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Commentary

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Palaeoclimates and Amazon biodiversity

The role of major environmental drivers such as Pleistocene climatic changes (i.e. glacial–interglacial cycles) and pre-Pleistocene palaeogeographical rearrangements (closure of the Panama Isthmus, Andean orogeny, drainage shifts, marine incursions, etc.) on the origin of extant Neotropical biodiversity is still controversial. Beyond the traditional proposals of ecological theory on the origin of latitudinal diversity gradients (environmental stability, niche differentiation, area, energy availability, intensity of biotic interactions), the issue has been addressed from an empirical perspective using palaeoecological and DNA phylogenetic evidence. The solution is not straightforward, as shown by recent meta-analyses on dated DNA phylogenies that favour a complex scenario of environmental drivers acting synergistically at different spatial (local to regional) and temporal (Neogene to Quaternary) scales (Rull, 2008; Turchetto-Zolet *et al.*, 2013). An important caveat of these studies is that patterns and processes derived from individual case studies, as for example one or few taxonomic groups or geographical regions, cannot be extrapolated to the whole Neotropics.

A recent palaeoclimatic reconstruction of the last glacial cycles (250,000 years to present), based on oxygen isotopic records from speleothems as a proxy for precipitation changes through time, revealed a significant time–space variability of precipitation patterns across the Amazon Basin (Cheng *et al.*, 2013). This reconstruction is a landmark in Neotropical palaeoeclimatology, as it provides a sub-millennial record of the last 250,000 years and documents the high palaeoenvironmental heterogeneity of the Amazon Basin during this time. In particular, these authors found significant differences in precipitation amounts and distribution between western (wetter) and eastern (drier) Amazonia owing to differential effects of the South American monsoon (SAM) circulation and the El Niño–Southern Oscillation (ENSO), and called this phenomenon the South American Precipitation Dipole (SAPD). Cheng *et al.* (2013) also discuss the implications of their palaeoclimatic records for the origins of biodiversity from the perspective of climatic stability versus instability. According to their results, eastern Amazonia underwent significant precipitation shifts during the last two glacial–interglacial cycles, whereas the western side of the basin has remained fairly stable since about 250,000 years. Using this scheme as a model for the Pleistocene glacial cycles, the authors combine the SAPD asymmetry with an alleged west–east diversity gradient and suggest that their data favour the stability hypothesis for diversification, whereas climatic instability would have promoted loss rather than gain in biodiversity. The influence of Pleistocene climatic instability on Neotropical diversification is supported by ample empirical evidence but the case seems not to be as simple as Cheng *et al.* (2013) propose, and deserves further consideration. Here, I discuss this issue on the basis of three main points: (1) the last glacial as a general model for Pleistocene glaciations, (2) the west–east biodiversity gradient, and (3) the climatic stability as a diversity driver.

Concerning the first point, studies on marine cores have documented the existence of *c.* 40 climatic shifts of glacial magnitude during the Pleistocene. These cycles have been driven by Earth's orbital variations of a 40,000-year period until about 800,000 years ago, when the periodicity changed to 100,000 years (Lisiecki & Raymo, 2005). Moreover, high-resolution palaeoclimatic reconstructions on polar ice cores have shown significant differences in timing, rates and intensity of climatic shifts for the last eight cycles (EPICA Community, 2004). In addition, it is uncertain whether the same spatial precipitation patterns in Amazonia for the last glaciation can be extended to all Pleistocene glacial phases. Even in the case that the west–east precipitation gradient was more or less constant, its strength and local manifestations may have varied. Palaeoecological data suggest that, while temperature shifts would have been of regional extent in the Neotropics, precipitation patterns may have been largely controlled by more local factors. As a consequence, it seems too risky to use the last glacial cycles alone to represent the whole Pleistocene variability, either in time trends or in spatial patterns.

Second, the assumed west–east biodiversity gradient in Amazonia is based on selected evidence from some particular groups of plants and animals (Hoorn *et al.*, 2010) and, as mentioned before, extrapolations on this subject are still premature. Also, previous studies have shown that different organism groups have contrasting spatial patterns and evolutionary histories that cannot be generalized (Rull, 2008; Hoorn *et al.*, 2010; Turchetto-Zolet *et al.*, 2013). Moreover, in a huge (*c.* 7 million km^2), diverse and comparatively unexplored region such as the Amazon Basin (of similar size to Europe), heterogeneities in sampling effort are highly relevant, precluding a sound appraisal of spatial biodiversity patterns, thereby introducing an additional methodological bias (Nelson *et al.*, 1990).

Third, the argument that climatic instability may have triggered biodiversity loss rather than promoting diversification ignores abundant palaeoecological evidence supporting a close connection between palaeoclimatic variability and diversification, not only during the Pleistocene but also across the geological time-scale (Erwin, 2009). This is manifest in the Neotropics and also in other tropical regions world-wide (Bush *et al.*, 2011). Cheng *et al.* (2013) mentioned the refuge hypothesis (RH) – i.e. the recurrent alternation of rain forest fragmentation during arid glacials, fostering vicariance and endemism, and forest coalescence during wet interglacials, promoting gene flow – as a possible scenario for eastern Amazonia. Contrary to the predictions of this hypothesis, which was originally proposed to explain the high Neotropical diversity, these authors considered the RH as a means of biotic impoverishment; however, the potential mechanism for this to have occurred is not specified. In addition, the RH has been seriously questioned in the Neotropics by recent palaeoecological and genetic evidence. This does not mean, however, that Pleistocene diversification should be dismissed, as a number of alternative mechanisms (e.g. disturbance-vicariance hypothesis, river hypothesis, gradient hypothesis, canopy-density hypothesis, edaphic hypothesis, etc.) have been proposed and, in several cases, tested with appropriate evidence (Nores, 1999; Haffer, 2008; Rull, 2011).

In spite of these considerations, the palaeoclimatic records of Cheng *et al.* (2013) are indeed able to render new insights on the issue of Neotropical diversification under Pleistocene climatic forcing. On the one hand, these high-resolution reconstructions stress the occurrence of complex patterns of millennial and orbital-scale variability. Particularly interesting is the finding of abrupt millennial-scale oscillations such as the Younger Dryas, the Dansgaard–Oeschger cycles and several Heinrich events, which are in phase with other Southern Hemisphere records and out of phase with their Neotropical Northern Hemisphere counterparts (including northen Amazonia). Hence, the big picture for the Amazon Basin as a whole, during the last glacial cycles, is a complex scenario of superimposed climatic shifts of different durations, coupled with high spatial precipitation variability, not only from east to west but also from north to south. This, together with the evidence for biotic elevational migrations of *c*. 1000 m as a response to glacial–interglacial temperature shifts of about 5 ºC (Liu & Colinvaux, 1985), the highly dynamic nature of drainage patterns, as well as the geomorphological, physiographical and edaphic heterogeneity of Amazonia, suggest a highly complex scenario in both space and time. In such a framework, biotic diversification is likely to be the result of complex interactions and feedbacks among multiple environmental drivers acting together at different scales.

In summary, the novel and sound palaeoclimatic evidence provided by Cheng *et al.* (2013) supports a complex diversification scenario, rather than a more simplistic stability versus instability framework. In fact, these palaeoclimatic reconstructions show that, despite manifest regional differences, neither eastern nor western Amazonia has been climatically stable during the time interval studied. More similar studies are needed to extend the records back in time, in order to unravel the palaeoclimatic trends for older glacial and interglacial periods. It is hoped that the current bourgeoning of DNA phylogenetic studies will furnish the necessary speciation chronologies to be compared with palaeoenvironmental records.

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