biology letters

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Biol. Lett. 2007 **3**, 566-569
doi: 10.1098/rsbl.2007.0287

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Biol. Lett. (2007) **3**, 566–569
doi:10.1098/rsbl.2007.0287
Published online 7 August 2007

Phylogeny

Steady diversification of derived liverworts under Tertiary climatic fluctuations

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Tropical forests contain the majority of extant plant diversity and their role as a cradle and/or museum of biodiversity is an important issue in our attempts to assess the long-term consequences of global climate change for terrestrial biomes. Highly diverse groups of liverworts are an often ignored but extremely common element in rainforests, and thus their evolution may shed light on the ecological robustness of rainforest biomes to climate fluctuations. We record a remarkable constant accumulation of diversity through time for the most species-rich family of liverworts, Lejeuneaceae, inferred by divergence time estimates. The observed pattern supports the recently developed concept of a dual role of the tropics as both a museum and a cradle of biodiversity.

Keywords: divergence time estimates; Lejeuneaceae; liverworts

1. INTRODUCTION

The current biodiversity crisis, especially in relation to the array of anthropogenic threats to the highly diverse tropical forests, has enhanced our general interest in the role of the tropics in the maintenance and recovery of biodiversity (Pimm *et al.* 1995; Laurance 2007). Detailed knowledge about these processes may enable us to develop models to predict the response of biodiversity to global warming (Jablonski *et al.* 2006; Marshall 2006). The tropics are often interpreted as either museums or cradles of biodiversity (Stebbins 1974), but their contribution may be more dynamic. A dual function as both a museum and a cradle of biodiversity may be the more suitable scenario for most organisms (Jablonski *et al.* 2006; Marshall 2006; McKenna & Farell 2006).

Traditionally, the inference of macroevolutionary patterns relied mainly on the fossil record to infer the origin and extinction of lineages through time. This restricted such studies to organisms with a good fossil record and excluded lineages with poor to nearly absent fossil records, such as many land plant lineages. Liverworts are occasionally well preserved as amber inclusions, but adequate conditions for their preservation in the fossil record have occurred only sporadically in time and space (Grolle & Meister 2004). Recent advancements in bioinformatics and molecular biology now allow us to explore the macroevolution of these lineages using DNA sequence data to estimate divergence times (Kumar 2005). Divergence time estimates are widely used to explore macroevolutionary patterns and processes, e.g. the coinciding diversification of ferns and angiosperms (Schneider *et al.* 2004), and global patterns of major animal and plant lineages (Brady *et al.* 2006; Danforth *et al.* 2006; Hughes *et al.* 2006; Moreau *et al.* 2006; Roelants *et al.* 2007). These studies offer important new insights, which are not possible using the fossil record alone.

These achievements motivated us to investigate the role of the tropics in the sustainability of biodiversity under the pressure of global climate change. Recent studies reported divergent interpretations of the high tropical diversity including evidence for faster evolution (Wright *et al.* 2006) and gradual accumulation of diversity (Bramley *et al.* 2004; McKenna & Farell 2006). Here, we infer the diversification pattern of a plant lineage with an arbitrarily distributed fossil record. Lejeuneaceae is the most species-rich family of liverworts and not only forms a particularly important component of the cryptogamic flora of tropical lowland forests, but also contributes substantially to the temperate liverwort flora (Gradstein 1993). Hence these liverworts are ideal candidates for inferring the origin of tropical diversity and their contribution to the non-tropical diversity. Recent studies have revealed their relationship to other liverworts as well as the relationships among the majority of genera within Lejeuneaceae (Wilson *et al.* 2007). Divergence time estimates have also shown that Lejeuneaceae started to diversify no earlier than the Mid-Cretaceous (Newton *et al.* 2006; Heinrichs *et al.* 2007); therefore, they are a further example of a seed-free land plant lineage diversifying in the shadow of angiosperms (Schneider *et al.* 2004). The biology of these taxa also provides an exceptional opportunity to compare the museum with the cradle hypothesis. These liverworts are generally good long-distance dispersers and their diversification pattern is probably little influenced by local-scale events (Schuster 1983). This renders them more capable of colonizing new habitats in times of climate change, where regions with a previously cooler climate become warmer.

2. MATERIAL AND METHODS

The dataset comprising 135 species and four genomic regions (*rbc*L/*psb*A/*trn*L-F/nrITS; 3773 aligned nucleotides) was generated and handled as described in our published exhaustive phylogenetic study on Lejeuneaceae (Wilson *et al.* 2007). Divergence time estimates were calculated employing a penalized likelihood approach using phylogenetic hypotheses generated in a Bayesian inference of phylogeny as described by Schneider *et al.* (2004). Lineage-through-time plots were generated for the whole Lejeuneaceae clade and major clades for 100 MCMC-based chronograms or the consensus chronogram.

3. RESULTS

Divergence time estimates provide evidence for a relatively rapid establishment of the major lineages in the Cretaceous (figure 1, nodes 7, 6, 10 and 14), but

Electronic supplementary material is available at http://dx.doi.org/10.1098/rsbl.2007.0287 or via http://www.journals.royalsoc.ac.uk.

Received 31 May 2007
Accepted 5 July 2007

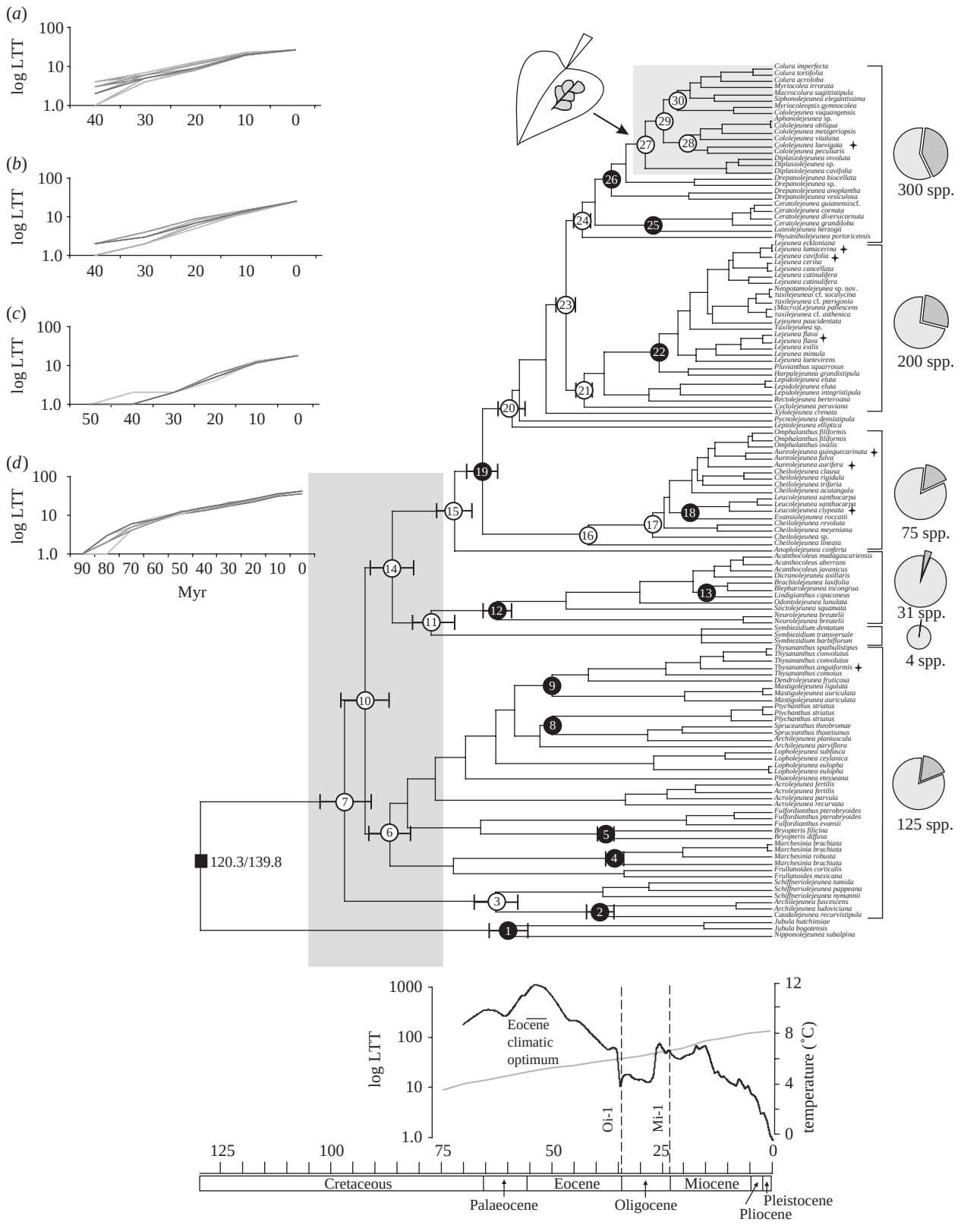

Figure 1. Phylogenetic chronogram for Lejeuneaceae plotted against geological time scale (Gradstein *et al.* 2004), using mean calibration point age of 130.1 Ma (Heinrichs *et al.* 2007). Ages for selected nodes (numbered) are given in the electronic supplementary material. Nodes with minimum age fossil constraints are indicated by black circles. Bars at nodes indicate age difference when using minimum and maximum fossil calibration points (120.3/139.8 Ma, respectively). Where no bar is present, difference is negligible. Shaded area at base of tree highlights initial diversification event. Shaded area at node 27 indicates the presence of epiphylly. Pie charts represent the proportion of extant Lejeuneaceae species in each clade. Taxa marked with + indicate temperate species. An averaged record of sea-surface temperatures (Zachos *et al.* 2001), a proxy for global climate, is presented against the geological time scale. Timing of Miocene (Mi-1) and Oligocene (Oi-1) glaciations and the Eocene climatic optimum are marked on the temperature curve. A mean lineage-through-time (LTT) plot is shown with the temperature curve. LTT plots of 25 randomly selected Bayesian inference trees are shown for nodes (*a*) 24, (*b*) 21, (*c*) 16 and (*d*) 6.

the majority of observed lineage establishments occurred during the Tertiary. Node 6 (figure 1), in particular, shows a more or less constant rate of separating lineages through the Tertiary. Lineage-through-time plots indicate a nearly constant rate of origin and extinction of lineages during the Tertiary. Net diversification rates do not vary substantially during this period (e.g. node 16, 0.0212; node 21, 0.0215; node 24, 0.0213). This is remarkable since neither the Eocene maximum temperature peak nor the Oligocene glaciations had a strong influence on the rate of origin and extinction of Lejeuneaceae. These patterns were also observed when selected lineages were studied separately. We did not find any evidence for an increased diversification rate for any particular clade, including the derived clade (figure 1, node 24), which includes plants with an epiphyllous habit (growth on living leaves), suggestive of a faster generation time (Gradstein *et al.* 2006). The taxon sampling, however, is most likely insufficient to infer the rates of clades that diversified after the Late Miocene. This limitation does not apply to the global pattern where a more or less constant rate of diversification was documented. The majority of lineages included in the chronogram occur predominantly to exclusively in the tropics and hence the data support the museum hypothesis. Temperate taxa originated from several independent colonizations as indicated by their distribution in the phylogeny and not from independent radiations into temperate regions. This pattern supports the tropics as the cradle of the current temperate Lejeuneaceae diversity.

4. DISCUSSION

The rapid divergence of the extant lineages of Lejeuneaceae in the Late Cretaceous is remarkable since the reconstructed phylogeny would indicate a long, static period throughout the Early Cretaceous. In addition, the sister clade of Lejeuneaceae (approx. 750 spp.), the Jubulaceae (approx. 6 spp.), is much less species rich. This pattern may fit a scenario of a rapid rise triggered by the rise of angiosperms (Schuster 1983; Heinrichs *et al.* 2007), reminiscent of the diversification of derived ferns (Schneider *et al.* 2004). However, alternative hypotheses involving extinction of ancestral sister lineages in the Late Cretaceous or at the Cretaceous–Tertiary boundary have to be considered. Similar patterns of diversification were documented for birds and mammals (Penny & Philips 2004; Brady *et al.* 2006). The coincidence of several independent diversifications of unrelated lineages combined with the putative replacement of more ancestral lineages leads to the hypothesis that the Middle and Late Cretaceous was a time of major reorganization of terrestrial habitats and underlying ecological networks (Schneider *et al.* 2004). Our results add evidence to previous reports of decoupling of diversity accumulation of plants and insects in the Early Tertiary (Wilf *et al.* 2006).

Observed static net divergence rates throughout the Cenozoic are very much in contrast to the pattern observed in the Cretaceous. Climatic fluctuations, such as the maximum temperature peaks in the Eocene and major global cooling in the Oligocene, appear to have had very limited influence on the net divergence rate in Lejeuneaceae. The lack of correlation with climate change is in contrast with divergence time estimates reported for some plant lineages, where dramatic fluctuations during the Miocene and Pleistocene correlate well with speciation (Won & Renner 2006). However, the net divergence rate is the composite of speciation and extinction rates, and therefore a constant net rate may result from a strong correlation between these two rates. In addition, some clades may have been more diverse in the past but were subsequently replaced by members of sister clades that diversified in later periods of the Cenozoic. The replacement of species by close relatives from the same genera or family where similar ecologies already exist is thought to be a significant contribution to the persistence and stability of plant communities over significant time periods (DiMichele & Philips 1996; Valiente *et al.* 2006).

In conclusion, the tropics appear to have constantly accumulated diversity within Lejeuneaceae throughout the Cenozoic, as suggested by the museum hypothesis. They are also the cradle for extant temperate Lejeuneaceae species since all temperate species are nested in clades comprising mainly tropical species. This is the first example of land plants demonstrating robustness of diversity in times of major climate fluctuations. The broad ecological range of most Lejeuneaceae species may be the cause for the observed stability. However, as shown by the pattern for the Cretaceous, the diversity of these plants may change drastically if the general structure of tropical terrestrial habitats is substantially modified.

This study was supported by DFG grants. We thank R. Grolle for discussions and B. Press, J. Vogel, A. Schmidt and an anonymous reviewer for their comments.

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