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The fossil record as a tool in cyclostratigraphy: the incidence of Milankovitch-scale palaeoenvironmental changes on palaeocommunities

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ABSTRACT

Cyclostratigraphic analysis at the Milankovitch scale has to date mainly been approached through the sedimentary record, although palaeontological data (the fossil record) is known to provide useful evidence of orbital-scale cycles of precession, obliquity and eccentricity. Orbitally induced marine and terrestrial palaeoenvironmental changes determine variable responses on the part of the resident communities. Aside from the disruption of communities, complex evolutionary responses including stasis, speciation and extinction phenomena may take place. Cyclic variations in the marine past-biota at the community level, or in some particular taxa, have often been associated with orbitally induced changes in palaeoenvironmental parameters. Cyclostratigraphic research into foraminifera, radiolaria and nannofossil data, mainly from Cretaceous sediments, may contribute significantly to our understanding of the planktonic community's response, whereas the response of the benthic community, deriving mainly from benthic foraminifera and trace fossils, has been studied to a lesser extent. Recognition of Milankovitch cycles from terrestrial palaeocommunities is relatively scarce and based mainly on the study of Pliocene-Miocene pollen assemblages. Astronomical forced climate changes determine well known variations in the distribution of terrestrial vegetation, but can also affect the terrestrial animal community, including hominid populations (migration, dispersion and colonisation).

Key words: cycle, fossil, Milankovitch, palaeontology, planktonic

El registro fósil como una herramienta en cicloestratigrafía. Incidencia de los cambios paleoambientales a escala de Milankovitch sobre las paleo-comunidades

RESUMEN

Tradicionalmente, el análisis cicloestratigráfico a escala de los ciclos de Milankovitch se ha realizado a partir del estudio del registro estratigráfico/sedimentológico. Sin embargo, los datos paleontológicos (registro fósil) poseen un gran potencial para caracterizar ciclos orbitales de precesión, oblicuidad y excentricidad. Cambios climáticos orbitalmente inducidos determinan variaciones paleoambientales en los medios marino y terrestre a los que responden de manera variable las comunidades que los habitan; fundamentalmente alteraciones y, en menor medida, cambios evolutivos, incluyendo fenómenos de especiación y extinción. Son numerosos los trabajos que ponen de manifiesto variaciones a nivel de comunidad o de algunos taxones concretos en respuesta a cambios cíclicos orbitalmente inducidos sobre el medio marino. La mayor información procede del medio plantónico como lo revelan los estudios sobre paleo-comunidades cretácicas de foraminíferos, radiolarios y nanofósiles, frente al ambiente bentónico comparativamente menos conocido, cuya respuesta proviene del estudio de foraminíferos bentónicos y trazas fósiles. La caracterización de ciclos de Milankovitch en el medio terrestre es relativamente escasa y fundamentalmente se debe al estudio de asociaciones de polen del Plioceno-Mioceno. Cambios climáticos orbitalmente inducidos han sido ampliamente reconocidos en el medio terrestre a partir de variaciones en la distribución de la vegetación, pero también afectan a la comunidad animal, con una especial atención a la respuesta de las poblaciones de homínidos (migración, dispersión, colonización).

Palabras clave: ciclo, fósil, Milankovitch, paleontología, plantónico

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Introducción

Tradicionalmente, el análisis cicloestratigráfico a escala de los ciclos de Milankovitch (ciclos de precesión, oblicuidad y excentricidad), en el rango de los 10^4-10^6 años (ver Fischer et al.*, 2004, para una revisión histórica; Fig. 1) se ha realizado a partir del estudio del registro estratigráfico/sedimentológico y del análisis de datos abióticos como el contenido mineralógico, tamaño de grano, litología, espesor de estratos, o susceptibilidad magnética, entre otros (por ejemplo Einsele and Seilacher, 1982; Berger* et al.*, 1984; Einsele* et al.*, 1991; Fischer and Bottjer, 1991; Schwarzacher, 1993, 2000; de Boer and Smith, 1994; House and Gale, 1995; Hinnov, 2000; Weedon, 2003; D'Argenio* et al.*, 2004). Sin embargo, los datos paleontológicos (registro fósil) poseen un gran potencial para caracterizar ciclos orbitales de precesión, oblicuidad y excentricidad.*

Ciclos de Milankovitch y registro fósil

La mayoría de los análisis cicloestratigráficos realizados sobre el componente biótico se han centrado en los microfósiles marinos, especialmente en el análisis isotópico de sus conchas en relación con variaciones en parámetros como temperatura, salinidad o nutrientes. Sin embargo, cambios climáticos orbitalmente inducidos determinan variaciones paleoambientales en los medios marino y terrestre a los que responden de manera variable las comunidades que los habitan (Fig. 2; Tabla 1); fundamentalmente alteraciones y, en menor medida, cambios evolutivos, incluyendo fenómenos de especiación y extinción, aunque la relación entre los ciclos de Milankovitch y estos cambios evolutivos son un tema de debate en la actualidad (Bennett, 1990, 1997, 2004; Dynesius and Jansson, 2000; Jansonn and Dynesius, 2002; Willis and Niklas, 2004; Van Dam et al.*, 2006; Haffer, 2008; Troost* et al.*, 2009; Clarke and Crame, 2010).*

Cambios en la insolación en el rango de los ciclos de Milankovitch determinan variaciones en la dinámica atmósfera-océano que afectan al régimen climático, masas de hielo, nivel del mar, disponibilidad de nutrientes, oxígeno y temperatura (Fig. 2; Tabla 1). La mayor parte de las investigaciones sobre ciclos de Milankovitch se han centrado en las comunidades marinas, frente a las terrestres, y especialmente en los microorganismos, frente a los macrofósiles.

Comunidades marinas

Son numerosos los trabajos que ponen de manifiesto variaciones a nivel de comunidad o de algunos taxones concretos en respuesta a cambios cíclicos orbitalmente inducidos sobre el medio marino, abarcando tanto las comunidades que habitan la columna de agua como el substrato. La mayor información procede del medio plantónico, siendo comparativamente escasa la referente a comunidades bentónicas. La estrecha relación entre los cambios climáticos orbitalmente inducidos y las comunidades planctónicas es consecuencia de la dependencia de estas a parámetros como la disponibilidad de luz y los nutrientes, estrechamente asociados a la insolación recibida en aguas superficiales.

Incidencia de los ciclos de Milankovitch en las comunidades planctónicas

Entre las comunidades planctónicas el mayor número de estudios cicloestratigráficos se ha llevado a cabo sobre foraminíferos, radiolarios y nanofósiles (Tabla 1).

Foraminíferos planctónicos.- Las asociaciones de foraminíferos planctónicos han sido tradicionalmente utilizadas para evidenciar la incidencia de los ciclos de Milankovitch, sobre la base de su estrecha relación con cambios, fundamentalmente, en temperatura y productividad. Si bien los primeros trabajos se realizaron sobre la composición isotópica de las conchas de los foraminíferos (desde Hays et al.*, 1976), la incidencia de los ciclos orbitales también se ha caracterizado a partir del estudio cicloestratigráfico de variaciones en la comunidades (abundancia, composición, o diversidad). La región mediterránea se ha revelado como un área clave para los análisis cicloestratigráficos, siendo los materiales de edad Cretácico Medio-Superior y especialmente Albiense, de Italia central, un referente para el reconocimiento de ciclos de precesión, oblicuidad y excentricidad (Premoli Silva* et al.*, 1989a,b; Tornagi* et al.*, 1989; Fischer* et al.*, 1991; Erba and Premoli Silva, 1994; Galeotti, 1998; Fiet* et al.*, 2001; Grippo* et al.*, 2004; ver Fischer* et al.*, 2009, para una reciente revisión). Otros intervalos geológicos y/o áreas de estudio han sido; sedimentos hemipelágicos de edad Maastrichtiense de Black Nose (MacLeod* et al.*, 2001), secuencias pelágicas paleocenas del Norte de Italia (Poletti* et al.*, 2004), secciones mediterráneas del Mioceno Medio tardío (Iaccarino* et al.*, 2004), o,* recientemente, materiales del Jurásico superior de las Cordilleras Béticas (Sur de España) (Rodríguez-Tovar et al., 2010).

Radiolarios.- Las asociaciones de radiolarios fueron uno de los primeros indicadores climáticos, especialmente en relación con cambios en la temperatura de las aguas superficiales, utilizados para caracterizar señales de Milankovitch (Hays et al., 1976), revelándose como una herramienta de gran utilidad. Análisis espectrales sobre datos de radiolarios se aplicaron en los primeros estudios cicloestratigráficos (Pisias and Leinen, 1984; Leinen, 1985). En los últimos años su interés se ha encaminado en interpretar la incidencia de los ciclos de Milankovitch sobre la dinámica de los monzones (pre- y post-Cuaternario), determinando cambios cíclicos en la productividad que afectan a las asociaciones de radiolarios (Chen et al., 2003; Gupta, 2003, 2009).

Nanofósiles.- La diversidad y abundancia de los cocolitofóridos está altamente condicionada por la incidencia del clima sobre las características de las aguas superficiales, induciendo fluctuaciones en su producción y distribución. Numerosos trabajos ponen de manifiesto variaciones en las asociaciones de nanofósiles en sedimentos pre-Cuaternarios, en relación con señales orbitales; Plioceno (Backman et al., 1986; Backman and Pestiaux, 1987; Chepstow-Lusty et al., 1989; Gibbs et al., 2004), Mioceno (Beafort and Aubry, 1990), Cretácico (Erba et al., 1992; Bellanca et al., 1996; Mutterlose and Ruffel, 1999; Herrle et al., 2003a,b; Bornermann et al., 2005), y Jurásico (Claps et al., 1995; Mattioli, 1997; Walsworth-Bell et al., 2000; Walsworth-Bell, 2001; Olivier et al., 2004).

Comunidades bentónicas y ciclos de Milankovitch

La mayor parte de los estudios cicloestratigráficos en el bentos se han realizado sobre foraminíferos bentónicos y trazas fósiles (Tabla 1).

Foraminíferos bentónicos.- Variaciones en la composición de las asociaciones de foraminíferos bentónicos y en algunos grupos particulares se han asociado a cambios climáticos de Milankovitch ligados, entre otros factores ambientales, a fluctuaciones en la oxigenación de las aguas del fondo, temperatura o características del substrato. Sucesiones rítmicas europeas cretácicas han sido ampliamente estudiadas, con ejemplos del Hauteribiense y Barremense del Este de Inglaterra y Norte de Alemania (Mutterlose and Rufell, 1999), Albiense-Aptiense de Italia Central (Coccioni and Galeotti, 1993; Galeotti, 1998), y Cenomaniense del Sur de Inglaterra (Leary et al., 1989; Leary and Hart, 1992) o de la Cuenca de Paris (Mitchell and Carr, 1998). Ejemplos de otras edades son comparativamente escasos; más recientes como Plioceno (Becker et al., 2005) y Cuaternario (Badawi et al., 2005), o más antiguos como Jurásico superior (Rodríguez-Tovar et al., 2010). En este último caso destaca la diferente respuesta a los ciclos de Milankovitch registrada entre los foraminíferos bentónicos (fundamentalmente afectados por precesión y excentricidad) y planctónicos (especialmente sensibles a fluctuaciones de oblicuidad), en relación con los parámetros implicados en ambos ambientes (Rodríguez-Tovar et al., 2010).

Trazas fósiles.- El análisis cicloestratigráfico de las asociaciones de trazas fósiles (ausencia/ocurrencia de bioturbación, tipo de trazas, densidad, diámetros, etc.), registradas en sedimentos del Cretácico, Paleoceno y Eoceno ha puesto de manifiesto variaciones orbitales cíclicas, fundamentalmente asociadas a cambios en la productividad superficial y oxigenación (Molinie and Ogg, 1992; Erba and Premoli-Silva, 1994; Sageman et al., 1998; Grippo et al., 2004; Poletti et al., 2004; Heard et al., 2008). Recientemente se ha evidenciado la relación entre la distribución de Zoophycos y ciclos de Milankovitch, en respuesta a cambios climáticos, actividad de los monzones y variaciones en los parámetros ambientales, incluyendo el aporte de material orgánico (Rodríguez-Tovar et al., 2008, 2011).

Comunidades terrestres

La caracterización de ciclos de Milankovitch en el medio terrestre es relativamente escasa, fundamentalmente a partir de variaciones en la distribución de la vegetación en relación con la incidencia de los cambios climáticos sobre temperatura y precipitación (Tabla 1). Destacan los estudios sobre asociaciones de polen del Plioceno-Mioceno (Versteegh, 1994; Mommersteeg et al., 1995; Santarelli et al., 1998; Willis et al., 1999; Popescu, 2001; Popescu et al., 2006), aunque también se han analizado registros del Cretácico (Tribovillard and Gorin, 1991), Jurásico (Waterhouse, 1999) y de la transición Jurásico-Triásico (Bonis et al., 2010). Respecto a la comunidad animal, aunque es ampliamente aceptada la incidencia de los cambios paleoambientales climáticamente inducidos sobre la evolución de las comunidades terrestres (cambios en diversidad, origen y extinción), son escasas las alusiones a variaciones a escala de Milankovitch (Retallack et al., 2004 para el Oligoceno o Van Dam et al., 2006 para el Neógeno). Una futura y fascinante línea de investigación se atisba en la respuesta de las poblaciones de homínidos (migración, dispersión, colonización) a escala orbital (deMenocal 2004; Dennell, 2008; Campisano 2012).

Introduction

Orbital signatures in the Milankovitch frequency band (precession, obliquity and eccentricity) at quasi-periodic 10^4-10^6 year cycles (Milankovitch cycles) have been recognised in sedimentary sequences since the first description of these cycles by Milutin Milankovitch (Milankovitch, 1941) (see Fischer *et al*., 2004, for a historical review). Primary orbital variations in the Milankovitch frequency band of 19-406 kyr, corresponding to the cycles of precession (at about 19 and 23 kyr, with extremes of 14 and 28 kyr), obliquity (most power at 41 kyr, with minor components at about 28 and 54 kyr), and eccentricity (short term at about 100 kyr, with major components at about 97 and 127 kyr, and long term at about 404 kyr) (see Hinnov, 2000 for a review) were modulated to add long-period components in the range of 2-2.8 Myr (Hinnov, 2000; Fischer *et al*., 2004; Fig. 1).

As a generalised assumption, the connection between orbitally forced latitudinal and temporal variations in insolation, climatic changes and variations in ecological and sedimentary parameters has been demonstrated in the Quaternary and pre-Quaternary. In the wake of the significant paper by Hays *et al*. (1976), using a time-series analysis of the oxygen isotope record of deep-sea sediments, various proxies have been applied to trace Milankovitch signals. Special

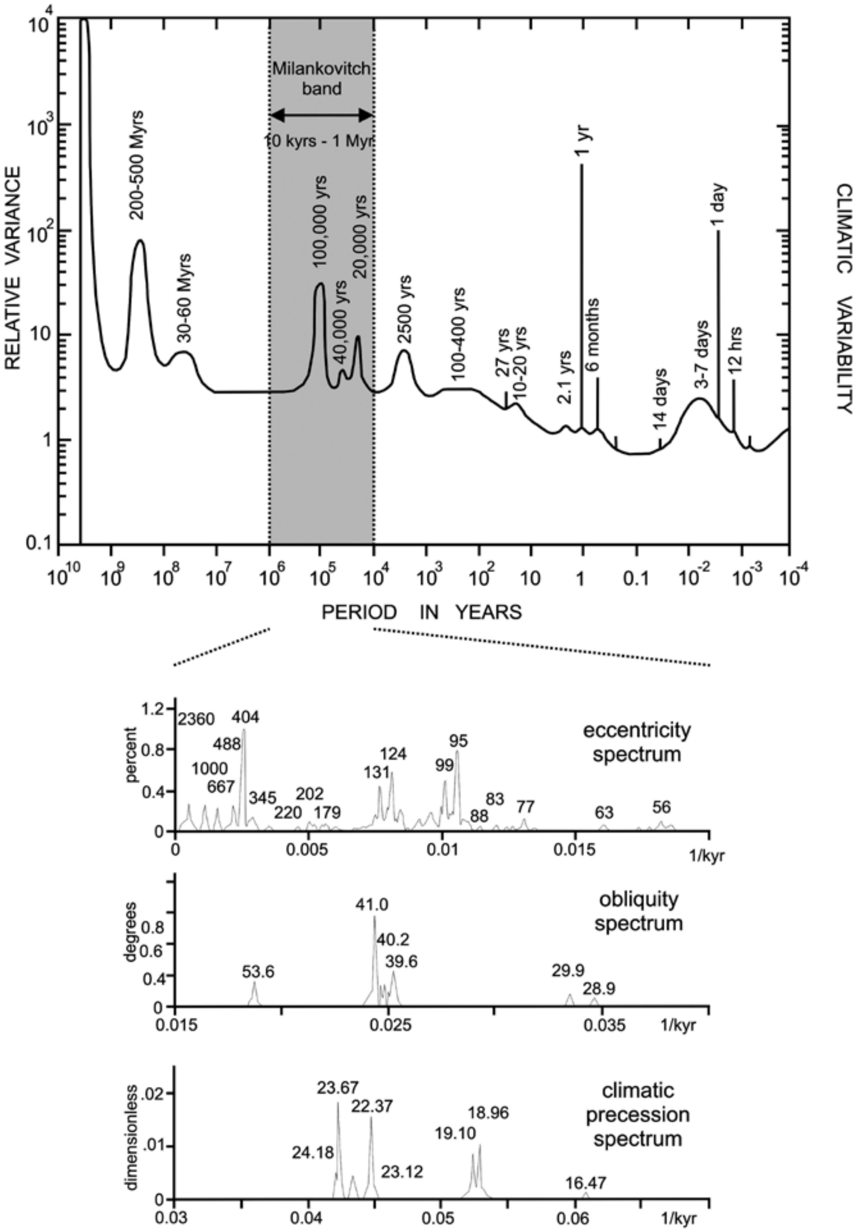

Figure 1. Above: Idealised sketch of the planetary climate variability spectrum (slightly modified from Mitchell 1976). Below: Evolution of the Earth's orbital parameters over the past 10 Myrs, adapted from Hinnov (2003).

Figura 1. *Arriba: Representación idealizada del espectro de variabilidad climática planetaria (ligeramente modificado de Mitchell, 1976). Abajo: Evolución de los parámetros orbitales terrestres en los últimos 10 Ma, adaptado de Hinnov (2003).*

attention is given to the stratigraphic/sedimentary record and abiotic features (mineralogical content, grain size, lithology, bed thickness, magnetic susceptibility etc. (*cf.* Einsele and Seilacher, 1982; Berger *et al.*, 1984; Einsele *et al.*, 1991; Fischer and Bottjer, 1991; Schwarzacher, 1993, 2000; de Boer and Smith, 1994; House and Gale, 1995; Hinnov, 2000; Weedon, 2003; D'Argenio *et al.*, 2004). As for the biotic component, most analyses focus on marine microfossils, and in particular the isotope analysis of shells and their probable relationship to changes in seawater features such as temperature and nutrient availability. Nevertheless, changes in biotic assemblages (composition, abundance, diversity etc.) are a very valuable tool for the recognition of different scale Milankovitch variations in terrestrial and marine environments. Thus, numerous recent papers have focused on time-series analyses of palaeocommunities (the fossil record) to characterize Milankovitch-type cyclical changes, even though this approach is still scarce compared to the abundance of studies concerning their abiotic components (the stratigraphic/ sedimentary record).

This paper offers a review of the many different features — from marine to terrestrial, macro- to microfossils, planktonic and benthic fauna, Quaternary and pre-Quaternary — that support the usefulness of fossil assemblages in revealing cyclic variations in the Milankovitch band. The incidence of orbital forcing on palaeocommunities is also explored.

Orbital forcing and the evolutionary process

The evolutionary response of species to palaeoenvironmental changes determined by orbital forcing at the Milankovitch scale is a topic of considerable debate at the moment, partly owing to the resolution of the fossil record and the absence of absolute time scales. A three-tier hierarchy was proposed by Gould (1985) to describe evolutionary changes: the first tier processes acting on organisms at ecological moments, the second tier consisting of speciation (species extinction and origination) on a scale of millions of years, and the third tier for periodic mass extinctions and major taxonomic replacements on an ultra-long timescale. Bennett (1990, 1997) supplemented this proposal by including a new tier for evolutionary process on the Milankovitch time-scale from 10 to100 kyr; the new second tier is characterized by the disruption of communities and loss of small adaptative changes that could have accumulated during the first tier, with communities re-sorting environmental changes throughout Milankovitch time-scales. Accordingly, speciation occurs at the following third tier in geographically isolated populations created by constant environmental changes on Milankovitch time-scales. In a later review of the role of Quaternary environmental changes for macroevolution, Bennett (2004) concluded that although speciation and extinction within the Quaternary did occur in response to orbitally forced climatic changes, these were certainly uncommon (some examples are discussed in Bennett, 2004), stasis being the typical response of species to Milankovitch oscillations in evolutionary terms.

In the wake of Bennett, cycles of contraction/expansion of available habitats induced by Milankovitch climate variability have been regarded as a major feature in the evolution of terrestrial biota; thus, major changes in terms of the size and location of species' geographical distributions (the orbitally forced species' range dynamics, the ORD of Dynesius and Jansson, 2000), or of clades at any level of genealogical inclusiveness (the orbitally forced range dynamics, ORD in Jansonn and Dynesius, 2002). Somewhat later, the Refuge hypothesis was presented by Haffer (2008) to explain the origins of species in Amazonia, evoking a plausible mechanism of faunal differentiation in the tropics and at higher latitudes through the formation of ecological refuges due to Milankovitch cycles. Changes in vegetation owing to Milankovitch cycles during the Quaternary and Tertiary ages presumably initiated many speciation processes, which may have been completed during one, two or even three cycles. Haffer (2008) concludes that there is no correlation between Milankovitch cycles and the duration of the speciation process (the latter depending on the size of a given isolated population, the degree of separation and other factors). Refuge theory therefore does not refer to a particular time of speciation but rather to a mode of speciation; to the postulated origin of species in ecological refugia irrespective of the geological time periods. Similarly, oscillations in the ice-sheet according to Milankovitch frequencies would have periodically eradicated and exposed continental shelf habitats, influencing evolutionary dynamics in marine fauna at high latitudes (Clarke and Crame, 2010).

Debate continues, however, centred largely on the second and third tiers as well as the incidence of orbital forcing on communities, with several papers diverging from the notions initially proposed by Bennett. The incidence of Quaternary climatic changes at Milankovitch frequencies upon plant evolution have been compared to previous time intervals (Willis and Niklas, 2004), concluding that, while in previous times, such as the Late Pliocene, for example, the effect of climate changes at Milankovitch time-scales mainly resulted in changes in the dominant species in plant communities, climatic changes at Milankovitch time-scales during the Quaternary determined individual, complex responses in plant species, with the recognition of stasis, speciation and extinction phenomena. Van Dam *et al.* (2006) recognised cyclic mammalian species variations (origination, extinction and turnover) in rodent lineages, with periods of 2.4-2.5 and 1.0 Myr, related by the authors to low-frequency modulations of Milankovitch oscillations and thus controlled by astronomically forced climate change. Obliquity nodes at the million-year-scale could represent short episodes of ice-sheet expansion, cooling and aridification, causing perturbation in terrestrial biota due to reduced food availability, resulting in habitat fragmentation and extinction, together with migration and lineage splitting. Cyclic species turnover occurring during eccentricity minima at periods of around 2.37 Myr could be interpreted in the light of climate-induced changes. Although these authors conclude that the astronomical hypothesis may explain third-tier processes, the question remains as to whether such species variations should be included in the third tier given the time involved (2.4-2.5 and 1.0 Myr, considering a periodicity of 1-10 million years for this tier in Bennett, 2004), or in the second tier by virtue of the cause determining the evolutionary process (orbital forcing for the second tier in Bennett, 2004). Simulations of the evolutionary response of rodent body size to a Milankovitch-type forcing climate and food density showed that below a certain seasonality threshold, body size will decrease rapidly, leading to extinction (Troost *et al.*, 2009).

Milankovitch signals in fossil communities

Global climate change and associated variations in palaeoenvironmental parameters on the scale of Milankovitch cyclicity are known to exert a significant effect on biota (Table 1). Changes in insolation lead to variations in the atmosphere-ocean dynamics, affecting climate regimes, ice-mass, sea level changes, nutrient availability, oxygen distribution, and temperature (Fig. 2; Table 1). Marine and terrestrial environments as well as their inhabiting communities are therefore affected by orbital-induced climatic changes, although the incidence and response can show great variation among communities (Fig. 2). For the most part, Milankovitch cycles are characterized in marine communities in relation to the terrestrial biota, and in the former mainly on microorganisms compared to macrofossils.

Marine environment

Marine microfossils provide information about palaeoceanographic and palaeoclimatic conditions, and can help to characterize limiting ecological and sedimentary parameters by conforming their ecological niche. Nutrient availability, oxygenation, temperature, salinity, oceanographic dynamics, and water masses are parameters that can be interpreted on the basis of marine microfossil communities. Many factors constraining the marine environment are directly associated to changes in insolation tied to Milankovitch-scale forcing. Hence, micropalaeontological communities have been extensively studied in marine environments as an approach to orbital-scale variations, frequently by applying spectral analysis. In any case (as exemplified for mid-Cenomanian data of numbers of planktonic and benthic foraminifera and ostracods), a specific counting technique is needed when working with microfossils for Milankovitch analysis (Paul, 1992).

From planktonic to sub-sea-floor environments

There is a clear correspondence between the number of studies revealing Milankovitch-scale input on marine biota and the local environment inhabiting the water column and substrate. The extensive information obtained regarding upper waters, or the planktonic environment, contrasts sharply with the scarce data from the sea-floor (bottom waters and within-sediment habitats), corresponding to the benthic environment.

Incidence of Milankovitch input on planktonic communities

Plankton consists of zooplankton and phytoplankton communities living in different habitats and occupying variable depths in the water column, depending mainly on the light and nutrients available. Both these factors are closely related to changes in insolation determined by orbital-Milankovitch-scale climatic changes.

Planktonic foraminifera.- Planktonic foraminifera live in upper ocean levels and are principally affected by changes in temperature, productivity and/or hydrography, whilst salinity and water depth are considered secondary co-variant factors (*cf.* Berger, 1969 *versus* Bijma *et al.*, 1990 and Morey *et al.*, 2005). Planktonic foraminifera assemblages have traditionally been used to identify Milankovitch-forcing. From the initial research to recent approaches, oxygen isotope ratios

Environment	**Major Communities**	**Environmental Parameters**	**Main groups affected**	**Periods**
MARINE	**PLANKTONIC**	**Sea-surface temperature** **Nutrients** Hydrography Salinity	**Nannoplankton**	Pleistocene Pliocene Miocene **Cretaceous** Jurassic
			Radiolaria	**Quaternary** Miocene
			Foraminifera	Quaternary Miocene Palaeocene **Cretaceous** Jurassic
	BENTHIC	**Oxygenation** **Nutrients** Temperature Substrate features	**Foraminifera**	Quaternary Pliocene **Cretaceous** Jurassic
			Bioturbation	Pleistocene Miocene Palaeogene **Cretaceous** Jurassic
			Molluscs	Pleistocene Miocene Cretaceous
TERRESTRIAL	PLANTS	Temperature Precipitation	**Pollen**	Pleistocene **Pliocene** **Miocene** Cretaceous Jurassic
	ANIMALS	Seasonality	Small mammals	Neogene Oligocene
			Hominids	Pleistocene Pliocene

Table 1. Milankovitch cycles in the fossil record. Marine and terrestrial communities, environmental parameters, main groups affected and frequent time record.
Note: Black indicates the most significant.
Tabla 1. *Ciclos de Milankovitch en el registro fósil. Comunidades marinas y terrestres, parámetros ambientales, principales grupos afectados e intervalo temporal más frecuente.*
Nota: En negro los más significativos.

in calcitic foraminifera have been resorted to as indicators of palaeotemperatures in sea water and global ice volume with respect to orbital-scale insolation (from Hays *et al.*, 1976, see Fischer *et al.*, 2004 for a historical review). In addition, cyclic Milankovitch-scale influence can be seen when analysing changes in the abundance, composition and diversity of planktonic foraminifera assemblages. Early papers applied spectral analyses to planktonic foraminiferal abundance, such as that in the Aptian-Albian Piobbico core (central Italy). They reflect cycles of precession, obliquity and eccentricity, and were interpreted in terms of productivity cycles (Premoli Silva *et al.*, 1989a). Later, the distribution pattern of different planktonic

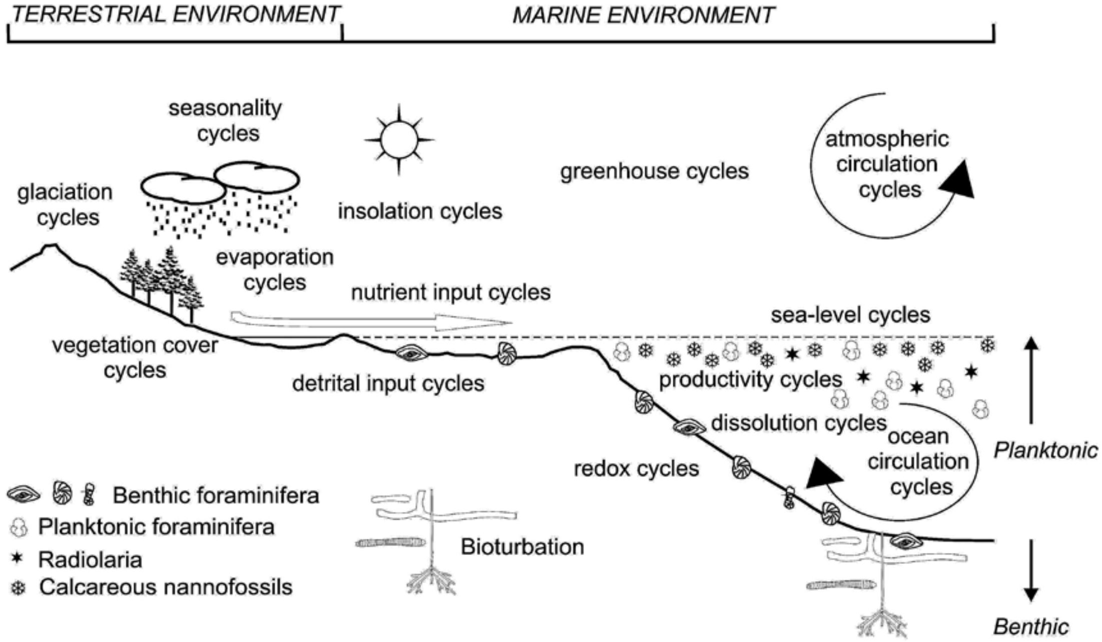

Figure 2. Sketch illustrating the complex climatic system, including atmospheric, oceanic, sedimentary, and biological subsystems, influenced by orbitally induced changes in insolation, with differentiation of terrestrial and marine (planktonic and benthic) environments (modified from Strasser *et al.* 2006).

Figura 2. *Esquema ilustrando el complejo sistema climático, incluyendo los subsistemas atmosférico, oceánico, sedimentario y biológico influenciados por cambios en la insolación inducidos orbitalmente, con diferenciación de los ambientes terrestre y marino (planctónico y bentónico) (modificado de Strasser* et al.*, 2006).*

foraminifera genera was linked to orbitally induced nutrient supply and surface water temperature (Galeotti, 1998). Cyclostratigraphic analysis of biogenic components (Premoli Silva *et al.*, 1989a, b; Tornagi *et al.*, 1989; Fischer *et al.*, 1991; Erba and Premoli Silva, 1994) showed that carbonate content was dominated by an abundance of coccoliths and that the abundance and taxonomic diversity of planktonic foraminifera run counter to coccolith productivity, reaching their maximum in the least calcareous marls.

The Mediterranean region is key to cyclostratigraphic analyses (Fischer *et al.*, 2009, for a recent review), the Middle-Upper Cretaceous, and Albian sediments in particular (coccolith-globigerinacean marls) from the Umbria-Marche Basin being a reference for such studies (Fiet *et al.*, 2001; Grippo *et al.*, 2004). Time series analyses of the abundance of two opportunistic foraminifera genera from Cretaceous sediments in the southern Tethys likewise point to the probability of Milankovitch precession and eccentricity cycles governing surface water fertility (Soua, 2010). Other geological intervals and/or areas highlight the potential of planktonic foraminifera assemblages in the context of Milankovitch cycles. Precession cycles recognised in Maastrichtian hemipelagic strata at the Black Nose indicate cyclic variations in the abundance of planktonic and benthic foraminifera linked to changes in productivity; *Heterohelix* spp., *Globigerinelloides* spp., and *Laeviheterohelix glabrans* were relatively abundant during times of high productivity, whereas *Globotruncana* spp. and *Pseudoguembelina* spp. were more abundant when productivity was low (MacLeod *et al.*, 2001). Fertility cycles induced by precession, obliquity and eccentricity cycles can be traced in Palaeocene pelagic sequences in the Southern Alps (Northern Italy) by the abundance and composition of planktonic foraminifera, among other data (Poletti *et al.*, 2004). Spectral analyses of the relative abundance of the planktonic foraminifer Globigerinoides reflect precession and long- and short-eccentricity as being dominant forces in Late Middle Miocene Mediterranean sections (Iaccarino *et al.*, 2004). Analyses of planktonic foraminiferal assemblages in the Sea of Japan during the last 2 My show significant cyclical replacements of the taxonomical structure associated with Milankovitch cycles of eccentricity, obliquity and precession (Pletnev and Sukhanov, 2006). Planktonic foraminiferal analysis conducted on Upper Jurassic materials from the Tethys (Rodríguez-Tovar *et al.*, 2010) has recently given the following results:

Radiolarian.- Radiolarian assemblages were one of the first indices of global climate used to characterize Milankovitch-scale signals. Hays *et al.* (1976) applied spectral techniques to *Ts* (summer sea-surface temperatures deriving from statistical analysis of radiolarian assemblages), and the percentage of *Cycladophora davisiana* (relative abundance of one radiolarian species not used in estimating *Ts*). This landmark report identifies radiolarian assemblages as representing a very useful tool in the recognition of cyclic orbital changes. It provided the first documented evidence of global palaeoclimatic changes through the precession, obliquity and eccentricity components in the radiolarian community during the Quaternary ice ages. Since then, temporal series of palaeo-sea-surface temperatures (SSTs), as estimated according to radiolarian transfer functions, have generally been used as palaeothermometres (*cf.* Gupta *et al.*, 1996; Cortese and Abelmann, 2002). Spectral analysis of radiolaria data associated with variations in productivity has also been applied to the study of Milankovitch periodicities (Pisias and Leinen, 1984; Leinen, 1985). Most recently, radiolarian assemblages have been used as proxy-monsoon Milankovitch cycles. Detailed spectral analysis of radiolaria test abundance for the Late Quaternary in Central Indian Ocean sediments reveals multiple cycles in the Milankovitch band (eccentricity, obliquity and precession) and in sub-orbital bands, related to cyclic changes in summer-monsoon productivity (Gupta, 2003, 2009). Variations in radiolarian abundance, diversity and accumulation rate have been used as palaeomonsoon proxies from the late Miocene (Chen *et al.*, 2003), which may very well be linked to upwelling variations linked to Milankovitch-climate forcing.

Nannofossil assemblages.- The diversity and abundance of coccolithophorids are highly determined by climate and environmental conditions in upper waters, climatic changes having a great impact on their production and distribution during the past. Numerous papers describe the relationship between coccolithophore productivity and long-term climatic signals (McIntyre and Bé, 1967; Okada and McIntyre, 1979; Molfino and McIntyre, 1990; Samtleben and Schröder, 1992; Giradeau *et al.*, 1993; Winter and Siesser, 1994; Flores *et al.*, 1997; Kinkel *et al.*, 2000; Marino *et al.*, 2008; Marino *et al.*, 2009). Milankovitch-scale forcing (at cycles of precession, obliquity and eccentricity) in pre-Quaternary records can be seen in the relative abundance of particular key taxa, related to variations in sea-surface fertility and water temperature in response to insolation climatic fluctuations. Several papers provide evidence of variations in nannofossil assemblages after orbital signals during the Pliocene (*cf.* Backman *et al.*, 1986; Backman and Pestiaux, 1987; Chepstow-Lusty *et al.*, 1989; Gibbs *et al.*, 2004), Miocene (Beafort and Aubry, 1990), the Cretaceous (*cf.* Erba *et al.*, 1992; Bellanca *et al.*, 1996; Mutterlose and Ruffel, 1999; Herrle *et al.*, 2003a,b; Bornermann *et al.*, 2005) and the Jurassic (*cf.* Claps *et al.*, 1995; Mattioli, 1997; Walsworth-Bell *et al.*, 2000; Walsworth-Bell, 2001; Olivier *et al.*, 2004). Recently, spectral analysis of coccolith-sized variations in Early Jurassic materials has given rise to the finding that changes in water transparency influenced by orbitally controlled frequency and intensity of storms may have affected group sizes (Suchéras-Marx *et al.*, 2010). Quantitative analyses of nannofossil assemblages with regard to their composition and diversity index (H) (Flores *et al.*, 2003; Marino *et al.*, 2008, 2009, 2011) also signal orbital-scale changes during the Pleistocene; cyclic fluctuation in nannofossil abundance during the mid-Pleistocene could be attributed to a change in the glacial-interglacial periodicity of obliquity and eccentricity (Marino *et al.*, 2008, 2009, 2011). No such obvious linear relationships between nannoflora changes and Milankovitch input are to be found however (Marino *et al.*, 2009).

The integrating of data concerning calcareous nannofossils and planktonic foraminifera in Tethyan Cenomanian black shales and Mediterranean sapropels reveals that both were deposited when the water column was stratified, in the light of the increased abundance of deep-dwelling rotaliporids and the euryhaline surface dweller *Globigerinoides ruber*, indicating freshwater superficial layers (Negri *et al.*, 2003). The greater abundance of surface-subsuface-tolerant foraminiferal species such as *Heterohelix reussi* and the opportunistic calcareous nannofossil *Watznaueria barnesae* suggest a similar ecological significance. Spectral analysis applied to calcareous nannofossils shows a close relationship with Milankovitch precession and eccentricity cycles in both the black shales and the sapropels (Negri *et al.*, 2003).

Epi- to endobenthic communities and Milankovitch input

Relationships between marine benthos and substrate vary according to the depth at which they dwell in the substrate, there being differences between the epifauna inhabiting the sediment surface and the infauna living shallow to deeply within the sediment. Benthic foraminifera consist mainly of epifauna or shallow infauna components, whilst deep sediments are occupied by other benthos such as macrobenthos (producing biogenic structures at varying depths). Oxygenation, temperature and the availability and type of nutrients have a major impact, being in some cases determined by orbitally controlled atmosphere/ocean dynamics. Benthic foraminifera and trace-makers can underline these orbitally induced environmental changes, thereby serving as proxies to elucidate Milankovitch cycles. Other benthic communities, on the other hand, have scarcely been studied to this end.

Benthic foraminifera.- Apart from the isotopic analysis conducted on benthic foraminifera tests to elucidate cyclic fluctuations at the Milankovitch frequencies (*cf.* Tian *et al.*, 2008; Ridente *et al.*, 2009 for recent examples), variations in the total composition of benthic associations and in particular taxonomic groups — relative abundances, variations in size or in the planktonic:benthic ratios — have been considered in the light of Milankovitch-scale influence on the flux of organic matter, bottom-water oxygenation, temperature and substrate features, among other ecological factors. European Cretaceous rhythmic successions have been extensively studied, not always using spectral analysis. Orbitally induced cyclical fluctuations have been distinguished by changes in particular benthic groups and variations in size in the case of Cenomanian rhythmic sediments in southern England (Leary *et al.*, 1989; Leary and Hart, 1992), changes in trophic structures and the composition of benthic foraminiferal assemblages in the organic-rich Aptian-Albian Scisti a Fucoidi Formation in Central Italy (Coccioni and Galeotti, 1993; Galeotti, 1998), the relative abundance of benthic foraminifera in the Cenomanian of the Anglo-Paris Basin (Mitchell and Carr, 1998) and variations in the abundance/diversity of benthic foraminifera in the Hauterivian and Barremian of eastern England and northern Germany (Mutterlose and Rufell, 1999). Younger and older examples are comparatively scarce. Fluctuations in the abundance, diversity and species composition of benthic foraminifera, including the relative abundance of particular species commonly associated with specific environmental features have been used to form an idea of Milankovitch scale cycles in the Pliocene (Becker *et al.*, 2005) and the Quaternary (Badawi *et al.*, 2005). With regard to older materials, Rodríguez-Tovar *et al.* (2010) recently studied foraminiferal assemblages in Upper Jurassic materials from the Tethys to integrate and compare responses between the two major groups of planktonic *versus* benthic forms. In this case the parameters analysed were the relative abundances (planktonic and benthic percentages within the foraminiferal assemblage) and absolute abundances (number of foraminifera/cm^2) of the two differentiated groups. Cyclostratigraphic analysis shows differences in the spectral cycles registered between planktonic and benthic components, interpreted in terms of a variable incidence of external forcing on the environmental limiting parameters, hence on the corresponding biota. The planktonic foraminifera group appears to have been especially sensitive to obliquity-scale fluctuations at 41 kyr, related with changes affecting upper waters, mainly with regard to their temperature. The benthic component is affected overall by the precession cycle (cycles at 24, 20, and 19 kyr) and in secondary terms by short eccentricity variability (123 kyr), associated with high-frequency Milankovitch climatic variations affecting environmental parameters such as nutrient availability and substrate oxygenation at the bottom level. To refine the inferences obtained concerning the role of Milankovitch forcing in the foraminifera community, research in progress is further focused on the benthic community. Depending upon the depth within the sediment which they inhabit, three groups can be distinguished; epifaunal (living on the sediment surface and above weeds or in the topmost centimetre), shallow infaunal (living in the sediment at a depth of less than 5 cm) and potentially deep infaunal, or ubiquitous (embracing a wide range of microhabitats from epifaunal to deep infaunal) (Olóriz *et al.*, 2003, 2006; Reolid *et al.*, 2008a, b).

High-resolution cyclostratigraphic analysis of the three benthic subgroups described above would prove to be of special interest in attempts to enhance our palaeoecological characterization of benthic foraminifera and their probable differential response to environmental changes induced by Milankovitch input.

Trace fossils.- Communities colonizing the benthic environment at depth, as revealed by the trace fossil record, may reveal Milankovitch input. Alternations of bioturbated limestones and of laminated marl or calcareous claystone characterizing Atlantic-Tethyan oceanic sedimentation during the Early Cretaceous reflect fluctuations in surface productivity and in dissolved oxygen levels in bottom waters associated with Milankovitch cycles (Molinie and Ogg, 1992 and references therein). Subsequently, detailed semi-quantitative studies and spectral analyses of Cretaceous, Palaeocene and Eocene sediments have been conducted on trace fossil data (i.e., absence/occurrence of bioturbation, type of trace fossils, density and degree of bioturbation, maximum burrow diameter etc.), showing periodicities correlated with precession, obliquity and eccentricity cycles (Erba and Premoli-Silva, 1994; Sageman *et al.*, 1998; Grippo *et al.*, 2004; Poletti *et al.*, 2004; Heard *et al.*, 2008). Time-series analysis of the distribution of the trace fossil *Zoophycos* in a deep-sea piston core recovered from the north-eastern South China Sea and covering the last 425 ka, revealed Milankovitch orbital-scale cycles in short-term eccentricity, obliquity, and precessional cycle bands (Rodríguez-Tovar *et al.*, 2008, 2011). This variable Milankovitch-scale cyclicity was interpreted as underlining the complex interaction of variable processes with East Asian monsoon dynamics. Thus, monsoon variability at Milankovitch orbital-scale cycles could bear a relation to cyclical changes in the climate system determining changes in environmental conditions, including alterations in the organic material reaching the sea floor, and in turn influencing the cyclical occurrence of *Zoophycos* trace makers. Meanwhile, variations in deeply buried (sub-sea-floor) microbial populations registered in the ODP Leg 201, Site 1226, eastern equatorial Pacific (Miocene-Pleistocene) have been interpreted as being ultimately controlled by different periods of Milankovitch orbital-forcing influencing palaeoproductivity, and therefore affecting subsurface populations (Aiello and Bekins, 2010).

Applications of other benthic communities to the study of cyclic variations are comparatively scarce. In some cases the inferred relationship with orbital climatic changes at the Milankovitch-scale lacks any spectral analysis. Shallow marine mollusc species can be considered a reliable indicator of water depth, due to their limited adaptational ranges to water depth conditions, and the ensuing temporal variations in the composition of mollusc fauna can be used to register environmental changes due to sea-level fluctuations associated to marine climate. Cyclic changes registered in offshore Pleistocene benthic mollusc associations in Japan have been interpreted as the result of sea-level changes over periods of 41 kyr, corresponding to orbital-insolation obliquity cycles (Kitamura *et al.*, 1994; Kitamura, 2004). Similarly, cyclic variations in gastropod and pelecipod fossil associations in Miocene materials from Jawa (Indonesia) were related to sea-level fluctuations between non-marine, supratidal, intertidal and open-marine conditions. The authors conclude that the main cause of the cyclic variations seen in mollusc associations is that of orbitally induced climatic changes in 41-kyr Milankovitch-scale obliquity cycles (Aswan, 2006). In Cenomanian cyclic chalk-marl sediments representing Milankovitch precession forcing, variations in benthic macrofauna (bivalves, brachiopods, and echinoderms, as the dominant faunal groups, together with bryozoans, serpulids, corals, sponges, and cirripides) and community structure, between chalk and marl samples could represent a biological response to long-term climatic and oceanographic changes of Milankovitch origin (Lauridsen *et al.*, 2009).

Integrative analysis of several groups of microfossils has occasionally shed light on different responses to Milankovitch forcing. Such is the case of Weber *et al.* (2001), based on a quantitative analysis of planktonic and benthic foraminifera, calcareous nannofossils, and radiolaria in Albian sediments. The authors document the biological response to Milankovitch-scale forcing at obliquity and precession ranges in particular, and differences between planktonic and benthic foraminifer species. The extensively studied Upper Albian Amadeus Segment (central Italy) gave rise to a review by Galeotti *et al.* (2003) of proxies previously used to identify Milankovitch cycles, including micropalaeontological data such as planktonic and benthic foraminifera, calcareous nannofossils and palynomorphs.

Terrestrial environment

Milankovitch variations in climate, especially when related to changes in the growth of large terrestrial ice sheets, had a major impact on terrestrial communities of flora and fauna, showing significant changes in geographic distribution. Yet studies on the incidence of Milankovitch input on terrestrial ecosystems are comparatively scarce.

Terrestrial vegetation and Milankovitch forcing

In recent years, the incidence of climatic fluctuations associated to Milankovitch-induced input on terrestrial vegetation has been mainly reflected through high-resolution palynological analyses. Since the first papers were published reporting on the use of spectral techniques to find evidence of Milankovitch-scale forcing on pollen records from the Pleistocene (*cf.* Molfino *et al.*, 1984; Pestiaux *et al.*, 1988; Hooghiemstra *et al.*, 1993; Hooghiemstra and Melice, 1994), the influence of astronomical forcing on pollen assemblages has been recognised in pre-Pleistocene sediments, especially from Pliocene and Miocene times (i.e., Versteegh, 1994; Mommersteeg *et al.*, 1995; Santarelli *et al.*, 1998; Willis *et al.*, 1999; Popescu, 2001; Popescu *et al.*, 2006). Relative abundance between selected ecological groups (i.e. thermophilous *vs.* altitudinal elements, or thermophilous *vs.* mesothermic elements) in the pollen assemblages of lacustrine deposits from the Miocene in Hungary and Spain has shown signs of astronomically forced climate changes in the distribution of vegetation, with dominating cycles of obliquity and short-term eccentricity, which affected both temperature and precipitation (Jiménez-Moreno *et al.*, 2005, 2007). Milankovitch-scale palynological changes have likewise been recognised in older times. Orbital cycles have been identified in Cretaceous palynofacies on the basis of terrestrial palynological debris (Tribovillard and Gorin, 1991), whereas palynofacies from the Jurassic succession in France and the United Kingdom have revealed precession cycles influencing the terrestrial environment, probably via climate-controlled variations in runoff that affected terrestrial organic debris (Waterhouse, 1999). Time-series analyses of terrestrial palynomorph proxy data from the Triassic-Jurassic transition showed significant cyclic patterns in the palynomorph record, with cycles tentatively assigned to eccentricity and precession, associated in turn to variations in monsoon strength and precipitation and/or humidity (Bonis *et al.*, 2010).

Evolutionary response in terrestrial animal communities

A widely accepted recent hypothesis is that of the incidence of palaeoenvironmental changes climatically imposed upon terrestrial past-community evolution (changes in diversity, origination and extinction; *cf.* Fortelius *et al.*, 2006, Badgley *et al.*, 2008; Liow *et al.*, 2008; Eronen *et al.*, 2009; Casanovas-Vilar *et al.*, 2010 for mammal communities). Despite recognition of the impact of prolonged climatic forcing, explicit allusions to variations in terrestrial animal communities in response to environmental changes at the Milankovitch-scale are only occasionally considered. Variations in the composition of the fossil record (including snails, mammals and trace fossils) in palaeosoils in the Oligocene of central Oregon have revealed palaeoclimatic and ecosystem oscillations at the Milankovitch-scale in the order of 41-100 kyr (Retallack *et al.*, 2004). bearing in mind that ice caps did not extend across North America during the Oligocene, the registered cyclic variations have been interpreted as reflecting the amplification of weak orbital signals by greenhouse gases due to changing carbon budgets in the sea and on land (Retallack *et al.*, 2004).

More recently, however, several papers focusing on rodent assemblages have been published. As commented earlier, spectral analysis of rodent assemblages from Neogene fluvio-lacustrine sections in Spain reveals mammal speciation, featuring turnover cycles with periods of 2.4-2.5 and 1.0 Myr, related to the long-period eccentricity modulation and nodes of the 1.2 Myr obliquity cycle (van Dam *et al.*, 2006). Long-term astronomical climate forcing was one major cause of species variations in the small mammals studied. Simulations of the evolutionary response of body size to environmental changes occurring at the Milankovitch scale have been documented, affirming that below a certain seasonality threshold body size will decrease rapidly, leading to extinction (Troost *et al.*, 2009).

One fascinating new research topic is the analysis of human responses to climate changes over long timescales — once again Milankovitch scales — at a regional to continental scale. Palaeoseasonality in Equatorial Africa during hominid evolution can be recognised at an orbital scale as having significant effects on early hominid evolution due to its incidence on primate foraging and ranging (Kingston, 2005). Diversifications in the hominid lineage during the Plio-Pleistocene were related to changes in African climate between markedly wetter and drier conditions, induced by the Earth´s orbital variations of precession, obliquity and eccentricity (deMenocal 2004; Campisano 2012).

From glacial to interglacial cycles, the analysis of human migration, dispersion and colonization poses a challenge for future research. The spreading of hominins within Europe in the Early Pleistocene and its colonization in the Mid Pleistocene; the expansion of Acheulean from the Levant to western Europe and India after 600 ka; and the response of hominin populations to Milankovitch-length climatic changes during the Middle Pleistocene, are all highly appealing research topics (Dennell, 2008).

Conclusions

The fossil record holds high potential for providing credible evidence for Milankovitch Band cycles (precession, obliquity and eccentricity). This affirmation is founded on the incidence of orbitally induced palaeoenvironmental impact on marine and terrestrial environments and their inhabiting communities. The evolutionary response of palaeocommunities to orbital-scale palaeoenvironmental changes is still however a controversial topic, probably because of limitations imposed by time resolution of the fossil record and the absence of absolute time scales. While the disruption of communities has long been recognised, other complex evolutionary responses —stasis, speciation, extinction — are only now coming under the spotlight of research efforts. Milankovitch cycles have been mainly characterized in marine palaeocommunities, especially on microfossils, rather than terrestrial biota.

The marine environment reflects variations at the community level (abundance, composition, diversity), and in certain taxa these are related to orbitally induced changes in palaeoenvironmental parameters, such as nutrient availability, oxygenation, temperature, salinity, oceanographic dynamics and water masses. Extensive information from the planktonic environment (e.g. foraminifera, radiolaria and nannofossils) contrasts with the relatively scarce data from the benthic habitat (benthic foraminifera and trace fossils). Marine examples from Cretaceous successions overshadow other pre-Quaternary intervals.

Cyclostratigraphic analyses at the Milankovitch Band from terrestrial palaeocommunities are relatively scarce and mainly conducted on Pliocene-Miocene pollen assemblages. Astronomical forced climate changes affecting temperature and precipitation are known to determine variations in the distribution of terrestrial vegetation yet few papers have analysed the incidence of Milankovitch palaeoenvironmental changes on the evolution (diversity, origination and extinction) of the terrestrial animal community or the effect of the Earth´s orbital climatic variations on hominid populations (migration, dispersion and colonization).

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