Does Forest Promote Terrestrialisation of Life History Strategies in East African Amphibians?

H. Christoph Liedtke[1], Hendrik Müller[2], Michele Menegon[3], Jan Beck[1], Liliana Ballesteros[1], Peter Nagel[1] and Simon P. Loader[1]

[1]University of Basel, Dept. of Environmental Sciences (Biogeography), Klingelbergstrasse 27, CH-4056 Basel, Switzerland [2]Institute of Systematic Zoology and Evolutionary Biology with Phyletic Museum, Friedrich-Schiller-University Jena, Erbertstrasse 1, 07743 Jena, Germany [3]Tropical Biodiversity Section, Tridentine Museum of Natural Sciences, Via Calepina 14, I–38100 Trento, Italy

Introduction

Terrestrialisation of breeding biology has occured at multiple times across the amphibian tree of life, though it is unclear what causal mechanisms are linked to this. Predation and habitat have been proposed as driving factors and while the influence of predation has been repeatedly investigated, abiotic pressures have largely been ignored. Poynton (1964) suggested that the humid, sylvicolous environments such as montane forests enable the evolution of terrestrialisation by protecting eggs from dessication and creating a multitude of sheltered microhabitats for egg deposition and larval development. Due to their species richness and diverse habitats, the Eastern Arc Mountains (EAM) and adjacent Tanzanian coastal lowlands (Figure 1) provide a suitable study area for investigating correlations of habitat with the evolution of terrestrialisation in amphibian breeding strategies.

Methods

TAXA SAMPLING Our dataset comprised 180 amphibian species showing 3 breeding strategies: complete aquatic, semi-terrestrial (terrestrial eggs, aquatic larvae) and complete terrestrial development, distributed across 4 habitats: montane grasslands, montane forest, coastal lowland forest and coastal lowland others (savanna, grassland or shrubland) following the IUCN Red List habitat categories with modifications based on Poynton (2000).
PHYLOGENY A genus level phylogeny was reconstructed based on 16S and RAG1 genes of 33 ingroup taxa. All other taxa were added as polytomies.
COMPARATIVE ANALYSIS A phylogentic Generalized Least Squares (pGLS) model correcting for phylogenetic non-independence, tested the effect of different habitats on breeding strategy. The DESCRETE module in BayesTraits was used to uncover differences in correlated evolution of habitat and terrestrial egg-laying and habitat and terrestrial larval development.

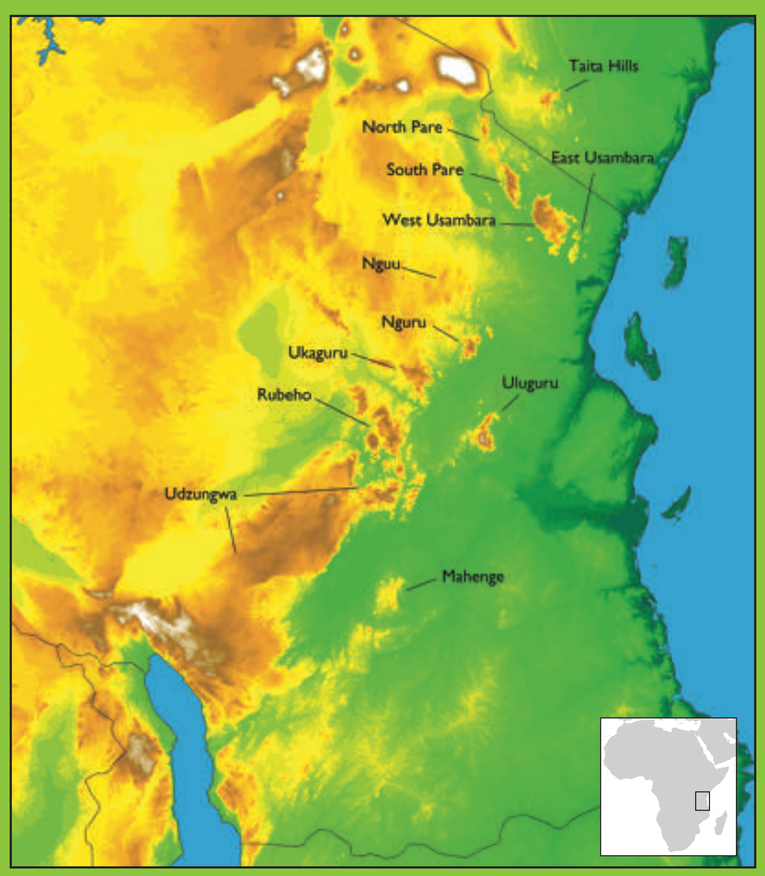

Figure 1. Map of Eastern Arc Mountains and adjacent coastal lowlands of Tanzania.

Montane forest: Nguru

Savanna: Serengeti

Montane grasslands: Kitulo

Results

Both montane forest and coastal lowland forest have a significant positive effect on terrestrialisation of breeding strategies (Table 1). Furthermore, there is strong evidence for correlated evolution of terrestrial egg-laying with forest in general, but terrestrial larval development is more closely associated with montane forest than coastal lowland forest (Table 2).

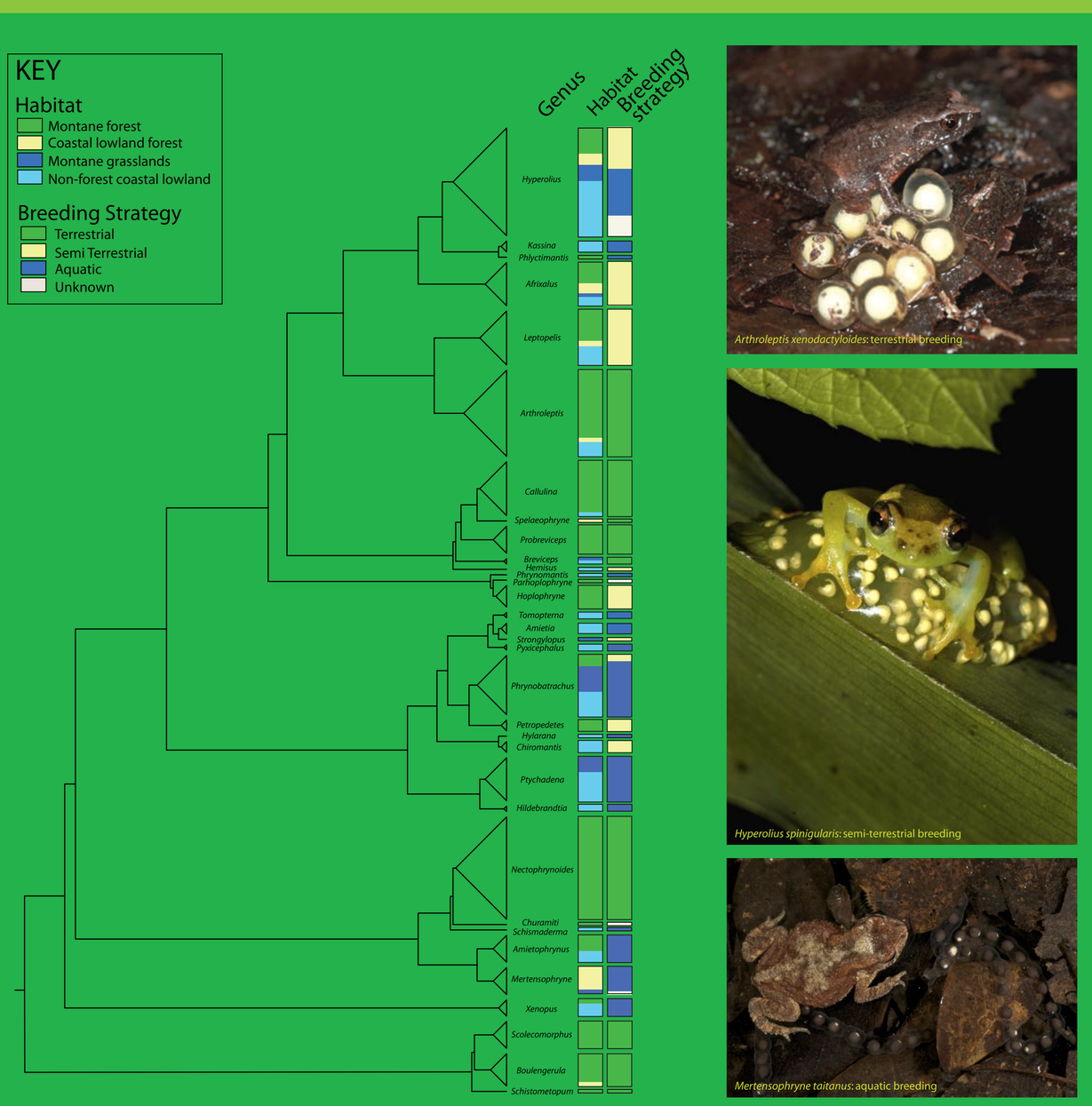

Figure 2. ML phylogeny of 180 EAM and coastal lowland amphibian species. Stacked bars show habitat and breeding biology composition per genus. Strong phylogentic clustering of both habitat and breeding strategies

Table 1. Explanatory variables of the pGLS analysis implimenting a Pagel's λ model of evolution (where λ =0.987).

	Coefficient ± SE	t-value	*p-value*
Intercept	1.199 ± 0.876	1.368	*p=0.1733*
Costal lowland forest	0.256 ± 0.080	3.193	***p<0.05***
Montane forest	0.158 ± 0.048	3.266	***p<0.05***
Montane grassland	0.036 ± 0.066	0.550	*p=0.5831*

Table 2. Analysis of correlated evolution: comparing dependent and independent trait evolution models using Likelihood method implemented in BayesTraits

	Log Likelihood Independent	Log Likelihood Dependent	Likelihood Ratio	*p-value*
Terrestrial egg - Montane Forest	-147.113	-132.862	28.503	***p<0.001***
Terrestrial Larva - Montane Forest	-105.969	-99.011	13.918	***p<0.05***
Terrestrial egg – Coastal lowland forest	-92.741	-87.180	11.121	***p<0.05***
Terrestrial Larva - Coastal lowland forest	-51.597	-51.449	0.296	*p=0.990*

Discussion

In East Africa, terrestrial forms of breeding are strongly associated with forest environments. Habitat with dense, moist undergrowth may have facilitated deposition of eggs on land, allowing species to escape competitive pressures and egg predation in an aquatic environment. Interestingly, the transition to complete terrestrial reproduction is only correlated with montane forests. Goin and Goin (1962) proposed that fast flowing streams and the lack of standing bodies of water in montane environments may limit aquatic breeding of amphibians. This is clearly reflected by taxa with stream-adapted tadpoles such as *Petropedets* or examples of ovoviviparity in *Nectophrynoides*, both of which inhabit montane forests. We therefore conclude that moist forest habitats are crucial for the evolution of terrestrial egg laying and speculate that potential lack of suitable aquatic breeding sites in topographically complex montane regions may favour the evolution of terrestrially adapted larva.

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