Cycad diversification and tropical biodiversity

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Editor: J. López-Pujol

Received 29 February 2012; Accepted 30 April 2012

Abstract

Cycad diversification and tropical biodiversity.— The recent unexpected discovery that living Cycadales are not Jurassic-Cretaceous (200–65 Mya) relicts, as all their extant genera began to diversify during the Late Miocene (12 Mya), has challenged a classical evolutionary myth. This brief note shows how this finding may also provide new clues on the shaping of the high tropical biodiversity.

Key words: climatic change; Cycadales; latitudinal diversity gradients; paleobiogeography; speciation timing.

The ongoing debate regarding the origin of biodiversity patterns on Earth (Hoorn et al., 2010, 2011; Rull, 2011a) may benefit significantly from the latest discovery that extant cycads (Cycadales), traditionally considered as living plant fossils, are remarkably younger than previously expected (Nagalingum et al., 2011). The cycads emerged in the Permian, around 270 million years ago (Mya), and are now represented by approximately 300 extant species of pantropical distribution, with some subtropical representatives (Fig. 1). The cycads have been considered the ancestors of the flowering plants, and are thought to have attained most of their diversity during the Jurassic-Cretaceous (200–65 Mya). However, a molecular phylogenetic study of approximately 200 species recently published by Nagalingum et al. (2011) concludes that extant cycad species originated during the last 12 Myr, thus challenging the former view. The evolutionary significance of these results has been highlighted, particularly in terms of morphological stasis, competition with angiosperms, and plant–animal coevolution (Nagalingum et al., 2011; Renner, 2011). Thus far, the emphasis has been placed on the unexpectedly recent initial diversification events.
within each genera and their striking synchrony, but a detailed analysis of the age of origin of individual species reveals interesting clues for the understanding of the origin of tropical biodiversity, as shown in this paper.

A variety of ecological and evolutionary mechanisms have been proposed to explain Earth’s latitudinal diversity gradients (Mittelbach et al., 2007) but the ultimate cause for natural selection relies on environmental factors or “agents of selection” (MacColl, 2011). The high level of tropical diversity, especially in the Neotropics, has been a favorite topic since the times of Humboldt and Darwin. Continental drift ruled by plate tectonics has been acknowledged as a fundamental evolutionary agent leading to the waxing and waning of migration barriers and pathways and determining new chances for vicariance or gene flow, as well as for colonization opportunities on newly created mountain and island habitats. Climate changes are thought to have shaped similar evolutionary outcomes via such changes as altitudinal, latitudinal, and sea-level shifts (Rull, 2011b).

The recent development of molecular dating techniques has revitalized the controversy between the defenders of either Quaternary (the last 2.6 Myr) climatic changes or Neogene (the period between 23.0 and 2.6 Mya, comprising the Miocene and the Pliocene, with a boundary of 5.3 Mya) tectonically driven paleogeographic reorganizations as speciation agents. Comprehensive surveys, however, favor a complex interaction of these agents on different spatial and temporal scales (Rull, 2008). The study by Nagalingum et al. (2011) shows that the diversification within the extant cycad genera (or the crown diversification) occurred during the Late Miocene—between approximately 10 and 5 Mya—, with the exception of Ceratozamia Brongn., whose diversification initiated in the Pliocene. Therefore, crown dating suggests that Neogene speciation agents would have been important in the initial diversification of extant cycads.

Nagalingum et al. (2011) performed species dating as well, thus allowing a more careful examination of the complexity of speciation trends. However, these data have not yet been exploited to their full potential. Globally, 26 (13.2%) of the extant cycad species studied originated in the Late Miocene, 98 (49.8%) originated in the Pliocene and 67 (34.0%) originated in the Pleistocene; in other words, more than a tenth of living cycad species originated after 12 Mya, almost the half originated after 5 Mya, and more than a third are less than 2.6 million years old (Fig. 2). Among the genera, Pliocene species dominate in Encephalartos Lehm. (32 sp., 60.4%), Cycas L. (38 sp., 59.4%) and Mac-
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rozamia Miq. (14 sp., 56.0%), whereas Pleistocene species predominate in Zamia L. (24 sp., 68.6%) and Ceratozamia (67 sp., 40.0%). Late Miocene speciation is not dominant but is significant in Encephalartos (11 sp., 20.8%) and Cycas (10 sp., 15.6%), whereas Pleistocene speciation is also important in these two genera (10 sp., 18.9% and 14 sp., 21.9%, respectively) and in Macrozamia (9 sp., 36.0%). From a biogeographical perspective, Pliocene speciation dominates in Africa (32 sp., 60.4%) and Australasia (52 sp., 57.1%), whereas Pleistocene speciation prevails in the Neotropics (34 sp., 64.2%). Conversely, Miocene speciation is comparatively low, averaging ~13% in the three regions. Of note, approximately two thirds of living neotropical cycad species originated in the Pleistocene, whereas approximately one quarter are of Pliocene origin (only ~5% emerged during the Miocene).

In summary, the conclusion of Nagalingum et al. (2011) that extant cycad diversity originated since the Late Miocene can be further pushed by a detailed analysis of their own data at species level, which shows that more than 80% of these species are even more recent and have originated during the Pliocene (< 5 Mya) and the Pleistocene (< 2.6 Mya). These a priori unexpectedly high rates of Pliocene and Pleistocene diversification have been explained in terms of climate, as a consequence of: (1) changes in general circulation patterns, due to the attainment of a paleogeographic configuration similar to the present, which developed in more seasonal climates, and (2) a significant global cooling that initiated around the Mio-Pliocene (~5 Mya) and led to Pleistocene glaciations (Nagalingum et al., 2011; Renner, 2011).

Hence, there is more than the end of a classical evolutionary myth in the findings of Nagalingum et al. (2011). They also show that, even in a lineage as old as the cycads, most of the extant tropical biodiversity has been originated after ~5 Mya, when climate changes have been the norm. It is particularly striking the large proportion of species emerged during the Pleistocene (especially in the Neotropics), when glacial-interglacial cycles have been the dominant environmental forcing. Most arguments denying Quaternary speciation and favoring Neogene diversification are based on

Figure 2. Histogram showing the number of extant cycad species originated since the Late Miocene to the Pleistocene, based on the raw data from Nagalingum et al. (2011). Only genera with more than one species studied are included.
crown dating alone (Hoorn et al., 2010; Wesselingh et al., 2010). The case of cycads reinforces the view that both crown and individual species dating are needed to unravel the complexity of diversification, both in the tropics and in extratropical regions (Rull, 2011b). Indeed, molecular phylogenetic evidence on Pleistocene speciation in relation to climate shifts is growing elsewhere (e.g. Weir & Schluter, 2007; Janssens et al., 2009; Valente et al., 2010; Mullen et al., 2011). The role of the different speciation agents in the shaping of present-day biodiversity patterns should be addressed taking into account that biodiversity is made of species and sub-specific clades, and any study on this subject should be based on specific and sub-specific categories rather than on genera and other supra-specific taxa (Rull, 2012).

ACKNOWLEDGEMENTS

Funding has been provided by projects CGL2009-07069/BOS (Ministry of Science and Innovation) and BIOCON 08-031 (BBVA Foundation).

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