could sometimes give different results even if the stratigraphic intervals and the taxonomic level of investigation were the same (e.g. Alroy, 1996; Prothero and Heaton, 1996). More importantly, Barnosky (2001); (Barnosky et al., 2003) pointed out that the geographic and temporal scales of observation are important in revealing what the main determinants of land mammals community evolution are. He argued that if the geographical scale is small, and the temporal scale is shorter than a Milankovitch cycle, then species interactions (mainly interspecific competition and predation) shape community evolution relentlessly (in agreement with the Red Queen hypothesis, Van Valen, 1973). At larger scales in both time and space (but for the spatially largest) community changes seem to obey the climate-forcing hypotheses (the Court Jester hypothesis in Barnosky, 2001).

Italian Plio-Pleistocene large mammal faunas have been extensively studied (and recently reviewed) for a long time (Alberdi et al., 1997; Gliozzi et al., 1997; Caloi and Palombo, 1998; Sardella et al., 1998; Palombo et al., 2003). These studies typically have either a biochronologic or a systematic target. As for the study of community changes, a worthy contribution were two papers from Azzaroli and colleagues (Azzaroli, 1983; Azzaroli et al., 1988), and various authors summarizing the 'dispersals events' occurred in Europe (von Koenigswald and Werdelin, 1992). Azzaroli et al. (1988) referred to community evolution during the Plio-Pleistocene as marked by a few, yet massive dispersal events. They qualitatively argued that each event correlates with some major change in climate, the latter being in turn driven from the onset of a glaciation.

The aim of this study is to understand if climate or biological interactions affected the evolution of large