

Biodiversity patterns and conservation of the coastal forests of Eastern Africa

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Introduction

Biodiversity patterns in space and time

Biological diversity is distributed unevenly across the earth. Well known current biodiversity gradients such as the latitudinal (e.g. Fig. 1), altitudinal diversity gradients and the mid-domain effect have contributed significantly to our understanding of diversity patterns. However, how biodiversity has changed over time is also an important factor that can explain past and current patterns (Mannion et al., 2014). In the past decades, significant progress in our understanding of biodiversity at spatial and temporal scales have been made (Rosenzweig, 1995; Gaston & Blackburn, 2007), and how this relates to global change and conservation (Kerr et al., 2007). Endemism, and the persistence of biodiversity over time is hypothesized to be strongly influenced by long-term climatic stability and topography (Sandel et al., 2011; Harrison & Noss, 2017). Over millions of years, refugia are suspected to play a crucial role in maintaining biodiversity during times of geological and climate change (Mayr & O'Hara, 1986, Moreau, 1933, Dynesius & Jansson, 2000). The persistence of diversity over time in refugia is known to lead to areas that support unique biodiversity that has become locally extinct elsewhere. This is especially true in areas with complex topography where a species may only need to move a small distance in response to climate change compared to the large distance that a species in a flat landscape would need to move to adapt to the same climate change conditions. Recent studies using the concept of climate change velocity as a measure of long-term climate stability have shown that areas subjected to high levels of climate change are associated with a marked absence of small ranged birds, mammals and amphibians (Sandel et al., 2011), with areas that are comparatively stable identified as essential refugia for narrow-ranged species that are sensitive to habitat change.

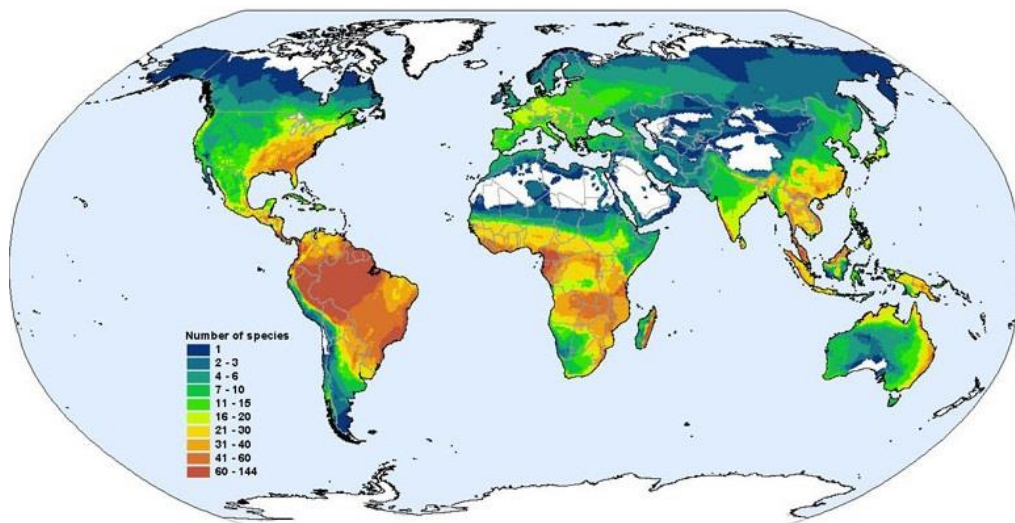


Fig. 1. Global patterns of amphibian species richness, from the Global Amphibian Assessment.

Conservation of biodiversity

Biodiversity is essential as it forms the foundation for all natural resources that humans need to survive and persist. Although it is an extremely broad and sometimes ambiguously used term, 'biodiversity' may be simply summarised as the variety of life (the variation of species, functional traits and genes). The multiple facets of biodiversity provide the foundation for ecosystem functions that control the movement of energy (e.g. primary production, nutrient cycling, decomposition), and the ecosystem services they provide to humanity (e.g. direct

benefits such as water, food, medicine, fuel, climate regulation, disease control) (Blackburn, 2008). Soon after the 1992 Earth Summit in Rio de Janeiro, interest in understanding biodiversity loss and how it may affect ecosystem functioning and services increased dramatically. This led to a proliferation of research in these fields and the establishment of several major global initiatives such as the Global Biodiversity Assessment launched by the United Nations Environment Programme, and the biodiversity science research agenda produced by Diversitas, (now the Future Earth project within the International Council for Science). In the quarter of a century since the Rio Earth Summit, there is now unequivocal evidence that biodiversity loss is intricately linked to ecosystem functioning (Cottingham et al., 2001; Balvanera et al., 2006; Cardinale et al., 2007) and is a major driver of global change (Tilman et al., 2014). Moreover, evolutionarily diverse communities have been shown to increase ecosystem stability over time and their functioning (Cadotte et al., 2008; Cadotte, 2013). Linking biodiversity with the direct benefits provided to humans through ecosystem services have proven to be more complex (Cardinale et al., 2012; Balvanera et al., 2014), though there is now evidence of the direct correlation between biodiversity and some provisioning and regulating ecosystem services (Harrison et al. 2014). Protecting biodiversity is therefore a major concern for humanity. Biodiversity is under threat due to climate change and human induced impact, to the point that the earth has been described as being in the midst of a major sixth extinction event (Kolbert, 2014; Ceballos et al., 2015). Reducing biodiversity loss both now and in the future are urgent conservation priorities and key components of the Aichi targets for 2020 by parties to the United Nations Convention on Biological Diversity (Pereira et al., 2013), especially after the failure to meet 2010 targets. To manage biological resources effectively given predicted future human impacts and climate change we need to collectively improve our capacity to assess biodiversity, both now and in the future.

Increasing knowledge of biodiversity patterns and what causes areas of rich biodiversity to form are vital steps towards prioritizing where and why we should focus future conservation efforts. Methods to measure biodiversity have typically focused at the species level, using metrics such as species richness that simply count the number of species present within a given area. The degree of endemism present may also be inferred if the known ranges of species are incorporated with this data. Species richness and endemism are the fundamental measurements of biodiversity which are currently used for conservation efforts at most scales, for example, defining the world's biodiversity hotspots (Myers et al., 2000) or establishing protected areas. Despite the wealth of biodiversity knowledge that is now available to scientists and conservation planners, several problems remain when using traditional methods for assessing biodiversity. Knowledge about biodiversity remains insufficient because the majority of species have still not been described (the Linnean shortfall), and the distributions of most are not fully understood or have significant sampling gaps, especially at local scales (the Wallacean shortfall) (Whittaker et al., 2005). These shortfalls are a serious problem for conservation planning in poorly developed regions of the world which often support high biodiversity but lack the appropriate infrastructure to document and assess it (Bini et al., 2006). Although traditional measures have provided a solid basis for biodiversity assessment and conservation, it has become increasingly clear that species diversity alone misses out on the full patterns of biodiversity present. Biodiversity is optimally represented by the full set of nested clades representing phylogenetic relationships and genetic diversity at all levels within the tree of life, and not just species (Mishler et al., 2014). However, even if we were to describe all of the species on earth and fully account for their distributions we would still have a problem due to a lack of available phylogenetic information for most organisms (the Darwinian shortfall, Diniz-Filho et al., 2013). Therefore, the documentation of biodiversity with molecular

tools and techniques provides the basis for understanding the diversity within and between organisms, and is crucial to integrate the information they can provide to complement traditional measures in future biodiversity assessment and conservation, especially in highly diverse tropical regions.

Molecular tools for estimating biodiversity

The low cost and effort of generating sequence data has led to a proliferation of molecular based biodiversity assessment techniques for rapid biodiversity assessment. One of the most common, DNA barcoding, is a tool that uses a standardized locus of DNA (typically between 400 and 800 base pairs in length) which can be easily amplified and sequenced across a wide range of organisms, showing variability within and between species. Massive online digital libraries of sequences from known species serve as the standard to match an unknown sample, allow its identification (Moritz & Cicero, 2004; Hebert & Gregory, 2005; Lahaye et al., 2008; Nagy et al., 2012), and in vertebrates is typically the mitochondrial *16S* rRNA or cytochrome oxidase subunit 1 (*COI*) genes (Vences et al., 2005). To gain more detailed data, extra loci such as recombinant nuclear genes may be chosen to supplement barcoding genes to increase phylogenetic signal and resolution, or fast evolving loci such as microsatellites may be used for microevolutionary processes acting at the level of populations such as allele frequency changes over time (Tautz & Schlötterer, 1994). With the advent of high throughput Next Generation Sequencing (NGS) techniques and their increasing affordability, it has now become feasible to conduct both macroevolutionary (phylogenomics) and microevolutionary (population genomics) research with unprecedented amounts of sequence data, in the order of thousands to millions of base pairs, for a relatively small cost (Lemmon & Lemmon, 2013). This data is increasingly contributing to the understanding of biodiversity patterns in the world's biologically rich regions (Carew et al., 2013; Joly & Faure, 2015). The last ten years in particular have highlighted the growing importance of phylogenetic perspectives on biodiversity conservation problems (Purvis et al., 2005; Cadotte & Davies, 2010; Davies & Buckley, 2011; Rolland et al., 2012). Phylogenetic information is now a critical component of modern ecology, particularly within macro- and community ecology and conservation (Tucker et al., 2016). The use of phylogenies acknowledges that the topology and branch length of a phylogenetic tree reflects genetic, phenotypic and trait differences between species and populations (Harvey & Pagel, 1991) and may be used to explain or predict evolutionary and ecological processes. Over seventy phylogeny based metrics are available, each of which may be used to address a range of ecological, evolutionary or conservation questions (Winter et al., 2013). Phylogeny based diversity indices first appeared in conservation as a response to the notion that minimising the loss of evolutionary diversity should be a priority (Vane-Wright et al., 1991). Phylogenetic diversity (PD) emerged as a metric to maximise the evolutionary diversity of a set of taxa in a given area (Faith, 1992) as that should also represent maximal feature diversity. The use of phylogenetics in macroecology and community ecology has tended to focus more on relatedness indices between communities (Webb et al., 2002) or to explain the causes of macro-scale patterns of diversity (Winter et al., 2009; Fritz & Rahbek, 2012; Jetz et al., 2012; Rosauer & Jetz, 2015, Voskamp et al. 2017). The phylogenetic endemism (PE) metric described by Rosauer et al. (2009) in particular has broad applications to conservation, including the identification of geographical concentrations of evolutionary history in refugia (Moore & Redding, 2009; Carnaval et al., 2014; Laity et al., 2015).

Using amphibians in the East African coastal forests as a model system, this thesis investigates how field work and molecular techniques (DNA barcoding and genomics), spatial data and taxonomic approaches can be

used to improve our knowledge of biodiversity patterns. Furthermore, the thesis seeks to establish the environmental and historical correlations with areas of high biodiversity and endemism to help identify priority areas for conservation.

Coastal forests of Eastern Africa, endemism, and environmental influences

Since the breakup of Pangaea around the Permian (ca. 225 million years ago) Africa became increasingly more isolated from other landmasses before its reunion with Eurasia in the Miocene (ca. 20 million years ago). The continent remained in a relatively stable equatorial position compared to other continents, which continued to move long into the Cenozoic period (Livingstone, 1993). Despite the relative stability of its geographical position, Africa has undergone significant periods of tectonic activity (Sepulchre et al., 2006; Partridge et al., 2010; Moucha & Forte, 2011; Kaufmann & Romanov, 2012) and historical climate oscillations (Demenocal, 1995; Maslin et al., 2014) which have resulted in the topographically complex and highly diverse habitats we see today. The high habitat diversity in Africa supports a quarter (nine) of the world's biodiversity hotspots (Myers et al., 2000), with a mixture of ancient relicts that have persisted through major global extinction events as well as relatively young species formed by recent processes. Africa supports many wide-ranging species including the world's most intact megafaunal assemblage (Fjeldså et al., 2004), but also many range-restricted endemics that are highly threatened. Understanding these biodiversity patterns and implementing them in conservation efforts at the continental scale is essential to protect African biodiversity (Brooks et al., 2001).

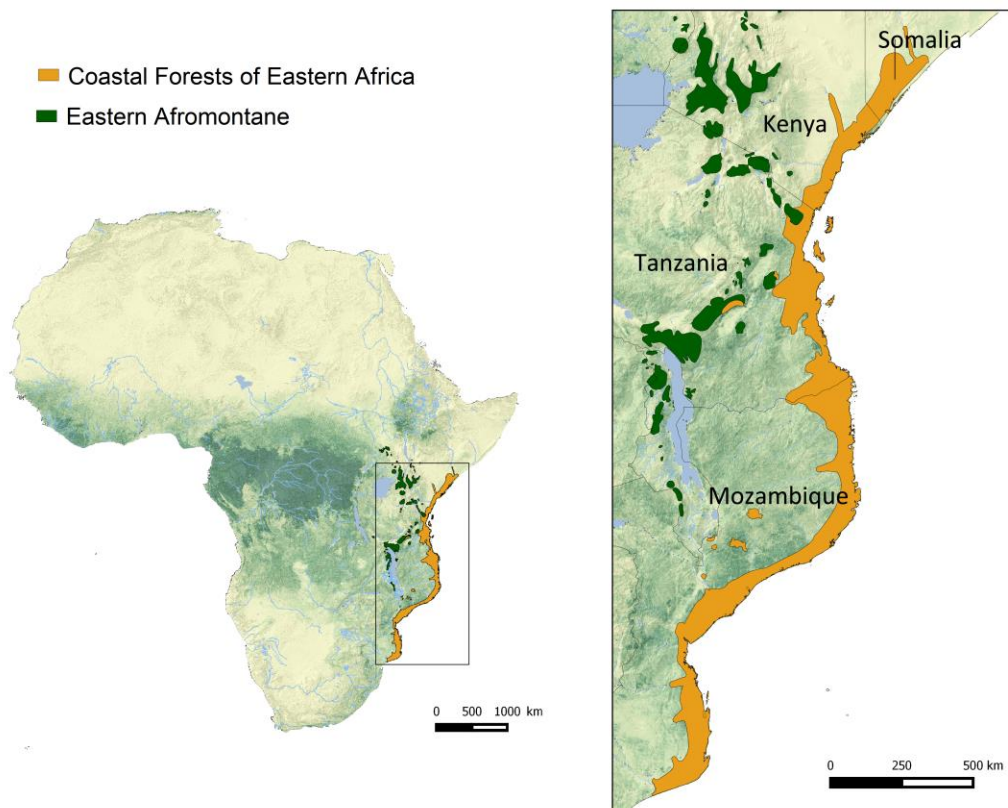


Fig. 2. The Coastal Forests of Eastern Africa (in orange) and the adjacent Eastern Afromontane biodiversity hotspot (in dark green).

The Coastal Forests of Eastern Africa (Fig. 2) are one of Africa's foremost biodiversity conservation priorities, and along with the adjacent Eastern Arc mountains form a highly threatened centre of endemism for plants and vertebrates (CEPF, 2007). In addition to their exceptionally high levels of plant endemism, coastal forests support high species richness and endemism of other taxonomic groups including mammals, birds, reptiles, amphibians and invertebrates (Burgess et al., 1998). However, the coastal forests and its rich biological diversity is severely threatened by human impact and predicted future climate change (Azeria et al., 2007; Burgess et al., 2007), and has been described as a 'vanishing refuge' (Burgess et al., 1998). The consensus view is that the coastal forests are the remaining fragments of a once continuous forest that covered tropical Africa during the Early Tertiary (ca. 40 million years ago) (Burgess et al., 1998; Couvreur et al., 2008; Kissling et al., 2012). The slow desiccation of Africa since the Oligocene is hypothesized to have led to natural fragmentation of this larger forest (Axelrod & Raven, 1978; Mumbi et al., 2008), but the increasing human population have drastically accelerated this process. Today the coastal forests consist of a fragmented network of tiny forest patches, mostly less than 20 km² in size, following the Eastern coastline of Africa through Somalia, Kenya, Tanzania and Mozambique. These forest patches are often unique in their community structure and species composition, making comparisons between areas difficult to make (Burgess et al., 1998). To quantify biodiversity and endemism patterns, subcentres of endemism within the Swahili regional centre of endemism were previously identified using species distributional data from a number of plant, vertebrate and invertebrate groups. Based on these data a number of important locations supporting high proportions of endemics were identified in Kenya and Tanzania (Tana river, Arabuko-Sokoke, East Usambara-Kwale, Pemba island, Uluguru, Udzungwa, Pugu hills and Lindi) and Mozambique (Bazaruto archipelago and Mount. Mulanje). The endemic species responsible for these patterns are generally distributed within areas of higher elevation, some of which overlap with the adjacent Eastern Afromontane biodiversity hotspot and other plateaux, and "are best interpreted as relicts and not the result of recent evolution" (Burgess et al. 1998).

Amphibians

Amphibians are tetrapod vertebrates that evolved from osteolepiform fish in the Devonian period (ca. 350-400 million years ago) (Carroll, 2001), comprising of three extant orders and 7,642 currently recognised species globally (Frost et al. 2017). Anurans (frogs and toads, 6,742 species) are the most widespread and species rich order with a near global distribution, whereas Caudates (salamanders and newts, 695 species) are found almost exclusively in the northern hemisphere with the exception of their recent colonization of South America (Elmer et al., 2013). Gymnophiona (caecilians, 205 species) are the least well known amphibian order, and are restricted to tropical regions only. The evolutionary relationships between these three orders have long been debated (Duellman & Trueb 1994), with the recent consensus being that the Gymnophiona are sister to Anurans and Caudates (Roelants et al., 2007; Pyron & Wiens, 2011). Globally, amphibians are known to be declining faster than most other vertebrate groups, with a large proportion of species that are threatened. The causes of these declines are many and varied, though human induced habitat modification is thought to be one of the major drivers of amphibian declines, especially for forest and water dependent species (Stuart et al., 2004). Due to their diverse life histories, ease of sampling and sensitivity to habitat modification and climate change during both aquatic and terrestrial life stages, amphibians have been proposed as useful indicators of the overall health of an ecosystem (Blaustein et al., 1994). As such, they are a suitable taxonomic group to use for assessing biodiversity, particularly

in tropical regions such as Sub-Saharan Africa where biological richness, human induced habitat modification and predicted future climate change are all high.

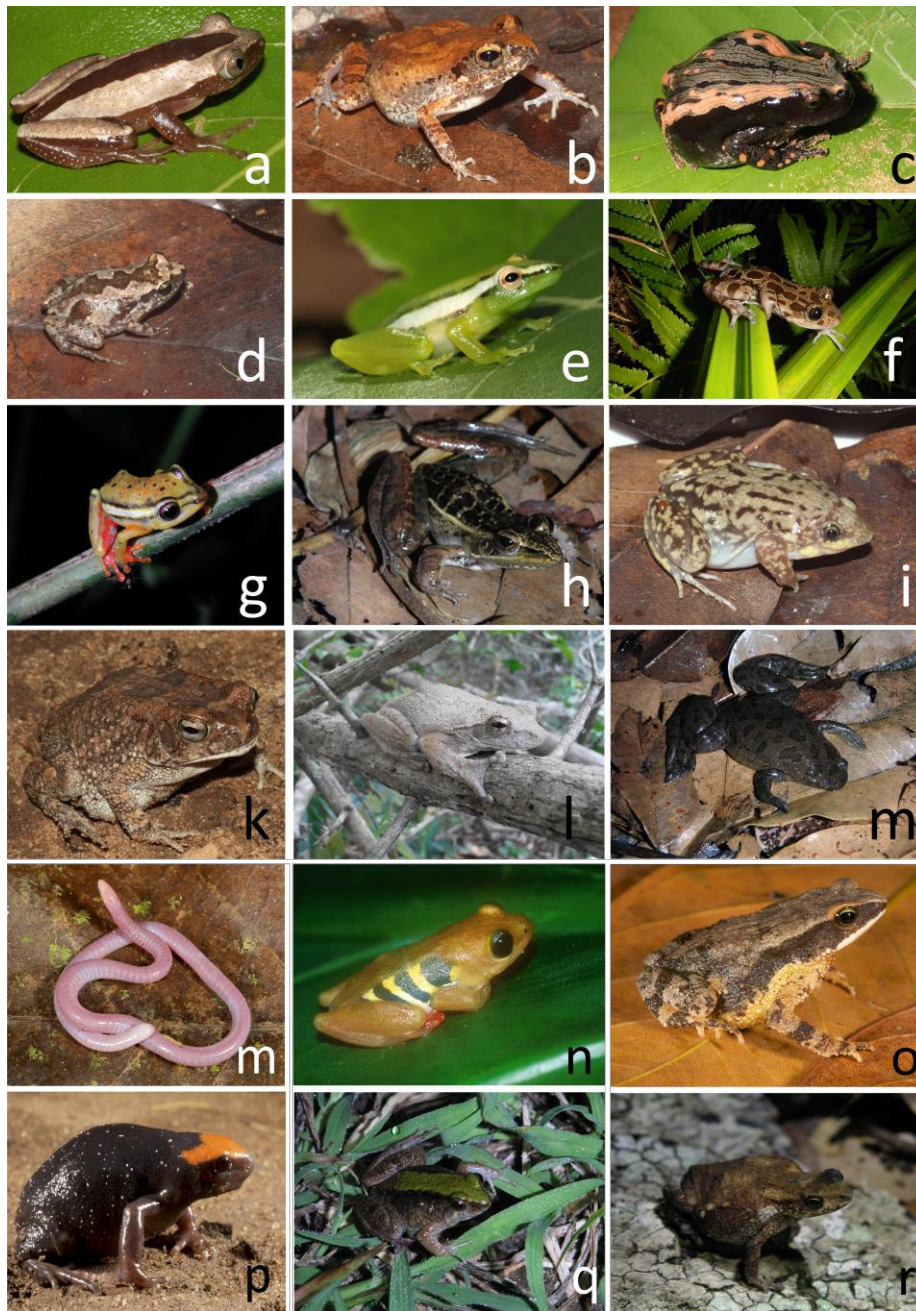


Fig. 2. A selection of amphibians found in the coastal forests, representing their diverse life histories. a) *Afrivalus fornasini*, b) *Arthroleptis stenodactylus*, c) *Phrynomantis bifasciatus*, d) *Arthroleptis xenodactyloides*, e) *Hyperolius parkeri*, f) *Kassina maculata*, g) *Hyperolius mitchelli*, h) *Ptychadena mascareniensis*, i) *Hemisis marmoratus*, j) *Sclerophrys pusilla*, k) *Chiromantis xerampelina*, l) *Xenopus muelleri*. m) *Boulengerula uluguruensis*, n) *Hyperolius reesi*, o) *Mertensophryne howelli*, p) *Spelaeophryne methneri*, q) *Phrynobatrachus acridoides* r) *Mertensophryne micranotis*. Photographs: Chris Barratt, Michele Menegon, Christoph Liedtke, Gabriela Bittencourt-Silva.

The known amphibian assemblage of the coastal forests of Eastern Africa region is currently around sixty species, though it is difficult to give a precise number due to the poor sampling across most of Mozambique and Somalia. The amphibians of the coastal forests received fairly little research attention until the scramble for Africa in the middle of the nineteenth century after European colonization (Harper et al. 2010). The first described species from the coastal forests was the treefrog, *Leptopelis flavomaculatus* in 1864 by Albert Günther, and subsequent work by early European naturalists including Wilhelm Peters, Fritz Nieden, George Boulenger and Ernst Ahl slowly began increasing our knowledge of the amphibians present in this region. The Welshman, Arthur Loveridge made a significant contribution to species descriptions in the early to mid- twentieth century while he was based at the Museum of Comparative Zoology alongside Thomas Barbour. After a slow-down in the number species descriptions after the Second World War, many more species were described by Jean-Luc Perret, Robert Drewes, Alice Grandison, Arne Schiøtz and John Poynton. These efforts continue to this day with over 21 species described in the past 15 years. In Tanzania the lowland (coastal forest) assemblage consists of fifty one species (Poynton et al., 2007), with several additional species from coastal Kenya (Harper et al. 2010) or recently described (Barratt et al. 2017) inflating that number to at least fifty five. Although several of these species are narrow ranged-endemics which are very conspicuous and easily identifiable, many widespread species occur across the coastal forests and adjacent areas of suitable habitat (e.g. savannah and bushland). The systematics of many of these widespread species are very poorly understood (e.g. Poynton, 2006), but some show strong phylogeographic structuring (Channing et al. 2013; Barratt et al. in review) and poorly defined species boundaries possibly representing many additional undescribed cryptic species (Zimkus et al., 2010; 2012; 2017, Harper et al. 2010).

Objectives

The amphibians of the coastal forests of Eastern Africa offer an ideal opportunity to integrate molecular and spatial data for assessing biodiversity and conservation planning. By improving our knowledge of the evolutionary relationships and distribution data for multiple species with markedly varied life histories, we can make broad inferences on the biodiversity patterns across the region. At finer scales, the inclusion of large numbers of samples per species allows cryptic diversity to be clearly quantified for the first time, and the geographic distributions of intraspecific lineages to be clarified.

This thesis is focused on categorizing and documenting amphibian biodiversity across the coastal forests by supplementing existing museum and literature data with new field work and molecular data. The work aims to identify refugia in this region, and understand if environmental factors can explain observed biodiversity patterns. Recent research in other geographic areas have established correlations between climatic stability, forest stability and topography in promoting endemism in small ranged species such as amphibians (Carnaval et al., 2014; Rosauer et al., 2015; Sandel et al., 2011). The links between long-term climate stability and endemism of small-ranged taxa has long been speculated, though this remains to be conclusively tested in East Africa. The long history of species identifications and collections across the coastal forest region have laid the groundwork for this thesis. With additional sampling and data assimilation, using new sequencing technologies and statistical methods, the thesis attempts to explain which factors may be responsible for the biodiversity patterns across the coastal forests, and how this may be important for conservation of this biodiversity hotspot in the future.

Chapter overview

Chapter 1: Next generation sequencing and landscape analyses reveal the importance of paleo-climate, geography and hydrology in the population structure of lowland amphibians in East Africa

Authors: Christopher D. Barratt, Beryl A. Bwong, Robert Jehle, Michele Menegon, Daniel M. Portik, Gabriela B. Bittencourt-Silva, H. Christoph Liedtke, Peter Nagel & Simon P. Loader

Status: Draft manuscript (target journal: Evolution)

Using next generation sequencing we reveal phylogeographic patterns in five co-distributed amphibian clades across East Africa. The work improves previous estimates of relationships in these clades, supports the common biogeographic patterns known for this region, and shows that genetic diversity is correlated with geography, hydrology and historical climate. We demonstrate that next generation sequencing is an efficient and cost effective method for assessing genetic variation within poorly defined groups, and will be crucial in the future for assessing tropical diversity.

Chapter 2: Environmental correlates of phylogenetic endemism in amphibians and the conservation of refugia in the Coastal Forests of Eastern Africa

Authors: Christopher D. Barratt, Beryl A. Bwong, Renske E. Onstein, Dan F. Rosauer, Michele Menegon, Nike Doggart, Peter Nagel, W. Daniel Kissling & Simon P. Loader

Status: revision in review (Diversity and Distributions)

Based on large scale DNA barcoding project we estimate phylogenetic endemism (a measure of the evolutionary history of a community contained in a given area) across a well sampled portion of the coastal forest and lowland Eastern Afromontane region in Tanzania and Kenya. We utilise cryptic diversity represented by multiple distinct lineages within species to improve fine scale estimates of endemism. We show that benign current climate and climatic stability in the Quaternary are strong predictors of endemism, supporting the hypothesis that these areas are refugia. We show that the current protected area network is insufficient to protect the endemism supported in these areas.

Chapter 3: Museums or cradles of diversity? Paleo- and Neo- endemism patterns in the East African lowlands using near complete assemblage phylogenetic data from amphibians

Authors: Christopher D. Barratt, Beryl A. Bwong, Peter Nagel & Simon P. Loader

Status: Draft manuscript (target journal: Journal of Biogeography)

For close to the complete lowland amphibian assemblage (fifty-five species) across Tanzania and Kenya, we estimate phylogenetic endemism and use a null model hypothesis testing framework to distinguish the different endemism types present and their geographic distributions. We show that while the coastal forests can be considered as museums of diversity that support ancient relicts, they can in some cases be cradles of diversity, supporting recently evolved forms, and several places support complex mixtures of endemism types. We discuss the results in context of the general geological, climate and hydrological history of the East African lowlands.

Chapter 4: A new, narrowly distributed, and critically endangered species of spiny-throated reed frog (Anura: Hyperoliidae) from a highly threatened coastal forest reserve in Tanzania

Authors: Christopher D. Barratt, Lucinda P. Lawson, Gabriela B. Bittencourt-Silva, Nike Doggart, Theron Morgan-Brown, Peter Nagel & Simon P. Loader

Status: Published (Herpetological Journal)

We describe a new, critically endangered amphibian from the coastal forests of Tanzania (Ruvu South Forest Reserve) using morphological and genetic approaches. The new species is the first lowland member of the montane spiny-throated reed frog clade, and is the sixth endemic amphibian for the Tanzanian coastal forests. Using remote sensing images we demonstrate the catastrophic levels of habitat destruction that have occurred in Ruvu South since 1998, highlighting the urgency of improving conservation protection in this area and also more broadly across the coastal forest region.

Additional Outputs

In addition to the chapters within this thesis, a number of additional outputs have arisen from the work and data collected during this PhD:

Peer-reviewed:

Zimkus B., Lawson L.P., Barej M., Barratt C.D., Channing A., Dehling J.M., Gehring S., Greenbaum E., Gvodzik V., Harvey J., Kielgast J., Kusamba C., Nagy Z., Pabijan M., Penner J., Du Preez L., Rödel M.O., Vences M., Weber K., Lötters S. (2017). Leapfrogging into new territory: how Mascarene ridged frogs have diversified across Africa. *Molecular Phylogenetics and Evolution*, **106**, 254-269.

Bwong B.A., Nyamache J.O., Malonza P.K., Wasonga D.V., Ngwava J.M., Barratt C.D., Nagel P., Loader S.P. (in press). Amphibian diversity in Shimba Hills National Reserve, Kenya: a comprehensive list of specimens and species. *Journal of East African Natural History*.

Bwong B.A., Lawson L.P., Nyamache J.O., Barratt C.D., Menegon M., Portik D.M., Malonza P.K., Nagel P., Loader S.P. (in review). Phylogenetic, ecological and morphological variation in the congeners *Hyperolius mitchelli* and *Hyperolius rubrovermiculatus* from East Africa. *Acta Herpetologica*.

Bittencourt-Silva G.B., Lawson L.P., Tolley K.A., Portik D.M.P., Barratt C.D., Nagel P., Loader S.P. (in review). Integrating phylogeny and ecological niche models to reconstruct the phylogeographical history of the East African reed frog *Hyperolius substriatus* Ahl 1931. *Journal of Biogeography*.

Popular press (non- peer reviewed):

Barratt C.D, Tonelli E., Menegon M., Doggart N., Ngalason W., Howell K. (2014). Fragmented habitats and species: the challenges of amphibian conservation in Tanzania today. *Froglog*, **111**, 63-64.

Mongabay (2017) Newly discovered Tanzanian frog already facing extinction.

<https://news.mongabay.com/2017/03/newly-discovered-tanzanian-frog-already-facing-extinction/>

References

Axelrod D.I., Raven P.H. (1978) Late Cretaceous and Tertiary vegetation history of Africa. M. Werger (Ed.), *Biogeography and Ecology of Southern Africa*, Junk, The Hague (1978), pp. 77–130.

Azeria E.T., Sanmartin I., As S., Carlson A., & Burgess N. (2007) Biogeographic patterns of the East African coastal forest vertebrate fauna. *Biodiversity and Conservation*, **16**, 883–912.

- Balvanera P., Pfisterer A.B., Buchmann N., He J.S., Nakashizuka T., Raffaelli D., & Schmid B. (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters*, **9**, 1146–1156.
- Balvanera P., Siddique I., Dee L., Paquette A., Isbell F., Gonzalez A., Byrnes J., O'Connor M.I., Hungate B.A., & Griffin J.N. (2014) Linking biodiversity and ecosystem services: Current uncertainties and the necessary next steps. *BioScience*, **64**, 49–57.
- Barratt C.D., Lawson L.P., Bittencourt-Silva G.B., Doggart N., Morgan-Brown T., Nagel P. & Loader S.P. (2017) A new, narrowly distributed, and critically endangered species of spiny-throated reed frog (Anura: Hyperoliidae) from a highly threatened coastal forest reserve in Tanzania. *Herpetological Journal*, **27**, 13-24.
- Barratt C.D., Bwong B.A., Onstein R.E., Rosauer D.F., Menegon M., Doggart N., Nagel P., Kissling W.D., Loader S.P. (in review) Environmental correlates of phylogenetic endemism in amphibians and the conservation of refugia in the Coastal Forests of Eastern Africa. *Diversity and Distributions*.
- Bini L.M., Diniz-Filho J.A.F., Rangel T.F.L.V.B., Bastos R.P., & Pinto M.P. (2006) Challenging Wallacean and Linnean shortfalls: Knowledge gradients and conservation planning in a biodiversity hotspot. *Diversity and Distributions*, **12**, 475–482.
- Blackburn D.C. (2008) Biogeography and evolution of body size and life history of African frogs: Phylogeny of squeakers (*Arthroleptis*) and long-fingered frogs (*Cardioglossa*) estimated from mitochondrial data. *Molecular Phylogenetics and Evolution*, **49**, 806–826.
- Blaustein A.R., Wake D.B., & Sousa W.P. (1994) Amphibian declines: Judging stability, persistence, and susceptibility of populations to local and global extinctions. *Conservation Biology*, **8**, 60–71.
- Brooks T., Balmford A., Burgess N., Fjeldsø J., Hansen L. a., Moore J., Rahbek C., & Williams P. (2001) Toward a Blueprint for Conservation in Africa. *BioScience*, **51**, 613.
- Burgess N., Fjeldsa J., Howell K., Kilahama F., Loader S.P., Lovett J.C., & Mbilinyi B. (2007) The biological importance of the Eastern Arc Mountains of Tanzania and Kenya. *Biological Conservation*, **134**, 209–231.
- Burgess N.D., Clarke G.P., & Rodgers W.A. (1998) Coastal forests of eastern Africa: status, endemism patterns and their potential causes. *Biological Journal of the Linnean Society*, **64**, 337–367.
- Cadotte M.W. (2013) Experimental evidence that evolutionarily diverse assemblages result in higher productivity. *Proceedings of the National Academy of Sciences*, **110**, 8996–9000.
- Cadotte M.W., Cardinale B.J., & Oakley T.H. (2008) Evolutionary history and the effect of biodiversity on plant productivity. *Proceedings of the National Academy of Sciences of the USA*, **105**, 17012–17017.
- Cadotte M.W. & Davies T.J. (2010) Rarest of the rare: advances in combining evolutionary distinctiveness and scarcity to inform conservation at biogeographical scales. *Diversity and Distributions*, **16**, 376–385.
- Cardinale B.J., Duffy J.E., Gonzalez A., Hooper D.U., Perrings C., Venail P., Narwani A., Mace G.M., Tilman D., Wardle D., Kinzig A.P., Daily G.C., Loreau M., Grace J.B., Larigauderie A., Srivastava D.S., & Naeem S. (2012) Biodiversity loss and its impact on humanity. *Nature*, **489**, 326–326.
- Cardinale B.J., Wright J.P., Cadotte M.W., Carroll I.T., Hector A., Srivastava D.S., Loreau M., & Weis J.J. (2007) Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proceedings of the National Academy of Sciences*, **104**, 18123–18128.

- Carew M.E., Pettigrove V.J., Metzeling L., & Hoffmann A. (2013) Environmental monitoring using next generation sequencing: Rapid identification of macroinvertebrate bioindicator species. *Frontiers in Zoology*, **10**, 45.
- Carnaval A.C., Waltari E., Rodrigues M.T., Rosauer D.F., VanDerWal J., Damasceno R., Prates I., Strangas M., Spanos Z., Rivera D., Pie M.R., Firkowski C.R., Bornschein M.R., Ribeiro L.F., & Moritz C. (2014a) Prediction of phylogeographic endemism in an environmentally complex biome. *Proceedings of the Royal Society B: Biological Sciences*, **281**, 20141461.
- Carroll R.L. (2001) The Origin and Early Radiation of Terrestrial Vertebrates. *Journal of Paleontology*, **75**, 1202–1213.
- Ceballos G., Ehrlich P.R., Barnosky A.D., García A., Pringle R.M., & Palmer T.M. (2015) Accelerated modern human – induced species losses: entering the sixth mass extinction. *Science Advances*, **1**, 1–5.
- Channing A., Hillers A., Lötters S., Rodel M.O., Schick S., Conradie W., Rödder D., Mercurio V., Wagner P., Dehling J.M., Du Preez L.H., Kielgast J., Burger M.. (2013). Taxonomy of the super-cryptic *Hyperolius nasutus* group of long reed frogs of Africa (Anura: Hyperoliidae), with descriptions of six new species. *Zootaxa*, **3620**, 301-350.
- Cottingham K.L., Brown B.L., & Lennon J.T. (2001) Biodiversity may regulate the temporal variability of ecological systems. *Ecology Letters*, **4**, 72–85.
- Couvreur T.L.P., Chatrou L.W., Sosef M.S.M., & Richardson J.E. (2008) Molecular phylogenetics reveal multiple tertiary vicariance origins of the African rain forest trees. *BMC Biology*, **6**, 54.
- Critical Ecosystem Partnership Fund. (2007). Fact Sheet: Eastern Arc Mountains and Coastal Forest Fact Sheet. Available from: <<http://www.cepf.net/Documents/cepf.easternarc.factsheet.pdf>>. Accessed: 9th March 2017.
- Davies T.J. & Buckley L.B. (2011) Phylogenetic diversity as a window into the evolutionary and biogeographic histories of present-day richness gradients for mammals. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **366**, 2414–2425.
- Deménil P.B. (1995) Plio-Pleistocene African climate. *Science*, **270**, 53–59.
- Diniz-Filho J.A.F., Loyola R.D., Raia P., Mooers A.O., & Bini L.M. (2013) Darwinian shortfalls in biodiversity conservation. *Trends in Ecology & Evolution*, **28**, 689–695.
- Duellman W.E., Trueb L. (1994). *Biology of Amphibians*. Johns Hopkins University Press, Baltimore.
- Dynesius M. & Jansson R. (2000) Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. *Proceedings of the National Academy of Sciences*, **97**, 9115–9120.
- Elmer K.R., Bonett R.M., Wake D.B., & Lougheed S.C. (2013) Early Miocene origin and cryptic diversification of South American salamanders. *BMC Evolutionary Biology*, **13**, 59.
- Faith D.P. (1992) Conservation evaluation and phylogenetic diversity. *Biological Conservation*, **61**, 1–10.
- Fjeldså J., Burgess N.D., Blyth S., & de Klerk H.M. (2004) Where are the major gaps in the reserve network for Africa's mammals? *Oryx*, **38**, 2004.
- Fritz S.A. & Rahbek C. (2012) Global patterns of amphibian phylogenetic diversity. *Journal of Biogeography*, **39**, 1373–1382.
- Gaston K.J. & Blackburn T.M. (2007) *Pattern and process in macroecology*. Blackwell Science Ltd.

- Harper E.B., Measey G.J., Patrick D.A., Menegon M., Vonesh J.R. (2010) *Field guide to the amphibians of the Eastern Arc Mountains and Coastal Forests of Tanzania and Kenya*. Camerapix International, Nairobi, Kenya.
- Harrison S, Noss R. (2017). Endemism hotspots are linked to stable climate refugia. *Annals of Botany*, **119**, 207-214.
- Harvey P.H. & Pagel M.D. (1991) *The Comparative Method In Evolutionary Biology*. Oxford Series in Ecology and Evolution, 239 pp.
- Hebert P.D.N. & Gregory T.R. (2005) The promise of DNA barcoding for taxonomy. *Systematic Biology*, **54**, 852–859.
- Jetz W., Thomas G.H., Joy J.B., Hartmann K., & Mooers A.O. (2012) The global diversity of birds in space and time. *Nature*, **491**, 444–448.
- Joly D. & Faure D. (2015) Next-generation sequencing propels environmental genomics to the front line of research. *Heredity*, **114**, 429–430.
- Kaufmann G. & Romanov D. (2012) Landscape evolution and glaciation of the Rwenzori Mountains, Uganda: Insights from numerical modeling. *Geomorphology*, **138**, 263–275.
- Kerr J.T., Kharouba H.M., & Currie D.J. (2007) The macroecological contribution to global change solutions. *Science*, **316**, 1581–1584.
- Kissling W.D., Eiserhardt W.L., Baker W.J., Borchsenius F., Couvreur T.L.P., Balslev H., & Svenning J.-C. (2012) Cenozoic imprints on the phylogenetic structure of palm species assemblages worldwide. *Proceedings of the National Academy of Sciences*, **109**, 7379–7384.
- Kolbert E. (2014) *The Sixth Extinction*. Henry Holt & Co.
- Lahaye R., van der Bank M., Bogarin D., Warner J., Pupulin F., Gigot G., Maurin O., Duthoit S., Barraclough T.G., & Savolainen V. (2008) DNA barcoding the floras of biodiversity hotspots. *Proceedings of the National Academy of Sciences*, **105**, 2923–2928.
- Laity T., Laffan S.W., González-Orozco C.E., Faith D.P., Rosauer D.F., Byrne M., Miller J.T., Crayn D., Costion C., Moritz C., & Newport K. (2015) Phylodiversity to inform conservation policy: An Australian example. *Science of the Total Environment*, **534**, 131–143.
- Lemmon E.M. & Lemmon A.R. (2013) High-Throughput Genomic Data in Systematics and Phylogenetics. *Annual Review of Ecology, Evolution, and Systematics*, **44**, 99–121.
- Livingstone, D.A. (1993). Evolution of African climate. In: Goldblatt P, editor. *Biological relationships between Africa and South America*. New Haven and London: Yale University Press. p. 456-472.
- Mannion P.D., Upchurch P., Benson R.B.J., & Goswami A. (2014) The latitudinal biodiversity gradient through deep time. *Trends in Ecology and Evolution*, **29**, 42–50.
- Maslin M.A., Brierley C.M., Milner A.M., Shultz S., Trauth M.H., & Wilson K.E. (2014) East african climate pulses and early human evolution. *Quaternary Science Reviews*, **101**, 1–17.
- Mishler B.D., Knerr N., González-Orozco C.E., Thornhill A.D., Laffan S.W., & Miller J.T. (2014) Phylogenetic measures of biodiversity and neo- and paleo-endemism in Australian Acacia. *Nature Communications*, **5**, 4473.
- Mooers A.O. & Redding D.W. (2009) Where the rare species are. *Molecular Ecology*, **18**, 3955–3957.
- Moritz C. & Cicero C. (2004) DNA barcoding: Promise and pitfalls. *PLoS Biology*, **2**, e354.

doi:10.1371/journal.pbio.0020354

- Moucha R. & Forte A.M. (2011) Changes in African topography driven by mantle convection. *Nature Geoscience*, **4**, 707–712.
- Mumbi C.T., Marchant R., Hooghiemstra H., & Wooller M.J. (2008) Late Quaternary vegetation reconstruction from the Eastern Arc Mountains, Tanzania. *Quaternary Research*, **69**, 326–341.
- Myers N., Mittermeier R.A., Mittermeier C.G., Fonseca G.A.B., & Kent J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.
- Nagy Z.T., Sonet G., Glaw F., & Vences M. (2012) First Large-Scale DNA Barcoding Assessment of Reptiles in the Biodiversity Hotspot of Madagascar, Based on Newly Designed COI Primers. *PLoS ONE*, **7**, e34506.
- Partridge T.C., Dollar E.S., Moolman J., & Dollar L.H. (2010) The geomorphic provinces of South Africa, Lesotho and Swaziland: A physiographic subdivision for earth and environmental scientists. *Transactions of the Royal Society of South Africa*, **65**, 1–47.
- Pereira H.M., Ferrier S., Walters M., Geller G.N., Jongman R.H.G., Scholes R.J., Bruford M.W., Brummitt N., Butchart S.H.M., Cardoso A.C., Coops N.C., Dulloo E., Faith D.P., Freyhof J., Gregory R.D., Heip C., Höft R., Hurr G., Jetz W., Karp D.S., McGeoch M.A., Obura D., Onoda Y., Pettorelli N., Reyers B., Sayre R., Scharlemann J.P.W., Stuart S.N., Turak E., Walpole M., & Wegmann M. (2013) Essential Biodiversity Variables. *Science*, **339**, 277–278.
- Poynton J. (2006) On dwarf spiny reedfrogs in Tanzanian eastern lowlands (Anura: Afrixalus). *African Journal of Herpetology*, **55**, 167–169.
- Poynton J.C., Loader S.P., Sherratt E., & Clarke B.T. (2007) Amphibian diversity in East African biodiversity hotspots: Altitudinal and latitudinal patterns. *Biodiversity and Conservation*, **16**, 1103–1118.
- Purvis A., Gittleman J.L., & Brooks T.M. (2005) *Phylogeny and Conservation*. 448 pp. Cambridge University Press.
- Pyron R.A. & Wiens J.J. (2011) A large-scale phylogeny of Amphibia including over 2800 species, and a revised classification of extant frogs, salamanders, and caecilians. *Molecular Phylogenetics and Evolution*, **61**, 543–583.
- Roelants K., Gower D.J., Wilkinson M., Loader S.P., Biju S.D., Guillaume K., Moriau L., & Bossuyt F. (2007) Global patterns of diversification in the history of modern amphibians. *Proceedings of the National Academy of Sciences*, **104**, 887–892.
- Rolland J., Cadotte M.W., Davies J., Devictor V., Lavergne S., Mouquet N., Pavoine S., Rodrigues A., Thuiller W., Turcati L., Winter M., Zupan L., Jabot F., & Morlon H. (2012) Using phylogenies in conservation: new perspectives. *Biology Letters*, **8**, 692–694.
- Rosauer D.F., Catullo R.A., Vanderwal J., & Moussalli A. (2015) Lineage range estimation method reveals fine-scale endemism linked to Pleistocene stability in Australian rainforest herpetofauna. *PLoS ONE*, **10**, e0126274.
- Rosauer D.F. & Jetz W. (2015) Phylogenetic endemism in terrestrial mammals. *Global Ecology and Biogeography*, **24**, 168–179.
- Rosenzweig M. (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge.

- Sandel B., Arge L., Dalsgaard B., Davies R.G., Gaston K.J., Sutherland W.J., & Svenning J.-C. (2011) The Influence of Late Quaternary Climate-Change Velocity on Species Endemism. *Science*, **334**, 660–664.
- Sepulchre P., Ramstein G., Fluteau F., Schuster M., Tiercelin J.-J., & Brunet M. (2006) Tectonic uplift and Eastern Africa aridification. *Science*, **313**, 1419–1423.
- Stuart S.N., Chanson J.S., Cox N. a, Young B.E., Rodrigues A.S.L., Fischman D.L., & Waller R.W. (2004) Status and trends of amphibian declines and extinctions worldwide. *Science*, **306**, 1783–1786.
- Tautz D. & Schlötterer C. (1994) Simple sequences. *Current Opinion in Genetics and Development*, **4**, 832–837.
- Tilman D., Isbell F., & Cowles J.M. (2014) Biodiversity and Ecosystem Functioning. *Annual Reviews in Ecology Evolution and Systematics*, **45**, 471–93
- Tucker C.M., Cadotte M.W., Carvalho S.B., Davies T.J., Ferrier S., Fritz S.A., Grenyer R., Helmus M.R., Jin L.S., Mooers A.O., Pavoine S., Purschke O., Redding D.W., Rosauer D.F., Winter M., & Mazel F. (2016) A guide to phylogenetic metrics for conservation, community ecology and macroecology. *Biological Reviews*, doi: 10.1111/brv.12252.
- Vane-Wright R.I., Humphries C.J., & Williams P.H. (1991) What to protect?-Systematics and the agony of choice. *Biological Conservation*, **55**, 235–254.
- Vences M., Thomas M., van der Meijden A., Chiari Y., & Vieites D.R. (2005) Comparative performance of the 16S rRNA gene in DNA barcoding of amphibians. *Frontiers in zoology*, **2**, 5.
- Voskamp A., Baker D.J., Stephens P.A., Valdes P.J., Willis S.G. (2017). Global patterns in the divergence between phylogenetic diversity and species richness in terrestrial birds. *Journal of Biogeography*, early view. doi: 10.1111/jbi.12916.
- Webb C.O., Ackerly D.D., McPeck M.A., & Donoghue M.J. (2002) Phylogenies and Community Ecology. *Annual Review of Ecology and Systematics*, **33**, 475–505.
- Whittaker R.J., Araujo M.B., Jepson, P., Ladle R.J., Watson J.E.M., & Willis K.J. (2005) Conservation biogeography: assessment and prospect. *Diversity and Distributions*, **11**, 3–23.
- Winter M., Devictor V., & Schweiger O. (2013) Phylogenetic diversity and nature conservation: where are we? *Trends in Ecology & Evolution*, **28**, 199–204.
- Winter M., Schweiger O., Klotz S., Nentwig W., Andriopoulos P., Arianoutsou M., Basnou C., Delipetrou P., Didziulis V., Hejda M., Hulme P.E., Lambdon P.W., Pergl J., Pyšek P., Roy D.B., & Kühn I. (2009) Plant extinctions and introductions lead to phylogenetic and taxonomic homogenization of the European flora. *Proceedings of the National Academy of Sciences*, **106**, 21721–5.
- Zimkus B.M., Lawson L., Loader S.P., & Hanken J. (2012) Terrestrialization, miniaturization and rates of diversification in african puddle frogs (anura: Phrynobatrachidae). *PLoS ONE*, **7**, e35118.
- Zimkus B.M., Rodel M.O., & Hillers A. (2010) Complex patterns of continental speciation: Molecular phylogenetics and biogeography of sub-Saharan puddle frogs (*Phrynobatrachus*). *Molecular Phylogenetics and Evolution*, **55**, 883–900.
- Zimkus B.M., Lawson L.P., Barej M.F., Barratt C.D., Channing A., Dash K.M., Dehling J.M., Du Preez L., Gehring P-S., Greenbaum E., Gvodzik V., Harvey J., Kielgast J., Kusamba C., Nagy Z., Pabijan M., Penner J., Rödel M.O., Vences M. & Lötters S. (2017). Leapfrogging into new territory: how

Mascarene ridged frogs have diversified across Africa. *Molecular Phylogenetics and Evolution*, **106**, 254-269.

Chapter I

Next generation sequencing and landscape analyses reveal the importance of paleo-climate, geography and hydrology in the population structure of lowland amphibians in East Africa

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Next generation sequencing and landscape analyses reveal the importance of paleo-climate, geography and hydrology in the population structure of lowland amphibians in East Africa

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Abstract

Genetic variation is often considered the most fundamental dimension of biodiversity as it provides the critical foundation for adaptation to new environmental conditions through evolutionary change. Conservation strategies must therefore be informed by detailed knowledge of genetic diversity, how it is distributed, and the environmental factors that are responsible for these patterns. In the East African lowlands, clear phylogeographic structure is evident across many varied species groups, strongly influenced by the geological and climatic history of Africa, though the reasons for this structure often depend on specific functional and life history characteristics. Here, we attempt to resolve the phylogeography of five widespread amphibian clades across Tanzania, Kenya, Zimbabwe, Malawi and Mozambique using thousands of genome-wide loci using next generation sequencing (RAD-seq). Our data represent wide geographical sampling across over 2000 km of East Africa, with 27-59 individuals per species group sampled across 8-27 localities. For each clade we infer phylogenetic relationships using up to 1,475,958 bp of sequence data, and estimate population structure using up to 38,642 unlinked single nucleotide polymorphisms. We use environmental connectivity modelling and electrical circuit theory to test correlations between genetic distance (F_{ST}) and environmental data related to geography, habitat suitability, paleo-climate, and hydrology. High phylogeographic structure is present in three of the five clades (*Afrivalus stuhlmanni*, *Leptopelis argenteus* and *Arthroleptis xenodactyloides*), and genetic distances between localities are strongly correlated with paleo-climatic stability dating back to the Pliocene, geographic distance and slope, and the spatial arrangement of hydrological basins. The remaining two clades (*Afrivalus fornasini* and *Leptopelis flavomaculatus*) show lower phylogeographic structure, with less clear environmental correlates of F_{ST} . The results reaffirm consistent phylogeographic breaks which are recovered across clades, corresponding to known vegetation zones, terrestrial ecoregions, suggesting that paleo-climatic fluctuations and the spatial location of refugia play a key role in biodiversity patterns. The work here provides a case study of how knowledge of biodiversity in East Africa can be improved by new sequencing technologies, which are likely to become crucial in the near future for measuring biodiversity and informing conservation strategies.

Key words: conservation, phylogeography, connectivity, NGS, circuit theory, gene flow

Introduction

Understanding the distribution of genetic diversity and the factors responsible for observed diversity patterns are both fundamental goals in evolutionary biology. Genetic diversity provides the foundation for evolutionary change (Lewontin, 1975), and to complement ongoing large scale estimates of biodiversity, phylogeographic studies within species are needed for local and regional scale conservation (Miraldo et al. 2016). Habitat fragmentation is known to diminish the ability of populations to make evolutionary responses to environmental change by reducing gene flow (Hoffmann et al., 2015), which may in some cases be mitigated by restoring connectivity between isolated populations. In tropical biodiversity hotspots, landscapes are often highly heterogeneous, often caused by natural habitat fragmentation, though this has in many areas been exacerbated by human activity. This fragmented and human modified landscape tends to lead to highly structured genetic diversity, which may compromise the connectivity, gene flow and resilience of populations (Frankham, 1996), but in some cases can promote speciation (Seehausen et al., 2014). Phylogeographic studies can help to prioritize areas of high conservation value as they identify population structure and unique evolutionary lineages (see Evolutionary Significant Units, Moritz, 1994). Knowledge of these patterns below the species level is important as some populations or lineages may require special conservation. The majority of phylogeographic studies have typically been based on mitochondrial DNA (mtDNA), mainly because sequence data is easy to generate at a low cost. Though mtDNA loci are useful and affordable for large scale studies, they are unable to represent all contemporary and historical population level processes due to being heritable from the maternal line only (Hoelzer, 1997). To gain fully reliable estimations of genetic diversity, the inclusion of recombinant nuclear genes inherited from both parents is required (Karl & Avise, 1993). However, the sequencing of nuclear genes can often require repeated sequencing efforts due to their lower cell copy numbers, and in some cases the development of species-specific primer sets or optimization of lab protocols may be needed (Zhang & Hewitt, 2003). These complications can quickly render the cost of a project prohibitive if large numbers of individuals are necessary.

The timely development of high throughput next-generation sequencing (NGS) technologies enables large numbers of both nuclear and mitochondrial loci to be genotyped simultaneously, and has revolutionized evolutionary research (Hickerson et al., 2010; Davey et al., 2011; Carstens et al., 2012; Lemmon & Lemmon, 2013; McCormack & Faircloth, 2013). In a single sequencing run, NGS generates thousands of loci across multiple individuals, which can be used to address a number of evolutionary questions at both deep and shallow time scales. Restriction-site Associated DNA sequencing (RAD-seq) has gained popularity as an alternative to costly whole genome sequencing due to its flexibility, with a variety of protocols that can be tailored to address specific evolutionary and ecological questions (McCormack & Faircloth, 2013; Andrews & Luikart, 2014; Andrews et al., 2016). Furthermore, these techniques can easily be applied to non-model organisms without an available reference genome at an affordable cost. RAD-seq is a reduced representation library method, which samples a subset of the genome to identify loci, represented by single nucleotide polymorphisms (SNPs) that are homologous across multiple samples. In brief, high molecular weight genomic DNA is digested with one or more restriction enzymes, and sequencing adapters are ligated to the loose ends flanking the cut sites. Several size selection and PCR cleanup steps enable the researcher to choose the size of the fragments to sequence, and unique barcode adapters to each individual can be ligated to enable pooling of hundreds of samples into a single genomic library with sequences per individual later processed by bioinformatic tools (see Fig. 1A for a workflow summary). These methods have been used for a number of evolutionary questions in many model and non-model

organisms, for both population (Etter et al., 2011; Seeb et al., 2011; Eaton, 2014) and phylogenomics (Cariou et al., 2013; Leaché et al., 2014; Pante et al., 2014; Leache et al., 2015), and are likely to continue to do so for the foreseeable future (Davey & Blaxter, 2010; McCormack & Faircloth, 2013). Exciting new applications with genomic data are now being used for biodiversity and conservation research, including for high resolution phylogeographic (Emerson et al., 2010; Lexer et al., 2013, 2014; Jeffries et al., 2015; Macher et al., 2015), and the emerging field of landscape genomics, which incorporates elements of population genetics and landscape ecology to identify the factors that shape variation across the genome (Bragg et al., 2015; Rellstab et al., 2015).

Genomic data greatly expands the potential of landscape genetics approaches (Storfer et al., 2007) for understanding what drives patterns of genetic diversity, and is likely to provide vital information to underpin future conservation strategies (Jeffries et al., 2015). In lowland East Africa, two adjacent biodiversity hotspots, the coastal forests of Eastern Africa and the Eastern Afromontane region comprise a highly diverse and heterogeneous habitat mosaic (Burgess et al. 2004). Habitat heterogeneity in this region is hypothesized to be influenced by a number of environmental factors including current climate and topography, but also historical aspects such as mountain building and paleo-climatic changes, thought to be responsible for changes in the structure of hydrobasins, sea level changes and the expansion and contraction of habitats. Species diversity and biogeographic patterns across many groups with varied life histories closely matches this habitat heterogeneity, and many clades often exhibit clear phylogeographic structure, which is a reflection of the environmental changes that have occurred in this region over time. The amphibians of this region are highly diverse, but despite much recent work to refine species distributions, taxonomy and phylogenetic relationships (Blackburn, 2008; Lawson, 2010; Zimkus et al., 2010, 2012; Liedtke et al., 2014; Loader et al., 2015), there remains a lack of studies that have examined intraspecific genetic diversity in high detail. The few papers that have looked at intraspecific diversity typically found high phylogenetic and phylogeographic structure, but have been extremely limited by spatial sampling as they have mostly focused on narrow ranged species which are notoriously difficult to sample adequately (Loader et al., 2014; Lawson et al., 2015). Furthermore, a distinct lack of adequate population genetic resources for African taxa in general such as microsatellites or anonymous nuclear loci have prohibited accurate quantification of genetic diversity and fine scale population structure (e.g. Barratt et al., 2012)

Amphibians are an ideal study organism to investigate the effects of the environment on genetic diversity because they are poor dispersers (Wiens, 1993), and sensitive to climate and habitat changes (Zeisset & Beebee, 2008). Widespread clades may be especially informative as they often consist of a number of unique evolutionary lineages that have been shaped by geographic distance, topography, hydrological features, and current and historical habitat suitability, especially in the tropics (Lawson, 2013). In this paper, we employ next generation sequencing (RAD-seq) to investigate phylogeographic patterns, genetic diversity and their environmental correlates. With new field sampling from across the region, we focus on five widespread species including Fornasini's spiny reed frog, *Afrixalus fornasini* (Bianconi 1849), the Yellow spotted tree frog, *Leptopelis flavomaculatus*, (Günther 1864), and the Dwarf squeaker *Arthroleptis xenodactyloides* (Hewitt 1933). A further two species clades that likely represent species complexes are investigated, the Silvery treefrog, *Leptopelis argenteus* (Pfeffer 1893) group which includes *L. broadleyi* (Poynton 1985) and *L. concolor* (Ahl 1929), and Dwarf spiny reed frogs including *Afrixalus stuhlmanni* (Pfeffer 1893), *A. sylvaticus* (Schiotz 1974), *A. brachycnemis* (Boulenger 1896) and *A. delicatus* (Pickersgill 1984). Using high resolution genomic data for each clade we i) resolve phylogenetic relationships and phylogeographic structure, and ii) test the most likely

environmental correlates which explain genetic distances between localities (F_{ST}) by using electrical circuit theory and connectivity modelling.

Materials and methods

Sample collection

Samples were collected across the study region in 2013-2015 with fresh tissue samples (leg muscle, liver or toe clips) stored in 100% ethanol to preserve DNA. Additional samples held in collections at the University of Basel, University of Jena, Natural History Museum, London, Science Museum of Trento, Museum of Comparative Zoology, Harvard and Museum of Vertebrate Zoology, Berkeley (collected between 2001 and 2012) were used to complement new field data. A summary of samples used for RAD-seq library preparation along with the total numbers of reads is shown below in Table 1.

Table 1. Summary of samples and unique locality numbers per species used in this study. Total number of sequence reads for each clade is also shown. A full list of all samples and their matching locality data is provided in Table S1.

	No. samples	No. unique localities	Total number of sequence reads (bp)
<i>Afrixalus fornasini</i>	44	30	182,663,928
<i>Leptopelis flavomaculatus</i>	59	25	299,581,783
<i>Afrixalus stuhlmanni</i>	50	32	243,690,376
<i>Arthroleptis xenodactyloides</i>	54	35	199,514,898
<i>Leptopelis argenteus</i>	27	17	154,933,766

DNA extraction and RAD library preparation

Genomic DNA was extracted following the DNeasy Blood & Tissue Kit (Qiagen) procedure for all samples across the five clades. Verification of species identifications were made using the BLAST tool (NCBI, 2016) against our own 16S DNA barcoding database of amphibians across the region. DNA was quantified prior to RAD-seq library preparation using a Qubit fluorometer and visual inspection on agarose gel to verify that DNA was intact. DNA concentration varied from 6–500 ng/ μ l). We included samples to represent outgroups for each clade, which are included in Table 1. The number of samples in RAD-seq libraries ranged from included 44 *Afrixalus fornasini* from 30 localities, 59 *Leptopelis flavomaculatus* from 24 localities, 50 *Afrixalus stuhlmanni* from 32 localities, 27 *Leptopelis argenteus* from 17 localities, and 54 *Arthroleptis xenodactyloides* from 35 localities. We spread all samples across six RAD libraries with between 45 and 51 samples per library each with an individual barcode adapter to demultiplex sequences bioinformatically. To work with an even concentration of 6 ng/ μ l for each library, different amounts of DNA and water were mixed for each sample in order to obtain a solution of 50 μ l. Following the RAD-seq library preparation protocol of Etter et al. (2011), 5.0 μ l of 10x NEB Buffer 4 and 1.5 μ l of the restriction enzyme HF *SbfI* (New England Biolabs) were added to the 50 μ l solution, for a total of 56.5 μ l total reaction volume. Samples were then put on a heatblock at 37°C for 65 minutes. 5 μ l of P1 adapter were added to the sample along with 1 μ l 10x NEB buffer 2, 0.6 μ l of rATP, 0.5 μ l T4 DNA Ligase, 2.9 μ l H₂O and incubated at room temperature for 45 min. Samples were again heat-inactivated for 20 min at 65°C, pooled, and

randomly sheared (Bioruptor UDC-300) to an average size of 500 bp. Sheared product was cleaned using “MinElute Clean-Up Kit” (Qiagen). Samples were then run out on a 1.25% agarose, 0.5x TBE gel and DNA ranging in size 300 bp to 500 bp was isolated using a “MinElute Gel Purification Kit” (Qiagen). The Quick Blunting Kit (NEB) was used to end repair the DNA. Samples were then purified using a QIAquick column and 3 µl of Klenow Fragment was used to add adenine overhangs on the 3’ end of the DNA at 37°C for 30 min. After another purification, 1 µl of P2 adapter was ligated to the DNA fragments. Samples were again purified and eluted in 52 µl EB buffer. 5 µl of this product was used in a PCR amplification with 25.5 µl Phusion Master Mix, 1.2 µl of forward and 1.2 µl of reverse 10 uM Solexa amplification primers, and 20.5 µl H₂O. PCR product was then purified and run on a gel, DNA 300-500 bp excised and eluted in 25 µl EB. The final eluted product was sequenced (single-end) on an Illumina Hi-seq 2500 at the D-BSSE sequencing facility in Basel, Switzerland.

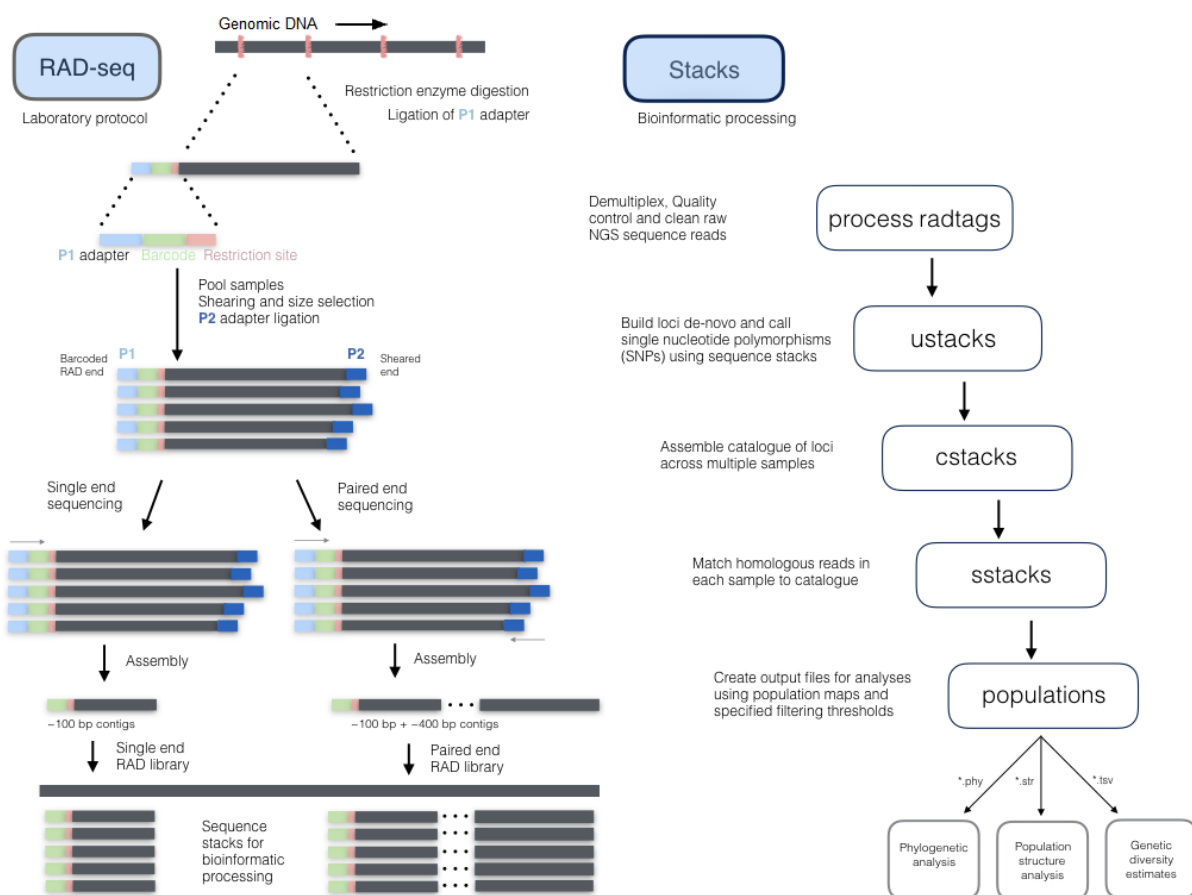


Fig. 1. Workflows for data generation in this study. A) RAD-seq laboratory protocol, B) Stacks bioinformatics.

Data filtering, SNP calling

We used STACKS v.1.41 (Catchen et al., 2011, 2013) to process RAD-seq data and produce single nucleotide polymorphism (SNP) datasets. We used the *process_radtags.pl* script to demultiplex each individual sample into its own .fastq file containing all sequence data based on its barcoded adapter during library preparation. The standard workflow of *ustacks*, *cstacks* and *sstacks* modules were then used to align reads into stacks, build a catalogue of consensus loci by merging alleles across individuals together, and match individuals to the catalogue of loci, respectively (see Fig. 1B). As with most recommendations for RAD-seq studies due to the uniqueness of

each dataset (Cruaud et al., 2014; Huang & Knowles, 2016), and the varying sequencing quality and effort across samples, we initially explored our data with different filtering parameters to investigate the effects of missing data caused by allelic dropout, which is a common problem of RAD-seq datasets caused by uneven sequencing effort across samples (datasets summarized in Table S2). Despite checking DNA quality and molecular weight before sequencing, our sampling still contained several samples with low numbers of sequence reads compared to the rest, so we also created datasets with the removal of any sample with less than 100MB sequence data (hereafter referred to as ‘poorly sequenced samples’). We did this because the inclusion of these samples reduced the homology of SNPs, and the overall number of loci, especially for population and genetic diversity analyses (Graham et al., 2015). This resulted in the removal of 9 *A. fornasini*, 5 *A. stuhlmanni*, 1 *L. argenteus*, 1 *L. flavomaculatus* and 18 *A. xenodactyloides* samples. Our final catalogue of loci for each dataset used a conservative minimum depth of sequencing coverage of 5x (default = 2x). Based on this catalogue, data matrices were generated using the *populations* module for downstream analyses in each software pipeline using specific output file types and parameters (details in each following section).

Phylogeny

Appropriate sister taxa outgroups for each clade were selected based on known phylogenetic relationships (Frost, 2016). We used *Afrivalus osorioi* and *Afrivalus quadrivittatus* as outgroups for *Afrivalus fornasini* and *Afrivalus stuhlmanni*, respectively. For the *Leptopelis* datasets we used a single sample from each dataset as an outgroup in the other as they are closely related (i.e. a single *L. argenteus* in the *L. flavomaculatus* dataset and vice versa), and *Arthroleptis stenodactylus* as the outgroup for *A. xenodactyloides*. After data filtering, we exported full phylip files for constructing phylogenies which included all SNPs including adjacent RAD-tag sequences as per Leache et al. (2015). We created three datasets for each species group with differing degrees of missing data based on the minimum proportion of the total samples (30, 40 and 50%), with a minimum of 5x coverage for each RAD locus. The phylip files were then imported into RAxML 8.2 (Stamatakis, 2014), relevant outgroups were defined, and we ran the ML + rapid bootstrap algorithm with the GTR+GAMMA+ Γ model. We set the bootstrap replicates parameter to AUTOMRE with the Lewis ascertainment bias correction, which accounts for the omission of constant invariant sites from the data matrix, which may lead to branch length overestimation (Leache et al., 2015).

Population structure

To generate population structure datasets we first removed outgroups and used a stricter minimum sequencing coverage per locus of 7x, and the maximum amount of missing data in the matrix set to 40%. For all population structure analyses we restricted data matrices to only include a single SNP per locus to avoid problems of high linkage disequilibrium between variable sites in the same locus (Andrews et al., 2016). We used discriminant analysis of principal components (DAPC) in the Adegenet R package (Jombart et al., 2008), first converting structure files into fstat format using PGDSpider 2.1.0.3 (Lischer & Excoffier, 2012). We defined multiple values of k (population clusters) between 1 (i.e. a single panmictic population) and the maximum number of individuals in each dataset. For each value of k , the Bayesian Information Criterion (BIC) is calculated, with lower scores indicating a higher probability of that number of population clusters. Unlike other software such as Structure (Pritchard et al., 2000) and FastStructure (Raj et al., 2014), the DAPC method is free of assumptions regarding the population genetic laws of Hardy-Weinberg equilibrium which are likely to be violated by small population

sizes and low numbers of samples per population, which is highly likely in our amphibian data. Furthermore, DAPC has been shown to perform as well or better than other comparable methods for assessing population structure, (Jombart et al., 2008; Jeffries et al., 2015). After preliminary DAPC examination of each clade in full (Fig. S2), we created finer-scale datasets which removed the highly divergent samples, as they were so genetically diverse they masked the population structure detected with the other samples.

Genetic distances and correlations with environmental data

An F_{ST} matrix between individuals from sampled localities per clade was used to test correlations of genetic distance (F_{ST}) with environmental data using multiple regression, Mantel and partial Mantel tests (see Lawson et al., 2013). For calculations of genetic distances (F_{ST}) we opted for an extremely strict minimum coverage of 20x, with missing data minimized (no more than 30% missing data in the matrix) and restricted the number of SNPs to a single site within each RAD locus, again removing poorly sequenced specimens as these would also bias the F_{ST} estimates. For environmental data we selected variables that could be expected to influence observed genetic distances in amphibians, related to geography (Euclidean distance, topographic slope), habitat suitability now and in the past (Last Glacial Maximum), paleo-climate (absolute temperature and precipitation anomalies in the LGM and Pliocene as a proxy of climatic stability), and hydrological features (hydrological connectivity via waterways, and hydrological basins). Euclidean distance between cells was calculated in ArcGIS 10.2.1 using the EucDistance.py script, along with slope which was calculated using the surface analysis tool based on a digital elevation model at 30 arc-second resolution. (GTOPO30; USGS, available from: <http://csgtm.iscgm.org/dataset/gtopo30>). Current habitat suitability was estimated using a distribution model for each clade in MAXENT 3.3.3k (Phillips et al., 2006), using nine uncorrelated Bioclim variables (Pearson's $r < 0.7$) from the Worldclim database (Hijmans et al., 2005). Known presence localities and model parameterization settings for species distribution models follow Barratt et al. (in review). The LGM habitat suitability was generated by projecting the current suitability model onto the matching nine Bioclim variables from the LGM time period (Braconnot et al., 2006). Paleo-climate data used a measure of climate change velocity following Sandel et al (2011), estimating the absolute difference between the temperature and precipitation for the LGM, the Pliocene and the present. Low measures of change indicate more stable climatic conditions over time. Downscaled and geo-processed paleo-climate data was supplied Dr. W.D. Kissling (University of Amsterdam) for the LGM ca. 21 kya (Braconnot et al., 2006), and late Pliocene ca. 3 mya (Haywood & Valdes, 2004). Current climate data (1960-1990) was downloaded from the Worldclim database (Hijmans et al., 2005). Hydrological data for mapping of river systems was based on a shapefile of inland waterways (USGS, 2016), and we differentiated hydrological basins using the HydroBASINS shapefile (Lehner & Grill, 2013). All environmental data were clipped to our study region using ArcGIS 10.2.1.

For each environmental variable we created a distance matrix matching the dimensions of the F_{ST} matrix so we could test correlations between variables and genetic distance across species clades. For the current habitat suitability, LGM habitat suitability, slope and hydrology (waterways) we used Circuitscape (McRae & Beier, 2007) to generate connectivity matrices between each sampling site (Fig. 2). Circuitscape transforms the landscape (represented by each environmental variable individually) into a conductivity surface, with values ranging from 0 (complete resistance) to 1 (complete connectivity) based on electrical circuit theory. The least cost paths are calculated (i.e. most suitable routes) between sampling localities through environmental space, and dispersal

routes are shown as high values on conductivity maps, with less suitable routes shown as low numbers. Maxent outputs were used for current and LGM habitat suitability (higher suitability pixels had higher conductance), slope was scaled (0 = vertical, 1 = flat), and waterways were assigned a value of 1 (non-waterways as 0). Because values of 0 are interpreted as absolute barriers to gene flow, we transformed all zero occurrences to extremely low values of 0.0001 in our data matrices before running Circuitscape. For geographic distance between sampling localities we used the Euclidean distance matrix from ArcGIS, and for hydrological basins we counted the minimum number of hydrobasins separating each sampling locality. Measures of connectivity during the LGM and Pliocene were calculated using least cost paths calculated in SDMtoolbox (Brown, 2014).

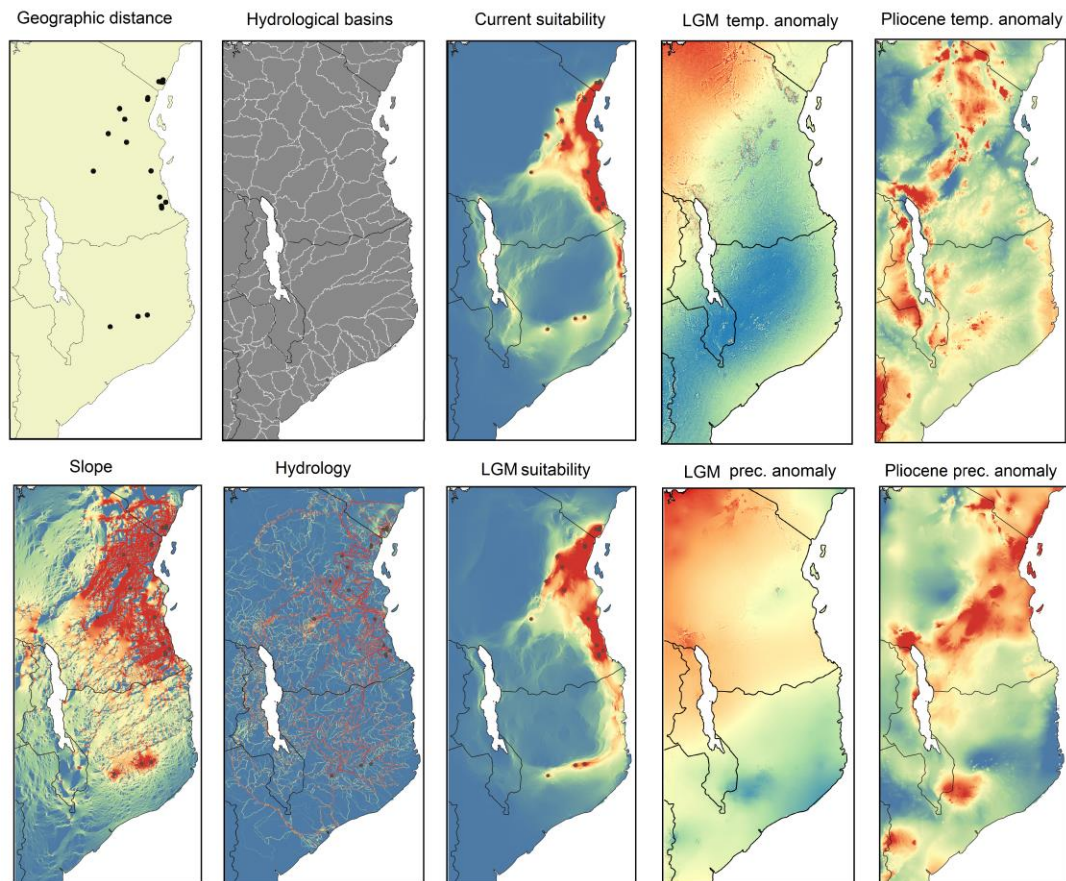


Fig. 2. Environmental variables tested against genetic distances. Example shown is *Afrixalus stuhlmann* clade ii (shown on phylogeny in Fig. 3). Variables represent geography (Geographic distance, slope), hydrology (hydrological basins, waterway connectivity), habitat suitability now and in the past (current, LGM) and paleo-climate (LGM and Pliocene anomalies of temperature and precipitation). Warmer colours represent higher connectivity for geographic, hydrological and habitat variables, and higher stability for paleo-climate variables. Sampling points shown as black dots overlaid on the geographic distance variable.

Results

Data quality, SNP calling and processing

We obtained single-end Illumina reads of 90 bp length for 44 *Afrixalus fornasini* (182,663,928 reads), 50 *Afrixalus stuhlmanni* (243,690,376 reads), 27 *Leptopelis argenteus* (154,933,766 reads), 59 *Leptopelis flavomaculatus*

(299,581,783 reads) and 54 *Arthroleptis xenodactyloides* individuals (199,514,898 reads) (Table 1). Phylogenetic datasets contained between 46,699-185,591 variable sites from 2,380-7,559 loci, with the complete sequences (including non-variable sites) exported as phylip files (464,651-1,475,958 bp) for phylogenetic analyses, and population structure datasets contained 2,257-38,462 unlinked SNPs from 2,272-38,659 loci (Table S2). Genetic diversity (F_{ST}) datasets contained between 1,266 and 3,075 loci. Within three datasets (*A. fornasini*, *A. stuhlmanni*, *A. xenodactyloides*) we observed a fairly large amount of allelic dropout when exporting data matrices across all samples probably due to poorly sequenced samples with degraded DNA at RAD-seq *SbfI* enzyme cut sites, these samples were mostly museum derived, not freshly collected tissue samples. In general the *Leptopelis* (*L. argenteus*, *L. flavomaculatus*) datasets were much more robust to allele dropout as they contained far fewer poorly sequenced samples (n=1 for each dataset).

Phylogeny

Phylogenetic relationships (Fig. 3) were consistent across trees generated from different datasets with the exception of varying node support and minor differences in the placement of certain individuals likely due to large amounts of missing data even in small matrices because of sequencing effort (Fig. S1). Our phylogenetic analyses show that the three clades exhibiting high divergences (*A. stuhlmanni*, *L. argenteus*, *A. xenodactyloides*) appear to be species complexes containing multiple species. *Afrivalus stuhlmanni* consists of two deeply diverged subclades (i and ii) on the phylogeny, the first appears to correspond with samples *A. delicatus* (previously recognized as *A. brachycnemis*) and a second subclade containing *A. stuhlmanni* and *A. sylvaticus*. In *Leptopelis argenteus*, two main subclades are present, matching the southern *L. argenteus*, with *L. broadleyi* part of the *L. argenteus* clade (subclade i), and northern *L. concolor* (subclade ii). *Arthroleptis xenodactyloides* also shows an extremely strong signal of high differentiation, with two deeply diverged subclades likely representing *A. xenodactyloides* (subclade i) and the closely related but unconfirmed species, *A. stridens* (subclade ii) (Pickersgill 2007) which was described from Kambai and Longuza forest reserves in East Usambara. The clear differentiation shown by these three clades is markedly less so in the remaining two clades, though *A. fornasini* and *L. flavomaculatus* do show phylogenetic structuring, which is generally restricted to the deep divergence between samples from the southern part of the coastal forest and surrounding areas (e.g. Mozambique, Malawi).

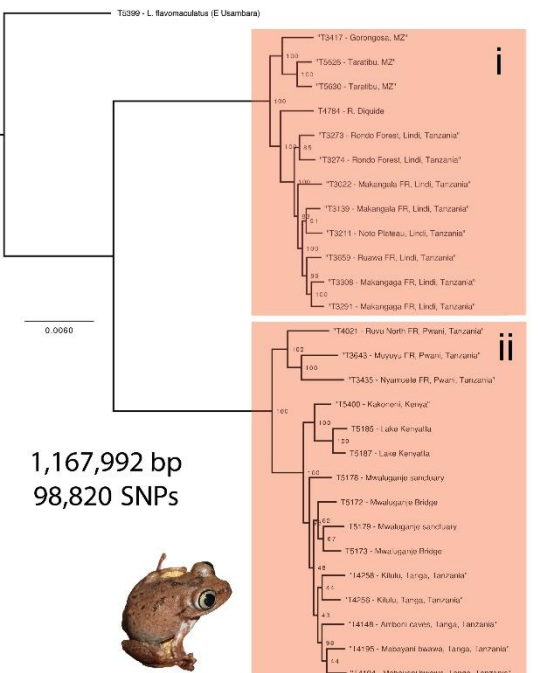
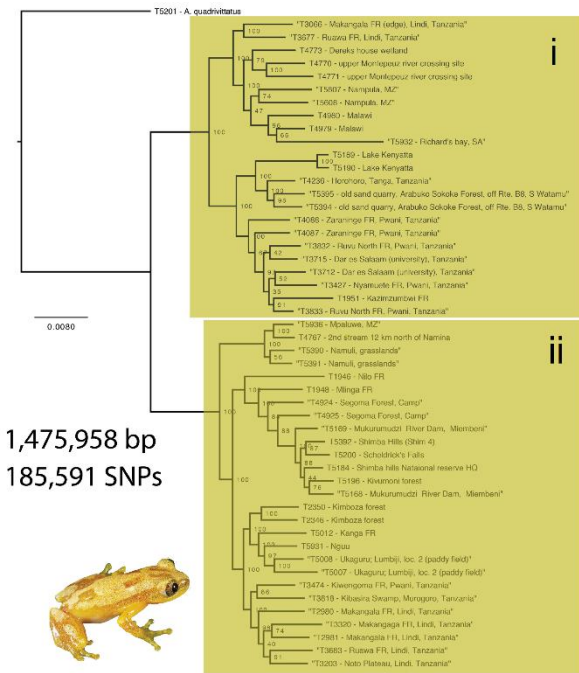
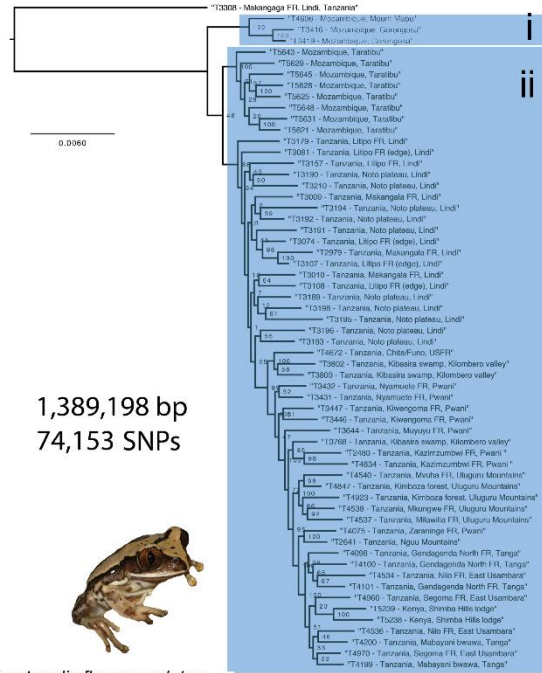
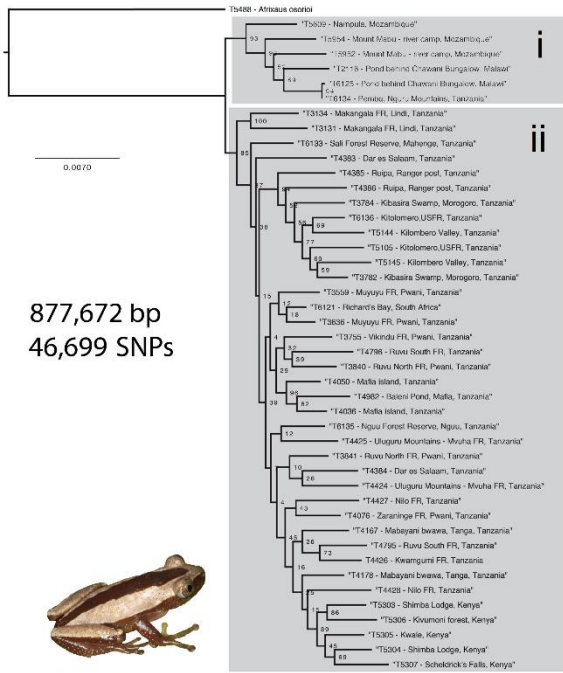


Fig. 3. Phylogeny for each clade revealed by RAD-seq (50% missing datasets shown). Note the deep phylogenetic structure present in *A. stuhlmanni*, *A. xenodactyloides* and *L. argenteus* with high node support, compared to the shallower divergences exhibited by *A. fornasini* and *L. flavomaculatus* and comparatively poor node support. Fig. S1 shows the same topologies with the 40% missing datasets. Each major subclade is numbered.

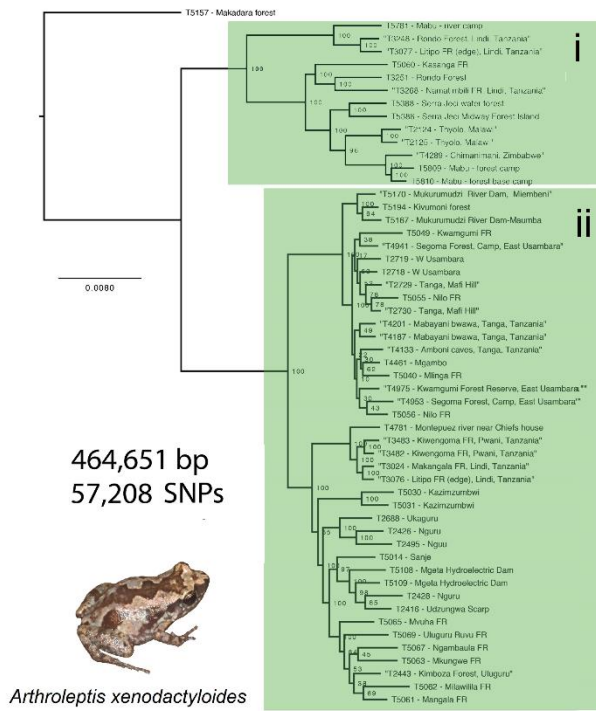


Fig. 3. (continued).

Population structure

Data matrices allowed population and phylogeographic structure to be detected with high statistical power from thousands of unlinked loci (Fig. 4). The analysis for each dataset revealed high congruence with the phylogenetic results, but the presence of highly divergent populations in Mozambique and Malawi in some cases (e.g. *Afrixalus fornasini*, *Leptopelis flavomaculatus*) masked the signal of population structure in the more closely related individuals (Fig. S2). However, once removing these outliers, the population structure became much clearer, displaying between 3 and 6 population clusters per clade based on the lowest BIC scores (3 population clusters for *A. fornasini*, *L. flavomaculatus*, and 6 for *A. xenodactyloides*, *L. argenteus* and *A. stuhlmanni*). These clusters of populations were clearly geographically structured across clades, matching phylogenetic patterns (Fig. 4, Mozambique and Malawi *A. fornasini* and *L. flavomaculatus* not shown due to low sample numbers).

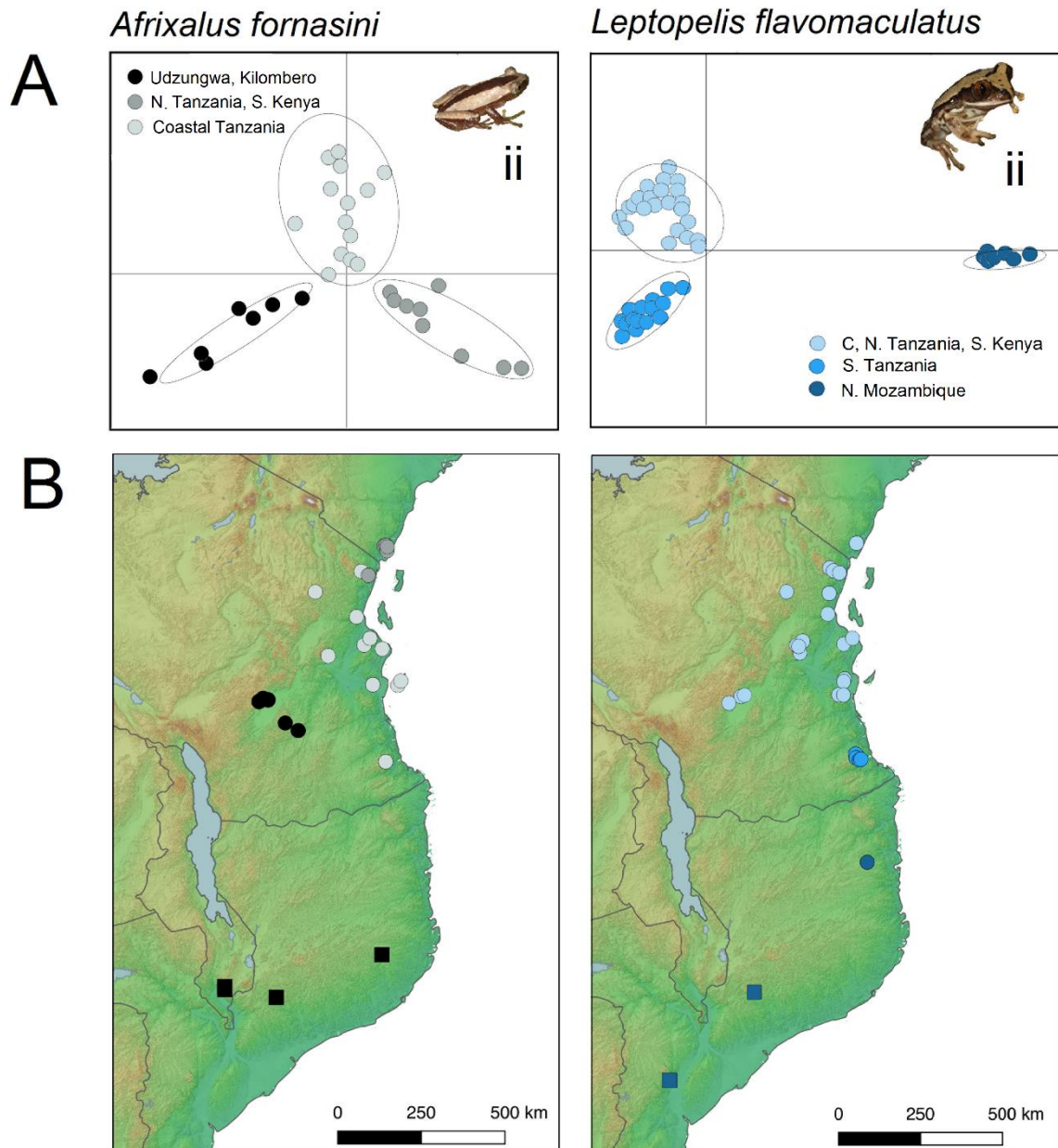


Fig. 4. A) Fine scale population structure across each subclade using discriminant analyses of principal components (Jombart et al., 2008). Numbers next to species photos refer to matching subclade identified by phylogeny in Fig. 3 (subclade i for *Leptopelis flavomaculatus* and *Afrixalus fornasini* not shown due to low sample numbers). Inferred population clusters are separated by different colours. B) Map of the distribution of each population cluster in geographical space.

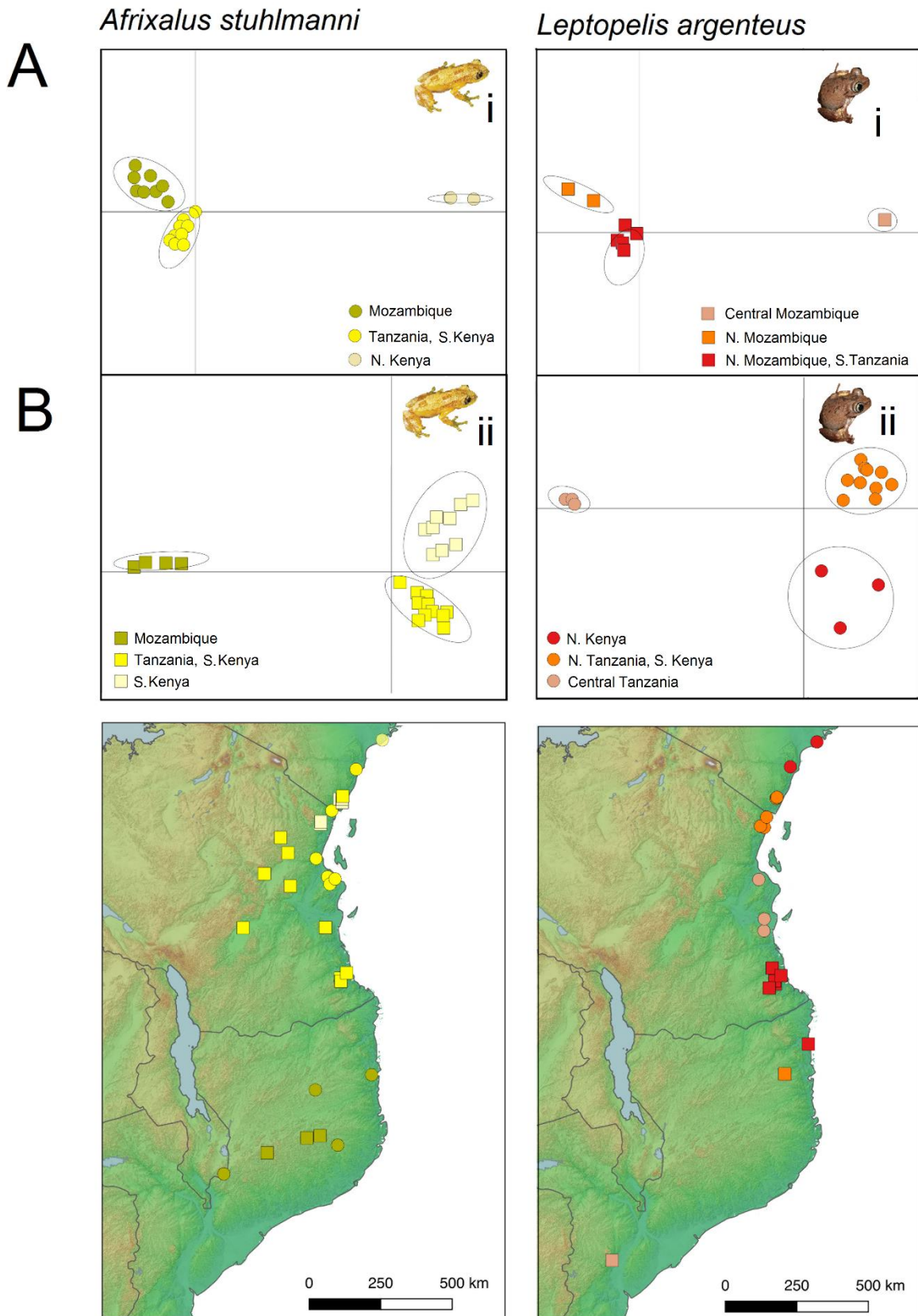


Fig. 4. (continued).

Arthroleptis xenodactyloides

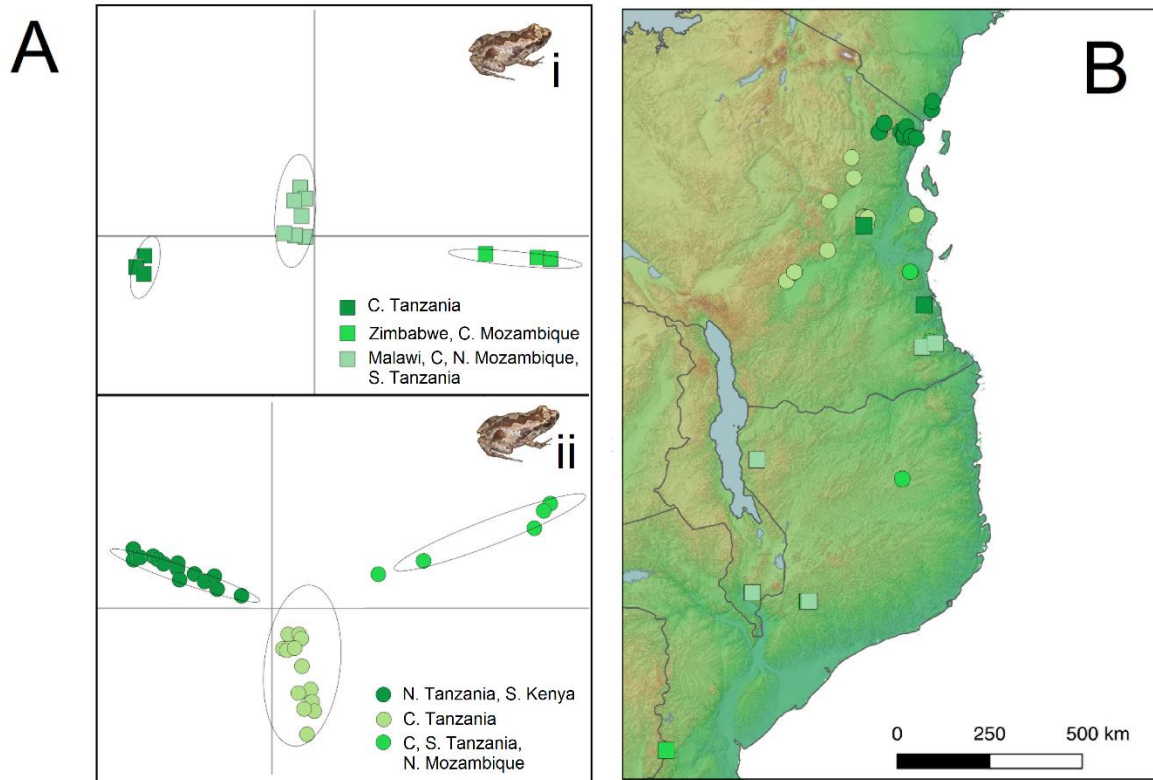


Fig. 4. (continued).

Genetic distances and correlations with environmental data

Although each of the clades we investigate here are widespread, we would expect different levels and routes of connectivity due to their unique ecologies and response to environmental change which may influence their phylogenetic and population structure. Multiple regression, Mantel and partial Mantel tests show the relationships between genetic distance (F_{ST}) and environmental data distance matrices representing geography (Euclidean distance, Slope), habitat suitability (current, LGM), paleo-climate (LGM and Pliocene precipitation and temperature anomalies), and hydrological features (hydrological basins, hydrology) (Table 2, Table S3). Results show that F_{ST} estimates for *Afrixalus stuhlmanni*, *Leptopelis argenteus* and *Arthroleptis xenodactyloides* are highly correlated with measures of historical habitat connectivity and the spatial arrangement of hydrological basins, but these correlations are less evident in the remaining two (*Leptopelis flavomaculatus* and *Afrixalus fornasini*). Multiple regression analyses show the importance of current, historical and geographic factors in explaining genetic distances, which are significantly correlated variables with F_{ST} within all of the three clades that display high levels of divergence (*A. stuhlmanni*, *L. argenteus*, *A. xenodactyloides*). No clades are closely associated with hydrological features using multiple regression. Overall, the fit of the linear models were significantly different from random (Fisher's scores, Table S3). Mantel tests reveal that in addition to geographical and historical factors, habitat and hydrological basins are significantly correlated to F_{ST} across all species clades except for *A. fornasini*. These correlations are confirmed by controlling for geographic distance (partial Mantel tests) in all clades except for *A. fornasini* and *L. flavomaculatus*. Together, results from multiple regression, Mantel and partial Mantel tests show the clear differences between environmental correlates of F_{ST} across clades,

and point toward the importance of historical climate and habitat connectivity along with hydrobasin structure, especially for species clades that are highly structured. The analyses clearly reflect the differences shown by *A. fornasini* and *L. flavomaculatus* which show comparatively low population divergences compared to *A. stuhlmanni*, *L. argenteus* and *A. xenodactyloides*.

Table 2. Summary of statistically significant ($p < 0.05$) environmental correlations with F_{ST} using multiple regression, partial Mantel and Mantel tests. Results are summarized for each of the eight subclades matching Fig. 4. Full results are shown in the supplementary material (Table S3).

	Multiple regression	Partial Mantel	Mantel
<i>Afrivalus fornasini</i> (subclade ii)			Pliocene prec., Pliocene temp.
<i>Leptopelis flavomaculatus</i> (subclade ii)			Pliocene prec., Pliocene temp., Hydrobasins
<i>Afrivalus stuhlmanni</i> (subclade i)		Hydrobasins, Pliocene prec.	Geographic distance, Hydrobasins, Pliocene prec.
<i>Afrivalus stuhlmanni</i> (subclade ii)	Current habitat, LGM temp.		Geographic distance, current habitat, LGM habitat, LGM temp., LGM prec., Pliocene temp., Pliocene prec., Hydrobasins
<i>Leptopelis argenteus</i> (subclade i)	Geographic distance, Slope	LGM temp., LGM prec., Hydrobasins	Geographic distance, current habitat, LGM habitat, LGM temp., LGM prec., Pliocene temp., Pliocene prec., Hydrobasins
<i>Leptopelis concolor</i> (subclade ii)		Current habitat, Hydrobasins, Pliocene prec.	Geographic distance, current habitat, LGM temp., Pliocene prec., Pliocene temp., Hydrobasins, Hydrology
<i>Arthroleptis xenodactyloides</i> (subclade i)	Slope		
<i>Arthroleptis xenodactyloides</i> (subclade ii)	LGM prec., Pliocene prec.	LGM prec., LGM temp., Pliocene prec., Pliocene temp., Hydrobasins	LGM prec., LGM temp., Pliocene prec., Pliocene temp., Hydrobasins

Discussion

The genomic techniques that we employ in this manuscript provide high resolution genomic data for five poorly understood clades, showing distinct phylogenetic structure in each. Major divergences between populations in northern and southern coastal forest lineages are clearly shown. This general congruence supports the broad biogeographical breaks between East African terrestrial ecoregions and species turnover patterns, caused by differences in vegetation structure and hydrological features, reflecting contemporary and historical climate processes in this region. However, though similar at broad scales, finer scale population structure patterns are not entirely congruent across clades and subclades. Environmental correlates of genetic distance highlight these differences, with F_{ST} in the three highly diverged clades highly correlated with historical factors and hydrological basin structure, and weak correlations with environmental variables in the remaining two clades with shallow divergences. The differences between these taxa demonstrate the importance of understanding diversity patterns across multiple species and geographic scales, as studies of single species may provide a somewhat limited perspective of biodiversity patterns. To this end, genomic data will play a key role in the future to provide useful information for conservation planning at multiple spatial and taxonomic scales.

Biogeography and phylogeography

The major biogeographic breaks and deep phylogeographic structure in our data is a clear reflection of the known biogeographic affinities in lowland East Africa for several other taxonomic groups (Tolley et al., 2011; Linder et al., 2012; Lorenzen et al., 2012; Smits et al., 2013; Zinner et al., 2013; Demos et al., 2015; McDonough et al., 2015; Bertola et al., 2016; Pozzi, 2016) and reinforces known diversity patterns corresponding to our knowledge of vegetation types and terrestrial ecoregions in East (White, 1983; Fayolle et al., 2014, Burgess et al. 2004). The division between the Northern and Southern Zanzibar Inhambane coastal forest mosaics is evident in each of the three deeply divergent clades (*A. stuhlmanni*, *L. argenteus*, *A. xenodactyloides*) and also to a lesser extent in *L. flavomaculatus* and *A. fornasini*. The divergences detected in all phylogenies are also recovered within population structure analyses, which detect even clearer genetic clusters of populations across clades. This structure provides clues to the biogeographic relationships between coastal forests and adjacent areas in East Africa.

Almost twenty years ago, Burgess et al. (1998) showed that several parts of the coastal forest region could be considered as refugia as they support a number of range restricted species that are endemic to small forest patches. Just under a decade later, Azeria et al. (2007) investigated the biogeographic patterns of the same coastal forest patches in Tanzania and Kenya with distribution data for birds, mammals and reptiles, concluding that the consistent clustering of species in coastal forest patches in the Usambara-Kwale and Lindi regional subcentres of endemism implied that these areas should be considered as distinct biogeographic provinces. The same paper (Azeria et al. 2007) also demonstrated that though patterns between areas can be generalized across a large number of species, they are strongly influenced by life history traits, in particular dispersal abilities, which could be an explanation for the highly disjunct distributions of reptiles. The authors suggested that reptiles, as poor dispersers, could be good candidates for tracing the effects of past environmental history using phylogeny-based approaches. Our use of amphibians which are generally considered poor dispersers with highly structured amphibians support the existence of coastal forest refugia (Burgess et al. 1998) and the distinct biogeographic provinces identified in several coastal forest areas (Azeria et al. 2007). Furthermore our analyses point toward the importance of paleo-

climate, hydrological basin structure and geographic features in determining the observed phylogeographic patterns.

Environmental correlates of genetic diversity

It is well established that many biodiversity patterns can be explained by contemporary environmental factors such as climate and topography (Rosenzweig, 1995). These factors are in part responsible for the present day vegetation structure in Africa (White, 1983; Fayolle et al., 2014), the distribution of terrestrial ecoregions (Burgess et al. 2004), and hydrological structure (Salzburger et al., 2014). However, historical processes are clearly also important in explaining biodiversity patterns, (Ricklefs, 2004; Sandel et al., 2011, Harrison & Noss, 2017), and there is little doubt that history has a strong influence on present day biodiversity (Jetz et al., 2004). These concepts apply to genetic diversity within species as well as more generally to species richness and endemism patterns, though disentangling contemporary and historical drivers of biodiversity remain difficult to prove.

A number of hypotheses discussed by Burgess et al. (1998) to explain endemism patterns of species in the coastal forests are directly relevant to understanding which factors may contribute to the patterns of genetic diversity and population structure outlined in this paper. These hypotheses include the potential effects of historical climate, sea level change and recent evolution on diversity patterns. The aridification of East Africa combined with Milankovitch climate oscillations since the Miocene fragmented once continuous areas of forest into isolated patches (Axelrod & Raven, 1978; Demenocal, 1995; Trauth et al., 2005; Sepulchre et al., 2006; Maslin et al., 2014). Though wetter periods during the late Miocene and Pliocene (Lovett, 1993) may have offered opportunities to reconnect isolated forest patches, the general trend of aridification and forest fragmentation present a plausible explanation for the high genetic diversity and population structure in most of our study clades. Repeated sea level fluctuations since the Miocene have also affected the coastal forest and surrounding areas, with significant inundations that are likely to have completely covered most low-lying areas of coastal forest at some point, and in many cases, repeatedly (Burgess & Clarke, 2000). Areas of higher ground are therefore probable refugia during periods of sea level change, particularly the raised plateau systems across the coastal forests and lowland Eastern Afrotropical. The deep divergences shown by our data appear to refute the possibility that recent evolution has occurred in the coastal forest amphibians however, supported by a mtDNA time-calibrated phylogeny placing most of the divergence times between major subclades as occurring between 2 and 8 million years ago (Barratt et al. in review). These dates seem to suggest the importance of the climatic and tectonic upheaval in East Africa beginning throughout the Miocene, which not only affected forest distribution and sea levels but also dramatically altered the hydrology of the region (Salzburger et al. 2014).

Hydrological structure was not discussed by Burgess et al (1998) as a potential driver of endemism patterns in the coastal forest but can be expected to be a major influence on the genetic structure of amphibians. Tectonic uplift since the Miocene had a profound effect on the hydrology of Africa, where in some cases progressive rifting even reversed the flow of major rivers such as the Congo which is estimated to have once formed a substantial delta around the Rufiji river in Tanzania up to 500 km wide (Stankiewicz & de Wit, 2006). The structure of hydrological basins is a correlate of genetic diversity across most of the studied clades in this paper, and is also reported in other literature as an explanatory factor for differentiation between species and populations in this region (Measey et al., 2007; Lawson, 2013). Major rivers may have also acted as barriers which facilitated genetic isolation (Voelker et al., 2013), examples such as the Ruvuma river separating Mozambique

from Tanzania and would explain some of the major biogeographic breaks we observe in our data, particularly the splits between Tanzania/Kenya and Mozambique/Malawi (Lorenzen et al., 2012). Other major rivers appear to be reasonable explanations for the phylogeographic structure such as those shown across Tanzania and Kenya (Zinner et al., 2013; Zimkus et al. 2017) which can be seen by visually inspecting Fig. 4, particularly the Rufiji (*A. fornasini*, *A. xenodactyloides*), Pangani (*A. stuhlmanni*, *L. argenteus*, *A. fornasini*, *A. xenodactyloides*), and Wami (*L. argenteus*) in Tanzania and the Tana (*A. stuhlmanni*) and Galana (*A. stuhlmanni*, *L. argenteus*) rivers in Kenya.

These multiple lines of evidence combined with the known large numbers of relictual taxa that are represented by plants, birds and mammals (Fjeldsa & Lovett, 1997; Burgess & Clarke, 2000; Dimitrov et al., 2012. Bryja et al., 2016) in the coastal forests all suggest that the patterns of genetic diversity are caused by environmental heterogeneity, and likely to be a result of historical changes in the environment. This supports the idea that the areas of coastal forests are now facilitating this diversity, and can be considered as refugia (and in some cases micro-refugia) that have persisted through climatic change and deserve special conservation focus to protect them against future climate change and anthropogenic activity. Examples of this that are consistent across the studied species here include the Lindi and Usambara-Kwale subcentres of endemism which appear to be important in supporting unique elements of biodiversity which are not found anywhere else within the study region. Future directions for conservation of the coastal forest region, as for other biodiversity hotspots worldwide should consider the myriad of advantages that large scale genomic data can bring in terms of increasing the numbers of individuals, populations and species that can be sequenced with high throughput NGS technology. Uncovering the intraspecific genetic diversity patterns within multiple species, and identifying refugia is certain to provide useful information for future conservation planning at local and broad scales.

Systematics and taxonomy

A number of taxonomic implications also arise from our analyses, which should be considered in any future systematic work in the clades and species used in this paper. Though untangling the taxonomy of these species is beyond the scope of this paper, further work is most certainly required to refine the taxonomic definition and ranges of species aided by morphological and acoustic analyses. This is particularly relevant for *Afrixalus stuhlmanni*, *Leptopelis argenteus* and *Arthroleptis xenodactyloides* species clades in particular which display deep divergences on the phylogeny (Fig. 3), high genetic variation and poorly known distributions (Poynton, 2006, Blackburn & Measey et al. 2010, Pickersgill, 2007, Schiøtz, 1999). In East African amphibians this is a common pattern which is also reflected by a number of other species complexes in this region (Zimkus et al. 2017, Liedkte et al. 2016, Channing et al, 2013, Bwong et al. in review, Bittencourt-Silva et al. in review).

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Supplementary material

Fig. S1. RAD-seq phylogenetic trees using 40% missing data.

Fig. S2. Population analyses (DAPC) showing BIC scores for full species clade analyses.

Fig. S3. Population analyses (DAPC) showing BIC scores for subclades.

Appendix S1. Additional methodological information.

Table S1. IDs for samples used in RAD-seq library preparation.

Table S2. Summary of phylogenetic, population and F_{ST} datasets used for analyses.

Table S3. Multiple regression, Mantel and partial Mantel test results for environmental correlations with F_{ST} .

References

- Andrews K.R., Good J.M., Miller M.R., Luikart G., & Hohenlohe P.A. (2016) Harnessing the power of RADseq for ecological and evolutionary genomics. *Nature Reviews Genetics*, **17**, 81–92.
- Andrews K.R. & Luikart G. (2014) Recent novel approaches for population genomics data analysis. *Molecular Ecology*, **23**, 1661–1667.
- Axelrod D.I., Raven P.H. (1978) Late Cretaceous and Tertiary vegetation history of Africa. M. Werger (Ed.), *Biogeography and Ecology of Southern Africa*, Junk, The Hague (1978), pp. 77–130.
- Azeria E., Sanmartín I., Ås S., Carlson A., & Burgess N. (2007) Biogeographic patterns of the East African coastal forest vertebrate fauna. *Vertebrate Conservation and Biodiversity*, **16**, 883–912.
- Barratt C.D., Horsburgh G.J., Dawson D.A., Gower D.J., Wilkinson M., Loader S.P., & Jehle R. (2012) Characterisation of nine microsatellite loci in the caecilian amphibian *Boulengerula uluguruensis* (Gymnophiona), and their cross-species utility in three congeneric species. *Conservation Genetics Resources*, **4**, 225–229.
- Barratt C.D., Bwong B.A., Onstein R.E., Rosauer D.F., Menegon M., Nagel P., Kissling W.D., Loader S.P. (in review). Environmental correlates of phylogenetic endemism and the conservation of centres of endemism in the coastal forests of Eastern Africa. *Diversity and Distributions*.
- Bertola L.D., Jongbloed H., Van Der Gaag K.J., De Knijff P., Yamaguchi N., Hooghiemstra H., Bauer H., Henschel P., White P.A, Driscoll C.A, Tende T., Ottosson U., Saidu Y., Vrieling K., & De Iongh H.H. (2016) Phylogeographic Patterns in Africa and High Resolution Delineation of Genetic Clades in the Lion (*Panthera leo*). *Scientific Reports*, **6**, 30807.

- Blackburn D.C. (2008) Biogeography and evolution of body size and life history of African frogs: Phylogeny of squeakers (*Arthroleptis*) and long-fingered frogs (*Cardioglossa*) estimated from mitochondrial data. *Molecular Phylogenetics and Evolution*, **49**, 806–826.
- Braconnot P., Harrison S., & Joussaume S. (2006) Coupled simulations of the mid-Holocene and Last Glacial Maximum : new results from PMIP2. *Climate of the Past*, **3**, 1293–1346.
- Bragg J.G., Supple M.A., Andrew R.L., & Borevitz J.O. (2015) Genomic variation across landscapes: Insights and applications. *New Phytologist*, **207**, 953–967.
- Brown J.L. (2014) SDMtoolbox: A python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *Methods in Ecology and Evolution*, **5**, 694–700.
- Bryja J., Mikula O., Šumbera R., Meheretu Y., Aghová T., Lavrenchenko L.A., Mazoch V., Oguge N., Mbau J.S., Welegerima K., Amundala N., Colyn M., Leirs H. & Verheyen E. (2014). Pan-African phylogeny of *Mus* (subgenus *Nannomys*) reveals one of the most successful mammal radiations in Africa. *BMC Evolutionary Biology*, **14**, 256.
- Bryja J., Šumbera R., Kerbis Peterhans J.C., Aghova T., Bryjova A., Mikula O., Vicolas V., Denys C., Verheyen E. (2016) Evolutionary history of the thicket rats (genus *Grammomys*) mirrors the evolution of African Forests since late Miocene. *Journal of Biogeography*, **44**, 182–194.
- Burgess N. & Clarke G.P. (2000) *Coastal Forests of Eastern Africa*. IUCN Forest Conservation Programme, **2010**, 443 pp.
- Burgess N.D., Clarke G.P., & Rodgers W.A. (1998) Coastal forests of eastern Africa: status, endemism patterns and their potential causes. *Biological Journal of the Linnean Society*, **64**, 337–367.
- Cariou M., Duret L., & Charlat S. (2013) Is RAD-seq suitable for phylogenetic inference? An in silico assessment and optimization. *Ecology and Evolution*, **3**, 846–52.
- Carstens B., Lemmon A.R., & Lemmon E.M. (2012) The Promises and Pitfalls of Next-Generation Sequencing Data in Phylogeography. *Systematic Biology*, **61**, 713–715.
- Cruaud A., Gautier M., Galan M., Foucaud J., Saune L., Genson G., Dubois E., Nidelet S., Deuve T., & Rasplu J.-Y. (2014) Empirical Assessment of RAD Sequencing for Interspecific Phylogeny. *Molecular Biology and Evolution*, **31**, 1272–1274.
- Davey J.L. & Blaxter M.W. (2010) RADseq: Next-generation population genetics. *Briefings in Functional Genomics*, **9**, 416–423.
- Davey J.W., Hohenlohe P.A., Etter P.D., Boone J.Q., Catchen J.M., & Blaxter M.L. (2011) Genome-wide genetic marker discovery and genotyping using next-generation sequencing. *Nature Reviews Genetics*, **12**, 499–510.
- Demenocal P.B. (1995) Plio-Pleistocene African climate. *Science*, **270**, 53–59.
- Demos T.C., Kerbis Peterhans J.C., Joseph T.A., Robinson J.D., Agwanda B., & Hickerson M.J. (2015) Comparative population genomics of African montane forest mammals support population persistence across a climatic gradient and quaternary climatic cycles. *PLoS ONE*, **10**, e031800.
- Dimitrov D., Nogués-Bravo D., & Scharff N. (2012) Why do tropical mountains support exceptionally high biodiversity? The Eastern Arc mountains and the drivers of *Saintpaulia* diversity. *PloS ONE*, **7**, e48908.
- Eaton D. a R. (2014) PyRAD: assembly of de novo RADseq loci for phylogenetic analyses. *Bioinformatics*, **30**, 1844–1849.

- Emerson K.J., Merz C.R., Catchen J.M., Hohenlohe P. a, Cresko W. a, Bradshaw W.E., & Holzapfel C.M. (2010) Resolving postglacial phylogeography using high-throughput sequencing. *Proceedings of the National Academy of Sciences*, **107**, 16196–16200.
- Etter P.D., Bassham S., Hohenlohe P.A., Johnson E.A., & Cresko W.A. (2011) SNP discovery and genotyping for evolutionary genetics using RAD sequencing. *Methods in Molecular Biology*, **772**, 157–178.
- Fayolle A., Swaine M.D., Bastin J.-F., Bourland N., Comiskey J., Dauby G., Doucet J.-L., Gillet J.-F., Gourlet-Fleury S., Hardy O.J., Kirunda B., Kouamé F.N., & Plumptre A.J. (2014) Patterns of tree species composition across tropical African forests. *Journal of Biogeography*, **41**, 2320–2331.
- Fjeldså J. & Lovett J.C. (1997) Biodiversity and environmental stability. *Biodiversity and Conservation*, **6**, 315–323.
- Frankham R. (1996) Relationship of genetic variation to population size in wildlife. *Conservation Biology*, **10**, 1500–1508.
- Frost D.R. (2016) Amphibian species of the world 6.0: an online reference. Available at: <http://research.amnh.org/vz/herpetology/amphibia/>. Accessed 1st February 2017.
- Graham C.F., Glenn T.C., McArthur A.G., Boreham D.R., Kieran T., Lance S., Manzon R.G., Martino J.A., Pierson T., Rogers S.M., Wilson J.Y., & Somers C.M. (2015) Impacts of degraded DNA on restriction enzyme associated DNA sequencing (RADSeq). *Molecular Ecology Resources*, **6**, 1304–1315.
- Haywood A.M. & Valdes P.J. (2004) Modelling Pliocene warmth: Contribution of atmosphere, oceans and cryosphere. *Earth and Planetary Science Letters*, **218**, 363–377.
- Hickerson M.J., Carstens B.C., Cavender-Bares J., Crandall K.A., Graham C.H., Johnson J.B., Rissler L., Victoriano P.F., & Yoder A.D. (2010) Phylogeography’s past, present, and future: 10 years after Avise, 2000. *Molecular Phylogenetics and Evolution*, **54**, 291–301.
- Hijmans R.J., Cameron S.E., Parra J.L., Jones P.G., & Jarvis A. (2005) WORLDCLIM - a set of global climate layers (climate grids). *International Journal of Climatology*, **25**, 1965–1978.
- Hoelzer G.A. (1997) Inferring phylogenies from mtDNA variation: mitochondrial-gene trees versus nuclear-gene trees revisited. *Evolution*, **51**, 622–626.
- Hoffmann A., Griffin P., Dillon S., Catullo R., Rane R., Byrne M., Jordan R., Oakeshott J., Weeks A., Joseph L., Lockhart P., Borevitz J., & Sgrò C. (2015) A framework for incorporating evolutionary genomics into biodiversity conservation and management. *Climate Change Responses*, **2**, 1.
- Huang H. & Knowles L. (2016) Unforeseen consequences of excluding missing data from next-generation sequences: Simulation study of rad sequences. *Systematic Biology*, **65**, 357–365.
- Jeffries D.L., Copp G.H., Lawson Handley L.-J., Olsén H., Sayer C.D., & Hänfling B. (2015) Comparing RADseq and microsatellites to infer complex phylogeographic patterns, a real data informed perspective in the Crucian carp, *Carassius carassius*, L. *Molecular Ecology*, **25**, 2997–3018.
- Jetz W., Rahbek C., & Colwell R.K. (2004) The coincidence of rarity and richness and the potential signature of history in centres of endemism. *Ecology Letters*, **7**, 1180–1191.
- Jombart T., Ahmed I., Calboli F., Cori A., Reiners T.E., Solymos P., & Jombart M.T. (2008) Package “adeget”. *Bioinformatics Application Note*, **24**, 1403–1405.
- Karl S. & Avise J.C. (1993) PCR-based assays of mendelian polymorphisms from anonymous single-copy nuclear DNA: techniques and applications for population genetics. *Molecular Biology and Evolution*, **10**,

342–361.

- Lawson L.P. (2010) The discordance of diversification : evolution in the tropical-montane frogs of the Eastern Arc Mountains of Tanzania. *Molecular Ecology*, **19**, 4046–4060.
- Lawson L.P. (2013) Diversification in a biodiversity hot spot: Landscape correlates of phylogeographic patterns in the African spotted reed frog. *Molecular Ecology*, **22**, 1947–1960.
- Lawson L.P., Bates J.M., Menegon M., & Loader S.P. (2015) Divergence at the edges: peripatric isolation in the montane spiny throated reed frog complex. *BMC Evolutionary Biology*, **15**, 128.
- Leache A.D., Chavez A.S., Jones L.N., Grummer J.A., Gottscho A.D., & Linkem C.W. (2015) Phylogenomics of Phrynosomatid Lizards: Conflicting Signals from Sequence Capture versus Restriction Site Associated DNA Sequencing. *Genome Biology and Evolution*, **7**, 706–719.
- Leaché A.D., Fujita M.K., Minin V.N., & Bouckaert R.R. (2014) Species delimitation using genome-wide SNP Data. *Systematic Biology*, **63**, 534–542.
- Lehner B. & Grill G. (2013) Global river hydrography and network routing: Baseline data and new approaches to study the world’s large river systems. *Hydrological Processes*, **27**, 2171–2186.
- Lemmon E.M. & Lemmon A.R. (2013) High-Throughput Genomic Data in Systematics and Phylogenetics. *Annual Review of Ecology, Evolution, and Systematics*, **44**, 99–121.
- Lewontin R. (1975) The Genetic Basis of Evolutionary Change. *The American Journal of Human Genetics*, **27**, 249–251.
- Lexer C., Mangili S., Bossolini E., Forest F., Stölting K.N., Pearman P.B., Zimmermann N.E., & Salamin N. (2013) “Next generation” biogeography: towards understanding the drivers of species diversification and persistence. *Journal of Biogeography*, **40**, 1013–1022.
- Lexer C., Wüest R.O., Mangili S., Heuertz M., Stölting K.N., Pearman P.B., Forest F., Salamin N., Zimmermann N.E., & Bossolini E. (2014) Genomics of the divergence continuum in an African plant biodiversity hotspot, I: drivers of population divergence in *Restio capensis* (Restionaceae). *Molecular Ecology*, **23**, 4373–4386.
- Liedtke H.C., Müller H., Hafner J., Nagel P., & Loader S.P. (2014) Interspecific patterns for egg and clutch sizes of African Bufonidae (Amphibia: Anura). *Zoologischer Anzeiger*, **253**, 309–315.
- Linder H.P., de Klerk H.M., Born J., Burgess N.D., Fjeldså J., & Rahbek C. (2012) The partitioning of Africa: Statistically defined biogeographical regions in sub-Saharan Africa. *Journal of Biogeography*, **39**, 1189–1205.
- Lischer H.E.L. & Excoffier L. (2012) PGDSpider: An automated data conversion tool for connecting population genetics and genomics programs. *Bioinformatics*, **28**, 298–299.
- Loader S.P., Lawson L.P., Portik D.M., & Menegon M. (2015) Three new species of spiny throated reed frogs (Anura : Hyperoliidae) from evergreen forests of Tanzania. *BMC Research Notes*, **8**, 167.
- Loader S.P., Ceccarelli F.S., Menegon M., Howell K.M., Kassahun R., Mengistu A.A., Saber S.A., Gebresenbet F., de Sá R., Davenport T.R.B., Larson J.G., Müller H., Wilkinson M., & Gower D.J. (2014) Persistence and stability of Eastern Afromontane forests: Evidence from brevipitid frogs. *Journal of Biogeography*, **41**, 1781–1792.
- Lorenzen E.D., Heller R., & Siegismund H.R. (2012) Comparative phylogeography of African savannah ungulates. *Molecular Ecology*, **21**, 3656–3670.

- Lovett J.C. (1993) Climatic history and forest distribution in eastern Africa. In: *Biogeography and Ecology of the Rainforests of Eastern Africa* (Eds. Lovett, J.C. & Wasser, S.K.). pp. 23–31.
- Macher J.-N., Rozenberg A., Pauls S.U., Tollrian R., Wagner R., & Leese F. (2015) Assessing the phylogeographic history of the montane caddisfly *Thremma gallicum* using mitochondrial and restriction-site-associated DNA (RAD) markers. *Ecology and Evolution*, **5**, 648–662.
- Maslin M.A., Brierley C.M., Milner A.M., Shultz S., Trauth M.H., & Wilson K.E. (2014) East african climate pulses and early human evolution. *Quaternary Science Reviews*, **101**, 1–17.
- McCormack J.E. & Faircloth B.C. (2013) Next-generation phylogenetics takes root. *Molecular Ecology*, **22**, 19–21.
- McDonough M.M., Šumbera R., Mazoch V., Ferguson A.W., Phillips C.D., & Bryja J. (2015) Multilocus phylogeography of a widespread savanna-woodland-adapted rodent reveals the influence of Pleistocene geomorphology and climate change in Africa's Zambezi region. *Molecular Ecology*, **24**, 5248–5266.
- McRae B.H. & Beier P. (2007) Circuit theory predicts gene flow in plant and animal populations. *Proceedings of the National Academy of Sciences*, **104**, 19885–19890.
- Measey G.J., Galbusera P., Breyne P., & Matthysen E. (2007) Gene flow in a direct-developing, leaf litter frog between isolated mountains in the Taita Hills, Kenya. *Conservation Genetics*, **8**, 1177–1188.
- Moritz C. (1994) Defining Evolutionarily-Significant-Units for Conservation. *Trends in Ecology & Evolution*, **9**, 373–375.
- Pante E., Abdelkrim J., Viricel A., Gey D., France S.C., Boisselier M.C., & Samadi S. (2014) Use of RAD sequencing for delimiting species. *Heredity*, **114**, 450–459.
- Phillips S.J., Anderson R.P., & Schapire R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, **190**, 231–259.
- Pozzi L. (2016) The role of forest expansion and contraction in species diversification among galagos (Primates: Galagidae). *Journal of Biogeography*, **43**, 1930–1941.
- Pritchard J.K., Stephens M., & Donnelly P. (2000) Inference of population structure using multilocus genotype data. *Genetics*, **155**, 945–59.
- Raj A., Stephens M., & Pritchard J.K. (2014) FastSTRUCTURE: Variational inference of population structure in large SNP data sets. *Genetics*, **197**, 573–589.
- Rellstab C., Gugerli F., Eckert A.J., Hancock A.M., & Holderegger R. (2015) A practical guide to environmental association analysis in landscape genomics. *Molecular Ecology*, **24**, 4348–4370.
- Ricklefs R.E. (2004) A comprehensive framework for global patterns in biodiversity. *Ecology Letters*, **7**, 1–15.
- Rosenzweig M. (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge.
- Salzburger W., Bocxlaer B. Van, & Cohen A.S. (2014) Ecology and Evolution of the African Great Lakes and Their Faunas. *Annual Review of Ecology, Evolution and Systematics*, **45**, 519–545.
- Sandel B., Arge L., Dalsgaard B., Davies R.G., Gaston K.J., Sutherland W.J., & Svenning J.-C. (2011) The Influence of Late Quaternary Climate-Change Velocity on Species Endemism. *Science*, **334**, 660–664.
- Seeb J.E., Carvalho G., Hauser L., Naish K., Roberts S., & Seeb L.W. (2011) Single-nucleotide polymorphism (SNP) discovery and applications of SNP genotyping in nonmodel organisms. *Molecular Ecology Resources*, **11**, 1–8.
- Seehausen O., Butlin R.K., Keller I., Wagner C.E., Boughman J.W., Hohenlohe P.A., Peichel C.L., Saetre G.-P.,

- Bank C., Brannstrom A., Brelsford A., Clarkson C.S., Eroukhmanoff F., Feder J.L., Fischer M.C., Foote A.D., Franchini P., Jiggins C.D., Jones F.C., Lindholm A.K., Lucek K., Maan M.E., Marques D.A., Martin S.H., Matthews B., Meier J.I., Most M., Nachman M.W., Nonaka E., Rennison D.J., Schwarzer J., Watson E.T., Westram A.M., & Widmer A. (2014) Genomics and the origin of species. *Nature Reviews Genetics*, **15**, 176–192.
- Sepulchre P., Ramstein G., Fluteau F., Schuster M., Tiercelin J.-J., & Brunet M. (2006) Tectonic uplift and Eastern Africa aridification. *Science*, **313**, 1419–1423.
- Smitz N., Berthouly C., Cornélis D., Heller R., van Hooft P., Chardonnet P., Caron A., Prins H., van Vuuren B.J., de Iongh H., & Michaux J. (2013) Pan-African Genetic Structure in the African Buffalo (*Syncerus caffer*): Investigating Intraspecific Divergence. *PLoS ONE*, **8**, e56235.
- Stamatakis A. (2014) RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, **30**, 1312–1313.
- Stankiewicz J. & de Wit M.J. (2006) A proposed drainage evolution model for Central Africa - Did the Congo flow east? *Journal of African Earth Sciences*, **44**, 75–84.
- Storfer A., Murphy M., Evans J.S., Goldberg C.S., Robinson S., Spear S.F., Dezzani R., Delmelle E., Vierling L., & Waits L.P. (2007) Putting the “landscape” in landscape genetics. *Heredity*, **98**, 128–42.
- Tolley K.A., Tilbury C.R., Measey G.J., Menegon M., Branch W.R., & Matthee C.A. (2011) Ancient forest fragmentation or recent radiation? Testing refugial speciation models in chameleons within an African biodiversity hotspot. *Journal of Biogeography*, **38**, 1748–1760.
- Trauth M.H., Maslin M.A., Deino A., & Strecker M.R. (2005) Late Cenozoic moisture history of East Africa. *Science*, **309**, 2051–2053.
- Voelker G., Marks B.D., Kahindo C., A’genonga U., Bapeamoni F., Duffie L.E., Huntley J.W., Mulotwa E., Rosenbaum S.A., & Light J.E. (2013) River barriers and cryptic biodiversity in an evolutionary museum. *Ecology and Evolution*, **3**, 536–545.
- White F. (1983) *The vegetation of Africa: a descriptive memoir to accompany the UNESCO/AETFAT/UNSO vegetation map of Africa*. Unesco Natural Resources Research, 352 pp.
- Wiens J.J. (1993) Herpetology an introductory biology of amphibians and reptiles. *Systematic Biology*, **42**, 592–596.
- Zeisset I. & Beebe T.J.C. (2008) Amphibian phylogeography: a model for understanding historical aspects of species distributions. *Heredity*, **101**, 109–119.
- Zhang D.-X. & Hewitt G.M. (2003) Nuclear DNA analyses in genetic studies of populations: practice, problems and prospects. *Molecular ecology*, **12**, 563–584.
- Zimkus B.M., Lawson L., Loader S.P., & Hanken J. (2012) Terrestrialization, miniaturization and rates of diversification in african puddle frogs (anura: Phrynobatrachidae). *PLoS ONE*, **7**, e35118.
- Zimkus B.M., Rödel M.O., & Hillers A. (2010) Complex patterns of continental speciation: Molecular phylogenetics and biogeography of sub-Saharan puddle frogs (Phrynobatrachus). *Molecular Phylogenetics and Evolution*, **55**, 883–900.
- Zimkus B.M., Lawson L.P., Barej M.F., Barratt C.D., Channing A., Dash K.M., Dehling J.M., Du Preez L., Gehring P-S., Greenbaum E., Gvodzik V., Harvey J., Kielgast J., Kusamba C., Nagy Z., Pabijan M.,

- Penner J., Rödel M.O., Vences M. & Lötters S. (2017) Leapfrogging into new territory: how Mascarene ridged frogs have diversified across Africa. *Molecular Phylogenetics and Evolution*, **106**, 254-269.
- Zinner D., Wertheimer J., Liedigk R., Groeneveld L.F., & Roos C. (2013) Baboon phylogeny as inferred from complete mitochondrial genomes. *American Journal of Physical Anthropology*, **150**, 133–140.

Chapter II

Environmental correlates of phylogenetic endemism in amphibians and the conservation of refugia in the Coastal Forests of Eastern Africa

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Environmental correlates of phylogenetic endemism in amphibians and the conservation of refugia in the Coastal Forests of Eastern Africa

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Abstract

Aims: To quantify the spatial distribution of amphibian phylogenetic endemism (PE), an indicator of potential refugia, to test PE for correlations with current and historical environmental predictors, and to evaluate the effectiveness of current protected areas at conserving evolutionary history.

Location: Coastal Forests of Eastern Africa (CFEA) and the adjacent low elevation Eastern Afromontane (EA).

Methods: We integrated new and existing spatial and phylogenetic data to map PE for almost the full amphibian assemblage (41 of 55 species), including 35 intraspecific lineages from several species and complexes showing high phylogeographic structure. Using spatial and non-spatial regressive models we tested whether PE can be predicted by measures of Quaternary climate change, forest stability, topographic heterogeneity, and current climate. PE results were intersected with the protected area network to evaluate current conservation effectiveness.

Results: We detect refugia in Tanzania and coastal Kenya previously identified as CFEA centres of endemism but also new areas (lowland Tanga region and Pangani river, Zaraninge forest, Mafia island, Matumbi hills). Results show that refugia for amphibians (high PE) are located in areas with long-term Quaternary climate stability and benign current climate (high precipitation of driest quarter, high annual precipitation), with climatically unstable areas demonstrating low PE. Conservation analyses revealed that ten PE hotspots account for over 25% of the total PE, but less than 3% of this is under formal protection.

Main Conclusions: Utilizing cryptic diversity from novel phylogeographic data and distribution modelling improves our understanding of endemism patterns, with climate stability being strongly correlated with the distribution of PE. Our analyses point towards high PE areas being refugia, which require an urgent need to consolidate protected areas within centres of endemism in this highly threatened biodiversity hotspot.

Key words: amphibians, cryptic diversity, niche models, refugia, spatial phylogenetics

Introduction

Biological diversity is concentrated in the tropics but faces unprecedented anthropogenic impact, which has led to the earth being described as in the midst of a major sixth extinction event (Kolbert, 2014, Ceballos et al., 2015). The race to mitigate the loss of biodiversity is therefore an urgent priority, and explaining why some areas are biologically richer than others is a vital step towards prioritizing what should be conserved and why. At global and regional scales, high biodiversity and species endemism has been shown to be correlated with contemporary and historical climate regimes and topography (Ricklefs, 2005; Sandel et al., 2011; Kissling et al., 2012, Kissling et al., 2016), but comprehensive tests within biodiversity hotspots are mostly lacking. Africa holds rich biodiversity with over a quarter of the world's biodiversity hotspots (Myers et al., 2000), though often in small and fragmented areas. Major advances in understanding Africa's biodiversity has been made in recent years (e.g., Jetz et al., 2004, Lorenzen et al., 2012; Linder et al., 2012; Burgess et al., 1992, 1998; Rovero et al., 2014; Levinsky et al., 2013), though many taxonomic groups remain under-sampled, with cryptic diversity often under-represented. Incorporating this intraspecific diversity within species is particularly important for understanding the correlates of biodiversity patterns and prioritizing conservation efforts at local scales.

The Coastal Forests of Eastern Africa (CFEA, Fig. 1) are a global conservation priority. However, they remain severely threatened (Azeria et al., 2007; Burgess et al., 2007) and have been described as a 'vanishing refuge' (Burgess et al. 1998). The majority of the CFEA hotspot is lowland (<300m a.s.l.) with several raised areas along the coastline and inland where the CFEA overlaps with parts of the Eastern Afromontane (EA) region up to around 1000m (Udzungwa, Uluguru, Usambara in the Eastern Arc mountains, Tanzania, see Fig. 1A, B). It is thought the fragmented lowland forests of the CFEA and EA region are the remnants of a once continuous forest that covered tropical Africa during the Early Tertiary (Couvreur et al., 2008; Kissling et al., 2012). Historical climate change since the Miocene led to significant contraction and expansion of forests during glacial and interglacial periods (Axelrod & Raven, 1978; Trauth et al., 2005; Maslin et al., 2014), subjecting many low elevation areas to repeated inundation from sea level fluctuations (Burgess & Clarke, 2000; Kent et al. 1971). Climate stability and topography are therefore likely to be important factors in the persistence of this region's biodiversity and the location of refugia (e.g. Moreau, 1933; Haffer, 1969; Mayr & O'Hara, 1986).

Previously, centres of endemism within the Swahili regional centre of endemism across the CFEA were identified using species distributional data from a number of plant, vertebrate and invertebrate groups (Burgess et al., 1998, Fig. 1C). However, phylogenetic information and environmental data have not yet been integrated to validate these findings. The inclusion of phylogenetic information to supplement traditional biodiversity measures such as species richness was popularized by Faith (1992), using phylogenetic diversity (PD) to measure an area's evolutionary history based on the sum of the branch lengths connecting each tip on a phylogenetic tree to its root. Rosauer et al. (2009) extended PD's utility by combining it with weighted endemism (WE; Crisp et al., 2001), to derive phylogenetic endemism (PE). By subdividing the length of each phylogenetic branch across the areas it occurs, PE indicates where substantial components of PD are spatially restricted. A particularly desirable property of PE is that it circumvents the need for formal taxonomic classification by utilizing branch lengths rather than species units. As PE can incorporate cryptic diversity, it has gained popularity in an increasing number of macroecological and conservation studies (Carnaval et al., 2014, Gudde et al., 2013, Laity et al., 2014, Rosauer et al., 2015; 2016). Areas of high PE are typically found where phylogenetic branches with few close relatives are geographically restricted, and are important in a conservation context because they have been used to indicate

refugia where a large proportion of evolutionary history has accumulated over time (Rosauer & Jetz, 2014; Carnaval et al. 2014; Rosauer et al. 2009).

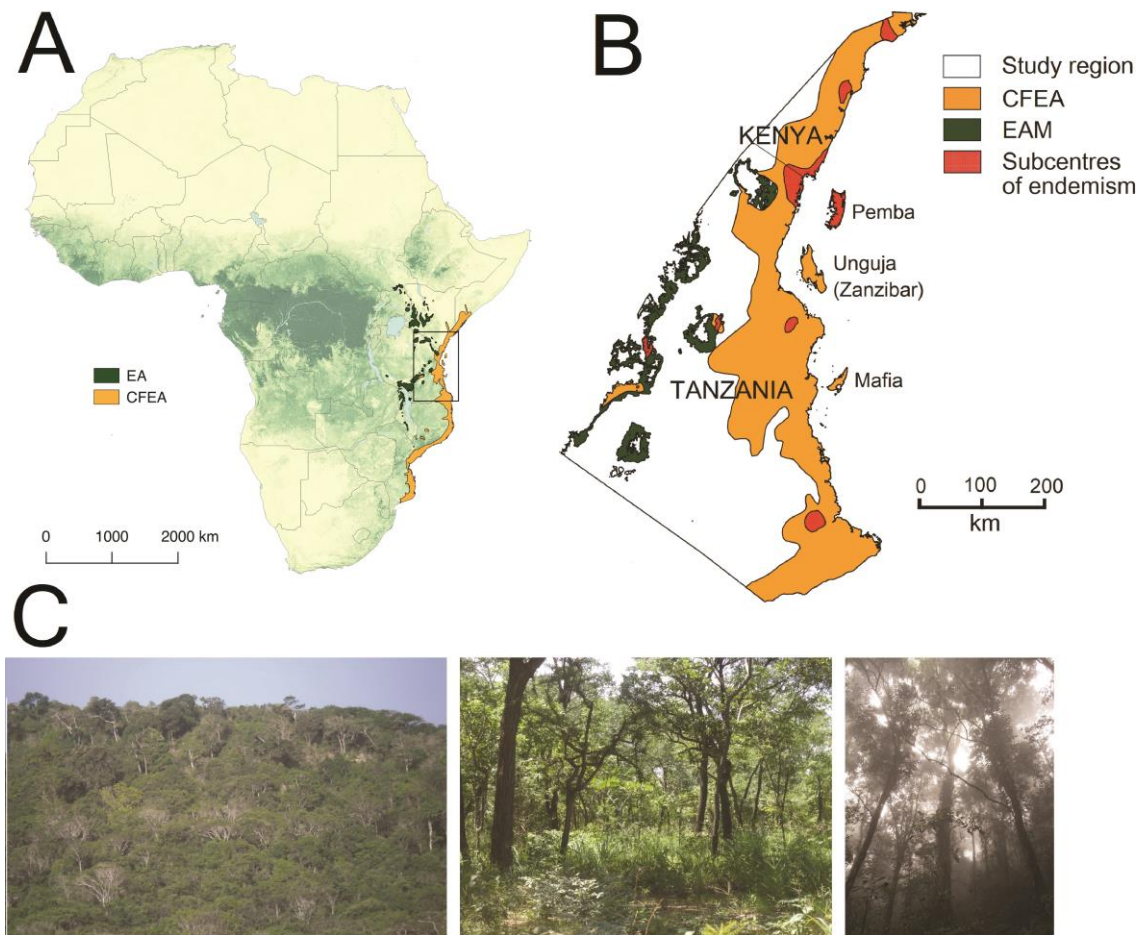


Fig. 1. Distribution of forests in the study region within East Africa. A) Map showing the location of the Coastal Forests of Eastern Africa (CFEA) and their proximity to the Eastern Afromontane (EA) region. B) Study region encompassing major elements of CFEA and lowland EA forests as well as intervening habitat in Kenya and Tanzania, including centres of endemism identified by Burgess et al. (1998). C) Examples of CFEA, with coastal dry forest in Shimba hills, Kenya (left), miombo woodland in Kiwengoma FR, Tanzania (middle), and EA habitat represented by montane forest in Kitolomero FR, Udzungwa (right).

Amphibians offer an excellent model to investigate biodiversity patterns due to their relatively poor dispersal abilities and sensitivity to habitat changes compared with other taxa (but see Van Bocxlaer et al., 2010). The known CFEA species assemblage of Tanzania consists of fifty one species (Poynton et al., 2007), with several additional species from coastal Kenya (Harper et al. 2010) or recently described (Barratt et al. 2017) inflating that number to at least fifty five. Although several of these species are narrow ranged endemics, many are widespread and occur across adjacent areas of suitable habitat (e.g. savannah and bushland). The systematics of many CFEA species are very poorly understood, but some show strong phylogeographic structure with poorly defined species boundaries (e.g. Channing et al. 2013). Phylogeographic data from amphibians has never been utilized for

understanding biodiversity patterns in the CFEA but given their suitability compared to traditional measures, they are likely to provide vital insights into this threatened biodiversity hotspot.

In this paper we integrate new and existing phylogenetic and spatial data for amphibians to investigate PE across a major part of the CFEA across Tanzania and Kenya. Utilizing cryptic diversity for the first time, we focus on combining species data with intraspecific diversity in widespread species (hereafter referred to as ‘lineages’) which likely indicate refugia where biodiversity has persisted during times of climatic instability. Given the extreme climate oscillations and forest cover change across the CFEA since at least the Miocene, we hypothesize that measures of climate stability have a major influence on phylogeographical patterns and the distribution of refugial areas for amphibians, and are good predictors of PE. Using almost the full species assemblage with spatial and phylogenetic data and including intraspecific diversity within multiple species and species complexes, we map the geographic distribution of evolutionary history (PE) and test our two main hypotheses: i) that PE predicts refugia, and is positively correlated with long term climatic stability, and ii) the current protected area network in the region does not effectively conserve refugia for amphibians.

Methods

Lineage discovery and phylogeny

We aimed to integrate as much of the CFEA amphibian assemblage as possible for phylogenetic endemism analyses. We therefore included molecular data from species but also from intraspecific lineages within species where sampling was sufficient. To build a phylogeny representing the amphibian assemblage of the study region (Fig. 2) we first compiled genetic data from recent fieldwork and museum sampling. Genetic samples were collected across the CFEA and lowland parts of the EA over a total of ten non-consecutive field seasons spanning 2001 to 2015. DNA was extracted from fresh tissue samples (leg muscle, liver or toe clip) collected in the field (2013-2015), or from samples held in collections (collected between 2001 and 2012) stored in 100% ethanol. We built a DNA barcoding database using the *16S* rRNA mitochondrial gene fragment, screening over 1,500 individual samples. Species identifications were verified against published GenBank sequences, and our own and collaborators unpublished sequences (Breda Zimkus, Daniel Portik, pers. comm.). We examined thoroughly sampled species and complexes with adequate spatial and genetic data to define the intraspecific lineages present within each group based on *16S* data. Based on structure in neighbor joining trees from *16S* data we then amplified an additional mitochondrial gene for a single representative per lineage (cytochrome oxidase subunit I; *COI*). Intraspecific lineages were defined using a minimum of 2% sequence divergence across a concatenated alignment of both genes, a reasonable threshold for quantifying divergence at the intraspecific level (see Vences et al., 2005, Fouquet et al. 2014, Chambers & Hebert, 2016). To ensure our analyses were not affected by oversplitting the lineages within species we ran sensitivity analyses whereby lineages were defined by a more conservative threshold of 5% sequence divergence across the two genes. All subsequent analyses were repeated on this dataset and are included in the supplemental information. Details of the molecular procedures follow Barratt et al. (2017) for *16S* and Poynton et al. (2016) for *COI*. All DNA sequences are deposited in GenBank, and accession codes for newly generated sequences from this study can be found in Table S1. Sequences were edited in GENEIOUS 6 and aligned with MUSCLE before Bayesian analyses were performed in BEAST 2.1.3 (Bouckaert et al., 2014) on the concatenated alignment, using the optimal models of evolution per partition (Table S1) according to the Bayesian Information Criterion determined by PARTITIONFINDER 1.1.1 (Lanfear et al. 2013). A full description of

the parameters used for the BEAST analysis can be found under the subheading *Phylogenetic tree* in Supplemental Appendix S1.

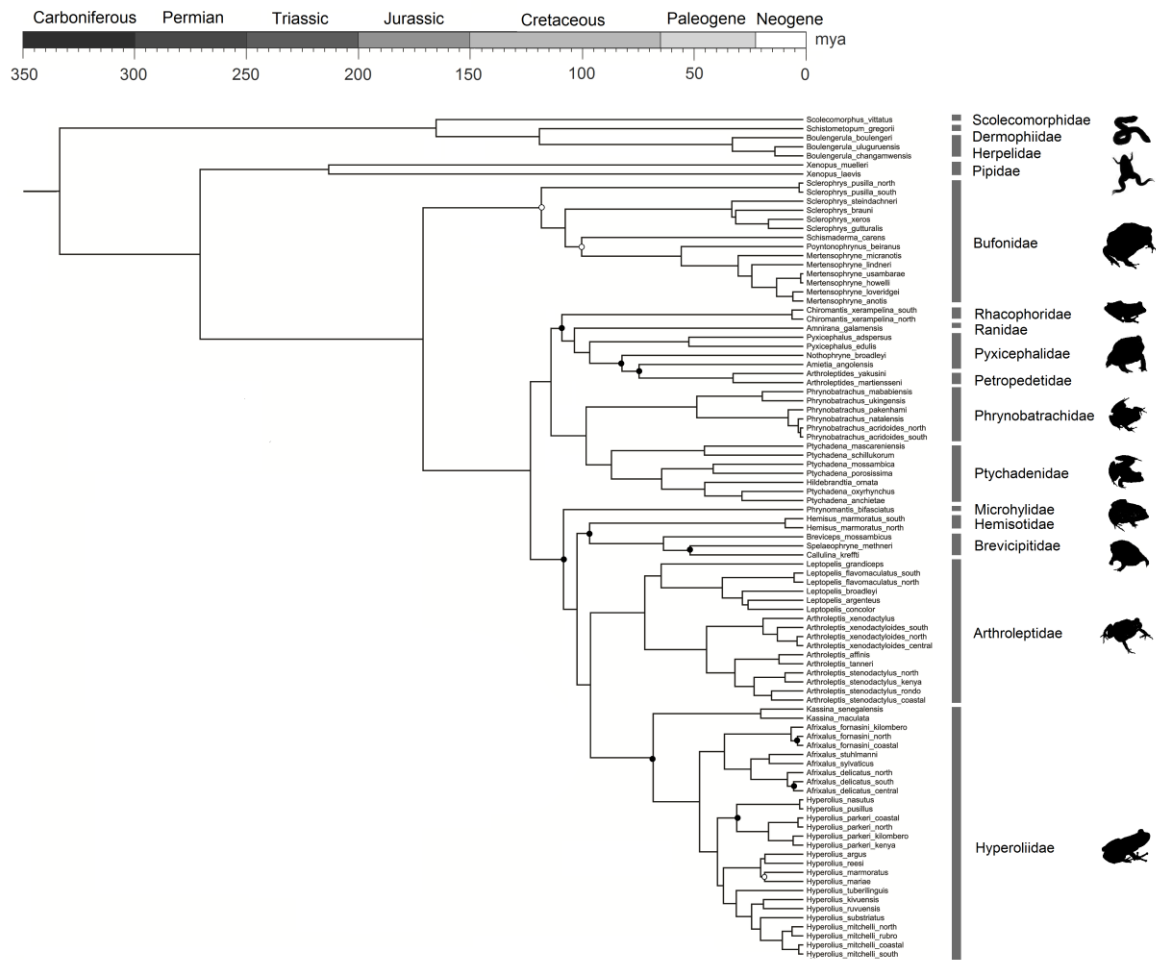


Fig. 2. Phylogeny representing the amphibian species assemblage for the Coastal Forests of Eastern Africa and surrounding lowland Eastern Afrotropical region based on genetic sampling. Intraspecific lineages ($n = 35$) are also represented in the phylogeny, and have been included in calculations of phylogenetic endemism. Posterior probability for each node is > 0.95 unless indicated by black ($pp < 0.95$) or white circles ($pp < 0.5$).

Distribution data

Spatial sampling covered a significant portion of the CFEA across Tanzania and Kenya, including overlapping areas of the adjacent EA region up to 1000 m elevation. With recent field work, this area is more comprehensively sampled compared to the adjacent CFEA in Mozambique and Somalia. We collated data for i) known locations of sequenced specimens (identified to species, or to intraspecific lineage where possible) based on molecular data, and ii) known locations for specimens from museums, GBIF records and CFEA literature without molecular data. These were included in species distribution modelling, to estimate which lineage they belong to provided we could definitively identify to species or species complex (see below). We conducted a rigorous filtering and correction

procedure to our spatial dataset prior to analyses (see *Spatial data filtering*, Appendix S1). The final dataset comprised of 9,184 occurrence records (2,161 unique points; Table S2 and Table S3).

We used species distribution modelling (SDM) to estimate the geographic distribution of each species, and for lineages by following the framework outlined by Rosauer et al. (2015). The method uses a modelling approach informed by known species and lineage point data, partitioning a SDM into its constituent lineage distribution models which are informed by the habitat suitability of grid cells between points where lineages are known from (see example in Fig. 3). Lineage distribution probability for a grid cell is conditional on i) the habitat suitability of the cell for the species as a whole and ii) the habitat connectivity of that cell with known locations of that lineage. We constructed species distribution models (SDMs) in MAXENT 3.3.3k, which uses a machine-learning algorithm based on the principles of maximum entropy (Phillips et al., 2006), shown to be highly effective at predicting distributions using presence only data (Elith et al., 2011). We followed recommendations by Merow et al. (2013) to avoid bias in our SDMs. We used only six bioclimatic layers that were not closely correlated (Pearson's $r < 0.6$); bio2 (mean diurnal temperature range), bio4 (temperature seasonality), bio5 (max temperature of warmest month), bio12 (annual precipitation), bio14 (precipitation of driest month), and bio18 (precipitation of warmest quarter). These variables were obtained from the Worldclim database based on the CCSM global circulation model (Hijmans et al., 2005) and a digital elevation model (DEM) (GTOPO30; USGS, available from: <http://csgtm.iscgm.org/dataset/gtopo30>) at 30 arc-second resolution (approximately 1km² grid cells). For all SDMs we used the subsample algorithm with a logistic output, and tested a range of regularization multiplier values between 0 and 3. We chose to use a regularization multiplier of 1 for our SDMs as it produced the most accurate distribution maps based on our own knowledge and IUCN range maps, whilst minimizing overfitting of the models. We ensured all SDMs used an adequate number of unique presence locations (minimum 10 points except for endemics known to have narrow ranges, see Table S2). Background data used 10,000 points within a buffered radius of land 100 km around presence points to emphasize factors locally relevant in distinguishing suitable sites. To account for sampling bias (see Kramer-Schadt et al., 2013; Merow et al., 2013, 2014), presence data was rarefied prior to creating SDMs, with a minimum of 10 km distance allowed between retained points. This distance was chosen as it reduced the spatial autocorrelation of environmental data used to build the models whilst retaining a sufficient number of points per species to model an adequate number of species. We took the average of 25 model replicates for each SDM, evaluating model performance using the area under the curve (AUC) statistic. Models were corrected for over-prediction using the minimum convex polygon method in SDMTOLBOX 1.1c (Brown et al., 2014) supplemented by our own knowledge of coastal forest amphibians and species range maps (IUCN, 2016). Each SDM was subsequently partitioned into its constituent lineage distribution models (LDMS) using cost distances, jointly informed by the species ecological niche and known locations of each lineage based on geo-referenced genetic data (Rosauer et al., 2015). LDMS were estimated using customized python scripts (<https://github.com/DanRosauer/phylospatial>). We retained suitability surfaces (likelihood of occurrence per grid cell) per species and lineage as a continuous variable between 0 and 1, which were then used to estimate PE.

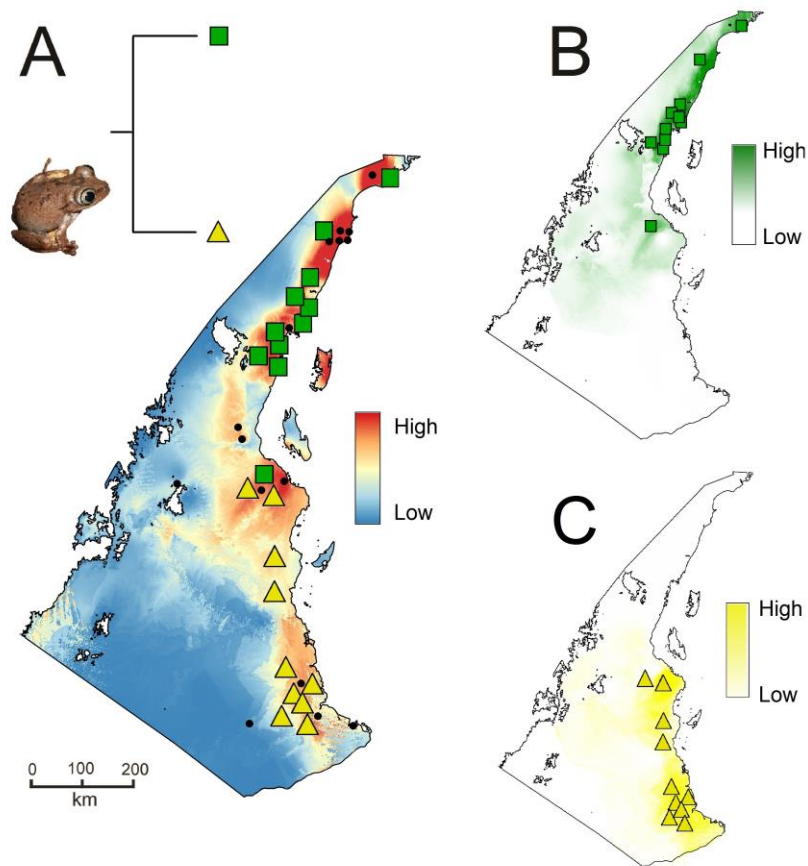


Fig. 3. Example of a poorly understood species group (*Leptopelis argenteus*) with two intraspecific lineages. A) Schematic representation of the two clades present in this species and its corresponding species distribution model (green squares = northern lineage, yellow triangles = southern lineage, black dots = species records without DNA to verify to which lineage they belong). B) and C) Lineage distribution models for each of the two intraspecific lineages after partitioning the SDM following Rosauer et al. (2015). For each lineage the relative likelihood of occurrence is shown, demonstrating the overlap of likelihood occurrences for both lineages towards the centre of the map where both have been recorded.

Phylogenetic endemism

We customized R scripts (<https://github.com/DanRosauer/phylospatial>) to estimate PE, using the phylogeny shown in Fig. 2 and the spatial occurrence of each tree tip (represented by SDM and LDM scores per grid cell at 1 km² resolution as described above). Each of the branch lengths of the phylogeny included in this study was partitioned into the grid cells where it occurs based on the SDM and LDM suitability scores ranging between 0 and 1. For LDMs the method uses the formula below where b is one of n branches linking lineages in a grid cell to the root, with local suitability as the LDM score for that grid cell, and the total suitability as the sum of all grid cells within the SDM:

$$Model_weighted_PE = \sum_{1..n}^b (local\ suitability[b] / total\ suitability[b]) \times length[b]$$

The output from these calculations is a map of the PE per grid cell, where the values of all cells sum to the total length of all corresponding branches on the phylogeny. We follow the basis of Laity et al. (2016) and Rosauer et al. (2015; 2016), utilizing summed PE per grid cell across the region for further analyses.

Environmental correlates of phylogenetic endemism

To test for correlations with PE we first prepared a selection of environmental predictors related to historical stability, topography, and climate that could be expected to influence amphibian phylogenetic endemism. For historical stability, we used two measures of Quaternary climate change, measured as the absolute difference in mean annual temperature and precipitation between the Last Glacial Maximum (LGM) and the present (see Kissling et al. 2012). These measures serve as proxies to represent the effect of climatic oscillations during the Quaternary (Eiserhardt et al., 2015; Sandel et al., 2011). We also prepared a measure of historical forest stability over time following Graham et al. (2010). In brief, forest points ($n = 500$) were randomly generated within an area classified as evergreen forest according to Tuanmu & Jetz (2014). We then constructed a distribution model in MAXENT using the same variables and model parameters used for SDMs. The model was then projected onto past climate data (mid- Holocene 6 ka BP, last glacial maximum 21 ka BP, last interglacial 120 ka BP). The forest stability measure was then obtained by averaging the log values of suitability for forest in each grid cell across each of the time periods (see *Forest modelling*, Appendix S1). Topographic heterogeneity was calculated as the difference between the minimum and maximum elevation appearing in each grid cell, using the GTOPO30 (USGS) 30 arc second dataset (more detailed information can be found under the *Forest modelling* section of Appendix S1, with a map of modelled forest stability shown in Fig. S2). We included four bioclimatic variables using available climate data; bio1 (annual mean temperature), bio4 (temperature seasonality), bio12 (annual mean precipitation) and bio14 (precipitation of the driest month).

We used Generalized Linear Models (GLM) and spatially autoregressive models (SAR) to test the relationship between PE (response variable) and the environmental variables mentioned above (predictor variables). We ensured predictor variables were not highly correlated with Pearson's $r < 0.7$ in all cases (Table S4). All rasters were resampled to

2.5 arc minutes ($\sim 5 \text{ km}^2$ resolution) for environmental predictor analyses to reduce computational requirements, and summarized in Fig. S3. We fitted GLMs for all grid cells in the '*Glmulti*' (Calcagno & Mazancourt, 2010) R package, with log transformed PE as the response and scaled predictors. We tested all combinations of predictors, with main effects only (level = 1), resulting in 128 possible models. We used the corrected Akaike Information Criterion (AICc) for model selection, assessing models using AICc weight. To account for spatial autocorrelation using an SAR, Moran's I was calculated for the log transformed PE results and for the residuals of the best GLM using correlograms (full details of the process are described in *Spatial autocorrelation*, Appendix S1). Distance classes were defined at 10 km intervals. We observed spatial autocorrelation at lower distance classes so prepared a spatial weights matrix and re-ran the best GLM with a SAR error model using the *errorsarlm* function in the R package '*spdep*' (Bivand & Piras, 2015). To define a spatial weights matrix we used the *knearneigh* function (with $k = 1$), deriving the minimum distance connecting each cell to at least one neighbor. Using this minimum distance we then defined the neighborhood structure using the *dnearneigh* function, and created a spatial weights matrix using the *nb2listw* function (Kissling & Carl, 2008).

Conservation

We follow Laity et al. (2014) and Rosauer et al. (2016) to demonstrate the effectiveness of the protected area network at conserving evolutionary history (PE). As PE is a measure of the spatial range of each branch on a phylogeny, summing the total PE across an area of interest estimates the total diversity found there (weighted for each branch by its distribution). Thus by intersecting summed PE with shapefiles of the protected area network it is possible to make conservation analyses of how much evolutionary history (i.e. refugia) is currently protected and where shortfalls may lie. We extracted the top 10% of all grid cell values for the PE results to reveal hotspots that contain a disproportionately high share of the total PE and are likely refugia using the *raster* package in R (Hijmans & van Etten, 2012). For each hotspot we calculated the area size, summed PE, and summed PE that falls within protected areas, representing this as a proportion of the whole study region. This was repeated for the top 2.5% and 5% of all grid cell values (Table S8). The shapefiles of the current protected area network across the study region to intersect PE results were obtained from the Critical Ecosystem Partnership Fund (<http://www.cepf.net>) and World Resources Institute (<http://www.wri.org>).

An extended version of these methods can be found in Appendix S1, with a schematic summary of the workflow in Fig. S4.

Results

Lineage discovery and phylogeny

Within nine thoroughly sampled species (*Arthroleptis stenodactylus*, *A. xenodactyloides*, *Leptopelis flavomaculatus*, *Sclerophrys pusilla*, *Hemisis marmoratus*, *Afrixalus fornasini*, *Hyperolius parkeri*, *Phrynobatrachus acridoides* and *Chiromantis xerampelina*) we defined twenty four intraspecific lineages (Fig. S1). A further eleven lineages were identified within three poorly understood complexes which we refer to as *Leptopelis argenteus* (including *L. concolor*), *Afrixalus stuhlmanni* (including *A. delicatus* and *A. sylvaticus*) and *Hyperolius mitchelli* (including *H. rubrovermiculatus*). The phylogeny captures this cryptic diversity along with several closely related species from the surrounding area (several CFEA species known from Mozambique and the adjacent EA mountains). Phylogenetic results are largely concordant with previous large-scale amphibian tree reconstructions in terms of topology and branch lengths, with high posterior probability, thus we regard the tree as an accurate representation of the inter- and intra- relationships of CFEA amphibians (Fig. 2).

Distribution data

Species distribution models (SDMs) performed well, with mean AUC values from 25 model runs >0.75 in all cases (range = 0.75-0.98, median = 0.83, mean = 0.83; Table S5), indicating ‘good’ model performance. Variable contributions towards each SDM were generally highest for precipitation of driest month (bio14) and elevation, with the mean contribution of these variables together affecting 59.66% of the predictions across all SDMs, but with high variation across species (Table S5). Forest models show similar variable contributions and are shown in Fig. S3. LDMs created from each SDM clearly delineate the spatial distribution of each lineage (Fig. 3), showing how the method avoids drawing arbitrary boundaries between lineages by accounting for probabilistic uncertainty with lower modelled suitability scores towards the periphery of each lineage range.

Phylogenetic endemism

Phylogenetic endemism is unevenly distributed across our study region, with several aggregations of high PE in ten hotspots, covering a large part of coastal Kenya, and in Tanzania around the lowlands of the EA region surrounding Uluguru and East Usambara mountains (including the Pangani river), the Pugu hills, Matumbi hills and Mafia island. Several smaller hotspots of high PE are represented in Tanzania on Pemba island and Zaraninge forest, and in the fragmented forests of Lindi region surrounding the Rondo Plateau (Fig. 3B).

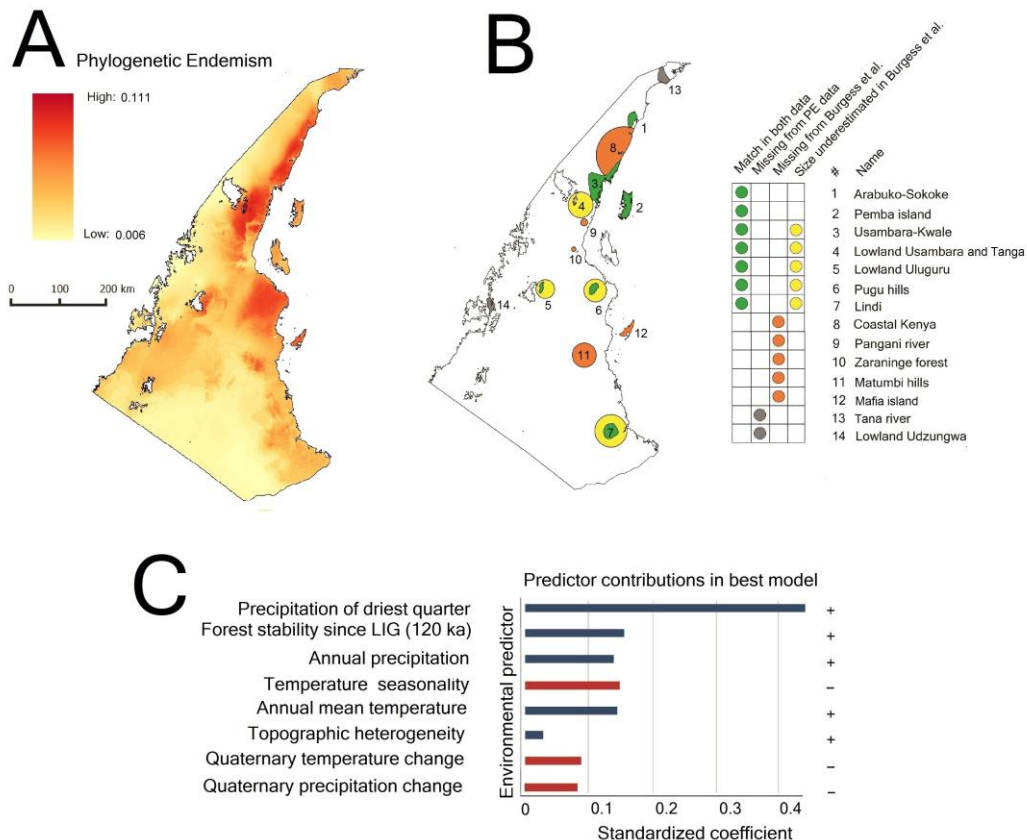


Fig. 4. Distribution and drivers of phylogenetic endemism (PE) in the Coastal Forests of Eastern Africa (CFEA). A) Summed PE of all species and intraspecific lineages used in this study. B) Comparison of PE results with centres of endemism described in Burgess et al. (1998); green = match in both data, orange = missing from Burgess et al. (1998), yellow = size underestimated in Burgess et al. (1998) grey = area listed in Burgess et al. (1998) but not recovered in our PE analyses. C) Standardized coefficients of predictor variables contributing to explain PE (the response variable) in the best Generalized Linear Model). Blue bars denote positive effects on PE, red bars denote negative effects. Results of spatially autoregressive models are provided in Table S6.

Environmental correlates of phylogenetic endemism

Complex models that included many predictor variables performed best (Table S6) based on AICc scores. Of all possible GLM combinations we tested, the model with the highest Akaike weight (0.99) and lowest AICc score (delta AIC = 0) included all predictors. In this model, the most important predictors positively correlated with PE (in descending order) included precipitation of driest month (bio14), forest stability since the last interglacial, annual mean temperature, annual precipitation, and topographic heterogeneity. Quaternary climate oscillations

(anom_bio1, anom_bio12) and temperature seasonality (bio4) showed a negative correlation with PE (Fig. 4C, Table S6). The spatial model of the best GLM fully accounted for spatial autocorrelation at all distance classes (Table S6) and confirmed the importance of most key predictors in the non-spatial model. Sensitivity analyses of the data using lineages defined by the more conservative 5% divergence cutoff showed the same results in terms of the importance and correlation of predictors (Table S7), indicating that results are consistent even when removing lineages with lower divergences from conspecifics (i.e. between 2 and 5%) from the analysis. This was also the case with the removal of bio14 (which contributes significantly to most SDMs and the forest model). Environmental correlates with amphibian PE were generally consistent between spatial and non-spatial regression models in all datasets including sensitivity analyses, although some predictor variables (forest stability and topographic heterogeneity) showed smaller effect sizes in the spatial models (Table S7).

Conservation

The ten identified hotspots of PE (Fig. 5A) account for a relatively small area size but support a disproportionately high amount of the total PE found across the study region. Up to 25.5% of the total PE is accounted for by these hotspots based on using the upper 10% of all grid cells. (Table 1). The protected area network across this region is extensive. However, intersecting it with the PE results revealed that only a very small proportion of the amphibian evolutionary history in the region is formally protected. Overlaying the hotspots with the protected area network, demonstrated that only small parts of the areas containing high PE are covered (Fig. 5), with less than 3% of the total PE in the study region protected. A list of major protected areas per hotspot is provided in Table S9. As with the environmental correlate analyses, sensitivity analyses using the 5% divergence cutoff dataset showed similar results (Table S8).

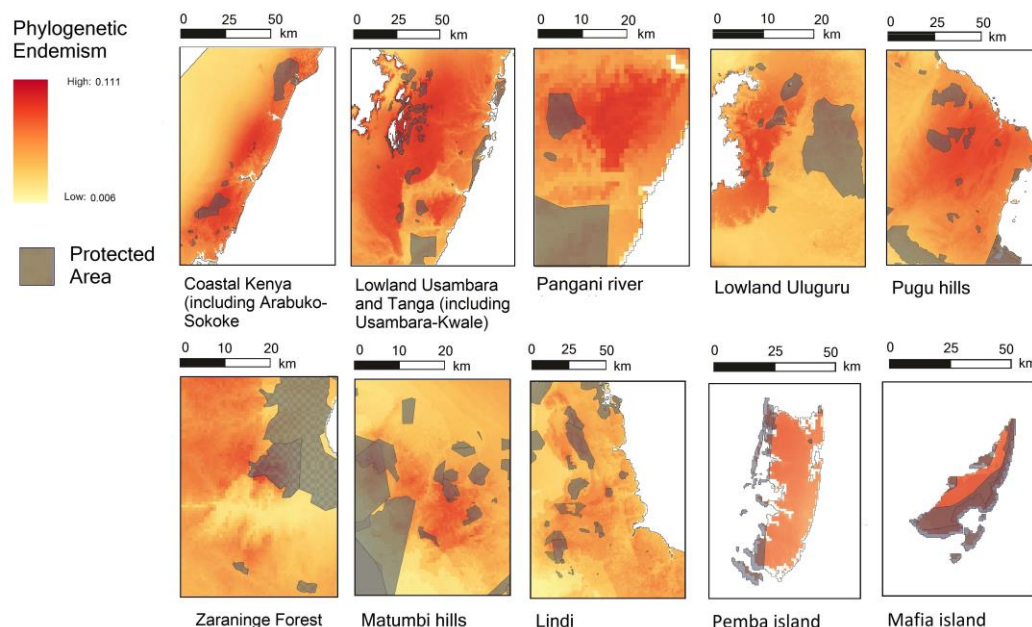


Fig. 5. Phylogenetic endemism (PE) hotspots, with the protected area network displayed in blue. The location of hotspots within the region is illustrated in Fig. 4B. Maps demonstrate that only a small proportion of high PE grid cells are protected, with results summarized for each hotspot in Table 1 and major protected areas per PE hotspot listed in Table S9.

Table 1. Hotspots of phylogenetic endemism categorized using the top 10% of all PE scores across grid cells, numbers refer to Fig. 4B. Size of each area is shown in km² and as a percentage of the total study area, with the protected area proportions (%) also indicated. Similarly, PE summed across each area is shown both as an absolute value and as a percentage, with the proportional representation (%) of the total indicated. Results are summarized in bold across all hotspots. Sensitivity analyses of this data can be found in Table S8.

Hotspot	Area (km ²)	% of total area	% of total area currently protected	PE	% of total PE	% of total PE currently protected
1. and 8. Coastal Kenya (including Arabuko-Sokoke)	6374	2.27	0.30	462.39	5.89	0.82
2. Pemba island	109	0.04	0.00	6.08	0.08	0.01
3. and 4. Lowland Usambara and Tanga (including Usambara-Kwale)	8351	2.98	0.18	644.77	8.22	0.58
5. Lowland Uluguru	1021	0.36	0.07	65.56	0.84	0.15
6. Pugu hills	10028	3.58	0.35	682.76	8.70	0.87
7. Lindi	31	0.01	0.01	1.73	0.02	0.02
9. Pangani river	625	0.22	0.02	42.54	0.55	0.05
10. Zaraninge forest	398	0.14	0.02	23.59	0.30	0.04
11. Matumbi hills	661	0.24	0.04	40.41	0.51	0.10
12. Mafia island	481	0.17	0.11	30.95	0.39	0.26
Total	28079	10.02	1.11	2000.78	25.50	2.89

Discussion

This study integrates phylogenetic and spatial data to provide the first comprehensive analysis of CFEA amphibian patterns. The CFEA is one of the highest priority ecosystems for conservation worldwide (Azeria et al., 2007) despite our limited knowledge of how inter- and intra-specific diversity is distributed. Our results demonstrate the utility of measures such as PE that can provide more meaningful measures than species distribution data alone for local scale conservation efforts. Analyses of PE correlations with environmental predictors strongly support our hypothesis that high levels of Quaternary climate stability, in particular for precipitation, are positively correlated with PE, suggesting the presence of refugial areas. Conservation analyses using PE demonstrate the worrying reality that only a tiny proportion of the identified refugial areas (endemism hotspots) are formally protected for conservation. Based on these analyses we suggest the protected areas covering high PE should be prioritized and consolidated to maintain the biodiversity that has accumulated and persisted there.

Environmental correlates of PE

The lowland areas of the CFEA have been subjected to more severe and prolonged climatic changes compared to adjacent higher elevation areas (Burgess & Clarke, 2000; Mumbi et al., 2008) which have likely influenced biodiversity in this region, probably since the Tertiary (Azeria et al., 2007). Environmental predictors (Fig. S4) demonstrate the heterogeneous nature of the study region with several areas that have remained more stable than others in terms of Quaternary precipitation and temperature change. These measures are a useful proxy for historical climatic stability through deeper time (see Sandel et al. 2011), and can help to explain biogeographic breaks and endemism at the species level not only in many amphibians (e.g. Barratt et al. 2017, Loader et al. 2014, Zimkus et al. 2017) but also across other taxonomic groups. Broad biogeographic breaks are common in many other vertebrate taxa across other parts of sub-Saharan Africa including ungulates (Arctander et al., 1999; Lorenzen et al., 2012), small mammals (Mynhardt et al. 2015), birds (Habel et al., 2015), and reptiles (Tolley et al. 2011). This points towards the importance of refugia in the persistence of biodiversity during long-term climate change (Fjelds  & Lovett, 1997).

Our results on environmental correlates or PE are consistent with other literature linking climate and habitat stability to endemism patterns and glacial refugia globally (Sandel et al. 2011, Kissling et al. 2016), in other parts of the world (Bell et al., 2010; Carnaval et al., 2014; Weber et al., 2013, 2014; Rosauer et al., 2015), and in sub-Saharan Africa (e.g. Hamilton, 1976, Fjelds  & Lovett, 1997; Gehrke & Linder, 2011; Tolley et al., 2011; Loader et al., 2014; Levinsky et al., 2013). While our results can be indicative of endemism patterns in non-volant species with poor dispersal abilities (Zug et al. 2001), the integration of data from taxa across larger parts of the tree of life within the CFEA would be beneficial to fully describe biodiversity patterns and evolutionary processes (e.g. Gonz lez-Orozco et al., 2015)..

Conservation

Conservation prioritization across the CFEA, as in many other biodiversity hotspots, can be boosted by fine-scale data to determine how best to effectively apply the limited conservation resources that are allocated. To achieve this, policy makers require more detailed knowledge of biodiversity and endemism patterns than are currently available to supplement existing information. In this paper we have shown that the integration of phylogenetic, spatial data and distribution modeling can include cryptic diversity in well sampled taxonomic groups, and may be particularly useful for confirming known hotspots of endemism and highlighting new areas. The congruence of our PE results with those derived from existing species distribution data for this region (Burgess et al. 1998) is striking despite fundamental differences in the datasets used (both taxonomically and methodologically). Burgess et al.'s (1998) analysis investigated endemism using a large proportion of known endemic CFEA species (i.e. almost 800 endemic plants, invertebrates, and vertebrates). Our results support the recognition of many of Burgess et al.'s (1998) centres of endemism, but show that several of these areas are likely underestimated in extent, and we highlight additional and previously unrecognized areas of high PE.

Integrative measures such as PE that include cryptic diversity with distribution modelling can reveal finer scale endemism patterns than species occurrence data alone. Such data at finer resolution are particularly important for understanding local scale patterns and processes (e.g. Carnaval et al. 2014; Rosauer et al., 2015), and show the strength of using measures such as PE that are not reliant on formal taxonomic classification. Although it appears that there is an extensive protected area network across the CFEA region, our data reveal

large gaps in this network. Nevertheless, it should be noted that our data is modelled and as such does not account for the substantial anthropogenic landscape modification that has occurred (e.g. Godoy et al. 2012, Hall et al., 2009). Combined with relatively low levels of legal enforcement, anthropogenic modification poses a major conservation concern across the CFEA, which will be exacerbated by future population growth and climate change. The high levels of threatened biodiversity and the rapidly increasing human population make conservation efforts in this region extremely challenging, especially given the limited funding and resources.

Conservationists are rarely afforded the luxury of planning new protected areas, and in most cases it is a race against time to protect whatever is possible before it disappears. Given the rapid loss of most forests outside governmental reserves, particularly in the East Usambaras and surrounding areas, our research suggests that strengthening protected areas that fall within identified PE hotspots would perhaps be the best strategy to conserve the biodiversity and evolutionary history of this region. We further suggest that existing frameworks for effective conservation prioritization based on phylogenetic and spatial data (e.g. Pollock et al., 2015) could be used to optimize conservation management efforts in this region. The conceptual framework in this manuscript is applicable to discover the distribution of biodiversity in any area, at any scale, and including cryptic diversity, allowing a flexible and objective means to identify important areas that should be considered for future conservation prioritization.

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Supplementary material

Fig. S1. Spatial sampling used in this study.

Fig. S2. Forest stability models.

Fig. S3. Environmental predictors.

Fig. S4. Schematic workflow of analyses.

Fig. S5. Lineage distribution models for all 35 intraspecific lineages included in this study.

Appendix S1. Additional methodological information.

Table S1. Sequences used in this study and evolutionary models per partition.

Table S2. Spatial and genetic dataset summary.

Table S3. Spatial point data.

Table S4. Correlations of environmental data.

Table S5. SDM, forest model contributions.

Table S6. Environmental correlates of PE.

Table S7. Sensitivity analyses – environmental correlations.

Table S8. Sensitivity analyses – conservation analyses.

Table S9. Major protected areas that intersect each of the eight PE hotspots shown in Fig. 5 and Table 1.

References

- Arctander, P., Johansen, C. & Coutellec-Vreto, M.-A. (1999) Phylogeography of three closely related African bovids (tribe Alcelaphini). *Molecular Biology and Evolution*, **16**, 1724-1739.
- Axelrod, D.I., & Raven, P.H. (1978) Late Cretaceous and Tertiary vegetation history of Africa. *Biogeography and Ecology of Southern Africa* (ed. Werger, M.J.A.). Springer, Netherlands.
- Azeria, E.T., Sanmartin, I., As, S., Carlson, A. & Burgess, N. (2007) Biogeographic patterns of the East African coastal forest vertebrate fauna. *Biodiversity and Conservation*, **16**, 883-912.
- Barratt, C.D., Lawson, L.P., Bittencourt-Silva, G.B., Duggart, N., Morgan-Brown, T., Nagel, P. & Loader, S.P. (2017) A new, narrowly distributed, and critically endangered species of spiny-throated reed frog (Anura: Hyperoliidae) from a highly threatened coastal forest reserve in Tanzania. *Herpetological Journal*, **27**, 13-24.
- Bell, R.C., Parra, J.L., Tonione, M., Hoskin, C.J., MacKenzie, J.B., Williams, S.E. & Moritz C. (2010) Patterns of persistence and isolation indicate resilience to climate change in montane rainforest lizards. *Molecular Ecology*, **19**, 2531-2544.
- Bivand, R. & Piras, G. (2015) Comparing implementations of estimation methods for spatial econometrics. *Journal of Statistical Software*, **63**, 1-36. Available from: <http://www.jstatsoft.org/v63/i18/>.
- Bouckaert, R., Heled, J., Kühnert, D., Vaughan, T., Wu, C-H., Xie, D., Suchard, M.A., Rambaut, A., & Drummond, A.J. (2014). BEAST 2: A Software platform for Bayesian evolutionary analysis. *PLoS Computational Biology*, **10**, e1003537. doi:10.1371/journal.pcbi.1003537.
- Brown, J.L., Cameron, A., Yoder, A.D., & Vences, M. (2014) A necessarily complex model to explain the biogeography of the amphibians and reptiles of Madagascar. *Nature Communications*, **5**, 5046.
- Burgess, N. & Clarke, G.P (eds.). (2000) *Coastal Forests of Eastern Africa*. IUCN Forest Conservation Programme, Gland, Switzerland and Cambridge, UK.
- Burgess, N., Fjeldså, J., Howell, K., Kilahama, F., Loader, S.P., Lovett, J.C. & Mbilinyi B. (2007) The biological importance of the Eastern Arc Mountains of Tanzania and Kenya. *Biological Conservation*, **134**, 209-231.
- Burgess, N.D., Clarke, G.P. & Rodgers, W.A. (1998) Coastal forests of eastern Africa : status, endemism patterns and their potential causes. *Biological Journal of the Linnean Society* **64**, 337-367.
- Burgess, N.D., Mwasumbi, L.B., Hawthorne, W.J., Dickinson, A. & Doggett, R.A. (1992) Preliminary assessment of the distribution, status and biological importance of coastal forests in Tanzania. *Biological Conservation*, **62**, 205-218.
- Calcagno, V. & de Mazancourt, C. (2010) glmulti : An R package for easy automated model selection with (generalized) linear models. *Journal of Statistical Software*, **34**, 1-29.
- Carnaval, A.C., Waltari, E., Rodrigues, M.T., Rosauer, D.F, Vanderwal, J., Damasceno, R., Prates, I., Strangas, M., Spanos, Z., Rivera, D., Pie, M.R., Firkowski, C.R., Bornschein, M.R., Ribeiro, L.F., Moritz, C (2014) Prediction of phylogeographic endemism in an environmentally complex biome. *Proceedings of the Royal*

- Society B*, **281**, doi: 10.1098/rspb.2014.1461.
- Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M. & Palmer T.M. (2015) Accelerated modern human – induced species losses: entering the sixth mass extinction. *Sciences Advances*, **1**, 1-5.
- Channing, A., Hillers, A., Lötters, S., Rödel, M.-O., Schick, S., Conradie, W., Rödder, D., Mercurio, V., Wagner, P., Dehling, J.M., Du Preez, L. H., Kielgast, J. & Burger, M. (2013) Taxonomy of the super-cryptic *Hyperolius nasutus* group of long reed frogs of Africa (Anura: Hyperoliidae), with descriptions of six new species. *Zootaxa*, **3620**, 301-350.
- Couvreur T.L.P., Chatrou L.W., Sosef M.S.M., & Richardson J.E. (2008) Molecular phylogenetics reveal multiple tertiary vicariance origins of the African rain forest trees. *BMC biology*, **6**, 54.
- Crisp, M.D, Laffan, S., Linder, H.P. & Monro, A. (2001) Endemism in the Australian flora. *Journal of Biogeography*, **28**, 183-198.
- Eiserhardt, W.L., Borchsenius, F., Sandel, B., Kissling, W.D. & Svenning, J.C. (2015) Late Cenozoic climate and the phylogenetic structure of regional conifer floras world-wide. *Global Ecology and Biogeography*, **24**, 1136-1148.
- Faith, D.P. (1992) Conservation evaluation and phylogenetic diversity. *Biological Conservation*, **61**, 1-10.
- Fjeldså, J. & Lovett, J.C. (1997) Geographical patterns of old and young species in African forest biota: the significance of specific montane areas as evolutionary centres. *Biodiversity and Conservation*, **6**, 325-346.
- Gehrke, B. & Linder, H.P. (2011) Time, space and ecology: Why some clades have more species than others. *Journal of Biogeography*, **38**, 1948-1962.
- Godoy, F.L., Tabor, K., Burgess, N.D., Mbilinyi, B.P., Kashaigili, J.J. & Steininger, M.K. (2011) Deforestation and CO2 emissions in coastal Tanzania from 1990 to 2007. *Environmental Conservation*, **39**, 62-71.
- González-Orozco, C.E., Mishler, B.D., Miller, J.T., Laffan, S.W., Knerr, N., Unmack, P., Georges, A., Thornhill, A.H., Rosauer, D.F. & Gruber, B. (2015) Assessing biodiversity and endemism using phylogenetic methods across multiple taxonomic groups. *Ecology and Evolution*, **5**, 5177-5192.
- Graham, C.H., VanDerWal, J., Phillips, S.J., Moritz, C. & Williams, S.E. (2010) Dynamic refugia and species persistence: Tracking spatial shifts in habitat through time. *Ecography*, **33**, 1062-1069.
- Gudde, R.M., Joy, J.B. & Mooers, A.O. (2013) Imperilled phylogenetic endemism of Malagasy lemuriformes. *Diversity and Distributions*, **19**, 664-675.
- Habel, J.C., Borghesio, L., Newmark, W.D., Day, J.J., Lens, L., Husemann, M. & Ulrich W. (2015) Evolution along the Great Rift Valley: phenotypic and genetic differentiation of East African white-eyes (Aves, Zosteropidae). *Ecology and Evolution*, **5**, 4849-4862.
- Haffer, J. (1969) Speciation in Amazonian forest birds. *Science*, **165**, 131-137.
- Hall, J., Burgess, N.D., Lovett, J., Mbilinyi, B. & Gerau, R.E. (2009) Conservation implications of deforestation across an elevational gradient in the Eastern Arc Mountains, Tanzania. *Biological Conservation*, **142**, 2510-2521.
- Hamilton, A.C. (1976) The significance of patterns of distribution shown by forest plants and animals in tropical Africa for the reconstruction of upper Pleistocene palaeo-environments: a review. *Palaeoecology of Africa*, **9**, 63-97.

- Harper, E.B., Measey, G.J., Patrick, D.A., Menegon, M., Vonesh, J.R. (2010) *Field guide to the amphibians of the Eastern Arc Mountains and Coastal Forests of Tanzania and Kenya*. Camerapix International, Nairobi, Kenya.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965-1978.
- Jetz W., Rahbek C., & Colwell R.K. (2004) The coincidence of rarity and richness and the potential signature of history in centres of endemism. *Ecology Letters*, **7**, 1180–1191.
- Kent, P.E., Hunt, J.A. & Johnstone, D.W. (1971) *Geophysics of coastal Tansania*. Institute of Geological Sciences, Geophysical papers, 101 pp.
- Kissling, W.D. & Carl, G. (2008) Spatial autocorrelation and the selection of simultaneous autoregressive models. *Global Ecology and Biogeography*, **17**, 59-71.
- Kissling, W.D., Blach-Overgaard, A., Zwaan, R.E. & Wagner, P. (2016) Historical colonization and dispersal limitation supplement climate and topography in shaping species richness of African lizards (Reptilia: Agaminae). *Scientific Reports*, **6**, 34014.
- Kissling, W.D., Eiserhardt, W.L., Baker, W.J., Borchsenius, F., Couvreur, T.L.P., Balslev, H., & Svenning, J.-C. (2012) Cenozoic imprints on the phylogenetic structure of palm species assemblages worldwide. *Proceedings of the National Academy of Sciences USA*, **109**, 7379-7384.
- Kolbert, E. (2014) *The Sixth Extinction*. Henry Holt and Company, New York.
- Kramer-Schadt S., Niedballa J., Pilgrim J.D., Schröder B., Lindenborn J., Reinfelder V., Stillfried M., Heckmann I., Scharf A.K., Augeri D.M., Cheyne S.M., Hearn A.J., Ross J., Macdonald D.W., Mathai J., Eaton J., Marshall A.J., Semiadi G., Rustam R., Bernard H., Alfred R., Samejima H., Duckworth J.W., Breitenmoser-Wuersten C., Belant J.L., Hofer H., & Wilting A. (2013) The importance of correcting for sampling bias in MaxEnt species distribution models. *Diversity and Distributions*, **19**, 1366–1379.
- Laity, T., Laffan, S.W., Gonzalez-Orozco, C.E., Faith, D.P., Rosauer, D.F., Byrne, M., Miller, J.T., Crayn, D., Costion, C., Moritz, C.C. & Newport, K. (2014) Phylodiversity to inform conservation policy: An Australian example. *Science of the Total Environment*, **534**, 131-143.
- Lanfear, R., Calcott, B., Ho, S.Y.W., & Guindon, S. (2012) PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution*, **29**, 1695–1701.
- Levinsky, I., Araújo, M.B., Nogués-Bravo, D., Haywood, A.M., Valdes, P.J. & Rahbek C. (2013) Climate envelope models suggest spatio-temporal co-occurrence of refugia of African birds and mammals. *Global Ecology and Biogeography*, **22**, 351-363.
- Linder, H.P., de Klerk, H.M., Born, J., Burgess, N.D., Fjeldså, J. & Rahbek, C. (2012) The partitioning of Africa: Statistically defined biogeographical regions in sub-Saharan Africa. *Journal of Biogeography*, **39**, 1189-1205.
- Loader, S.P., Ceccarelli, F.S., Menegon, M., Howell, K.M., Kassahun, R., Mengistu, A.A., Saber, S.A., Gebresenbet, F. & Gower, D.J. (2014) Persistence and stability of Eastern Afromontane forests : evidence from brevicipitid frogs. *Journal of Biogeography*, **41**, 1781-1792.
- Lorenzen, E.D., Heller, R., & Siegmund, H.R. (2012) Comparative phylogeography of African savannah ungulates. *Molecular Ecology*, **21**, 3656-3670.

- Maslin, M.A., Brierley, C.M., Milner, A.M., Shultz, S., Trauth, M.H., & Wilson, K.E. (2014) East african climate pulses and early human evolution. *Quaternary Science Reviews*, **101**, 1-17.
- Mayr, E. & O'Hara, R.J. (1986) The biogeographic evidence supporting the Pleistocene forest refuge hypothesis. *Evolution*, **40**, 55-67.
- Merow C., Smith M.J., Edwards T.C., Guisan A., McMahon S.M., Normand S., Thuiller W., Wüest R.O., Zimmermann N.E., & Elith J. (2014) What do we gain from simplicity versus complexity in species distribution models? *Ecography*, **37**, 1267–1281.
- Merow C., Smith M.J., & Silander J.A. (2013) A practical guide to MaxEnt for modeling species' distributions: What it does, and why inputs and settings matter. *Ecography*, **36**, 1058–1069.
- Moreau, R.E. (1933) Pleistocene climatic changes and the distribution of life in East Africa. *Journal of Ecology*, **21**, 415-435.
- Mumbi, C.T., Marchant, R., Hooghiemstra, H., & Wooller M.J. (2008) Late Quaternary vegetation reconstruction from the Eastern Arc Mountains, Tanzania. *Quaternary Research*, **69**, 326-341.
- Myers, N., Mittermeier R.A., Mittermeier, C.G., Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853-858.
- Pollock, L.J., Rosauer, D.F., Thornhill, A.H., Kujala, H., Crisp, M.D., Miller, J.T. & McCarthy M.A. (2015) Phylogenetic diversity meets conservation policy: small areas are key to preserving eucalypt lineages. *Philosophical Transactions of the Royal Society B*, **370**, doi: 10.1098/rstb.2014.0007.
- Ricklefs, R.E., Bermingham, E., Dick, C.W. & Moritz, C. (2005) Phylogenetic perspectives on patterns of regional and local species richness. in: *Tropical Rainforest: past, present, and future* (pp. 16-40). University of Chicago Press.
- Rosauer, D., Laffan, S.W., Crisp, M.D., Donnellan, S.C. & Cook, L.G. (2009) Phylogenetic endemism: a new approach for identifying geographical concentrations of evolutionary history. *Molecular Ecology*, **18**, 4061-4072.
- Rosauer, D.F., Blom, M.P.K., Bourke, G., Catalano, S., Donnellan, S., Gillespie, G., Mulder, E., Oliver, P.M., Potter, S., Pratt, R.C., Rabosky, D.L., Skipwith, P.L. & Moritz, C. (2016) Phylogeography, hotspots and conservation priorities: an example from the Top End of Australia. *Biological Conservation*, doi: 10.1016/j.biocon.2016.05.002
- Rosauer, D.F., Catullo, R.A., Vanderwal, J., & Moussalli, A. (2015) Lineage range estimation method reveals fine-scale endemism linked to Pleistocene stability in Australian rainforest herpetofauna. *PLoS One*, doi:10.1371/journal.pone.0126274.s001
- Rovero, F., Menegon, M., Fjeldså, J., Collett, L., Doggart, N., Leonard, C., Norton, G., Owen, N., Perkin, A., Spitale, D., Ahrends, A. & Burgess N.D. (2014) Targeted vertebrate surveys enhance the faunal importance and improve explanatory models within the Eastern Arc Mountains of Kenya and Tanzania. *Diversity and Distributions*, **20**, 1438-1449.
- Sandel, B., Arge, L., Dalsgaard, B., Davies, R.G., Gaston, K.J., Sutherland, W.J. & Svenning, J.-C. (2011) The Influence of late Quaternary climate-change velocity on species endemism. *Science*, **334**, 660-664.
- Tolley, K.A., Tilbury, C.R., Measey, G.J., Menegon, M., Branch, W.R., & Matthee, C.A. (2011) Ancient forest fragmentation or recent radiation? Testing refugial speciation models in chameleons within an African biodiversity hotspot. *Journal of Biogeography*, **38**, 1748-1760.

- Trauth, M.H., Maslin, M.A., Deino, A. & Strecker, M.R. (2005) Late Cenozoic moisture history of East Africa. *Science*, **309**, 2051-2053.
- Tuanmu, M.N. & Jetz, W. (2014) A global 1-km consensus land-cover product for biodiversity and ecosystem modelling. *Global Ecology and Biogeography*, **23**, 1031-1045.
- Van Bocxlaer I., Loader S.P., Roelants K., Biju S.D., Menegon M., & Bossuyt F. (2010) Gradual adaptation toward a range-expansion phenotype initiated the global radiation of toads. *Science*, **327**, 679–682.
- Weber, L.C., Vanderwal, J., Schmidt, S., McDonald, W.J.F. & Shoo, L.P. (2014) Patterns of rain forest plant endemism in subtropical Australia relate to stable mesic refugia and species dispersal limitations. *Journal of Biogeography*, **41**, 222-238.
- Wisz, M.S., Pottier, J., Kissling, W.D., Pellissier, L., Damgaard, C.F., Dormann, C.F., Forchhammer, M.C., Grytnes, J., Guisan, A., Heikkinen, R.K., Høye, T.T., Ockinger, E., Schmidt, N.M., Termansen, M., Wardle, D.A., Aastrup, P. & Svenning, J-C. (2013) The role of biotic interactions in shaping distributions and realised assemblages of species : implications for species distribution modelling. *Biological Reviews of the Cambridge Philosophical Society*, **8**, 15-30.
- Zimkus B.M., Lawson L.P., Barej M.F., Barratt C.D., Channing A., Dash K.M., Dehling J.M., Du Preez L., Gehring P-S., Greenbaum E., Gvodzik V., Harvey J., Kielgast J., Kusamba C., Nagy Z., Pabijan M., Penner J., Rödel M.O., Vences M. & Lötters S. (2017). Leapfrogging into new territory: how Mascarene ridged frogs have diversified across Africa. *Molecular Phylogenetics and Evolution*, **106**, 254-269.

Chapter III

Museums or cradles of diversity? Paleo- and Neo- endemism patterns in the East African lowlands using near complete assemblage phylogenetic data from amphibians

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Museums or cradles of diversity? Paleo- and Neo- endemism patterns in the East African lowlands using near complete assemblage phylogenetic data from amphibians

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Abstract

Identifying centres of endemism and the processes that contribute to their formation is fundamental in biogeography and macroecology. Two non-mutually exclusive hypotheses have examined whether range restricted species accumulate in an area due to low extinction rates ('museums of diversity') or high rates of speciation ('cradles of diversity'). In East Africa, lowland forest patches are generally interpreted as museums supporting ancient relicts caused by historical forest fragmentation since the Miocene. However, traditional measures such as species richness and endemism are unable to empirically test this hypothesis as they only consider species in geographical space and do not account for the temporal aspect of their diversification. To address this shortfall, we use phylogenetic and spatial data with a recently described statistical framework to identify centres of endemism, and distinguish between museums (paleo-endemism) and cradles of diversity (neo-endemism). Results confirm previous speculations of refugia, with paleo-endemism mainly distributed around lowland parts of the Eastern Afromontane and coastal forests in Kenya. Interestingly, neo-endemism was detected in miombo woodland, grasslands and island habitats. Several super-endemic areas supporting simultaneous paleo- and neo- endemism suggest that some parts of coastal forest, along with the Eastern Afromontane are key refugia for maintaining biodiversity in this region (museums), as well as being centres for recent radiations (cradles). The use of empirical data to categorize endemism types and how they are geographically distributed is a first for this region, and provides vital information which may be useful for future biodiversity conservation in this global biodiversity hotspot.

Key words: spatial phylogenetics, conservation, null models, Tanzania, Kenya, spatial data.

Introduction

Biodiversity is unevenly distributed across geographical space, with rich tropical regions supporting many centres of endemism that contain high numbers of range-restricted species. Centres of endemism are exceptionally important for biodiversity because range-restricted species are often unable to survive in areas other than those in which they are found. As such, these endemic areas and many of the species within them are worldwide conservation priorities due to anthropogenic impacts and climate change (Myers et al., 2000). Suitable habitats for species shift over time, with historical climate in particular considered as a major factor in explaining current biodiversity patterns (Sandel et al., 2011; Fjelds  & Lovett, 1997; Dimitrov et al., 2012). Hypotheses about how centres of endemism form has focused on the competing ideas that they may be ‘museums’ of diversity that support ancient paleo-endemic survivors of past widespread extinction events, ‘cradles’ of diversity supporting high numbers of relatively recently evolved neo-endemic species, or combinations of the two (Jablonski et al., 2006; Chown & Gaston, 2000; Gaston & Blackburn, 2007). However, traditional measures of biodiversity that only account for species numbers and their geographic distributions are unable to distinguish between paleo- and neo- endemism as they provide no information on the temporal aspect of species diversification. To this end, phylogenetic information can greatly assist our understanding of biodiversity patterns across space and time (Rosenzweig, 1995). A recently published statistical framework (Mishler et al., 2014) developed a novel metric, relative phylogenetic endemism (RPE), which enables the categorization of endemism types based on the community phylogenetic composition of any given area. Using phylogenetic branch lengths (see Rosauer et al., 2009), the type of endemism present can be categorized based on whether it holds an over-representation of deeper branch lengths (paleo-endemism), an over-representation of shorter branch lengths (neo-endemism), or some mixture of the two. Distinguishing the types of endemism present in biodiversity hotspots may lead to a more thorough understanding of the processes that lead to current biodiversity patterns, and provide a fundamental basis to understand the reasons why some areas are richer than others.

In lowland East Africa, two adjacent biodiversity hotspots (Myers et al., 2000) hold a significant proportion of the region’s endemic species. The Coastal Forests of Eastern Africa (CFEA, Fig. 1) span across coastal East Africa from Somalia, through Kenya, Tanzania and Mozambique, and in several places (less than 1000 m elevation) overlap with the Eastern Afromontane hotspot (EA, specifically the Eastern Arc forests). The CFEA and surrounding areas are a highly heterogeneous habitat mosaic, supporting moist and dry forest, coastal thicket, miombo woodland, savannah, swamp, and mangroves close to the coast. Many of the lower elevation areas of this region have been subjected to severe climate oscillations since at least the Miocene, with some higher elevation habitats such as the EA and raised plateaus within the CFEA thought to have remained relatively stable (Mumbi et al., 2008; Newmark, 2002). Paleo-climatic stability has undoubtedly had a profound effect on the habitat and species diversity across this region with the contraction and expansion of forest closely linked to the pulses of glacial and interglacial periods (Axelrod & Raven, 1978; Maslin et al., 2014; Trauth et al., 2005; Demenocal, 1995; Sepulchre et al., 2006). Parts of this region are likely to have acted as refugia for biodiversity during the late Pleistocene (Diamond & Hamilton, 1980; Fjelds  & Lovett, 1997; Voelker et al., 2010; Dimitrov et al., 2012) and probably much earlier, minimally to the Miocene (Bryja et al., 2014; Tolley et al., 2011; Loader et al., 2014; Demos et al., 2015). Putative refugia and centres of endemism within the CFEA and lowland EA have been identified using species distributional data in Tanzania (lowlands of the Udzungwa and Uluguru mountains, Lindi, Pugu hills, Pemba island, Usambara-Kwale), and Kenya (Arabuko-Sokoke and Tana river)

(Burgess et al. 1998). These refugia are hypothesized to support ancient paleo- endemic diversity, with limited recent evolution (neo-endemism), though this has so far only been speculated, without empirical tests using appropriate phylogenetic data (Burgess et al., 1998). Amphibians represent an excellent model system to test the spatial distribution of endemism types across the region because compared to most other vertebrates they are poor dispersers and sensitive to climate change over time. The CFEA and surrounding grasslands and woodland habitats supports at least fifty-one amphibian species in total (Poynton et al., 2007; IUCN, 2015), with many range-restricted species that demonstrate a remarkable variety of life histories (Müller et al., 2013).

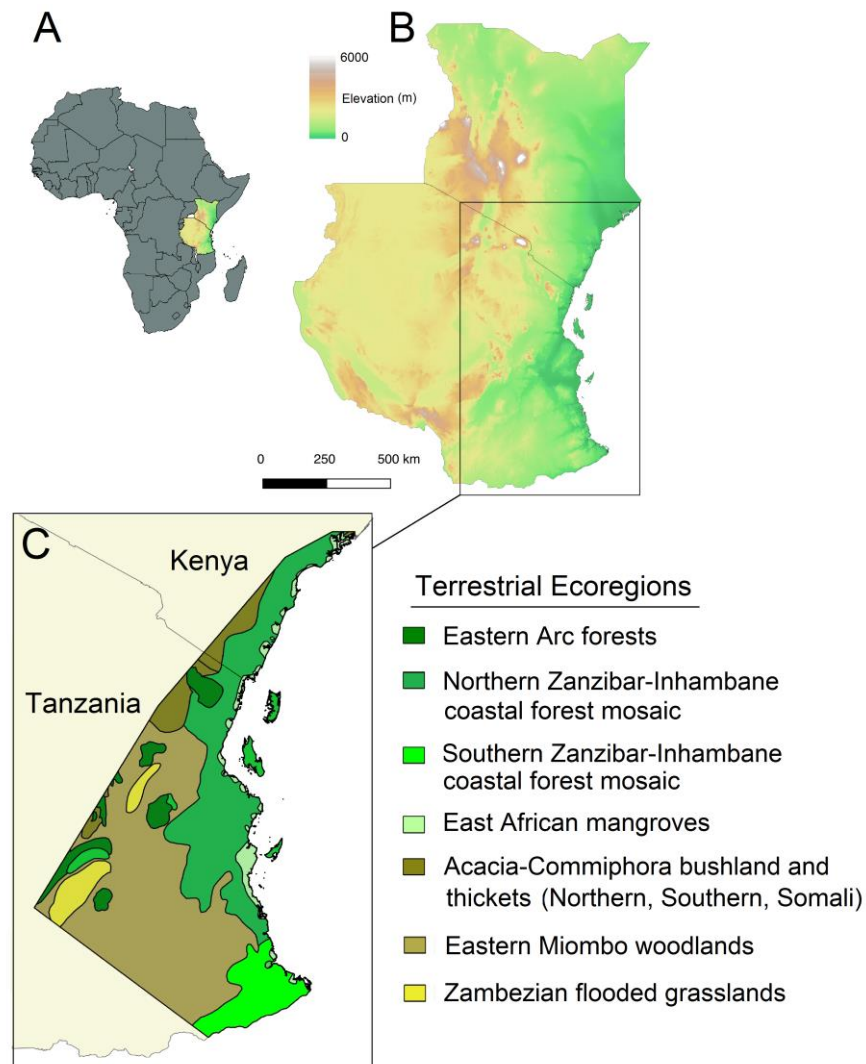


Fig. 1. A) Location of the study area in East Africa. B) Elevation profile, C) Extent of spatial sampling within Tanzania and Kenya, showing the terrestrial ecoregions that are represented.

In this paper we use phylogenetic and spatial data for amphibians to investigate biodiversity and endemism patterns in a thoroughly sampled part of the East African lowlands. We hypothesize that in line with previous speculations, paleo-endemism is the dominant type to explain amphibian assemblages in the CFEA, and especially so in higher elevation areas such as plateaux and lowland parts of the EA. To test this hypothesis, we sampled near complete species level amphibian data across lowland Tanzania and Kenya. The extensive dataset

we compiled allows us to: i) map the distribution of biodiversity and endemism by comparing species richness (SR), phylogenetic diversity (PD) and phylogenetic endemism (PE), and ii) distinguish the types of endemism present and how it is geographically distributed across the region.

Methods

Data collection and integration

We used data from a large-scale study of phylogenetic endemism across the CFEA investigating intra-specific endemism patterns, supplemented with additional species that covered the lowland EA (Barratt et al. in review). A full description of the methods used can be found in the methods section of that paper. In brief, genetic samples were collected across the CFEA and EA over numerous field seasons (2001-2015) and a phylogeny was reconstructed using BEAST 2.1.3 (Bouckaert et al., 2014) with the caecilian, *Scolecophorus vittatus* (Gymnophiona) as an outgroup. The phylogeny included individual representatives of each species (n = 55) using partial fragments of the mitochondrial genes *16S* rRNA and cytochrome oxidase subunit 1 (*COI*). The phylogeny from Barratt et al. (in review) was trimmed to match our species dataset (Fig. S1). Spatial sampling matches the phylogenetic data, together covering an area of Tanzania and Kenya that is relatively well known in terms of species composition (compared to the poorly sampled remainder of the CFEA in Mozambique and Somalia). We restrict our study to this area to account for the uncertainty of species identifications in other regions of coastal forest, and the lack of phylogenetic and spatial data for these taxa. We combined recent field sampling with existing spatial data collected from museum and literature sources (Burgess & Clarke, 2000 and references within) and collaborators databases (Kim Howell pers. comm.). We used occurrence data to build species distribution models (SDMs) in MAXENT 3.3.3k (Phillips et al., 2006) for each species, spatially rarefying all occurrence data first to ensure that models were not biased towards collecting localities. Our species level dataset after filtering and correction in ARCMAP 10.2.1 comprised of 9,987 individual records for the 55 species with phylogenetic data (Table 1). This dataset covers almost the entire known coastal forest amphibians in this area and includes peripheral coastal forest species present in this area that are members of montane clades that extend into the CFEA (Poynton et al., 2007). We ran a sensitivity analysis of the full data, to account for the removal of 11 species that are geographically restricted, predominantly occurring in the lowland EA. Though these species occur within the study area the level of their interaction with the lowland assemblage is uncertain, so we ran all subsequent analyses on the 44 species dataset, (Table 1), and results are supplied in the appendix. (Fig. S2, S3).

Table 1. Summary of species used in this study for the 55 and 44 species datasets. * species were removed for the sensitivity analysis using the 44 species dataset.

Family	Genus	Species	Spatial records	Unique spatial records	Unique spatial records after rarefying	
Arthroleptidae	<i>Arthroleptis</i>	<i>affinis</i> *	320	23	13	
	<i>Arthroleptis</i>	<i>stenodactylus</i>	761	174	62	
	<i>Arthroleptis</i>	<i>taneri</i> *	65	4	2	
	<i>Arthroleptis</i>	<i>xenodactyloides</i>	738	137	37	
	<i>Arthroleptis</i>	<i>xenodactylus</i> *	78	18	7	
	<i>Leptopelis</i>	<i>argenteus</i>	51	12	9	
	<i>Leptopelis</i>	<i>concolor</i>	141	37	24	
	<i>Leptopelis</i>	<i>flavomaculatus</i>	230	87	33	
	<i>Leptopelis</i>	<i>grandiceps</i> *	38	14	7	
	Bufonidae	<i>Sclerophrys</i>	<i>brauni</i> *	50	20	7
<i>Sclerophrys</i>		<i>gutturialis</i>	99	64	30	
<i>Sclerophrys</i>		<i>pusilla</i>	76	41	18	
<i>Mertensophryne</i>		<i>howelli</i>	13	1	2	
<i>Mertensophryne</i>		<i>lindneri</i>	28	16	9	
<i>Mertensophryne</i>		<i>loveridgei</i>	65	14	7	
<i>Mertensophryne</i>		<i>micranotis</i>	78	37	16	
<i>Mertensophryne</i>		<i>usambarae</i>	7	4	2	
Brevicipitidae		<i>Breviceps</i>	<i>mossambicus</i>	88	24	14
	<i>Callulina</i>	<i>krefftii</i>	257	7	3	
Hemisotidae	<i>Hemisus</i>	<i>marmoratus</i>	282	91	47	
Herpeliidae	<i>Boulengerula</i>	<i>changamwensis</i>	18	3	2	
	<i>Boulengerula</i>	<i>uluguruensis</i>	9	6	5	
Hyperoliidae	<i>Afrixalus</i>	<i>fornasini</i>	647	116	57	
	<i>Afrixalus</i>	<i>delicatus</i>	64	12	10	
	<i>Afrixalus</i>	<i>stuhlmanni</i>	290	64	36	
	<i>Afrixalus</i>	<i>sylvaticus</i>	78	24	17	
	<i>Hyperolius</i>	<i>argus</i>	250	60	34	
	<i>Hyperolius</i>	<i>mariae</i>	380	60	32	
	<i>Hyperolius</i>	<i>mittelli</i>	201	28	28	
	<i>Hyperolius</i>	<i>nasutus</i>	156	33	21	
	<i>Hyperolius</i>	<i>parkeri</i>	171	52	35	
	<i>Hyperolius</i>	<i>pusillus</i>	215	38	17	
	<i>Hyperolius</i>	<i>reesi</i>	77	9	6	
	<i>Hyperolius</i>	<i>rubrovermiculatus</i>	63	6	2	
	<i>Hyperolius</i>	<i>ruvuensis</i>	4	1	1	
	<i>Hyperolius</i>	<i>substriatus</i>	946	76	19	
	<i>Hyperolius</i>	<i>tuberilinguis</i>	590	94	48	
	<i>Kassina</i>	<i>maculata</i>	78	34	21	
	<i>Kassina</i>	<i>senegalensis</i>	291	52	26	
Microhylidae	<i>Phrynomantis</i>	<i>bifasciatus</i>	64	30	16	
Petropedetidae	<i>Arthroleptides</i>	<i>martiensseni</i> *	53	25	6	
	<i>Arthroleptides</i>	<i>yakusini</i> *	14	5	5	
Phrynobatrachidae	<i>Phrynobatrachus</i>	<i>acridoides</i>	574	138	62	
	<i>Phrynobatrachus</i>	<i>mababiensis</i>	123	52	29	
Ptychadenidae	<i>Hildebrandtia</i>	<i>ornata</i>	8	6	6	
	<i>Ptychadena</i>	<i>anchietae</i>	307	91	38	
	<i>Ptychadena</i>	<i>mossambica</i>	49	28	19	
	<i>Ptychadena</i>	<i>mascareniensis</i>	61	27	18	
Pyxicephalidae	<i>Amietia</i>	<i>angolensis</i> *	111	26	14	
	<i>Pyxicephalus</i>	<i>edulis</i>	35	20	14	
Ranidae	<i>Amnirana</i>	<i>galamensis</i>	80	21	16	
Rhacophoridae	<i>Chiromantis</i>	<i>xerampelina</i>	287	87	49	
Pipidae	<i>Xenopus</i>	<i>laevis</i> *	11	5	5	
	<i>Xenopus</i>	<i>muelleri</i>	245	76	39	
Σ	14	21	55	9,987	2,222	1,094

Biodiversity and endemism patterns

We integrated species occurrences and matching phylogenetic data in the software BIODIVERSE 1.99 (Laffan et al., 2010) as 10km² grid cells. This size of grid cells was chosen due to computational constraints when randomizing the data. As Biodiverse requires presence/absence data to calculate biodiversity metrics we used the minimum training presence threshold of each SDM to transform each model into a binary distributional matrix (1 = present, 0 = absent). We supplied a parameter file to match phylogenetic tips on the tree to their SDMs and calculated species richness (SR), weighted endemism (WE), phylogenetic diversity (PD), phylogenetic endemism (PE) and a new metric known as relative phylogenetic endemism (RPE, Mishler et al. 2014) for later categorization of endemism types using the *spatial analyses* function in Biodiverse (hereafter referred to as observed results). When calculating RPE, an alternative PE score per grid cell is first estimated (PE_{null}), using a phylogenetic tree with equalized branch lengths but the same number of taxa in each grid cell. This serves as a null model to test the observed PE scores per grid cell (PE) against, and RPE is then calculated as a ratio between PE and PE_{null} for each grid cell.

We randomized the data using the *rand_structure* feature for 999 iterations (hereafter referred to as randomized results). During each randomization, the taxa on the phylogeny are randomly assigned to a grid cell without replacement, therefore keeping the number of grid cells per species and the species richness of each grid cell constant. The calculations of PE, PE_{null} and RPE are made at each iteration, and form a null distribution that is used to test the significance of observed results with non-parametric tests.

Categorical analysis of neo- and paleo- endemism

We followed a method named categorical analysis of neo- and paleo- endemism (CANAPE, Mishler et al., 2014) to compare observed and randomized PE results. The workflow for the estimation of biodiversity metrics, significance testing and CANAPE method is shown in Fig. 2. The method is designed to investigate if an area supports more or less PE than would be expected by chance compared to a null model after multiple randomizations of the data. By testing significance levels of observed PE values per grid cell compared to the null expectation (PE_{null}), CANAPE firstly identifies areas of endemism which significantly differ from the null distribution after multiple randomizations, and secondly categorizes these areas into their endemism types by thresholding the RPE metric with observed PE values as a ratio. Areas are parsed into their types of endemism present based on whether there is an overrepresentation of shorter or longer branch lengths (neo- or paleo- or mixtures of these two).

From the calculations made in BIODIVERSE 1.99, we exported observed and randomized results into separate files and modified an R script to fit our data and run the CANAPE classification (https://github.com/NunzioKnerr/biodiverse_pipeline). Results were classified with two-tailed non-parametric tests, first looking for significantly high PE or PE_{null} (i.e. $p < 0.05$), with cells meeting this requirement then assessed for the significance of RPE to determine paleo- or neo- endemism. Significantly high RPE ($p < 0.05$) means that PE is consistently higher than PE_{null}, indicating paleo-endemism, where significantly low means that PE is consistently lower than PE_{null}, indicating neo-endemism. If RPE is not significant, then a mixture of paleo- and neo- endemism is present; with areas of PE and PE_{null} that are both significantly high ($p < 0.01$) in these cases being termed super-endemic grid cells.

Categorical Analysis of Neo- and Paleo- endemism

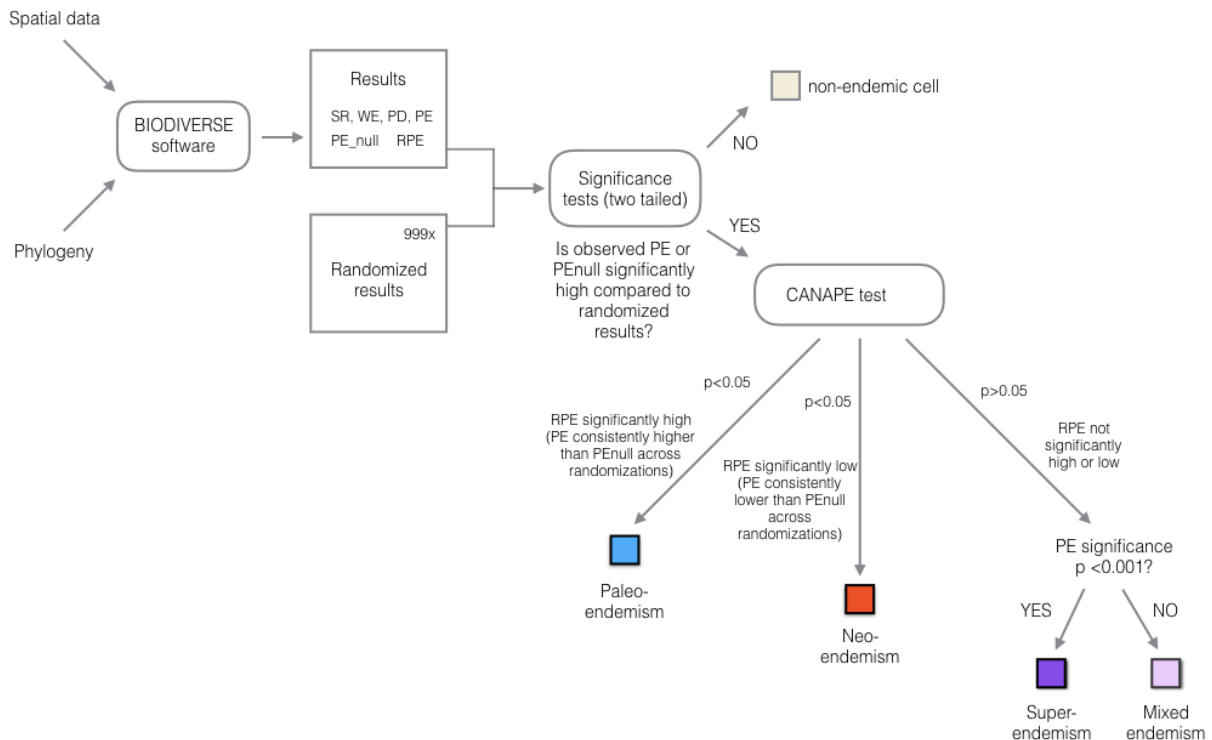


Fig. 2. Workflow for this paper, explaining the steps to calculate PE, RPE and how the CANAPE method categorizes endemism types.

Results

Biodiversity and endemism patterns

The first step of our analysis was to estimate and compare SR, PD and PE. Areas of high SR and PD are widespread across our sampling area but generally higher in the northern parts, corresponding to the northern Zanzibar-Inhambane coastal forest mosaic (White, 1968, 1983). This includes parts of the lowland EA (Usambara, Uluguru) and northern parts of the CFEA (Pugu hills and around the city of Dar es Salaam). Phylogenetic endemism is generally low across the study region, but is comparatively higher in several areas (East Usambara, Uluguru, Pugu hills in Tanzania and the southern part of coastal Kenya around Mombasa) (Fig. 3, A-C). Bivariate plots and linear regression analyses investigating relationships among these variables reveal that SR and PD are closely correlated, though PE accounts geographic rarity by identifying distinct concentrations of evolutionary history that are not always represented by high species richness (Fig. 3 D-F). These results demonstrate the utility of phylogenetic endemism in highlighting grid cells that are rich in evolutionary history but not necessarily species richness/phylogenetic diversity.

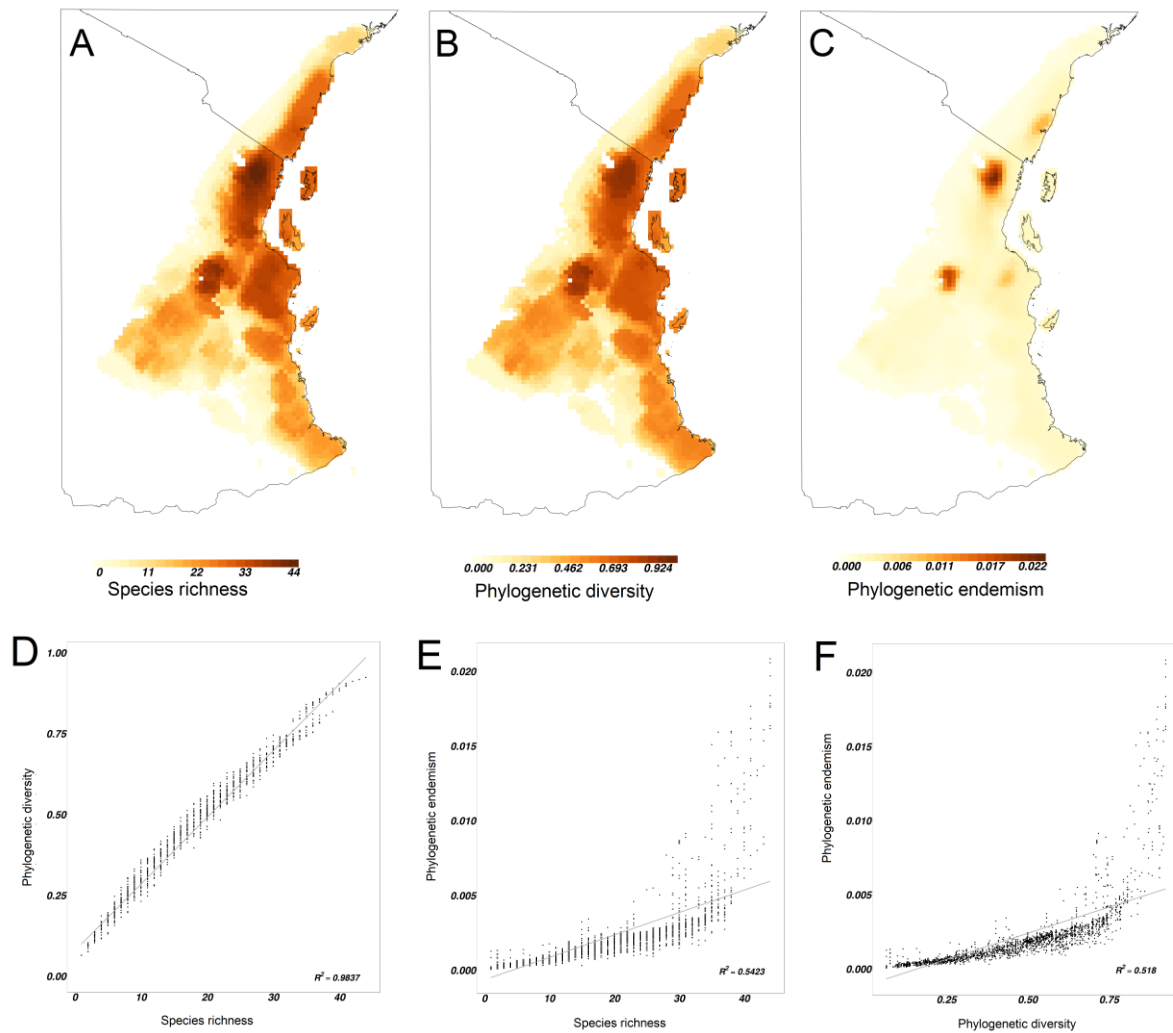


Fig. 3. A) Species richness (SR), B) Phylogenetic diversity (PD), C) Phylogenetic endemism (PE) across the study area (upper panel). Darker colours represent higher scores, results shown are for the 55 species dataset. Relationships between biodiversity indices used are shown in the lower panel; D) phylogenetic diversity vs species richness, E) phylogenetic endemism vs species richness, F) phylogenetic endemism vs phylogenetic diversity. Scattered data points in E and F show areas with high levels of phylogenetic endemism that are not highly correlated with species richness or phylogenetic diversity.

Categorical analysis of neo- and paleo- endemism

We identified several areas dominated by paleo-endemism (blue) in lowland East Africa, supporting our hypothesis that paleo-endemism – or museums of diversity - have significantly contributed to the present-day amphibian diversity in the area. However, these are mainly located in lowland parts of the EA (West and East Usambara, Uluguru, Nguru), and only one in coastal forest in southern Kenya (Fig. 4A). We also detected areas dominated by neo-endemism (red), these included the Selous Game reserve and Lindi region in Tanzania, Kilombero Valley and Mahenge mountains, Mafia island and East Usambara in Tanzania, and also the Shimba Hills in Kenya. Super-endemic areas that comprise of high levels of both paleo- and neo- endemism together (dark purple) include lowland EA (Uluguru, Udzungwa, Usambara, Nguru), a large area in the Kilombero Valley, the

Pugu hills (Tanzania) and around Mombasa (Kenya). Mixed endemism (light purple) is found on the periphery of all other paleo-, neo- or super- endemic areas. The statistical significance of PE and RPE when compared with randomized null models, and the relationship between PE and PE_{null} for each statistically significant grid cell are shown in Fig. 4 B-C, respectively.

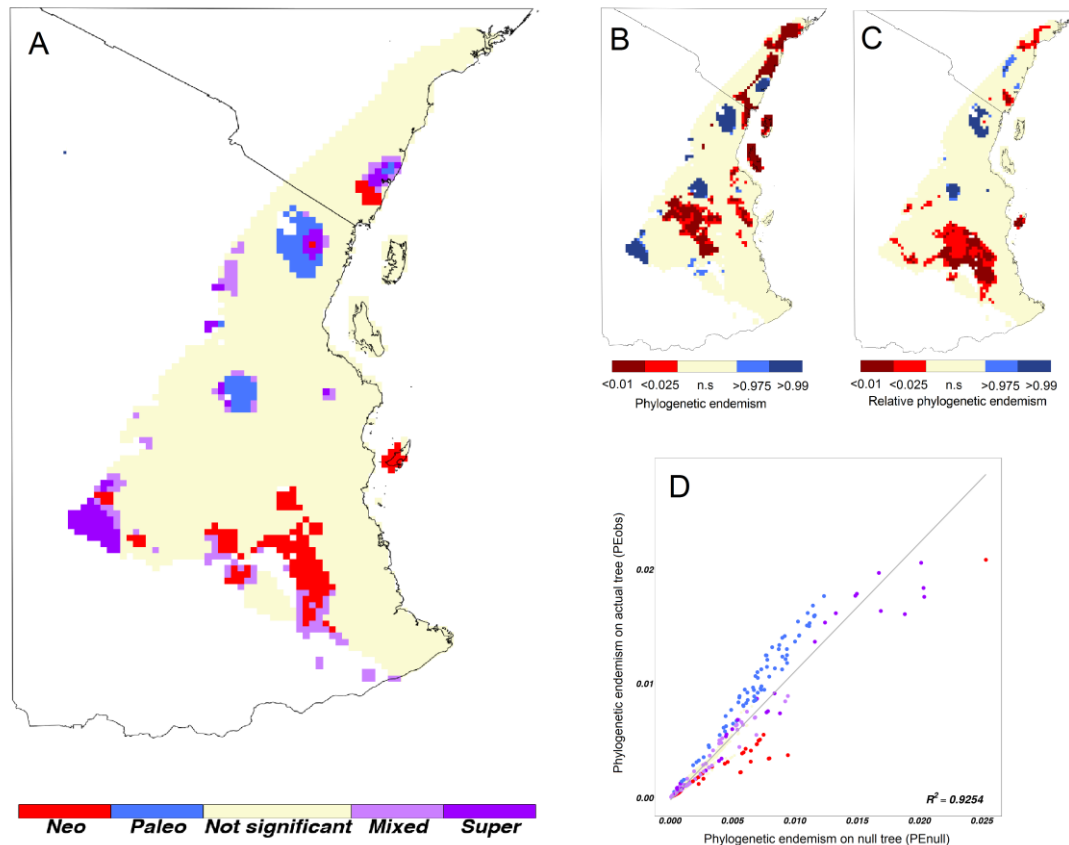


Fig. 4. A) Categorization of neo- and paleo- endemism (CANAPE) based on the significance tests of B) phylogenetic endemism, C) relative phylogenetic endemism, D) shows the relationship between phylogenetic endemism on the actual tree (PE) and phylogenetic endemism on the null tree (PE_{null}) after randomization, which is used along with significance tests of PE and RPE to categorize endemic grid cells into neo-, paleo-, mixed and super categories.

Discussion

Our results demonstrate that PE offers a valuable tool for assessing biodiversity and endemism, and unlike PD, which is linked to species richness patterns, can reveal concentrations of evolutionary history that are not necessarily species rich. The distinction between endemism types enhances our understanding of the evolutionary processes that have led to current biodiversity patterns and further underlines the complexity of the diversity patterns in lowland East Africa. The randomization and null model framework show that many areas of PE are statistically significant (all non-beige coloured grid cells in Fig. 4A). By employing the new RPE metric within the CANAPE hypothesis-testing framework we show that there is geographical complexity in the results. For the first time we prove with phylogenies that many concentrations of paleo-endemism in lowland East Africa exist,

the majority of these in the lowland EA, but some in coastal forests. Results for neo-endemism suggest that grassland and miombo woodland habitats in particular are important centres for neo-endemism in amphibians.

Paleo-endemism indicates an over-representation of long-branch lengths compared what would be expected by chance, suggesting that ancient diversity may have persisted in those areas, gradually becoming endemic relicts with increased extinction in the surrounding areas. The distribution of paleo-endemism revealed by our results is in agreement with previous hypotheses of refugia in lowland parts of this region (Burgess et al. 1998), mainly concentrated in coastal forest areas that overlap with lowland parts of the EA (Usambara, Uluguru, Nguu, Nguru, Udzungwa). Relictual paleo-endemic coastal forest diversity is also detected in Mombasa. Super-endemism in adjacent coastal Kenya and the Pugu hills in Tanzania lend support to the idea that some part of the coastal forests are museums of diversity that can best be described as a ‘vanishing refuge’ (Burgess et al. 1998). Results recover several of the subcentres of endemism speculated by Burgess et al. (1998). The dominance of paleo- and super-endemism in the northern part of our study region (lowland EA and parts of the CFEA) confirm that these places are, at least in part, museums of diversity that support relicts that gradually became extinct in surrounding areas over time (Burgess et al., 1998; Azeria et al., 2007; Diamond & Hamilton, 1980). This might be linked to close proximity of the EA to the northern coastal region, compared to the central and south parts – with the Uluguru’s being the only EA refugia relatively close to central coastal region. Other major geographical changes are likely to be important in shaping the paleo-endemism patterns we recover. The major tectonic uplift that created the Great Lakes and African Rift Valley from the Miocene onwards likely contributed significantly to the vicariant evolution of many species in this region (Tolley et al., 2011; Loader et al., 2014; Lawson et al., 2015; Demos et al., 2015; Bryja et al., 2014). Repeated historical climate and sea level fluctuations since Miocene, but especially during the Pleistocene, accompanied by the slow desiccation of African habitats are thought to have played a major role in the fragmentation of a more pan-African forest (Trauth et al., 2005; Maslin et al., 2014; Demenocal, 1995). Such large scale retraction of forests likely explains the high levels of paleo-endemism detected, where ancient relicts could only have persisted in particular areas that remained stable over long time periods (Burgess et al., 2007; Fjeldsa & Lovett, 1997; Loader et al., 2014; Tolley et al., 2011).

Neo-endemism, in contrast, is caused by an over-representation of shorter branch lengths than expected by chance, signifying that endemism is caused by recent evolution. The dominance of neo-endemism in areas that correspond to miombo woodland and grasslands such as the Selous Game Reserve and the Kilombero valley indicate that the relatively low stability and shifting climate of these landscapes, which are partially maintained by seasonal fire (Frost, 1996), may be key in the evolution of new lineages (e.g., Morley, 2000). The categorization of Mafia island as a centre of neo-endemism is also interesting in this respect, as it formed part of the mainland up to around 9,000 years ago in the Last Glacial Maximum when it became isolated (Prendergast et al. 2016), which may have led to recent evolution in situ. Neo-endemism is not detected on other islands such as Zanzibar and Pemba however, which may be explained by relatively poor sampling for most species in these areas which may have had a reduced prediction of occurrence across species by SDMs. Neo-endemism patterns confirm previous hypotheses that most of the coastal forests are not important centres of recent evolution (Burgess et al. 1998). However, neo-endemism in coastal forest areas such as Mafia island and the Shimba hills suggests that these parts of the CFEA should be considered as cradles of diversity, reflecting recent radiations.

Geographically, it is perhaps notable that areas representing museums of diversity (i.e. paleo- and super-endemism) are generally concentrated in the northern parts of the study region, corresponding to the Northern

Zanzibar-Inhambane coastal forest mosaic, and in closer proximity to the EA. The EA, along with northern parts of the coastal forests is predicted to have remained more climatically stable than the Southern Zanzibar-Inhambane coastal forest mosaic, which receives less rainfall due to being in the rain shadow of Madagascar, and has also undergone less extreme sea level changes since the Miocene (Burgess & Clarke, 2000). Though major parts of the CFEA and EA can certainly be considered as museums of relictual diversity which aligns with previous studies, there is evidence from our results to suggest that several areas are cradles of diversity that promote speciation. Using empirical data to categorize the types of endemism and their distribution is novel for this region, and provides vital preliminary information and a framework that may be useful to guide future biodiversity conservation in this global biodiversity hotspot. Complex mixtures of endemism types are present across this part of East Africa, and generalizations are not easy to make, as previous studies of this region have noted (Burgess & Clarke, 2000). However, the CFEA and EA regions are clearly unique as they support paleo-endemic relicts of ancient processes alongside neo-endemics from recent processes, with both signatures detectable in our data. This is unsurprising given the high habitat heterogeneity of the coastal forests in particular, and the unique characteristics and histories of many coastal forest patches, though it has not been quantified before despite being suggested (Burgess et al. 1998).

The interplay between historical and environmental factors in shaping biodiversity patterns remains poorly understood. Our data show patterns across parts of lowland East Africa suggest the existence of both cradles and museums of diversity. These findings are in line with other recent studies in other geographic regions (Couvreur et al., 2011; Pennington et al., 2015, Koenen et al., 2015) but in Sub-Saharan Africa cradles of diversity are generally more concentrated in grassland type habitats (Linder et al., 2014), supporting the idea that forest habitats are important museums of diversity in this region. Our findings have broad implications for the understanding of tropical biodiversity hotspots in Africa, but is also applicable to other biologically rich areas worldwide.

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Supplementary material

Fig. S1. Trimmed phylogenetic tree from Barratt et al. (in review) to match species level dataset.

Fig. S2. Sensitivity analyses with 44 species dataset showing SR, PD, PE and their relationships.

Fig. S3. Sensitivity analyses (CANAPE) for 44 species dataset.

References

- Axelrod D.I., Raven P.H. (1978) Late Cretaceous and Tertiary vegetation history of Africa. In: M. Werger (Ed.), *Biogeography and Ecology of Southern Africa*, Junk, The Hague (1978), pp. 77–130.
- Azeria E.T., Sanmartin I., As S., Carlson A., & Burgess N. (2007) Biogeographic patterns of the East African coastal forest vertebrate fauna. *Biodiversity and Conservation*, **16**, 883–912.
- Bouckaert R., Heled J., Kühnert D., Vaughan T., Wu C.H., Xie D., Suchard M.A., Rambaut A. & Drummond A.J. (2014) BEAST 2: A Software Platform for Bayesian Evolutionary Analysis. *PLoS Computational Biology*, **10**, 1003537.
- Bryja J., Mikula O., Šumbera R., Meheretu Y., Aghová T., Lavrenchenko L.A., Mazoch V., Oguge N., Mbau J.S., Welegerima K., Amundala N., Colyn M., Leirs H. & Verheyen E. (2014) Pan-African phylogeny of *Mus* (subgenus *Nannomys*) reveals one of the most successful mammal radiations in Africa. *BMC Evolutionary Biology*, **14**, 256.
- Burgess N. & Clarke G.P. (2000) *Coastal Forests of Eastern Africa*. IUCN Forest Conservation Programme, **2010**, 443 pp.
- Burgess N., Fjeldsa J., Howell K., Kilahama F., Loader S.P., Lovett J.C., & Mbilinyi B. (2007) The biological importance of the Eastern Arc Mountains of Tanzania and Kenya. *Biological Conservation*, **134**, 209–231.
- Burgess N.D., Clarke G.P., & Rodgers W.A. (1998) Coastal forests of eastern Africa: status, endemism patterns and their potential causes. *Biological Journal of the Linnean Society*, **64**, 337–367.
- Chown S.L. & Gaston K.J. (2000) Areas cradles and museums: The latitudinal gradient in species richness. *Trends in Ecology and Evolution*, **15**, 311–315.
- Couvreur T., Forest F. & Baker W.J. (2011) Origin and global diversification patterns of tropical rain forests: inferences from a complete genus-level phylogeny of palms. *BMC Biology*, **9**, 44
- Demenocal P.B. (1995) Plio-Pleistocene African climate. *Science*, **270**, 53–59.
- Demos T.C., Kerbis Peterhans J.C., Joseph T.A., Robinson J.D., Agwanda B., & Hickerson M.J. (2015) Comparative population genomics of African montane forest mammals support population persistence across a climatic

- gradient and quaternary climatic cycles. *PLoS ONE*, **10**, e031800.
- Diamond A.W. & Hamilton A.C. (1980) The distribution of forest passerine birds and Quaternary climatic change in tropical Africa. *Journal of Zoology*, **191**, 379–402.
- Dimitrov D., Nogués-Bravo D. & Scharff N. (2012) Why do tropical mountains support exceptionally high biodiversity? The Eastern Arc mountains and the drivers of Saintpaulia diversity. *PLoS ONE*, **7**, e48908.
- Fjeldsa J. & Lovett J.C. (1997) Biodiversity and environmental stability. *Biodiversity and Conservation*, **6**, 315–323.
- Frost, P. (1996) The Ecology of Miombo Woodlands. In: Campbell, B. (ed.), *The Miombo in transition: woodlands and welfare in Africa*. Center for International Forestry Research, 273 pp.
- Gaston K.J. & Blackburn T.M. (2007) *Pattern and process in macroecology*. Blackwell Science Ltd.
- IUCN (2015) IUCN Red List of Threatened Species. Available from: <<http://www.iucnredlist.org>>. Accessed: 6th September 2015.
- Jablonski D., Roy K. & Valentine J.W. (2006) Out of the Tropics: Evolutionary Dynamics of the Latitudinal Diversity Gradient. *Science*, **314**, 102–106.
- Koenen E.J.M., Clarkson J.J., Pennington T.D., Chatrou L.W. (2015) Recently evolved diversity and convergent radiations of rainforest mahoganies (Meliaceae) shed new light on the origins of rainforest hyperdiversity. *New Phytologist*, **207**, 327–339.
- Laffan S.W., Lubarsky E. & Rosauer D.F. (2010) Biodiverse, a tool for the spatial analysis of biological and related diversity. *Ecography*, **33**, 643–647.
- Lawson L.P., Bates J.M., Menegon M., & Loader S.P. (2015) Divergence at the edges: peripatric isolation in the montane spiny throated reed frog complex. *BMC Evolutionary Biology*, **15**, 128.
- Linder, H.P., Pennington, T. & Schneider, H. (2014) The evolution of African plant diversity. *Frontiers in Ecology and Evolution*, **2**, 1–14.
- Loader S.P., Ceccarelli F.S., Menegon M., Howell K.M., Kassahun R., Mengistu A.A., Saber S.A., Gebresenbet F., de Sá R., Davenport T.R.B., Larson J.G., Müller H., Wilkinson M., & Gower D.J. (2014) Persistence and stability of Eastern Afromontane forests: Evidence from brevicipitid frogs. *Journal of Biogeography*, **41**, 1781–1792.
- Maslin M.A., Brierley C.M., Milner A.M., Shultz S., Trauth M.H., & Wilson K.E. (2014) East african climate pulses and early human evolution. *Quaternary Science Reviews*, **101**, 1–17.
- Mishler B.D., Knerr N., González-Orozco C.E., Thornhill A.D., Laffan S.W. & Miller J.T. (2014) Phylogenetic measures of biodiversity and neo- and paleo-endemism in Australian Acacia. *Nature Communications*, **5**, 4473.
- Morley R.J. (2000) *Origin and Evolution of Tropical Rain Forests*. Chichester: Wiley, 378 pp.
- Müller H.M., Liedtke H.C., Menegon M. Beck J., Ballesteros-Mejia L., Nagel P., Loader S.P. (2013) Forests as promoters of terrestrial life-history strategies in East African amphibians. *Biology Letters*, **9**, doi: 10.1098/rsbl.2012.1146.
- Mumbi C.T., Marchant R., Hooghiemstra H. & Wooller M.J. (2008) Late Quaternary vegetation reconstruction from the Eastern Arc Mountains, Tanzania. *Quaternary Research*, **69**, 326–341.
- Myers N., Mittermeier R.A., Mittermeier C.G., Fonseca G.A.B. & Kent J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.
- Newmark W.D. (2002) *Conserving biodiversity in East African forests. A study of the Eastern Arc Mountains*. Springer.

- Pennington R.T., Hughes M. & Moonlight P.W. (2015) The Origins of Tropical Rainforest Hyperdiversity. *Trends in Plant Science*, **20**, 693–695.
- Phillips S.J., Anderson R.P. & Schapire R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, **190**, 231–259.
- Poynton J.C., Loader S.P., Sherratt E. & Clarke B.T. (2007) Amphibian diversity in East African biodiversity hotspots: Altitudinal and latitudinal patterns. *Biodiversity and Conservation*, **16**, 1103–1118.
- Rosenzweig M. (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge.
- Sandel B., Arge L., Dalsgaard B., Davies R.G., Gaston K.J., Sutherland W.J., & Svenning J.-C. (2011) The Influence of Late Quaternary Climate-Change Velocity on Species Endemism. *Science*, **334**, 660–664.
- Sepulchre P., Ramstein G., Fluteau F., Schuster M., Tiercelin J.-J., & Brunet M. (2006) Tectonic uplift and Eastern Africa aridification. *Science*, **313**, 1419–1423.
- Tolley, K.A., Tilbury, C.R., Measey, G.J., Menegon, M., Branch, W.R. & Matthee, C.A. (2011). Ancient forest fragmentation or recent radiation? Testing refugial speciation models in chameleons within an African biodiversity hotspot. *Journal of Biogeography*, **38**, 1748–1760.
- Trauth M.H., Maslin M.A., Deino A., & Strecker M.R. (2005) Late Cenozoic moisture history of East Africa. *Science*, **309**, 2051–2053.
- Voelker G., Marks B.D., Kahindo C., A'genonga U., Bapeamoni F., Duffie L.E., Huntley J.W., Mulotwa E., Rosenbaum S.A., & Light J.E. (2013) River barriers and cryptic biodiversity in an evolutionary museum. *Ecology and Evolution*, **3**, 536–545.

Chapter IV

A new, narrowly distributed, and critically endangered species of spiny-throated reed frog (Anura: Hyperoliidae) from a highly threatened coastal forest reserve in Tanzania

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A new, narrowly distributed, and critically endangered species of spiny-throated reed frog (Anura: Hyperoliidae) from a highly threatened coastal forest reserve in Tanzania

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Amphibians are in decline globally due to increasing anthropogenic changes, and many species are at risk of extinction even before they are formally recognised. The Coastal Forests of Eastern Africa is a hotspot of amphibian diversity but is threatened by recent land use changes. Based on specimens collected in 2001 we identify a new species from the coastal forests of Tanzania. The new species belongs to the spiny-throated reed frog complex that comprises a number of morphologically similar species with highly fragmented populations across the Eastern Afrotropical Region, an adjacent biodiversity hotspot comprising of numerous isolated montane forests. The new species is the first coastal forest member of this otherwise montane clade. We formally describe this species, assess its distribution and conservation threat, and provide a revised key to species of the spiny-throated reed frog complex. We highlight the most important characters distinguishing the new species from the other similar reed frog species. Recent surveys at the type locality and also more broadly across the region failed to find this new species. The conservation threat of this species is critical as the only known locality (Ruvu South Forest Reserve) is currently subjected to devastating land use changes.

Key words: Coastal Forests of Eastern Africa, conservation, habitat destruction, *Hyperolius ruvuensis* sp. n., *Hyperolius spinigularis*, Tanzania
Ruvu South Forest Reserve

INTRODUCTION

Amphibians are threatened by extinction across the globe (Stuart et al., 2004), with extinction rates exceeding those of other vertebrate groups (Hof et al., 2011). Adding to the increased threat to amphibians, the distribution of areas with the highest species richness often corresponds with areas impacted disproportionately by multiple threat factors, such as climate change, land use changes, and chytridiomycosis (Hof et al., 2011). The current challenge faced by biologists, particularly those in tropical countries where biodiversity is most concentrated, is the race to describe species before they go extinct.

The Coastal Forests of Eastern Africa represent an area of high amphibian species richness (e.g., Poynton et al., 2007) but many of the small remaining forest patches are relatively poorly known (Barratt et al., 2014). The area has long been identified as an area of importance for

biodiversity (Burgess et al., 1992; 1998; Burgess & Clarke, 2000) but has suffered major land use changes (Burgess et al., 1992, Tanzania Forest Conservation Group, 2012; Godoy et al., 2011). The long-term survival potential of species in these forests therefore remains uncertain given current trends in anthropogenic threats. Given the rapid rate of change, efforts in highlighting the biodiversity of this region, identifying key areas for conservation, and monitoring the health of populations are of the utmost importance.

In 2001 four specimens of a hyperoliid frog species were collected from a coastal forest in Tanzania identifiable to a clade of spiny-throated reed frogs. This clade exhibits a distinctive gular flap, with almost all species having asperities on the gular, and some with spines on the chest, and/or groin (*Hyperolius burgessi* Loader et al., 2015, *H. davenporti* Loader et al., 2015, *H. minutissimus* Schiøtz and Westergaard 2000, *H. spinigularis* Stevens 1971, *H. tanneri* Schiøtz 1982, *H. ukwiva* Loader et al.,

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2015). The spiny-throated reed frogs comprise a clade of several morphologically similar species that are found on isolated mountains across the Eastern Afrotropical (EAM hereafter) region adjacent to the Coastal Forests of Eastern Africa (Lawson et al., 2015, Loader et al., 2015). These coastal specimens were not taxonomically evaluated and remained in the herpetology collection of the Natural History Museum in London. Recent fieldwork in the coastal forests of Tanzania has failed to secure any further individuals assigned to this coastal population.

In this study we assess the population of *H. cf. spinigularis* collected from Ruvu South Forest Reserve, a coastal forest patch less than 45 km from the major city of Dar es Salaam. Given that this material is the only non-montane record of the spiny-throated reed frogs, rare and apparently not recently collected, we review its taxonomic placement, biogeographic significance and conservation risk.

MATERIAL AND METHODS

Molecular Data

Specimens were collected by Frontier Tanzania (stored at the Natural History Museum, London, see collecting details in type description) and stored in 70% ethanol. Samples of muscle and/or liver were taken from representative individuals and preserved in 95% ethanol. Specimens included in this study are listed in Table 1, with expected occurrence data per species and Genbank numbers (KX455694-KX455723). Phylogenetic relationships of *H. cf. spinigularis* from Ruvu South Forest Reserve and all other known spiny-throated reed frogs (based on Loader et al., 2015, Lawson et al., 2015) were estimated between all individuals using a previously published gene dataset including one mitochondrial (ND2) and three nuclear (*c-Myc*, *POMC*, *RAG1*) genes, with *Hyperolius mitchelli* used as an outgroup. In addition we included from a smaller sampling of individuals one mitochondrial partial gene (16SrRNA). To reconstruct relationships, sequences were aligned using MUSCLE (Edgar, 2004), excluding poorly aligned regions of all genes using GBlocks (Castresana, 2000). The optimal model of molecular evolution for our gene partition (GTR+G) was found using PartitionFinder v.1.1.1 (Lanfear et al., 2012). For the complete concatenated alignment, intra- and inter-clade distances were calculated using the Species Delimitation plugin v1.04 for Geneious Pro (Masters et al., 2011). Molecular phylogenies were constructed using Bayesian and maximum likelihood (ML) approaches in BEAST (v.2.1.3) and RAxML v.8.0.0 (Ronquist et al., 2012, Stamatakis, 2014). To examine species boundaries across the reconstructed phylogeny we applied a Bayesian implementation of the General Mixed Yule-Coalescent model (“bGMYC” package v.1.0.2 for R, Reid & Carstens, 2012) using trees from the BEAST analysis. In BEAST, the first 10% of generations were discarded as burnin for both convergence and tree estimates. Convergence was investigated using Tracer v.1.6 (Rambaut et al., 2014) through a visual inspection of adequate mixing and ESS estimates >200. The maximum clade credibility tree was calculated for BEAST using TreeAnnotator. ML node

support in RAxML was evaluated by non-parametric bootstrapping with 1000 replicates. BEAST analysis was run with a coalescent, constant size tree-prior and a strict molecular clock (as recommended for recent population-level analyses). Each locus was rate scaled to reflect the faster evolution times in mtDNA using rates outlined in Lawson et al. (2015). To address alternative phylogenetic hypotheses, we enforced topological constraints on our RAxML trees and performed AU, KH and SH topology tests in CONSEL v.0.20 (Shimodaira & Hasegawa, 2001).

Morphology

Material was examined from the Natural History Museum, London (BMNH) in addition to material previously documented in Loader et al. (2015). Morphological measurements were taken to the nearest 0.1 mm using Mitutoyo Absolute Digimatic Calipers (CD-6”C) with the aid of a Leica MZ8 stereo microscope (Leica Microsystems GmbH, Wetzlar, Germany). Sex was determined by the presence or absence of the gular flap in adult specimens. Measurements in this analysis match those in Loader et al. (2015) and include: Snout-Urostyle Length (SUL), Head Width (HW), Head Length Diagonal from corner of mouth (HLD), Head Length Diagonal from jawbone end (HLDJ), Nostril-Snout (NS), Inter-narial (IN), Eye to Nostril (EN), Eye Distance (EE), Inter-orbital (IO), Tibiafibula Length (TL), Thigh Length (THL), Tibiale Fibulare Length (TFL), Foot Length (FL), Forelimb Length (FLL), Hand Length (HL), Width of Gular Flap (WGF), and Height of Gular Flap (HGF). Qualitative characters were further investigated: gular shape, proportions and spinosity to assess differences from congeneric species. In order to assess the overall pattern of morphometric variation in these species (see Table 1 for specimen list) we also conducted a principal component analysis on log-transformed data using the Ggbiplot package in R (R Development Core Team, 2014; Wickham, 2009; Venables & Ripley, 2002).

Coastal forest surveys and remote sensing analysis of habitats

The geographic distribution of *H. cf. spinigularis* from Ruvu South Forest Reserve was mapped using the original collection records made by Frontier Tanzania in 2001. Additionally, we constructed a map of the points where major surveys have been conducted in other parts of the coastal forests of Tanzania using our own data and other published literature (Fig. 4). The data were accumulated on the basis of major collections in the region including Arthur Loveridge (Loveridge, 1942), Frontier Tanzania and Kim Howell (Appendix 7 in Burgess & Clarke, 2000), Frontier Tanzania (2001), and Barratt (unpublished data) (see Online Appendix 1).

We conducted an analysis of the habitat change in Ruvu South Forest Reserve since 1998 (Fig. 5A, Online Appendix 2). The land-cover change analysis covers Ruvu South Forest Reserve and two other nearby forest reserves (Pugu and Kazimzumbwi), which historically contained similar forest types. The most recent image used in the analysis was a Landsat 8 image dated 13 June 2014, chosen as the most recent cloud free image

Table 1. Details of specimens included in this study for molecular and morphological analyses (Modified from Table 3 in Lawson et al., 2015). Genbank accession numbers of new sequences generated for this study (KX455694-KX455723) are shown per gene, for all other sequences please see Lawson et al. (2015).

Species	Altitudinal range occurrence	Habitat	Expected Occurrence	Voucher numbers	GenBank accession numbers of new sequences			
					16s	ND2	C Myc	POMC
<i>H. burgessi</i>	East Usambara: 900–1100 m Nguru: 900–1000 m Uluguru: 980 m	Submontane forest	14,774 km ²	FMNH18989	KX455710			
				FMNH 274258	KX455709			
				FMNH 274259				
				FMNH 274310				
				FMNH 274311				
				FMNH 274312				
				FMNH 274313				
				FMNH 274314				
				FMNH 274321				
				FMNH 274322				
				FMNH 274323				
				FMNH 274324	KX455706			
				FMNH 274482				
				FMNH 274483				
				FMNH 274484				
				FMNH 274944	KX455705			
				MTSN 8238				
				MTSN 8240				
				MTSN 8259				
				MTSN 8260				
MTSN 8267								
MTSN 8273								
<i>H. davenporti</i>	Livingstone: 2010 m	Montane forest edge	28 km ²	MTSN 7453	KX455703			
				MTSN 7464	KX455695	KX455714	KX455722	KX455719
				MTSN 7465	KX455694	KX455715	KX455723	KX455718
				MTSN 7467		KX455716		KX455717
<i>H. minutissimus</i>	Njombe: 2010 m	Montane forest edge and grassland	14,904 km ²	FMNH 274290				
				MUSE 11023				
				MUSE 11024				
				MUSE 11026				
				MUSE 11028				
				MCZ DK R771421	KX455702			
				MCZ DK R771422	KX455701			
				MCZ DK R771423	KX455700			
				MCZ DK R771424	KX455699			
				MCZ DK R771426				
MCZ DK R771432	KX455698							
<i>H. ruvuensis</i> sp. n.	lowland Tanzania: 230m	Coastal forest thicket, swamp	2 km ²	BMNH 2002.410				
				BMNH 2002.411	KX455696	KX455712		KX455721
				BMNH 2002.412				
				BMNH 2002.413	KX455697	KX455713		KX455720

Table 1. Continued.

Species	Altitudinal range occurrence	Habitat	Expected Occurrence	Voucher numbers	GenBank accession numbers of new sequences			
					16s	ND2	C Myc	POMC
<i>H. spinigularis</i>	Malawi: 690 m	Submontane forest and forest edge	5,488 km ²	FMNH 274894				
				FMNH 274943				
	Mozambique: 1250 m			FMNH 274945				
				FMNH 274947				
				FMNH 274949				
				FMNH 274950				
	MVZ 266050							
<i>H. tanneri</i>	West Usambara:	Submontane forest and forest edge	4 km ²	FMNH274287				
				FMNH274288	KX455708			
				FMNH274289	KX455707			
				FMNH 18804	KX455711			
<i>H. ukwiva</i>	Rubeho: 1660 m	Montane forest edge	1,179 km ²	KMH36053				

of the area. The historical image used in the analysis was a Landsat 5 image dated 16 May 1998, selected as the most cloud free Landsat image covering the three forest reserves near the year that the specimens were collected (2001).

As separate training data were chosen for each scene, no preprocessing was performed on the Landsat imagery, with the exception of improving the georeferencing of the 1998 Landsat 5 scene using the georeferencer plugin in QGIS. In 1998, the three different forest types that dominated Ruvu South Forest Reserve were East African coastal dry forest, East African coastal scrub forest, and degraded variants of each (Burgess & Clarke, 2000). There were also large portions of wooded grassland with a mixture of larger trees and bushes. Training data for the classifications was based on expert knowledge of the area and high-resolution imagery on Google Earth ranging in dates from 2004 to 2014. For the 1998 scene, 232 training polygons were drawn, while for the 2014 scene, 154 training polygons were drawn.

To make better use of limited training data, the Landsat images were segmented using mean-shift segmentation from the Orfeo Toolbox. The spatial radius was set to 5 pixels, the range radius was set to 2 pixels, and the minimum object size to 5 pixels. These settings were chosen after visual experimentation to arrive at a segmentation that did not appear to lump different land-cover types into the same segments. The segment size, mean and variance were then calculated for bands corresponding to Landsat 5 bands 1–5, and 7, 1-arc SRTM elevation data, slope, and a hillshade image corresponding to the particular Landsat scene. The segments were classified in R (R Development Core Team, 2013) using Random Forest and output as TIFF images. Several classifications were generated for each Landsat scene and compared with high-resolution imagery until

there was good visual agreement. The classifications for the two years were then compared using raster algebra in R to arrive at a map of land-cover change. To remove small areas of change due to georeferencing disagreements and speckle, a 5 pixel orthogonal sieve was applied to arrive at the final land-cover change map.

RESULTS

Phylogeny

Bayesian and Maximum Likelihood methods both agreed on previously published evolutionary relationships within the spiny-throated clade (see Fig. 1, Loader et al., 2015, Lawson et al., 2015). The smaller sampling dataset of 16S mtDNA also agreed on the topology recovered with our multilocus dataset, though support and pairwise distances between species were consistently lower. Intra- and inter-clade distances using the Species Delimitation tool are given in Table 4 for the larger gene and individual sampled dataset. Analysis using the Species Delimitation plugin in Geneious Pro support previous taxonomic units (as in Loader et al., 2015) in addition to the new species here described. As in Loader et al., (2015) it seems that *H. burgessi* and *H. minutissimus* might consist of more than one species (See Table 4). Comparing all individual gene trees, our phylogenetic results appear largely reliant upon the fully resolved mtDNA relationships within this lineage, as many of the nuclear loci appear to retain ancestral polymorphisms, particularly in more recently divergent species.

Topology tests using likelihood scores (Table 2) indicated a significant difference between our optimal tree (*H. ruvuensis* sp. n. as sister taxon to a clade containing *H. spinigularis*, *H. burgessi* and *H. davenporti*) and alternative topologies, thus refuting the grouping of *H. ruvuensis* sp. n. with either *H. davenporti* or *H.*

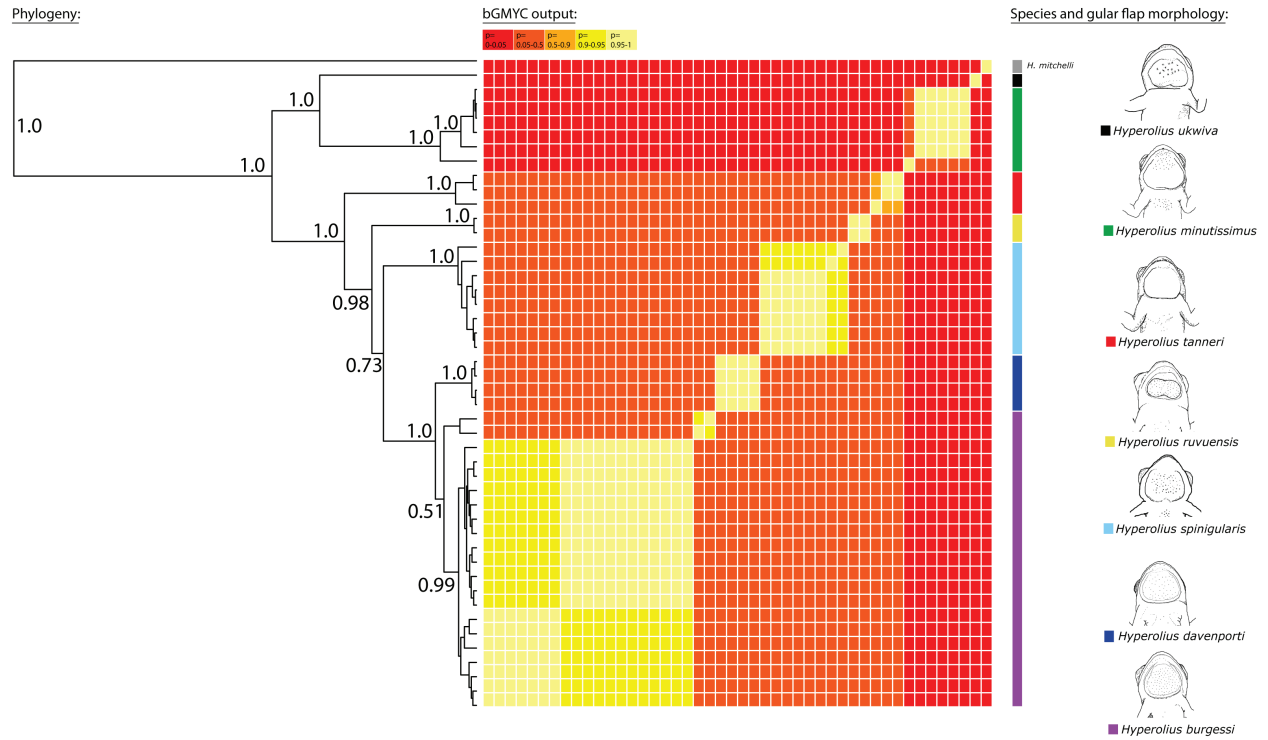


Fig. 1. Bayesian phylogeny of the spiny-throated reed frog species complex including *Hyperolius ruvuensis* sp. n. Support for clades is shown on nodes as well as bGMYC species delimitation results shown in colour coding and male gular flap morphology.

burgessi (Table 2). Topology test scores from trees pairing *H. ruvuensis* sp. n. with *H. spinigularis* from Mozambique and Malawi were consistently lower than our optimal tree but not significantly different.

Morphology

Measurements for specimens examined are given in Table 3. Principal component analysis of *H. ruvuensis* sp. n. males and females separately including morphological data from Loader et al. 2015 shows largely overlapping results (Fig. 2), and does not distinguish *H. ruvuensis* sp. n. based on morphometric measures as unique from the rest of the *H. spinigularis* complex. The main trait to distinguish *Hyperolius ruvuensis* sp. n. from the other members of the spiny-throated reed frog complex is the distinctive bilobed shape, disc-like platform, and spinosity of the gular flap, which is evident in both male specimens included in this study, and the relatively large snout-urostyle length in females (See Loader et al., 2015).

Systematics

***Hyperolius ruvuensis* sp. n.** Barratt, Lawson and Loader
Ruvu spiny reed frog
Figs. 3A, B

Holotype.— BMNH 2002.410 (male, field tag KMH 23565, held at the Natural History Museum, London) collected on 18 May 2001 in Ruvu South Forest Reserve (07° 02' 21.1" S; 38° 54' 58.3" E, 230 m a.s.l.) by Frontier-Tanzania.

Paratypes.— Male: BMNH 2002.412 (field tag KMH 23567). Females: BMNH 2002.411 (field tag KMH 23566), BMNH 2002.413 (field tag KMH 23569) collected at same locality and date as of the Holotype.

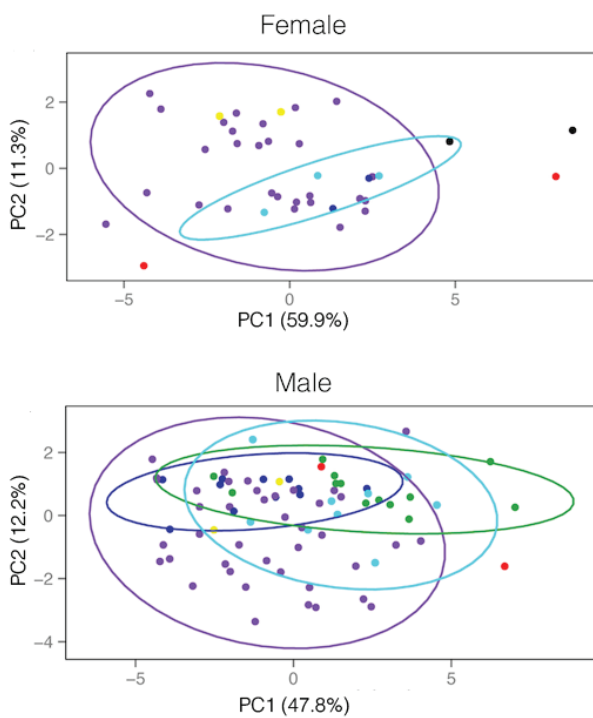
Diagnosis.— Horizontal pupil with distinctive gular flap in males. As with most other members of the spiny-throated clade (*H. burgessi*, *H. davenporti*, *H. minutissimus*, *H. spinigularis*, *H. ukwiva*), *H. ruvuensis* sp. n. also has the presence of dermal asperities (including on the body and chin region) on the ventrum, unique

Table 2. Results from topology tests of alternative relationships. Most likely tree topologies displayed in rank order from top to bottom. Key: 1 – optimal tree (as in Fig. 1), 2 – *H. ruvuensis* sp. n. and *H. spinigularis* constraint, 3 – *H. ruvuensis* sp. n. and *H. burgessi* constraint, 4 – *H. ruvuensis* sp. n. and *H. davenporti* constraint, obs – the observed log-likelihood difference, bp – bootstrap probability, np – bootstrap probability calculated from multiscale bootstrap, pp=Bayesian posterior probability. AU – Approximately Unbiased test, KH, Kishino-Hasegawa test, SH – Shimodaira-Hasegawa test, WKH – Weighted Kishino-Hasegawa test, WSH – Weighted Shimodaira-Hasegawa test. *significantly different than optimal tree.

	obs	bp	np	pp	AU	KH	SH	WKH	WSH
1	-1.6	0.656	0.656	0.837	0.687	0.671	0.823	0.671	0.864
2	1.6	0.344	0.344	0.163	0.317	0.329	0.626	0.329	0.547
3*	48.5	0	1e-04	7e-22	3e-04	0.001	0.001	0.001	0.001
4*	48.5	0	1e-04	7e-22	3e-04	0.001	0.001	0.001	0.001

Table 3. *Hyperolius ruvuensis* sp. n. morphology. All measurements in to the nearest 0.1 millimetres, with * indicating the holotype.

Genus	<i>Hyperolius</i>	<i>Hyperolius</i>	<i>Hyperolius</i>	<i>Hyperolius</i>
Species	<i>ruvuensis</i> sp. n.	<i>ruvuensis</i> sp. n.	<i>ruvuensis</i> sp. n.	<i>ruvuensis</i> sp. n.
Museum Number	BMNH 2002.410*	BMNH 2002.411	BMNH 2002.412	BMNH 2002.413
Country	Tanzania	Tanzania	Tanzania	Tanzania
Sex	M	F	M	F
SUL	16.8	25.4	18.7	24.2
Head Width (HW)	6.1	9.2	6.2	8.3
Head Length Diagonal (HLD) corner of mouth	5.3	7.2	5.4	6.9
Head Length Diagonal (HLD) from jawbone end	6.3	8.3	6.4	8.1
Nostril-Snout (NS)	1.0	1.3	1.1	1.2
Inter-narial (IN)	2.1	2.5	2.1	2.3
Eye to Nostril (EN)	1.9	2.3	1.9	2.2
Eye Distance (EE)	3.6	4.0	3.7	4.0
Inter-orbital (IO)	3.1	4.8	2.7	4.5
Tibiafibula Length (TL)	8.7	12.3	9.1	11.8
Thigh Length (THL)	8.5	11.8	9.2	11.4
Tibiale Fibulare Length (TFL)	5.3	7.3	5.8	7.1
Foot Length (FL)	7.4	10.3	7.6	10.1
Forelimb Length (FLL)	4.2	5.3	4.8	5.2
Hand Length (HL)	4.9	6.7	4.8	6.6
Gular Flap: Width	4.8	-	5.1	-
Gular Flap Height	3.2	-	3.6	-

**Fig. 2.** Principal Component Analysis of morphological divergence between species. Raw morphological measurements for *H. ruvuensis* sp. n. shown in Table 3. For the other species in the complex we used data from Additional file 2 in Loader et al. 2015.

amongst hyperoliids. The presence of asperities on the gular flap diagnoses this species from *H. tanneri*, for which they are absent. The distribution of dermal asperities in two distinct circular patches differs from the anteriorly positioned distribution of asperities in *H. minutissimus* and *H. ukwiva*, and the evenly distributed asperities on the gular flap in *H. burgessi*, *H. davenporti* and *H. spinigularis*. Furthermore, *H. ruvuensis* sp. n. males have a bilobed and rounded gular flap - distinctive from the rounded gular flap of *H. burgessi*, *H. davenporti* and *H. minutissimus* (see Fig. 1). The bilobed gular flap in *H. ruvuensis* sp. n. is similar to that seen in *H. spinigularis* from Malawi and *H. ukwiva* from Rubeho, although in *H. ruvuensis* sp. n. it is much more pronounced and raised, forming a disc-like structure on the gular flap (see Figs. 1, 3B). This raised disc like gular flap is a diagnostic character for males of *H. ruvuensis* sp. n. Based on molecular data the species is genetically distinct from close relatives, and is the sister taxon to a clade comprising of *H. davenporti*, *H. burgessi* and *H. spinigularis*, being minimally 5.9% pairwise divergent from its closest relative (*H. davenporti*) based on ND2, C Myc, POMC and RAG1 genes. *Hyperolius ruvuensis* sp. n. further has an allopatric distribution with respect to other species in the complex and is the only member found at low elevation within the coastal forest belt of Eastern Africa (Fig. 4).

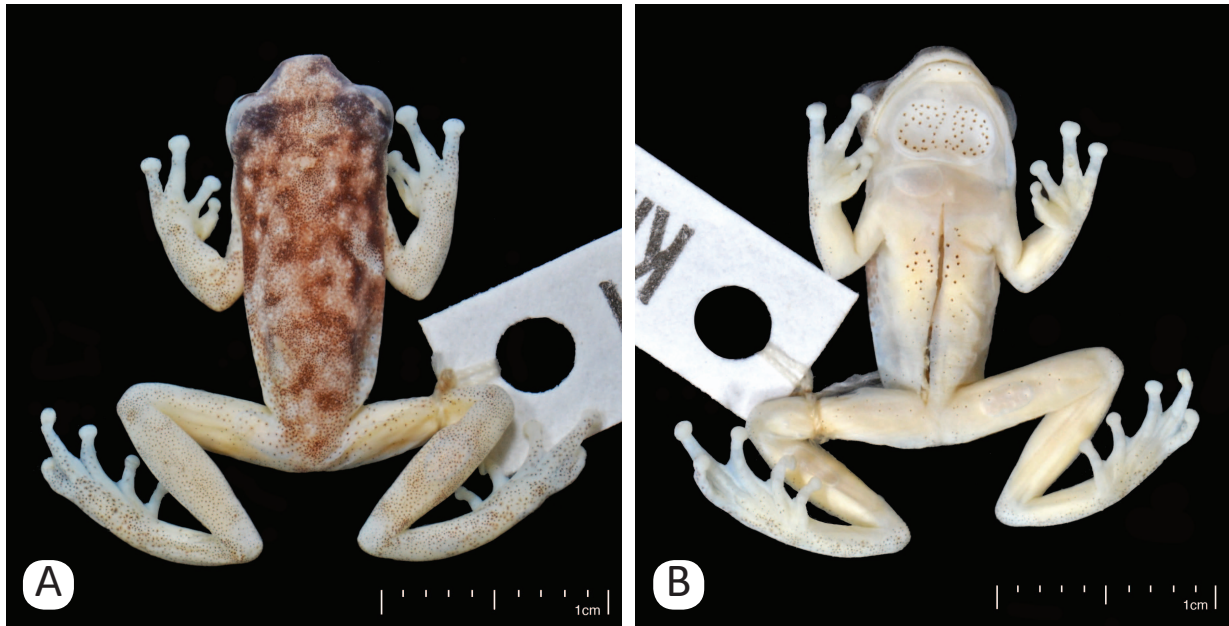


Fig. 3. Dorsal (A) and ventral (B) views of the holotype of *H. ruvuensis* sp. n. BMNH 2002.410. Scale bar = 1cm.

Description of holotype.— Small to moderate sized hyperoliid. Pupil horizontal. Snout blunt and slightly rounded. Canthus rostralis angular, being slightly convex on the horizontal plane and slightly concave on the vertical plane. Distance between eyes is 3.6 mm and interorbital distance is 3.1 mm. The inter-narial distance is 2.1 mm, greater than narial distance to the eye (1.9 mm). The nostril to snout is 1.0 mm. The width of head (6.1 mm) equals 0.36 of the body length (16.8 mm). The gular flap width is more than (4.8 mm) the height (3.2 mm). The gular flap is raised and bilobed, anteriorly narrowing. It is marked by black asperities (ca. 65) distributed across the gular flap in two distinct patches on each lobe. Asperities are evenly distributed on each lobe, though a small patch without asperities is present towards the lower central part of each lobe. Tibio-tarsal articulation of the addressed hind limb reaching the eye. Tibio-tarsal (8.7 mm) is almost equal to thigh length (8.5 mm). The tibiale fibulare length is 5.3 mm. Toes have expanded fleshy discs with the foot being 7.4 mm. Webbing is extensive almost reaching the base of the fleshy discs on all toes apart from the first toe where it only reaches the first tubercle. The forelimb length is 3.3 mm, less than the hand length (4.8 mm). The hands have expanded, rounded fleshy discs. Webbing just reaching distal subarticular tubercle of the outer finger and slightly reduced on all other fingers. Dorsal skin surface granular with a single minute black asperity surmounting many of the granules. Ventral skin surface strongly granular with black asperities on the mentum (ca. 8), gular flap (ca. 60), abdomen (ca. 40) and undersurfaces of the femur (ca. 20 on each femur). Ventral asperities much more prominent than those of the dorsum.

Paratypes.— Head and body proportions in close agreement with those of the holotype (Fig. 3, Table 3). The distribution of the asperities of the male paratype is in close agreement with that of the holotype. As with other *H. spinigularis* group species the proportions of the gular flap in males, diagnostic for the species, shows slight

variation which means care needs to be taken in applying this character, though the unique shape and spinosity of *H. ruvuensis* sp. n. should enable clear differentiation from other members of the complex (Figs. 1, 3B). Webbing of all the material conforms to that of the holotype.

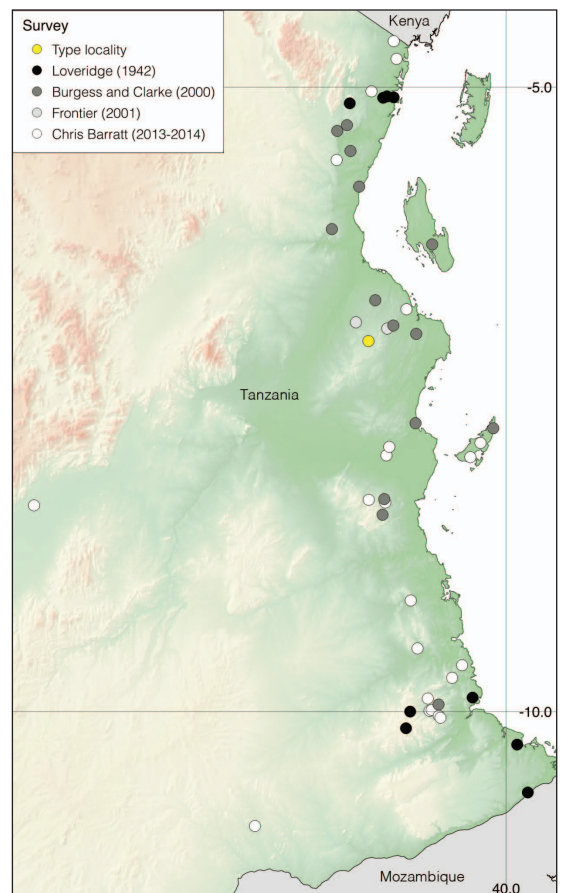


Fig. 4. Map of coastal Tanzania showing the type locality of *H. ruvuensis* sp. n. (yellow circle) and additional coastal forest localities that have been surveyed but did not yield members of the spiny-throated reed frog complex. See Online Appendix 1 for locality data and sources.

Table 4. Species delimitation results for the spiny-throated reed frog complex using the Species Delimitation Plugin for Genious Pro (Masters et al., 2011) with our Bayesian phylogeny from Figure 1. Delimitation results show all taxa are monophyletic, and show the closest relative for each species. Intra-dist shows intra-specific genetic distance between samples within each species (values of 0 indicate a single representative per species), Inter-dist shows inter-specific genetic distance to the closest relative.

Species	Closest relative	Monophyletic?	Intra-dist	Inter-dist
<i>H. mitchelli</i>	<i>H. ukwiva</i>	yes	0	0.164
<i>H. ukwiva</i>	<i>H. minutissimus</i>	yes	0	0.06
<i>H. minutissimus</i>	<i>H. ukwiva</i>	yes	0.01	0.06
<i>H. tanneri</i>	<i>H. davenporti</i>	yes	0.007	0.049
<i>H. ruvuensis</i> sp. n.	<i>H. davenporti</i>	yes	0.003	0.059
<i>H. spinigularis</i>	<i>H. davenporti</i>	yes	0.007	0.041
<i>H. davenporti</i>	<i>H. burgessi</i>	yes	0.003	0.018
<i>H. burgessi</i>	<i>H. davenporti</i>	yes	0.01	0.018

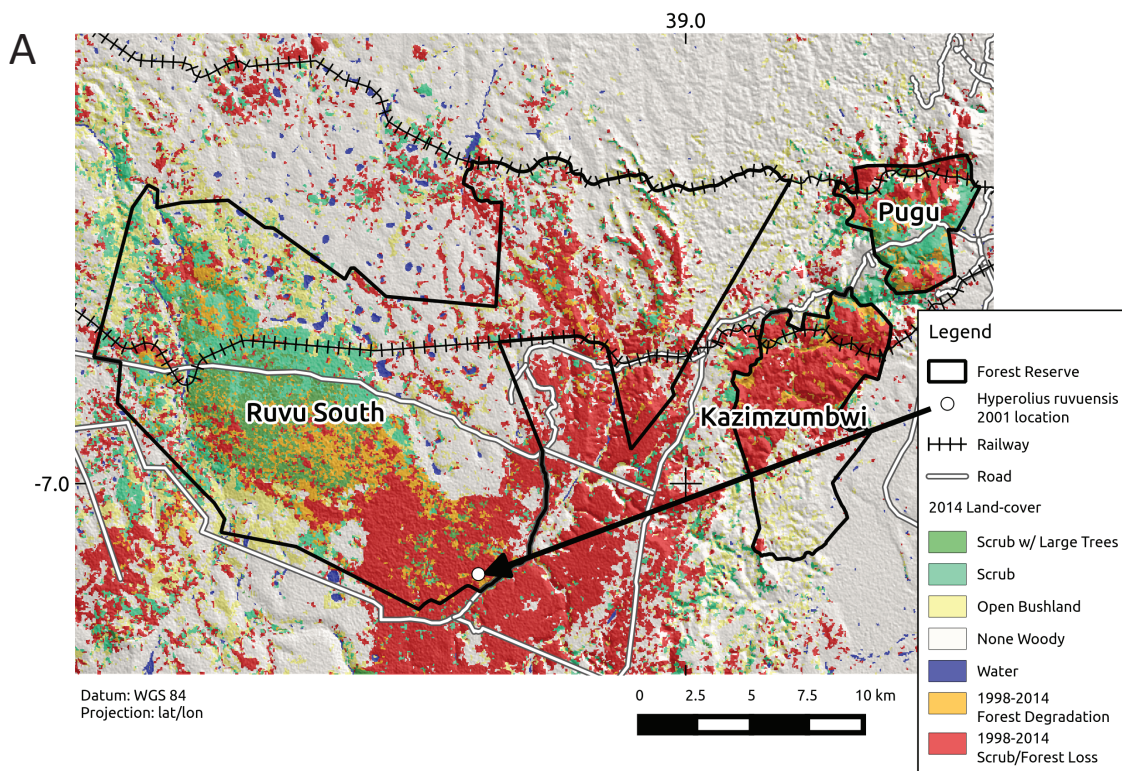


Fig. 5. Habitat change and photographs of Ruvu South Forest Reserve in April 2015. (A) Habitat change from 1998–2014, see also Online Appendix 2. (B) Grassland swamp area of type locality based on original GPS co-ordinates, (C) Charcoal being transported by motorbike illegally from Ruvu South Forest Reserve, a common sight in the coastal forests.

Colour patterning of adults.— *In life*: Head and dorsum is brown with a creamy white mottling on back, in some individuals the mottling extends along the side of the animal from the anterior end. The ventrum side is generally white with the exception of the asperities in males which are dark brown/black. Forelimbs and hindlimbs are mottled creamy white colour matching the dorsum, with flashes of orange on the thighs and feet and faded white heel spots. *In preservative*: The holotype (BMNH 2002.410) is a creamy colour, with the asperities and pigmentation of chromatophores on the dorsum resulting in a brown mottled appearance. Forelimbs, hindlimbs and feet are cream coloured with scattered brown chromatophores on the dorsal side. The ventral side is cream coloured with the exception of the asperities on the abdomen, gular flap and mentum. The male paratype (BMNH 2002.412) resembles the holotype in basic patterning but the colour is largely absent from the dorsum and head. The female paratypes also exhibit colour and pattern variation, BMNH 2002.411 is cream coloured with several small patches of brown on the dorsum, legs and forelimbs, and BMNH 2002.413 is cream with more subtle brown patches. Both female specimens have scattered patches of cream colour where the brown pigment is reduced. All specimens had lateral dark edged white stripes (either thin or irregular in size and outline) ending anteriorly in a narrow stripe meeting at the snout.

Sexual dimorphism.— Females attain a much larger size than the males (Table 3). Asperities of the dorsum are slightly weaker in the females and completely absent from the ventral side. Males are easily distinguished from the females by their characteristic bilobed and raised gular flap (Fig. 3B).

Advertisement Call.— No advertisement call is known.

Etymology.— The species is named after Ruvu South Forest Reserve where the specimens were collected and is the current extent of the species occurrence.

Distribution and habitat.— The species is likely endemic to Ruvu South Forest Reserve in Tanzania (See Figs. 4, 5A). Specimens were collected by Mr. David Emmett who provided valuable information on the habitat of the type locality. Specimens were found on reeds and bushes in a swampy open grassland area beside a permanent pond on a lowland plain (230 m a.s.l.). Adjacent to the grassland was some sparse forest cover which kept the type locality partially shaded during the day (canopy height of <10 m, ground vegetation layer >50 % cover and shrub layer <10 % cover). One of the authors of the paper (SL) was able to revisit Ruvu South Forest Reserve in April 2015, where a rapid survey was conducted. The survey failed to discover any individuals of this species with a one day survey conducted at the type locality and two night surveys in varied habitats (swamp and forest) located in the northern part of the Forest Reserve. Figure 5A shows habitat classifications in Ruvu South Forest Reserve with the location of the type locality. Estimates of forest loss and severe habitat degradation are also given and show severe habitat degradation around the type locality – as also evidenced by ground truthing (see also Figs. 5B–D). Furthermore, on a broader scale, surveys across the coastal region in Tanzania failed to

find any specimens referable to this species (Fig. 4). The apparent restriction of *Hyperolius ruvuensis* sp. n. solely to Ruvu South Forest Reserve seems plausible and not due to sampling deficiencies across the region.

IUCN red listing.— Because the area of occupancy is probably less than 10 km², all individuals are in a single sub-population and the extent of its habitat and possibly the number of reproductively active individuals are declining, we recommend the species to be listed as Critically Endangered based on the IUCN red list criteria (IUCN, 2012). The species cannot be classified as Extinct due to the lack of exhaustive surveys in known and expected habitat.

Key to the East African Spiny-throated Reed Frogs

As in Loader et al. (2015) we present a key that should identify adult male specimens of all presently described species.

1a	Gular flap with black dotted asperities, species not found in West Usambara Mountains	2
1b	Gular flap lacking any asperities, species found in West Usambara Mountains	<i>H. tanneri</i>
2a	Black dotted asperities evenly distributed across the gular flap	3
2b	Black dotted asperities distributed on anterior and mid region of the gular flap	6
3a	Gular flap bilobed	4
3b	Gular flap not bilobed	5
4a	Gular flap strongly bilobed, with asperities distributed into two discernable circular raised platforms, demarcating the area, species found in coastal forests of Tanzania.	<i>H. ruvuensis</i> sp. n.
4b	Gular flap bilobed, with asperities distributed regularly across the gular flap. Species found in Malawi and Mozambique	<i>H. spinigularis</i>
5a	Gular flap rounded with posterior and anterior ends more equal. The gular flap is usually either equal or wider than height, species found in Southern Highlands of Tanzania.	<i>H. davenporti</i>
5b	Gular flap narrowly tapering anteriorly and usually equal or greater in height, species found in East Usambara, Nguru, and Uluguru Mountains	<i>H. burgessi</i>
6a	Gular flap not bilobed and found in Udzungwa Mountains. Females reach a moderate size 18–24mm	<i>H. minutissimus</i>
6b	Gular flap bilobed, and found in Rubeho Mountains. Females reach a large size >25mm	<i>H. ukwiva</i>

DISCUSSION

Biogeography

Our phylogenetic reconstruction of the spiny-throated reed frog clade is consistent with the multi-locus gene tree of Lawson et al. (2015), showing generally high divergence between species. Our analyses places *H.*

ruvuensis sp. n. as sister taxon to a clade containing *H. burgessi*, *H. davenporti* and *H. spinigularis* (see Fig. 1) though the relationships between the latter clade are not well resolved. Topology tests on alternative relationships suggest most are significantly worse, however, an alternative topology with *H. ruvuensis* sp. n. forming a clade with *H. spinigularis* in Malawi and Mozambique was not significantly worse. The lack of resolution prevents robust biogeographic conclusions but we can speculate upon a potential scenario given the best topology and known distribution of species. The position of *H. ruvuensis* sp. n. and *H. tanneri* – two geographically widely separated populations, relative to the *H. spinigularis*, *H. davenporti* and *H. burgessi* clade – lends support to a formerly relatively widespread coastal and montane ancestor that became increasingly fragmented and restricted to both montane and coastal regions. Such a scenario has been previously speculated upon in other groups (Kingdon, 1989; Burgess et al., 1998) with a number of examples of sister group relationships among coastal and montane regions embedded in montane or coastal clades. This has been specifically shown in birds (e.g. Roy et al., 1997) and plants (e.g. Dimitrov et al., 2012) occurring in both montane and lowland rainforest habitats.

Climate fluctuations have been important in expanding and contracting forest habitats in East Africa (Burgess & Clarke, 2000), and such fluctuations were likely important in speciation processes that produced the current extant species in the *H. spinigularis* complex with their currently restricted distributions. Such changes in species ranges were documented in Lawson et al. (2015) potentially producing peripatric populations (e.g. *H. tanneri*, *H. davenporti*) and the new species documented here could comprise another example – particularly given the potential niche shift to coastal forest, open woodland type habitat. Furthermore, *H. ruvuensis* sp. n. restricted to the coastal forests and a relatively divergent species (based on molecular differences) provides a piece of evidence that might suggest the relative longevity of coastal forests. Burgess and Clarke (2000) argued that endemism in coastal forests was likely in part attributed to the old age, or non-inundated habitats in the region). This was also shown in African violets (*Saintpaulia* spp.), in a study by Dimitrov et al. (2012) who suggested the presence of micro-endemic species in their analysis supports the existence of lowland refugia even during glacial maxima.

Conservation

The coastal forests are an important ecosystem for conservation in Africa due to its rich biodiversity (Myers et al., 2000, Azeria et al., 2007). However, many coastal forests have either disappeared completely or have been reduced to extremely small patches less than 20 km² in size (Burgess et al., 1998). Across the Coastal Forests of Eastern Africa, there are over 1750 endemic plant and 100 endemic vertebrate species respectively, which are in many cases present in several forests (Conservation International, 2015), however similarly to *H. ruvuensis* sp. n. there are also micro-endemics likely restricted to single

sites (e.g. several millipede and amphibian species see Burgess et al., 1998). The type locality and only known location of *H. ruvuensis* sp. n., Ruvu South Forest Reserve, is one of the few remaining areas of coastal forest near to Dar es Salaam, and in recent years has undergone severe deforestation for fuelwood, timber and biofuel production (Gwegime et al., 2013; see Figs. 5A–C). Our analysis of the forest reserve shows habitat change over the last 16 years (1998–2014) with particularly high rates of deforestation in areas formerly covered in coastal forest relative to the areas that are dominated by coastal thicket. Particularly worrying is the level of habitat change in the southern parts of the reserve, which includes the precise type locality of *H. ruvuensis* sp. n.

Assessing the impact of habitat change has on amphibian assemblage in Ruvu South Forest Reserve is currently not possible given the lack of data on the spatial distribution of species and population numbers. Gross habitat changes (Fig. 5A, Online Appendix 2), as recorded for this area, however are likely to impact amphibian assemblage but it is unclear how this might specifically impact the new species here described, only recorded once from grassland swamps that adjoin forest in 2001. Our rapid surveys in both the type locality and northern parts of the reserve with historically similar habitat in 2015 failed to find the species, though more extensive survey efforts are necessary to better validate its potential absence. Today the adjoining areas are heavily degraded woodland with evidence of extensive charcoal burning, which could have had an impact on the species but this remains speculative and requires a monitoring program to better understand whether the species is indeed absent or declining.

All members of the spiny-throated reed frog complex have small distributions, with the consequence that all species are classified as threatened in recently compiled IUCN red list assessments. *Hyperolius ruvuensis* sp. n. in particular is of high conservation concern due to the high rates of deforestation in Ruvu South Forest Reserve, and its extremely small extent of occurrence (Table 1, Fig. 4). For all East African spiny-throated reed frogs, it will be important to establish the full extent of their distributions, with future sampling of the Eastern Afromontane and Coastal Forests of Eastern Africa, as these data have important conservation implications.

Beyond the conservation of this newly described species – Ruvu South Forest Reserve and, more broadly, the coastal forests of Tanzania are highly threatened habitats that require further conservation attention. These habitats provide important sustainable resources for human populations (Burgess et al., 1992; Tanzania Forest Conservation Group, 2012) but forest resources are currently being used unsustainably and in many cases, illegally, depleted. The region is currently being subjected to an unprecedented level of human induced habitat change, and without drastic intervention the forests will be entirely lost in the coming years.

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REFERENCES

- Azeria, E.T., Sanmartín, I., Ås, S., Carlson, A. & Burgess, N. (2007). Biogeographic patterns of the East African coastal forest vertebrate fauna. *Biodiversity and Conservation* 16, 883–912.
- Barratt, C.D., Tonelli, E., Menegon, M., Doggart, N., et al. (2014). Fragmented habitats and species: The challenges of amphibian conservation in Tanzania today. *FrogLog* 111, 63–64.
- Burgess, N.D., Clarke, G.P. & Rodgers, W.A. (1998). Coastal forests of eastern Africa: status, endemism patterns and their potential causes. *Biological Journal of the Linnean Society* 64, 337–367.
- Burgess, N.D., Mwasumbi, L.B., Hawthorne, W.J., Dickinson, A. & Doggett, R.A. (1992). Preliminary assessment of the distribution, status and biological importance of coastal forests in Tanzania. *Biological Conservation* 62, 205–218.
- Burgess, N.D. & Clarke, G.P. (eds.). (2000). *Coastal Forests of Eastern Africa*. IUCN Forest Conservation Programme, Gland, Switzerland and Cambridge, England.
- Castresana, J. (2000). Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution* 17, 540–552.
- Conservation International. (2015). *Coastal Forests of Eastern Africa*. Critical Ecosystem Partnership Fund. Available from: <<http://www.cepf.net/resources/hotspots/africa/Pages/Coastal-Forests-of-Eastern-Africa.aspx>>. Accessed: 9 September 2015.
- Dimitrov, D., Nogués-Bravo, D. & Scharff, N. (2012). Why do tropical mountains support exceptionally high biodiversity? The Eastern Arc Mountains and the drivers of *Saintpaulia* diversity. *PLoS One*: DOI: 10.1371/journal.pone.0048908.
- Edgar, R.C. (2004). MUSCLE: Multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32, 1792–1797.
- Godoy, F.L., Tabor, K., Burgess, N.D., Mbilinyi, B.P., et al. (2011). Deforestation and CO₂ emissions in coastal Tanzania from 1990 to 2007. *Environmental Conservation* 39, 62–71.
- Gwegime, J., Mwangoka, M., Mulungu, E., Perkin, A. & Nowak, K. (2013). The biodiversity and forest condition of Ruvu South Forest Reserve. TFCG Technical Paper 37. Dar es Salaam, Tanzania.
- Hof, C., Araújo, M.B., Jetz, W., Rahbek, C. (2011). Additive threats from pathogens, climate and land-use change for global amphibian diversity. *Nature* 480, 516–519.
- IUCN (2012). *IUCN Red List Categories and Criteria: Version 3.1*. IUCN Species Survival Commission. IUCN, Gland, Switzerland and Cambridge, UK. ii + 30 pp.
- Kingdon, J. (1989). *Island Africa: The Evolution of Africa's Rare Animals and Plants*. Princeton University Press, Princeton, New Jersey.
- Lanfear, R., Calcott, B., Ho, S.Y.W., Guindon, S. (2012). PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution* 29, 1695–1701.
- Lawson, L.P. (2010). The discordance of diversification: evolution in the tropical-montane frogs of the Eastern Arc Mountains of Tanzania. *Molecular Ecology* 19, 4046–4060.
- Lawson, L.P., Bates, J., Menegon, M. & Loader, S.P. (2015). Divergence at the edges: Peripatric isolation in the montane Spiny Throated Reed Frog complex. *BMC Evolutionary Biology* 15, 128.
- Loader, S.P., Lawson, L.P., Portik, D.M. & Menegon, M. (2015). Three new species of spiny throated treefrogs (Anura: Hyperoliidae) from evergreen forests of Tanzania. *BMC Research Notes* 8, 167.
- Loveridge, A. (1942). Scientific results of a fourth expedition to forested areas in east and central Africa. V. Amphibians. *Bulletin of the Museum of Comparative Zoology* XCI, 237–373.
- Masters, B.C., Fan, V. & Ross, H.A. (2011). Species Delimitation: a Geneious plugin for the exploration of species boundaries. *Molecular Ecology Resources* 11, 154–157.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature* 403, 853–858.
- Poynton, J.C., Loader, S.P., Sherratt, E. & Clarke, B.C. (2007). Amphibian diversity in East African biodiversity hotspots: altitudinal and latitudinal patterns. *Biodiversity and Conservation* 16, 1103–1118.
- Rambaut, A., Suchard, M.A., Xie, D. & Drummond, A.J. (2014). Tracer v1.6, Available from: <<http://beast.bio.ed.ac.uk/Tracer>>.

- Reid, N.M., Carstens, B.C. (2012). Phylogenetic estimation error can decrease the accuracy of species delimitation: a Bayesian implementation of the general mixed Yule-coalescent model. *BMC Evolutionary Biology* 12, 196.
- R Development Core Team. (2013). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing Vienna, Austria. Available from: <<http://www.R-project.org>>.
- Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., et al. (2012). MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61, 539–542.
- Roy, M.S., Da Silva, J.M.C., Arctander, P., Garcia-Moreno, J., Fjeldså, J. (1997). The speciation of South American and African birds in montane regions. In *Avian molecular evolution and systematics*. San Diego : Academic Press, Incorporated, p. 325–343.
- Shimodaira, H. & Hasegawa, M. (2001). CONSEL: for assessing the confidence of phylogenetic tree selection. *Bioinformatics* 17, 1246–1247.
- Stamatakis, A. (2014). RAxML Version 8: a tool for Phylogenetic Analysis and Post-Analysis of Large Phylogenies. *Bioinformatics* 30, 1312–1313.
- Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., et al. (2004). Status and trends of amphibian declines and extinctions worldwide. *Science* 306, 1783–1786.
- Tanzania Forest Conservation Group. (2012). *Coastal forests under threat*. Available from: <<http://coastalforests.tfcg.org/threats.html>>. Accessed: 9 September 2015.
- Venables, W.N. & Ripley, B.D. (2002). *Modern Applied Statistics with S*. Springer. New York.
- Wickham, H. (2009). *Ggplot2: Elegant Graphics for Data Analysis*. Springer. New York.

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Synthesis

Synthesis

“The coastal forests are interpreted as a ‘vanishing refuge’ with the endemic species gradually becoming more and more relict (and presumably extinct) due historically to climatic desiccation and more recently to human destruction” – Burgess et al. (1998).

The research in this thesis provides the most extensive biodiversity assessment to date for the amphibians of the coastal forests of Eastern Africa biodiversity hotspot, and demonstrates the intricate interplay between current biodiversity patterns and the environment. Previous biodiversity assessments of the coastal forest region have showed that several coastal forest patches support a disproportionately high number of endemic species, and that these places are best interpreted as refugia where species have become increasingly relictualized due to environmental change and human activity (Burgess et al. 1998). Though this information vastly improved our knowledge of the coastal forest region, the patterns were inferred by aggregating relatively coarse-scale species distributions, and did not include molecular data, which is particularly important to test the links between biodiversity patterns and past environmental change. This thesis was dedicated to understanding coastal forest biodiversity patterns in finer spatial detail, by using modelling approaches and molecular data for the whole amphibian assemblage, along with spatial analyses of environmental data.

Using next generation sequencing (RAD-seq) datasets, I demonstrated that intraspecific relationships and cryptic diversity patterns can be well resolved, even for poorly understood species clades (chapter I), and that knowledge of these intraspecific relationships can be applied to broader scale analyses of endemism using phylogenies and spatial data (Rosauer et al., 2009). By accounting for intraspecific diversity within phylogeny-based endemism analyses, I showed that endemism can be measured using phylogenetic branch lengths and spatial rarity, and used to identify places where high levels of evolutionary history have accumulated. These places have significant conservation value because they hold a disproportionately high amount of unique biodiversity. With my analyses, I showed that these data can improve knowledge of endemism patterns, with thirty-five distinct lineages within several species that are endemic to specific microrefugia (chapter II). Importantly my work has led to the identification of three previously unrecognised endemic areas in Tanzania, which are likely to be of critical conservation concern. Accounting for intraspecific diversity in biodiversity assessment is a growing field (Rosauer et al., 2015; Tarroso et al., 2015), and enables a broader perspective on biodiversity conservation, especially in poorly understood tropical regions where cryptic diversity is often high (Miraldo et al., 2016). Phylogeny-based measures of endemism for the complete species assemblage of amphibians (fifty-five species) in the region demonstrate that places supporting high numbers of species do not necessarily correspond to high levels of evolutionary history, and that complex mixtures of ancient paleo-endemic and recent neo-endemic diversity are present within the coastal forest region. In line with previous work I proved that coastal forests surrounding the lowland Eastern Afromontane region are dominated by ancient relicts, and should be considered as museums of diversity but also that there are several areas that have facilitated recent evolution, along with mixtures of endemism types (chapter III).

With environmental data, I demonstrated that genetic diversity within species (chapter I) is strongly linked to past environmental stability dating as far back as the late Pliocene (ca. 3 mya), topography, and the spatial structure of hydrological basins. For analyses of biodiversity patterns incorporating intraspecific diversity

(chapter II), I showed that higher phylogenetic endemism is clustered in places with benign current climate, that have experienced habitat and climate stability since at least the late Quaternary, but most probably further back in time. Together, analyses of genetic diversity and endemism patterns in this thesis strongly support the hypothesis that several major areas of coastal forest are refugia, and especially around the lowland parts of the Eastern Afromontane. These refugia have allowed biodiversity to persist over time while climate change and anthropogenic activities have reduced forest cover across East Africa. The spatial analyses I undertook in chapters II and IV indicate that many of these refugia are highly threatened and poorly conserved, and the description of the coastal forests as a “vanishing refuge” (Burgess et al. 1998) is appropriate given the ancient diversity they support and their highly threatened status.

Caveats

There are a number of limitations regarding the molecular data analysed in this thesis that need to be outlined. Although DNA barcoding is an important tool for confirming species identifications of poorly known tropical taxa, it is by no means a ‘silver bullet’ solution to quantifying biodiversity. Using only mitochondrial DNA for large scale phylogenetic reconstruction is not optimal as it does not capture all population level processes because it is only maternally inherited (Hoelzer, 1997). Though our phylogenies used for phylogenetic endemism estimates in chapter II and III represent expected species relationships, extra nuclear genes should ideally be sequenced to help to fully resolve the trees and account for the shortcomings of mitochondrial DNA. In addition, a lack of adequate fossil data for African amphibians hinders the calibration of accurately dated phylogenies which are particularly useful for verifying the topology and branch length estimation across phylogenies. The dated Bayesian phylogenies in this thesis (chapter II and III) were built using secondary calibrations, which are based on previous results of molecular dating studies to infer the timing of divergence dates on specific parts of the phylogeny. Although methods to estimate evolutionary divergence times have improved a great deal since the first introduction of the molecular clock (Morlon et al., 2011), the use of secondary calibrations still remain suboptimal. Secondary calibrations offer a relatively good estimate of phylogenetic relationships when no fossil data is available, but are no substitute, in many cases failing to accurately reproduce results from primary fossil data studies (Schenk, 2016).

Despite large quantities of sequence data for the RAD-seq analyses in chapter I, accurate fine-scale population structure is difficult to detect because of a lack of dense population sampling, however broad-scale phylogeographic patterns were well resolved. The RAD-seq strategy was designed to account for wide geographical sampling, which enabled the detection of broad spatial patterns that are evident in each study. However, to gain a better understanding of population processes, such as estimating effective population sizes, inbreeding co-efficients and identifying genetic bottlenecks in isolated populations, larger numbers of individuals from each locality would be required (Luikart et al., 1998). Such sampling intensity was beyond the scope of this PhD. With denser population sampling, it would also be possible to examine demographic histories of specific populations in more detail, which may be particularly informative for supporting the existence of refugia in the coastal forests highlighted in chapters II and III. Identifying distinct colonization events that may have led to current population structure would have been particularly informative (Gutenkunst et al., 2009; Pickrell & Pritchard, 2012). Chapter IV, which describes a new species of frog that has not been seen since 2001, reminds us that despite the rapid developments in sequencing technologies, taxonomy and systematic work still remains

an essential part of biodiversity assessment. Formal descriptions of species, and not molecular based units of biodiversity, are fundamental to designate threat status, and remain the cornerstone of current conservation policy.

The spatial sampling in this thesis is comprehensive, though is still restricted mainly to the coastal forests of Tanzania and southern Kenya (chapters II, III and IV) where sampling intensity is now relatively even. Inadequate sampling across coastal forests in Mozambique, northern Kenya and Somalia, both in terms of DNA samples but also geographic records restricts the inferences that can be made about these areas, even with the use of species distribution modelling techniques. Species distribution modelling has provided great promise for biodiversity and conservation, to estimate distributions of biodiversity but is not without its pitfalls (Elith & Leathwick, 2009; Merow et al., 2013). The quality of environmental data, both for species distribution modelling and for environmental correlation analyses presented in this thesis is not optimal. The environmental data I used within this thesis is based on data recorded from a low number of weather stations and then interpolated to produce global climate layers (Hijmans et al., 2005). This interpolated data is imperfect, due to its failure to capture local scale climate variation accurately in some cases, but is currently the only available opportunity for investigating paleo-climatic history. New cloud-cover based climate layers from remote sensing data (Wilson & Jetz, 2016) deal with the problem of data interpolation, and offer great promise for biodiversity monitoring in the future, though they are not yet applicable to paleo-climate models. In this thesis, species distribution modelling approaches are somewhat crude, and must be interpreted carefully as they may overestimate distributions of species and lineages based on inaccurate measures of habitat suitability. When building and assessing species distribution models I accounted for all possible errors to maximise their quality (Merow et al. 2013), and adopted further quality checking including comparing known distributions to IUCN range maps. A further problem of the species distribution models in this thesis are that the anthropogenic impacts by humans are not accounted for sufficiently by the environmental data, and many of the refugia detected may actually be much smaller due to human activities which the environmental data is unable to verify. The species distribution models and detection of refugia based on phylogenetic endemism scores ideally need to be ground-truthed with future survey work, though the inaccessibility of many areas in the tropics due to steep topography or political problems still remains one of the biggest stumbling blocks to fully understanding tropical biodiversity patterns worldwide.

Shortcomings in our knowledge and future research directions

The work in this thesis has made several advances in understanding the biodiversity patterns and environmental correlates of amphibians in the coastal forests of East Africa, including using phylogenetic data to validate some of the previous hypotheses about the biodiversity of the region (Burgess et al., 1998; Azeria et al., 2007). However, my research does not answer all of the questions about this regions rich biodiversity, and a number of fruitful avenues for future research are summarized below.

Quantifying tropical diversity

The tropics are known to support high levels of biodiversity, though this is often poorly categorized (Magurran, 2004) and subject to exceptionally high anthropogenic threat (Kolbert, 2014). Rapid biodiversity assessments facilitated by DNA barcoding (chapter I, II, III) and next generation sequencing (chapter I) are already becoming an increasingly important aspect of biodiversity conservation (Taberlet et al. 2012, Joly & Faure, 2015) that can provide higher resolution estimates of biodiversity patterns. In the future, molecular methods are set to increase

in importance, and next generation sequencing in particular provide data that are useful for unravelling relationships in taxonomically complex groups as I demonstrated (chapter I). These methods are already being employed in South and East Africa for plants (Lexer et al., 2013, 2014), fish (Wagner et al., 2013; Brawand et al., 2014) and small mammals (Demos et al., 2015) but the RAD-seq approach adopted in this thesis was the first ever application for amphibians in this region, and provides a case study of how this can be applied to understand cryptic diversity. Expansion of these methods is likely to continue for other taxa, and exciting times lie ahead for quantifying tropical biodiversity, though it is a race to categorize biodiversity before it disappears, as sadly may be the case with the new species described in chapter IV. Though we clearly still have a long way to go to fully explain the diversity of the tropics, the molecular tools at our disposal, their decreasing cost, and massive online repositories of available sequence data to identify species will aid the challenge significantly. In the future, I would suggest that sampling efforts are targeted within and around the endemism hotspots identified within this thesis, not only for amphibians but also for other taxonomic groups, and in particular reptiles, which are another poorly understood taxonomic group in this region. The development of a facility for in-country DNA barcoding, although difficult to establish and maintain, would come relatively cheap, and provide an exceptionally timely boost to the categorization of biodiversity and subsequent conservation efforts of the coastal forest region. This should be combined with the ongoing collection of geo-referenced DNA samples and species records by local organization and international collaborations. The subsequent databasing and open access publication of biodiversity data in findable, accessible, interoperable and reusable formats (Wilkinson et al., 2016) will therefore be essential to communicate biodiversity knowledge to stakeholders and policymakers.

Phylogenetics to identify centres of endemism and refugia

I have shown that the adoption of phylogenetic community-based biodiversity metrics such as phylogenetic endemism (chapters II and III) provide an efficient means of incorporating molecular data into biodiversity assessment and identifying refugia (Purvis et al., 2005; Rolland et al., 2012). Furthermore, branch-length based estimates of biodiversity enable the evolutionary history of an area to be categorized depending on the type of endemism present (chapter III), which may be particularly relevant for making conservation decisions, such as the conservation prioritization of ancient (paleo-endemic) diversity (Avice, 2008; Mishler et al., 2014). Refinements of these methods are ongoing (Tucker et al., 2016) alongside improved modelling techniques for distribution data (Merow et al. 2016). These methods are already being applied at global (Fritz & Rahbek, 2012; Rosauer & Jetz, 2015), and continental scales to predict the effects of future climate change on biodiversity (González-Orozco et al., 2016). However, at the scale of the African continent they are sorely lacking, and I aim to continue my research to aid biodiversity knowledge in Africa. Excitingly, improvements to our knowledge of the tree of life such as near-complete phylogenies (Jetz et al., 2012; Faurby & Svenning, 2015; Tonini et al., 2016), and the availability of matching spatial datasets (BirdLife & NatureServe, 2014; IUCN, 2015; GARD, 2017) enable phylogenetic endemism analyses to be conducted comprehensively for the first time across Africa. With these available phylogenetic and spatial datasets across multiple taxonomic groups, large scale analyses of African diversity becomes possible, especially by accounting for evolutionary history to allow the identification of centres of endemism and refugia. Advances in complementarity-based spatial conservation prioritization software (Leathwick et al., 2010) now facilitate conservation prioritization based on biodiversity patterns informed by evolutionary history (Pollock et al., 2015), but can also take into account aspects of functional diversity (Tilman

et al. 1997, Petchey et al. 2002). Combined with molecular data, I believe that these approaches can be employed to establish the optimal configuration of protected area networks that most efficiently capture biodiversity across taxonomic groups at broad scales which may be key to implementing a cohesive conservation plan which has so far been lacking in Africa (Brooks et al., 2001). At fine-scales, such as across the coastal forests of Eastern Africa, high resolution analyses of endemism patterns may help to protect ecosystem function and services which may be integral to the maintenance of this rich biodiversity (Cardinale et al., 2012). In a global context it is critically important to fill in biodiversity threat gaps by synthesizing available high quality biodiversity datasets that are up to date, assessed by experts, and repeated over time in appropriate spatial resolutions (Joppa et al., 2016). The ongoing collection of biodiversity data that meets these criteria will provide the basis for assessing anthropogenic biodiversity threats and how these can be counteracted to preserve biodiversity in the future.

Conclusion

This thesis has demonstrated that amphibian biodiversity is unevenly distributed across the Coastal forests of Eastern Africa, and that environmental factors, and in particular long term-stability, play a key role in the spatial distribution of this biodiversity. With this work I have shown that molecular data is key to the ongoing categorization of biodiversity in rich tropical regions, and that next generation sequencing in particular can resolve difficult taxonomic groups, and holds rich promise for future tropical research. The phylogenetic endemism measure that I used demonstrates how community evolutionary history can be measured to identify refugia, and the categorization of these endemism types showed that coastal forests are mainly museums of diversity supporting the persistence of ancient paleo-endemic lineages, but in some cases cradles that support recently evolved neo-endemics. Together, the analyses within this thesis support previously described centres of endemism in the coastal forest region, proving this with phylogenetic data for the first time. With spatial analyses I confirmed that many areas supporting high levels of endemism are highly threatened and poorly conserved, and it is critical that conservation efforts in this region are increased to protect the biodiversity that exists in these places.

References

- Awise J.C. (2008) Colloquium paper: three ambitious (and rather unorthodox) assignments for the field of biodiversity genetics. *Proceedings of the National Academy of Sciences*, **105 Suppl**, 11564–70.
- Azeria E.T., Sanmartin I., As S., Carlson A., & Burgess N. (2007) Biogeographic patterns of the East African coastal forest vertebrate fauna. *Biodiversity and Conservation*, **16**, 883–912.
- BirdLife & NatureServe (2014) Bird species distribution maps of the world. Available at: <<http://datazone.birdlife.org/>>. Accessed on 1st March 2017.
- Brawand D., Wagner C.E., Li Y.I., Malinsky M., Keller I., Fan S., Simakov O., Ng A.Y., Lim Z.W., Bezault E., Turner-Maier, J. Johnson J., Alcazar R., Noh H.J., Russell P., Aken B., Alföldi J., Amemiya C., Azzouzi N., Baroiller J.-F., Barloy-Hubler F., Berlin A., Bloomquist R., Carleton K.L., Conte M. a., D’Cotta H., Eshel O., Gaffney L., Galibert F., Gante H.F., Gnerre S., Greuter L., Guyon R., Haddad N.S., Haerty W., Harris R.M., Hofmann H., Hourlier T., Hulata G., Jaffe D.B., Lara M., A.P. L., MacCallum I., Mwaiko S., Nikaïdo M., Nishihara H., Ozouf-Costaz C., Penman D.J., Przybylski D., Rakotomanga M., Renn S.C.P., Ribeiro F.J., Ron M., Salzburger W., Sanchez-Pulido L., Santos M.E., Searle S., Sharpe T., Swofford R., Tan F.J., Williams L., Young S., Yin S., Okada N., Kocher T.D., Miska E. a., Lander E.S., Venkatesh B.,

- Fernald R.D., Meyer A., Ponting C.P., Streelman J.T., Lindblad-Toh K., Seehausen O., & Di Palma F. (2014) The genomic substrate for adaptive radiation in African cichlid fish. *Nature*, **513**, 375-381.
- Brooks T., Balmford A., Burgess N., Fjeldså J., Hansen L., Moore J., Rahbek C., & Williams P. (2001) Toward a Blueprint for Conservation in Africa. *BioScience*, **51**, 613.
- Burgess N.D., Clarke G.P., & Rodgers W.A. (1998) Coastal forests of eastern Africa: status, endemism patterns and their potential causes. *Biological Journal of the Linnean Society*, **64**, 337-367.
- Cardinale B.J., Duffy J.E., Gonzalez A., Hooper D.U., Perrings C., Venail P., Narwani A., Mace G.M., Tilman D., A.Wardle D., Kinzig A.P., Daily G.C., Loreau M., Grace J.B., Larigauderie A., Srivastava D.S., & Naeem S. (2012) Biodiversity loss and its impact on humanity. *Nature*, **489**, 326-326.
- Demos T.C., Kerbis Peterhans J.C., Joseph T.A., Robinson J.D., Agwanda B., & Hickerson M.J. (2015) Comparative population genomics of African montane forest mammals support population persistence across a climatic gradient and quaternary climatic cycles. *PLoS ONE*, **10**, e031800.
- Elith J. & Leathwick J.R. (2009) Species Distribution Models : Ecological Explanation and Prediction Across Space and Time. *Annual Review of Ecology, Evolution and Systematics*, **40**, 677-697.
- Faurby S. & Svenning J.C. (2015) A species-level phylogeny of all extant and late Quaternary extinct mammals using a novel heuristic-hierarchical Bayesian approach. *Molecular Phylogenetics and Evolution*, **84**, 14-26.
- Fritz S.A. & Rahbek C. (2012) Global patterns of amphibian phylogenetic diversity. *Journal of Biogeography*, **39**, 1373-1382.
- González-Orozco C.E., Pollock L.J., Thornhill A.H., Mishler B.D., Knerr N., Laffan S.W., Miller J.T., Rosauer D.F., Faith D.P., Nipperess D.A., Kujala H., Linke S., Butt N., Külheim C., Crisp M.D., & Gruber B. (2016) Phylogenetic approaches reveal biodiversity threats under climate change. *Nature Climate Change*, **1**, 1-6.
- Gutenkunst R.N., Hernandez R.D., Williamson S.H., & Bustamante C.D. (2009) Inferring the Joint Demographic History of Multiple Populations from Multidimensional SNP Frequency Data. *PLoS Genetics*, **5**, e1000695.
- Hijmans R.J., Cameron S.E., Parra J.L., Jones P.G., & Jarvis A. (2005) WORLDCLIM - a set of global climate layers (climate grids). *International Journal of Climatology*, **25**, 1965-1978.
- Hoelzer G.A. (1997) Inferring phylogenies from mtDNA variation: mitochondrial-gene trees versus nuclear-gene trees revisited. *Evolution*, **51**, 622-626.
- IUCN (2015) IUCN Red List of Threatened Species. *Version 2015.3*, Available from: <<http://www.iucnredlist.org>>. Accessed: 3rd February 2017.
- Jetz W., Thomas G.H., Joy J.B., Hartmann K., & Mooers A.O. (2012) The global diversity of birds in space and time. *Nature*, **491**, 444-448.
- Joly D. & Faure D. (2015) Next-generation sequencing propels environmental genomics to the front line of research. *Heredity*, **114**, 429-430.
- Joppa L.N., O'Connor B., Visconti P., Smith C., Geldmann J., Hoffmann M., Watson J.E.M., Butchart S.H.M., Virah-Sawmy M., Halpern B.S., Ahmed S.E., Balmford A., Sutherland W.J., Harfoot M., Hilton-Taylor C., Foden W., Minin E. Di, Pagad S., Genovesi P., Hutton J., & Burgess N.D (2016) Filling in biodiversity threat gaps. *Science*, **352**, 416-418.

- Kolbert E. (2014) *The Sixth Extinction*. Henry Holt & Co.
- Leathwick J.R., Moilanen A., Ferrier S., & Julian K. (2010) Complementarity-based conservation prioritization using a community classification, and its application to riverine ecosystems. *Biological Conservation*, **143**, 984–991.
- Lexer C., Mangili S., Bossolini E., Forest F., Stölting K.N., Pearman P.B., Zimmermann N.E., & Salamin N. (2013) “Next generation” biogeography: towards understanding the drivers of species diversification and persistence. *Journal of Biogeography*, **40**, 1013–1022.
- Lexer C., Wüest R.O., Mangili S., Heuertz M., Stölting K.N., Pearman P.B., Forest F., Salamin N., Zimmermann N.E., & Bossolini E. (2014) Genomics of the divergence continuum in an African plant biodiversity hotspot, I: drivers of population divergence in *Restio capensis* (Restionaceae). *Molecular Ecology*, **23**, 4373–4386.
- Luikart G., Allendorf F.W., Cornuet J.M., & Sherwin W.B. (1998) Distortion of allele frequency distributions provides a test for recent population bottlenecks. *Journal of Heredity*, **89**, 238–247.
- Magurran A. (2004) Introduction: measurement of (biological) diversity. *Measuring Biological Diversity*, p. 1–17. Blackwell Science Ltd.
- Merow C., Smith M.J., & Silander J.A. (2013) A practical guide to MaxEnt for modeling species’ distributions: What it does, and why inputs and settings matter. *Ecography*, **36**, 1058–1069.
- Merow C., Allen J.M., Aiello-Lamens M., Silander J.A. Jr (2016) Improving niche and range estimates with Maxent and point process models by integrating spatially explicit information. *Global Ecology and Biogeography*, **25**, 1022–1036.
- Miraldo A., Li S., Borregaard M.K., Florez-Rodriguez A., Gopalakrishnan S., Rizvanovic M., Wang Z., Rahbek C., Marske K.A., & Nogues-Bravo D. (2016) An Anthropocene map of genetic diversity. *Science*, **353**, 1532–1535.
- Mishler B.D., Knerr N., González-Orozco C.E., Thornhill A.D., Laffan S.W., & Miller J.T. (2014) Phylogenetic measures of biodiversity and neo- and paleo-endemism in Australian Acacia. *Nature Communications*, **5**, 4473.
- Morlon H., Parsons T.L., & Plotkin J.B. (2011) Reconciling molecular phylogenies with the fossil record. *Proceedings of the National Academy of Sciences*, **108**, 16327–16332.
- Pickrell J.K. & Pritchard J.K. (2012) Inference of population splits and mixtures from genome-wide allele frequency data. *PLoS Genetics*, **8**, e1002967.
- Pollock L.J., Rosauer D.F., Thornhill A.H., Kujala H., Crisp M.D., Miller J.T., & McCarthy M.A. (2015) Phylogenetic diversity meets conservation policy: small areas are key to preserving eucalypt lineages. *Philosophical Transactions of the Royal Society London B Biological Sciences*, **370**, 20140007.
- Purvis A., Gittleman J.L., & Brooks T.M. (2005) *Phylogeny and Conservation*. 448 pp. Cambridge University Press.
- Rolland J., Cadotte M.W., Davies J., Devictor V., Lavergne S., Mouquet N., Pavoine S., Rodrigues A., Thuiller W., Turcati L., Winter M., Zupan L., Jabot F., & Morlon H. (2012) Using phylogenies in conservation: new perspectives. *Biology Letters*, **8**, 692–694.
- Rosauer D., Laffan S.W., Crisp M.D., Donnellan S.C., & Cook L.G. (2009) Phylogenetic endemism: a new approach for identifying geographical concentrations of evolutionary history. *Molecular Ecology*, **18**,

4061–4072.

- Rosauer D.F., Catullo R.A., Vanderwal J., & Moussalli A. (2015) Lineage range estimation method reveals fine-scale endemism linked to Pleistocene stability in Australian rainforest herpetofauna. *PLoS ONE*, **10**, e0126274.
- Rosauer D.F. & Jetz W. (2015) Phylogenetic endemism in terrestrial mammals. *Global Ecology and Biogeography*, **24**, 168–179.
- Schenk J.J. (2016) Consequences of secondary calibrations on divergence time estimates. *PLoS ONE*, **11**, DOI:10.1371/journal.pone.014822.
- Schmidt-Lebuhn A.N., Knerr N.J., Miller J.T., & Mishler B.D. (2015) Phylogenetic diversity and endemism of Australian daisies (Asteraceae). *Journal of Biogeography*, **42**, 1114–1122.
- Taberlet P., Coissac E., Pompanon F, Brochmann C., Willerslev E. (2012) Towards next-generation biodiversity assessment using DNA metabarcoding. *Molecular Ecology* **21**, 2045–2050.
- Tarroso P., Velo-Antón G., & Carvalho S.B. (2015) PHYLIN: An R package for phylogeographic interpolation. *Molecular Ecology Resources*, **15**, 349–357.
- Tonini J.F.R., Beard K.H., Ferreira R.B., Jetz W., & Pyron R.A. (2016) Fully-sampled phylogenies of squamates reveal evolutionary patterns in threat status. *Biological Conservation*, **204**, 23–31.
- Tucker C.M., Cadotte M.W., Carvalho S.B., Davies T.J., Ferrier S., Fritz S.A., Grenyer R., Helmus M.R., Jin L.S., Mooers A.O., Pavoine S., Purschke O., Redding D.W., Rosauer D.F., Winter M., & Mazel F. (2016) A guide to phylogenetic metrics for conservation, community ecology and macroecology. *Biological Reviews*, doi: 10.1111/brv.12252.
- Wagner C.E., Keller I., Wittwer S., Selz O.M., Mwaiko S., Greuter L., Sivasundar A., & Seehausen O. (2013) Genome-wide RAD sequence data provide unprecedented resolution of species boundaries and relationships in the Lake Victoria cichlid adaptive radiation. *Molecular Ecology*, **22**, 787–798.
- Wilkinson M.D., Dumontier M., Aalbersberg Ij.J., Appleton G., Axton M., Baak A., Blomberg N., Boiten J.-W., da Silva Santos L.B., Bourne P.E., Bouwman J., Brookes A.J., Clark T., Crosas M., Dillo I., Dumon O., Edmunds S., Evelo C.T., Finkers R., Gonzalez-Beltran A., Gray A.J.G., Groth P., Goble C., Grethe J.S., Heringa J., 't Hoen P., Hooft R., Kuhn T., Kok R., Kok J., Lusher S.J., Martone M.E., Mons A., Packer A.L., Persson B., Rocca-Serra P., Roos M., van Schaik R., Sansone S.-A., Schultes E., Sengstag T., Slater T., Strawn G., Swertz M., Thompson M., van der Lei J., van Mulligen E., Velterop J., Waagmeester A., Wittenburg P., Wolstencroft K., Zhao J., & Mons B. (2016) The FAIR Guiding Principles for scientific data management and stewardship. *Scientific Data*, **3**, 160018.
- Wilson A.M. & Jetz W. (2016) Remotely Sensed High-Resolution Global Cloud Dynamics for Predicting Ecosystem and Biodiversity Distributions. *PLoS Biology*, **14**, e1002415.

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Thank you to my family - my parents, Gill and Steve, and my sisters Claire and Amy who have supported me throughout my entire life, in every endeavour. As far back as I can remember I've always been mesmerised by the natural world – whether that be catching grasshoppers in buckets, studying rockpools on Cawsand beach, fishing trips at Penlee point, collecting frogs in leftover sweet jars or watching David Attenborough programmes open-mouthed on early Sunday evenings! I also thank my extended family, including John and Luke for always making trips home a lot of fun – especially with Ollie and the new arrivals!

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Supplementary Materials

DNA Barcoding

A large-scale DNA barcoding project formed the basis of this thesis, with use of existing sequence data from within Dr. Simon Loader's lab group at the University of Basel (ca. 200 genetic samples). My own field work across the Tanzanian coastal forests provided almost 1000 genetic samples which contributed to this database, and several hundred additional samples from Kenya, Mozambique and Malawi were obtained. The following people and institutions contributed to the additional samples collected, either from tissue loans or recent field work, resulting in a total of 1,532 amphibian DNA samples from the coastal forests and surrounding areas:

Simon P. Loader (University of Basel)

Beryl Akoth Bwong (National Museums of Kenya)

Gabriela Bittencourt-Silva (University of Basel)

Michele Menegon (Museum of Science, Trento, Italy)

David Gower, Mark Wilkinson, John Poynton (Natural History Museum, London)

Hendrik Mueller (University of Jena, Germany)

Lucinda Lawson (Field Museum of Natural History, Chicago, USA)

Breda Zimkus, Joanna Larson (Museum of Comparative Zoology, Harvard, USA)

Daniel Portik (Museum of Vertebrate Zoology, Berkeley, USA)

Werner Conradie (Port Elizabeth museum, South Africa)

Harith Farooq (Universidade Lurio, Nampula, Mozambique)

Alan Channing (University of Western Cape, Cape Town, South Africa)

Kim Howell (University of Dar es Salaam, Tanzania)

For each sample, genomic DNA was first extracted using the DNeasy Blood & Tissue Kit (Qiagen). To generate DNA barcode data, the commonly used mitochondrial *16S* rRNA gene (Vences et al. 2005) was amplified, and the PCR products were visualized under UV light on 1.5% agarose gels. PCR products of expected size (ca. 500 base pairs) were Sanger sequenced by Microsynth AG sequencing facility, Balgach, Switzerland. Sequence data was cleaned and verified using Codoncode Aligner 7.0.1 (CodonCode Corporation, Dedham, Massachusetts, USA), and consensus sequences were queried against existing GenBank sequences using the NCBI BLAST tool (NCBI Resource Coordinators, 2016) to verify species identifications. All sequences were given a unique ID number, and the sequence, locality data, voucher specimen GPS coordinates were recorded in an internal MySQL database created by Reto Hagmann (Table S1).

Table S1. All coastal forest amphibians used in this PhD thesis, including their unique ID numbers (T no.), Species IDs, Voucher numbers, and locality data including GPS coordinates (WGS84 format).

T no.	Species ID	Voucher ID	Cnt	Locality	Long	Lat
T1942	<i>Afrivalus brachycnemis</i>	BM 2002.376	TZ	Ruvu South	38.878	-6.948
T1944	<i>Afrivalus brachycnemis</i>	BM 2002.997	TZ	Uluguru	37.838	-7.179
T1951	<i>Afrivalus brachycnemis</i>	BM 2005.915	TZ	Kazizumbwi	39.040	-6.945
T1952	<i>Afrivalus brachycnemis</i>	BM 2002.372	TZ	Ruvu South	38.813	-6.895
T2710	<i>Afrivalus brachycnemis</i>	HM 1660	MWI	Thyolo town, Thyolo	35.137	-16.063
T2711	<i>Afrivalus brachycnemis</i>	HM 1661	MWI	Thyolo town, Thyolo	35.137	-16.063
T3427	<i>Afrivalus brachycnemis</i>	CB 13.338	TZ	Nyamuete FR, Pwani, Tanzania	39.034	-8.326
T3428	<i>Afrivalus brachycnemis</i>	CB 13.339	TZ	Nyamuete FR, Pwani, Tanzania	39.034	-8.326
T3429	<i>Afrivalus brachycnemis</i>	CB 13.340	TZ	Nyamuete FR, Pwani, Tanzania	39.034	-8.326
T3434	<i>Afrivalus brachycnemis</i>	CB 13.345	TZ	Nyamuete FR, Pwani, Tanzania	39.034	-8.326
T3712	<i>Afrivalus brachycnemis</i>	CB 13.504	TZ	Dar es Salaam (university), Tanzania	39.204	-6.779
T3713	<i>Afrivalus brachycnemis</i>	CB 13.505	TZ	Dar es Salaam (university), Tanzania	39.204	-6.779
T3714	<i>Afrivalus brachycnemis</i>	CB 13.506	TZ	Dar es Salaam (university), Tanzania	39.204	-6.779
T3715	<i>Afrivalus brachycnemis</i>	CB 13.507	TZ	Dar es Salaam (university), Tanzania	39.204	-6.779
T3716	<i>Afrivalus brachycnemis</i>	CB 13.508	TZ	Dar es Salaam (university), Tanzania	39.204	-6.779
T3717	<i>Afrivalus brachycnemis</i>	CB 13.509	TZ	Dar es Salaam (university), Tanzania	39.204	-6.779
T3832	<i>Afrivalus brachycnemis</i>	CB 13.626	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T3833	<i>Afrivalus brachycnemis</i>	CB 13.627	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T3834	<i>Afrivalus brachycnemis</i>	CB 13.628	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T3835	<i>Afrivalus brachycnemis</i>	CB 13.629	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T3836	<i>Afrivalus brachycnemis</i>	CB 13.630	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T3837	<i>Afrivalus brachycnemis</i>	CB 13.631	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T3838	<i>Afrivalus brachycnemis</i>	CB 13.632	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T3853	<i>Afrivalus brachycnemis</i>	CB 13.647	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T3854	<i>Afrivalus brachycnemis</i>	CB 13.648	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T3855	<i>Afrivalus brachycnemis</i>	CB 13.649	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T3856	<i>Afrivalus brachycnemis</i>	CB 13.650	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T3857	<i>Afrivalus brachycnemis</i>	CB 13.651	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T4087	<i>Afrivalus brachycnemis</i>	CB 13.737	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4088	<i>Afrivalus brachycnemis</i>	CB 13.738	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4089	<i>Afrivalus brachycnemis</i>	CB 13.739	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4090	<i>Afrivalus brachycnemis</i>	CB 13.740	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4091	<i>Afrivalus brachycnemis</i>	CB 13.741	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4092	<i>Afrivalus brachycnemis</i>	CB 13.742	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4093	<i>Afrivalus brachycnemis</i>	CB 13.743	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4094	<i>Afrivalus brachycnemis</i>	CB 13.744	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4236	<i>Afrivalus brachycnemis</i>	CB 13.886	TZ	Horohoro, Tanga, Tanzania	39.102	-4.632
T4762	<i>Afrivalus brachycnemis</i>	MMA-16	MZ	Mnt Mabu	36.588	-16.313
T5020	<i>Afrivalus brachycnemis</i>	BM 2002.373	TZ	Ruvu South FR	38.813	-6.895
T5021	<i>Afrivalus brachycnemis</i>	BM 2002.374	TZ	Ruvu South FR	38.878	-6.948
T5022	<i>Afrivalus brachycnemis</i>	BM 2002.375	TZ	Ruvu South FR	38.878	-6.948
T5382	<i>Afrivalus brachycnemis</i>	MVZ 265821	MZ	Serra Jeci Grassland drainage banana plant 1	35.173	-12.867
T5383	<i>Afrivalus brachycnemis</i>	MVZ 265822	MZ	Serra Jeci Grassland drainage banana plant 1	35.173	-12.867
T5384	<i>Afrivalus brachycnemis</i>	MVZ 265823	MZ	Serra Jeci Grassland savannah pond	35.184	-12.877
T5389	<i>Afrivalus brachycnemis</i>	MVZ 265824	MZ	Namuli, grasslands	37.072	-15.384
T5390	<i>Afrivalus brachycnemis</i>	MVZ 265825	MZ	Namuli, grasslands	37.072	-15.384
T5391	<i>Afrivalus brachycnemis</i>	MVZ 265826	MZ	Namuli, grasslands	37.072	-15.384
T5394	<i>Afrivalus brachycnemis</i>	MVZ:226254	KN	old sand quarry, Arabuko Sokoke Forest	39.867	-3.333
T5395	<i>Afrivalus brachycnemis</i>	MVZ:226255	KN	old sand quarry, Arabuko Sokoke Forest	39.867	-3.333
T4763	<i>Afrivalus cf. delicatus</i>	WC-DNA-1227	MZ	Revubo river below Tenge Hill	33.772	-15.719
T4766	<i>Afrivalus cf. delicatus</i>	WC-DNA-1349	MZ	Revubo river below Tenge Hill	33.772	-15.719
T2930	<i>Afrivalus delicatus</i>	GPN 032	MZ	Gorongosa N.P.	34.805	-18.665
T2931	<i>Afrivalus delicatus</i>	GPN 061	MZ	Gorongosa N.P.	34.814	-18.644

T2932	<i>Afrivalus delicatus</i>	GPN 063	MZ	Gorongosa N.P.	34.814	-18.644
T2933	<i>Afrivalus delicatus</i>	GPN 158	MZ	Gorongosa N.P.	34.676	-19.031
T3066	<i>Afrivalus delicatus</i>	CB 13.089	TZ	Makangala FR (edge), Lindi, Tanzania	39.369	-9.982
T3675	<i>Afrivalus delicatus</i>	CB 13.467	TZ	Ruawa FR, Lindi, Tanzania	39.569	-9.730
T3676	<i>Afrivalus delicatus</i>	CB 13.468	TZ	Ruawa FR, Lindi, Tanzania	39.569	-9.730
T3677	<i>Afrivalus delicatus</i>	CB 13.469	TZ	Ruawa FR, Lindi, Tanzania	39.569	-9.730
T3678	<i>Afrivalus delicatus</i>	CB 13.470	TZ	Ruawa FR, Lindi, Tanzania	39.569	-9.730
T3679	<i>Afrivalus delicatus</i>	CB 13.471	TZ	Ruawa FR, Lindi, Tanzania	39.569	-9.730
T3680	<i>Afrivalus delicatus</i>	CB 13.472	TZ	Ruawa FR, Lindi, Tanzania	39.569	-9.730
T4764	<i>Afrivalus delicatus</i>	WC-DNA-1228	MZ	Revubo river below Tenge Hill	33.772	-15.719
T4765	<i>Afrivalus delicatus</i>	WC-DNA-1230	MZ	Revubo river below Tenge Hill	33.772	-15.719
T4767	<i>Afrivalus delicatus</i>	WC-DNA-1154	MZ	2nd stream 12 km north of Namina	38.735	-14.847
T4768	<i>Afrivalus delicatus</i>	WC-DNA-1157	MZ	2nd stream 12 km north of Namina	38.735	-14.847
T4769	<i>Afrivalus delicatus</i>	WC-DNA-1085	MZ	dammed area just west of Syrah camp	37.631	-13.337
T4770	<i>Afrivalus delicatus</i>	WC-DNA-1109	MZ	upper Montepeuz river crossing site	38.587	-13.408
T4771	<i>Afrivalus delicatus</i>	WC-DNA-1113	MZ	upper Montepeuz river crossing site	38.587	-13.408
T4772	<i>Afrivalus delicatus</i>	WC-DNA-1416	MZ	Dereks house wetland	40.354	-12.933
T4773	<i>Afrivalus delicatus</i>	WC-DNA-1418	MZ	Dereks house wetland	40.354	-12.933
T4774	<i>Afrivalus delicatus</i>	ENI 02	MZ	R. Diquide	40.428	-11.883
T4979	<i>Afrivalus delicatus</i>	FMNH 274871	MWI	Malawi	35.711	-16.048
T4980	<i>Afrivalus delicatus</i>	FMNH 274881	MWI	Malawi	35.711	-16.048
T4981	<i>Afrivalus delicatus</i>	FMNH 274867	MWI	Malawi	35.711	-16.048
T5010	<i>Afrivalus delicatus</i>	MTSN 5851	TZ	Mang'ula	NULL	NULL
T5011	<i>Afrivalus delicatus</i>	MTSN 5852	TZ	Mang'ula	36.890	-7.843
T3131	<i>Afrivalus fornasini</i>	CB 13.154	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3134	<i>Afrivalus fornasini</i>	CB 13.157	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3553	<i>Afrivalus fornasini</i>	CB 13.417	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3558	<i>Afrivalus fornasini</i>	CB 13.422	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3559	<i>Afrivalus fornasini</i>	CB 13.423	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3635	<i>Afrivalus fornasini</i>	CB 13.427	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3636	<i>Afrivalus fornasini</i>	CB 13.428	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3755	<i>Afrivalus fornasini</i>	CB 13.547	TZ	Vikindu FR, Pwani, Tanzania	39.297	-6.994
T3782	<i>Afrivalus fornasini</i>	CB 13.574	TZ	Kibasira Swamp, Morogoro, Tanzania	36.228	-8.349
T3783	<i>Afrivalus fornasini</i>	CB 13.575	TZ	Kibasira Swamp, Morogoro, Tanzania	36.228	-8.349
T3784	<i>Afrivalus fornasini</i>	CB 13.576	TZ	Kibasira Swamp, Morogoro, Tanzania	36.228	-8.349
T3785	<i>Afrivalus fornasini</i>	CB 13.577	TZ	Kibasira Swamp, Morogoro, Tanzania	36.228	-8.349
T3788	<i>Afrivalus fornasini</i>	CB 13.592	TZ	Kibasira Swamp, Morogoro, Tanzania	36.228	-8.349
T3791	<i>Afrivalus fornasini</i>	CB 13.583	TZ	Kibasira Swamp, Morogoro, Tanzania	36.228	-8.349
T3803	<i>Afrivalus fornasini</i>	CB 13.597	TZ	Kibasira Swamp, Morogoro, Tanzania	36.228	-8.349
T3812	<i>Afrivalus fornasini</i>	CB 13.606	TZ	Kibasira Swamp, Morogoro, Tanzania	36.318	-8.312
T3827	<i>Afrivalus fornasini</i>	CB 13.621	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T3828	<i>Afrivalus fornasini</i>	CB 13.622	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T3840	<i>Afrivalus fornasini</i>	CB 13.634	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T3841	<i>Afrivalus fornasini</i>	CB 13.635	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T3842	<i>Afrivalus fornasini</i>	CB 13.636	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T4036	<i>Afrivalus fornasini</i>	CB 13.686	TZ	Mafia island, Tanzania	39.714	-7.963
T4050	<i>Afrivalus fornasini</i>	CB 13.700	TZ	Mafia island, Tanzania	39.795	-7.849
T4076	<i>Afrivalus fornasini</i>	CB 13.726	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4165	<i>Afrivalus fornasini</i>	CB 13.815	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4166	<i>Afrivalus fornasini</i>	CB 13.816	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4167	<i>Afrivalus fornasini</i>	CB 13.817	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4168	<i>Afrivalus fornasini</i>	CB 13.818	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4169	<i>Afrivalus fornasini</i>	CB 13.819	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4170	<i>Afrivalus fornasini</i>	CB 13.820	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4178	<i>Afrivalus fornasini</i>	CB 13.828	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4383	<i>Afrivalus fornasini</i>	MTSN 5143	TZ	Dar es Salaam	39.286	-6.787
T4384	<i>Afrivalus fornasini</i>	MTSN 5144	TZ	Dar es Salaam	NULL	NULL
T4385	<i>Afrivalus fornasini</i>	MTSN 8121	TZ	Ruipa, Ranger post	37.035	-9.169
T4386	<i>Afrivalus fornasini</i>	MTSN 8122	TZ	Ruipa, Ranger post	37.035	-9.169
T4387	<i>Afrivalus fornasini</i>	MTSN 8125	TZ	Ruipa, Ranger post	37.035	-9.169
T4423	<i>Afrivalus fornasini</i>	BM 2002.998	TZ	Uluguru Mountians - Mvuha FR	37.838	-7.179
T4424	<i>Afrivalus fornasini</i>	BM 2002.999	TZ	Uluguru Mountians - Mvuha FR	37.838	-7.179

T4425	<i>Afrivalus fornasini</i>	BM 2002.1000	TZ	Uluguru Mountians - Mvuha FR	37.838	-7.179
T4426	<i>Afrivalus fornasini</i>	BM 2000.825	TZ	Kwangumi FR	38.733	-4.923
T4427	<i>Afrivalus fornasini</i>	BM 2002.551	TZ	Nilo FR	38.663	-4.904
T4428	<i>Afrivalus fornasini</i>	BM 2002.552	TZ	Nilo FR	38.663	-4.904
T4795	<i>Afrivalus fornasini</i>	BM 2002.377	TZ	Ruvu South FR	38.813	-6.895
T4796	<i>Afrivalus fornasini</i>	BM 2002.378	TZ	Ruvu South FR	38.762	-6.901
T4982	<i>Afrivalus fornasini</i>	MCZ A-32090	TZ	Baleni Pond, Mafia	39.803	-7.850
T5144	<i>Afrivalus fornasini</i>	MUSE 11052	TZ	Mgeta Hydroelectric Dam	36.091	-8.312
T5145	<i>Afrivalus fornasini</i>	MUSE 11053	TZ	Mgeta Hydroelectric Dam	36.091	-8.312
T5201	<i>Afrivalus quadrivittatus</i>	MW 04283	TZ	Igamba falls, Kigoma region	29.979	-5.182
T5023	<i>Afrivalus sp P&B</i>	BM 2002.561	TZ	Nilo FR	38.660	-4.904
T5024	<i>Afrivalus sp P&B</i>	BM 2002.562	TZ	Nilo FR	38.663	-4.904
T5026	<i>Afrivalus sp P&B</i>	BM 2002.566	TZ	Nilo FR	38.652	-4.929
T2346	<i>Afrivalus stuhlmanni</i>	MTSN 7703	TZ	Kimboza Forest	37.802	-7.002
T2347	<i>Afrivalus stuhlmanni</i>	MTSN 7704	TZ	Kimboza Forest	37.802	-7.002
T2348	<i>Afrivalus stuhlmanni</i>	MTSN 7705	TZ	Kimboza Forest	37.802	-7.002
T2349	<i>Afrivalus stuhlmanni</i>	MTSN 7706	TZ	Kimboza Forest	37.802	-7.002
T2350	<i>Afrivalus stuhlmanni</i>	MTSN 7722	TZ	Kimboza Forest	37.802	-7.002
T3805	<i>Afrivalus stuhlmanni</i>	CB 13.599	TZ	Kibasira Swamp, Morogoro, Tanzania	36.228	-8.349
T3806	<i>Afrivalus stuhlmanni</i>	CB 13.600	TZ	Kibasira Swamp, Morogoro, Tanzania	36.228	-8.349
T3818	<i>Afrivalus stuhlmanni</i>	CB 13.612	TZ	Kibasira Swamp, Morogoro, Tanzania	36.318	-8.312
T5008	<i>Afrivalus stuhlmanni</i>	SL 804	TZ	Ukaguru; Lumbiji, loc. 2 (paddy field)	36.984	-6.615
T1948	<i>Afrivalus sylvaticus</i>	BM 2002.318	TZ	Mlinga	38.748	-5.059
T2980	<i>Afrivalus sylvaticus</i>	CB 13.025	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T2981	<i>Afrivalus sylvaticus</i>	CB 13.026	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T2987	<i>Afrivalus sylvaticus</i>	CB 13.044	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3013	<i>Afrivalus sylvaticus</i>	CB 13.030	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3067	<i>Afrivalus sylvaticus</i>	CB 13.090	TZ	Makangala FR (edge), Lindi, Tanzania	39.369	-9.982
T3099	<i>Afrivalus sylvaticus</i>	CB 13.122	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3100	<i>Afrivalus sylvaticus</i>	CB 13.123	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3113	<i>Afrivalus sylvaticus</i>	CB 13.136	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3123	<i>Afrivalus sylvaticus</i>	CB 13.146	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3132	<i>Afrivalus sylvaticus</i>	CB 13.155	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3203	<i>Afrivalus sylvaticus</i>	CB 13.226	TZ	Noto Plateau, Lindi, Tanzania	39.374	-9.895
T3212	<i>Afrivalus sylvaticus</i>	CB 13.235	TZ	Noto Plateau, Lindi, Tanzania	39.374	-9.895
T3213	<i>Afrivalus sylvaticus</i>	CB 13.236	TZ	Noto Plateau, Lindi, Tanzania	39.374	-9.895
T3214	<i>Afrivalus sylvaticus</i>	CB 13.237	TZ	Noto Plateau, Lindi, Tanzania	39.374	-9.895
T3215	<i>Afrivalus sylvaticus</i>	CB 13.238	TZ	Noto Plateau, Lindi, Tanzania	39.374	-9.895
T3216	<i>Afrivalus sylvaticus</i>	CB 13.239	TZ	Noto Plateau, Lindi, Tanzania	39.374	-9.895
T3217	<i>Afrivalus sylvaticus</i>	CB 13.240	TZ	Noto Plateau, Lindi, Tanzania	39.374	-9.895
T3318	<i>Afrivalus sylvaticus</i>	CB 13.325	TZ	Makangaga FR, Lindi, Tanzania	39.292	-9.495
T3319	<i>Afrivalus sylvaticus</i>	CB 13.326	TZ	Makangaga FR, Lindi, Tanzania	39.292	-9.495
T3320	<i>Afrivalus sylvaticus</i>	CB 13.327	TZ	Makangaga FR, Lindi, Tanzania	39.292	-9.495
T3321	<i>Afrivalus sylvaticus</i>	CB 13.328	TZ	Makangaga FR, Lindi, Tanzania	39.292	-9.495
T3474	<i>Afrivalus sylvaticus</i>	CB 13.385	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3475	<i>Afrivalus sylvaticus</i>	CB 13.386	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3476	<i>Afrivalus sylvaticus</i>	CB 13.387	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3477	<i>Afrivalus sylvaticus</i>	CB 13.388	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3478	<i>Afrivalus sylvaticus</i>	CB 13.389	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3683	<i>Afrivalus sylvaticus</i>	CB 13.475	TZ	Ruawa FR, Lindi, Tanzania	39.569	-9.730
T4044	<i>Afrivalus sylvaticus</i>	CB 13.694	TZ	Mafia island, Tanzania	39.795	-7.849
T4388	<i>Afrivalus sylvaticus</i>	MTSN 8124	TZ	Ruipa, Ranger post	37.035	-9.169
T4848	<i>Afrivalus sylvaticus</i>	MTSN 7707	TZ	Kimboza Forest	37.804	-7.005
T4924	<i>Afrivalus sylvaticus</i>	MTSN 9517	TZ	Segoma Forest, Camp, East Usambara	38.758	-4.981
T4925	<i>Afrivalus sylvaticus</i>	MTSN 9518	TZ	Segoma Forest, Camp, East Usambara	38.758	-4.981
T4926	<i>Afrivalus sylvaticus</i>	MTSN 9519	TZ	Segoma Forest, Camp, East Usambara	38.758	-4.981
T4938	<i>Afrivalus sylvaticus</i>	MTSN 9524	TZ	Segoma Forest, Camp, East Usambara	38.758	-4.981
T4942	<i>Afrivalus sylvaticus</i>	MTSN 9528	TZ	Segoma Forest, Camp, East Usambara	38.758	-4.981
T4955	<i>Afrivalus sylvaticus</i>	MTSN 9547	TZ	Segoma Forest, Camp, East Usambara	38.762	-4.976
T4956	<i>Afrivalus sylvaticus</i>	MTSN 9548	TZ	Segoma Forest, Camp, East Usambara	38.762	-4.976
T4978	<i>Afrivalus sylvaticus</i>	MTSN 9574	TZ	Segoma Forest, Camp, East Usambara	38.762	-4.976
T5007	<i>Afrivalus sylvaticus</i>	SL 803	TZ	Ukaguru; Lumbiji, loc. 2 (paddy field)	36.984	-6.615

T5009	<i>Afrivalus sylvaticus</i>	SL 805	TZ	Ukaguru; Lumbiji, loc. 2 (paddy field)	36.984	-6.615
T5012	<i>Afrivalus sylvaticus</i>	MTSN 8375	TZ	Kanga FR	37.724	-5.960
T5013	<i>Afrivalus sylvaticus</i>	MTSN 8383	TZ	Kanga FR	37.724	-5.960
T5025	<i>Afrivalus sylvaticus</i>	BM 2002.563	TZ	Nilo FR	38.663	-4.904
T5392	<i>Afrivalus sylvaticus</i>	MVZ:234560	KN	Shimba Hills (Shim 4)	39.341	-4.266
T5393	<i>Afrivalus sylvaticus</i>	MVZ:234561	KN	Shimba Hills (Shim 4)	39.341	-4.266
T4586	<i>Amietia angolensis</i>	no number	TZ	Mgambo F.R.	NULL	NULL
T4587	<i>Amietia angolensis</i>	BM 2002.893	TZ	Mgambo F.R.	38.813	-4.792
T4588	<i>Amietia angolensis</i>	BM 2005.165	TZ	Uluguru Mountains - Kasanga FR	37.774	-7.191
T4589	<i>Amietia angolensis</i>	BM 2005.166	TZ	Uluguru Mountians - Mvuha FR	37.838	-7.179
T4590	<i>Amietia angolensis</i>	BM 2005.167	TZ	Uluguru Mountians - Uluguru Ruvu FR	37.863	-7.008
T5126	<i>Amietia angolensis</i>	MUSE 11034	TZ	Mgeta Hydroelectric Dam	36.091	-8.312
T4463	<i>Sclerophrys brauni</i>	BM 2002.335	TZ	Mlinga Forest Reserve	38.731	-5.061
T4464	<i>Sclerophrys brauni</i>	BM 2000.841	TZ	Kwamgumi FR	38.758	-4.943
T4465	<i>Sclerophrys brauni</i>	BM 2005.112	TZ	Uluguru Mountains - Kasanga FR	37.774	-7.191
T4929	<i>Sclerophrys brauni</i>	MTSN 9511	TZ	Segoma Forest, Camp, East Usambara	38.758	-4.981
T1657	<i>Sclerophrys gutturalis</i>	AC 2933	TZ	Ifakara	36.684	-8.134
T1689	<i>Sclerophrys gutturalis</i>	MTSN 5036	TZ	Handeni	38.032	-5.417
T3029	<i>Sclerophrys gutturalis</i>	CB 13.052	TZ	Lake Rutamba, Lindi, Tanzania	39.462	-10.033
T3063	<i>Sclerophrys gutturalis</i>	CB 13.086	TZ	Makangala FR (edge), Lindi, Tanzania	39.369	-9.982
T3149	<i>Sclerophrys gutturalis</i>	CB 13.172	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3152	<i>Sclerophrys gutturalis</i>	CB 13.175	TZ	Litipo FR, Lindi, Tanzania	39.475	-10.050
T3153	<i>Sclerophrys gutturalis</i>	CB 13.176	TZ	Litipo FR, Lindi, Tanzania	39.475	-10.050
T3154	<i>Sclerophrys gutturalis</i>	CB 13.177	TZ	Litipo FR, Lindi, Tanzania	39.475	-10.050
T3155	<i>Sclerophrys gutturalis</i>	CB 13.178	TZ	Litipo FR, Lindi, Tanzania	39.475	-10.050
T3156	<i>Sclerophrys gutturalis</i>	CB 13.179	TZ	Litipo FR, Lindi, Tanzania	39.475	-10.050
T3159	<i>Sclerophrys gutturalis</i>	CB 13.182	TZ	Litipo FR, Lindi, Tanzania	39.475	-10.050
T3160	<i>Sclerophrys gutturalis</i>	CB 13.183	TZ	Litipo FR, Lindi, Tanzania	39.475	-10.050
T3542	<i>Sclerophrys gutturalis</i>	CB 13.406	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3543	<i>Sclerophrys gutturalis</i>	CB 13.407	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3544	<i>Sclerophrys gutturalis</i>	CB 13.408	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3545	<i>Sclerophrys gutturalis</i>	CB 13.409	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3722	<i>Sclerophrys gutturalis</i>	CB 13.514	TZ	Dar es Salaam (university), Tanzania	39.204	-6.779
T3723	<i>Sclerophrys gutturalis</i>	CB 13.515	TZ	Dar es Salaam (university), Tanzania	39.204	-6.779
T3724	<i>Sclerophrys gutturalis</i>	CB 13.516	TZ	Dar es Salaam (university), Tanzania	39.204	-6.779
T3725	<i>Sclerophrys gutturalis</i>	CB 13.517	TZ	Dar es Salaam (university), Tanzania	39.204	-6.779
T3726	<i>Sclerophrys gutturalis</i>	CB 13.518	TZ	Dar es Salaam (university), Tanzania	39.204	-6.779
T3727	<i>Sclerophrys gutturalis</i>	CB 13.519	TZ	Dar es Salaam (university), Tanzania	39.204	-6.779
T3733	<i>Sclerophrys gutturalis</i>	CB 13.525	TZ	Vikindu FR, Pwani, Tanzania	39.299	-6.990
T3734	<i>Sclerophrys gutturalis</i>	CB 13.526	TZ	Vikindu FR, Pwani, Tanzania	39.299	-6.990
T3735	<i>Sclerophrys gutturalis</i>	CB 13.527	TZ	Vikindu FR, Pwani, Tanzania	39.299	-6.990
T3743	<i>Sclerophrys gutturalis</i>	CB 13.535	TZ	Vikindu FR, Pwani, Tanzania	39.299	-6.990
T4031	<i>Sclerophrys gutturalis</i>	CB 13.681	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T4095	<i>Sclerophrys gutturalis</i>	CB 13.745	TZ	Zaraninge FR, Pwani, Tanzania	38.495	-6.071
T4116	<i>Sclerophrys gutturalis</i>	CB 13.766	TZ	Gendagenda North FR, Tanga, Tanzania	38.646	-5.583
T4117	<i>Sclerophrys gutturalis</i>	CB 13.767	TZ	Gendagenda North FR, Tanga, Tanzania	38.646	-5.583
T4118	<i>Sclerophrys gutturalis</i>	CB 13.768	TZ	Gendagenda North FR, Tanga, Tanzania	38.646	-5.583
T4272	<i>Sclerophrys gutturalis</i>	CB 13.929	TZ	Kilulu, Tanga, Tanzania	39.117	-4.749
T4466	<i>Sclerophrys gutturalis</i>	BM 2002.362	TZ	Kazizumbwi FR	39.055	-6.931
T4467	<i>Sclerophrys gutturalis</i>	BM 2005.928	TZ	Kazizumbwi FR	NULL	NULL
T4468	<i>Sclerophrys gutturalis</i>	BM 2005.1298	TZ	Bombo Forest Reserve	38.703	-4.810
T4469	<i>Sclerophrys gutturalis</i>	BM 2005.1299	TZ	Bombo Forest Reserve	38.708	-4.820
T4470	<i>Sclerophrys gutturalis</i>	BM 2005.1300	TZ	Bombo Forest Reserve	38.681	-4.809
T4471	<i>Sclerophrys gutturalis</i>	BM 2005.113	TZ	Uluguru Mountains - Kasanga FR	37.774	-7.191
T4983	<i>Sclerophrys gutturalis</i>	MCZ A-32006	TZ	Dondwe Forest, near Mvuti	39.097	-7.065
T3051	<i>Sclerophrys pusilla</i>	CB 13.074	TZ	Makangala FR (edge), Lindi, Tanzania	39.369	-9.982
T3056	<i>Sclerophrys pusilla</i>	CB 13.079	TZ	Makangala FR (edge), Lindi, Tanzania	39.369	-9.982
T3057	<i>Sclerophrys pusilla</i>	CB 13.080	TZ	Makangala FR (edge), Lindi, Tanzania	39.369	-9.982
T3058	<i>Sclerophrys pusilla</i>	CB 13.081	TZ	Makangala FR (edge), Lindi, Tanzania	39.369	-9.982
T3064	<i>Sclerophrys pusilla</i>	CB 13.087	TZ	Makangala FR (edge), Lindi, Tanzania	39.369	-9.982
T3065	<i>Sclerophrys pusilla</i>	CB 13.088	TZ	Makangala FR (edge), Lindi, Tanzania	39.369	-9.982
T3150	<i>Sclerophrys pusilla</i>	CB 13.173	TZ	Makangala FR, Lindi, Tanzania	39.405	-9.987

T3169	<i>Sclerophrys pusilla</i>	CB 13.192	TZ	Litipo FR, Lindi, Tanzania	39.475	-10.050
T3175	<i>Sclerophrys pusilla</i>	CB 13.198	TZ	Litipo FR, Lindi, Tanzania	39.475	-10.050
T3180	<i>Sclerophrys pusilla</i>	CB 13.203	TZ	Litipo FR, Lindi, Tanzania	39.475	-10.050
T3181	<i>Sclerophrys pusilla</i>	CB 13.204	TZ	Litipo FR, Lindi, Tanzania	39.475	-10.050
T3300	<i>Sclerophrys pusilla</i>	CB 13.307	TZ	Makangaga FR, Lindi, Tanzania	39.292	-9.495
T4119	<i>Sclerophrys pusilla</i>	CB 13.769	TZ	Amboni caves, Tanga, Tanzania	39.048	-5.073
T4125	<i>Sclerophrys pusilla</i>	CB 13.775	TZ	Amboni caves, Tanga, Tanzania	39.048	-5.073
T4127	<i>Sclerophrys pusilla</i>	CB 13.777	TZ	Amboni caves, Tanga, Tanzania	39.048	-5.073
T4188	<i>Sclerophrys pusilla</i>	CB 13.838	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4398	<i>Sclerophrys pusilla</i>	MTSN 5446	TZ	Mikeregembe	NULL	NULL
T4400	<i>Sclerophrys pusilla</i>	MTSN 8123	TZ	Ruipa, Ranger post	37.035	-9.169
T4476	<i>Sclerophrys pusilla</i>	BM 2002.336	TZ	Mlinga Forest Reserve	38.751	-5.054
T4477	<i>Sclerophrys pusilla</i>	BM 2000.846	TZ	Kwamgumi FR	38.727	-4.950
T4478	<i>Sclerophrys pusilla</i>	BM 2002.853	TZ	Mgambo F.R.	38.814	-4.791
T4479	<i>Sclerophrys pusilla</i>	BM 2005.115	TZ	Uluguru Mountians - Uluguru Ruvu FR	37.863	-7.008
T4480	<i>Sclerophrys pusilla</i>	BM 2005.114	TZ	Uluguru Mountians - Uluguru Ruvu FR	37.750	-6.979
T4984	<i>Sclerophrys pusilla</i>	MCZ A-32195	TZ	Hondo Hondo Lodge, Udzungwa	36.884	-7.856
T5127	<i>Sclerophrys pusilla</i>	MUSE 11035	TZ	Mgeta Hydroelectric Dam	36.091	-8.312
T5128	<i>Sclerophrys pusilla</i>	MUSE 11036	TZ	Mgeta Hydroelectric Dam	36.091	-8.312
T5131	<i>Sclerophrys pusilla</i>	MUSE 11039	TZ	Mgeta Hydroelectric Dam	36.091	-8.312
T5141	<i>Sclerophrys pusilla</i>	MUSE 11049	TZ	Mgeta Hydroelectric Dam	36.091	-8.312
T4474	<i>Sclerophrys xeros</i>	BM 2005.896	TZ	Mkomazi GR (Ibaya hill)	NULL	NULL
T4475	<i>Sclerophrys xeros</i>	BM 2005.897	TZ	Mkomazi GR (Ibaya hill)	NULL	NULL
T4482	<i>Sclerophrys xeros</i>	BM 2002.395	TZ	Ruvu South FR	38.814	-6.909
T4404	<i>Arthroleptides cf. yakusini</i>	MTSN 8382	TZ	Kanga FR	37.724	-5.960
T4429	<i>Arthroleptides martiensseni</i>	BM 2002.320	TZ	Mlinga Forest Reserve	38.752	-5.058
T4430	<i>Arthroleptides martiensseni</i>	BM 2002.321	TZ	Mlinga Forest Reserve	38.752	-5.058
T4431	<i>Arthroleptides martiensseni</i>	BM 2002.322	TZ	Mlinga Forest Reserve	38.748	-5.059
T4432	<i>Arthroleptides martiensseni</i>	BM 2000.826	TZ	Kwamgumi FR	38.751	-4.921
T4433	<i>Arthroleptides martiensseni</i>	BM 2002.804	TZ	Mgambo F.R.	38.811	-4.793
T4434	<i>Arthroleptides martiensseni</i>	BM 2002.574	TZ	Nilo FR	38.673	-4.904
T4435	<i>Arthroleptides martiensseni</i>	BM 2002.577	TZ	Nilo FR	38.643	-4.955
T4436	<i>Arthroleptides martiensseni</i>	BM 2002.578	TZ	Nilo FR	NULL	NULL
T4437	<i>Arthroleptides yakusini</i>	BM 2005.012	TZ	Uluguru Mountains - Kasanga FR	37.774	-7.191
T4438	<i>Arthroleptides yakusini</i>	BM 2005.013	TZ	Uluguru Mountains - Kasanga FR	37.774	-7.191
T4439	<i>Arthroleptides yakusini</i>	BM 2005.014	TZ	Uluguru Mountains - Kasanga FR	37.774	-7.191
T5130	<i>Arthroleptides yakusini</i>	MUSE 11038	TZ	Mgeta Hydroelectric Dam	36.091	-8.312
T5132	<i>Arthroleptides yakusini</i>	MUSE 11040	TZ	Mgeta Hydroelectric Dam	36.091	-8.312
T5133	<i>Arthroleptides yakusini</i>	MUSE 11041	TZ	Mgeta Hydroelectric Dam	36.091	-8.312
T5134	<i>Arthroleptides yakusini</i>	MUSE 11042	TZ	Mgeta Hydroelectric Dam	36.091	-8.312
T5139	<i>Arthroleptides yakusini</i>	MUSE 11047	TZ	Mgeta Hydroelectric Dam	36.091	-8.312
T5140	<i>Arthroleptides yakusini</i>	MUSE 11048	TZ	Mgeta Hydroelectric Dam	36.091	-8.312
T636	<i>Arthroleptides yakusini</i>	MTSN 5679	TZ	Sanje	36.911	-7.772
T5018	<i>Arthroleptis affinis</i>	MTSN 8348	TZ	Kanga FR	37.724	-5.960
T5019	<i>Arthroleptis affinis</i>	MTSN 8369	TZ	Kanga FR	37.724	-5.960
T2444	<i>Arthroleptis cf. affinis</i>	MTSN 7721	TZ	Kimboza Forest	37.802	-7.002
T5027	<i>Arthroleptis sp.</i>	BM 2000.891	TZ	Kilombero Valley	NULL	NULL
T5028	<i>Arthroleptis sp.</i>	BM 2000.892	TZ	Kilombero Valley	NULL	NULL
T5029	<i>Arthroleptis sp.</i>	BM 2000.893	TZ	Kilombero Valley	NULL	NULL
T2318	<i>Arthroleptis stenodactylus</i>	BM 2002.593	TZ	Nilo FR	38.693	-4.928
T2319	<i>Arthroleptis stenodactylus</i>	BM 2002.594	TZ	Nilo FR	38.651	-4.863
T2322	<i>Arthroleptis stenodactylus</i>	BM 2005.033	TZ	Uluguru Mountains	37.774	-7.191
T2323	<i>Arthroleptis stenodactylus</i>	BM 2005.034	TZ	Uluguru Mountains	37.774	-7.191
T2324	<i>Arthroleptis stenodactylus</i>	BM 2005.035	TZ	Uluguru Mountains	37.759	-6.979
T2326	<i>Arthroleptis stenodactylus</i>	BM 2005.037	TZ	Uluguru Mountains	37.838	-7.179
T2327	<i>Arthroleptis stenodactylus</i>	BM 2005.038	TZ	Uluguru Mountains	37.838	-7.179
T2328	<i>Arthroleptis stenodactylus</i>	BM 2005.042	TZ	Uluguru Mountains	37.764	-6.985
T2334	<i>Arthroleptis stenodactylus</i>	BM 2005.923	TZ	Kazizumbwi FR	39.062	-6.955
T2540	<i>Arthroleptis stenodactylus</i>	AC 1265	TZ	Zaraninge	38.608	-6.137
T2541	<i>Arthroleptis stenodactylus</i>	AC 1266	TZ	Zaraninge	38.608	-6.137
T2991	<i>Arthroleptis stenodactylus</i>	CB 13.002	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3143	<i>Arthroleptis stenodactylus</i>	CB 13.166	TZ	Makangala FR, Lindi, Tanzania	39.387	-9.990

T3253	<i>Arthroleptis stenodactylus</i>	CB 13.261	TZ	Rondo Forest, Lindi, Tanzania	39.200	-10.119
T3255	<i>Arthroleptis stenodactylus</i>	CB 13.262	TZ	Rondo Forest, Lindi, Tanzania	39.199	-10.119
T3256	<i>Arthroleptis stenodactylus</i>	CB 13.263	TZ	Rondo Forest, Lindi, Tanzania	39.178	-10.118
T3257	<i>Arthroleptis stenodactylus</i>	CB 13.264	TZ	Rondo Forest, Lindi, Tanzania	39.178	-10.118
T3258	<i>Arthroleptis stenodactylus</i>	CB 13.265	TZ	Rondo Forest, Lindi, Tanzania	39.178	-10.118
T3259	<i>Arthroleptis stenodactylus</i>	CB 13.266	TZ	Rondo Forest, Lindi, Tanzania	39.178	-10.118
T4269	<i>Arthroleptis stenodactylus</i>	CB 13.923	TZ	Kilulu, Tanga, Tanzania	39.130	-4.765
T4287	<i>Arthroleptis stenodactylus</i>	AC 1265	TZ	Zaraninge Forest	NULL	NULL
T4288	<i>Arthroleptis stenodactylus</i>	AC 1266	TZ	Zaraninge Forest	NULL	NULL
T4440	<i>Arthroleptis stenodactylus</i>	BM 2002.379	TZ	Ruvu South FR	38.814	-6.909
T4441	<i>Arthroleptis stenodactylus</i>	BM 2002.383	TZ	Ruvu South FR	38.814	-6.909
T4442	<i>Arthroleptis stenodactylus</i>	BM 2002.357	TZ	Kazizumbwi FR	39.053	-6.932
T4443	<i>Arthroleptis stenodactylus</i>	BM 2005.918	TZ	Kazizumbwi FR	39.053	-6.943
T4444	<i>Arthroleptis stenodactylus</i>	BM 2000.894	TZ	Kilombero Valley	NULL	NULL
T4445	<i>Arthroleptis stenodactylus</i>	BM 2000.908	TZ	Kilombero Valley	NULL	NULL
T4446	<i>Arthroleptis stenodactylus</i>	BM 2000.829	TZ	Kwangumi FR	NULL	NULL
T4447	<i>Arthroleptis stenodactylus</i>	BM 2000.830	TZ	Kwangumi FR	NULL	NULL
T4448	<i>Arthroleptis stenodactylus</i>	BM 2000.831	TZ	Kwangumi FR	NULL	NULL
T4449	<i>Arthroleptis stenodactylus</i>	BM 2002.547	TZ	Namakutwa FR	NULL	NULL
T4450	<i>Arthroleptis stenodactylus</i>	BM 2002.595	TZ	Nilo FR	38.663	-4.908
T4451	<i>Arthroleptis stenodactylus</i>	BM 2005.1321	TZ	Bombo Forest Reserve	38.681	-4.809
T4452	<i>Arthroleptis stenodactylus</i>	BM 2005.1322	TZ	Bombo Forest Reserve	38.681	-4.809
T4453	<i>Arthroleptis stenodactylus</i>	BM 2005.032	TZ	Uluguru Mountains - Kasanga FR	37.774	-7.191
T4454	<i>Arthroleptis stenodactylus</i>	BM 2005.039	TZ	Uluguru Mountians - Mvuha FR	37.838	-7.179
T4455	<i>Arthroleptis stenodactylus</i>	BM 2005.040	TZ	Uluguru Mountians - Mvuha FR	37.838	-7.179
T4456	<i>Arthroleptis stenodactylus</i>	BM 2005.041	TZ	Uluguru Mountians - Mvuha FR	37.837	-7.180
T4457	<i>Arthroleptis stenodactylus</i>	BM 2005.045	TZ	Uluguru Mountians - Uluguru Ruvu FR	37.863	-7.008
T4458	<i>Arthroleptis stenodactylus</i>	BM 2005.046	TZ	Uluguru Mountians - Uluguru Ruvu FR	37.863	-7.008
T4802	<i>Arthroleptis stenodactylus</i>	?_multiple_07	TZ	Rondo plateau	NULL	NULL
T4803	<i>Arthroleptis stenodactylus</i>	?_multiple_08	TZ	Mbarawala	NULL	NULL
T4930	<i>Arthroleptis stenodactylus</i>	MTSN 9512	TZ	Segoma Forest, Camp, East Usambara	38.758	-4.981
T4933	<i>Arthroleptis stenodactylus</i>	MTSN 9515	TZ	Segoma Forest, Camp, East Usambara	38.758	-4.981
T4934	<i>Arthroleptis stenodactylus</i>	MTSN 9516	TZ	Segoma Forest, Camp, East Usambara	38.758	-4.981
T4939	<i>Arthroleptis stenodactylus</i>	MTSN 9525	TZ	Segoma Forest, Camp, East Usambara	38.758	-4.981
T4940	<i>Arthroleptis stenodactylus</i>	MTSN 9526	TZ	Segoma Forest, Camp, East Usambara	38.758	-4.981
T4943	<i>Arthroleptis stenodactylus</i>	MTSN 9529	TZ	Segoma Forest, Camp, East Usambara	38.758	-4.981
T4945	<i>Arthroleptis stenodactylus</i>	MTSN 9535	TZ	Segoma Forest, Camp, East Usambara	38.762	-4.976
T4946	<i>Arthroleptis stenodactylus</i>	MTSN 9536	TZ	Segoma Forest, Camp, East Usambara	38.762	-4.976
T4950	<i>Arthroleptis stenodactylus</i>	MTSN 9540	TZ	Segoma Forest, Camp, East Usambara	38.762	-4.976
T4964	<i>Arthroleptis stenodactylus</i>	MTSN 9556	TZ	Segoma Forest, Camp, East Usambara	38.762	-4.976
T5402	<i>Arthroleptis stenodactylus</i>	MVZ:233788	TZ			
T2720	<i>Arthroleptis stenodactylus</i>	MCZ 148779	TZ	Dar es Salaam, Dondwe Forest	39.097	-7.064
T2722	<i>Arthroleptis stenodactylus</i>	MCZ 148794	TZ	Lindi, Rondo Forest	39.178	-10.118
T2723	<i>Arthroleptis stenodactylus</i>	MCZ 148801	TZ	Lindi, Rondo Forest	39.178	-10.118
T2726	<i>Arthroleptis stenodactylus</i>	MCZ 148817	TZ	Lindi, Rondo Forest	39.178	-10.118
T2727	<i>Arthroleptis stenodactylus</i>	MCZ 148832	TZ	Dar es Salaam, Dondwe Forest	39.097	-7.064
T2728	<i>Arthroleptis stenodactylus</i>	MCZ 148833	TZ	Dar es Salaam, Dondwe Forest	39.097	-7.064
T2732	<i>Arthroleptis stenodactylus</i>	MCZ 148848	TZ	Tanga, Mafi Hill	38.141	-4.923
T2733	<i>Arthroleptis stenodactylus</i>	MCZ 148849	TZ	Tanga, Mafi Hill	38.141	-4.923
T2734	<i>Arthroleptis stenodactylus</i>	MCZ 148850	TZ	Tanga, Mafi Hill	38.141	-4.923
T5142	<i>Arthroleptis stenodactylus</i>	MUSE 11050	TZ	Mgeta Hydroelectric Dam	36.091	-8.312
T4783	<i>Arthroleptis tanneri</i>	no number	MZ	Mnt Mabu	36.588	-16.313
T2418	<i>Arthroleptis xenodactyloides</i>	MTSN 5680	TZ	Sanje	36.911	-7.772
T2441	<i>Arthroleptis xenodactyloides</i>	MTSN 7516	TZ	Segoma FR, East Usambara	38.761	-4.976
T2442	<i>Arthroleptis xenodactyloides</i>	MTSN 7681	TZ	Kimboza Forest	37.802	-7.002
T2443	<i>Arthroleptis xenodactyloides</i>	MTSN 7710	TZ	Kimboza Forest	37.802	-7.002
T2721	<i>Arthroleptis xenodactyloides</i>	MCZ 148791	TZ	Lindi, Rondo Forest	39.178	-10.118
T2724	<i>Arthroleptis xenodactyloides</i>	MCZ 148802	TZ	Lindi, Rondo Forest	39.178	-10.118
T2725	<i>Arthroleptis xenodactyloides</i>	MCZ 148803	TZ	Lindi, Rondo Forest	39.178	-10.118
T2729	<i>Arthroleptis xenodactyloides</i>	MCZ 148840	TZ	Tanga, Mafi Hill	38.141	-4.923
T2730	<i>Arthroleptis xenodactyloides</i>	MCZ 148841	TZ	Tanga, Mafi Hill	38.141	-4.923
T2731	<i>Arthroleptis xenodactyloides</i>	MCZ 148842	TZ	Tanga, Mafi Hill	38.141	-4.923

T4187	<i>Arthroleptis xenodactyloides</i>	CB 13.837	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4201	<i>Arthroleptis xenodactyloides</i>	CB 13.851	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4202	<i>Arthroleptis xenodactyloides</i>	CB 13.852	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4203	<i>Arthroleptis xenodactyloides</i>	CB 13.853	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4461	<i>Arthroleptis xenodactyloides</i>	BM 2002.851	TZ	Mgambo F.R.	38.813	-4.792
T4775	<i>Arthroleptis xenodactyloides</i>	WC-DNA-1148	MZ	between two inselbergs along Mecuburi	38.849	-14.700
T4776	<i>Arthroleptis xenodactyloides</i>	WC-DNA-1149	MZ	between two inselbergs along Mecuburi	NULL	NULL
T4777	<i>Arthroleptis xenodactyloides</i>	WC-DNA-1151	MZ	between two inselbergs along Mecuburi	38.849	-14.700
T4778	<i>Arthroleptis xenodactyloides</i>	WC-DNA-1152	MZ	between two inselbergs along Mecuburi	38.849	-14.700
T4779	<i>Arthroleptis xenodactyloides</i>	WC-DNA-1059	MZ	Montepuez river near Chiefs house	38.709	-13.318
T4780	<i>Arthroleptis xenodactyloides</i>	WC-DNA-1061	MZ	Montepuez river near Chiefs house	38.709	-13.318
T4781	<i>Arthroleptis xenodactyloides</i>	WC-DNA-1062	MZ	Montepuez river near Chiefs house	38.709	-13.318
T4782	<i>Arthroleptis xenodactyloides</i>	WC-DNA-1078	MZ	Montepuez river near Chiefs house	38.709	-13.318
T5016	<i>Arthroleptis xenodactyloides</i>	MTSN 8446	TZ	Mgeta	36.087	-8.339
T5017	<i>Arthroleptis xenodactyloides</i>	MTSN 8460	TZ	Mgeta	36.087	-8.339
T5030	<i>Arthroleptis xenodactyloides</i>	BM 2002.360	TZ	Kazizumbwi FR	39.053	-6.932
T5031	<i>Arthroleptis xenodactyloides</i>	BM 2002.361	TZ	Kazizumbwi FR	39.053	-6.932
T5032	<i>Arthroleptis xenodactyloides</i>	BM 2005.924	TZ	Kazizumbwi FR	39.073	-6.977
T5033	<i>Arthroleptis xenodactyloides</i>	BM 2005.925	TZ	Kazizumbwi FR	39.073	-6.977
T5034	<i>Arthroleptis xenodactyloides</i>	BM 2005.926	TZ	Kazizumbwi FR	39.053	-6.943
T5035	<i>Arthroleptis xenodactyloides</i>	BM 2000.930	TZ	Kilombero Valley	NULL	NULL
T5036	<i>Arthroleptis xenodactyloides</i>	BM 2000.951	TZ	Kilombero Valley	NULL	NULL
T5037	<i>Arthroleptis xenodactyloides</i>	BM 2000.925	TZ	Kilombero Valley	NULL	NULL
T5038	<i>Arthroleptis xenodactyloides</i>	BM 2000.944	TZ	Kilombero Valley	NULL	NULL
T5039	<i>Arthroleptis xenodactyloides</i>	BM 2000.926	TZ	Kilombero Valley	NULL	NULL
T5040	<i>Arthroleptis xenodactyloides</i>	BM 2002.325	TZ	Mlinga Forest Reserve	38.752	-5.058
T5041	<i>Arthroleptis xenodactyloides</i>	BM 2002.326	TZ	Mlinga Forest Reserve	38.748	-5.059
T5042	<i>Arthroleptis xenodactyloides</i>	BM 2002.327	TZ	Mlinga Forest Reserve	38.748	-5.059
T5043	<i>Arthroleptis xenodactyloides</i>	BM 2002.328	TZ	Mlinga Forest Reserve	38.748	-5.059
T5044	<i>Arthroleptis xenodactyloides</i>	BM 2002.329	TZ	Mlinga Forest Reserve	38.748	-5.059
T5045	<i>Arthroleptis xenodactyloides</i>	BM 2000.835	TZ	Kwangumi FR	NULL	NULL
T5046	<i>Arthroleptis xenodactyloides</i>	BM 2000.836	TZ	Kwangumi FR	NULL	NULL
T5047	<i>Arthroleptis xenodactyloides</i>	BM 2000.837	TZ	Kwangumi FR	NULL	NULL
T5048	<i>Arthroleptis xenodactyloides</i>	BM 2000.838	TZ	Kwangumi FR	NULL	NULL
T5049	<i>Arthroleptis xenodactyloides</i>	BM 2000.840	TZ	Kwangumi FR	38.751	-4.921
T5050	<i>Arthroleptis xenodactyloides</i>	BM 2002.883	TZ	Mgambo F.R.	38.813	-4.792
T5051	<i>Arthroleptis xenodactyloides</i>	BM 2002.884	TZ	Mgambo F.R.	38.813	-4.792
T5052	<i>Arthroleptis xenodactyloides</i>	BM 2002.885	TZ	Mgambo F.R.	38.813	-4.792
T5053	<i>Arthroleptis xenodactyloides</i>	BM 2002.886	TZ	Mgambo F.R.	38.813	-4.792
T5054	<i>Arthroleptis xenodactyloides</i>	BM 2002.888	TZ	Mgambo F.R.	38.813	-4.792
T5055	<i>Arthroleptis xenodactyloides</i>	BM 2002.597	TZ	Nilo FR	38.693	-4.928
T5056	<i>Arthroleptis xenodactyloides</i>	BM 2002.598	TZ	Nilo FR	38.665	-4.911
T5057	<i>Arthroleptis xenodactyloides</i>	BM 2002.599	TZ	Nilo FR	38.663	-4.908
T5058	<i>Arthroleptis xenodactyloides</i>	BM 2002.600	TZ	Nilo FR	38.659	-4.944
T5059	<i>Arthroleptis xenodactyloides</i>	BM 2002.601	TZ	Nilo FR	38.659	-4.944
T5060	<i>Arthroleptis xenodactyloides</i>	BM 2005.078	TZ	Uluguru Mountains - Kasanga FR	37.774	-7.191
T5061	<i>Arthroleptis xenodactyloides</i>	BM 2005.079	TZ	Uluguru Mountains - Mangala FR	37.759	-6.979
T5062	<i>Arthroleptis xenodactyloides</i>	BM 2005.080	TZ	Uluguru Mountians - Milawilia FR	37.750	-6.979
T5063	<i>Arthroleptis xenodactyloides</i>	BM 2005.081	TZ	Uluguru Mountains - Mkungwe FR	37.915	-6.869
T5064	<i>Arthroleptis xenodactyloides</i>	BM 2005.082	TZ	Uluguru Mountains	37.915	-6.869
T5065	<i>Arthroleptis xenodactyloides</i>	BM 2005.083	TZ	Uluguru Mountains - Mvuha FR	37.838	-7.179
T5066	<i>Arthroleptis xenodactyloides</i>	BM 2005.085	TZ	Uluguru Mountains	37.838	-7.179
T5067	<i>Arthroleptis xenodactyloides</i>	BM 2005.086	TZ	Uluguru Mountains - Ngambaula FR	37.764	-6.985
T5068	<i>Arthroleptis xenodactyloides</i>	BM 2005.087	TZ	Uluguru Mountians - Uluguru Ruvu FR	37.863	-7.008
T5069	<i>Arthroleptis xenodactyloides</i>	BM 2005.088	TZ	Uluguru Mountians - Uluguru Ruvu FR	37.863	-7.008
T5106	<i>Arthroleptis xenodactyloides</i>	MUSE 11056	TZ	Mgeta Hydroelectric Dam	-	-
T5107	<i>Arthroleptis xenodactyloides</i>	MUSE 11057	TZ	Mgeta Hydroelectric Dam	-	-
T5108	<i>Arthroleptis xenodactyloides</i>	MUSE 11059	TZ	Mgeta Hydroelectric Dam	36.091	-8.312
T5109	<i>Arthroleptis xenodactyloides</i>	MUSE 11058	TZ	Mgeta Hydroelectric Dam	36.091	-8.312
T5385	<i>Arthroleptis xenodactyloides</i>	MVZ 265870	MZ	Serra Jeci Midway Forest Island		
T5386	<i>Arthroleptis xenodactyloides</i>	MVZ 265871	MZ	Serra Jeci Midway Forest Island	35.181	-12.849
T5387	<i>Arthroleptis xenodactyloides</i>	MVZ 265872	MZ	Serra Jeci Drainage Forest, streamside	35.178	-12.844

T5388	<i>Arthroleptis xenodactyloides</i>	DMP 208	MZ	Serra Jeci water forest	35.178	-12.851
T4941	<i>Arthroleptis xenodactyloides</i>	MTSN 9527	TZ	Segoma Forest, Camp, East Usambara	38.758	-4.981
T4953	<i>Arthroleptis xenodactyloides</i>	MTSN 9543	TZ	Segoma Forest, Camp, East Usambara	38.762	-4.976
T4967	<i>Arthroleptis xenodactyloides</i>	MTSN 9560	TZ	Segoma Forest, Camp, East Usambara	38.762	-4.976
T4975	<i>Arthroleptis xenodactyloides</i>	MTSN 9569	TZ	Kwangumi Forest Reserve, East Usambara	38.737	-4.972
T4459	<i>Arthroleptis xenodactylus</i>	BM 2002.611	TZ	Nilo FR	38.663	-4.908
T4460	<i>Arthroleptis xenodactylus</i>	BM 2002.612	TZ	Nilo FR	38.643	-4.955
T5015	<i>Arthroleptis xenodactylus</i>	MTSN 8373	TZ	Kanga FR	37.724	-5.960
T4971	<i>Boulengerula boulengeri</i>	MTSN 9564	TZ	Segoma Forest, Camp, East Usambara	38.762	-4.976
T4972	<i>Boulengerula boulengeri</i>	MTSN 9565	TZ	Segoma Forest, Camp, East Usambara	38.762	-4.976
T243	<i>Boulengerula changamwensis</i>	KMH 23345	TZ	Kazizumbwi	39.033	-6.933
T1931	<i>Breviceps mossambicus</i>	MCZ 32076	TZ	Rondo Plateau	39.205	-10.144
T4601	<i>Breviceps mossambicus</i>	ENI 31	MZ	Cabo Delgado, Mozambique	39.321	-12.334
T4602	<i>Breviceps mossambicus</i>	WC-DNA-1363	MZ	Coastal dry forest, Mozambique	40.404	-12.767
T4603	<i>Breviceps mossambicus</i>	WC-DNA-1405	MZ	Coastal dry forest, Mozambique	40.404	-12.767
T4462	<i>Breviceps mossambicus</i>	BM 2005.927	TZ	Kazizumbwi FR	39.055	-6.931
T4800	<i>Breviceps sp.</i>	?_multiple_05	TZ	RONDO PLATEAU	NULL	NULL
T3185	<i>Chiromantis xerampelina</i>	CB 13.208	TZ	Noto Plateau, Lindi, Tanzania	39.374	-9.895
T3186	<i>Chiromantis xerampelina</i>	CB 13.209	TZ	Noto Plateau, Lindi, Tanzania	39.374	-9.895
T3187	<i>Chiromantis xerampelina</i>	CB 13.210	TZ	Noto Plateau, Lindi, Tanzania	39.374	-9.895
T3188	<i>Chiromantis xerampelina</i>	CB 13.211	TZ	Noto Plateau, Lindi, Tanzania	39.374	-9.895
T3207	<i>Chiromantis xerampelina</i>	CB 13.230	TZ	Noto Plateau, Lindi, Tanzania	39.374	-9.895
T3208	<i>Chiromantis xerampelina</i>	CB 13.231	TZ	Noto Plateau, Lindi, Tanzania	39.374	-9.895
T3209	<i>Chiromantis xerampelina</i>	CB 13.232	TZ	Noto Plateau, Lindi, Tanzania	39.374	-9.895
T3260	<i>Chiromantis xerampelina</i>	CB 13.267	TZ	Rondo Forest, Lindi, Tanzania	39.197	-10.121
T3261	<i>Chiromantis xerampelina</i>	CB 13.268	TZ	Rondo Forest, Lindi, Tanzania	39.197	-10.121
T3262	<i>Chiromantis xerampelina</i>	CB 13.269	TZ	Rondo Forest, Lindi, Tanzania	39.197	-10.121
T3263	<i>Chiromantis xerampelina</i>	CB 13.270	TZ	Rondo Forest, Lindi, Tanzania	39.197	-10.121
T3264	<i>Chiromantis xerampelina</i>	CB 13.271	TZ	Rondo Forest, Lindi, Tanzania	39.197	-10.121
T3266	<i>Chiromantis xerampelina</i>	CB 13.273	TZ	Rondo Forest, Lindi, Tanzania	39.197	-10.121
T3267	<i>Chiromantis xerampelina</i>	CB 13.274	TZ	Namatimbili FR, Lindi, Tanzania	39.238	-9.111
T3275	<i>Chiromantis xerampelina</i>	CB 13.282	TZ	Rondo Forest, Lindi, Tanzania	39.197	-10.121
T3276	<i>Chiromantis xerampelina</i>	CB 13.283	TZ	Rondo Forest, Lindi, Tanzania	39.197	-10.121
T3277	<i>Chiromantis xerampelina</i>	CB 13.284	TZ	Rondo Forest, Lindi, Tanzania	39.197	-10.121
T3278	<i>Chiromantis xerampelina</i>	CB 13.285	TZ	Rondo Forest, Lindi, Tanzania	39.197	-10.121
T3279	<i>Chiromantis xerampelina</i>	CB 13.286	TZ	Rondo Forest, Lindi, Tanzania	39.197	-10.121
T3284	<i>Chiromantis xerampelina</i>	CB 13.291	TZ	Makangaga FR, Lindi, Tanzania	39.292	-9.495
T3285	<i>Chiromantis xerampelina</i>	CB 13.292	TZ	Makangaga FR, Lindi, Tanzania	39.292	-9.495
T3286	<i>Chiromantis xerampelina</i>	CB 13.293	TZ	Makangaga FR, Lindi, Tanzania	39.292	-9.495
T3287	<i>Chiromantis xerampelina</i>	CB 13.294	TZ	Makangaga FR, Lindi, Tanzania	39.292	-9.495
T3288	<i>Chiromantis xerampelina</i>	CB 13.295	TZ	Makangaga FR, Lindi, Tanzania	39.292	-9.495
T3289	<i>Chiromantis xerampelina</i>	CB 13.296	TZ	Makangaga FR, Lindi, Tanzania	39.292	-9.495
T3311	<i>Chiromantis xerampelina</i>	CB 13.318	TZ	Makangaga FR, Lindi, Tanzania	39.292	-9.495
T3425	<i>Chiromantis xerampelina</i>	CB 13.336	TZ	Nyamute FR, Pwani, Tanzania	39.034	-8.326
T3426	<i>Chiromantis xerampelina</i>	CB 13.337	TZ	Nyamute FR, Pwani, Tanzania	39.034	-8.326
T3433	<i>Chiromantis xerampelina</i>	CB 13.344	TZ	Nyamute FR, Pwani, Tanzania	39.034	-8.326
T3437	<i>Chiromantis xerampelina</i>	CB 13.348	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3438	<i>Chiromantis xerampelina</i>	CB 13.349	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3439	<i>Chiromantis xerampelina</i>	CB 13.350	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3440	<i>Chiromantis xerampelina</i>	CB 13.351	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3441	<i>Chiromantis xerampelina</i>	CB 13.352	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3442	<i>Chiromantis xerampelina</i>	CB 13.353	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3451	<i>Chiromantis xerampelina</i>	CB 13.362	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3454	<i>Chiromantis xerampelina</i>	CB 13.365	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3455	<i>Chiromantis xerampelina</i>	CB 13.366	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3456	<i>Chiromantis xerampelina</i>	CB 13.367	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3457	<i>Chiromantis xerampelina</i>	CB 13.368	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3458	<i>Chiromantis xerampelina</i>	CB 13.369	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3459	<i>Chiromantis xerampelina</i>	CB 13.370	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3460	<i>Chiromantis xerampelina</i>	CB 13.371	TZ	Kiwengoma FR, Pwani, Tanzania	NULL	NULL
T3461	<i>Chiromantis xerampelina</i>	CB 13.372	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3462	<i>Chiromantis xerampelina</i>	CB 13.373	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304

T3463	<i>Chiromantis xerampelina</i>	CB 13.374	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3464	<i>Chiromantis xerampelina</i>	CB 13.375	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3465	<i>Chiromantis xerampelina</i>	CB 13.376	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3466	<i>Chiromantis xerampelina</i>	CB 13.377	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3467	<i>Chiromantis xerampelina</i>	CB 13.378	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3556	<i>Chiromantis xerampelina</i>	CB 13.420	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3557	<i>Chiromantis xerampelina</i>	CB 13.421	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3642	<i>Chiromantis xerampelina</i>	CB 13.434	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3656	<i>Chiromantis xerampelina</i>	CB 13.448	TZ	Ruawa FR, Lindi, Tanzania	39.569	-9.730
T3657	<i>Chiromantis xerampelina</i>	CB 13.449	TZ	Ruawa FR, Lindi, Tanzania	39.569	-9.730
T3658	<i>Chiromantis xerampelina</i>	CB 13.450	TZ	Ruawa FR, Lindi, Tanzania	39.569	-9.730
T3662	<i>Chiromantis xerampelina</i>	CB 13.454	TZ	Ruawa FR, Lindi, Tanzania	39.579	-9.746
T3663	<i>Chiromantis xerampelina</i>	CB 13.455	TZ	Ruawa FR, Lindi, Tanzania	39.579	-9.746
T3664	<i>Chiromantis xerampelina</i>	CB 13.456	TZ	Ruawa FR, Lindi, Tanzania	39.579	-9.746
T3665	<i>Chiromantis xerampelina</i>	CB 13.457	TZ	Ruawa FR, Lindi, Tanzania	39.579	-9.746
T3666	<i>Chiromantis xerampelina</i>	CB 13.458	TZ	Ruawa FR, Lindi, Tanzania	39.579	-9.746
T3667	<i>Chiromantis xerampelina</i>	CB 13.459	TZ	Ruawa FR, Lindi, Tanzania	39.579	-9.746
T3672	<i>Chiromantis xerampelina</i>	CB 13.464	TZ	Ruawa FR, Lindi, Tanzania	39.569	-9.730
T4102	<i>Chiromantis xerampelina</i>	CB 13.752	TZ	Gendagenda North FR, Tanga, Tanzania	38.645	-5.583
T4103	<i>Chiromantis xerampelina</i>	CB 13.753	TZ	Gendagenda North FR, Tanga, Tanzania	38.646	-5.583
T4104	<i>Chiromantis xerampelina</i>	CB 13.754	TZ	Gendagenda North FR, Tanga, Tanzania	38.646	-5.583
T4105	<i>Chiromantis xerampelina</i>	CB 13.755	TZ	Gendagenda North FR, Tanga, Tanzania	38.646	-5.583
T4106	<i>Chiromantis xerampelina</i>	CB 13.756	TZ	Gendagenda North FR, Tanga, Tanzania	38.646	-5.583
T4107	<i>Chiromantis xerampelina</i>	CB 13.757	TZ	Gendagenda North FR, Tanga, Tanzania	38.646	-5.583
T4108	<i>Chiromantis xerampelina</i>	CB 13.758	TZ	Gendagenda North FR, Tanga, Tanzania	38.646	-5.583
T4109	<i>Chiromantis xerampelina</i>	CB 13.759	TZ	Gendagenda North FR, Tanga, Tanzania	38.646	-5.583
T4110	<i>Chiromantis xerampelina</i>	CB 13.760	TZ	Gendagenda North FR, Tanga, Tanzania	38.646	-5.583
T4111	<i>Chiromantis xerampelina</i>	CB 13.761	TZ	Gendagenda North FR, Tanga, Tanzania	38.646	-5.583
T4112	<i>Chiromantis xerampelina</i>	CB 13.762	TZ	Gendagenda North FR, Tanga, Tanzania	38.646	-5.583
T4113	<i>Chiromantis xerampelina</i>	CB 13.763	TZ	Gendagenda North FR, Tanga, Tanzania	38.646	-5.583
T4262	<i>Chiromantis xerampelina</i>	CB 13.915	TZ	Kilulu, Tanga, Tanzania	39.117	-4.749
T4263	<i>Chiromantis xerampelina</i>	CB 13.916	TZ	Kilulu, Tanga, Tanzania	39.117	-4.749
T4264	<i>Chiromantis xerampelina</i>	CB 13.917	TZ	Kilulu, Tanga, Tanzania	39.117	-4.749
T4270	<i>Chiromantis xerampelina</i>	CB 13.924	TZ	Kilulu, Tanga, Tanzania	39.117	-4.749
T4415	<i>Chiromantis xerampelina</i>	MTSN 8314	TZ	Mtemere gate Selous	38.203	-7.751
T4416	<i>Chiromantis xerampelina</i>	MTSN 8319	TZ	Mtemere gate Selous	38.203	-7.751
T4422	<i>Chiromantis xerampelina</i>	MTSN 8588	TZ	Mang'ula	36.884	-7.849
T4483	<i>Chiromantis xerampelina</i>	BM 2005.931	TZ	Kazizumbwi FR	39.055	-6.931
T4484	<i>Chiromantis xerampelina</i>	BM 2002.862	TZ	Mgambo F.R.	38.814	-4.791
T4485	<i>Chiromantis xerampelina</i>	BM 2002.620	TZ	Nilo FR	38.663	-4.908
T4486	<i>Chiromantis xerampelina</i>	BM 2002.621	TZ	Nilo FR	38.663	-4.908
T4487	<i>Chiromantis xerampelina</i>	BM 2002.622	TZ	Nilo FR	38.650	-4.983
T4488	<i>Chiromantis xerampelina</i>	BM 2002.765	TZ	Nilo FR	38.663	-4.908
T4489	<i>Chiromantis xerampelina</i>	BM 2005.116	TZ	Uluguru Mountains - Kasanga FR	37.774	-7.191
T4841	<i>Chiromantis xerampelina</i>	MTSN 7673	TZ	Kimboza Forest	37.804	-7.005
T4842	<i>Chiromantis xerampelina</i>	MTSN 7674	TZ	Kimboza Forest	37.804	-7.005
T4948	<i>Chiromantis xerampelina</i>	MTSN 9538	TZ	Segoma Forest, Camp, East Usambara	38.762	-4.976
T4949	<i>Chiromantis xerampelina</i>	MTSN 9539	TZ	Segoma Forest, Camp, East Usambara	38.762	-4.976
T4963	<i>Chiromantis xerampelina</i>	MTSN 9555	TZ	Segoma Forest, Camp, East Usambara	38.762	-4.976
T4977	<i>Chiromantis xerampelina</i>	MTSN 9573	TZ	Segoma Forest, Camp, East Usambara	38.762	-4.976
T2743	<i>Hemismus marmoratus</i>	MCZ A-149023	TZ	Dar es Salaam, near Mvuti	39.097	-7.065
T2744	<i>Hemismus marmoratus</i>	MCZ A-148829	TZ	Mafia Island, Pwani, Baleni	39.803	-7.850
T2746	<i>Hemismus marmoratus</i>	MCZ A-148928	TZ	Mafia Island, Pwani, Baleni	39.803	-7.850
T3142	<i>Hemismus marmoratus</i>	CB 13.165	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3448	<i>Hemismus marmoratus</i>	CB 13.359	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3449	<i>Hemismus marmoratus</i>	CB 13.360	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3819	<i>Hemismus marmoratus</i>	CB 13.613	TZ	Kibasira Swamp, Morogoro, Tanzania	36.318	-8.312
T3868	<i>Hemismus marmoratus</i>	CB 13.662	TZ	Ruvu North FR, Pwani, Tanzania	38.871	-6.712
T4022	<i>Hemismus marmoratus</i>	CB 13.672	TZ	Ruvu North FR, Pwani, Tanzania	38.871	-6.712
T4226	<i>Hemismus marmoratus</i>	CB 13.876	TZ	Horohoro, Tanga, Tanzania	39.102	-4.632
T4227	<i>Hemismus marmoratus</i>	CB 13.877	TZ	Horohoro, Tanga, Tanzania	39.102	-4.632
T4228	<i>Hemismus marmoratus</i>	CB 13.878	TZ	Horohoro, Tanga, Tanzania	39.102	-4.632

T4233	<i>Hemismus marmoratus</i>	CB 13.883	TZ	Horohoro, Tanga, Tanzania	39.102	-4.632
T4250	<i>Hemismus marmoratus</i>	CB 13.903	TZ	Kilulu, Tanga, Tanzania	39.117	-4.749
T4251	<i>Hemismus marmoratus</i>	CB 13.904	TZ	Kilulu, Tanga, Tanzania	39.117	-4.749
T4252	<i>Hemismus marmoratus</i>	CB 13.905	TZ	Kilulu, Tanga, Tanzania	39.117	-4.749
T4271	<i>Hemismus marmoratus</i>	CB 13.925	TZ	Kilulu, Tanga, Tanzania	39.117	-4.749
T4490	<i>Hemismus marmoratus</i>	BM 2002.889	TZ	Mgambo F.R.	38.813	-4.792
T4491	<i>Hemismus marmoratus</i>	BM 2002.890	TZ	Mgambo F.R.	38.813	-4.792
T4492	<i>Hemismus marmoratus</i>	BM 2005.1301	TZ	Bombo Forest Reserve	38.681	-4.809
T4493	<i>Hemismus marmoratus</i>	BM 2000.988	TZ	Kilombero Valley	NULL	NULL
T4494	<i>Hemismus marmoratus</i>	BM 2000.989	TZ	Kilombero Valley	NULL	NULL
T4495	<i>Hemismus marmoratus</i>	BM 2000.990	TZ	Kilombero Valley	NULL	NULL
T4496	<i>Hemismus marmoratus</i>	BM 2000.991	TZ	Kilombero Valley	NULL	NULL
T4497	<i>Hemismus marmoratus</i>	BM 2000.992	TZ	Kilombero Valley	NULL	NULL
T4498	<i>Hemismus marmoratus</i>	BM 2000.993	TZ	Kilombero Valley	NULL	NULL
T4499	<i>Hemismus marmoratus</i>	BM 2002.579	TZ	Nilo FR	38.652	-4.929
T4605	<i>Hemismus marmoratus</i>	ENI 30	MZ	Pemba, Mozambique	40.523	-12.997
T4794	<i>Hemismus marmoratus</i>	AC 1243	TZ	Tanzania, Dar es Salaam	39.245	-6.825
T4797	<i>Hemismus marmoratus</i>	BM 2002.396	TZ	Ruvu South FR	38.813	-6.895
T4806	<i>Hemismus marmoratus</i>	BM 2002.397	TZ	Ruvu South FR	38.814	-6.909
T4807	<i>Hemismus marmoratus</i>	BM 2002.398	TZ	Ruvu South FR	38.814	-6.909
T4808	<i>Hemismus marmoratus</i>	BM 2002.399	TZ	Ruvu South FR	38.793	-6.910
T4830	<i>Hemismus marmoratus</i>	BM 2005.932	TZ	Kazizumbwi FR	39.062	-6.934
T4831	<i>Hemismus marmoratus</i>	BM 2005.933	TZ	Kazizumbwi FR	39.042	-6.947
T4832	<i>Hemismus marmoratus</i>	BM 2005.934	TZ	Kazizumbwi FR	39.042	-6.947
T4928	<i>Hemismus marmoratus</i>	MTSN 9509	TZ	Segoma Forest, Camp, East Usambara	38.758	-4.981
T4947	<i>Hemismus marmoratus</i>	MTSN 9537	TZ	Segoma Forest, Camp, East Usambara	38.762	-4.976
T4968	<i>Hemismus marmoratus</i>	MTSN 9561	TZ	Segoma Forest, Camp, East Usambara	38.762	-4.976
T4969	<i>Hemismus marmoratus</i>	MTSN 9562	TZ	Segoma Forest, Camp, East Usambara	38.762	-4.976
T4973	<i>Hemismus marmoratus</i>	MTSN 9566	TZ	Segoma Forest, Camp, East Usambara	38.762	-4.976
T4985	<i>Hemismus marmoratus</i>	MCZ A-32036	TZ	Kilongwe School pond, Mafia	39.819	-7.900
T4986	<i>Hemismus marmoratus</i>	MCZ A-32138	TZ	summit Mafi Hill, Tanga	38.141	-4.923
T3685	<i>Hildebrandtia ornata</i>	CB 13.477	TZ	Mkowela village, Ruvuma, Tanzania	37.993	-10.916
T3825	<i>Amnirana galamensis</i>	CB 13.619	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T3845	<i>Amnirana galamensis</i>	CB 13.639	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T3846	<i>Amnirana galamensis</i>	CB 13.640	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T3847	<i>Amnirana galamensis</i>	CB 13.641	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T3848	<i>Amnirana galamensis</i>	CB 13.642	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T3849	<i>Amnirana galamensis</i>	CB 13.643	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T3851	<i>Amnirana galamensis</i>	CB 13.645	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T3852	<i>Amnirana galamensis</i>	CB 13.646	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T4034	<i>Amnirana galamensis</i>	CB 13.684	TZ	Mafia island, Tanzania	39.714	-7.963
T4041	<i>Amnirana galamensis</i>	CB 13.691	TZ	Mafia island, Tanzania	39.717	-7.958
T4151	<i>Amnirana galamensis</i>	CB 13.801	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4152	<i>Amnirana galamensis</i>	CB 13.802	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4172	<i>Amnirana galamensis</i>	CB 13.822	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4175	<i>Amnirana galamensis</i>	CB 13.825	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4987	<i>Amnirana galamensis</i>	MCZ A-32030	TZ	Dondwe Forest, near Mvuti	39.097	-7.065
T4608	<i>Hyperolius acuticeps</i>	WC-DNA-579	MZ	Afungi stream crossing	40.484	-10.846
T4609	<i>Hyperolius acuticeps</i>	WC-DNA-1126	MZ	dambo 24 km north of Namina to Mecuburi	38.813	-14.750
T4610	<i>Hyperolius acuticeps</i>	ENI 10	MZ	R. Diquide	40.428	-11.883
T3637	<i>Hyperolius argus</i>	CB 13.429	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3731	<i>Hyperolius argus</i>	CB 13.523	TZ	Vikindu FR, Pwani, Tanzania	39.299	-6.990
T3732	<i>Hyperolius argus</i>	CB 13.524	TZ	Vikindu FR, Pwani, Tanzania	39.299	-6.990
T3744	<i>Hyperolius argus</i>	CB 13.536	TZ	Vikindu FR, Pwani, Tanzania	39.299	-6.990
T3745	<i>Hyperolius argus</i>	CB 13.537	TZ	Vikindu FR, Pwani, Tanzania	39.299	-6.990
T3746	<i>Hyperolius argus</i>	CB 13.538	TZ	Vikindu FR, Pwani, Tanzania	39.299	-6.990
T4037	<i>Hyperolius argus</i>	CB 13.687	TZ	Mafia island, Tanzania	39.714	-7.963
T4500	<i>Hyperolius argus</i>	BM 2000.856	TZ	Kwamgumi FR	38.733	-4.923
T4501	<i>Hyperolius argus</i>	BM 2000.857	TZ	Kwamgumi FR	38.733	-4.923
T4809	<i>Hyperolius argus</i>	BM 2002.400	TZ	Ruvu South FR	38.813	-6.895
T4810	<i>Hyperolius argus</i>	BM 2002.401	TZ	Ruvu South FR	38.813	-6.895
T4811	<i>Hyperolius argus</i>	BM 2002.402	TZ	Ruvu South FR	38.813	-6.895

T4812	<i>Hyperolius argus</i>	BM 2002.403	TZ	Ruvu South FR	NULL	NULL
T4418	<i>Hyperolius cf. mitchelli</i>	MTSN 8584	TZ	Mang'ula	NULL	NULL
T4419	<i>Hyperolius cf. mitchelli</i>	MTSN 8585	TZ	Mang'ula	NULL	NULL
T3813	<i>Hyperolius kivuensis</i>	CB 13.607	TZ	Kibasira Swamp, Morogoro, Tanzania	36.318	-8.312
T3814	<i>Hyperolius kivuensis</i>	CB 13.608	TZ	Kibasira Swamp, Morogoro, Tanzania	36.318	-8.312
T3815	<i>Hyperolius kivuensis</i>	CB 13.609	TZ	Kibasira Swamp, Morogoro, Tanzania	36.318	-8.312
T3816	<i>Hyperolius kivuensis</i>	CB 13.610	TZ	Kibasira Swamp, Morogoro, Tanzania	36.318	-8.312
T3817	<i>Hyperolius kivuensis</i>	CB 13.611	TZ	Kibasira Swamp, Morogoro, Tanzania	36.318	-8.312
T3820	<i>Hyperolius kivuensis</i>	CB 13.614	TZ	Kibasira Swamp, Morogoro, Tanzania	36.318	-8.312
T3750	<i>Hyperolius mariae</i>	CB 13.542	TZ	Vikindu FR, Pwani, Tanzania	39.299	-6.990
T4040	<i>Hyperolius mariae</i>	CB 13.690	TZ	Mafia island, Tanzania	39.714	-7.963
T4043	<i>Hyperolius mariae</i>	CB 13.693	TZ	Mafia island, Tanzania	39.795	-7.849
T4045	<i>Hyperolius mariae</i>	CB 13.695	TZ	Mafia island, Tanzania	39.795	-7.849
T4047	<i>Hyperolius mariae</i>	CB 13.697	TZ	Mafia island, Tanzania	39.795	-7.849
T4048	<i>Hyperolius mariae</i>	CB 13.698	TZ	Mafia island, Tanzania	39.795	-7.849
T4049	<i>Hyperolius mariae</i>	CB 13.699	TZ	Mafia island, Tanzania	39.717	-7.958
T4055	<i>Hyperolius mariae</i>	CB 13.705	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4056	<i>Hyperolius mariae</i>	CB 13.706	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4057	<i>Hyperolius mariae</i>	CB 13.707	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4058	<i>Hyperolius mariae</i>	CB 13.708	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4059	<i>Hyperolius mariae</i>	CB 13.709	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4060	<i>Hyperolius mariae</i>	CB 13.710	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4061	<i>Hyperolius mariae</i>	CB 13.711	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4063	<i>Hyperolius mariae</i>	CB 13.713	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4064	<i>Hyperolius mariae</i>	CB 13.714	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4065	<i>Hyperolius mariae</i>	CB 13.715	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4066	<i>Hyperolius mariae</i>	CB 13.716	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4067	<i>Hyperolius mariae</i>	CB 13.717	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4068	<i>Hyperolius mariae</i>	CB 13.718	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4069	<i>Hyperolius mariae</i>	CB 13.719	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4080	<i>Hyperolius mariae</i>	CB 13.730	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4081	<i>Hyperolius mariae</i>	CB 13.731	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4082	<i>Hyperolius mariae</i>	CB 13.732	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4115	<i>Hyperolius mariae</i>	CB 13.765	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4502	<i>Hyperolius mariae</i>	BM 2000.858	TZ	Kwamgumi FR	38.733	-4.923
T4508	<i>Hyperolius mariae</i>	BM 2000.859	TZ	Kwamgumi FR	38.733	-4.923
T4512	<i>Hyperolius mariae</i>	BM 2002.768	TZ	Nilo FR	38.617	-4.898
T4523	<i>Hyperolius mariae</i>	BM 2005.1302	TZ	Bombo Forest Reserve	38.708	-4.820
T4825	<i>Hyperolius mariae</i>	BM 2002.420	TZ	Ruvu South FR	38.878	-6.948
T4826	<i>Hyperolius mariae</i>	BM 2002.421	TZ	Ruvu South FR	38.878	-6.948
T4827	<i>Hyperolius mariae</i>	BM 2002.422	TZ	Ruvu South FR	38.878	-6.948
T4828	<i>Hyperolius mariae</i>	BM 2002.423	TZ	Ruvu South FR	38.878	-6.948
T4988	<i>Hyperolius mariae</i>	MCZ A-32048	TZ	Baleni Pond, Mafia	39.803	-7.850
T4989	<i>Hyperolius mariae</i>	MCZ A-32039	TZ	Kilongwe School pond, Mafia	39.819	-7.900
T2982	<i>Hyperolius mitchelli</i>	CB 13.028	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T2983	<i>Hyperolius mitchelli</i>	CB 13.029	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T2988	<i>Hyperolius mitchelli</i>	CB 13.045	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T2989	<i>Hyperolius mitchelli</i>	CB 13.046	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3000	<i>Hyperolius mitchelli</i>	CB 13.011	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3001	<i>Hyperolius mitchelli</i>	CB 13.012	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3012	<i>Hyperolius mitchelli</i>	CB 13.027	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3110	<i>Hyperolius mitchelli</i>	CB 13.133	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3111	<i>Hyperolius mitchelli</i>	CB 13.134	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3112	<i>Hyperolius mitchelli</i>	CB 13.135	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3121	<i>Hyperolius mitchelli</i>	CB 13.144	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3122	<i>Hyperolius mitchelli</i>	CB 13.145	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3126	<i>Hyperolius mitchelli</i>	CB 13.149	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3127	<i>Hyperolius mitchelli</i>	CB 13.150	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3128	<i>Hyperolius mitchelli</i>	CB 13.151	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3129	<i>Hyperolius mitchelli</i>	CB 13.152	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3130	<i>Hyperolius mitchelli</i>	CB 13.153	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3133	<i>Hyperolius mitchelli</i>	CB 13.156	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994

T3135	<i>Hyperolius mitchelli</i>	CB 13.158	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3136	<i>Hyperolius mitchelli</i>	CB 13.159	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3205	<i>Hyperolius mitchelli</i>	CB 13.228	TZ	Noto Plateau, Lindi, Tanzania	39.374	-9.895
T3206	<i>Hyperolius mitchelli</i>	CB 13.229	TZ	Noto Plateau, Lindi, Tanzania	39.374	-9.895
T3218	<i>Hyperolius mitchelli</i>	CB 13.241	TZ	Noto Plateau, Lindi, Tanzania	39.374	-9.895
T3219	<i>Hyperolius mitchelli</i>	CB 13.242	TZ	Noto Plateau, Lindi, Tanzania	39.374	-9.895
T3282	<i>Hyperolius mitchelli</i>	CB 13.289	TZ	Namatimbili FR, Lindi, Tanzania	39.238	-9.111
T3297	<i>Hyperolius mitchelli</i>	CB 13.304	TZ	Makangaga FR, Lindi, Tanzania	39.292	-9.495
T3298	<i>Hyperolius mitchelli</i>	CB 13.305	TZ	Makangaga FR, Lindi, Tanzania	39.292	-9.495
T3299	<i>Hyperolius mitchelli</i>	CB 13.306	TZ	Makangaga FR, Lindi, Tanzania	39.292	-9.495
T3312	<i>Hyperolius mitchelli</i>	CB 13.319	TZ	Makangaga FR, Lindi, Tanzania	39.292	-9.495
T3313	<i>Hyperolius mitchelli</i>	CB 13.320	TZ	Makangaga FR, Lindi, Tanzania	39.292	-9.495
T3314	<i>Hyperolius mitchelli</i>	CB 13.321	TZ	Makangaga FR, Lindi, Tanzania	39.292	-9.495
T3315	<i>Hyperolius mitchelli</i>	CB 13.322	TZ	Makangaga FR, Lindi, Tanzania	NULL	NULL
T3316	<i>Hyperolius mitchelli</i>	CB 13.323	TZ	Makangaga FR, Lindi, Tanzania	39.292	-9.495
T3468	<i>Hyperolius mitchelli</i>	CB 13.379	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3484	<i>Hyperolius mitchelli</i>	CB 13.395	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3485	<i>Hyperolius mitchelli</i>	CB 13.396	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3549	<i>Hyperolius mitchelli</i>	CB 13.413	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3771	<i>Hyperolius mitchelli</i>	CB 13.563	TZ	Kibasira Swamp, Morogoro, Tanzania	36.228	-8.349
T3772	<i>Hyperolius mitchelli</i>	CB 13.564	TZ	Kibasira Swamp, Morogoro, Tanzania	36.228	-8.349
T3773	<i>Hyperolius mitchelli</i>	CB 13.565	TZ	Kibasira Swamp, Morogoro, Tanzania	36.228	-8.349
T3774	<i>Hyperolius mitchelli</i>	CB 13.566	TZ	Kibasira Swamp, Morogoro, Tanzania	36.228	-8.349
T3775	<i>Hyperolius mitchelli</i>	CB 13.567	TZ	Kibasira Swamp, Morogoro, Tanzania	36.228	-8.349
T3776	<i>Hyperolius mitchelli</i>	CB 13.568	TZ	Kibasira Swamp, Morogoro, Tanzania	36.228	-8.349
T3777	<i>Hyperolius mitchelli</i>	CB 13.569	TZ	Kibasira Swamp, Morogoro, Tanzania	36.228	-8.349
T3778	<i>Hyperolius mitchelli</i>	CB 13.570	TZ	Kibasira Swamp, Morogoro, Tanzania	36.228	-8.349
T3779	<i>Hyperolius mitchelli</i>	CB 13.571	TZ	Kibasira Swamp, Morogoro, Tanzania	36.228	-8.349
T3780	<i>Hyperolius mitchelli</i>	CB 13.572	TZ	Kibasira Swamp, Morogoro, Tanzania	36.228	-8.349
T3781	<i>Hyperolius mitchelli</i>	CB 13.573	TZ	Kibasira Swamp, Morogoro, Tanzania	36.228	-8.349
T3792	<i>Hyperolius mitchelli</i>	CB 13.584	TZ	Kibasira Swamp, Morogoro, Tanzania	NULL	NULL
T3801	<i>Hyperolius mitchelli</i>	CB 13.595	TZ	Kibasira Swamp, Morogoro, Tanzania	36.228	-8.349
T3804	<i>Hyperolius mitchelli</i>	CB 13.598	TZ	Kibasira Swamp, Morogoro, Tanzania	36.228	-8.349
T4156	<i>Hyperolius mitchelli</i>	CB 13.806	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4157	<i>Hyperolius mitchelli</i>	CB 13.807	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4158	<i>Hyperolius mitchelli</i>	CB 13.808	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4159	<i>Hyperolius mitchelli</i>	CB 13.809	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4160	<i>Hyperolius mitchelli</i>	CB 13.810	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4161	<i>Hyperolius mitchelli</i>	CB 13.811	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4162	<i>Hyperolius mitchelli</i>	CB 13.812	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4163	<i>Hyperolius mitchelli</i>	CB 13.813	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4181	<i>Hyperolius mitchelli</i>	CB 13.831	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4182	<i>Hyperolius mitchelli</i>	CB 13.832	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4503	<i>Hyperolius mitchelli</i>	BM 2002.628	TZ	Nilo FR	38.617	-4.898
T4504	<i>Hyperolius mitchelli</i>	BM 2002.629	TZ	Nilo FR	38.617	-4.898
T4505	<i>Hyperolius mitchelli</i>	BM 2002.630	TZ	Nilo FR	38.629	-4.888
T4506	<i>Hyperolius mitchelli</i>	BM 2002.631	TZ	Nilo FR	38.645	-4.971
T4507	<i>Hyperolius mitchelli</i>	BM 2002.632	TZ	Nilo FR	38.659	-4.944
T4517	<i>Hyperolius mitchelli</i>	BM 2005.127	TZ	Uluguru Mountains - Kasanga FR	37.774	-7.191
T4843	<i>Hyperolius mitchelli</i>	MTSN 7675	TZ	Kimboza Forest	37.804	-7.005
T4844	<i>Hyperolius mitchelli</i>	MTSN 7676	TZ	Kimboza Forest	37.804	-7.005
T4845	<i>Hyperolius mitchelli</i>	MTSN 7682	TZ	Kimboza Forest	37.804	-7.005
T4846	<i>Hyperolius mitchelli</i>	MTSN 7683	TZ	Kimboza Forest	37.804	-7.005
T4849	<i>Hyperolius mitchelli</i>	MTSN 7708	TZ	Kimboza Forest	37.804	-7.005
T4850	<i>Hyperolius mitchelli</i>	MTSN 7709	TZ	Kimboza Forest	37.804	-7.005
T4937	<i>Hyperolius mitchelli</i>	MTSN 9523	TZ	Segoma Forest, Camp, East Usambara	38.758	-4.981
T4957	<i>Hyperolius mitchelli</i>	MTSN 9549	TZ	Segoma Forest, Camp, East Usambara	38.762	-4.976
T4992	<i>Hyperolius mitchelli</i>	MCZ A-32199	TZ	Hondo Hondo Lodge, Udzungwa	36.884	-7.856
T5143	<i>Hyperolius mitchelli</i>	MUSE 11051	TZ	Mgeta Hydroelectric Dam	36.091	-8.312
T5147	<i>Hyperolius mitchelli</i>	MUSE 11060	TZ	Mgeta Hydroelectric Dam	36.091	-8.312
T5148	<i>Hyperolius mitchelli</i>	MUSE 11061	TZ	Mgeta Hydroelectric Dam	36.091	-8.312
T5149	<i>Hyperolius mitchelli</i>	MUSE 11062	TZ	Mgeta Hydroelectric Dam	36.091	-8.312

T2472	<i>Hyperolius nasutus</i>	BM 2002.405	TZ	Ruvu South FR	38.878	-6.948
T4130	<i>Hyperolius nasutus</i>	CB 13.780	TZ	Amboni caves, Tanga, Tanzania	39.048	-5.073
T4814	<i>Hyperolius nasutus</i>	BM 2002.406	TZ	Ruvu South FR	38.878	-6.948
T2471	<i>Hyperolius parkeri</i>	BM 2002.409	TZ	Ruvu South FR	38.878	-6.948
T2473	<i>Hyperolius parkeri</i>	BM 2002.633	TZ	Nilo FR	38.652	-4.929
T2474	<i>Hyperolius parkeri</i>	BM 2002.634	TZ	Nilo FR	38.652	-4.929
T2475	<i>Hyperolius parkeri</i>	BM 2002.635	TZ	Nilo FR	38.617	-4.898
T2708	<i>Hyperolius parkeri</i>	MW 01814	TZ	Coastal Forest, Tanzania	NULL	NULL
T2709	<i>Hyperolius parkeri</i>	FSU >	TZ	Pet Trade	NULL	NULL
T3124	<i>Hyperolius parkeri</i>	CB 13.147	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3125	<i>Hyperolius parkeri</i>	CB 13.148	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3541	<i>Hyperolius parkeri</i>	CB 13.405	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3639	<i>Hyperolius parkeri</i>	CB 13.431	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3640	<i>Hyperolius parkeri</i>	CB 13.432	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3770	<i>Hyperolius parkeri</i>	CB 13.562	TZ	Kibasira Swamp, Morogoro, Tanzania	36.228	-8.349
T3800	<i>Hyperolius parkeri</i>	CB 13.594	TZ	Kibasira Swamp, Morogoro, Tanzania	36.228	-8.349
T4083	<i>Hyperolius parkeri</i>	CB 13.733	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4084	<i>Hyperolius parkeri</i>	CB 13.734	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4179	<i>Hyperolius parkeri</i>	CB 13.829	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4180	<i>Hyperolius parkeri</i>	CB 13.830	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4237	<i>Hyperolius parkeri</i>	CB 13.887	TZ	Horohero, Tanga, Tanzania	39.102	-4.632
T4528	<i>Hyperolius parkeri</i>	BM 2002.409	TZ	Ruvu South FR	NULL	NULL
T4607	<i>Hyperolius parkeri</i>	WC-DNA-495	MZ	roadside pan, 10 km South of Quionga	40.502	-10.681
T4615	<i>Hyperolius parkeri</i>	WC-DNA-584	MZ	roadside pan, 10 km South of Quionga	40.502	-10.681
T4616	<i>Hyperolius parkeri</i>	WC-DNA-1417	MZ	Dereks house wetland	40.354	-12.933
T4617	<i>Hyperolius parkeri</i>	ENI 11	MZ	R. Diquide	40.428	-11.883
T4414	<i>Hyperolius puncticulatus</i>	MTSN 5678	TZ	Sanje	NULL	NULL
T2762	<i>Hyperolius pusillus</i>	BM 2002.410	TZ	Ruvu South FR	38.916	-7.037
T4815	<i>Hyperolius pusillus</i>	BM 2002.407	TZ	Ruvu South FR	38.878	-6.948
T4816	<i>Hyperolius pusillus</i>	BM 2002.408	TZ	Ruvu South FR	38.878	-6.948
T3790	<i>Hyperolius reesi</i>	CB 13.582	TZ	Kibasira Swamp, Morogoro, Tanzania	36.228	-8.349
T3808	<i>Hyperolius reesi</i>	CB 13.602	TZ	Kibasira Swamp, Morogoro, Tanzania	36.228	-8.349
T3810	<i>Hyperolius reesi</i>	CB 13.604	TZ	Kibasira Swamp, Morogoro, Tanzania	36.318	-8.312
T3821	<i>Hyperolius reesi</i>	CB 13.615	TZ	Kibasira Swamp, Morogoro, Tanzania	36.318	-8.312
T5146	<i>Hyperolius reesi</i>	MUSE 11055	TZ	Mgeta Hydroelectric Dam	36.091	-8.312
T4039	<i>Hyperolius sp.</i>	CB 13.689	TZ	Mafia island, Tanzania	NULL	NULL
T4509	<i>Hyperolius sp.</i>	BM 2005.948	TZ	Kazizumbwi FR	NULL	NULL
T4513	<i>Hyperolius sp.</i>	BM 2002.764	TZ	Nilo FR	NULL	NULL
T4514	<i>Hyperolius sp.</i>	BM 2002.764	TZ	Nilo FR	38.617	-4.898
T4515	<i>Hyperolius sp.</i>	BM 2005.125	TZ	Kasanga FR	37.774	-7.191
T4516	<i>Hyperolius sp.</i>	BM 2005.126	TZ	Kasanga FR	37.774	-7.191
T4990	<i>Hyperolius sp.</i>	MCZ A-32049	TZ	Baleni Pond, Mafia	39.803	-7.850
T4991	<i>Hyperolius sp.</i>	MCZ A-32017	TZ	Dondwe Forest, near Mvuti	39.097	-7.065
T2763	<i>Hyperolius spinigularis</i>	BM 2002.411	TZ	Ruvu South FR	38.916	-7.037
T2765	<i>Hyperolius spinigularis</i>	BM 2002.413	TZ	Ruvu South FR	38.916	-7.037
T3204	<i>Hyperolius substriatus</i>	CB 13.227	TZ	Noto Plateau, Lindi, Tanzania	39.374	-9.895
T4510	<i>Hyperolius substriatus</i>	BM 2002.766	TZ	Nilo FR	38.617	-4.898
T4511	<i>Hyperolius substriatus</i>	BM 2002.769	TZ	Nilo FR	38.617	-4.898
T3317	<i>Hyperolius tuberlinguis</i>	CB 13.324	TZ	Makangaga FR, Lindi, Tanzania	39.292	-9.495
T3550	<i>Hyperolius tuberlinguis</i>	CB 13.414	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3551	<i>Hyperolius tuberlinguis</i>	CB 13.415	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3554	<i>Hyperolius tuberlinguis</i>	CB 13.418	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3555	<i>Hyperolius tuberlinguis</i>	CB 13.419	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3638	<i>Hyperolius tuberlinguis</i>	CB 13.430	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3718	<i>Hyperolius tuberlinguis</i>	CB 13.510	TZ	Dar es Salaam (university), Tanzania	39.204	-6.779
T3719	<i>Hyperolius tuberlinguis</i>	CB 13.511	TZ	Dar es Salaam (university), Tanzania	39.204	-6.779
T3720	<i>Hyperolius tuberlinguis</i>	CB 13.512	TZ	Dar es Salaam (university), Tanzania	39.204	-6.779
T3721	<i>Hyperolius tuberlinguis</i>	CB 13.513	TZ	Dar es Salaam (university), Tanzania	39.204	-6.779
T3786	<i>Hyperolius tuberlinguis</i>	CB 13.578	TZ	Kibasira Swamp, Morogoro, Tanzania	36.228	-8.349
T3787	<i>Hyperolius tuberlinguis</i>	CB 13.579	TZ	Kibasira Swamp, Morogoro, Tanzania	36.228	-8.349
T3830	<i>Hyperolius tuberlinguis</i>	CB 13.624	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T3831	<i>Hyperolius tuberlinguis</i>	CB 13.625	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713

T3850	<i>Hyperolius tuberlinguis</i>	CB 13.644	TZ	Ruvu North FR, Pwani, Tanzania	NULL	NULL
T3858	<i>Hyperolius tuberlinguis</i>	CB 13.652	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T3859	<i>Hyperolius tuberlinguis</i>	CB 13.653	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T3860	<i>Hyperolius tuberlinguis</i>	CB 13.654	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T3861	<i>Hyperolius tuberlinguis</i>	CB 13.655	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T3862	<i>Hyperolius tuberlinguis</i>	CB 13.656	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T3863	<i>Hyperolius tuberlinguis</i>	CB 13.657	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T3864	<i>Hyperolius tuberlinguis</i>	CB 13.658	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T4038	<i>Hyperolius tuberlinguis</i>	CB 13.688	TZ	Mafia island, Tanzania	39.717	-7.958
T4042	<i>Hyperolius tuberlinguis</i>	CB 13.692	TZ	Mafia island, Tanzania	39.795	-7.849
T4046	<i>Hyperolius tuberlinguis</i>	CB 13.696	TZ	Mafia island, Tanzania	39.795	-7.849
T4062	<i>Hyperolius tuberlinguis</i>	CB 13.712	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4070	<i>Hyperolius tuberlinguis</i>	CB 13.720	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4071	<i>Hyperolius tuberlinguis</i>	CB 13.721	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4077	<i>Hyperolius tuberlinguis</i>	CB 13.727	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4078	<i>Hyperolius tuberlinguis</i>	CB 13.728	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4079	<i>Hyperolius tuberlinguis</i>	CB 13.729	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4164	<i>Hyperolius tuberlinguis</i>	CB 13.814	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4171	<i>Hyperolius tuberlinguis</i>	CB 13.821	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4183	<i>Hyperolius tuberlinguis</i>	CB 13.833	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4184	<i>Hyperolius tuberlinguis</i>	CB 13.834	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4185	<i>Hyperolius tuberlinguis</i>	CB 13.835	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4192	<i>Hyperolius tuberlinguis</i>	CB 13.842	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4389	<i>Hyperolius tuberlinguis</i>	MTSN 5504	TZ	Mikeregembe	NULL	NULL
T4390	<i>Hyperolius tuberlinguis</i>	MTSN 5505	TZ	Mikeregembe	NULL	NULL
T4420	<i>Hyperolius tuberlinguis</i>	MTSN 8586	TZ	Mang'ula	36.884	-7.849
T4421	<i>Hyperolius tuberlinguis</i>	MTSN 8587	TZ	Mang'ula	36.884	-7.849
T4518	<i>Hyperolius tuberlinguis</i>	BM 2002.419	TZ	Ruvu South FR	38.878	-6.948
T4519	<i>Hyperolius tuberlinguis</i>	BM 2002.337	TZ	Mlinga Forest Reserve	38.731	-5.061
T4520	<i>Hyperolius tuberlinguis</i>	BM 2002.668	TZ	Nilo FR	38.652	-4.929
T4521	<i>Hyperolius tuberlinguis</i>	BM 2002.669	TZ	Nilo FR	38.652	-4.929
T4522	<i>Hyperolius tuberlinguis</i>	BM 2002.670	TZ	Nilo FR	38.643	-4.955
T4820	<i>Hyperolius tuberlinguis</i>	BM 2002.414	TZ	Ruvu South FR	38.813	-6.895
T4821	<i>Hyperolius tuberlinguis</i>	BM 2002.415	TZ	Ruvu South FR	38.813	-6.895
T4822	<i>Hyperolius tuberlinguis</i>	BM 2002.416	TZ	Ruvu South FR	38.813	-6.895
T4823	<i>Hyperolius tuberlinguis</i>	BM 2002.417	TZ	Ruvu South FR	38.878	-6.948
T4824	<i>Hyperolius tuberlinguis</i>	BM 2002.418	TZ	Ruvu South FR	38.878	-6.948
T4993	<i>Hyperolius tuberlinguis</i>	MCZ A-32032	TZ	Dondwe Forest, near Mvuti	39.097	-7.065
T4994	<i>Hyperolius tuberlinguis</i>	MCZ A-32005	TZ	Dondwe Forest, near Mvuti	39.097	-7.065
T4529	<i>Hyperolius viridiflavus</i>	BM 2000.360	TZ	Kilombero Valley	NULL	NULL
T4530	<i>Hyperolius viridiflavus</i>	BM 2000.361	TZ	Kilombero Valley	NULL	NULL
T4813	<i>Hyperolius viridiflavus mariae</i>	BM 2002.404	TZ	Ruvu South FR	38.878	-6.948
T4526	<i>Hyperolius viridiflavus reesi</i>	BM 2000.1000	TZ	Kilombero Valley	NULL	NULL
T4527	<i>Hyperolius viridiflavus reesi</i>	BM 2000.999	TZ	Kilombero Valley	NULL	NULL
T4525	<i>Hyperolius viridiflavus sp.</i>	BM 2000.860	TZ	Kwamgumi FR	38.733	-4.923
T4611	<i>Hyperolius viridiflavus sp.</i>	WC-DNA-1055	MZ	13 km NW of Rapale	39.065	-14.902
T4612	<i>Hyperolius viridiflavus sp.</i>	WC-DNA-1271	MZ	Revubo river junction, s of Tenge Hill	33.761	-15.744
T4613	<i>Hyperolius viridiflavus sp.</i>	WC-DNA-1231	MZ	Revubo river below Tenge Hill	33.772	-15.719
T4614	<i>Hyperolius viridiflavus sp.</i>	no number_02	MZ	Mt Namuli	37.011	-15.338
T4524	<i>Hyperolius viridiflavus subsp.</i>	BM 2000.362	TZ	Kilombero Valley	NULL	NULL
T2476	<i>Kassina maculata</i>	BM 2002.427	TZ	Ruvu South FR	38.878	-6.948
T3011	<i>Kassina maculata</i>	CB 13.024	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3681	<i>Kassina maculata</i>	CB 13.473	TZ	Ruawa FR, Lindi, Tanzania	39.569	-9.730
T3709	<i>Kassina maculata</i>	CB 13.501	TZ	Dar es Salaam (university), Tanzania	39.204	-6.779
T3710	<i>Kassina maculata</i>	CB 13.502	TZ	Dar es Salaam (university), Tanzania	39.204	-6.779
T3711	<i>Kassina maculata</i>	CB 13.503	TZ	Dar es Salaam (university), Tanzania	39.204	-6.779
T4789	<i>Kassina maculata</i>	MW 01818	TZ	Coastal Forest, Tanzania	NULL	NULL
T4804	<i>Kassina maculata</i>	KMH 29421	TZ	JNP, Zanzibar	39.410	-6.242
T3829	<i>Kassina senegalensis</i>	CB 13.623	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T4032	<i>Kassina senegalensis</i>	CB 13.682	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4033	<i>Kassina senegalensis</i>	CB 13.683	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4035	<i>Kassina senegalensis</i>	CB 13.685	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137

T4051	<i>Kassina senegalensis</i>	CB 13.701	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4052	<i>Kassina senegalensis</i>	CB 13.702	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4074	<i>Kassina senegalensis</i>	CB 13.724	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4086	<i>Kassina senegalensis</i>	CB 13.736	TZ	Zaraninge FR, Pwani, Tanzania	NULL	NULL
T2477	<i>Kassina senegalensis argreivittis</i>	BM 2002.425	TZ	Ruvu South FR	38.878	-6.948
T2478	<i>Kassina senegalensis argreivittis</i>	BM 2002.426	TZ	Ruvu South FR	38.878	-6.948
T4829	<i>Kassina senegalensis argreivittis</i>	BM 2002.424	TZ	Ruvu South FR	38.878	-6.948
T4833	<i>Kassina senegalensis argreivittis</i>	BM 2005.935	TZ	Kazizumbwi FR	39.042	-6.947
T2479	<i>Leptopelis argenteus</i>	BM 2005.936	TZ	Kazizumbwi	NULL	NULL
T2986	<i>Leptopelis argenteus</i>	CB 13.043	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3022	<i>Leptopelis argenteus</i>	CB 13.041	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3023	<i>Leptopelis argenteus</i>	CB 13.042	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3114	<i>Leptopelis argenteus</i>	CB 13.137	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3115	<i>Leptopelis argenteus</i>	CB 13.138	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3116	<i>Leptopelis argenteus</i>	CB 13.139	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3117	<i>Leptopelis argenteus</i>	CB 13.140	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3118	<i>Leptopelis argenteus</i>	CB 13.141	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3119	<i>Leptopelis argenteus</i>	CB 13.142	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3120	<i>Leptopelis argenteus</i>	CB 13.143	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3138	<i>Leptopelis argenteus</i>	CB 13.161	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3139	<i>Leptopelis argenteus</i>	CB 13.162	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3158	<i>Leptopelis argenteus</i>	CB 13.181	TZ	Litipo FR, Lindi, Tanzania	39.475	-10.050
T3170	<i>Leptopelis argenteus</i>	CB 13.193	TZ	Litipo FR, Lindi, Tanzania	39.475	-10.050
T3172	<i>Leptopelis argenteus</i>	CB 13.195	TZ	Litipo FR, Lindi, Tanzania	39.475	-10.050
T3173	<i>Leptopelis argenteus</i>	CB 13.196	TZ	Litipo FR, Lindi, Tanzania	39.475	-10.050
T3174	<i>Leptopelis argenteus</i>	CB 13.197	TZ	Litipo FR, Lindi, Tanzania	39.475	-10.050
T3178	<i>Leptopelis argenteus</i>	CB 13.201	TZ	Litipo FR, Lindi, Tanzania	39.475	-10.050
T3199	<i>Leptopelis argenteus</i>	CB 13.222	TZ	Noto Plateau, Lindi, Tanzania	39.374	-9.895
T3200	<i>Leptopelis argenteus</i>	CB 13.223	TZ	Noto Plateau, Lindi, Tanzania	39.374	-9.895
T3201	<i>Leptopelis argenteus</i>	CB 13.224	TZ	Noto Plateau, Lindi, Tanzania	39.374	-9.895
T3211	<i>Leptopelis argenteus</i>	CB 13.234	TZ	Noto Plateau, Lindi, Tanzania	39.374	-9.895
T3265	<i>Leptopelis argenteus</i>	CB 13.272	TZ	Rondo Forest, Lindi, Tanzania	NULL	NULL
T3270	<i>Leptopelis argenteus</i>	CB 13.277	TZ	Rondo Forest, Lindi, Tanzania	39.197	-10.121
T3271	<i>Leptopelis argenteus</i>	CB 13.278	TZ	Rondo Forest, Lindi, Tanzania	39.197	-10.121
T3272	<i>Leptopelis argenteus</i>	CB 13.279	TZ	Rondo Forest, Lindi, Tanzania	39.197	-10.121
T3273	<i>Leptopelis argenteus</i>	CB 13.280	TZ	Rondo Forest, Lindi, Tanzania	39.197	-10.121
T3274	<i>Leptopelis argenteus</i>	CB 13.281	TZ	Rondo Forest, Lindi, Tanzania	39.197	-10.121
T3290	<i>Leptopelis argenteus</i>	CB 13.297	TZ	Makangaga FR, Lindi, Tanzania	39.292	-9.495
T3291	<i>Leptopelis argenteus</i>	CB 13.298	TZ	Makangaga FR, Lindi, Tanzania	39.292	-9.495
T3292	<i>Leptopelis argenteus</i>	CB 13.299	TZ	Makangaga FR, Lindi, Tanzania	39.292	-9.495
T3293	<i>Leptopelis argenteus</i>	CB 13.300	TZ	Makangaga FR, Lindi, Tanzania	39.292	-9.495
T3294	<i>Leptopelis argenteus</i>	CB 13.301	TZ	Makangaga FR, Lindi, Tanzania	39.292	-9.495
T3295	<i>Leptopelis argenteus</i>	CB 13.302	TZ	Makangaga FR, Lindi, Tanzania	39.292	-9.495
T3296	<i>Leptopelis argenteus</i>	CB 13.303	TZ	Makangaga FR, Lindi, Tanzania	39.292	-9.495
T3307	<i>Leptopelis argenteus</i>	CB 13.314	TZ	Makangaga FR, Lindi, Tanzania	39.292	-9.495
T3308	<i>Leptopelis argenteus</i>	CB 13.315	TZ	Makangaga FR, Lindi, Tanzania	39.292	-9.495
T3430	<i>Leptopelis argenteus</i>	CB 13.341	TZ	Nyamuete FR, Pwani, Tanzania	39.034	-8.326
T3435	<i>Leptopelis argenteus</i>	CB 13.346	TZ	Nyamuete FR, Pwani, Tanzania	39.034	-8.326
T3436	<i>Leptopelis argenteus</i>	CB 13.347	TZ	Nyamuete FR, Pwani, Tanzania	39.034	-8.326
T3633	<i>Leptopelis argenteus</i>	CB 13.425	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3643	<i>Leptopelis argenteus</i>	CB 13.435	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3659	<i>Leptopelis argenteus</i>	CB 13.451	TZ	Ruawa FR, Lindi, Tanzania	39.569	-9.730
T3660	<i>Leptopelis argenteus</i>	CB 13.452	TZ	Ruawa FR, Lindi, Tanzania	39.569	-9.730
T3661	<i>Leptopelis argenteus</i>	CB 13.453	TZ	Ruawa FR, Lindi, Tanzania	39.569	-9.730
T3668	<i>Leptopelis argenteus</i>	CB 13.460	TZ	Ruawa FR, Lindi, Tanzania	39.579	-9.746
T3669	<i>Leptopelis argenteus</i>	CB 13.461	TZ	Ruawa FR, Lindi, Tanzania	39.579	-9.746
T3670	<i>Leptopelis argenteus</i>	CB 13.462	TZ	Ruawa FR, Lindi, Tanzania	39.579	-9.746
T3673	<i>Leptopelis argenteus</i>	CB 13.465	TZ	Ruawa FR, Lindi, Tanzania	39.569	-9.730
T3682	<i>Leptopelis argenteus</i>	CB 13.474	TZ	Ruawa FR, Lindi, Tanzania	39.569	-9.730
T3869	<i>Leptopelis argenteus</i>	CB 13.663	TZ	Ruvu North FR, Pwani, Tanzania	38.871	-6.712
T3870	<i>Leptopelis argenteus</i>	CB 13.664	TZ	Ruvu North FR, Pwani, Tanzania	38.871	-6.712
T3871	<i>Leptopelis argenteus</i>	CB 13.665	TZ	Ruvu North FR, Pwani, Tanzania	38.871	-6.712

T4016	<i>Leptopelis argenteus</i>	CB 13.666	TZ	Ruvu North FR, Pwani, Tanzania	38.871	-6.712
T4017	<i>Leptopelis argenteus</i>	CB 13.667	TZ	Ruvu North FR, Pwani, Tanzania	NULL	NULL
T4018	<i>Leptopelis argenteus</i>	CB 13.668	TZ	Ruvu North FR, Pwani, Tanzania	38.871	-6.712
T4019	<i>Leptopelis argenteus</i>	CB 13.669	TZ	Ruvu North FR, Pwani, Tanzania	38.871	-6.712
T4021	<i>Leptopelis argenteus</i>	CB 13.671	TZ	Ruvu North FR, Pwani, Tanzania	38.871	-6.712
T4136	<i>Leptopelis argenteus</i>	CB 13.786	TZ	Amboni caves, Tanga, Tanzania	39.048	-5.073
T4137	<i>Leptopelis argenteus</i>	CB 13.787	TZ	Amboni caves, Tanga, Tanzania	39.048	-5.073
T4138	<i>Leptopelis argenteus</i>	CB 13.788	TZ	Amboni caves, Tanga, Tanzania	39.048	-5.073
T4139	<i>Leptopelis argenteus</i>	CB 13.789	TZ	Amboni caves, Tanga, Tanzania	39.048	-5.073
T4148	<i>Leptopelis argenteus</i>	CB 13.798	TZ	Amboni caves, Tanga, Tanzania	39.048	-5.073
T4189	<i>Leptopelis argenteus</i>	CB 13.839	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4193	<i>Leptopelis argenteus</i>	CB 13.843	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4194	<i>Leptopelis argenteus</i>	CB 13.844	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4195	<i>Leptopelis argenteus</i>	CB 13.845	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4234	<i>Leptopelis argenteus</i>	CB 13.884	TZ	Horohoro, Tanga, Tanzania	39.102	-4.632
T4256	<i>Leptopelis argenteus</i>	CB 13.909	TZ	Kilulu, Tanga, Tanzania	39.117	-4.749
T4257	<i>Leptopelis argenteus</i>	CB 13.910	TZ	Kilulu, Tanga, Tanzania	39.117	-4.749
T4258	<i>Leptopelis argenteus</i>	CB 13.911	TZ	Kilulu, Tanga, Tanzania	39.117	-4.749
T4259	<i>Leptopelis argenteus</i>	CB 13.912	TZ	Kilulu, Tanga, Tanzania	39.117	-4.749
T4260	<i>Leptopelis argenteus</i>	CB 13.913	TZ	Kilulu, Tanga, Tanzania	39.117	-4.749
T4261	<i>Leptopelis argenteus</i>	CB 13.914	TZ	Kilulu, Tanga, Tanzania	39.117	-4.749
T4273	<i>Leptopelis argenteus</i>	CB 13.930	TZ	Kilulu, Tanga, Tanzania	39.117	-4.749
T5396	<i>Leptopelis argenteus</i>	MVZ::234054	KN	Kakoeni	39.863	-3.170
T5397	<i>Leptopelis argenteus</i>	MVZ:234055	KN	Kakoeni	39.863	-3.170
T5398	<i>Leptopelis argenteus</i>	MVZ: 234056	KN	Kakoeni	39.863	-3.170
T5400	<i>Leptopelis argenteus</i>	MVZ: 234592	KN	Kakoeni	39.863	-3.170
T5401	<i>Leptopelis argenteus</i>	MVZ:234591	KN	Kakoeni	39.863	-3.170
T4531	<i>Leptopelis barbouri</i>	BM 2002.864	TZ	Mgambo F.R.	38.813	-4.792
T4851	<i>Leptopelis barbouri</i>	MTSN 7712	TZ	Kimboza Forest	37.804	-7.005
T4784	<i>Leptopelis broadleyi</i>	ENI 01	MZ	R. Diquide	40.428	-11.883
T4785	<i>Leptopelis broadleyi</i>	ENI 06	MZ	R. Diquide	40.428	-11.883
T2480	<i>Leptopelis flavomaculatus</i>	BM 2005.938	TZ	Kazizumbwi	NULL	NULL
T2481	<i>Leptopelis flavomaculatus</i>	BM 2002.363	TZ	Coastal	NULL	NULL
T2577	<i>Leptopelis flavomaculatus</i>	MTSN 7698	TZ	Kimboza Forest	37.808	-7.017
T2578	<i>Leptopelis flavomaculatus</i>	MTSN 7699	TZ	Kimboza Forest	37.808	-7.017
T2583	<i>Leptopelis flavomaculatus</i>	MTSN 7701	TZ	Kimboza Forest	37.808	-7.017
T2624	<i>Leptopelis flavomaculatus</i>	MTSN 9522	TZ	Segoma Forest, Camp	38.750	-4.983
T2978	<i>Leptopelis flavomaculatus</i>	CB 13.021	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T2979	<i>Leptopelis flavomaculatus</i>	CB 13.022	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3009	<i>Leptopelis flavomaculatus</i>	CB 13.020	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3010	<i>Leptopelis flavomaculatus</i>	CB 13.023	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3074	<i>Leptopelis flavomaculatus</i>	CB 13.097	TZ	Litipo FR (edge), Lindi, Tanzania	39.507	-10.030
T3081	<i>Leptopelis flavomaculatus</i>	CB 13.104	TZ	Litipo FR (edge), Lindi, Tanzania	39.511	-10.032
T3107	<i>Leptopelis flavomaculatus</i>	CB 13.130	TZ	Litipo FR (edge), Lindi, Tanzania	39.388	-9.994
T3108	<i>Leptopelis flavomaculatus</i>	CB 13.131	TZ	Litipo FR (edge), Lindi, Tanzania	39.388	-9.994
T3137	<i>Leptopelis flavomaculatus</i>	CB 13.160	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3157	<i>Leptopelis flavomaculatus</i>	CB 13.180	TZ	Litipo FR, Lindi, Tanzania	39.475	-10.050
T3179	<i>Leptopelis flavomaculatus</i>	CB 13.202	TZ	Litipo FR, Lindi, Tanzania	39.475	-10.050
T3189	<i>Leptopelis flavomaculatus</i>	CB 13.212	TZ	Noto Plateau, Lindi, Tanzania	39.374	-9.895
T3190	<i>Leptopelis flavomaculatus</i>	CB 13.213	TZ	Noto Plateau, Lindi, Tanzania	39.374	-9.895
T3191	<i>Leptopelis flavomaculatus</i>	CB 13.214	TZ	Noto Plateau, Lindi, Tanzania	39.374	-9.895
T3192	<i>Leptopelis flavomaculatus</i>	CB 13.215	TZ	Noto Plateau, Lindi, Tanzania	39.374	-9.895
T3193	<i>Leptopelis flavomaculatus</i>	CB 13.216	TZ	Noto Plateau, Lindi, Tanzania	39.374	-9.895
T3194	<i>Leptopelis flavomaculatus</i>	CB 13.217	TZ	Noto Plateau, Lindi, Tanzania	39.374	-9.895
T3195	<i>Leptopelis flavomaculatus</i>	CB 13.218	TZ	Noto Plateau, Lindi, Tanzania	39.374	-9.895
T3196	<i>Leptopelis flavomaculatus</i>	CB 13.219	TZ	Noto Plateau, Lindi, Tanzania	39.374	-9.895
T3197	<i>Leptopelis flavomaculatus</i>	CB 13.220	TZ	Noto Plateau, Lindi, Tanzania	NULL	NULL
T3198	<i>Leptopelis flavomaculatus</i>	CB 13.221	TZ	Noto Plateau, Lindi, Tanzania	39.374	-9.895
T3210	<i>Leptopelis flavomaculatus</i>	CB 13.233	TZ	Noto Plateau, Lindi, Tanzania	39.374	-9.895
T3431	<i>Leptopelis flavomaculatus</i>	CB 13.342	TZ	Nyamute FR, Pwani, Tanzania	39.037	-8.309
T3432	<i>Leptopelis flavomaculatus</i>	CB 13.343	TZ	Nyamute FR, Pwani, Tanzania	39.037	-8.309
T3443	<i>Leptopelis flavomaculatus</i>	CB 13.354	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304

T3444	<i>Leptopelis flavomaculatus</i>	CB 13.355	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3445	<i>Leptopelis flavomaculatus</i>	CB 13.356	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3446	<i>Leptopelis flavomaculatus</i>	CB 13.357	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3447	<i>Leptopelis flavomaculatus</i>	CB 13.358	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3450	<i>Leptopelis flavomaculatus</i>	CB 13.361	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3470	<i>Leptopelis flavomaculatus</i>	CB 13.381	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3471	<i>Leptopelis flavomaculatus</i>	CB 13.382	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3472	<i>Leptopelis flavomaculatus</i>	CB 13.383	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3473	<i>Leptopelis flavomaculatus</i>	CB 13.384	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3486	<i>Leptopelis flavomaculatus</i>	CB 13.397	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3487	<i>Leptopelis flavomaculatus</i>	CB 13.398	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3552	<i>Leptopelis flavomaculatus</i>	CB 13.416	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3632	<i>Leptopelis flavomaculatus</i>	CB 13.424	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3644	<i>Leptopelis flavomaculatus</i>	CB 13.436	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3768	<i>Leptopelis flavomaculatus</i>	CB 13.560	TZ	Ngumburuni FR, Pwani, Tanzania	39.066	-7.881
T3794	<i>Leptopelis flavomaculatus</i>	CB 13.586	TZ	Kibasira Swamp, Morogoro, Tanzania	36.228	-8.349
T3795	<i>Leptopelis flavomaculatus</i>	CB 13.587	TZ	Kibasira Swamp, Morogoro, Tanzania	36.228	-8.349
T3796	<i>Leptopelis flavomaculatus</i>	CB 13.588	TZ	Kibasira Swamp, Morogoro, Tanzania	36.228	-8.349
T3797	<i>Leptopelis flavomaculatus</i>	CB 13.589	TZ	Kibasira Swamp, Morogoro, Tanzania	36.228	-8.349
T3798	<i>Leptopelis flavomaculatus</i>	CB 13.590	TZ	Kibasira Swamp, Morogoro, Tanzania	36.228	-8.349
T3802	<i>Leptopelis flavomaculatus</i>	CB 13.596	TZ	Kibasira Swamp, Morogoro, Tanzania	36.228	-8.349
T3809	<i>Leptopelis flavomaculatus</i>	CB 13.603	TZ	Kibasira Swamp, Morogoro, Tanzania	36.318	-8.312
T4075	<i>Leptopelis flavomaculatus</i>	CB 13.725	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4096	<i>Leptopelis flavomaculatus</i>	CB 13.746	TZ	Gendagenda North FR, Tanga, Tanzania	38.645	-5.583
T4097	<i>Leptopelis flavomaculatus</i>	CB 13.747	TZ	Gendagenda North FR, Tanga, Tanzania	38.645	-5.583
T4098	<i>Leptopelis flavomaculatus</i>	CB 13.748	TZ	Gendagenda North FR, Tanga, Tanzania	38.645	-5.583
T4099	<i>Leptopelis flavomaculatus</i>	CB 13.749	TZ	Gendagenda North FR, Tanga, Tanzania	38.645	-5.583
T4100	<i>Leptopelis flavomaculatus</i>	CB 13.750	TZ	Gendagenda North FR, Tanga, Tanzania	38.645	-5.583
T4101	<i>Leptopelis flavomaculatus</i>	CB 13.751	TZ	Gendagenda North FR, Tanga, Tanzania	38.645	-5.583
T4196	<i>Leptopelis flavomaculatus</i>	CB 13.846	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4197	<i>Leptopelis flavomaculatus</i>	CB 13.847	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4198	<i>Leptopelis flavomaculatus</i>	CB 13.848	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4199	<i>Leptopelis flavomaculatus</i>	CB 13.849	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4200	<i>Leptopelis flavomaculatus</i>	CB 13.850	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4532	<i>Leptopelis flavomaculatus</i>	BM 2002.340	TZ	Mlinga Forest Reserve	38.748	-5.059
T4533	<i>Leptopelis flavomaculatus</i>	BM 2002.687	TZ	Nilo FR	38.649	-4.930
T4534	<i>Leptopelis flavomaculatus</i>	BM 2002.688	TZ	Nilo FR	38.663	-4.904
T4535	<i>Leptopelis flavomaculatus</i>	BM 2002.691	TZ	Nilo FR	38.645	-4.971
T4536	<i>Leptopelis flavomaculatus</i>	BM 2002.689	TZ	Nilo FR	38.662	-4.906
T4537	<i>Leptopelis flavomaculatus</i>	BM 2005.128	TZ	Uluguru Mountians - Milawilia FR	37.750	-6.979
T4538	<i>Leptopelis flavomaculatus</i>	BM 2005.129	TZ	Uluguru Mountians - Mkungwe FR	37.915	-6.869
T4539	<i>Leptopelis flavomaculatus</i>	BM 2005.130	TZ	Uluguru Mountians - Mkungwe FR	37.915	-6.869
T4540	<i>Leptopelis flavomaculatus</i>	BM 2005.131	TZ	Uluguru Mountians - Mvuha FR	37.838	-7.179
T4541	<i>Leptopelis flavomaculatus</i>	BM 2005.132	TZ	Uluguru Mountians - Mvuha FR	37.837	-7.180
T4606	<i>Leptopelis flavomaculatus</i>	no number_06	MZ	Mnt Mabu	36.588	-16.313
T4834	<i>Leptopelis flavomaculatus</i>	BM 2005.937	TZ	Kazizumbwi FR	39.053	-6.943
T4847	<i>Leptopelis flavomaculatus</i>	MTSN 7702	TZ	Kimboza Forest	37.804	-7.005
T4922	<i>Leptopelis flavomaculatus</i>	MTSN 7719	TZ	Kimboza Forest	37.804	-7.005
T4923	<i>Leptopelis flavomaculatus</i>	MTSN 7720	TZ	Kimboza Forest	37.804	-7.005
T4935	<i>Leptopelis flavomaculatus</i>	MTSN 9520	TZ	Segoma Forest, Camp, East Usambara	38.758	-4.981
T4936	<i>Leptopelis flavomaculatus</i>	MTSN 9521	TZ	Segoma Forest, Camp, East Usambara	38.758	-4.981
T4944	<i>Leptopelis flavomaculatus</i>	MTSN 9530	TZ	Segoma Forest, Camp, East Usambara	38.758	-4.981
T4960	<i>Leptopelis flavomaculatus</i>	MTSN 9552	TZ	Segoma Forest, Camp, East Usambara	38.762	-4.976
T4970	<i>Leptopelis flavomaculatus</i>	MTSN 9563	TZ	Segoma Forest, Camp, East Usambara	38.762	-4.976
T5399	<i>Leptopelis flavomaculatus</i>	MVZ:234039	TZ	Amani pond, East Usambara	38.627	-5.100
T560	<i>Leptopelis flavomaculatus</i>	BM 2002.363	TZ	Coastal	39.062	-6.945
T3151	<i>Lygodactylus sp.</i>	CB 13.174	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T1891	<i>Mertensophryne lindneri</i>	BM 2005.930	TZ	Kazizumbwi FR	39.042	-6.947
T1892	<i>Mertensophryne lindneri</i>	BM 2002.394	TZ	Ruvu South	38.814	-6.909
T4472	<i>Mertensophryne lindneri</i>	BM 2005.929	TZ	Kazizumbwi FR	39.042	-6.947
T4473	<i>Mertensophryne lindneri</i>	BM 2005.930	TZ	Kazizumbwi FR	NULL	NULL
T4481	<i>Mertensophryne lindneri</i>	BM 2005.949	TZ	Kazizumbwi FR	NULL	NULL

T1932	<i>Mertensophryne loveridgei</i>	MCZ 32084	TZ	Rondo Plateau	39.205	-10.144
T3073	<i>Mertensophryne loveridgei</i>	CB 13.096	TZ	Litipo FR (edge), Lindi, Tanzania	39.507	-10.030
T3241	<i>Mertensophryne loveridgei</i>	CB 13.399	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T1882	<i>Mertensophryne micranotis</i>	MTSN 9558	TZ	Segoma Forest, Camp, East Usambara	38.762	-4.976
T1893	<i>Mertensophryne micranotis</i>	BM 2005.135	TZ	Uluguru	37.863	-7.008
T1894	<i>Mertensophryne micranotis</i>	BM 2002.428	TZ	Ruvu South	38.793	-6.910
T1895	<i>Mertensophryne micranotis</i>	BM 2002.364	TZ	Kazizumbwi	39.055	-6.931
T2291	<i>Mertensophryne micranotis</i>	BM 2002.343	TZ	Mlinga Forest Reserve	38.744	-5.070
T3242	<i>Mertensophryne micranotis</i>	CB 13.889	TZ	Kilulu hill, Tanga, Tanzania	39.125	-4.773
T3243	<i>Mertensophryne micranotis</i>	CB 13.890	TZ	Kilulu hill, Tanga, Tanzania	39.125	-4.773
T3244	<i>Mertensophryne micranotis</i>	CB 13.891	TZ	Kilulu hill, Tanga, Tanzania	39.125	-4.773
T3252	<i>Mertensophryne micranotis</i>	CB 13.920	TZ	Kilulu hill, Tanga, Tanzania	39.125	-4.773
T4391	<i>Mertensophryne micranotis</i>	MTSN 5443	TZ	Mikeregembe	36.526	-8.090
T4392	<i>Mertensophryne micranotis</i>	MTSN 5444	TZ	Mikeregembe	36.700	-8.167
T4393	<i>Mertensophryne micranotis</i>	MTSN 5445	TZ	Mikeregembe	36.526	-8.090
T4542	<i>Mertensophryne micranotis</i>	BM 2002.429	TZ	Ruvu South FR	38.845	-6.966
T4543	<i>Mertensophryne micranotis</i>	BM 2002.365	TZ	Kazizumbwi FR	39.055	-6.931
T4544	<i>Mertensophryne micranotis</i>	BM 2002.366	TZ	Kazizumbwi FR	39.055	-6.931
T4545	<i>Mertensophryne micranotis</i>	BM 2005.939	TZ	Kazizumbwi FR	39.042	-6.947
T4546	<i>Mertensophryne micranotis</i>	BM 2005.940	TZ	Kazizumbwi FR	39.035	-6.960
T4547	<i>Mertensophryne micranotis</i>	BM 2002.342	TZ	Mlinga Forest Reserve	38.754	-5.059
T4549	<i>Mertensophryne micranotis</i>	BM 2002.891	TZ	Mgambo F.R.	38.807	-4.757
T4927	<i>Mertensophryne micranotis</i>	MTSN 9557	TZ	Segoma Forest, Camp, East Usambara	38.762	-4.976
T4966	<i>Mertensophryne micranotis</i>	MTSN 9559	TZ	Segoma Forest, Camp, East Usambara	38.762	-4.976
T4974	<i>Mertensophryne micranotis</i>	MTSN 9568	TZ	Kwangumi Forest Reserve, East Usambara	38.737	-4.972
T1933	<i>Mertensophryne sp. nov.</i>	MCZ 32087	TZ	Rondo Plateau	39.205	-10.144
T1934	<i>Mertensophryne sp. nov.</i>	MCZ 32088	TZ	Rondo Plateau	39.205	-10.144
T1881	<i>Mertensophryne usambarae</i>	MTSN 9541	TZ	Segoma Forest, Camp, East Usambara	38.762	-4.976
T1883	<i>Mertensophryne usambarae</i>	MTSN 9570	TZ	Kwangumi Forest Reserve, East Usambara	38.737	-4.972
T4952	<i>Mertensophryne usambarae</i>	MTSN 9542	TZ	Segoma Forest, Camp, East Usambara	38.762	-4.976
T3148	<i>Philothamnus semivariiegata</i>	CB 13.171	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T2997	<i>Phrynobatrachus acridoides</i>	CB 13.008	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3082	<i>Phrynobatrachus acridoides</i>	CB 13.105	TZ	Litipo FR (edge), Lindi, Tanzania	NULL	NULL
T3088	<i>Phrynobatrachus acridoides</i>	CB 13.111	TZ	Litipo FR (edge), Lindi, Tanzania	NULL	NULL
T3301	<i>Phrynobatrachus acridoides</i>	CB 13.308	TZ	Makangaga FR, Lindi, Tanzania	39.292	-9.495
T3302	<i>Phrynobatrachus acridoides</i>	CB 13.309	TZ	Makangaga FR, Lindi, Tanzania	39.292	-9.495
T3303	<i>Phrynobatrachus acridoides</i>	CB 13.310	TZ	Makangaga FR, Lindi, Tanzania	39.292	-9.495
T3304	<i>Phrynobatrachus acridoides</i>	CB 13.311	TZ	Makangaga FR, Lindi, Tanzania	39.292	-9.495
T3305	<i>Phrynobatrachus acridoides</i>	CB 13.312	TZ	Makangaga FR, Lindi, Tanzania	39.292	-9.495
T3306	<i>Phrynobatrachus acridoides</i>	CB 13.313	TZ	Makangaga FR, Lindi, Tanzania	39.292	-9.495
T3309	<i>Phrynobatrachus acridoides</i>	CB 13.316	TZ	Makangaga FR, Lindi, Tanzania	39.292	-9.495
T3310	<i>Phrynobatrachus acridoides</i>	CB 13.317	TZ	Makangaga FR, Lindi, Tanzania	39.292	-9.495
T3452	<i>Phrynobatrachus acridoides</i>	CB 13.363	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3453	<i>Phrynobatrachus acridoides</i>	CB 13.364	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3641	<i>Phrynobatrachus acridoides</i>	CB 13.433	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3698	<i>Phrynobatrachus acridoides</i>	CB 13.490	TZ	Ngumburuni FR, Pwani, Tanzania	39.066	-7.881
T3699	<i>Phrynobatrachus acridoides</i>	CB 13.491	TZ	Ngumburuni FR, Pwani, Tanzania	39.066	-7.881
T3700	<i>Phrynobatrachus acridoides</i>	CB 13.492	TZ	Ngumburuni FR, Pwani, Tanzania	39.066	-7.881
T3701	<i>Phrynobatrachus acridoides</i>	CB 13.493	TZ	Ngumburuni FR, Pwani, Tanzania	39.066	-7.881
T3702	<i>Phrynobatrachus acridoides</i>	CB 13.494	TZ	Ngumburuni FR, Pwani, Tanzania	39.066	-7.881
T3703	<i>Phrynobatrachus acridoides</i>	CB 13.495	TZ	Ngumburuni FR, Pwani, Tanzania	39.066	-7.881
T3704	<i>Phrynobatrachus acridoides</i>	CB 13.496	TZ	Ngumburuni FR, Pwani, Tanzania	39.066	-7.881
T3747	<i>Phrynobatrachus acridoides</i>	CB 13.539	TZ	Vikindu FR, Pwani, Tanzania	39.299	-6.990
T3748	<i>Phrynobatrachus acridoides</i>	CB 13.540	TZ	Vikindu FR, Pwani, Tanzania	39.299	-6.990
T3749	<i>Phrynobatrachus acridoides</i>	CB 13.541	TZ	Vikindu FR, Pwani, Tanzania	39.299	-6.990
T3751	<i>Phrynobatrachus acridoides</i>	CB 13.543	TZ	Vikindu FR, Pwani, Tanzania	39.297	-6.994
T3752	<i>Phrynobatrachus acridoides</i>	CB 13.544	TZ	Vikindu FR, Pwani, Tanzania	39.297	-6.994
T3764	<i>Phrynobatrachus acridoides</i>	CB 13.556	TZ	Ngumburuni FR, Pwani, Tanzania	39.066	-7.881
T3765	<i>Phrynobatrachus acridoides</i>	CB 13.557	TZ	Ngumburuni FR, Pwani, Tanzania	39.066	-7.881
T3769	<i>Phrynobatrachus acridoides</i>	CB 13.561	TZ	Ngumburuni FR, Pwani, Tanzania	39.066	-7.881
T3839	<i>Phrynobatrachus acridoides</i>	CB 13.633	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T3866	<i>Phrynobatrachus acridoides</i>	CB 13.660	TZ	Ruvu North FR, Pwani, Tanzania	38.871	-6.712

T3867	<i>Phrynobatrachus acridoides</i>	CB 13.661	TZ	Ruvu North FR, Pwani, Tanzania	38.871	-6.712
T4023	<i>Phrynobatrachus acridoides</i>	CB 13.673	TZ	Ruvu North FR, Pwani, Tanzania	38.871	-6.712
T4024	<i>Phrynobatrachus acridoides</i>	CB 13.674	TZ	Ruvu North FR, Pwani, Tanzania	38.871	-6.712
T4124	<i>Phrynobatrachus acridoides</i>	CB 13.774	TZ	Amboni caves, Tanga, Tanzania	39.048	-5.073
T4128	<i>Phrynobatrachus acridoides</i>	CB 13.778	TZ	Amboni caves, Tanga, Tanzania	39.048	-5.073
T4129	<i>Phrynobatrachus acridoides</i>	CB 13.779	TZ	Amboni caves, Tanga, Tanzania	39.048	-5.073
T4143	<i>Phrynobatrachus acridoides</i>	CB 13.793	TZ	Amboni caves, Tanga, Tanzania	39.048	-5.073
T4144	<i>Phrynobatrachus acridoides</i>	CB 13.794	TZ	Amboni caves, Tanga, Tanzania	39.048	-5.073
T4145	<i>Phrynobatrachus acridoides</i>	CB 13.795	TZ	Amboni caves, Tanga, Tanzania	39.048	-5.073
T4146	<i>Phrynobatrachus acridoides</i>	CB 13.796	TZ	Amboni caves, Tanga, Tanzania	39.048	-5.073
T4147	<i>Phrynobatrachus acridoides</i>	CB 13.797	TZ	Amboni caves, Tanga, Tanzania	39.048	-5.073
T4153	<i>Phrynobatrachus acridoides</i>	CB 13.803	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4154	<i>Phrynobatrachus acridoides</i>	CB 13.804	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4155	<i>Phrynobatrachus acridoides</i>	CB 13.805	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4174	<i>Phrynobatrachus acridoides</i>	CB 13.824	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4177	<i>Phrynobatrachus acridoides</i>	CB 13.827	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4191	<i>Phrynobatrachus acridoides</i>	CB 13.841	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4216	<i>Phrynobatrachus acridoides</i>	CB 13.866	TZ	Horohoro, Tanga, Tanzania	39.102	-4.632
T4218	<i>Phrynobatrachus acridoides</i>	CB 13.868	TZ	Horohoro, Tanga, Tanzania	39.102	-4.632
T4235	<i>Phrynobatrachus acridoides</i>	CB 13.885	TZ	Horohoro, Tanga, Tanzania	39.102	-4.632
T4239	<i>Phrynobatrachus acridoides</i>	CB 13.892	TZ	Kilulu, Tanga, Tanzania	39.117	-4.749
T4240	<i>Phrynobatrachus acridoides</i>	CB 13.893	TZ	Kilulu, Tanga, Tanzania	39.117	-4.749
T4241	<i>Phrynobatrachus acridoides</i>	CB 13.894	TZ	Kilulu, Tanga, Tanzania	39.117	-4.749
T4242	<i>Phrynobatrachus acridoides</i>	CB 13.895	TZ	Kilulu, Tanga, Tanzania	39.117	-4.749
T4243	<i>Phrynobatrachus acridoides</i>	CB 13.896	TZ	Kilulu, Tanga, Tanzania	39.117	-4.749
T4244	<i>Phrynobatrachus acridoides</i>	CB 13.897	TZ	Kilulu, Tanga, Tanzania	39.117	-4.749
T4245	<i>Phrynobatrachus acridoides</i>	CB 13.898	TZ	Kilulu, Tanga, Tanzania	39.117	-4.749
T4246	<i>Phrynobatrachus acridoides</i>	CB 13.899	TZ	Kilulu, Tanga, Tanzania	39.117	-4.749
T4247	<i>Phrynobatrachus acridoides</i>	CB 13.900	TZ	Kilulu, Tanga, Tanzania	39.117	-4.749
T4248	<i>Phrynobatrachus acridoides</i>	CB 13.901	TZ	Kilulu, Tanga, Tanzania	39.117	-4.749
T4249	<i>Phrynobatrachus acridoides</i>	CB 13.902	TZ	Kilulu, Tanga, Tanzania	39.117	-4.749
T4267	<i>Phrynobatrachus acridoides</i>	CB 13.921	TZ	Kilulu, Tanga, Tanzania	39.117	-4.749
T4268	<i>Phrynobatrachus acridoides</i>	CB 13.922	TZ	Kilulu, Tanga, Tanzania	39.117	-4.749
T4396	<i>Phrynobatrachus acridoides</i>	MTSN 5863	TZ	Mang'ula	NULL	NULL
T4401	<i>Phrynobatrachus acridoides</i>	MTSN 8367	TZ	Kanga FR	37.724	-5.960
T4402	<i>Phrynobatrachus acridoides</i>	MTSN 8371	TZ	Kanga FR	37.724	-5.960
T4403	<i>Phrynobatrachus acridoides</i>	MTSN 8372	TZ	Kanga FR	37.724	-5.960
T4550	<i>Phrynobatrachus acridoides</i>	BM 2002.430	TZ	Ruvu South FR	38.813	-6.895
T4551	<i>Phrynobatrachus acridoides</i>	BM 2002.431	TZ	Ruvu South FR	38.813	-6.895
T4552	<i>Phrynobatrachus acridoides</i>	BM 2002.432	TZ	Ruvu South FR	38.796	-6.912
T4553	<i>Phrynobatrachus acridoides</i>	BM 2002.433	TZ	Ruvu South FR	38.796	-6.912
T4554	<i>Phrynobatrachus acridoides</i>	BM 2002.434	TZ	Ruvu South FR	38.878	-6.948
T4555	<i>Phrynobatrachus acridoides</i>	BM 2002.435	TZ	Ruvu South FR	38.878	-6.948
T4556	<i>Phrynobatrachus acridoides</i>	BM 2005.941	TZ	Kazizumbwi FR	39.073	-6.945
T4557	<i>Phrynobatrachus acridoides</i>	BM 2002.347	TZ	Mlinga Forest Reserve	38.748	-5.059
T4558	<i>Phrynobatrachus acridoides</i>	BM 2002.230	TZ	Kwamgumi FR	38.733	-4.923
T4559	<i>Phrynobatrachus acridoides</i>	BM 2002.231	TZ	Kwamgumi FR	38.733	-4.923
T4560	<i>Phrynobatrachus acridoides</i>	BM 2002.232	TZ	Kwamgumi FR	38.733	-4.923
T4561	<i>Phrynobatrachus acridoides</i>	BM 2002.734	TZ	Nilo FR	38.643	-4.955
T4562	<i>Phrynobatrachus acridoides</i>	BM 2002.735	TZ	Nilo FR	38.643	-4.955
T4563	<i>Phrynobatrachus acridoides</i>	BM 2002.736	TZ	Nilo FR	38.643	-4.955
T4564	<i>Phrynobatrachus acridoides</i>	BM 2002.737	TZ	Nilo FR	38.643	-4.955
T4565	<i>Phrynobatrachus acridoides</i>	BM 2002.738	TZ	Nilo FR	38.643	-4.955
T4566	<i>Phrynobatrachus acridoides</i>	BM 2002.739	TZ	Nilo FR	38.643	-4.955
T4567	<i>Phrynobatrachus acridoides</i>	BM 2005.136	TZ	Uluguru Mountians - Mvuha FR	37.838	-7.179
T4568	<i>Phrynobatrachus acridoides</i>	BM 2005.137	TZ	Uluguru Mountians - Mvuha FR	37.838	-7.179
T4569	<i>Phrynobatrachus acridoides</i>	BM 2005.138	TZ	Uluguru Mountians - Mvuha FR	37.838	-7.179
T4570	<i>Phrynobatrachus acridoides</i>	BM 2005.139	TZ	Uluguru Mountians - Mvuha FR	37.838	-7.179
T4792	<i>Phrynobatrachus acridoides</i>	WTS 8416	TZ	Unguja near Mchekeni village, Zanzibar	39.247	-6.190
T4793	<i>Phrynobatrachus acridoides</i>	WTS 8417	TZ	Unguja near Mchekeni village, Zanzibar	39.247	-6.190
T4835	<i>Phrynobatrachus acridoides</i>	MTSN 7660	TZ	Kimboza Forest	NULL	NULL
T4836	<i>Phrynobatrachus acridoides</i>	MTSN 7661	TZ	Kimboza Forest	37.804	-7.005

T4837	<i>Phrynobatrachus acridoides</i>	MTSN 7662	TZ	Kimboza Forest	37.804	-7.005
T4954	<i>Phrynobatrachus acridoides</i>	MTSN 9546	TZ	Segoma Forest, Camp, East Usambara	38.762	-4.976
T4958	<i>Phrynobatrachus acridoides</i>	MTSN 9550	TZ	Segoma Forest, Camp, East Usambara	38.762	-4.976
T4959	<i>Phrynobatrachus acridoides</i>	MTSN 9551	TZ	Segoma Forest, Camp, East Usambara	38.762	-4.976
T4996	<i>Phrynobatrachus acridoides</i>	MCZ A-32196	TZ	Hondo Hondo Lodge, Udzungwa	36.884	-7.856
T4997	<i>Phrynobatrachus acridoides</i>	MCZ A-32003	TZ	Dondwe Forest, near Mvuti	39.097	-7.065
T4998	<i>Phrynobatrachus acridoides</i>	MCZ A-32137	TZ	summit Mafi Hill, Tanga	38.141	-4.923
T3705	<i>Phrynobatrachus cf. mababiensis</i>	CB 13.497	TZ	Ngumburuni FR, Pwani, Tanzania	39.066	-7.881
T3706	<i>Phrynobatrachus cf. mababiensis</i>	CB 13.498	TZ	Ngumburuni FR, Pwani, Tanzania	39.066	-7.881
T3753	<i>Phrynobatrachus cf. mababiensis</i>	CB 13.545	TZ	Vikindu FR, Pwani, Tanzania	39.297	-6.994
T4025	<i>Phrynobatrachus cf. mababiensis</i>	CB 13.675	TZ	Ruvu North FR, Pwani, Tanzania	38.871	-6.712
T4085	<i>Phrynobatrachus cf. mababiensis</i>	CB 13.735	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T3008	<i>Phrynobatrachus mababiensis</i>	CB 13.019	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3084	<i>Phrynobatrachus mababiensis</i>	CB 13.107	TZ	Litipo FR (edge), Lindi, Tanzania	39.511	-10.032
T3090	<i>Phrynobatrachus mababiensis</i>	CB 13.113	TZ	Litipo FR (edge), Lindi, Tanzania	39.507	-10.030
T3281	<i>Phrynobatrachus mababiensis</i>	CB 13.288	TZ	Namatimbili FR, Lindi, Tanzania	39.238	-9.111
T3469	<i>Phrynobatrachus mababiensis</i>	CB 13.380	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3479	<i>Phrynobatrachus mababiensis</i>	CB 13.390	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3674	<i>Phrynobatrachus mababiensis</i>	CB 13.466	TZ	Ruawa FR, Lindi, Tanzania	39.569	-9.730
T4217	<i>Phrynobatrachus mababiensis</i>	CB 13.867	TZ	Horohero, Tanga, Tanzania	39.102	-4.632
T4219	<i>Phrynobatrachus mababiensis</i>	CB 13.869	TZ	Horohero, Tanga, Tanzania	39.102	-4.632
T4220	<i>Phrynobatrachus mababiensis</i>	CB 13.870	TZ	Horohero, Tanga, Tanzania	39.102	-4.632
T4221	<i>Phrynobatrachus mababiensis</i>	CB 13.871	TZ	Horohero, Tanga, Tanzania	39.102	-4.632
T4222	<i>Phrynobatrachus mababiensis</i>	CB 13.872	TZ	Horohero, Tanga, Tanzania	39.102	-4.632
T4223	<i>Phrynobatrachus mababiensis</i>	CB 13.873	TZ	Horohero, Tanga, Tanzania	39.102	-4.632
T4224	<i>Phrynobatrachus mababiensis</i>	CB 13.874	TZ	Horohero, Tanga, Tanzania	39.102	-4.632
T4225	<i>Phrynobatrachus mababiensis</i>	CB 13.875	TZ	Horohero, Tanga, Tanzania	39.102	-4.632
T4409	<i>Phrynobatrachus mababiensis</i>	KMH 17125	TZ	Kilombero Valley	NULL	NULL
T4410	<i>Phrynobatrachus mababiensis</i>	KMH 17199	TZ	Kilombero Valley	NULL	NULL
T4411	<i>Phrynobatrachus mababiensis</i>	KMH 17161	TZ	Kilombero Valley	NULL	NULL
T4412	<i>Phrynobatrachus mababiensis</i>	KMH 17193	TZ	Kilombero Valley	NULL	NULL
T4413	<i>Phrynobatrachus mababiensis</i>	KMH 17191	TZ	Kilombero Valley	NULL	NULL
T4571	<i>Phrynobatrachus mababiensis</i>	BM 2005.942	TZ	Kazizumbwi FR	NULL	NULL
T4572	<i>Phrynobatrachus mababiensis</i>	BM 2005.943	TZ	Kazizumbwi FR	NULL	NULL
T4995	<i>Phrynobatrachus mababiensis</i>	MCZ A-32018	TZ	Dondwe Forest, near Mvuti	39.097	-7.065
T2985	<i>Phrynobatrachus natalensis</i>	CB 13.037	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T2992	<i>Phrynobatrachus natalensis</i>	CB 13.003	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T2993	<i>Phrynobatrachus natalensis</i>	CB 13.004	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T2994	<i>Phrynobatrachus natalensis</i>	CB 13.005	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T2995	<i>Phrynobatrachus natalensis</i>	CB 13.006	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T2996	<i>Phrynobatrachus natalensis</i>	CB 13.007	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T2998	<i>Phrynobatrachus natalensis</i>	CB 13.009	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T2999	<i>Phrynobatrachus natalensis</i>	CB 13.010	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3002	<i>Phrynobatrachus natalensis</i>	CB 13.013	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3003	<i>Phrynobatrachus natalensis</i>	CB 13.014	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3004	<i>Phrynobatrachus natalensis</i>	CB 13.015	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3005	<i>Phrynobatrachus natalensis</i>	CB 13.016	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3006	<i>Phrynobatrachus natalensis</i>	CB 13.017	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3007	<i>Phrynobatrachus natalensis</i>	CB 13.018	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3015	<i>Phrynobatrachus natalensis</i>	CB 13.032	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3016	<i>Phrynobatrachus natalensis</i>	CB 13.033	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3017	<i>Phrynobatrachus natalensis</i>	CB 13.034	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3018	<i>Phrynobatrachus natalensis</i>	CB 13.035	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3019	<i>Phrynobatrachus natalensis</i>	CB 13.038	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3025	<i>Phrynobatrachus natalensis</i>	CB 13.048	TZ	Lake Rutamba, Lindi, Tanzania	39.462	-10.033
T3026	<i>Phrynobatrachus natalensis</i>	CB 13.049	TZ	Lake Rutamba, Lindi, Tanzania	39.462	-10.033
T3027	<i>Phrynobatrachus natalensis</i>	CB 13.050	TZ	Lake Rutamba, Lindi, Tanzania	39.462	-10.033
T3028	<i>Phrynobatrachus natalensis</i>	CB 13.051	TZ	Lake Rutamba, Lindi, Tanzania	39.462	-10.033
T3069	<i>Phrynobatrachus natalensis</i>	CB 13.092	TZ	Litipo FR (edge), Lindi, Tanzania	39.507	-10.030
T3070	<i>Phrynobatrachus natalensis</i>	CB 13.093	TZ	Litipo FR (edge), Lindi, Tanzania	39.507	-10.030
T3071	<i>Phrynobatrachus natalensis</i>	CB 13.094	TZ	Litipo FR (edge), Lindi, Tanzania	39.507	-10.030
T3083	<i>Phrynobatrachus natalensis</i>	CB 13.106	TZ	Litipo FR (edge), Lindi, Tanzania	39.511	-10.032

T3085	<i>Phrynobatrachus natalensis</i>	CB 13.108	TZ	Litipo FR (edge), Lindi, Tanzania	39.511	-10.032
T3086	<i>Phrynobatrachus natalensis</i>	CB 13.109	TZ	Litipo FR (edge), Lindi, Tanzania	39.511	-10.032
T3089	<i>Phrynobatrachus natalensis</i>	CB 13.112	TZ	Litipo FR (edge), Lindi, Tanzania	39.511	-10.032
T3101	<i>Phrynobatrachus natalensis</i>	CB 13.124	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3102	<i>Phrynobatrachus natalensis</i>	CB 13.125	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3162	<i>Phrynobatrachus natalensis</i>	CB 13.185	TZ	Litipo FR, Lindi, Tanzania	39.475	-10.050
T3163	<i>Phrynobatrachus natalensis</i>	CB 13.186	TZ	Litipo FR, Lindi, Tanzania	39.475	-10.050
T3164	<i>Phrynobatrachus natalensis</i>	CB 13.187	TZ	Litipo FR, Lindi, Tanzania	39.475	-10.050
T3165	<i>Phrynobatrachus natalensis</i>	CB 13.188	TZ	Litipo FR, Lindi, Tanzania	39.475	-10.050
T3176	<i>Phrynobatrachus natalensis</i>	CB 13.199	TZ	Litipo FR, Lindi, Tanzania	39.475	-10.050
T3177	<i>Phrynobatrachus natalensis</i>	CB 13.200	TZ	Litipo FR, Lindi, Tanzania	39.475	-10.050
T4786	<i>Phrynobatrachus pakenhami</i>	KMH 28800	TZ	Pemba	39.755	-5.142
T4787	<i>Phrynobatrachus pakenhami</i>	KMH 28801	TZ	Pemba	39.755	-5.142
T4788	<i>Phrynobatrachus pakenhami</i>	KMH 28802	TZ	Pemba	39.755	-5.142
T3766	<i>Phrynobatrachus ukingensis</i>	CB 13.558	TZ	Ngumburuni FR, Pwani, Tanzania	39.066	-7.881
T3767	<i>Phrynobatrachus ukingensis</i>	CB 13.559	TZ	Ngumburuni FR, Pwani, Tanzania	39.066	-7.881
T4576	<i>Phrynobatrachus ukingensis</i>	BM 2005.142	TZ	Uluguru Mountians - Uluguru Ruvu FR	37.867	-6.983
T4577	<i>Phrynobatrachus ukingensis</i>	BM 2005.143	TZ	Uluguru Mountians - Uluguru Ruvu FR	37.867	-6.983
T4578	<i>Phrynobatrachus ukingensis</i>	BM 2005.144	TZ	Uluguru Mountians - Uluguru Ruvu FR	37.867	-6.983
T4575	<i>Phrynobatrachus uzungwensis</i>	BM 2005.181	TZ	Uluguru Mountians - Mkungwe FR	NULL	NULL
T3671	<i>Phrynomantis bifasciatus</i>	CB 13.463	TZ	Ruawa FR, Lindi, Tanzania	39.569	-9.730
T3684	<i>Phrynomantis bifasciatus</i>	CB 13.476	TZ	Ruawa FR, Lindi, Tanzania	39.569	-9.730
T4054	<i>Phrynomantis bifasciatus</i>	CB 13.704	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4073	<i>Phrynomantis bifasciatus</i>	CB 13.723	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4397	<i>Phrynomantis bifasciatus</i>	MTSN 8591	TZ	Kilombero	36.892	-7.858
T4798	<i>Phrynomantis bifasciatus</i>	?_multiple_03	TZ	MAFIA ISLAND	NULL	NULL
T4999	<i>Phrynomantis bifasciatus</i>	MCZ A-32035	TZ	Dondwe Forest, near Mvuti	39.097	-7.065
T2975	<i>Ptychadena anchietae</i>	CB 13.926	TZ	Kilulu, Tanga, Tanzania	39.117	-4.749
T2976	<i>Ptychadena anchietae</i>	CB 13.927	TZ	Kilulu, Tanga, Tanzania	39.117	-4.749
T2990	<i>Ptychadena anchietae</i>	CB 13.001	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3014	<i>Ptychadena anchietae</i>	CB 13.031	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3020	<i>Ptychadena anchietae</i>	CB 13.039	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3021	<i>Ptychadena anchietae</i>	CB 13.040	TZ	Makangala FR, Lindi, Tanzania	39.388	-9.994
T3030	<i>Ptychadena anchietae</i>	CB 13.053	TZ	Makangala FR (edge), Lindi, Tanzania	39.369	-9.982
T3031	<i>Ptychadena anchietae</i>	CB 13.054	TZ	Makangala FR (edge), Lindi, Tanzania	39.369	-9.982
T3032	<i>Ptychadena anchietae</i>	CB 13.055	TZ	Makangala FR (edge), Lindi, Tanzania	39.369	-9.982
T3033	<i>Ptychadena anchietae</i>	CB 13.056	TZ	Makangala FR (edge), Lindi, Tanzania	39.369	-9.982
T3034	<i>Ptychadena anchietae</i>	CB 13.057	TZ	Makangala FR (edge), Lindi, Tanzania	39.369	-9.982
T3035	<i>Ptychadena anchietae</i>	CB 13.058	TZ	Makangala FR (edge), Lindi, Tanzania	39.369	-9.982
T3036	<i>Ptychadena anchietae</i>	CB 13.059	TZ	Makangala FR (edge), Lindi, Tanzania	39.369	-9.982
T3037	<i>Ptychadena anchietae</i>	CB 13.060	TZ	Makangala FR (edge), Lindi, Tanzania	39.369	-9.982
T3038	<i>Ptychadena anchietae</i>	CB 13.061	TZ	Makangala FR (edge), Lindi, Tanzania	39.369	-9.982
T3039	<i>Ptychadena anchietae</i>	CB 13.062	TZ	Makangala FR (edge), Lindi, Tanzania	39.369	-9.982
T3040	<i>Ptychadena anchietae</i>	CB 13.063	TZ	Makangala FR (edge), Lindi, Tanzania	39.369	-9.982
T3041	<i>Ptychadena anchietae</i>	CB 13.064	TZ	Makangala FR (edge), Lindi, Tanzania	39.369	-9.982
T3042	<i>Ptychadena anchietae</i>	CB 13.065	TZ	Makangala FR (edge), Lindi, Tanzania	39.369	-9.982
T3043	<i>Ptychadena anchietae</i>	CB 13.066	TZ	Makangala FR (edge), Lindi, Tanzania	39.369	-9.982
T3044	<i>Ptychadena anchietae</i>	CB 13.067	TZ	Makangala FR (edge), Lindi, Tanzania	39.369	-9.982
T3045	<i>Ptychadena anchietae</i>	CB 13.068	TZ	Makangala FR (edge), Lindi, Tanzania	39.369	-9.982
T3046	<i>Ptychadena anchietae</i>	CB 13.069	TZ	Makangala FR (edge), Lindi, Tanzania	39.369	-9.982
T3047	<i>Ptychadena anchietae</i>	CB 13.070	TZ	Makangala FR (edge), Lindi, Tanzania	39.369	-9.982
T3048	<i>Ptychadena anchietae</i>	CB 13.071	TZ	Makangala FR (edge), Lindi, Tanzania	39.369	-9.982
T3049	<i>Ptychadena anchietae</i>	CB 13.072	TZ	Makangala FR (edge), Lindi, Tanzania	39.369	-9.982
T3050	<i>Ptychadena anchietae</i>	CB 13.073	TZ	Makangala FR (edge), Lindi, Tanzania	39.369	-9.982
T3052	<i>Ptychadena anchietae</i>	CB 13.075	TZ	Makangala FR (edge), Lindi, Tanzania	39.369	-9.982
T3053	<i>Ptychadena anchietae</i>	CB 13.076	TZ	Makangala FR (edge), Lindi, Tanzania	39.369	-9.982
T3054	<i>Ptychadena anchietae</i>	CB 13.077	TZ	Makangala FR (edge), Lindi, Tanzania	39.369	-9.982
T3055	<i>Ptychadena anchietae</i>	CB 13.078	TZ	Makangala FR (edge), Lindi, Tanzania	39.369	-9.982
T3059	<i>Ptychadena anchietae</i>	CB 13.082	TZ	Makangala FR (edge), Lindi, Tanzania	39.369	-9.982
T3060	<i>Ptychadena anchietae</i>	CB 13.083	TZ	Makangala FR (edge), Lindi, Tanzania	39.369	-9.982
T3061	<i>Ptychadena anchietae</i>	CB 13.084	TZ	Makangala FR (edge), Lindi, Tanzania	39.369	-9.982
T3072	<i>Ptychadena anchietae</i>	CB 13.095	TZ	Litipo FR (edge), Lindi, Tanzania	39.507	-10.030

T3079	<i>Ptychadena anchietae</i>	CB 13.102	TZ	Litipo FR (edge), Lindi, Tanzania	39.511	-10.032
T3080	<i>Ptychadena anchietae</i>	CB 13.103	TZ	Litipo FR (edge), Lindi, Tanzania	39.511	-10.032
T3166	<i>Ptychadena anchietae</i>	CB 13.189	TZ	Litipo FR, Lindi, Tanzania	39.475	-10.050
T3167	<i>Ptychadena anchietae</i>	CB 13.190	TZ	Litipo FR, Lindi, Tanzania	39.475	-10.050
T3168	<i>Ptychadena anchietae</i>	CB 13.191	TZ	Litipo FR, Lindi, Tanzania	39.475	-10.050
T3171	<i>Ptychadena anchietae</i>	CB 13.194	TZ	Litipo FR, Lindi, Tanzania	39.475	-10.050
T3536	<i>Ptychadena anchietae</i>	CB 13.400	TZ	Kiwengoma FR, Pwani, Tanzania	38.903	-8.304
T3548	<i>Ptychadena anchietae</i>	CB 13.412	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3729	<i>Ptychadena anchietae</i>	CB 13.521	TZ	Vikindu FR, Pwani, Tanzania	39.299	-6.990
T3730	<i>Ptychadena anchietae</i>	CB 13.522	TZ	Vikindu FR, Pwani, Tanzania	39.299	-6.990
T3736	<i>Ptychadena anchietae</i>	CB 13.528	TZ	Vikindu FR, Pwani, Tanzania	39.299	-6.990
T3737	<i>Ptychadena anchietae</i>	CB 13.529	TZ	Vikindu FR, Pwani, Tanzania	39.299	-6.990
T3738	<i>Ptychadena anchietae</i>	CB 13.530	TZ	Vikindu FR, Pwani, Tanzania	39.299	-6.990
T3739	<i>Ptychadena anchietae</i>	CB 13.531	TZ	Vikindu FR, Pwani, Tanzania	39.299	-6.990
T3754	<i>Ptychadena anchietae</i>	CB 13.546	TZ	Vikindu FR, Pwani, Tanzania	39.297	-6.994
T3759	<i>Ptychadena anchietae</i>	CB 13.551	TZ	Ngumburuni FR, Pwani, Tanzania	39.066	-7.881
T3761	<i>Ptychadena anchietae</i>	CB 13.553	TZ	Ngumburuni FR, Pwani, Tanzania	39.066	-7.881
T4114	<i>Ptychadena anchietae</i>	CB 13.764	TZ	Gendagenda North FR, Tanga, Tanzania	38.646	-5.583
T4149	<i>Ptychadena anchietae</i>	CB 13.799	TZ	Amboni caves, Tanga, Tanzania	39.048	-5.073
T4173	<i>Ptychadena anchietae</i>	CB 13.823	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4176	<i>Ptychadena anchietae</i>	CB 13.826	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4204	<i>Ptychadena anchietae</i>	CB 13.854	TZ	Horohoro, Tanga, Tanzania	NULL	NULL
T4205	<i>Ptychadena anchietae</i>	CB 13.855	TZ	Horohoro, Tanga, Tanzania	39.102	-4.632
T4206	<i>Ptychadena anchietae</i>	CB 13.856	TZ	Horohoro, Tanga, Tanzania	39.102	-4.632
T4207	<i>Ptychadena anchietae</i>	CB 13.857	TZ	Horohoro, Tanga, Tanzania	39.102	-4.632
T4208	<i>Ptychadena anchietae</i>	CB 13.858	TZ	Horohoro, Tanga, Tanzania	39.102	-4.632
T4209	<i>Ptychadena anchietae</i>	CB 13.859	TZ	Horohoro, Tanga, Tanzania	39.102	-4.632
T4210	<i>Ptychadena anchietae</i>	CB 13.860	TZ	Horohoro, Tanga, Tanzania	39.102	-4.632
T4230	<i>Ptychadena anchietae</i>	CB 13.880	TZ	Horohoro, Tanga, Tanzania	39.102	-4.632
T4231	<i>Ptychadena anchietae</i>	CB 13.881	TZ	Horohoro, Tanga, Tanzania	39.102	-4.632
T4253	<i>Ptychadena anchietae</i>	CB 13.906	TZ	Kilulu, Tanga, Tanzania	39.117	-4.749
T4254	<i>Ptychadena anchietae</i>	CB 13.907	TZ	Kilulu, Tanga, Tanzania	39.117	-4.749
T4255	<i>Ptychadena anchietae</i>	CB 13.908	TZ	Kilulu, Tanga, Tanzania	39.117	-4.749
T4581	<i>Ptychadena anchietae</i>	BM 2005.164	TZ	Uluguru Mountians - Uluguru Ruvu FR	37.867	-6.983
T4838	<i>Ptychadena anchietae</i>	MTSN 7664	TZ	Kimboza Forest	37.804	-7.005
T4839	<i>Ptychadena anchietae</i>	MTSN 7665	TZ	Kimboza Forest	37.804	-7.005
T4840	<i>Ptychadena anchietae</i>	MTSN 7666	TZ	Kimboza Forest	37.804	-7.005
T4961	<i>Ptychadena anchietae</i>	MTSN 9553	TZ	Segoma Forest, Camp, East Usambara	38.762	-4.976
T4962	<i>Ptychadena anchietae</i>	MTSN 9554	TZ	Segoma Forest, Camp, East Usambara	38.762	-4.976
T5002	<i>Ptychadena anchietae</i>	MCZ A-32101	TZ	Amboni Caves	39.059	-5.074
T5003	<i>Ptychadena anchietae</i>	MCZ A-32008	TZ	Dondwe Forest, near Mvuti	39.097	-7.065
T5004	<i>Ptychadena anchietae</i>	MCZ A-32132	TZ	Mkalamo, Tanga	38.115	-4.991
T5129	<i>Ptychadena anchietae</i>	MUSE 11037	TZ	Mgeta Hydroelectric Dam	36.091	-8.312
T5135	<i>Ptychadena anchietae</i>	MUSE 11043	TZ	Mgeta Hydroelectric Dam	36.091	-8.312
T5136	<i>Ptychadena anchietae</i>	MUSE 11044	TZ	Mgeta Hydroelectric Dam	36.091	-8.312
T5137	<i>Ptychadena anchietae</i>	MUSE 11045	TZ	Mgeta Hydroelectric Dam	36.091	-8.312
T5138	<i>Ptychadena anchietae</i>	MUSE 11046	TZ	Mgeta Hydroelectric Dam	36.091	-8.312
T3078	<i>Ptychadena cf. mossambica</i>	CB 13.101	TZ	Litipo FR (edge), Lindi, Tanzania	39.511	-10.032
T3537	<i>Ptychadena cf. mossambica</i>	CB 13.401	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3538	<i>Ptychadena cf. mossambica</i>	CB 13.402	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3539	<i>Ptychadena cf. mossambica</i>	CB 13.403	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3540	<i>Ptychadena cf. mossambica</i>	CB 13.404	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3546	<i>Ptychadena cf. mossambica</i>	CB 13.410	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3547	<i>Ptychadena cf. mossambica</i>	CB 13.411	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3634	<i>Ptychadena cf. mossambica</i>	CB 13.426	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3646	<i>Ptychadena cf. mossambica</i>	CB 13.438	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3647	<i>Ptychadena cf. mossambica</i>	CB 13.439	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3648	<i>Ptychadena cf. mossambica</i>	CB 13.440	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3649	<i>Ptychadena cf. mossambica</i>	CB 13.441	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3650	<i>Ptychadena cf. mossambica</i>	CB 13.442	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3651	<i>Ptychadena cf. mossambica</i>	CB 13.443	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3652	<i>Ptychadena cf. mossambica</i>	CB 13.444	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948

T3653	<i>Ptychadena cf. mossambica</i>	CB 13.445	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3756	<i>Ptychadena cf. mossambica</i>	CB 13.548	TZ	Ngumburuni FR, Pwani, Tanzania	39.066	-7.881
T3757	<i>Ptychadena cf. mossambica</i>	CB 13.549	TZ	Ngumburuni FR, Pwani, Tanzania	39.066	-7.881
T3865	<i>Ptychadena cf. mossambica</i>	CB 13.659	TZ	Ruvu North FR, Pwani, Tanzania	38.871	-6.712
T4020	<i>Ptychadena cf. mossambica</i>	CB 13.670	TZ	Ruvu North FR, Pwani, Tanzania	38.871	-6.712
T4229	<i>Ptychadena cf. mossambica</i>	CB 13.879	TZ	Horohoro, Tanga, Tanzania	39.102	-4.632
T4582	<i>Ptychadena cf. mossambica</i>	BM 2005.945	TZ	Kazizumbwi FR	39.042	-6.947
T4583	<i>Ptychadena cf. mossambica</i>	BM 2002.436	TZ	Ruvu South FR	38.878	-6.948
T3793	<i>Ptychadena cf. nilotica</i>	CB 13.585	TZ	Kibasira Swamp, Morogoro, Tanzania	36.228	-8.349
T3799	<i>Ptychadena cf. nilotica</i>	CB 13.591	TZ	Kibasira Swamp, Morogoro, Tanzania	36.228	-8.349
T3807	<i>Ptychadena cf. nilotica</i>	CB 13.601	TZ	Kibasira Swamp, Morogoro, Tanzania	36.228	-8.349
T3811	<i>Ptychadena cf. nilotica</i>	CB 13.605	TZ	Kibasira Swamp, Morogoro, Tanzania	36.318	-8.312
T3822	<i>Ptychadena cf. nilotica</i>	CB 13.616	TZ	Kibasira Swamp, Morogoro, Tanzania	36.318	-8.312
T3823	<i>Ptychadena cf. nilotica</i>	CB 13.617	TZ	Kibasira Swamp, Morogoro, Tanzania	36.318	-8.312
T4417	<i>Ptychadena cf. nilotica</i>	MTSN 8127	TZ	Ruipa, Ranger post	37.035	-9.169
T5001	<i>Ptychadena cf. nilotica</i>	MCZ A-32198	TZ	Hondo Hondo Lodge, Udzungwa	36.884	-7.856
T3062	<i>Ptychadena nilotica</i>	CB 13.085	TZ	Makangala FR (edge), Lindi, Tanzania	39.369	-9.982
T3645	<i>Ptychadena nilotica</i>	CB 13.437	TZ	Muyuyu FR, Pwani, Tanzania	39.044	-7.948
T3728	<i>Ptychadena nilotica</i>	CB 13.520	TZ	Vikindu FR, Pwani, Tanzania	39.299	-6.990
T3740	<i>Ptychadena nilotica</i>	CB 13.532	TZ	Vikindu FR, Pwani, Tanzania	39.299	-6.990
T3741	<i>Ptychadena nilotica</i>	CB 13.533	TZ	Vikindu FR, Pwani, Tanzania	39.299	-6.990
T3742	<i>Ptychadena nilotica</i>	CB 13.534	TZ	Vikindu FR, Pwani, Tanzania	39.299	-6.990
T5000	<i>Ptychadena nilotica</i>	MCZ A-32046	TZ	Baleni Pond, Mafia	39.803	-7.850
T3707	<i>Ptychadena oxyrhynchus</i>	CB 13.499	TZ	Ngumburuni FR, Pwani, Tanzania	39.066	-7.881
T4394	<i>Ptychadena oxyrhynchus</i>	MTSN 5746	TZ	Kilombero fr	NULL	NULL
T4395	<i>Ptychadena oxyrhynchus</i>	MTSN 5747	TZ	Kilombero fr	NULL	NULL
T3654	<i>Ptychadena porosissima</i>	CB 13.446	TZ	Kiwengoma FR, Pwani, Tanzania	NULL	NULL
T3655	<i>Ptychadena porosissima</i>	CB 13.447	TZ	Muyuyu FR, Pwani, Tanzania	NULL	NULL
T4407	<i>Ptychadena porosissima</i>	MTSN 5770	TZ	Ruaha National Park	35.053	-7.507
T3708	<i>Ptychadena sp.</i>	CB 13.500	TZ	Ngumburuni FR, Pwani, Tanzania	39.066	-7.881
T3758	<i>Ptychadena sp.</i>	CB 13.550	TZ	Ngumburuni FR, Pwani, Tanzania	39.066	-7.881
T3760	<i>Ptychadena sp.</i>	CB 13.552	TZ	Ngumburuni FR, Pwani, Tanzania	39.066	-7.881
T4579	<i>Ptychadena sp.</i>	BM 2002.370	TZ	Kazizumbwi FR	39.051	-6.934
T4580	<i>Ptychadena sp.</i>	BM 2005.946	TZ	Kazizumbwi FR	39.046	-6.950
T4600	<i>Ptychadena sp.</i>	BM 2002.761	TZ	Segoma FR	38.617	-4.898
T4805	<i>Ptychadena sp.</i>	WTS 8415	TZ	Unguja near Mchekeni village, Zanzibar	39.247	-6.190
T3686	<i>Pyxicephalus adspersus</i>	CB 13.478	TZ	Ndimba FR, Lindi, Tanzania	39.648	-9.629
T3687	<i>Pyxicephalus adspersus</i>	CB 13.479	TZ	Ndimba FR, Lindi, Tanzania	39.648	-9.629
T3688	<i>Pyxicephalus adspersus</i>	CB 13.480	TZ	Ndimba FR, Lindi, Tanzania	39.648	-9.629
T3689	<i>Pyxicephalus adspersus</i>	CB 13.481	TZ	Ndimba FR, Lindi, Tanzania	39.648	-9.629
T3690	<i>Pyxicephalus adspersus</i>	CB 13.482	TZ	Ndimba FR, Lindi, Tanzania	39.648	-9.629
T3691	<i>Pyxicephalus adspersus</i>	CB 13.483	TZ	Ndimba FR, Lindi, Tanzania	39.648	-9.629
T3692	<i>Pyxicephalus adspersus</i>	CB 13.484	TZ	Ndimba FR, Lindi, Tanzania	39.648	-9.629
T3693	<i>Pyxicephalus adspersus</i>	CB 13.485	TZ	Ndimba FR, Lindi, Tanzania	39.648	-9.629
T4405	<i>Pyxicephalus adspersus</i>	MTSN 5293	TZ	Ruaha National Park	35.053	-7.507
T3824	<i>Pyxicephalus edulis</i>	CB 13.618	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T3843	<i>Pyxicephalus edulis</i>	CB 13.637	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T4026	<i>Pyxicephalus edulis</i>	CB 13.676	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T4027	<i>Pyxicephalus edulis</i>	CB 13.677	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T4028	<i>Pyxicephalus edulis</i>	CB 13.678	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T4029	<i>Pyxicephalus edulis</i>	CB 13.679	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T4030	<i>Pyxicephalus edulis</i>	CB 13.680	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T4053	<i>Pyxicephalus edulis</i>	CB 13.703	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4072	<i>Pyxicephalus edulis</i>	CB 13.722	TZ	Zaraninge FR, Pwani, Tanzania	38.608	-6.137
T4584	<i>Pyxicephalus edulis</i>	BM 2002.437	TZ	Ruvu South FR	NULL	NULL
T4585	<i>Pyxicephalus edulis</i>	BM 2002.438	TZ	Ruvu South FR	38.878	-6.948
T5005	<i>Pyxicephalus edulis</i>	MCZ A-32011	TZ	Dondwe Forest	39.097	-7.065
T4790	<i>Scolecophorus vittatus</i>	WTS 1572	TZ	Kwamgumi, East Usambara, Tanzania	38.717	-4.950
T4791	<i>Scolecophorus vittatus</i>	WTS 1548	TZ	Kwamgumi, East Usambara, Tanzania	38.717	-4.950
T1930	<i>Spelaophryne methneri</i>	MCZ 32061	TZ	Rondo Plateau	39.205	-10.144
T4591	<i>Spelaophryne methneri</i>	BM 2000.216	TZ	Uluguru Mountians - Milawilia FR	37.750	-6.979
T4592	<i>Spelaophryne methneri</i>	BM 2000.217	TZ	Uluguru Mountians - Milawilia FR	37.750	-6.979

T4406	<i>Tomopterna wambensis</i>	MTSN 5397	TZ	Ruaha National Park	35.053	-7.507
T4855	<i>Xenopus laevis</i>	MTSN 7716	TZ	Kimboza Forest	37.804	-7.005
T4856	<i>Xenopus laevis</i>	MTSN 7717	TZ	Kimboza Forest	37.804	-7.005
T4857	<i>Xenopus laevis</i>	MTSN 7718	TZ	Kimboza Forest	37.804	-7.005
T2977	<i>Xenopus muelleri</i>	CB 13.928	TZ	Kilulu, Tanga, Tanzania	39.117	-4.749
T3087	<i>Xenopus muelleri</i>	CB 13.110	TZ	Litipo FR (edge), Lindi, Tanzania	39.511	-10.032
T3103	<i>Xenopus muelleri</i>	CB 13.126	TZ	Litipo FR (edge), Lindi, Tanzania	39.507	-10.030
T3104	<i>Xenopus muelleri</i>	CB 13.127	TZ	Litipo FR (edge), Lindi, Tanzania	39.507	-10.030
T3109	<i>Xenopus muelleri</i>	CB 13.132	TZ	Litipo FR (edge), Lindi, Tanzania	39.388	-9.994
T3161	<i>Xenopus muelleri</i>	CB 13.184	TZ	Litipo FR, Lindi, Tanzania	39.475	-10.050
T3182	<i>Xenopus muelleri</i>	CB 13.205	TZ	Noto Plateau, Lindi, Tanzania	39.374	-9.895
T3183	<i>Xenopus muelleri</i>	CB 13.206	TZ	Noto Plateau, Lindi, Tanzania	39.374	-9.895
T3184	<i>Xenopus muelleri</i>	CB 13.207	TZ	Noto Plateau, Lindi, Tanzania	39.374	-9.895
T3202	<i>Xenopus muelleri</i>	CB 13.225	TZ	Noto Plateau, Lindi, Tanzania	39.374	-9.895
T3283	<i>Xenopus muelleri</i>	CB 13.290	TZ	Makangaga FR, Lindi, Tanzania	39.292	-9.495
T3694	<i>Xenopus muelleri</i>	CB 13.486	TZ	Ngumburuni FR, Pwani, Tanzania	39.066	-7.881
T3695	<i>Xenopus muelleri</i>	CB 13.487	TZ	Ngumburuni FR, Pwani, Tanzania	39.066	-7.881
T3696	<i>Xenopus muelleri</i>	CB 13.488	TZ	Ngumburuni FR, Pwani, Tanzania	39.066	-7.881
T3697	<i>Xenopus muelleri</i>	CB 13.489	TZ	Ngumburuni FR, Pwani, Tanzania	39.066	-7.881
T3762	<i>Xenopus muelleri</i>	CB 13.554	TZ	Ngumburuni FR, Pwani, Tanzania	39.066	-7.881
T3763	<i>Xenopus muelleri</i>	CB 13.555	TZ	Ngumburuni FR, Pwani, Tanzania	39.066	-7.881
T3789	<i>Xenopus muelleri</i>	CB 13.593	TZ	Kibasira Swamp, Morogoro, Tanzania	36.228	-8.349
T3826	<i>Xenopus muelleri</i>	CB 13.620	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T3844	<i>Xenopus muelleri</i>	CB 13.638	TZ	Ruvu North FR, Pwani, Tanzania	38.970	-6.713
T4126	<i>Xenopus muelleri</i>	CB 13.776	TZ	Amboni caves, Tanga, Tanzania	39.048	-5.073
T4140	<i>Xenopus muelleri</i>	CB 13.790	TZ	Amboni caves, Tanga, Tanzania	39.048	-5.073
T4141	<i>Xenopus muelleri</i>	CB 13.791	TZ	Amboni caves, Tanga, Tanzania	39.048	-5.073
T4142	<i>Xenopus muelleri</i>	CB 13.792	TZ	Amboni caves, Tanga, Tanzania	39.048	-5.073
T4150	<i>Xenopus muelleri</i>	CB 13.800	TZ	Amboni caves, Tanga, Tanzania	39.048	-5.073
T4190	<i>Xenopus muelleri</i>	CB 13.840	TZ	Mabayani bwawa, Tanga, Tanzania	38.924	-5.034
T4211	<i>Xenopus muelleri</i>	CB 13.861	TZ	Horohoro, Tanga, Tanzania	39.102	-4.632
T4212	<i>Xenopus muelleri</i>	CB 13.862	TZ	Horohoro, Tanga, Tanzania	39.102	-4.632
T4213	<i>Xenopus muelleri</i>	CB 13.863	TZ	Horohoro, Tanga, Tanzania	39.102	-4.632
T4214	<i>Xenopus muelleri</i>	CB 13.864	TZ	Horohoro, Tanga, Tanzania	39.102	-4.632
T4215	<i>Xenopus muelleri</i>	CB 13.865	TZ	Horohoro, Tanga, Tanzania	39.102	-4.632
T4232	<i>Xenopus muelleri</i>	CB 13.882	TZ	Horohoro, Tanga, Tanzania	39.102	-4.632
T4265	<i>Xenopus muelleri</i>	CB 13.918	TZ	Kilulu, Tanga, Tanzania	39.117	-4.749
T4266	<i>Xenopus muelleri</i>	CB 13.919	TZ	Kilulu, Tanga, Tanzania	39.117	-4.749
T4593	<i>Xenopus muelleri</i>	BM 2002.439	TZ	Ruvu South FR	38.813	-6.895
T4594	<i>Xenopus muelleri</i>	BM 2002.440	TZ	Ruvu South FR	38.813	-6.895
T4595	<i>Xenopus muelleri</i>	BM 2005.947	TZ	Kazizumbwi FR	39.062	-6.934
T4596	<i>Xenopus muelleri</i>	BM 2005.175	TZ	Uluguru Mountians - Mvuha FR	37.838	-7.179
T4597	<i>Xenopus muelleri</i>	BM 2005.176	TZ	Uluguru Mountians - Mvuha FR	37.838	-7.179
T4598	<i>Xenopus muelleri</i>	BM 2002.895	TZ	Mgambo F.R.	38.813	-4.792
T4599	<i>Xenopus muelleri</i>	BM 2002.371	TZ	Kazizumbwi FR	39.062	-6.934
T4852	<i>Xenopus muelleri</i>	MTSN 7713	TZ	Kimboza Forest	37.804	-7.005
T4853	<i>Xenopus muelleri</i>	MTSN 7714	TZ	Kimboza Forest	NULL	NULL
T4854	<i>Xenopus muelleri</i>	MTSN 7715	TZ	Kimboza Forest	37.804	-7.005
T4931	<i>Xenopus muelleri</i>	MTSN 9513	TZ	Segoma Forest, Camp, East Usambara	38.758	-4.981
T4932	<i>Xenopus muelleri</i>	MTSN 9514	TZ	Segoma Forest, Camp, East Usambara	38.758	-4.981
T5006	<i>Xenopus muelleri</i>	MCZ A-32044	TZ	Kilongwe	39.828	-7.878

Supplementary Materials: Chapter I

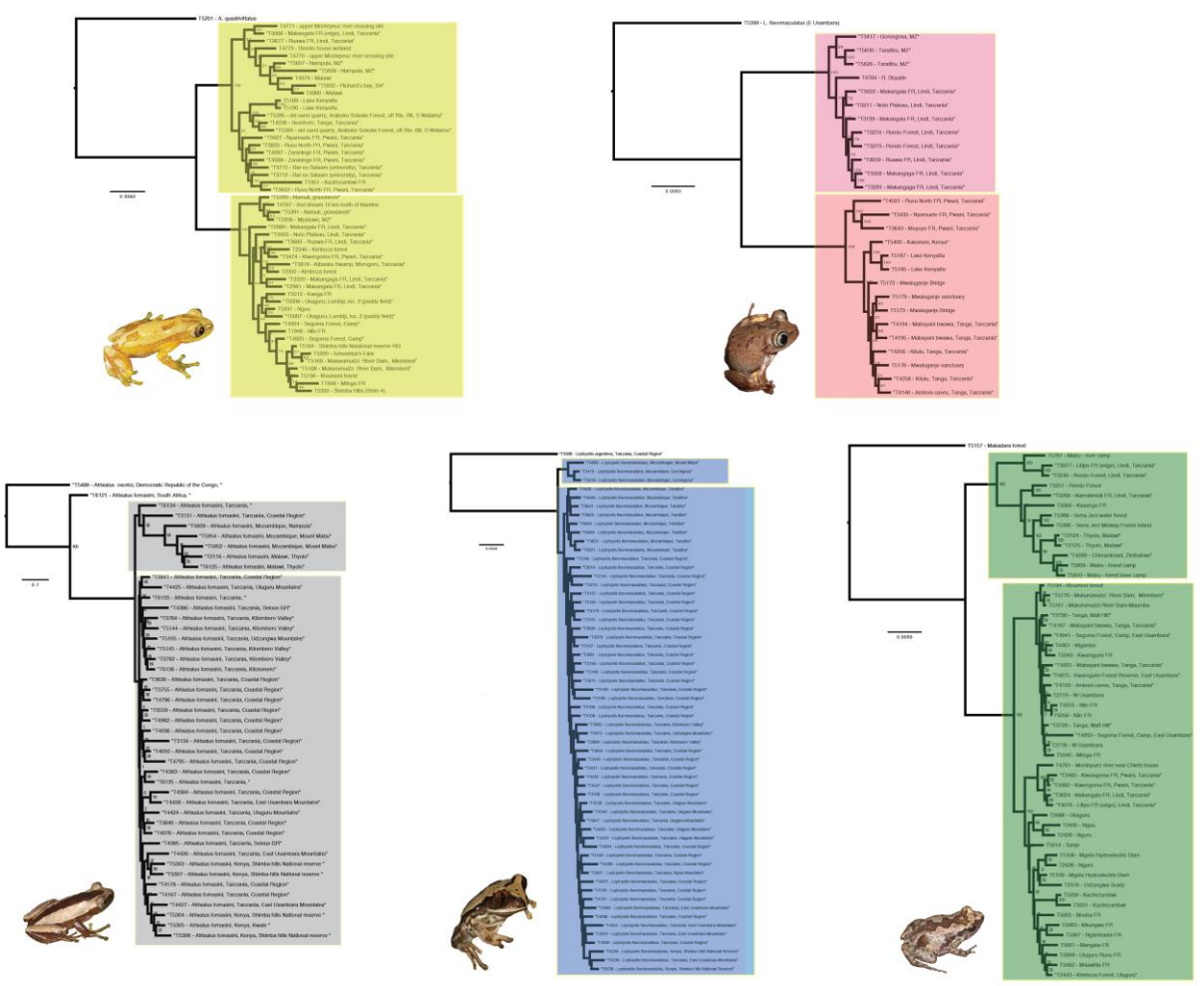


Fig. S1. Phylogenies from RAD-seq data using 40% missing data.

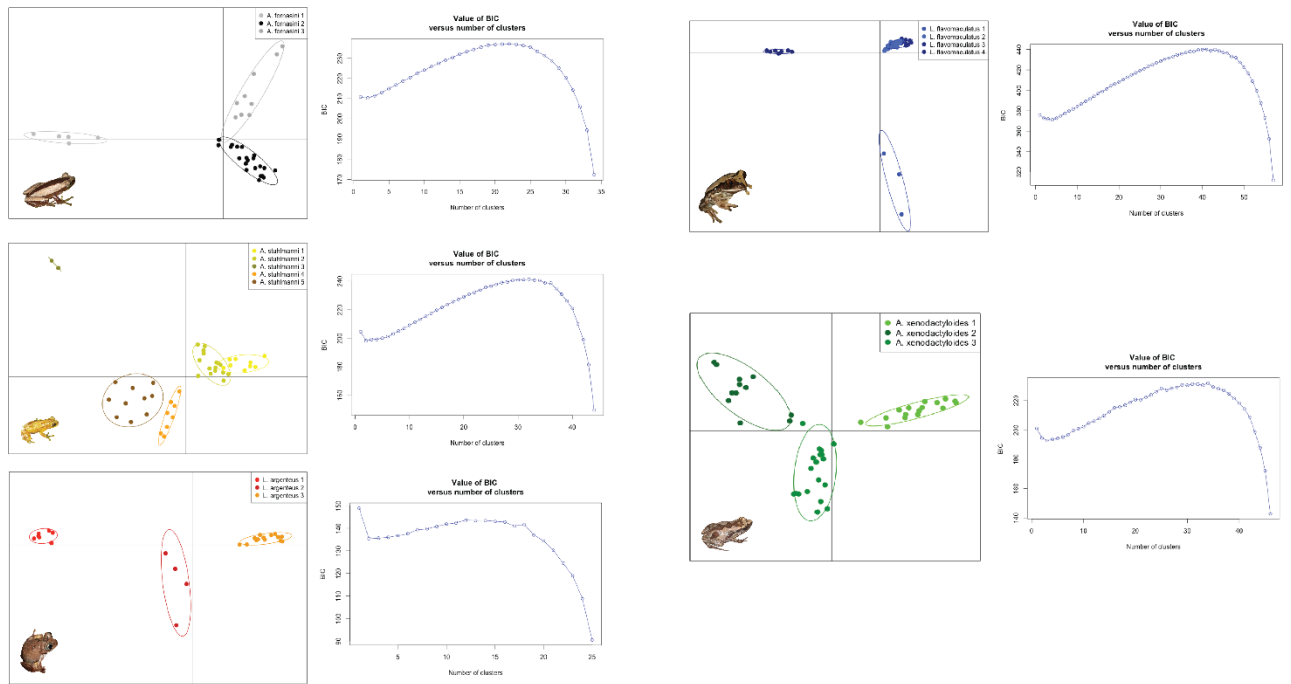


Fig. S2. Full species clade analysis using Discriminant Function analysis of Principal Components using the Adegenet R package. (Jombart et al. 2008). Number of clusters plotted along with corresponding BIC values.

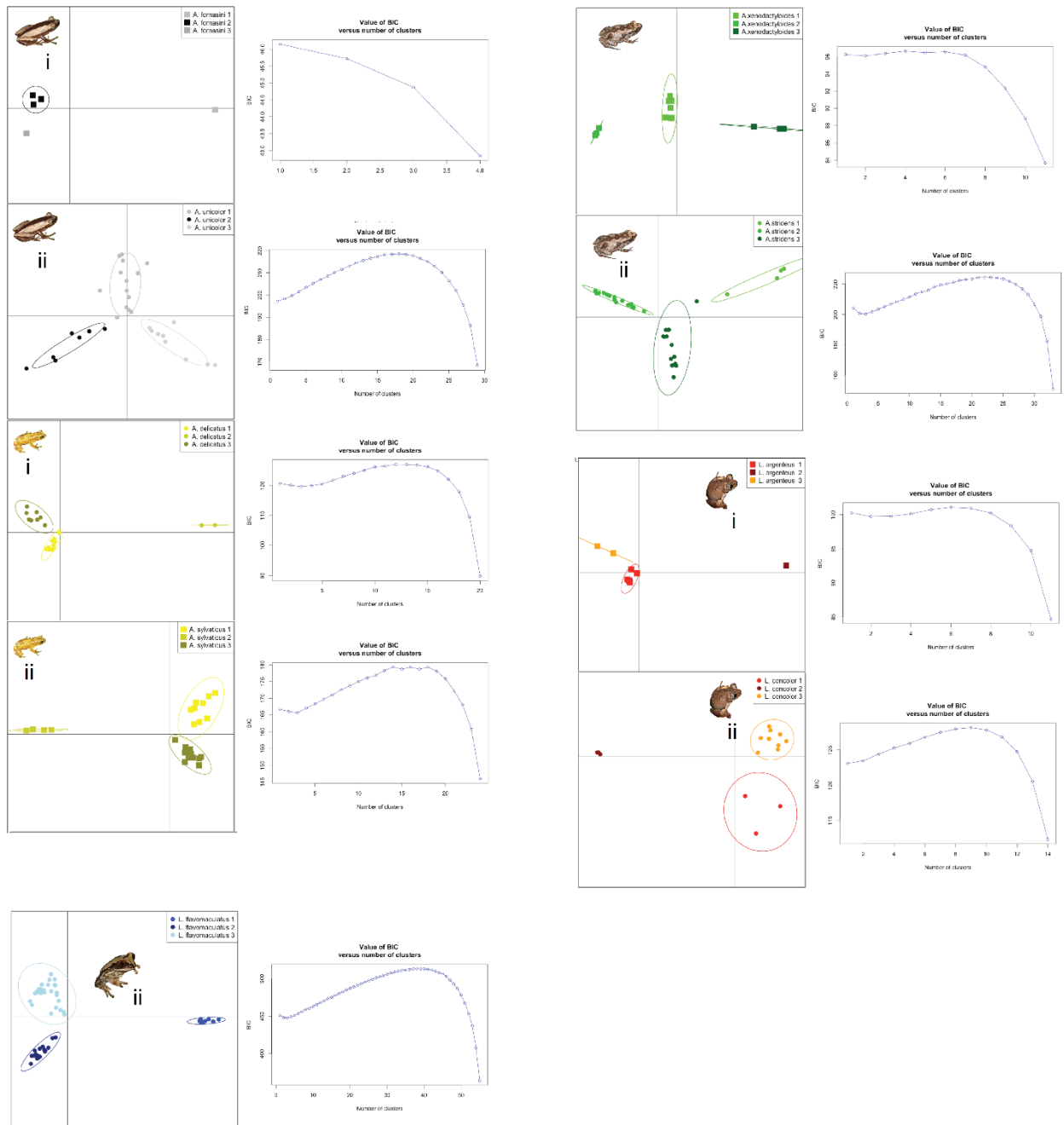


Fig. S3. Subclade analysis using Discriminant Function analysis of Principal Components using the Adegenet R package. (Jombart et al. 2008). . Number of clusters plotted along with corresponding BIC values.

Table S1. Sample IDs for RAD-seq individuals. ID name and locality, species clade, Subclade (identified on phylogeny), population (identified by DAPC analysis), and coordinates of where the sample was collected. * denotes that the sample was removed for population analysis due to poor sequence data or being an outgroup.

ID	Species clade	Subclade	population	Long	Lat
T3139 - Makangala FR, Lindi, Tanzania	<i>Leptopelis argenteus</i>	i	<i>argenteus_2</i>	39.38803	-9.99418
T3211 - Noto Plateau, Lindi, Tanzania	<i>Leptopelis argenteus</i>	i	<i>argenteus_2</i>	39.37409	-9.89532
T3273 - Rondo Forest, Lindi, Tanzania	<i>Leptopelis argenteus</i>	i	<i>argenteus_2</i>	39.19714	-10.12126
T3274 - Rondo Forest, Lindi, Tanzania	<i>Leptopelis argenteus</i>	i	<i>argenteus_2</i>	39.19714	-10.12126
T3291 - Makangaga FR, Lindi, Tanzania	<i>Leptopelis argenteus</i>	i	<i>argenteus_2</i>	39.29196	-9.49454
T3308 - Makangaga FR, Lindi, Tanzania	<i>Leptopelis argenteus</i>	i	<i>argenteus_2</i>	39.29196	-9.49454
T3417 - Gorongosa, MZ	<i>Leptopelis argenteus</i>	i	<i>argenteus_3</i>	34.26533	-18.678761
T3659 - Ruawa FR, Lindi, Tanzania	<i>Leptopelis argenteus</i>	i	<i>argenteus_2</i>	39.56871	-9.72995
T4784 - R. Diquide	<i>Leptopelis argenteus</i>	i	<i>argenteus_2</i>	40.42827	-11.883333
T5626 - Taratibu, MZ	<i>Leptopelis argenteus</i>	i	<i>argenteus_1</i>	39.68658	-12.821783
T5630 - Taratibu, MZ	<i>Leptopelis argenteus</i>	i	<i>argenteus_1</i>	39.68658	-12.821783
T3435 - Nyamuete FR, Pwani, Tanzania	<i>Leptopelis argenteus</i>	ii	<i>concolor_3</i>	39.03441	-8.32557
T3643 - Muyuyu FR, Pwani, Tanzania	<i>Leptopelis argenteus</i>	ii	<i>concolor_3</i>	39.04373	-7.94835
T4021 - Ruvu North FR, Pwani, Tanzania	<i>Leptopelis argenteus</i>	ii	<i>concolor_3</i>	38.8713	-6.71173
T4148 - Amboni caves, Tanga, Tanzania	<i>Leptopelis argenteus</i>	ii	<i>concolor_2</i>	39.04843	-5.0731
T4194 - Mabayani bwawa, Tanga, Tanzania	<i>Leptopelis argenteus</i>	ii	<i>concolor_2</i>	38.92436	-5.03361
T4195 - Mabayani bwawa, Tanga, Tanzania	<i>Leptopelis argenteus</i>	ii	<i>concolor_2</i>	38.92436	-5.03361
T4256 - Kilulu, Tanga, Tanzania	<i>Leptopelis argenteus</i>	ii	<i>concolor_2</i>	39.11713	-4.74908
T4258 - Kilulu, Tanga, Tanzania	<i>Leptopelis argenteus</i>	ii	<i>concolor_2</i>	39.11713	-4.74908
T5172 - Mwaluganje Bridge	<i>Leptopelis argenteus</i>	ii	<i>concolor_2</i>	39.41731	-4.15821
T5173 - Mwaluganje Bridge	<i>Leptopelis argenteus</i>	ii	<i>concolor_2</i>	39.41731	-4.15821
T5178 - Mwaluganje sanctuary	<i>Leptopelis argenteus</i>	ii	<i>concolor_2</i>	39.44002	-4.1278
T5179 - Mwaluganje sanctuary	<i>Leptopelis argenteus</i>	ii	<i>concolor_2</i>	39.44002	-4.1278
T5185 - Lake Kenyatta	<i>Leptopelis argenteus</i>	ii	<i>concolor_1</i>	40.69678	-2.3854444
T5187 - Lake Kenyatta	<i>Leptopelis argenteus</i>	ii	<i>concolor_1</i>	40.69678	-2.3854444
T5400 - Kakoneni, Kenya	<i>Leptopelis argenteus</i>	ii	<i>concolor_1</i>	39.86283	-3.1699667
T3022 - Makangala FR, Lindi, Tanzania	<i>Leptopelis argenteus</i>	i*	-	39.38803	-9.99418
T3416 - Mozambique, Gorongosa	<i>Leptopelis flavomaculatus</i>	i	<i>flavomaculatus_moz</i>	34.26533	-18.678761
T3419 - Mozambique, Gorongosa	<i>Leptopelis flavomaculatus</i>	i	<i>flavomaculatus_moz</i>	34.26533	-18.678761
T4606 - Mozambique, Mount Mabu	<i>Leptopelis flavomaculatus</i>	i	<i>flavomaculatus_moz</i>	36.58756	-16.313055
T3802 - Tanzania, Kibasira swamp, Kilombero valley	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_1</i>	36.2277	-8.34888
T2641 - Tanzania, Nguu Mountains	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_1</i>	37.47162	-5.539355
T4540 - Tanzania, Mvuhha FR, Uluguru Mountains	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_1</i>	37.8375	-7.179167
T4100 - Tanzania, Gendagenda North FR, Tanga	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_1</i>	38.64486	-5.58302
T3446 - Tanzania, Kiwengoma FR, Pwani	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_1</i>	38.90269	-8.30435
T3447 - Tanzania, Kiwengoma FR, Pwani	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_1</i>	38.90269	-8.30435
T4199 - Tanzania, Mabayani bwawa, Tanga	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_1</i>	38.92436	-5.03361
T4537 - Tanzania, Milawilia FR, Uluguru Mountains	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_1</i>	37.75	-6.979167
T4847 - Tanzania, Kimboza forest, Uluguru Mountains	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_1</i>	37.80356	-7.005459

T4538 - Tanzania, Mkungwe FR, Uluguru Mountains	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_1</i>	37.915	-6.868611
T4075 - Tanzania, Zaraninge FR, Pwani	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_1</i>	38.60755	-6.13694
T4098 - Tanzania, Gendagenda North FR, Tanga	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_1</i>	38.64486	-5.58302
T4101 - Tanzania, Gendagenda North FR, Tanga	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_1</i>	38.64486	-5.58302
T4534 - Tanzania, Nilo FR, East Usambara	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_1</i>	38.6625	-4.904444
T4960 - Tanzania, Segoma FR, East Usambara	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_1</i>	38.7615	-4.97643
T4970 - Tanzania, Segoma FR, East Usambara	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_1</i>	38.7615	-4.97643
T4200 - Tanzania, Mabayani bwawa, Tanga	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_1</i>	38.92436	-5.03361
T3431 - Tanzania, Nyamuete FR, Pwani	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_1</i>	39.03702	-8.30865
T2480 - Tanzania, Kazimzumbwi FR, Pwani	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_1</i>	39.04028	-6.944556
T3768 - Tanzania, Kibasira swamp, Kilombero valley	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_1</i>	39.06615	-7.88088
T4384 - Dar es Salaam, Tanzania	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_1</i>	39.28574	-6.786671
T5238 - Kenya, Shimba Hills lodge	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_1</i>	39.39564	-4.2375
T5239 - Kenya, Shimba Hills lodge	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_1</i>	39.39564	-4.2375
T3644 - Tanzania, Muyuyu FR, Pwani	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_1</i>	39.04373	-7.94835
T4672 - Tanzania, Chita/Funo, USFR	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_1</i>	35.89459	-8.5279245
T3809 - Tanzania, Kibasira swamp, Kilombero valley	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_1</i>	36.31764	-8.31238
T4923 - Tanzania, Kimboza forest, Uluguru Mountains	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_1</i>	37.80356	-7.005459
T3432 - Tanzania, Nyamuete FR, Pwani	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_1</i>	39.03702	-8.30865
T3189 - Tanzania, Noto plateau, Lindi	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_2</i>	39.37409	-9.89532
T3190 - Tanzania, Noto plateau, Lindi	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_2</i>	39.37409	-9.89532
T3191 - Tanzania, Noto plateau, Lindi	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_2</i>	39.37409	-9.89532
T3192 - Tanzania, Noto plateau, Lindi	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_2</i>	39.37409	-9.89532
T3193 - Tanzania, Noto plateau, Lindi	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_2</i>	39.37409	-9.89532
T3194 - Tanzania, Noto plateau, Lindi	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_2</i>	39.37409	-9.89532
T3195 - Tanzania, Noto plateau, Lindi	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_2</i>	39.37409	-9.89532
T3196 - Tanzania, Noto plateau, Lindi	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_2</i>	39.37409	-9.89532
T3198 - Tanzania, Noto plateau, Lindi	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_2</i>	39.37409	-9.89532
T3210 - Tanzania, Noto plateau, Lindi	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_2</i>	39.37409	-9.89532
T2979 - Tanzania, Makangala FR, Lindi	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_2</i>	39.38803	-9.99418
T3009 - Tanzania, Makangala FR, Lindi	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_2</i>	39.38803	-9.99418
T3010 - Tanzania, Makangala FR, Lindi	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_2</i>	39.38803	-9.99418
T3107 - Tanzania, Litipo FR (edge), Lindi	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_2</i>	39.38803	-9.99418
T3108 - Tanzania, Litipo FR (edge), Lindi	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_2</i>	39.38803	-9.99418
T3157 - Tanzania, Litipo FR, Lindi	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_2</i>	39.4752	-10.04952
T3179 - Tanzania, Litipo FR, Lindi	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_2</i>	39.4752	-10.04952
T3074 - Tanzania, Litipo FR (edge), Lindi	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_2</i>	39.50674	-10.03041
T3081 - Tanzania, Litipo FR (edge), Lindi	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_2</i>	39.51065	-10.03238
T5621 - Mozambique, Taratibu	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_3</i>	39.68658	-12.821783
T5625 - Mozambique, Taratibu	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_3</i>	39.68658	-12.821783
T5628 - Mozambique, Taratibu	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_3</i>	39.68658	-12.821783
T5629 - Mozambique, Taratibu	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_3</i>	39.68658	-12.821783
T5631 - Mozambique, Taratibu	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_3</i>	39.68658	-12.821783
T5643 - Mozambique, Taratibu	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_3</i>	39.68658	-12.821783
T5645 - Mozambique, Taratibu	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_3</i>	39.68658	-12.821783
T5648 - Mozambique, Taratibu	<i>Leptopelis flavomaculatus</i>	ii	<i>flavomaculatus_3</i>	39.68658	-12.821783

T3418 - Mozambique, Gorongosa	<i>Leptopelis flavomaculatus</i>	ii*	-	34.26533	-18.678761
T5399 - L. flavomaculatus (E Usambara)	<i>Leptopelis flavomaculatus</i>	ii*	-	38.62663	-5.100033
T2116 - Pond behind Chawani Bungalow, Malawi	<i>Afrixalus fornasini</i>	i	<i>fornasini</i>	35.0638	-16
T6125 - Pond behind Chawani Bungalow, Malawi	<i>Afrixalus fornasini</i>	i	<i>fornasini</i>	35.06446	-16.077674
T5952 - Mount Mabu - river camp, Mozambique	<i>Afrixalus fornasini</i>	i	<i>fornasini</i>	36.44378	-16.281528
T5954 - Mount Mabu - river camp, Mozambique	<i>Afrixalus fornasini</i>	i	<i>fornasini</i>	36.44378	-16.281528
T5609 - Nampula, Mozambique	<i>Afrixalus fornasini</i>	i	<i>fornasini</i>	39.28822	-15.14475
T6121 - Richard's Bay, South Africa	<i>Afrixalus fornasini</i>	i*	-	32.01	-28.78
T6134 - Pemba; Nguru Mountains, Tanzania	<i>Afrixalus fornasini</i>	i*	-	37.52477	-6.030439
T6136 - Kitolomero,USFR, Tanzania	<i>Afrixalus fornasini</i>	ii	<i>unicolor_1</i>	35.98376	-8.39463
T5144 - Kilombero Valley, Tanzania	<i>Afrixalus fornasini</i>	ii	<i>unicolor_1</i>	36.09133	-8.311798
T5145 - Kilombero Valley, Tanzania	<i>Afrixalus fornasini</i>	ii	<i>unicolor_1</i>	36.09133	-8.311798
T3782 - Kibasira Swamp, Morogoro, Tanzania	<i>Afrixalus fornasini</i>	ii	<i>unicolor_1</i>	36.2277	-8.34888
T3784 - Kibasira Swamp, Morogoro, Tanzania	<i>Afrixalus fornasini</i>	ii	<i>unicolor_1</i>	36.2277	-8.34888
T4385 - Ruiipa, Ranger post, Tanzania	<i>Afrixalus fornasini</i>	ii	<i>unicolor_1</i>	37.03472	-9.168889
T4386 - Ruiipa, Ranger post, Tanzania	<i>Afrixalus fornasini</i>	ii	<i>unicolor_1</i>	37.03472	-9.168889
T3559 - Muyuyu FR, Pwani, Tanzania	<i>Afrixalus fornasini</i>	ii	<i>unicolor_3</i>	39.04373	-7.94835
T3636 - Muyuyu FR, Pwani, Tanzania	<i>Afrixalus fornasini</i>	ii	<i>unicolor_3</i>	39.04373	-7.94835
T6135 - Nguu Forest Reserve, Nguu, Tanzania	<i>Afrixalus fornasini</i>	ii	<i>unicolor_3</i>	37.49361	-5.4791667
T4076 - Zaraninge FR, Pwani, Tanzania	<i>Afrixalus fornasini</i>	ii	<i>unicolor_3</i>	38.60755	-6.13694
T4426 - Kwamgumi FR. Tanzania	<i>Afrixalus fornasini</i>	ii	<i>unicolor_3</i>	38.73278	-4.923056
T4795 - Ruvu South FR, Tanzania	<i>Afrixalus fornasini</i>	ii	<i>unicolor_3</i>	38.8125	-6.895222
T4167 - Mabayani bwawa, Tanga, Tanzania	<i>Afrixalus fornasini</i>	ii	<i>unicolor_2</i>	38.92436	-5.03361
T4178 - Mabayani bwawa, Tanga, Tanzania	<i>Afrixalus fornasini</i>	ii	<i>unicolor_2</i>	38.92436	-5.03361
T3841 - Ruvu North FR, Pwani, Tanzania	<i>Afrixalus fornasini</i>	ii	<i>unicolor_3</i>	38.97007	-6.71349
T5306 - Kivumoni forest, Kenya	<i>Afrixalus fornasini</i>	ii	<i>unicolor_2</i>	39.35	-4.25
T5303 - Shimba Lodge, Kenya	<i>Afrixalus fornasini</i>	ii	<i>unicolor_2</i>	39.39564	-4.2375
T5304 - Shimba Lodge, Kenya	<i>Afrixalus fornasini</i>	ii	<i>unicolor_2</i>	39.39564	-4.2375
T5305 - Kwale, Kenya	<i>Afrixalus fornasini</i>	ii	<i>unicolor_2</i>	39.42547	-4.3752167
T5307 - Scheldrick's Falls, Kenya	<i>Afrixalus fornasini</i>	ii	<i>unicolor_2</i>	39.43096	-4.27553
T5105 - Kitolomero,USFR, Tanzania	<i>Afrixalus fornasini</i>	ii	<i>unicolor_1</i>	35.9824	-8.39521
T6133 - Sali Forest Reserve, Mahenge, Tanzania	<i>Afrixalus fornasini</i>	ii	<i>unicolor_1</i>	36.68831	-8.9659444
T4425 - Uluguru Mountains - Mvuha FR, Tanzania	<i>Afrixalus fornasini</i>	ii	<i>unicolor_3</i>	37.8375	-7.179167
T3840 - Ruvu North FR, Pwani, Tanzania	<i>Afrixalus fornasini</i>	ii	<i>unicolor_3</i>	38.97007	-6.71349
T3755 - Vikindu FR, Pwani, Tanzania	<i>Afrixalus fornasini</i>	ii	<i>unicolor_3</i>	39.29749	-6.99365
T3131 - Makangala FR, Lindi, Tanzania	<i>Afrixalus fornasini</i>	ii	<i>unicolor_3</i>	39.38803	-9.99418
T3134 - Makangala FR, Lindi, Tanzania	<i>Afrixalus fornasini</i>	ii	<i>unicolor_3</i>	39.38803	-9.99418
T4036 - Mafia island, Tanzania	<i>Afrixalus fornasini</i>	ii	<i>unicolor_3</i>	39.71429	-7.96261
T4050 - Mafia island, Tanzania	<i>Afrixalus fornasini</i>	ii	<i>unicolor_3</i>	39.79531	-7.84898
T4424 - Uluguru Mountains - Mvuha FR, Tanzania	<i>Afrixalus fornasini</i>	ii*	-	37.8375	-7.179167
T4427 - Nilo FR, Tanzania	<i>Afrixalus fornasini</i>	ii*	-	38.6625	-4.904444
T4428 - Nilo FR, Tanzania	<i>Afrixalus fornasini</i>	ii*	-	38.6625	-4.904444
T4796 - Ruvu South FR, Tanzania	<i>Afrixalus fornasini</i>	ii*	-	38.76217	-6.901083
T4834 - Tanzania, Kazimzumbwi FR, Pwani	<i>Afrixalus fornasini</i>	ii*	-	39.05347	-6.942528
T4383 - Dar es Salaam, Tanzania	<i>Afrixalus fornasini</i>	ii*	-	39.28574	-6.786671
T4982 - Baleni Pond, Mafia, Tanzania	<i>Afrixalus fornasini</i>	ii*	-	39.80253	-7.849772

T4087 - Zaraninge FR, Pwani, Tanzania	<i>Afrixalus stuhlmanni</i>	i	<i>delicatus_1</i>	38.60755	-6.13694
T4088 - Zaraninge FR, Pwani, Tanzania	<i>Afrixalus stuhlmanni</i>	i	<i>delicatus_1</i>	38.60755	-6.13694
T3832 - Ruvu North FR, Pwani, Tanzania	<i>Afrixalus stuhlmanni</i>	i	<i>delicatus_1</i>	38.97007	-6.71349
T3833 - Ruvu North FR, Pwani, Tanzania	<i>Afrixalus stuhlmanni</i>	i	<i>delicatus_1</i>	38.97007	-6.71349
T1951 - Kazimzumbwi FR	<i>Afrixalus stuhlmanni</i>	i	<i>delicatus_1</i>	39.04028	-6.944556
T3712 - Dar es Salaam (university), Tanzania	<i>Afrixalus stuhlmanni</i>	i	<i>delicatus_1</i>	39.20388	-6.77875
T3715 - Dar es Salaam (university), Tanzania	<i>Afrixalus stuhlmanni</i>	i	<i>delicatus_1</i>	39.20388	-6.77875
T4236 - Horohoro, Tanga, Tanzania	<i>Afrixalus stuhlmanni</i>	i	<i>delicatus_1</i>	39.10166	-4.63209
T5394 - old sand quarry, Arabuko Sokoke Forest	<i>Afrixalus stuhlmanni</i>	i	<i>delicatus_1</i>	39.86667	-3.33333
T5395 - old sand quarry, Arabuko Sokoke Forest	<i>Afrixalus stuhlmanni</i>	i	<i>delicatus_1</i>	39.86667	-3.33333
T5189 - Lake Kenyatta	<i>Afrixalus stuhlmanni</i>	i	<i>delicatus_3</i>	40.68583	-2.4088889
T5190 - Lake Kenyatta	<i>Afrixalus stuhlmanni</i>	i	<i>delicatus_3</i>	40.68583	-2.4088889
T4979 - Malawi	<i>Afrixalus stuhlmanni</i>	i	<i>delicatus_2</i>	35.71076	-16.04831
T4980 - Malawi	<i>Afrixalus stuhlmanni</i>	i	<i>delicatus_2</i>	35.71076	-16.04831
T4770 - upper Montepezuz river crossing site	<i>Afrixalus stuhlmanni</i>	i	<i>delicatus_2</i>	38.58678	-13.407944
T5607 - Nampula, MZ	<i>Afrixalus stuhlmanni</i>	i	<i>delicatus_2</i>	39.28822	-15.14475
T5608 - Nampula, MZ	<i>Afrixalus stuhlmanni</i>	i	<i>delicatus_2</i>	39.28822	-15.14475
T3066 - Makangala FR (edge), Lindi, Tanzania	<i>Afrixalus stuhlmanni</i>	i	<i>delicatus_2</i>	39.36913	-9.98237
T3677 - Ruawa FR, Lindi, Tanzania	<i>Afrixalus stuhlmanni</i>	i	<i>delicatus_2</i>	39.56871	-9.72995
T4773 - Dereks house wetland	<i>Afrixalus stuhlmanni</i>	i	<i>delicatus_2</i>	40.35416	-12.933333
T5932 - Richard's bay, SA	<i>Afrixalus stuhlmanni</i>	i*	-	32.01	-28.78
T4771 - upper Montepezuz river crossing site	<i>Afrixalus stuhlmanni</i>	i*	-	38.58678	-13.407944
T1946 - Nilo FR	<i>Afrixalus stuhlmanni</i>	i*	-	38.66253	-4.940944
T3427 - Nyamuete FR, Pwani, Tanzania	<i>Afrixalus stuhlmanni</i>	i*	-	39.03441	-8.32557
T3320 - Makangaga FR, Lindi, Tanzania	<i>Afrixalus stuhlmanni</i>	i*	-	39.29196	-9.49454
T5007 - Ukaguru; Lumbiji, loc. 2 (paddy field)	<i>Afrixalus stuhlmanni</i>	ii	<i>sylvaticus_2</i>	36.98424	-6.614667
T5008 - Ukaguru; Lumbiji, loc. 2 (paddy field)	<i>Afrixalus stuhlmanni</i>	ii	<i>sylvaticus_2</i>	36.98424	-6.614667
T5931 - Nguu	<i>Afrixalus stuhlmanni</i>	ii	<i>sylvaticus_2</i>	37.49361	-5.4791667
T5012 - Kanga FR	<i>Afrixalus stuhlmanni</i>	ii	<i>sylvaticus_2</i>	37.7243	-5.959949
T1948 - Mlinga FR	<i>Afrixalus stuhlmanni</i>	ii	<i>sylvaticus_3</i>	38.74781	-5.059417
T4924 - Segoma Forest, Camp	<i>Afrixalus stuhlmanni</i>	ii	<i>sylvaticus_3</i>	38.75825	-4.98094
T4925 - Segoma Forest, Camp	<i>Afrixalus stuhlmanni</i>	ii	<i>sylvaticus_3</i>	38.75825	-4.98094
T5392 - Shimba Hills (Shim 4)	<i>Afrixalus stuhlmanni</i>	ii	<i>sylvaticus_3</i>	39.3405	-4.2664167
T5168 - Mukurumudzi River Dam, Miembeni	<i>Afrixalus stuhlmanni</i>	ii	<i>sylvaticus_3</i>	39.42547	-4.3752167
T5169 - Mukurumudzi River Dam, Miembeni	<i>Afrixalus stuhlmanni</i>	ii	<i>sylvaticus_3</i>	39.42547	-4.3752167
T5200 - Scheldrick's Falls	<i>Afrixalus stuhlmanni</i>	ii	<i>sylvaticus_3</i>	39.43096	-4.27553
T5184 - Shimba hills Nataional reserve HQ	<i>Afrixalus stuhlmanni</i>	ii	<i>sylvaticus_3</i>	39.44453	-4.1760278
T5196 - Kivumoni forest	<i>Afrixalus stuhlmanni</i>	ii	<i>sylvaticus_2</i>	39.44453	-4.1760278
T3818 - Kibasira Swamp, Morogoro, Tanzania	<i>Afrixalus stuhlmanni</i>	ii	<i>sylvaticus_2</i>	36.31764	-8.31238
T2346 - Kimboza forest	<i>Afrixalus stuhlmanni</i>	ii	<i>sylvaticus_2</i>	37.80213	-7.002231
T2350 - Kimboza forest	<i>Afrixalus stuhlmanni</i>	ii	<i>sylvaticus_2</i>	37.80213	-7.002231
T3474 - Kiwengoma FR, Pwani, Tanzania	<i>Afrixalus stuhlmanni</i>	ii	<i>sylvaticus_2</i>	38.90269	-8.30435
T3203 - Noto Plateau, Lindi, Tanzania	<i>Afrixalus stuhlmanni</i>	ii	<i>sylvaticus_2</i>	39.37409	-9.89532
T2980 - Makangala FR, Lindi, Tanzania	<i>Afrixalus stuhlmanni</i>	ii	<i>sylvaticus_2</i>	39.38803	-9.99418
T2981 - Makangala FR, Lindi, Tanzania	<i>Afrixalus stuhlmanni</i>	ii	<i>sylvaticus_2</i>	39.38803	-9.99418
T3683 - Ruawa FR, Lindi, Tanzania	<i>Afrixalus stuhlmanni</i>	ii	<i>sylvaticus_2</i>	39.56871	-9.72995

T5390 - Namuli, grasslands	<i>Afrivalus stuhlmanni</i>	ii	<i>sylvaticus_1</i>	37.07196	-15.384275
T5391 - Namuli, grasslands	<i>Afrivalus stuhlmanni</i>	ii	<i>sylvaticus_1</i>	37.07196	-15.384275
T5936 - Mpaluwe, MZ	<i>Afrivalus stuhlmanni</i>	ii	<i>sylvaticus_1</i>	38.31645	-14.91522
T4767 - 2nd stream 12 km north of Namina	<i>Afrivalus stuhlmanni</i>	ii	<i>sylvaticus_1</i>	38.73536	-14.847361
T4289 - Chimanimani, Zimbabwe	<i>Arthroleptis xenodactyloides</i>	i	<i>xenodactyloides_2</i>	32.98439	-19.891993
T2124 - Thyolo, Malawi	<i>Arthroleptis xenodactyloides</i>	i	<i>xenodactyloides_3</i>	35.0638	-16.0769
T2125 - Thyolo, Malawi	<i>Arthroleptis xenodactyloides</i>	i	<i>xenodactyloides_3</i>	35.0638	-16.0769
T5388 - Serra Jeci water forest	<i>Arthroleptis xenodactyloides</i>	i	<i>xenodactyloides_3</i>	35.17778	-12.851208
T5386 - Serra Jeci Midway Forest Island	<i>Arthroleptis xenodactyloides</i>	i	<i>xenodactyloides_3</i>	35.18105	-12.849248
T5809 - Mabu - forest camp	<i>Arthroleptis xenodactyloides</i>	i	<i>xenodactyloides_2</i>	36.40006	-16.286222
T5810 - Mabu - forest base camp	<i>Arthroleptis xenodactyloides</i>	i	<i>xenodactyloides_2</i>	36.40006	-16.286222
T5060 - Kasanga FR	<i>Arthroleptis xenodactyloides</i>	i	<i>xenodactyloides_1</i>	37.77393	-7.191166
T3251 - Rondo Forest	<i>Arthroleptis xenodactyloides</i>	i	<i>xenodactyloides_1</i>	39.19999	-10.11922
T3268 - Namatimbili FR, Lindi, Tanzania	<i>Arthroleptis xenodactyloides</i>	i	<i>xenodactyloides_1</i>	39.23778	-9.11064
T5781 - Mabu - river camp	<i>Arthroleptis xenodactyloides</i>	i	<i>xenodactyloides_3</i>	36.44378	-16.281528
T3248 - Rondo Forest, Lindi, Tanzania	<i>Arthroleptis xenodactyloides</i>	i	<i>xenodactyloides_3</i>	39.19999	-10.11922
T3077 - Litipo FR (edge), Lindi, Tanzania	<i>Arthroleptis xenodactyloides</i>	i	<i>xenodactyloides_3</i>	39.51065	-10.03238
T2729 - Tanga, Mafi Hill	<i>Arthroleptis xenodactyloides</i>	ii	<i>stridens_1</i>	38.14093	-4.923429
T2730 - Tanga, Mafi Hill	<i>Arthroleptis xenodactyloides</i>	ii	<i>stridens_1</i>	38.14093	-4.923429
T2718 - W Usambara	<i>Arthroleptis xenodactyloides</i>	ii	<i>stridens_1</i>	38.27019	-4.714649
T2719 - W Usambara	<i>Arthroleptis xenodactyloides</i>	ii	<i>stridens_1</i>	38.27019	-4.714649
T5056 - Nilo FR	<i>Arthroleptis xenodactyloides</i>	ii	<i>stridens_1</i>	38.66461	-4.910778
T4975 - Kwamgumi Forest Reserve, East Usambara	<i>Arthroleptis xenodactyloides</i>	ii	<i>stridens_1</i>	38.73714	-4.97217
T5049 - Kwamgumi FR	<i>Arthroleptis xenodactyloides</i>	ii	<i>stridens_1</i>	38.75053	-4.920833
T5040 - Mlinga FR	<i>Arthroleptis xenodactyloides</i>	ii	<i>stridens_1</i>	38.75169	-5.058278
T4941 - Segoma Forest, Camp, East Usambara	<i>Arthroleptis xenodactyloides</i>	ii	<i>stridens_1</i>	38.75825	-4.98094
T4461 - Mgambo	<i>Arthroleptis xenodactyloides</i>	ii	<i>stridens_1</i>	38.81297	-4.792
T4187 - Mabayani bwawa, Tanga, Tanzania	<i>Arthroleptis xenodactyloides</i>	ii	<i>stridens_1</i>	38.92436	-5.03361
T4201 - Mabayani bwawa, Tanga, Tanzania	<i>Arthroleptis xenodactyloides</i>	ii	<i>stridens_1</i>	38.92436	-5.03361
T4133 - Amboni caves, Tanga, Tanzania	<i>Arthroleptis xenodactyloides</i>	ii	<i>stridens_1</i>	39.04843	-5.0731
T5170 - Mukurumudzi River Dam, Miembeni	<i>Arthroleptis xenodactyloides</i>	ii	<i>stridens_1</i>	39.42547	-4.3752167
T5167 - Mukurumudzi River Dam-Maumba	<i>Arthroleptis xenodactyloides</i>	ii	<i>stridens_1</i>	39.4292	-4.3753333
T5194 - Kivumoni forest	<i>Arthroleptis xenodactyloides</i>	ii	<i>stridens_1</i>	39.44453	-4.1760278
T2416 - Udzungwa Scarp	<i>Arthroleptis xenodactyloides</i>	ii	<i>stridens_3</i>	35.89459	-8.5279245
T5108 - Mgeta Hydroelectric Dam	<i>Arthroleptis xenodactyloides</i>	ii	<i>stridens_3</i>	36.09133	-8.311798
T5109 - Mgeta Hydroelectric Dam	<i>Arthroleptis xenodactyloides</i>	ii	<i>stridens_3</i>	36.09133	-8.311798
T5014 - Sanje	<i>Arthroleptis xenodactyloides</i>	ii	<i>stridens_3</i>	36.89217	-7.783333
T2688 - Ukaguru	<i>Arthroleptis xenodactyloides</i>	ii	<i>stridens_3</i>	36.94043	-6.594853
T2495 - Nguu	<i>Arthroleptis xenodactyloides</i>	ii	<i>stridens_3</i>	37.47162	-5.539355
T2426 - Nguru	<i>Arthroleptis xenodactyloides</i>	ii	<i>stridens_3</i>	37.52564	-6.0304394
T5061 - Mangala FR	<i>Arthroleptis xenodactyloides</i>	ii	<i>stridens_3</i>	37.75861	-6.979167
T5067 - Ngambaula FR	<i>Arthroleptis xenodactyloides</i>	ii	<i>stridens_3</i>	37.76417	-6.984722
T2443 - Kimboza Forest, Uluguru	<i>Arthroleptis xenodactyloides</i>	ii	<i>stridens_3</i>	37.80213	-7.002231
T5065 - Mvuha FR	<i>Arthroleptis xenodactyloides</i>	ii	<i>stridens_3</i>	37.8375	-7.179167
T5069 - Uluguru Ruvu FR	<i>Arthroleptis xenodactyloides</i>	ii	<i>stridens_3</i>	37.8625	-7.008056
T4781 - Montepuez river near Chiefs house	<i>Arthroleptis xenodactyloides</i>	ii	<i>stridens_2</i>	38.7094	-13.3184

T3482 - Kiwengoma FR, Pwani, Tanzania	<i>Arthroleptis xenodactyloides</i>	ii	<i>stridens_2</i>	38.90269	-8.30435
T3483 - Kiwengoma FR, Pwani, Tanzania	<i>Arthroleptis xenodactyloides</i>	ii	<i>stridens_2</i>	38.90269	-8.30435
T5030 - Kazimzumbwi	<i>Arthroleptis xenodactyloides</i>	ii	<i>stridens_3</i>	39.05344	-6.932306
T3024 - Makangala FR, Lindi, Tanzania	<i>Arthroleptis xenodactyloides</i>	ii	<i>stridens_2</i>	39.38803	-9.99418
T3076 - Litipo FR (edge), Lindi, Tanzania	<i>Arthroleptis xenodactyloides</i>	ii	<i>stridens_2</i>	39.50674	-10.03041
T2428 - Nguru	<i>Arthroleptis xenodactyloides</i>	ii*	-	35.89459	-8.5279245
T5062 - Milawilila FR	<i>Arthroleptis xenodactyloides</i>	ii*	-	37.75	-6.979167
T5063 - Mkungwe FR	<i>Arthroleptis xenodactyloides</i>	ii*	-	37.915	-6.868611
T5055 - Nilo FR	<i>Arthroleptis xenodactyloides</i>	ii*	-	38.69331	-4.928472
T4953 - Segoma Forest, Camp, East Usambara	<i>Arthroleptis xenodactyloides</i>	ii*	-	38.7615	-4.97643
T5031 - Kazimzumbwi	<i>Arthroleptis xenodactyloides</i>	ii*	-	39.05344	-6.932306
T5488 - Afrixalus osorioi	<i>A. fornasini</i> OG	outgroup	-		
T5201 - <i>A. quadrivittatus</i>	<i>A. stuhlmanni</i> OG	outgroup	-		
T5157 - Makadara forest	<i>A. xenodactyloides</i> OG	outgroup	-		

Table S2. Summary of RAD-seq datasets used for phylogeny, population (DAPC) and genetic distance analyses (F_{ST}).

Species clade	Dataset	phylip file size (bp)	loci	SNPs
<i>Afrixalus fornasini</i>	50% missing data phylogeny	877672	4539	46699
	40% missing data phylogeny	21300	109	1473
	30% missing data phylogeny	3936	20	336
	initial DAPC	-	4735	4735
	<i>Afrixalus fornasini</i> (i) DAPC	-	-	-
	<i>Afrixalus fornasini</i> (ii) DAPC	-	7320	6997
	<i>Afrixalus fornasini</i> (i) FST		1576	1576
	<i>Afrixalus fornasini</i> (ii) FST		1589	1589
<i>Afrixalus stuhlmanni</i>	50% missing data phylogeny	1475958	7559	185591
	40% missing data phylogeny	314970	1616	35981
	30% missing data phylogeny	19047	98	1970
	initial DAPC	-	1098	1098
	<i>Afrixalus stuhlmanni</i> (i) DAPC	-	2272	2257
	<i>Afrixalus stuhlmanni</i> (ii) DAPC	-	6370	6309
	<i>Afrixalus stuhlmanni</i> (i) FST		896	896
	<i>Afrixalus stuhlmanni</i> (ii) FST		1373	1373
<i>Leptopelis argenteus</i>	50% missing data phylogeny	1389198	7185	74153
	40% missing data phylogeny	385263	1992	20764
	30% missing data phylogeny	166900	863	8970
	initial DAPC	-	1885	1885
	<i>Leptopelis argenteus</i> (i) DAPC	-	24114	19163
	<i>Leptopelis argenteus</i> (ii) DAPC	-	25680	22143
	<i>Leptopelis argenteus</i> (i) FST		2901	2901
	<i>Leptopelis argenteus</i> (ii) FST		3848	3848

<i>Leptopelis flavomaculatus</i>	50% missing data phylogeny	1167992	6003	92820
	40% missing data phylogeny	252672	1300	19828
	30% missing data phylogeny	109178	562	8470
	initial DAPC	-	9829	9829
	<i>Leptopelis flavomaculatus</i> (i) DAPC	-	-	-
	<i>Leptopelis flavomaculatus</i> (ii) DAPC	-	38659	38462
	<i>Leptopelis flavomaculatus</i> (i) FST	-	-	-
	<i>Leptopelis flavomaculatus</i> (ii) FST	-	2662	2662
<i>Arthroleptis xenodactyloides</i>	50% missing data phylogeny	464651	2380	57208
	40% missing data phylogeny	34094	175	3878
	30% missing data phylogeny	3154	16	411
	initial DAPC	-	1030	1030
	<i>Arthroleptis xenodactyloides</i> (i) DAPC	-	9790	9688
	<i>Arthroleptis xenodactyloides</i> (ii) DAPC	-	4367	4345
	<i>Arthroleptis xenodactyloides</i> (i) FST	-	1651	1651
	<i>Arthroleptis xenodactyloides</i> (ii) FST	-	1481	1481

Table S3. Environmental correlates of genetic distance (F_{ST}) tested with multiple regression, partial Mantel and Mantel tests (using the *ecodist* and *vegan* R packages).

<i>Afrivalus stuhlmanni i</i>	Multiple regression		Partial Mantel		Mantel			Fisher's Exact test
	r	p	r	p	r	p		
Geographic distance	0.00560	0.762			0.2808	0.025	r ²	0.40493
Slope	0.00000	0.935	-0.1391	0.742	-0.147	0.79	p	0.296
Current habitat	0.03104	0.562	-0.2008	0.912	0.1625	0.146	F	6.12433
LGM habitat	-0.00003	0.791	-0.1072	0.694	-0.055	0.476	p	0.296
LGM prec. anomaly	-0.00361	0.627	0.039	0.26	0.185	0.12		
LGM temp. anomaly	0.96410	0.336	0.0906	0.188	0.2089	0.091		
Pliocene prec. anomaly	-0.03854	0.28	0.283	0.042	0.283	0.039		
Pliocene temp. anomaly	-0.25211	0.32	0.2136	0.085	0.2292	0.09		
Hydrobasins	0.00799	0.324	0.2486	0.019	0.3669	0.002		
Hydrology	-0.00001	0.404	-0.1817	0.979	-0.096	0.8		

<i>Afrivalus stuhlmanni ii</i>	Multiple regression		Partial Mantel		Mantel			Fisher's Exact test
	r	p	r	p	r	p		
Geographic distance	0.00477	0.86			0.4585	0.003	r ²	0.54
Slope	0.00001	0.429	-0.1078	0.701	-0.115	0.689	p	0.005
Current habitat	0.04163	0.001	0.0814	0.28	0.4428	0.012	F	21.2073
LGM habitat	-0.00008	0.836	-0.0672	0.551	0.0639	0.318	p	0.005
LGM prec. anomaly	-0.01460	0.145	0.035	0.344	0.4523	0.001		
LGM temp. anomaly	0.32490	0.005	0.0665	0.123	0.3681	0.001		
Pliocene prec. anomaly	0.21078	0.918	-0.0888	0.793	0.4152	0.002		
Pliocene temp. anomaly	-0.17110	0.504	-0.0551	0.539	0.4218	0.016		
Hydrobasins	-0.00099	0.93	0.0153	0.333	0.3554	0.001		
Hydrology	0.00001	0.709	0.0155	0.337	0.0055	0.164		

<i>Afrivalus fornasini ii</i>	Multiple regression		Partial Mantel		Mantel			Fishers' Exact test
	r	p	r	p	r	p		
Geographic distance	0.01899	0.262			-0.006	0.45	r ²	0.20925
Slope	-0.00001	0.422	0.1657	0.133	0.1655	0.125	p	0.348
Current habitat	-0.00935	0.53	0.0117	0.364	0.0092	0.4	F	6.49801
LGM habitat	0.00067	0.664	-0.066	0.603	-0.007	0.583	p	0.348
LGM prec. anomaly	-0.01252	0.575	0.2329	0.115	0.2288	0.111		
LGM temp. anomaly	0.15191	0.538	0.2349	0.085	0.2304	0.103		
Pliocene prec. anomaly	0.00001	0.244	0.3271	0.059	0.3242	0.005		
Pliocene temp. anomaly	0.56635	0.197	0.3217	0.062	0.32	0.049		
Hydrobasins	0.00011	0.989	0.0431	0.208	0.0289	0.278		
Hydrology	0.00002	0.157	0.0917	0.13	0.0917	0.117		

<i>Leptopelis argenteus i</i>	Multiple regression		Partial Mantel		Mantel			Fisher's Exact test
	r	p	r	p	r	p		
Geographic distance	0.05640	0.044			0.4841	0.004	r ²	0.87224
Slope	0.00001	0.039	0.119	0.261	-0.044	0.542	p	0.038
Current habitat	-0.12775	0.352	-0.5575	0.93	0.4111	0.006	F	13.6542
LGM habitat	0.00155	0.39	-0.0046	0.451	0.4482	0.006	p	0.038
LGM prec. anomaly	-0.25384	0.084	0.5796	0.01	0.6834	0.004		
LGM temp. anomaly	-0.17185	0.182	0.5987	0.01	0.6987	0.008		
Pliocene prec. anomaly	0.18430	0.411	-0.2352	0.886	0.4387	0.003		
Pliocene temp. anomaly	-0.83955	0.369	0.1339	0.254	0.4966	0.008		
Hydrobasins	0.04386	0.904	0.6728	0.009	0.7495	0.01		
Hydrology	0.00002	0.924	-0.0767	0.59	0.1623	0.195		

<i>Leptopelis argenteus ii</i>	Multiple regression		Partial Mantel		Mantel			Fisher's Exact test
	r	p	r	p	r	p		
Geographic distance	-0.04477	0.958			0.699	0.001	r ²	0.86512
Slope	-0.61788	0.993	-0.3343	0.927	0.2815	0.064	p	0.012
Current habitat	0.06361	0.321	0.6777	0.001	0.8322	0.001	F	24.9426
LGM habitat	-0.00142	0.223	-0.4119	0.958	-0.083	0.491	p	0.012
LGM prec. anomaly	1.41157	0.305	-0.3927	0.969	0.1988	0.153		
LGM temp. anomaly	-1.68396	0.297	-0.3732	0.973	0.3288	0.028		
Pliocene prec. anomaly	0.18202	0.98	0.2881	0.049	0.7256	0.003		
Pliocene temp. anomaly	-0.14651	0.895	-0.5353	0.997	0.4179	0.008		
Hydrobasins	-0.00526	0.629	0.6613	0.002	0.843	0.001		
Hydrology	-0.00004	0.514	-0.3764	0.976	-0.065	0.582		

<i>Leptopelis flavomaculatus ii</i>	Multiple regression		Partial Mantel		Mantel			Fisher's Exact test
	r	p	r	p	r	p		
Geographic distance	-0.05033	0.207			0.2964	0.059	r ²	0.86512
Slope	7.88727	0.035	-0.0162	0.389	0.0459	0.249	p	0.012
Current habitat	0.16900	0.34	-0.2489	0.995	-0.063	0.517	F	24.9426
LGM habitat	-0.00001	0.19	-0.2687	0.992	0.0063	0.376	p	0.012
LGM prec. anomaly	0.88715	0.032	-0.013	0.911	0.2259	0.069		
LGM temp. anomaly	-0.14856	0.714	-0.0031	0.424	0.221	0.062		
Pliocene prec. anomaly	-0.62723	0.023	0.0847	0.175	0.3072	0.042		
Pliocene temp. anomaly	-0.07801	0.466	0.0715	0.222	0.3019	0.046		
Hydrobasins	0.01247	0.652	0.1626	0.053	0.3245	0.005		
Hydrology	0.00000	0.928	0.0229	0.338	0.005	0.392		

<i>Arthroleptis xenodactyloides i</i>	Multiple regression		Partial Mantel		Mantel		Fisher's Exact test	
	r	p	r	p	r	p		
Geographic distance	-0.00652	0.453			0.0357	0.382	r ²	0.47637
Slope	0.09825	0.044	0.3134	0.095	0.3039	0.084	p	0.342
Current habitat	0.05046	0.651	0.1108	0.24	0.0835	0.276	F	3.53796
LGM habitat	0.00219	0.981	0.0622	0.332	0.0668	0.298	p	0.342
LGM prec. anomaly	0.01950	0.672	0.0762	0.317	0.0789	0.32		
LGM temp. anomaly	-0.15614	0.542	0.0212	0.387	0.0414	0.385		
Pliocene prec. anomaly	0.05481	0.528	0.0103	0.42	-0.009	0.501		
Pliocene temp. anomaly	-0.08489	0.781	-0.02	0.513	0.0458	0.333		
Hydrobasins	0.02216	0.448	-0.0067	0.496	0.0265	0.41		
Hydrology	-0.00002	0.362	-0.0701	0.647	-0.067	0.688		

<i>Arthroleptis xenodactyloides ii</i>	Multiple regression		Partial Mantel		Mantel		Fisher's Exact test	
	r	p	r	p	r	p		
Geographic distance	0.00057	0.631			-0.01	0.863	r ²	0.54115
Slope	0.00001	0.883	-0.1186	0.895	-0.114	0.895	p	0.001
Current habitat	-0.00003	0.961	0.0433	0.255	0.0408	0.254	F	44.6842
LGM habitat	-0.00059	0.284	0.0428	0.257	0.0405	0.257	p	0.001
LGM prec. anomaly	0.30326	0.005	0.4604	0.001	0.455	0.001		
LGM temp. anomaly	-0.24026	0.124	0.5582	0.001	0.5542	0.001		
Pliocene prec. anomaly	0.04280	0.001	0.3747	0.001	0.3708	0.001		
Pliocene temp. anomaly	0.60619	0.0142	0.2372	0.018	0.2323	0.021		
Hydrobasins	-0.00183	0.281	0.5978	0.001	0.5895	0.001		
Hydrology	0.00001	0.321	-0.0065	0.458	-0.015	0.522		

Supplementary Materials: Chapter II

Appendix S1. Supplementary methods.

Phylogenetic tree

Sequences were edited in GENEIOUS 6 and aligned with MUSCLE before Bayesian analyses were performed in BEAST 2.1.3 (Bouckaert et al., 2014) on the concatenated 1,271 bp alignment with a secondary calibration point of 350 million years (normal prior, $\sigma = 10.0$) as an approximate divergence date between caecilians (Gymnophiona) and frogs (Anura) following Wilkinson et al. (2011). We used the optimal models of evolution per partition (Table S2) according to the Bayesian Information Criterion determined by PARTITIONFINDER 1.1.1 (Lanfear et al. 2013). For all partitions trees were linked, and models and clocks were unlinked. Markov Chain Monte Carlo (MCMC) simulations were run for 100 million iterations, with sampling every 5000 iterations. We checked for convergence using TRACER 1.6, and investigated parameter variations including strict, relaxed and log normal clocks, and Yule/coalescent priors, but found the relaxed clock log normal model with a Yule prior as the best parameter combination (adequate mixing and ESS values >200). We combined two independent runs in LOGCOMBINER 2.1.3 and calculated the maximum clade credibility tree (Fig. 2) with TREANNOTATOR 2.1.2 which was used for further analyses, after the removal of 10% burn-in. Phylogenetic results are largely concordant with previous large-scale amphibian tree reconstructions in terms of topology and branch lengths (Roelants et al., 2007; Frost, 2016; Pyron & Wiens, 2011).

Spatial data filtering

All lineage data was compiled from our own and collaborators field work since 2001, relevant CFEA literature (Burgess and Clarke, 2000), and available distribution records from the Global Biodiversity Information Facility (GBIF). We utilized spatial records from amphibian collections housed at the University of Dar es Salaam, National Museums of Kenya, Natural History Museum London, Science Museum of Trento, Museum of Vertebrate Zoology Berkeley, Museum of Comparative Zoology Harvard, and Field Museum of Natural History Chicago. Due to uncertainty in some data sources such as GBIF and museum records we were conservative regarding which data points were retained, only keeping spatial data which we could be certain were accurate. To assess this, a rigorous filtering and correction procedure to these data prior to further analysis was made. We excluded records not present in our CFEA study region <1000m in altitude (i.e. specific EA restricted species and other species not considered as part of or interacting with the CFEA assemblage) and used only occurrence data that accurately matched the recorded locality names. Species names were corrected to reflect currently recognized taxonomy following Frost et al. (2016), excluding ambiguous records listed as "sp." or "indet." that could not be confidently matched to a species tip on the tree.

Forest modelling

As no accurate historical vegetation maps of sub-Saharan Africa exist for the time-scales we investigate, we use modelling methods to estimate forest distribution, firstly in the present time and then projected back onto global circulation model climate data for the mid-Holocene (6 ka BP), Last Glacial Maximum (LGM; 21 ka BP) and Last Interglacial (LIG; 120 ka BP) time periods (Hijmans et al. 2005, Braconnot et al., 2007, Otto-Bliesner et al., 2006). Current forest extent was estimated by creating a forest distribution model using the global 1km consensus land cover product (Tuanmu and Jetz, 2015) to classify the study region based on evergreen forest presence (excluding mangroves which are not part of the CFEA). Firstly we reclassified their raster layer, taking only pixels

representing the top 10% of all values for evergreen forest to ensure an accurate representation of current forest was maintained. We transformed the resulting raster into a single polygon and generated 500 random points within this area, with a constraint that the points had a buffer of at least 10 km apart to minimize bias (sensu Graham et al. 2010). We verified that the points covered an accurate representation of current forest habitat by overlaying them on satellite imagery from Google Earth and ground truthing based on first-hand knowledge of the region from recent fieldwork. We subsequently created a predictive model of current forest cover in MAXENT 3.3.3k using bioclimatic variables (bio2, bio4, bio5, bio12, bio14, bio18 from the CCSM global circulation model) and a digital elevation model (GTOPO30; USGS, available from: <http://csgtm.iscgm.org/dataset/gtopo30>) at 30 arc-second resolution (approximately 1 km²) with the subsample modeling algorithm, and regularization multiplier of 1. After inspection of the predictive forest model to verify that it accurately represented currently forested habitats, we created historical projections based on past climate data, by projecting the model onto the three time slices with available historical climate data. We followed Graham et al. (2010) to derive a measure of forest stability over time by transforming the forest model at each time slice into its log value and averaging the values across the four time periods (i.e. from the present back to the LIG over 120k years). The exponent of this average value (EXP function in ARCGIS raster calculator) was then used to transform the resulting number into a continuous variable, representing a measure of forest stability in each grid cell (ranging from 0 to 1) following Rosauer et al. (2015) and Graham et al. (2010).

The forest model performed well, with a high AUC values (0.811). Variable contribution was highest for bio14 (53.73%) with each other variable contributing between 6.33 and 13.69% with the exception of bio5 (Table S6). Forest projections at 6 ka BP, 21 ka BP, 120 ka BP and the calculated forest stability surface measure over this time period show that several areas have retained high stability throughout. These areas correspond to lowland parts of the EA and surrounding areas, parts of central coastal Tanzania, with additional areas scattered along the coastline to the east of our map. Remaining low elevation areas and those extending inland have mainly been unstable in terms of forest cover, probably affected by sea level inundation and periods of severe climate change (Fig. S3).

Spatial autocorrelation

To test for spatial autocorrelation we examined the correlation structure of the log transformed response variable (PE) and residuals of the best GLM, visualizing correlograms of Moran's *I* across distance classes of 10 km increments. Model residuals of the GLM were spatially autocorrelated at small distance classes (i.e. Moran's *I* values > 0.7 up to 20 km distance between grid cells), suggesting the need for a spatial model. To define a spatial weights matrix we used the *knearneigh* function (with *k* = 1) to derive the minimum distance connecting each cell to at least one neighbor. Using this minimum distance we then defined the neighborhood structure using the *dnearneigh* function, and created a spatial weights matrix using the *nb2listw* function, for details see Kissling & Carl (2008). We then used the best GLM and ran a spatial autoregressive error model with the spatial weights matrix to account for spatial autocorrelation using the *errorsarlm* function in R package '*spdep*' (Bivand & Piras, 2015). This spatial autoregressive error model accounted for spatial autocorrelation in GLM residuals across all distance classes (Tables S6, S7).

References

- Bivand, R. & Piras, G. (2015) Comparing implementations of estimation methods for spatial econometrics. *Journal of Statistical Software*, **63**, 1-36. Available from: <http://www.jstatsoft.org/v63/i18/>.
- Bouckaert, R., Heled, J., Kühnert, D., Vaughan, T., Wu, C-H., Xie, D., Suchard, M.A., Rambaut, A., & Drummond, A.J. (2014). BEAST 2: A Software platform for Bayesian evolutionary analysis. *PLoS Computational Biology*, **10**, e1003537. doi:10.1371/journal.pcbi.1003537.
- Braconnot, P., Otto-Bliesner, B., Harrison, S., Joussaume, S., Peterchmitt, J.-Y., Abe-Ouchi, A., Crucifix, M., Driesschaert, E., Fichefet, T., Hewitt, C.D., Kageyama, M., Kitoh, A., Lâiné, A., Loutre, M.-F. , Marti, O., Merkel, U., Ramstein, G., Valdes, P., Weber, S.L., Yu, Y., Zhao, Y. (2007) Results of PMIP2 coupled simulations of the Mid-Holocene and Last Glacial Maximum - Part 1: experiments and large-scale features. *Climate of the Past*, **3**, 279–276.
- Calcagno, V. & de Mazancourt, C. (2010) glmulti : An R package for easy automated model selection with (generalized) linear models. *Journal of Statistical Software*, **34**, 1-29.
- Frost, D.R. (2016) Amphibian Species of the World: an Online Reference. Version 6.0 (1 October 2016). Electronic Database available from: <http://research.amnh.org/herpetology/amphibia/index.html>. American Museum of Natural History, New York, USA.
- Graham, C.H., VanDerWal, J., Phillips, S.J., Moritz, C. & Williams, S.E. (2010) Dynamic refugia and species persistence: Tracking spatial shifts in habitat through time. *Ecography*, **33**, 1062-1069.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965-1978.
- Kissling, W.D. & Carl, G. (2008) Spatial autocorrelation and the selection of simultaneous autoregressive models. *Global Ecology and Biogeography*, **17**, 59-71.
- Lanfear, R., Calcott, B., Ho, S.Y.W., & Guindon, S. (2012) PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution*, **29**, 1695–1701.
- Otto-Bliesner, B.L., Marshall, S.J., Overpeck, J.T., Miller, G.H., Hu, A., & CAPE Last Interglacial Project members (2006) Simulating Arctic climate warmth and icefield retreat in the last interglaciation. *Science*, **311**, 1751-1753.
- Pyron, R.A. & Wiens, J.J. (2011) A large-scale phylogeny of Amphibia including over 2800 species, and a revised classification of extant frogs, salamanders, and caecilians. *Molecular Phylogenetics and Evolution*, **61**, 543-583.
- Roelants, K., Gower, D.J., Wilkinson, M., Loader, S.P., Biju, S.D., Guillaume, K., Moriau, L. & Bossuyt, F. (2007) Global patterns of diversification in the history of modern amphibians. *Proceedings of the National Academy of Sciences*, **104**, 887-892.
- Tuanmu, M.N. & Jetz, W. (2014) A global 1-km consensus land-cover product for biodiversity and ecosystem modelling. *Global Ecology and Biogeography*, **23**, 1031-1045.
- Wilkinson, M., San Mauro, D., Sherratt, E. & Gower, D.J. (2011). A nine-family classification of caecilians (Amphibia: Gymnophiona). *Zootaxa*, **2874**, 41-64.

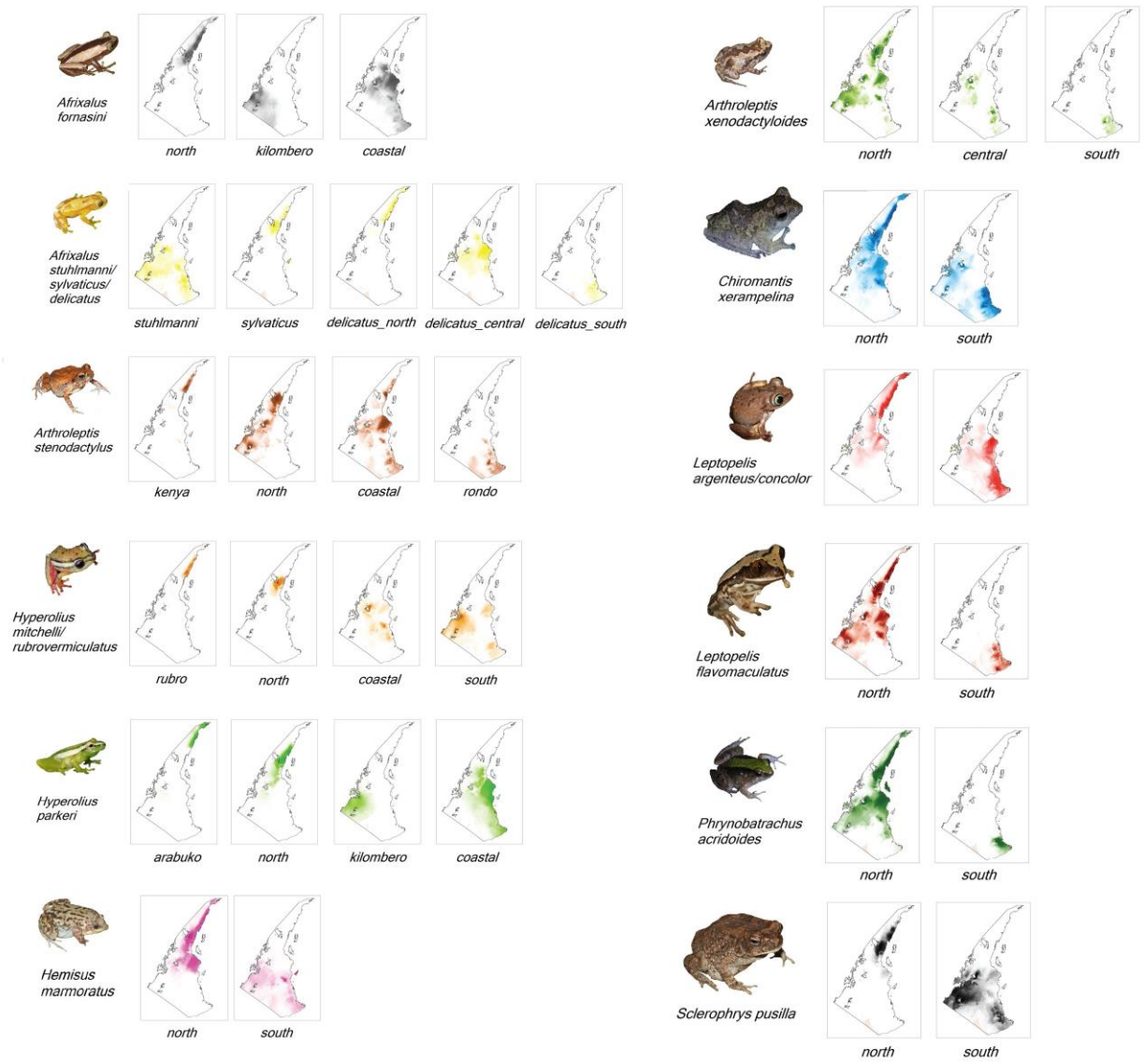


Fig. S1. Lineage distribution models used in this study highlighting the distributions of 35 intraspecific lineages.

Modelled forest suitability

Forest stability (120 ka)

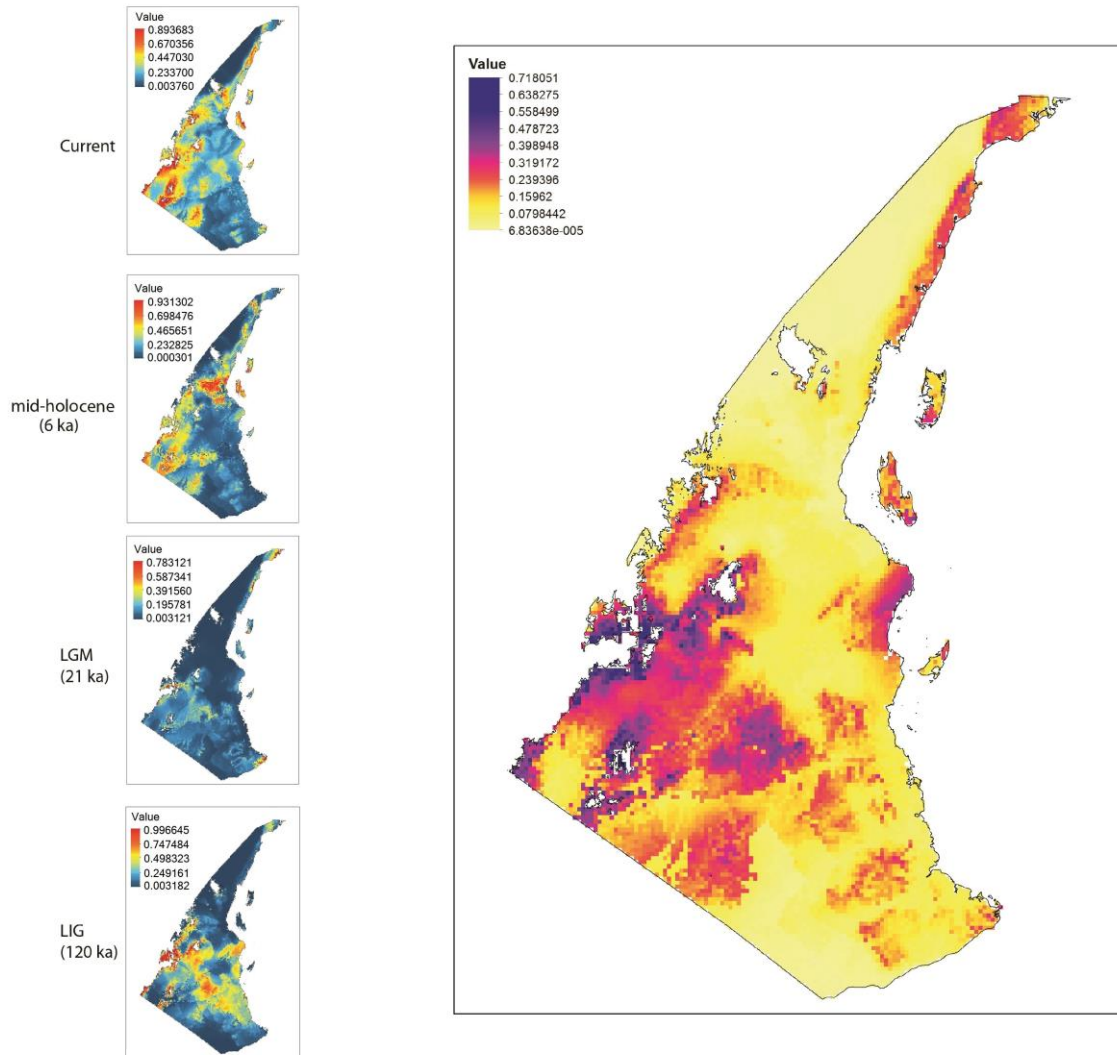


Fig. S2. Projected forest stability measures for the current, mid-Holocene, Last Glacial Maximum and Last Interglacial time periods.

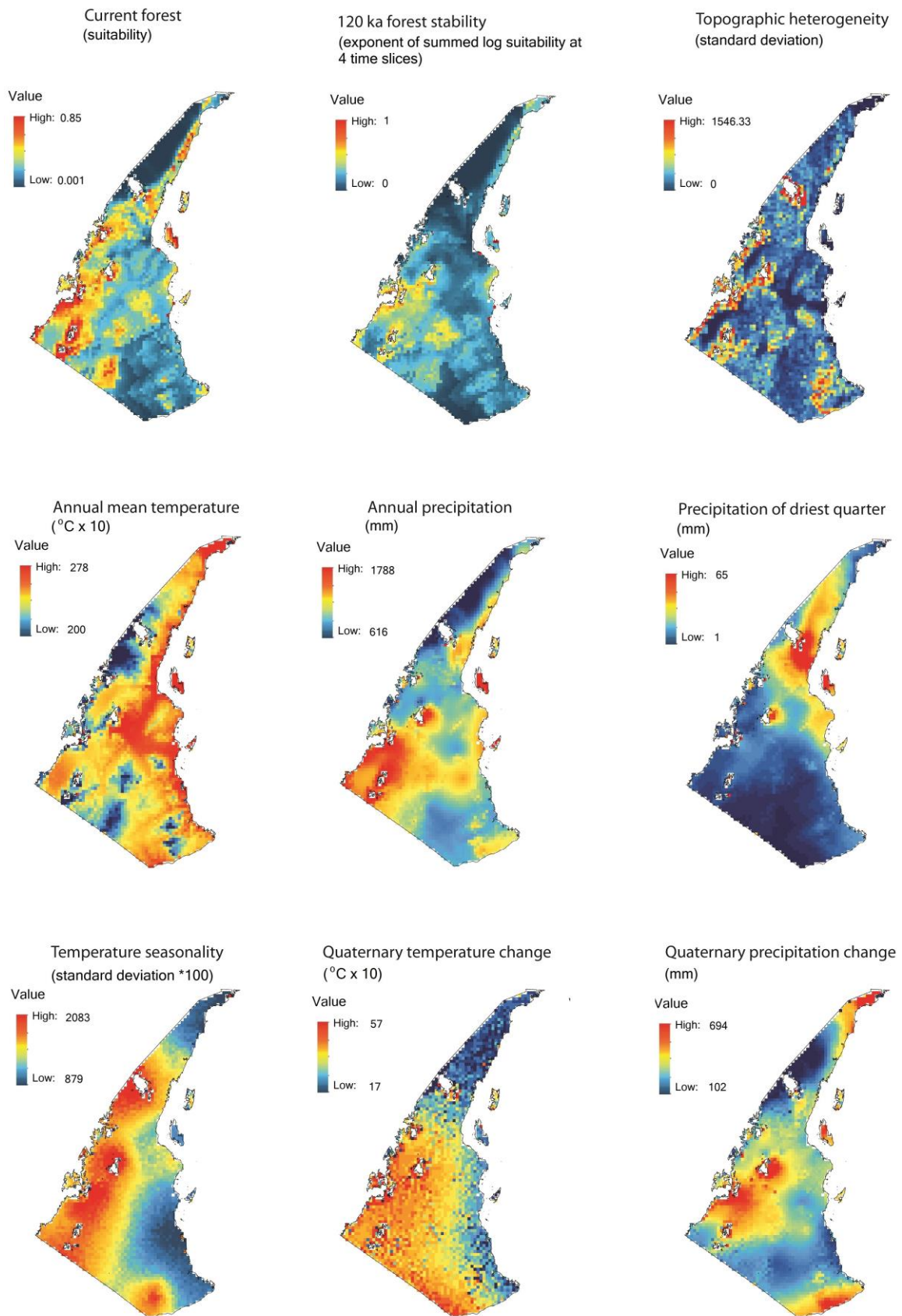


Fig. S3. Environmental predictors used in analyses.

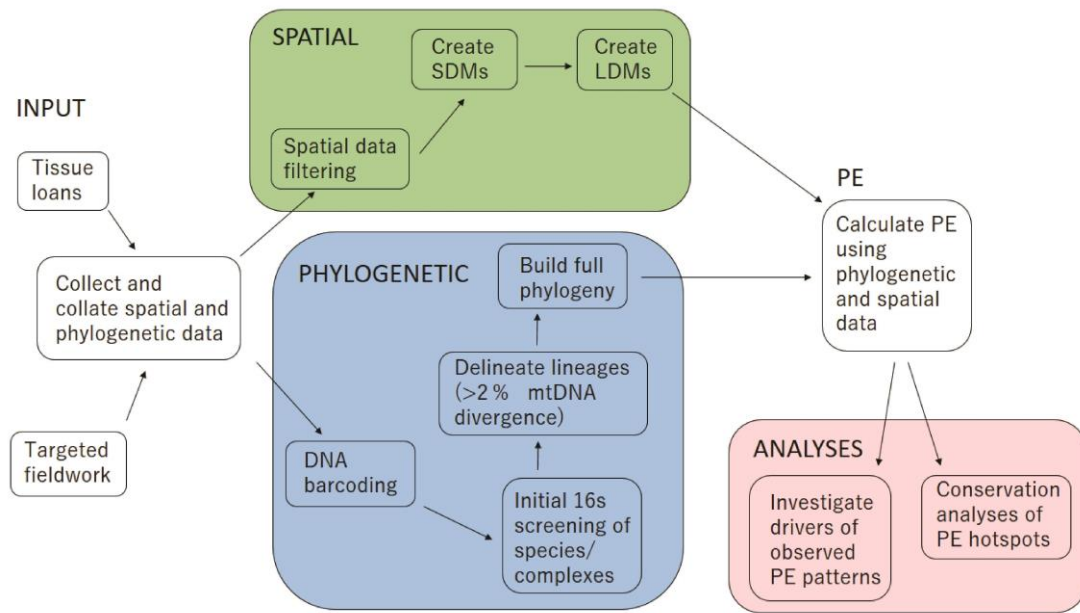


Fig. S4. Workflow representing the steps taken in this study.

Table S1. Sequences used in this study (species and intraspecific lineages) and evolutionary models for each partition. Published GenBank Numbers are supplied for 16S and COI sequences.

Intraspecific lineages:

ID	Species	Locality	Long	Lat	Lineage	16S	COI
T4170	<i>Afrixalus fornasini</i>	Mabayani bwawa,	38.92436	-5.03361	North	KY177039	KY177132
T4425	<i>Afrixalus fornasini</i>	Mvuha FR	37.8375	-7.179167	Coastal	KY177040	KY177116
T5144	<i>Afrixalus fornasini</i>	Mgeta Hydro Dam	36.091327	-8.311798	Kilombero	KY177041	KY177131
T3113	<i>Afrixalus stuhlmanni</i>	Makangala FR	39.38803	-9.99418	stuhlmanni	KY177045	KY177133
T3679	<i>Afrixalus stuhlmanni</i>	Ruawa FR, Lindi	39.56871	-9.72995	delicatus_south	KY177042	KY177136
T3832	<i>Afrixalus stuhlmanni</i>	Ruvu North FR	38.97007	-6.71349	delicatus_central	KY177043	KY177137
T5158	<i>Afrixalus stuhlmanni</i>	Mwaluganje	39.41731	-4.15821	sylvaticus	KY177046	KY177135
T5395	<i>Afrixalus stuhlmanni</i>	Arabuko Sokoke	39.86667	-3.33333	delicatus_north	KY177044	KY177134
T2727	<i>Arthroleptis stenodactylus</i>	Dar, Dondwe	39.096969	-7.064294	Coastal	KY177080	KY177167
T3259	<i>Arthroleptis stenodactylus</i>	Rondo Forest, Lindi	39.17774	-10.11795	Rondo	KY177079	KY177165
T5142	<i>Arthroleptis stenodactylus</i>	Mgeta Hydro Dam	36.091327	-8.311798	North	KY177077	KY177162
T5320	<i>Arthroleptis stenodactylus</i>	Makadara forest	39.395639	-4.237556	Kenya	KY177078	KY177164
T3096	<i>Arthroleptis xenodactyloides</i>	Litipo FR	39.50674	-10.03041	South	KY177071	KY177161
T5060	<i>Arthroleptis xenodactyloides</i>	Kasanga FR	37.773925	-7.191166	Central	KY177072	KY177158
T5069	<i>Arthroleptis xenodactyloides</i>	Uluguru Ruvu FR	37.8625	-7.008056	North	KY177074	KY177160
T3289	<i>Chiromantis xerampelina</i>	Makangaga FR	39.29196	-9.49454	South	KY177003	KY177113
T3464	<i>Chiromantis xerampelina</i>	Kiwengoma FR	38.90269	-8.30435	North	KY177004	KY177112
T3448	<i>Hemisus marmoratus</i>	Kiwengoma FR	38.90269	-8.30435	South	KY176997	KY177086
T4973	<i>Hemisus marmoratus</i>	Segoma Forest	38.7615	-4.97643	North	KY176998	KY177087
T2983	<i>Hyperolius mitchelli</i>	Makangala FR, Lindi	39.38803	-9.99418	South	KY177030	KY177144
T3297	<i>Hyperolius mitchelli</i>	Makangaga FR, Lindi	39.29196	-9.49454	Coastal	KY177029	KY177143
T4957	<i>Hyperolius mitchelli</i>	Segoma Forest	38.7615	-4.97643	North	KY177027	KY177141
T5221	<i>Hyperolius mitchelli</i>	Scheldrick's Falls	39.43096	-4.27553	rubro	KY177028	KY177142
T3124	<i>Hyperolius parkeri</i>	Makangala FR	39.38803	-9.99418	Coastal	KY177035	KY177155
T3770	<i>Hyperolius parkeri</i>	Kibasira Swamp	36.2277	-8.34888	Kilombero	KY177037	KY177154
T5364	<i>Hyperolius parkeri</i>	Base TitaniumArea	39.45095	-2.39755	North	KY177036	KY177153
T6295	<i>Hyperolius parkeri</i>	Arabuko sokoke	39.975806	-3.262667	Arabuko	KY177038	KY177152
T3295	<i>Leptopelis argenteus</i>	Makangaga FR	39.29196	-9.49454	South	KY177068	KY177129

T5165	<i>Leptopelis argenteus</i>	Mukurumudzi River	39.42535	-4.42535	North	KY177070	KY177128
T3179	<i>Leptopelis flavomaculatus</i>	Litipo FR, Lindi	39.4752	-10.04952	South	KY177066	KY177126
T5237	<i>Leptopelis flavomaculatus</i>	Shimba Lodge	39.395639	-4.2375	North	KY177067	KY177127
T2997	<i>Phrynobatrachus acridoides</i>	Makangala FR	39.38803	-9.99418	South	KY177050	KY177110
T5247	<i>Phrynobatrachus acridoides</i>	Shimba Lodge	39.395639	-4.2375	North	KY177048	KY177114
T3065	<i>Sclerophrys pusilla</i>	Makangala FR	39.36913	-9.98237	South	KY177014	KY177095
T4188	<i>Sclerophrys pusilla</i>	Mabayani bwawa	38.92436	-5.03361	North	KY177013	KY177096

Species level data:

ID	Species	16s	COI
T1754	<i>Amietia angolensis</i>	KY177064	-
T3825	<i>Ammirana galamensis</i>	KY177053	KY177117
T4431	<i>Arthroleptides martiensseni</i>	KY177002	KY177157
T510	<i>Arthroleptides yakusini</i>	KY177001	KY177156
T1872	<i>Arthroleptis affinis</i>	KY177075	KY177124
T594	<i>Arthroleptis tanneri</i>	KY177076	-
T2683	<i>Arthroleptis xenodactylus</i>	KY177073	KY177159
T4792	<i>Boulengerula boulengeri</i>	KY176991	-
T2511	<i>Boulengerula changamwensis</i>	KY176994	KY177092
T243	<i>Boulengerula uluguruensis</i>	KY176993	KY177091
T1931	<i>Breviceps mossambicus</i>	KY177082	KY177111
T6265	<i>Callulina krefftii</i>	KY177081	KY177088
T3685	<i>Hildebrandtia ornata</i>	KY177054	-
T3731	<i>Hyperolius argus</i>	KY177021	KY177151
T3813	<i>Hyperolius kivuensis</i>	KY177031	KY177145
T4047	<i>Hyperolius mariae</i>	KY177024	KY177148
T3392	<i>Hyperolius marmoratus</i>	KY177022	-
T4130	<i>Hyperolius nasutus</i>	KY177019	KY177149
T6373	<i>Hyperolius pusillus</i>	KY177020	KY177150
T3808	<i>Hyperolius reesi</i>	KY177023	KY177147
T4819	<i>Hyperolius ruvuensis</i>	KY177032	KY177146
T3204	<i>Hyperolius substriatus</i>	KY177026	KY177140
T4994	<i>Hyperolius tuberilinguis</i>	KY177025	KY177125
T5227	<i>Kassina maculata</i>	KY177034	KY177139
T4035	<i>Kassina senegalensis</i>	KY177033	KY177138
T5626	<i>Leptopelis broadleyi</i>	KY177069	KY177130
T2582	<i>Leptopelis grandiceps</i>	KY177000	KY177115
T5650	<i>Mertensophryne anotis</i>	KY177010	KY177102
T2202	<i>Mertensophryne howelli</i>	KY177008	KY177107
T1892	<i>Mertensophryne lindneri</i>	KY177006	KY177098
T1932	<i>Mertensophryne loveridgei</i>	KY177009	KY177103
T1882	<i>Mertensophryne micranotis</i>	KY177005	KY177099
T1881	<i>Mertensophryne usambarae</i>	KY177007	KY177101
T5639	<i>Nothophryne broadleyi</i>	KY177063	KY177163
T3008	<i>Phrynobatrachus mababiensis</i>	KY177051	KY177120
T3101	<i>Phrynobatrachus natalensis</i>	KY177049	-
T4787	<i>Phrynobatrachus pakenhami</i>	KY177047	-
T4577	<i>Phrynobatrachus ukingensis</i>	KY177052	KY177119
T3684	<i>Phrynomantis bifasciatus</i>	KY177065	KY177118
T5647	<i>Poyntonophryne beiranus</i>	KY177012	KY177106
T5268	<i>Ptychadena anchietae</i>	KY177056	KY177084
T3062	<i>Ptychadena mascareniensis</i>	KY177059	KY177083
T3757	<i>Ptychadena mossambica</i>	KY177057	KY177109
T5290	<i>Ptychadena oxyrhynchus</i>	KY177055	-
T5286	<i>Ptychadena porosissima</i>	KY177058	KY177108
T6652	<i>Ptychadena schillukorum</i>	KY177060	-

T3691	<i>Pyxicephalus adspersus</i>	KY177061	KY177123
T3824	<i>Pyxicephalus edulis</i>	KY177062	KY177122
T1958	<i>Schismaderma carens</i>	KY177011	KY177100
T2507	<i>Schistometopum gregorii</i>	KY176992	KY177085
T2292	<i>Sclerophrys brauni</i>	KY177017	-
T3156	<i>Sclerophrys pusilla</i>	KY177016	KY177097
T5318	<i>Sclerophrys steindachneri</i>	KY177018	-
T1649	<i>Sclerophrys xeros</i>	KY177015	KY177104
T4791	<i>Scolecophorus vittatus</i>	KY176990	KY177089
T4591	<i>Spelaophryne methneri</i>	KY176999	-
T4855	<i>Xenopus laevis</i>	KY176996	KY177093
T3104	<i>Xenopus muelleri</i>	KY176995	KY177094

Models of evolution for phylogeny in Fig. 1 (16s, COI):

Partition	Length (bp)	Best model (BIC)
16s	368	GTR+I+G
co1 p1	301	TrNef+I+G
co1 p2	301	HKY+I+G
co1 p3	301	TrN+G

Table S3. Spatial data. Large file with almost 10,000 spatial records. Available from my personal website: <https://christopherdbarratt.files.wordpress.com/2016/02/table-s3-spatial-point-data.xlsx>.

Table S4. Correlation structure of environmental variables.

SDM modelling variables:

	DEM	bio2	bio4	bio5	bio12	bio14	bio15
DEM		0.419	0.513	-0.531	0.015	-0.219	0.176
bio2			0.254	0.333	0.524	0.155	-0.224
bio4				0.085	0.231	0.075	-0.019
bio5					-0.254	0.318	-0.465
bio12						-0.011	0.499
bio14							-0.519

Environmental predictor variables:

	120k_forest stability	anom_bio1	anom_bio12	bio1	bio12	bio14	bio4	topographic heterogeneity
120k_forest stability		0.339	-0.471	-0.259	0.680	-0.296	0.216	0.310
anom_bio1			-0.326	-0.100	0.331	-0.453	0.502	0.095
anom_bio12				-0.244	-0.555	0.050	-0.186	-0.085
bio1					0.026	0.099	-0.332	-0.413
bio12						-0.065	0.294	0.230
bio14							0.082	0.039
bio4								0.211

Table S5. Variable contributions for SDM and forest model.

SDM	DEM	bio12	bio14	bio18	bio2	bio4	bio5	AUC
<i>Afrixalus_stuhlmanni</i>	0.77	9.55	73.00	1.71	8.10	4.26	2.61	0.83
<i>Afrixalus_fornasini</i>	2.01	12.58	65.28	5.01	7.62	1.92	5.58	0.78
<i>Amietia_angolensis</i>	17.46	23.27	55.57	1.03	1.31	0.90	0.46	0.84
<i>Sclerophrys_gutturialis</i>	8.74	5.61	70.49	1.32	5.37	0.19	8.27	0.79
<i>Arthroleptis_stenodactylus</i>	5.32	9.23	61.96	6.63	5.96	3.07	7.83	0.82
<i>Arthroleptis_xenodactyloides</i>	8.87	11.78	62.09	1.97	4.70	2.40	8.20	0.90
<i>Breviceps_mossambicus</i>	0.01	0.16	29.84	1.37	0.45	9.14	59.04	0.77
<i>Chiromantis_xerampelina</i>	1.18	11.26	63.46	1.80	7.21	6.93	8.17	0.78
<i>Hemisus_marmoratus</i>	2.03	9.82	57.52	4.03	21.20	0.78	4.62	0.83
<i>Amnirana_galamensis</i>	66.25	2.50	26.39	0.00	3.25	0.83	0.78	0.79
<i>Hyperolius_argus</i>	34.01	6.48	24.21	21.30	6.92	3.88	3.21	0.88
<i>Hyperolius_mariae</i>	4.21	8.49	36.19	8.63	39.71	2.02	0.75	0.84
<i>Hyperolius_mitchelli</i>	6.46	9.22	66.70	2.86	7.38	0.69	6.69	0.87
<i>Hyperolius_nasutus</i>	44.19	7.92	23.19	18.64	2.65	0.92	2.49	0.85
<i>Hyperolius_parkeri</i>	28.28	13.22	41.98	5.80	2.78	2.25	5.68	0.83
<i>Hyperolius_pusillus</i>	32.63	4.70	21.36	27.88	8.03	1.22	4.19	0.83
<i>Hyperolius_reesi</i>	0.46	39.16	15.37	3.22	18.38	5.43	17.97	0.98
<i>Hyperolius_substriatus</i>	0.79	2.89	66.69	3.98	1.15	23.65	0.86	0.87
<i>Hyperolius_tuberilinguis</i>	6.56	18.25	44.67	13.51	7.59	2.93	6.50	0.85
<i>Kassina_maculata</i>	40.11	9.38	27.44	14.33	4.38	4.19	0.18	0.79
<i>Kassina_senegalensis</i>	14.19	10.94	37.92	14.85	10.73	1.39	9.98	0.84
<i>Leptopelis_argenteus</i>	38.39	9.63	13.97	32.11	1.33	0.39	4.19	0.88
<i>Leptopelis_flavomaculatus</i>	6.45	7.81	69.40	0.85	8.62	3.50	3.37	0.90
<i>Mertensophryne_lindneri</i>	5.95	0.09	73.91	5.06	2.23	0.05	12.70	0.80
<i>Mertensophryne_loveridgei</i>	1.54	2.76	3.21	0.00	2.62	9.06	80.81	0.75
<i>Mertensophryne_microanotis</i>	13.32	8.79	58.53	5.23	11.23	0.01	2.90	0.91
<i>Phrynobatrachus_acridoides</i>	2.32	13.01	59.90	4.44	15.23	2.58	2.53	0.85
<i>Phrynobatrachus_mababiensis</i>	12.79	3.47	56.38	11.71	2.94	9.05	3.68	0.77
<i>Phrynobatrachus_natalensis</i>	0.00	0.46	20.00	0.00	7.64	0.00	71.91	0.74
<i>Phrynomantis_bifasciatus</i>	26.60	2.86	37.16	11.88	15.79	2.34	3.37	0.84
<i>Ptychadena_anchietae</i>	1.70	12.34	67.62	4.71	7.48	0.80	5.33	0.85
<i>Ptychadena_mascareniensis</i>	6.52	2.91	21.84	5.97	60.60	0.33	1.83	0.81
<i>Ptychadena_mossambica</i>	71.62	0.55	13.07	2.83	3.42	1.64	6.89	0.82
<i>Ptychadena_oxyrhynchus</i>	14.11	19.00	71.63	0.00	0.00	0.04	5.21	0.83
<i>Pyxicephalus_edulis</i>	35.80	0.05	14.40	29.51	7.01	5.75	7.48	0.75
<i>Sclerophrys_pusillus</i>	13.85	6.47	56.13	9.93	2.24	6.38	5.01	0.84
<i>Spelaophryne_methneri</i>	10.32	15.83	2.75	52.33	0.00	0.00	18.76	0.81
<i>Xenopus_muelleri</i>	2.01	11.46	68.50	2.18	12.27	0.31	3.29	0.84
total	587.80	343.86	1679.73	338.61	335.52	121.19	403.29	31.56
mean	15.47	9.05	44.20	8.91	8.83	3.19	10.61	0.83
median	7.65	9.00	50.12	4.86	6.97	1.97	5.11	0.83

forest model	DEM	bio12	bio14	bio18	bio2	bio4	bio5	Test AUC
current	7.7527	10.9807	53.7315	6.3303	13.6942	6.5145	0.9961	0.811

Table S6. Environmental correlates of PE. Predictor importance (consistent results for SAR and GLM highlighted in blue). Also shown is a plot showing how the SAR model completely accounts for spatial autocorrelation.

Best GLM				
formula	AIC	delta_AIC	weight	
div ~ 1 + foreststability_120k+topographic_heterogeneity + bio1 + bio4 + bio12 + bio14 + anom_bio1 + anom_bio12	2307.629	0	0.99	

Model contributions		GLM		SAR	
Predictor		Estimate	p	st. coeff	p
forest stability		0.155	0.025	0.01	2.31E-01
bio1		0.14	0.019	-0.056	6.18E-07
bio4		-0.146	0.02	0.026	2.22E-01
bio12		0.129	2.30E-02	0.052	4.26E-02
bio14		0.447	1.90E-02	0.178	9.86E-12
topographic_heterogeneity		0.035	0.017	-0.019	1.41E-05
anom_bio1		-0.098	0.022	-0.003	0.52595
anom_bio12		-0.085	0.019	-0.101	1.35E-11

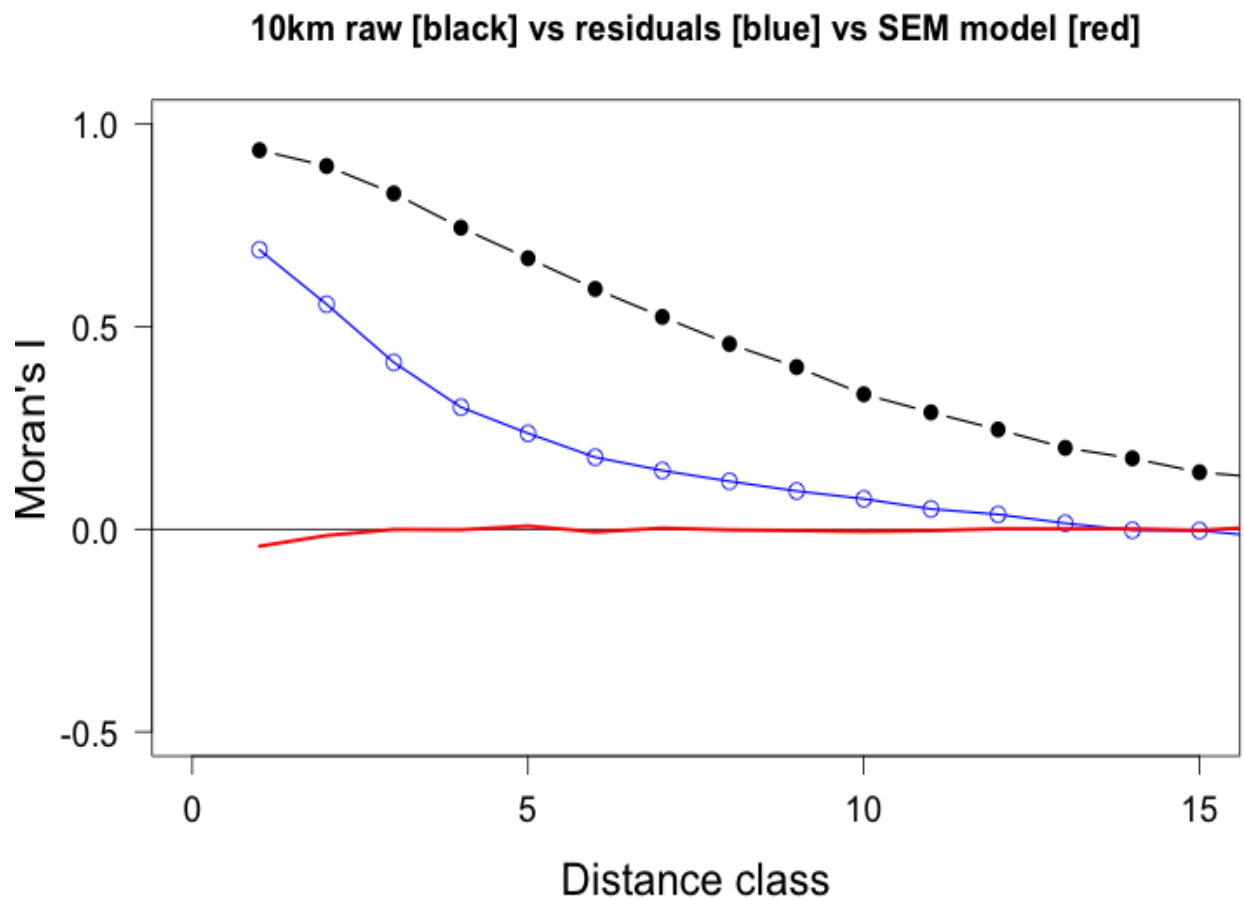
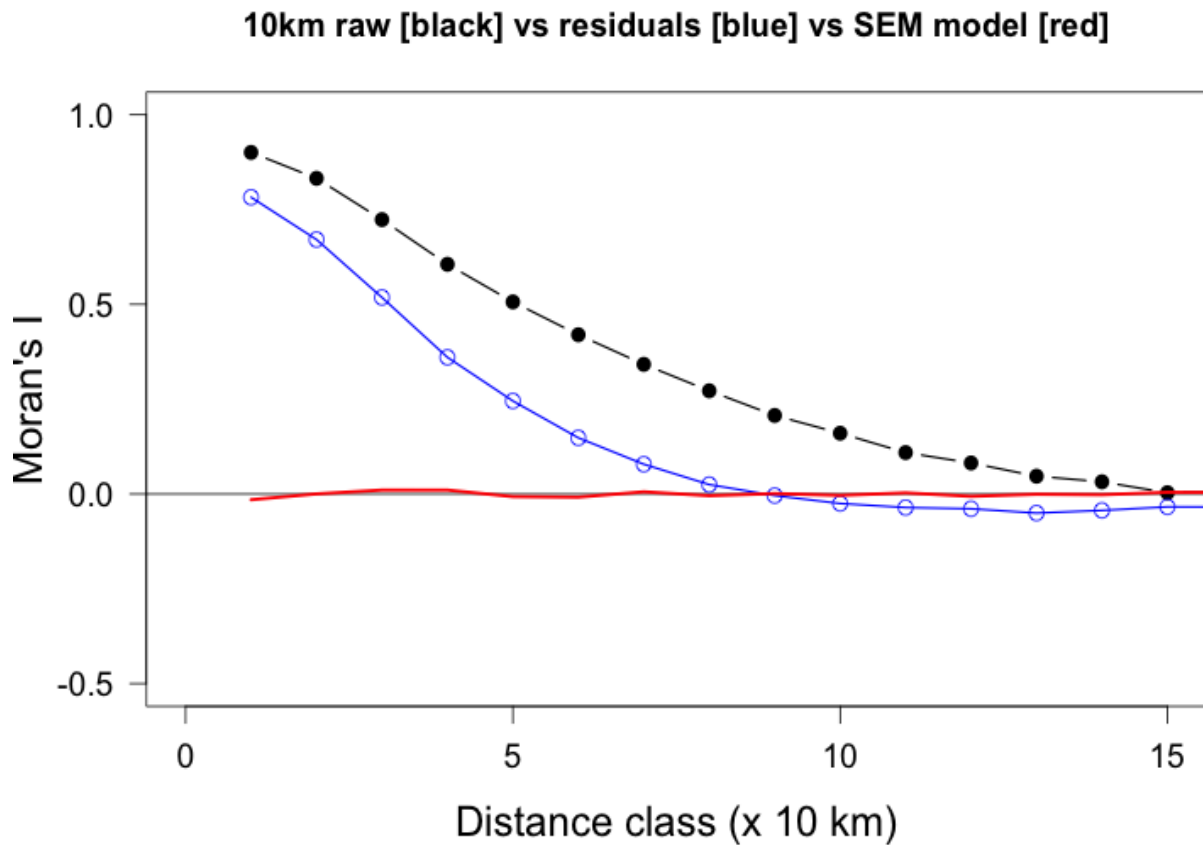


Table S7. Sensitivity analyses - Environmental correlates of PE. Predictor importance (consistent results for SAR and GLM highlighted in blue). Also shown is a plot showing how the SAR model completely accounts for spatial autocorrelation.

All predictors, 5% divergence dataset

formula	AIC	delta_AIC	weight
div ~ 1 + foreststability_120k + topographic_heterogeneity + bio1 + bio4 + bio12 + bio14 + anom_bio1 + anom_bio12	2266.51	0	0.98

Model contributions	GLM		SAR	
Predictor	Estimate	p	std. coeff	p
foreststability_120k	0.148	2.50E-02	0.006	4.58E-01
bio1	0.134	0.019	-0.061	7.56E-08
bio4	-0.154	0.02	0.032	0.13
bio12	0.122	2.30E-02	0.036	1.50E-01
bio14	0.466	0.019	0.185	1.77E-12
topographic_heterogeneity	0.028	0.017	0.016	0.0001
anom_bio1	-0.099	0.022	-0.003	0.54
anom_bio12	-0.091	0.019	-0.099	3.26E-11



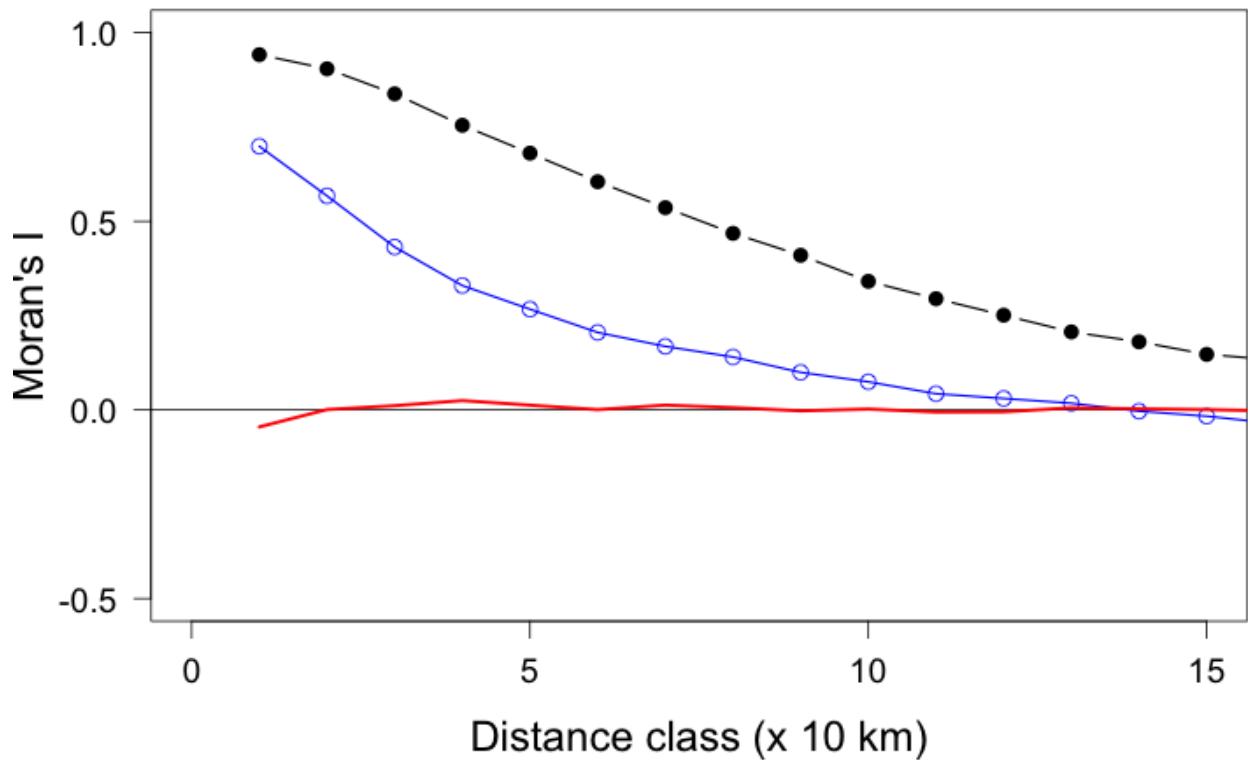
Removed bio14, 2% divergence dataset

Best GLM

formula	AIC	delta_AIC	weight
div ~ 1+ topographic_heterogeneity + bio1 + bio4 + bio12 + anom_bio1 + anom_bio12	3804.20	0	0.70

Model contributions	GLM		SAR	
Predictor	Estimate	p	std. coeff	p
bio1	0.174	0.025	-0.062	7.28E-06
bio4	0.042	0.025	0.041	6.10E-02
bio12	0.2	2.70E-02	0.131	2.49E-08
topographic_heterogeneity	0.083	0.022	-0.017	9.19E-05
anom_bio1	-0.391	0.024	-0.003	0.563
anom_bio12	-0.148	0.025	-0.087	3.88E-09

10km raw [black] vs residuals [blue] vs SEM model [red]



Removed bio14, 5% divergence dataset

Best GLM

formula	AIC	delta_AIC	weight
div ~ 1+ topographic_heterogeneity + bio1 + bio4 + bio12 + anom_bio1 + anom_bio12	3804.20	0	0.52

Model contributions Predictor	GLM Estimate	p	SAR std. coeff	p
bio1	0.171	0.027	-0.067	7.40E-09
bio4	0.042	0.026	0.048	0.029
bio12	0.193	3.10E-02	0.118	5.37E-07
topographic_heterogeneity	0.078	0.023	-0.015	0.001
anom_bio1	-0.405	0.024	-0.003	0.588
anom_bio12	-0.154	0.027	-0.086	1.07E-08

10km raw [black] vs residuals [blue] vs SEM model [red]

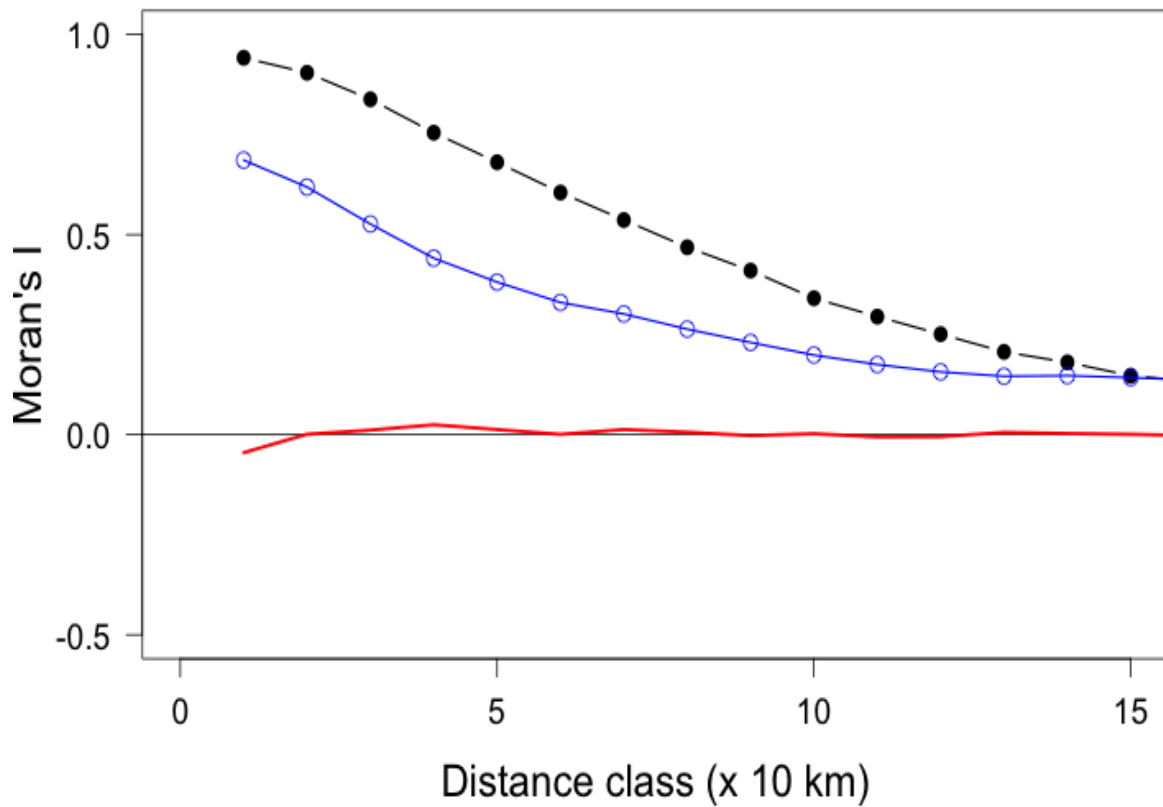


Table S8. Sensitivity analyses (Conservation analysis).

2% divergence dataset										
% of cells	Hotspot	Area (km2)	% of total area	% of total area currently protected	PE	% of total PE	% of total PE currently protected	Area of hotspot currently protected (km2)	PE currently protected	
top 2.5%	1. and 8. Coastal Kenya (including Arabuko-Sokoke)	1796	0.64	0.12	155.33	1.98	0.39	349	30.96	
	2. Pemba island									
	3. and 4. Lowland Usambara and Tanga (including Usambara-Kwale)	3817	1.36	0.14	34.29	0.44	0.50	404	38.9	
	5. Lowland Uluguru									
	6. Pugu hills	1253	0.45	0.06	101.29	1.29	0.16	156	12.73	
	7. Lindi									
	9. Pangani river	197	0.07	0.01	16.82	0.21	0.02	19	1.56	
	10. Zaraninge forest									
	11. Matumbi hills									
	12. Mafia island									
	Total		7063	2.52	0.33	307.73	3.92	1.07		
	top 5%	1. and 8. Coastal Kenya (including Arabuko-Sokoke)	3660	1.31	0.22	293.35	3.74	0.64	612	50.46
2. Pemba island										
3. and 4. Lowland Usambara and Tanga (including Usambara-Kwale)		5377	1.92	0.15	460.69	5.87	0.52	428	40.68	
5. Lowland Uluguru		229	0.08	0.01	16.81	0.21	0.03	29	2.07	
6. Pugu hills		4431	1.58	0.17	337.52	4.30	0.46	464	35.78	
7. Lindi										
9. Pangani river		338	0.12	0.02	27.27	0.35	0.05	47	3.68	
10. Zaraninge forest		22	0.01	0.01	1.57	0.02	0.01	16	1.14	
11. Matumbi hills		637	0.23	0.04	39.05	0.50	0.08	104	6.43	
12. Mafia island										
Total			14694	5.02	0.61	1176.3	14.99	1.79		
top 10%		1. and 8. Coastal Kenya (including Arabuko-Sokoke)	6374	2.27	0.30	462.39	5.89	0.82	828	64.22
	2. Pemba island	109	0.04	0.00	6.08	0.08	0.01	9	0.50	
	3. and 4. Lowland Usambara and Tanga (including Usambara-Kwale)	8351	2.98	0.18	644.77	8.22	0.58	516	45.84	
	5. Lowland Uluguru	1021	0.36	0.07	65.56	0.84	0.15	187	11.88	
	6. Pugu hills	10028	3.58	0.35	682.76	8.70	0.87	991	67.96	
	7. Lindi	31	0.01	0.01	1.73	0.02	0.02	24	1.34	
	9. Pangani river	625	0.22	0.02	42.54	0.55	0.05	62	4.07	
	10. Zaraninge forest	398	0.14	0.02	23.59	0.30	0.04	47	3.01	
	11. Matumbi hills	661	0.24	0.04	40.41	0.51	0.10	126	7.69	
	12. Mafia island	481	0.17	0.11	30.95	0.39	0.26	313	20.14	
	Total		28079	10.02	1.11	2000.8	25.50	2.89		

5% divergence dataset

% of cells	Hotspot	Area (km2)	% of total area	% of hotspot currently protected	PE	% of total PE	% of total PE currently protected	Area of hotspot currently protected (km2)	PE currently protected	
top 2.5%	1. and 8. Coastal Kenya (including Arabuko-Sokoke)	1351	0.48	0.11	112.11	1.45	0.32	295	24.96	
	2. Pemba island									
	3. and 4. Lowland Usambara and Tanga (including Usambara-Kwale)	3659	1.31	0.14	318.26	4.13	0.48	406	37.37	
	5. Lowland Uluguru									
	6. Pugu hills	1870	0.67	0.07	148.72	1.93	0.21	197	15.85	
	7. Lindi									
	9. Pangani river	202	0.07	0.01	16.89	0.22	0.02	17	1.35	
	910. Zaraninge forest									
	911. Matumbi hills									
	912. Mafia island									
	Total	7082	2.53	0.33	595.98	7.73	1.03			
top 5%	1. and 8. Coastal Kenya (including Arabuko-Sokoke)	3190	1.14	0.21	245.58	3.19	0.59	576	45.29	
	2. Pemba island	29	0.01	0.00	2.02	0.03	0.00	3	0.21	
	3. and 4. Lowland Usambara and Tanga (including Usambara-Kwale)	5135	1.83	0.15	425.34	5.52	0.51	432	39.27	
	5. Lowland Uluguru	149	0.05	0.00	10.51	0.14	0.01	6	0.42	
	6. Pugu hills	4791	1.71	0.17	361.18	4.68	0.47	472	36.04	
	7. Lindi									
	9. Pangani river	345	0.12	0.02	27.34	0.35	0.05	47	3.57	
	10. Zaraninge forest	22	0.01	0.01	1.54	0.02	0.01	16	1.12	
	11. Matumbi hills	77	0.03	0.01	5.41	0.07	0.02	18	1.27	
	12. Mafia island	346	0.12	0.08	25.18	0.33	0.22	231	16.81	
		Total	14084	5.03	0.64	1104.1	14.32	1.87		
	top 10%	1. and 8. Coastal Kenya (including Arabuko-Sokoke)	6120	2.18	0.29	427.66	5.55	0.79	822	60.80
2. Pemba island		592	0.21	0.03	36.3	0.47	0.07	86	5.23	
3. and 4. Lowland Usambara and Tanga (including Usambara-Kwale)		8135	2.90	0.18	611.11	7.93	0.56	497	43.15	
5. Lowland Uluguru		905	0.32	0.06	56.84	0.74	0.13	167	10.39	
6. Pugu hills		10067	3.59	0.35	686.26	8.90	0.87	979	66.89	
7. Lindi		17	0.01	0.00	0.95	0.01	0.01	13	0.73	
9. Pangani river		616	0.22	0.02	43.83	0.57	0.05	55	4.07	
10. Zaraninge forest		300	0.11	0.02	17.88	0.23	0.04	44	2.81	
11. Matumbi hills		676	0.24	0.05	41.94	0.54	0.11	132	8.16	
12. Mafia island		493	0.18	0.12	34.71	0.45	0.30	325	22.82	
		Total	27921	9.96	1.11	1957.5	25.39	2.92		

Table S9. Major protected areas that intersect each of the PE hotspots shown in Fig. 4 and Table 1.

Hotspot	Name	Designation
Coastal Kenya	Arabuko Sokoke	Forest Reserve
	Buda	Forest Reserve
	Kaya Chonyi	Sacred Kaya Forest
	Kaya Jibana	Sacred Kaya Forest
	Kaya Kambe	Sacred Kaya Forest
	Kaya Ribe	Sacred Kaya Forest
	Shimba Hills	National Reserve
Lowland Usambara and Tanga	Amani	Nature Reserve
	Bamba Ridge	Forest Reserve
	Bombo West/East	Forest Reserve
	Kwangumi	Forest Reserve
	Kwani/Makinyumbi	Forest Reserve
	Longuza	Forest Reserve
	Magoroto	Forest Reserve
	Manga	Forest Reserve
	Mgambo	Forest Reserve
	Mlinga	Forest Reserve
	Mtai	Forest Reserve
	Mvuha	Forest Reserve
	Nilo	Nature Reserve
	Semdoe/Msige	Forest Reserve
	South Gendagenda	Forest Reserve
Tongwe	Forest Reserve	
Pangani river	Msumbugwe	Forest Reserve
	Zaranninge forest	Forest Reserve
Lowland Uluguru	Kimboza	Forest Reserve
	Mangala	Forest Reserve
	Milawilila	Forest Reserve
	Ukutu	Wildlife Management Area
	Uluguru-Ruvu	Forest Reserve
Pugu hills	Kazimzumbwi	Forest Reserve
	Pande	Game Reserve
	Pugu - Kisarawe	Forest Reserve
	Ruvu South	Forest Reserve
Matumbi hills	Kiwengoma	Forest Reserve
	Kwamrimba	Forest Reserve
	Tong'omba	Forest Reserve
Lindi	Chitoa	Forest Reserve
	Litipo	Forest Reserve
	Makangala	Forest Reserve
	Matapwa	Forest Reserve
	Ndimba	Forest Reserve
	Rondo	Forest Reserve
	Ruawa	Forest Reserve
Mafia island	Mlola	Forest Reserve
	Rufiji-Mafia-Kilwa	RAMSAR ste
Pemba island	Ngezi	Forest Reserve
	Ras Kiuyu	Forest Reserve
	Msitu Mkuu	Forest Reserve
	Pemba channel	Conservation area

Supplementary Materials: Chapter III

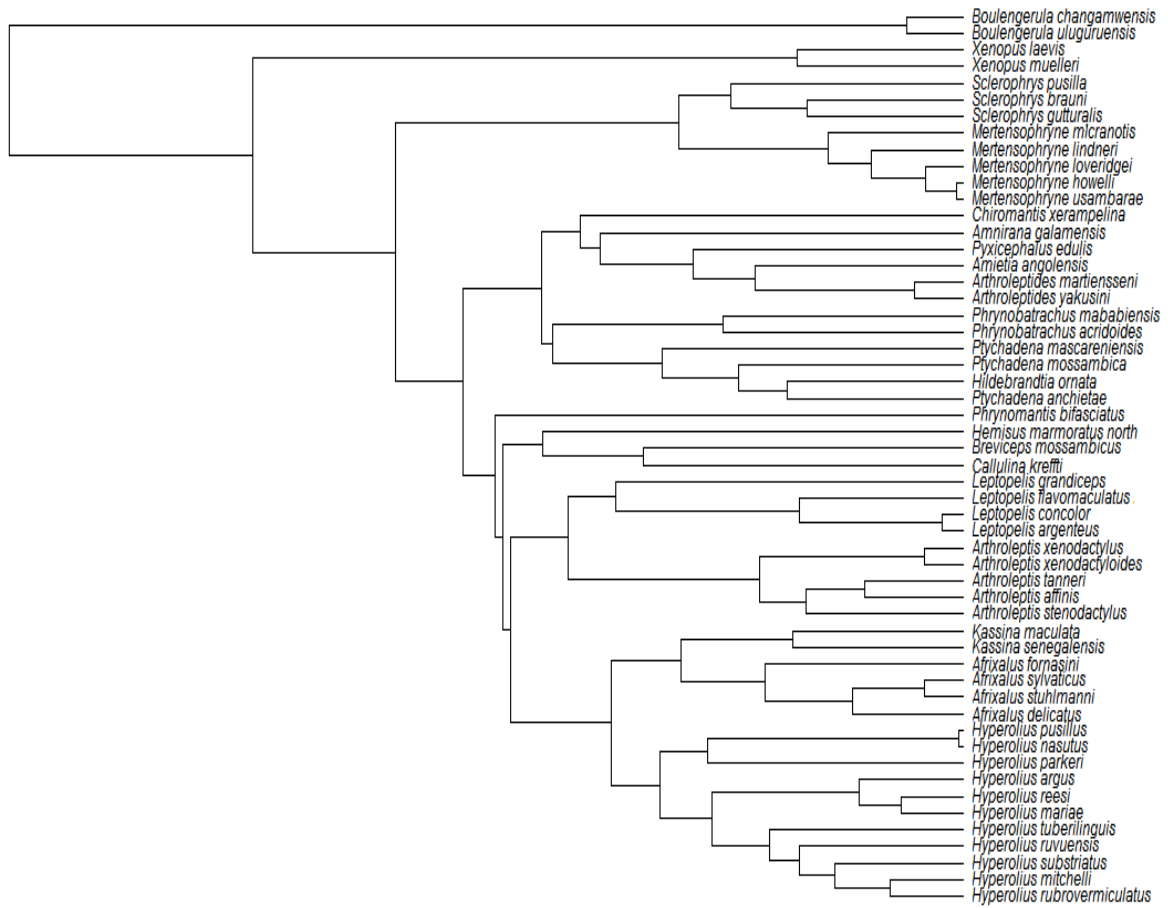


Fig. S1. Pruned phylogeny from Barratt et al (in review) representing species level relationships between coastal forest amphibians.

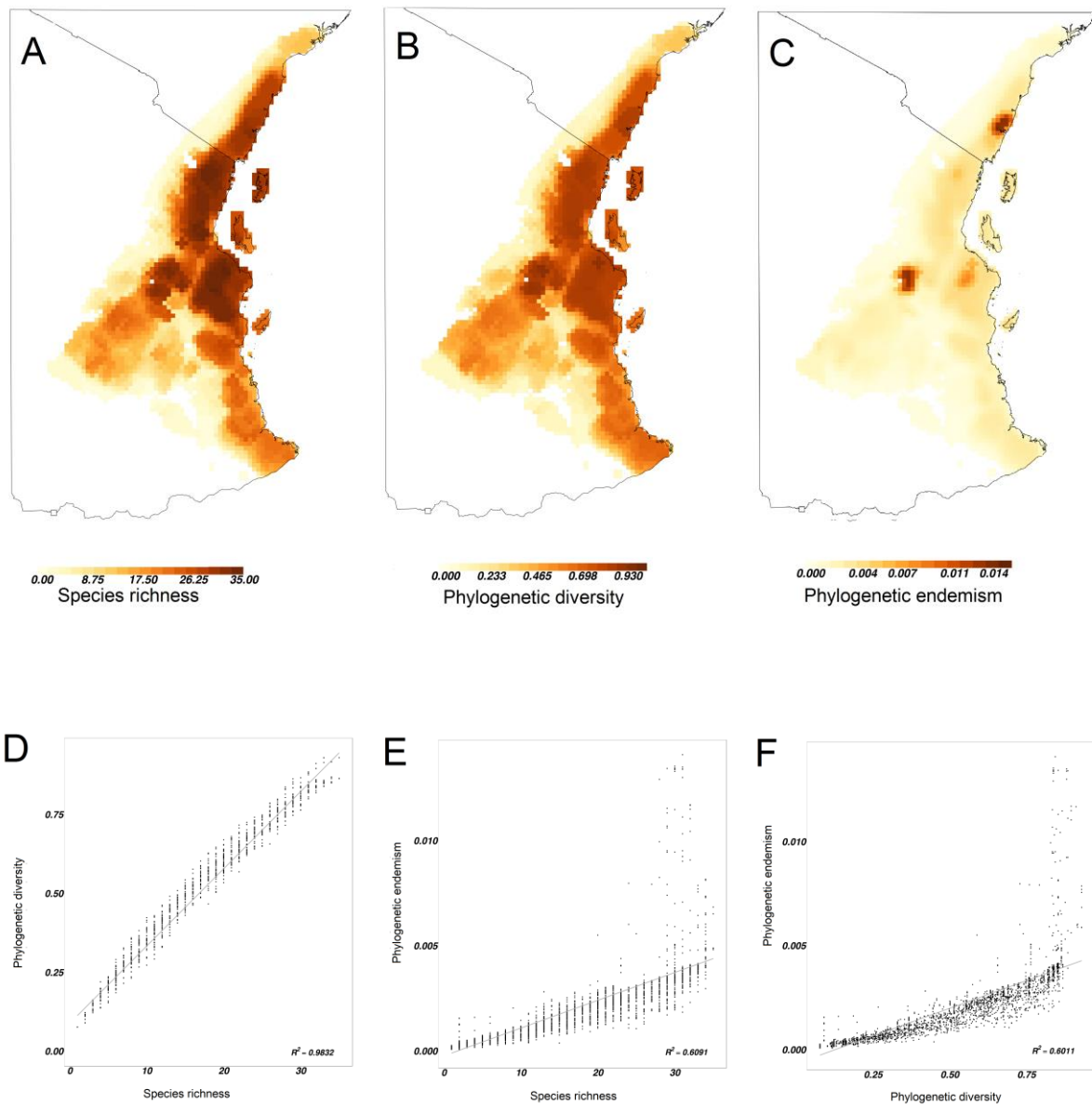


Fig. S2. Sensitivity analysis using 44 species dataset. A) Species richness (SR), B) Phylogenetic diversity (PD), C) Phylogenetic endemism (PE) across the study area (upper panel). Darker colours represent higher scores. Relationships between biodiversity indices used are shown in the lower panel; D) phylogenetic diversity vs species richness, E) phylogenetic endemism vs species richness, F) phylogenetic endemism vs phylogenetic diversity. Scattered data points in E and F show areas with high levels of phylogenetic endemism that are not highly correlated with species richness or phylogenetic diversity.

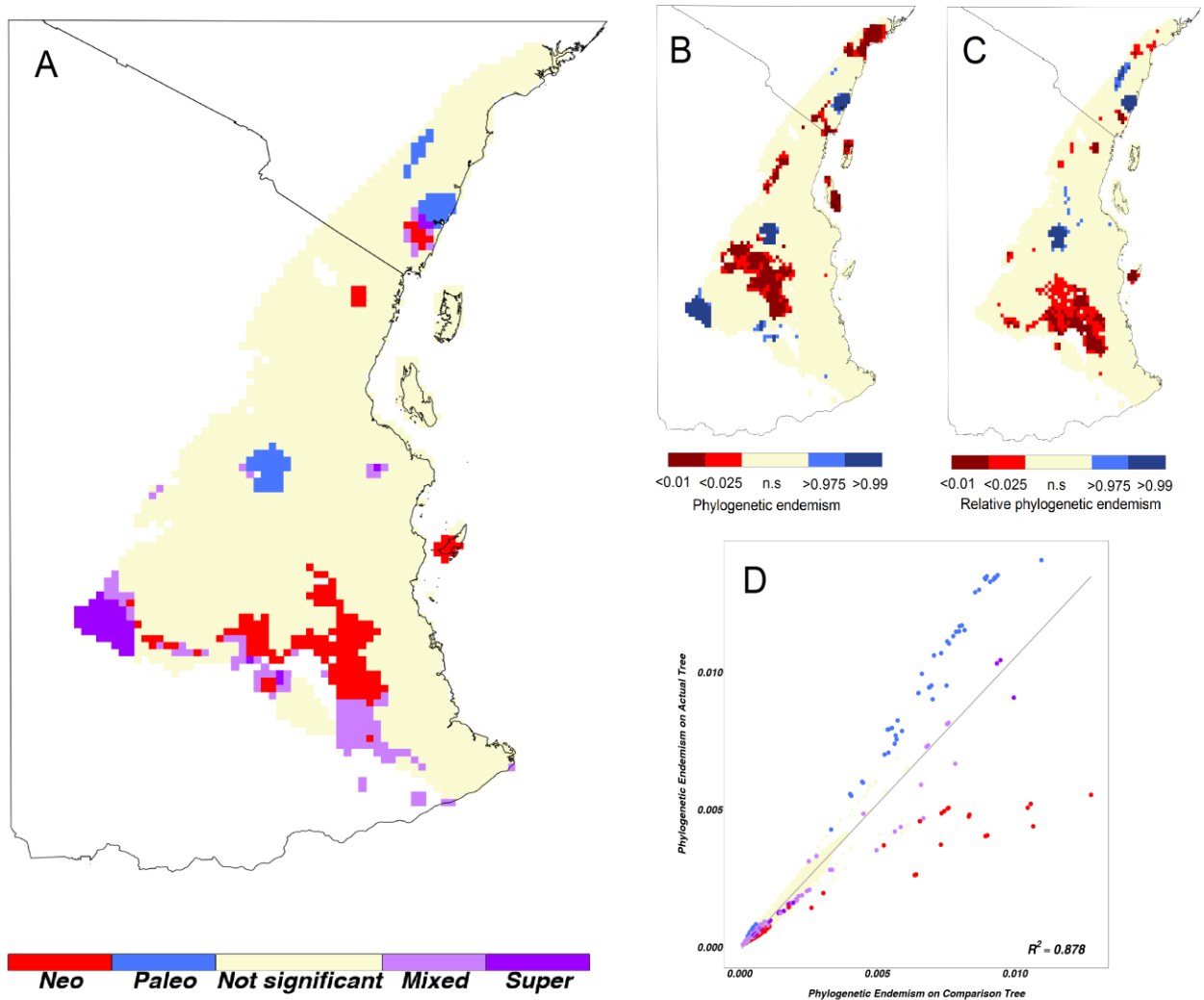


Fig. S3. Sensitivity analysis using 44 species dataset. A) Categorization of neo- and paleo- endemism (CANAPE) based on the significance tests of B) phylogenetic endemism, C) relative phylogenetic endemism, D) shows the relationship between phylogenetic endemism on the actual tree (PE) and phylogenetic endemism on the null tree (PE_{null}) after randomization, which is used along with significance tests of PE and RPE to categorize endemic grid cells into neo-, paleo-, mixed and super categories.

Supplementary Materials: Chapter IV



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Appendix 1. Locality data for previously surveyed coastal forest patches in Tanzania based on Loveridge (1942), Burgess and Clarke (2000), Frontier Tanzania and recent fieldwork by the author Barratt (unpublished). Frontier Tanzania records for various years were obtained from the library of the Natural History Museum, London.

Locality	Region	Longitude	Latitude	Source
Amboni caves	Tanga	39.04843	-5.07310	Loveridge (1942), Barratt (unpublished), Frontier Tanzania
Amboni estate	Tanga	39.01745	-5.08526	Loveridge (1942)
Baleni (Mafia island)	Pwani	39.79531	-7.84898	Barratt (unpublished)
Chitoo	Lindi	39.45987	-9.94324	Burgess and Clarke (2000), Barratt (unpublished), Frontier Tanzania
Dar es Salaam	Pwani	39.20388	-6.77875	Barratt (unpublished)
Gendagenda	Tanga	38.75633	-5.51091	Burgess and Clarke (2000)
Gendagenda North	Tanga	38.64593	-5.58329	Barratt (unpublished)
Horohoro	Tanga	39.10166	-4.63209	Barratt (unpublished)
Jozani	Zanzibar South	39.40948	-6.25973	Burgess and Clarke (2000)
Kazizumbwi	Pwani	39.05000	-6.93333	Frontier Tanzania
Kibasira	Morogoro	36.22770	-8.34888	Barratt (unpublished)
Kilulu hill	Tanga	39.12460	-4.77332	Barratt (unpublished), Frontier Tanzania
Kilulu village	Tanga	39.11713	-4.74908	Barratt (unpublished)
Kinyope village	Lindi	39.40525	-9.98720	Barratt (unpublished)
Kitaya	Mtwara	40.17337	-10.64777	Loveridge (1942)
Kiwengoma	Pwani	38.90269	-8.30435	Burgess and Clarke (2000), Barratt (unpublished), Frontier Tanzania
Lake Rutamba	Lindi	39.46164	-10.03348	Loveridge (1942), Barratt (unpublished)
Lindi, Southern Province	Lindi	39.23333	-10.00000	Loveridge (1942)
Litipo (edge)	Lindi	39.51065	-10.03238	Barratt (unpublished)
Litipo, Lindi	Lindi	39.47520	-10.04952	Barratt (unpublished), Frontier Tanzania
Mabayani bwawa	Tanga	38.92436	-5.03361	Barratt (unpublished)
Magrotto mountain	Tanga	38.75043	-5.12940	Loveridge (1942), Frontier Tanzania
Makangaga	Lindi	39.29196	-9.49454	Barratt (unpublished)
Makangala	Lindi	39.38803	-9.99418	Barratt (unpublished)
Makangala (edge)	Lindi	39.36913	-9.98237	Barratt (unpublished)
Mbanja	Mtwara	39.73186	-9.88789	Loveridge (1942)
Mchungu	Pwani	39.27662	-7.69087	Burgess and Clarke (2000), Frontier Tanzania
Mikindani	Mtwara	40.08797	-10.26437	Loveridge (1942)
Mkowela village	Ruvuma	37.99328	-10.91619	Barratt (unpublished)
Mkwaja	Tanga	38.82594	-5.79666	Burgess and Clarke (2000), Frontier Tanzania
Mrora	Pwani	39.89728	-7.73156	Burgess and Clarke (2000)
Muyuyu	Pwani	39.04373	-7.94835	Barratt (unpublished)
Namatimbili	Lindi	39.23778	-9.11064	Barratt (unpublished)

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Appendix 1. Continued.

Locality	Region	Longitude	Latitude	Source
Ndimba	Lindi	39.64829	-9.62917	Barratt (unpublished)
Ngumburuni	Pwani	39.06615	-7.88088	Barratt (unpublished)
Noto Plateau	Lindi	39.37409	-9.89532	Barratt (unpublished)
Namakutwa /Nyamuete	Pwani	39.03441	-8.32557	Burgess and Clarke (2000), Barratt (unpublished), Frontier Tanzania
Pangani falls	Tanga	38.65083	-5.35037	Burgess and Clarke (2000)
Pugu	Pwani	39.09876	-6.90893	Frontier Tanzania (2001), Frontier Tanzania
Rondo Forest	Lindi	39.17774	-10.11795	Loveridge (1942), Barratt (unpublished)
Ruawa	Lindi	39.56871	-9.72995	Barratt (unpublished)
Ruvu North	Pwani	38.95441	-6.70644	Burgess and Clarke (2000), Barratt (unpublished)
Ruvu South	Pwani	38.86667	-6.93333	Burgess and Clarke (2000), Frontier Tanzania
Tanga	Tanga	39.10137	-5.08171	Loveridge (1942)
Tong'omba	Lindi	39.01279	-8.42413	Burgess and Clarke (2000), Frontier Tanzania
Tongwe	Tanga	38.72840	-5.30438	Burgess and Clarke (2000)
Utende (Mafia island)	Pwani	39.71429	-7.96261	Barratt (unpublished)
Vikindu	Pwani	39.29910	-6.99017	Burgess and Clarke (2000), Barratt (unpublished), Frontier Tanzania
Zaranninge	Pwani	38.60755	-6.13694	Burgess and Clarke (2000), Barratt (unpublished)

Appendix 2. Natural vegetation change in Ruvu South Forest Reserve based on Landsat images from 1998 and 2014.

Class Code	Land cover	May 1998 (ha)	June 2014 (ha)
1	Mixed Dry Forest	4,796	0
2	Coastal Scrub Forest	4,119	2,148
3	Scrub Thicket	7,978	7,535
4	Wooded Grassland	10,515	7,096
5	Grassland with short bushes	4,142	10,475
6	Cleared / Sparse Vegetation	660	5,213
7	Wetland	230	480
8	Woodland	562	83
9	Cloud or Shadow	28	0

Curriculum Vitae

Christopher David Barratt

Personal Information:

- Full Name: Christopher David Barratt
- Date of Birth: 20th August 1982
- Nationality: British
- Institution address: Department of Environmental Sciences, Biogeography, University of Basel, Buro-raum 01-03 Klingelbergstr. 27, 4056 Basel, Switzerland.
- Correspondence address: Valkenburgerstraat 152 ii, 1011 NB Amsterdam, The Netherlands.
- Mobile: +41 786707793, +44 7582481893
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- ORCID: 0000-0003-3267-8855
- Google Scholar: <https://scholar.google.com/citations?user=9Qx6KAIAAAAJ&hl=en>
- Personal website: <https://christopherdbarratt.wordpress.com/>

Education and academic qualifications:

University of Basel, Switzerland (September 2013–)	PhD - Biodiversity value of the coastal forests of Eastern Africa (supervisor: Dr. Simon P. Loader)	Defence on 28th April 2017.
University of Salford, The Crescent, Salford (July 2010–July 2012)	MSc by research - Developing microsatellite markers for East African caecilian amphibians (supervisor: Dr. Robert Jehle)	Pass.
University of Salford, The Crescent, Salford (September 2003–June 2007)	BSc (Hons) - Wildlife and Practical Conservation (supervisor: Dr. P.A.Rees)	1 st class.

Relevant skills:

- Computing: Competence in phylogenetic and spatial software including RAxML, BEAST, MrBayes, Geneious, ArcGIS, qGIS, R, Unix scripting and high performance computing cluster operations, python scripting.
- Communication: Fluent in English, basic French, Italian, Dutch and Swahili.
- Additional skills: Driver's licence for class B vehicles.

Presentations and posters:

- Jan 2017 *Drivers of phylogenetic endemism and the conservation of centres of endemism in the Coastal Forests of Eastern Africa.* International Biogeography Society biennial, Tucson, AZ, USA (talk).
- April 2016 *A phylogenetic approach to explain amphibian endemism in the East African coastal forests.* Estación Biológica de Doñana, Seville, Spain. (invited talk).
- April 2016 *Linking phylogenies and spatial data to explain amphibian endemism in the East African coastal forests.* Natural History Museum of Bern, Switzerland. (invited talk).
- March 2016 *Using Next Generation Sequencing and DNA barcoding to reveal the biodiversity value of the Coastal forests of Eastern Africa.* Department of Life Sciences, University of Roehampton, UK. (invited talk).
- Dec 2015 *Phylogenetic Endemism of a highly threatened biodiversity hotspot.* Young Systematists Forum, Natural History Museum, London, UK. (talk)
- April 2015 *Using NGS and barcode data to explain diversity patterns in the CFEA.* Humer Foundation general annual meeting. University of Salzburg, Austria. (invited talk).
- March 2014 *Vanishing refuge: The Coastal Forests of Eastern Africa.* 16th African Amphibian Working Group conference, Bwindi, Uganda (talk).
- April 2011 *Newly developed microsatellite markers for the East African caecilian, Boulengerula uluguruensis and their utility in congeneric species.* British Herpetological Symposium, Bangor, Wales (talk).

- Feb 2016 *Are the Coastal forests of Eastern Africa a source area of diversity? Biology 16, Swiss Zoological Society, University of Lausanne, Switzerland (poster).*
- Aug 2015 *Are the Coastal forests of Eastern Africa a source area of diversity? Systematics Association biennial, Oxford UK (poster).*
- July 2015 *Are the Coastal forests of Eastern Africa a source area of diversity? Amphibian Conservation Research Symposium, University of Cambridge, UK (poster).*
- June 2015 *Are the Coastal forests of Eastern Africa a source area of diversity? Genotyping By Sequencing course, The Genome Analysis Centre, Norwich, UK (prize for best poster).*
- Feb 2015 *Speciation patterns in the Coastal Forests of Eastern Africa. Biology 15, Swiss Zoological Society, Duberdorf, Switzerland (poster).*
- Jan 2015 *Speciation patterns in the lowland forests of Eastern Africa. International Biogeography Society 7th biennial, University of Bayreuth, Germany (poster).*
- Sept 2014 *Speciation patterns in the lowland forests of Eastern Africa. Genomics of the speciation continuum workshop, University of Fribourg, Switzerland (poster).*

Grants:

- Feb 2016 Swiss Zoological Society travel grant to attend 8th International Biogeography Society meeting in Tucson, AZ, US. (1'000 CHF)
- Oct 2016 Freiwillige Akademischen Gesellschaft Basel - PhD extension grant for 6 months (12'000 CHF)
- Jan 2015 Departmental travel grant to attend International 7th Biogeography Society biennial conference in Bayreuth, Germany (600 CHF).
- Aug 2014 European Science Foundation ConGenOmics – Short grant to visit NHM London (1'350 EUR).
- May 2014 Departement Umweltwissenschaften, University of Basel – Travel grant to attend 16th African Amphibian Working Group meeting, Bwindi, Uganda (800 CHF).
- April 2014 Freiwillige Akademischen Gesellschaft Basel – Field work grant for Tanzania (3'500 CHF).
- Sept 2013 Humer Foundation for Academic Talent – PhD scholarship (3 years stipend).

Teaching and supervision: (see Work experience for more):

- Nov 2014 Co-supervised Mr. Marco Crotti MSc (Imperial College London). “Empirical data from a species of African frog support the negative consequences of excluding missing data from RADseq analyses”.
- Oct 2015 Ran two half-day workshops at the Institute of Biogeography, University of Basel: ‘Spatial analysis in R’ and ‘An introduction to next generation sequencing in unix’ (Students: Beryl Bwong, Reto Hagmann, Christoph Liedtke, Gabriela Bittencourt-Silva, Stefan Leiser)

Professional services:

IUCN red list assessor for East African amphibians (2016).
 Reviewer for *Conservation Genetics Resources, Molecular Phylogenetics and Evolution, Herpetological Bulletin*
 Associate editor for the *Herpetological Bulletin*

Fieldwork: UK (2004-2008), Principe, West Africa (2005), Tanzania (2004, 2007, 2008, 2013,

Memberships:

Member of Herpetological Association of Africa (2013-), African Amphibian Working Group (2011-), and IUCN red list assessor for East African amphibians
 Reviewer for *Conservation Genetics Resources, Molecular Phylogenetics and Evolution, the Herpetological Bulletin*
 Member of International Biogeography Society (2014-), British Herpetological Society (2010-), Swiss Zoological Society (2013-2017), Swiss Systematics Society (2013-2016)

Work experience:

The Herpetological Journal
Managing Editor (freelance)
(Dec 2011 – Dec 2016)

Managing the production of a quarterly published, internationally recognised peer-reviewed journal. Responsible for content management, proof reading and typesetting of papers. My work also involved regularly liaising with the Editor, society secretary, printers and authors to produce press quality journal issues.

Wolters Kluwer London
(Nov 2012 – Sept 2013)

Production editor and manager for 8 medical journals in a large international publishing house. Duties included contacting editors, authors, typesetters and proofreaders to maintain scheduled publication dates of print and online files.

University of Salford
Demonstrator
(Sept 2010 – Nov 2012)

Assisting in the teaching of undergraduate practicals based in the laboratory and leading field work on excursions in the School of Environment and Life Sciences during university term time.

Frontier Tanzania Savannah
Research Project
Research Officer
(Aug 2008 – May 2009)

Research office for a conservation NGO in Tanzania. Responsible for design and supervision of all amphibian and mammal research undertaken. Trained and supervised Research Assistants in all survey techniques for science programme. Managed logistics, budget, and seven staff. Supervised up to 25 research assistants at any one time. BTEC in Tropical Habitat Conservation mentor and assessor.

Endemic bird habitat mapping
GIS project, Principe Island,
West Africa
(August – Dec 2005)

Production of GIS maps - gathered data relating to habitats of endemic bird species by conducting field work, contacting environmental organisations such as ECOFAC (www.ecofac.org) and working with forest guides and local people.

Training courses and workshops attended:

- Jan 2017* Cleaning Biodiversity Data, International Biogeography Society biennial meeting, Tucson, AZ, USA.
July 2016 East African Amphibian Conservation IUCN discussion group, Natural History Museum, London.
Feb 2016 Adaptation for Bioinformatics Genomics Winter School, Swiss Federal Institute of Technology, held in Weggis, Switzerland.
Oct 2015 Introduction to high performance computing cluster use. Swiss Institute for Bioinformatics/ University of Basel, Switzerland.
June 2015 Genotyping By Sequencing. The Genome Analysis Centre, Norwich, UK.
Oct 2014 Genomics of the speciation continuum. University of Fribourg, Switzerland.

Referees: (Additional academic and professional referees can be obtained on request)

Dr. Simon Loader - PhD supervisor. Department of Environmental Sciences, Biogeography, University of Basel, Klingelbergstr. 27, Switzerland, CH-4056 Basel and Curator of Vertebrates, Natural History Museum, Cromwell Road, London, UK, SW7 5BD (simon.p.loader@gmail.com)

Dr. David Gower - Life Sciences department, LS Vertebrates Division, Natural History Museum, Cromwell Road, London, UK, SW7 5BD (d.gower@nhm.ac.uk)

Dr. Robert Jehle - MSc supervisor, Editor - Herpetological Journal. School of Environment and Life Sciences, Centre for Environmental Systems Research, University of Salford, Peel Building, Salford Crescent, Salford, Greater Manchester, UK, M5 4WT (r.jehle@salford.ac.uk)

Publications in peer reviewed journals:

- Bwong BA, Nyecheme J, Malonza PK, Wasonga V, **Barratt CD**, Nagel P, Loader SP (in press). Amphibian diversity in Shimba Hills National Reserve, Kenya: a comprehensive list of specimens and species. *Journal of East African Natural History*.
- Barratt CD**, Lawson LP, Bittencourt-Silva GB, Doggart N, Morgan-Brown T, Nagel P, Loader SP (2017). A new, narrowly distributed, and critically endangered species of spiny-throated reed frog (Anura: Hyperoliidae) from a highly threatened coastal forest reserve in Tanzania. *Herpetological Journal* 27, 13-24.
- Zimkus B, Lawson L, Barej M, **Barratt CD**, Channing A, Dehling JM, Gehring S, Greenbaum E, Gvodzik V, Harvey J, Kielgast J, Kusamba C, Nagy Z, Pabijan M, Penner J, Du Preez L, Rödel MO, Vences M, Weber K, Lötters S. (2017). Leapfrogging into new territory: how Mascarene ridged frogs have diversified across Africa. *Molecular Phylogenetics and Evolution* 106, 254-269.
- Sala-Bozano M, Mariani S, **Barratt CD**, Sacchi H, Boufana B, Coscia I. (2015). Spatio-temporal variability in the population structure in North-East Atlantic stocks of horse mackerel (*Trachurus trachurus*). *Proceedings of the Royal Irish Academy: Biology and Environment* 115B, 211-220.
- O'Brien CD, Hall JE, Orchard D., **Barratt CD**, Arntzen JW, Jehle R. (2015). Extending the natural range of a declining species: Genetic evidence for native great crested newt (*Triturus cristatus*) populations in the Scottish Highlands. *European Journal of Wildlife Research* 61, 27-33.
- Barratt CD**, Horsburgh GJ, Dawson, DA, Gower DJ, Wilkinson M, Loader SP, Jehle R (2012). Isolation and characterisation of nine polymorphic microsatellites for the caecilian amphibian *Boulengerula uluguruensis*, and cross-species amplification with four congeneric species. *Conservation Genetics Resources* 4, 225–229.

Submitted but not yet accepted publications:

- Barratt CD**, Bwong BA, Onstein RE, Rosauer DF, Menegon M, Doggart N, Nagel P, Kissling WD, Loader SP (in revision). Environmental correlates of phylogenetic endemism in amphibians and the conservation of refugia in the coastal forests of Eastern Africa. *Diversity and Distributions*.
- Bwong BA, Lawson LP, Nyecheme J, **Barratt CD**, Menegon M, Portik DM, Malonza PK Nagel P, Loader SP (in review). Phylogenetic, ecological and morphological variation in the congeners *Hyperolius mitchelli* and *Hyperolius rubrovermiculatus* from East Africa. *Acta Herpetologica*.
- Bittencourt-Silva GB, Tolley K, Lawson LP, Portik DM, **Barratt CD**, Nagel P, Loader SP (in review). Impact of species delimitation and sampling on niche models and phylogeographical inference: a case study of the East African reed frog *Hyperolius substriatus* Ahl 1931. *Journal of Biogeography*.

(2 first author papers and 4 co-authored papers in prep)