Macroevolutionary processes shaping monocots diversity: the new era of phylogenetics

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How phylogenetic studies allow to test hypotheses about evolutionary history of organisms?

Zuckerland and Pauling (1965): “[...] we first have to determine to what extent the phylogenetic tree derived from molecular data in independence from the results of organismal biology coincides with the phylogeny constructed on the basis of organismal biology. If the two trees are in agreement (topology and branching events), the best available proof of the reality of macro-evolution would be furnished!”
Evolutionary processes

- biogeographical diversification (island biogeography)
- adaptive radiation (Caribbean anoles, African cichlids)
- diversity-dependent diversification (niche filling)
- tempo and mode of environmental pressures (ecological filtering…)
- key innovations (deceptive orchids)
All those could be identified and quantified using phylogenetic trees by:

• ancestral ecology (habitat, soil/water requirements that need to be recorded systematically) reconstructions

• molecular dating (fossil records)

• biogeographical optimizations (species distribution coding)

• tests of diversification models (birth-death, diversity-dependent…)

• Complete species-level sampling!!
Complete taxonomical species-level sampling

A taxonomical group (genus, tribe, order...) of 5 species

60% sampling

100% sampling

Time in Mya
DNA barcoding:

- identifying specimens
- conservation (i.e. biodiversity monitoring, habitat protection etc)
- forensics
- international trade regulation
- food security
• The onset of DNA Barcoding led to a rapid increase of DNA sequencing at population, species and genus levels

• DNA Barcoding is a sequencing effort towards comprehensive species sampling
Simpson’s view on radiations (1944): Entering an ecological opportunity triggers a radiation

Examples: Ericaceae and *Lupinus* radiations triggered by orogenies (Drummond et al., 2012; Schwery et al., 2015)
The paradigm of temporal progression of radiations

Density-dependent radiation due to niche conservatism: Bounded diversification

Example: Caribbean anolids (Rabosky and Glor, 2010)
The paradigm of temporal progression of radiations

Radiation in the absence of niche conservatism: Unbounded diversification

Examples: Neotropical honeycreepers (Derryberry et al., 2011), African catfishes (Day et al., 2013)
The Cape Floristic Region

- ~ 90,000 km$^2$
- ~ 9,000 species
- Species richness result from a limited number of radiations (Linder, 2003)

- Old Paleogene cape fold mountains
- Miocene-Pliocene uplift exposed coastal plains
- Increase in seasonality with the onset of the winter rainfall in the late Miocene
The case of African Restionaceae

- Monophyletic Restionoideae (340 sp.)
- Dominant in fynbos vegetation
- Coastal plains to high mountain peaks, wetlands to well-drained soils
- Part of the evolving fynbos vegetation throughout the Cenozoic

Hypotheses:

- Any shifts in diversification rates of Restios during the middle-late Miocene?
- Faster rates in different habitats?
- Niche conservatism?
Methods

• 335 Restios species (98% of total species number) using 5 chloroplast markers: time-calibrated phylogeny

• Selection of best diversification model for African Restionaceae: TESS (Höhna et al., 2016)


Rouget et al. (2003)
Results

- Unbounded pattern of species proliferation: constant birth-death model

- Evolutionary model for habitat preferences is kappa model (kappa~0): transitions are related to the number of speciation events

<table>
<thead>
<tr>
<th>Models</th>
<th>-(InL)</th>
<th>AICc</th>
<th>Bayes Factor</th>
<th>Significance</th>
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<tr>
<td>Kappa</td>
<td>304.84 (299.50-310.90)</td>
<td>636.86 (626.18-648.98)</td>
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<td>Lambda</td>
<td>311.66 (303.61-345.66)</td>
<td>650.49 (634.39-690.15)</td>
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<td>Delta</td>
<td>318.88 (309.90-331.03)</td>
<td>664.42 (642.78-685.07)</td>
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<tr>
<td>None</td>
<td>320.32 (311.26-331.93)</td>
<td>665.66 (647.52-688.86)</td>
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<td>EB</td>
<td>351.11 (339.66-359.54)</td>
<td>729.44 (710.32-752.65)</td>
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</tbody>
</table>
Results

- Ancestral habitats are montane wetlands and/or drylands

- First origin of coastal lineages in the early-middle Miocene (~20-15 Ma)

- Frequent transitions: 69% from Montane drylands to Montane and Coastal wetlands
Discussion

• Absence of a density dependent (DD) radiation in restios: is it unusual for the Cape flora?

    DD reports: *Tetraria* (Slingsby et al. 2014), *Protea* (Hoffmann et al. 2015; Valente et al. 2010), *Stoebe* (Asteraceae), *Moraea* (Iridaceae), and *Satyrium* (Orchidaceae) (Hoffmann et al. 2015)

• Presence of unbounded patterns:

    Richness of 19 Cape lineages scaled with age of the lineages, suggesting no DD (Valente and Vargas 2013)

• Habitat transitions are followed by small radiations, that result from allopatric speciation through ecological differentiation

• **Further questions:**
  - Role of long-term stability of the CFR?
  - How common this process in other biodiversity hotspots?
The case of Danthonioideae (Poaceae)

- Dominant in temperate open systems of Southern continents (~300 sp.)
- Spatial variation in species richness among continents

Linder et al. (2014) Journal of Biogeography
• Parallel radiations in Africa (*Pentameris*) and Australia/New Zealand/South America (*Rytidosperma*) at the Miocene/Pliocene transition: increase in seasonality and aridification (decrease of the canopy, increase in fire regimes…etc)

• Miocene/Pliocene transition: increase in seasonality and aridification (decrease of the canopy, increase in fire regimes…etc)

• Diversity-dependent diversification for both radiations: DDD 3.3 (Etienne et al., 2012)

• 90% species sampling
Traits potentially linked to the radiations

- Orthophyll
- Sclerophyll

- ~ 100 characters scored (transverse, adaxial and abaxial surfaces)
- Non-metric multidimensional scaling (NTSYSpc)
- Ordination axes were used to score the species for the degree of sclerenchyma.

| Plant height (mm) | Degree of sclerophylly | Orthophyll | Sclerophyll |
Pentameris

Rytidosperma

B

0.00 6.10 12.21 18.31 24.42

-1.0 -0.5 0.0 0.5

phenotype

C

T

ran

0.00 0.2 0.4 0.6 0.8 1.0

05 1 0 1 5 2 0 2 5

density.default(x = data$theta1)

N = 100   Bandwidth = 0.004992

Density

phenotype

Density

A

Time (Ma)

C

D

Tr

ran

0.00 0.2 0.4 0.6 0.8 1.0

05 1 0 1 5 2 0 2 5

Schismus

Dendrobaena

Blattaria

Collembola

Nematoda

Pseudoschizaphis

Schizaphis

Chironomus

Diptera

Trichoptera

Lepidoptera

Hymenoptera

Siphonaptera

Mammalia

Aves

Reptilia

Amphibia

Chordata

Protista

Fungi

Archaea

Bacteria

Eukarya

Eukarya
• The drying trend throughout the Miocene and early Pliocene may have been of the cause of the two simultaneous radiations in Africa and Australia/South America; at least for *Rytidosperma*, there was an evolutionary pathway towards short life cycle (small height and orthophylly).

• More traits are needed (in progress) to confidently identify the causalities of these two evolutionary radiations.
Conclusions

- DNA barcoding helped and is helping achieving comprehensive species-level phylogenetic frameworks, that are crucial for understanding the evolution histories of living organisms

- The development of analytical tools (computing packages, algorithms…) that now allow to analyze large datasets and implement complex evolutionary models

- A new era in phylogenetics is emerging thanks to the (rapid) accumulation of molecular data and the increasing statistical power of phylogenetic comparative methods

- Even though DNA barcoding was developed primarily for conservation and management, it provides a great opportunity for evolutionary biologists to test and develop biological concepts
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Thanks for your attention....