impact of change

diversitication of freshwater fliers

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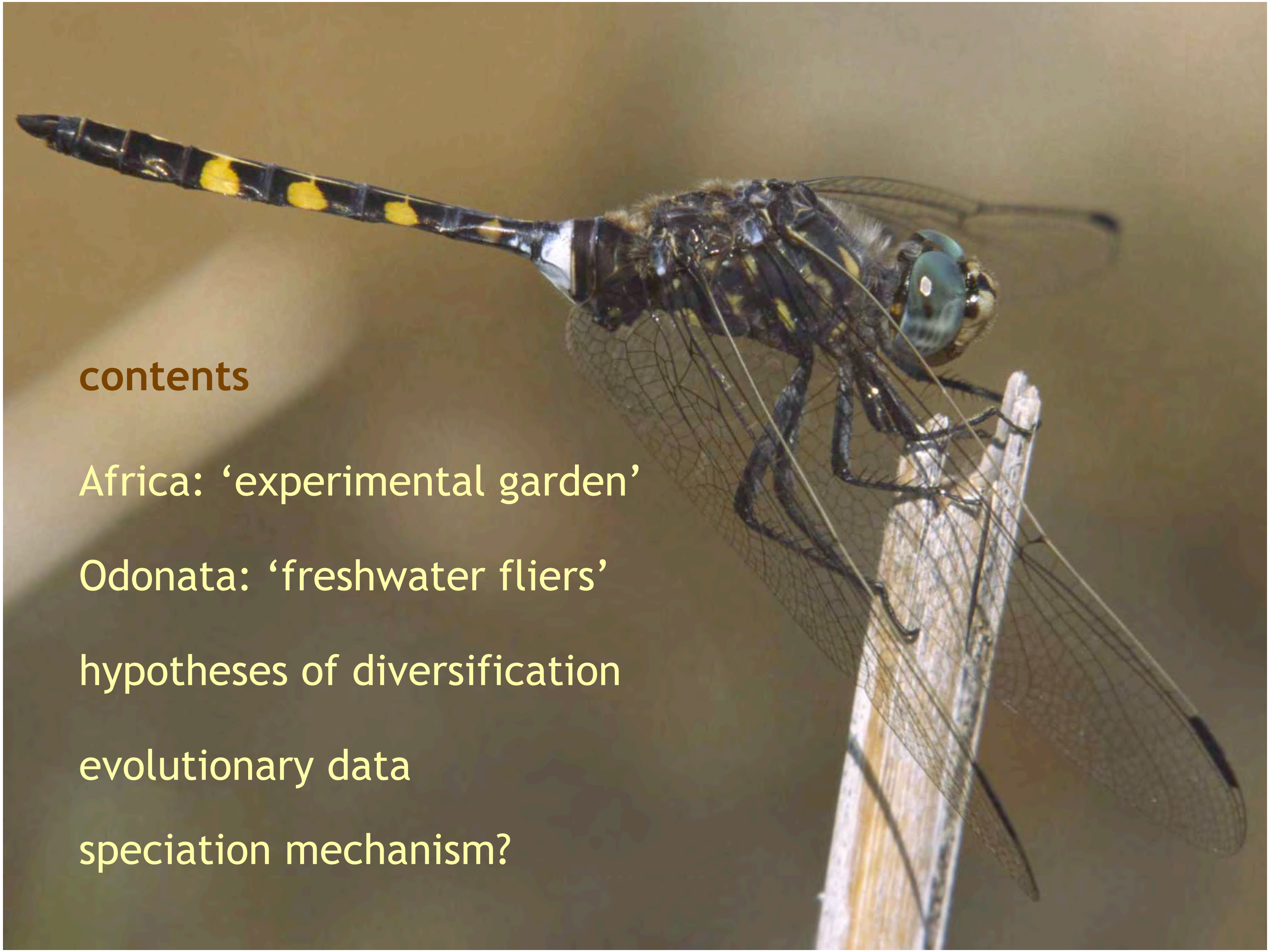

contents
Africa: ‘experimental garden’
Odonata: ‘freshwater fliers’
hypotheses of diversification
evolutionary data
speciation mechanism?

Africa as ‘experimental garden’ of global change

- once largely forested, savanna expanded 16-8 m.y.a.
- dry: 80% of past 1 million years less rainforest than now
- unstable: only 10% of the current rainforest area just 20-12,000 years ago, but Sahara much wetter 8000 y.a.
- climate in Africa is still more seasonal, more irregular and drier than in tropical Asia and America

nearest neighbour: Africa versus Asia

- Africa's climate varied while its geology was comparatively stable, but conditions in Asia were 'relatively reversed'
- contact between Africa and Asia (from about 16 m.y.a.) coincided with drying climate: with the closing of a marine barrier (Tethys Sea), a terrestrial hurdle (Sahara) opened

hypotheses of African biodiversity's history

- high selective pressures: extensive extinction <u>and</u> speciation
- ecologically-diverse species-rich groups became dominant
- much of Africa's older rainforest diversity lost, many current specialists evolved locally from ancestors of open habitats
- African (forest) diversity as 'broad', but less 'deep', than Asian

questions of ecological diversification in time and space

How frequent are ecological shifts, and which are prevalent?

Are certain ecologies ancestral, or are older species just those tolerant enough to survive?

Did different groups respond similarly to environmental history?

In which realms, regions and habitats are older and younger, or sensitive and tolerant, species?

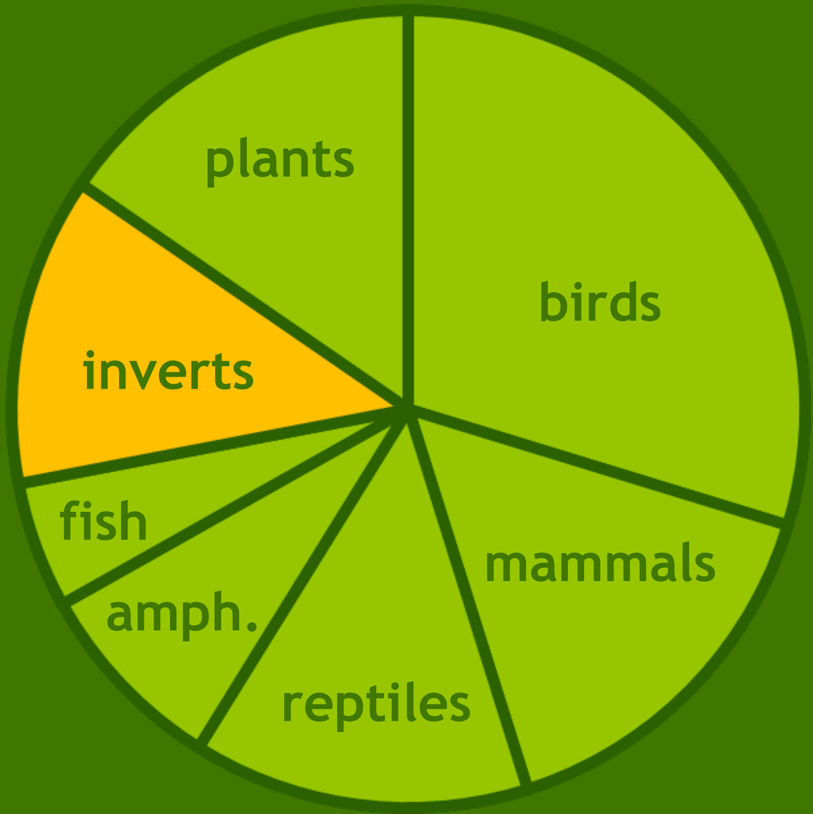
freshwater fliers

- climate change affects density, size, permanence, flow and vegetation of aquatic habitats

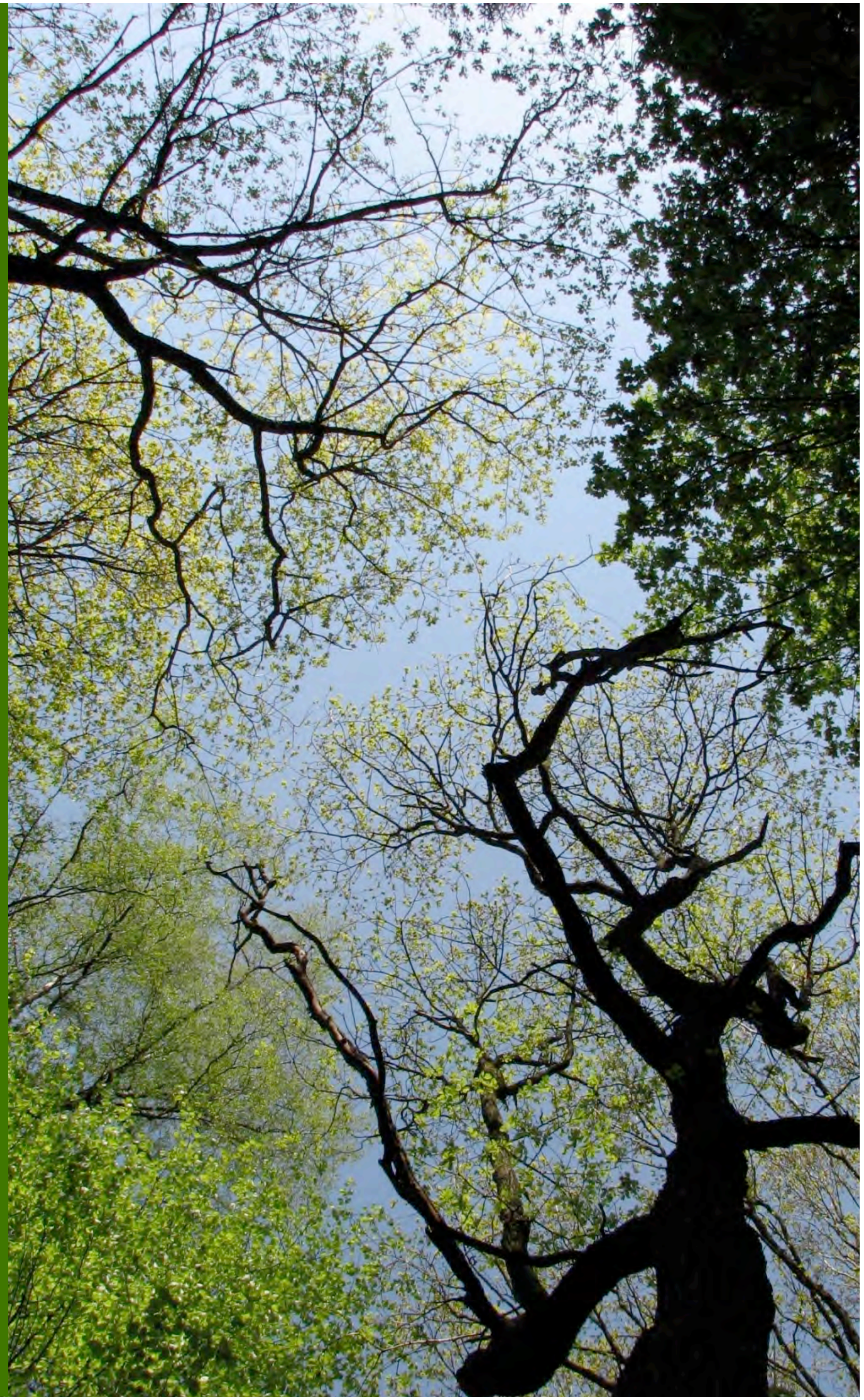
- amphibious insects are affected directly by change and can also respond instantly by dispersal: range follows change

- honest indicators of environmental change, with limited influence of other geological, ecological and human factors (contra e.g. fish, mammals, many insects)

focus of phylogenies



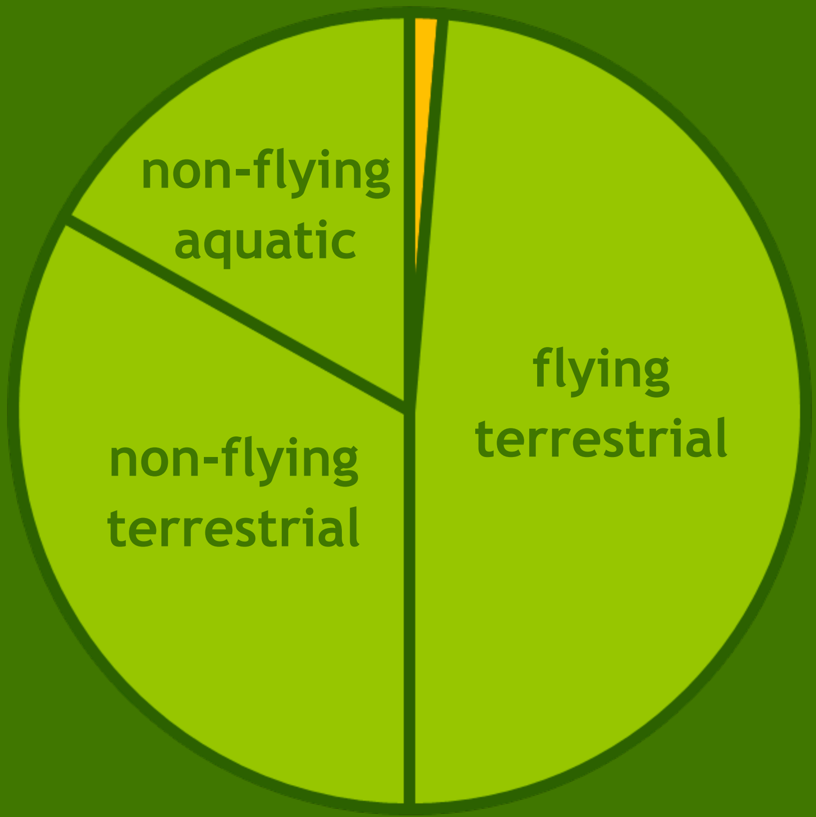
taxonomic focus of 175 molecular papers since 2000 with Afrotropical taxa



focus of phylogenies

ecological focus of 175 molecular papers since 2000 with Afrotropical taxa

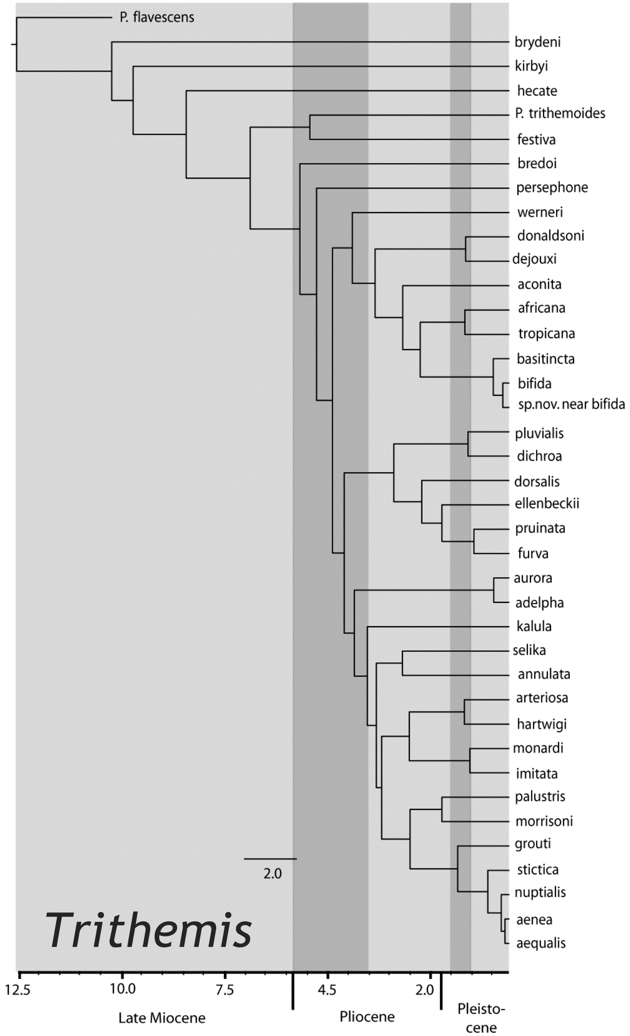
focus of phylogenies

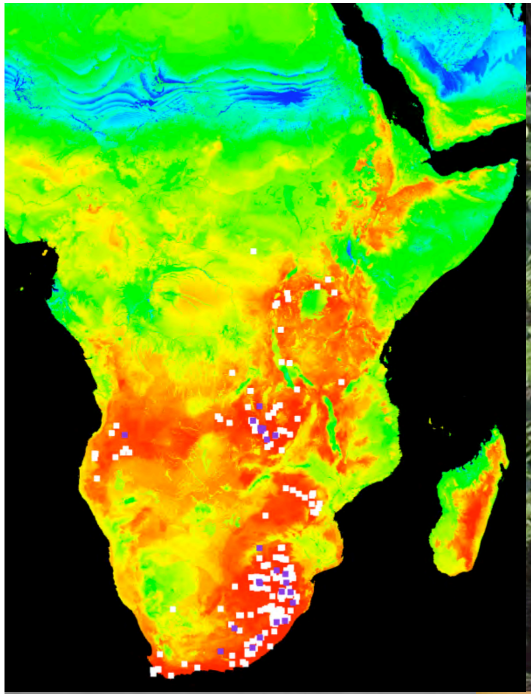


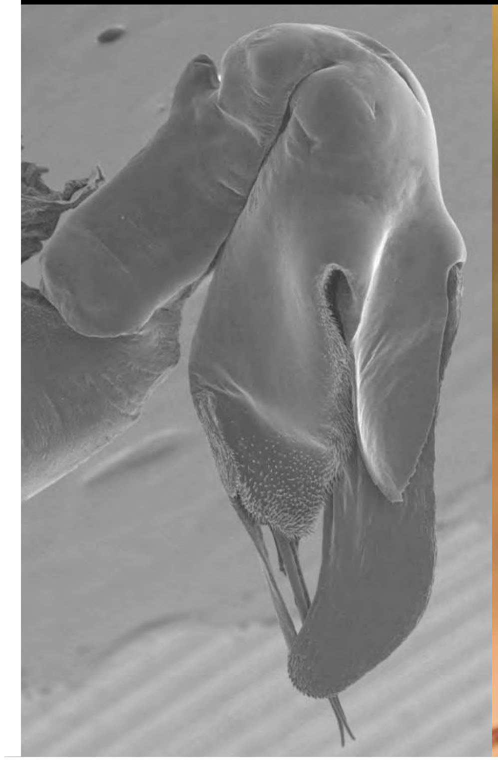
dispersal and ecology in 148 molecular papers with Afrotropical animals

> real gap in knowledge!

data: morphology, geography, phylogeny, ecology, behaviour

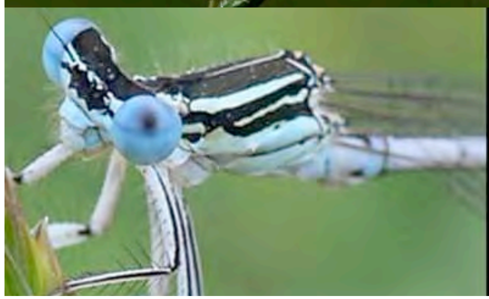
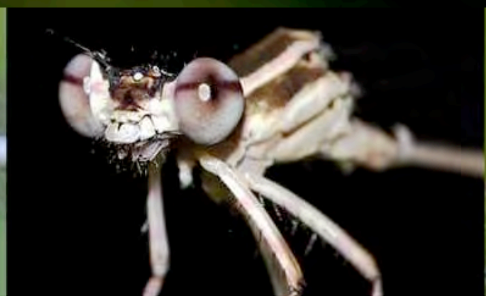


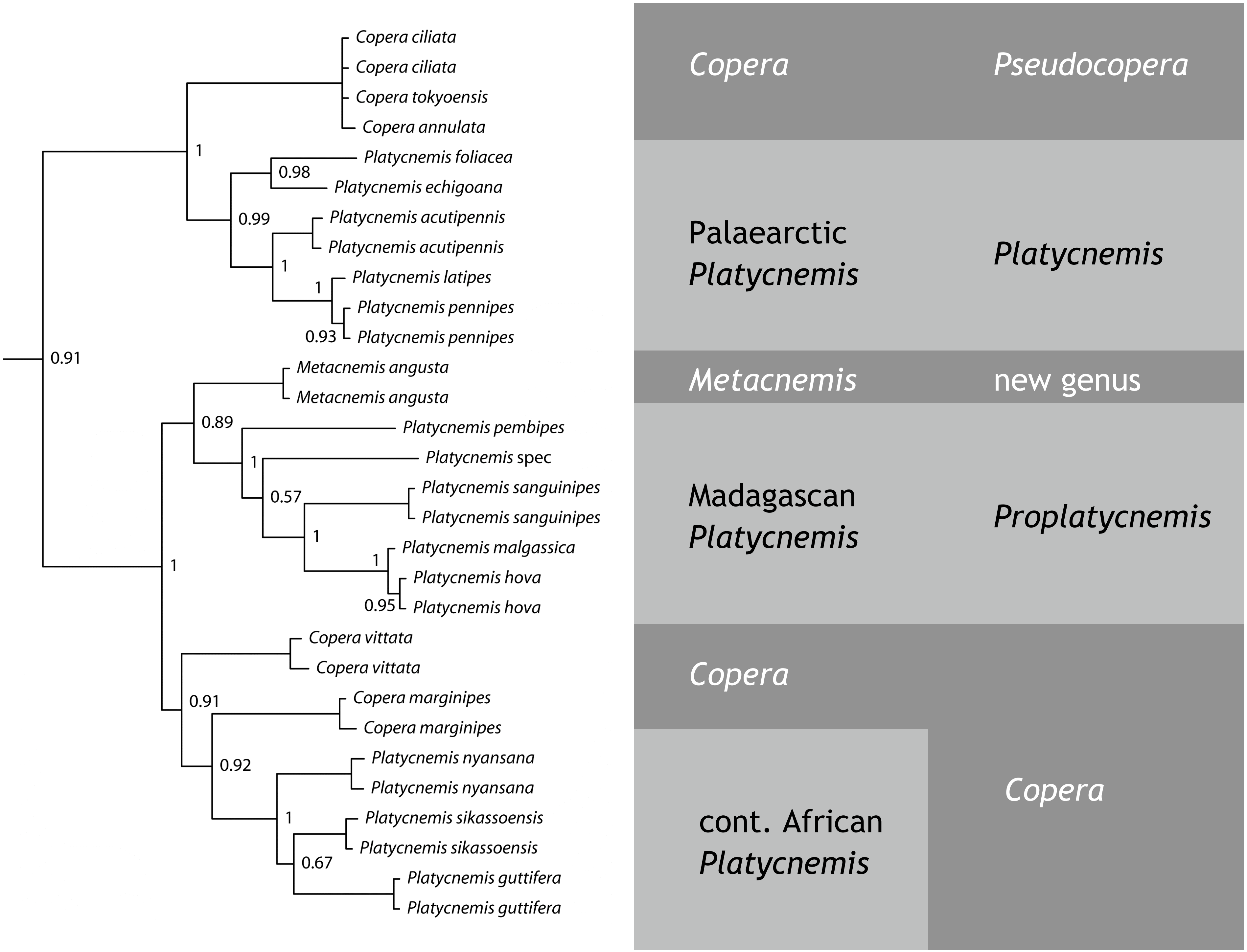


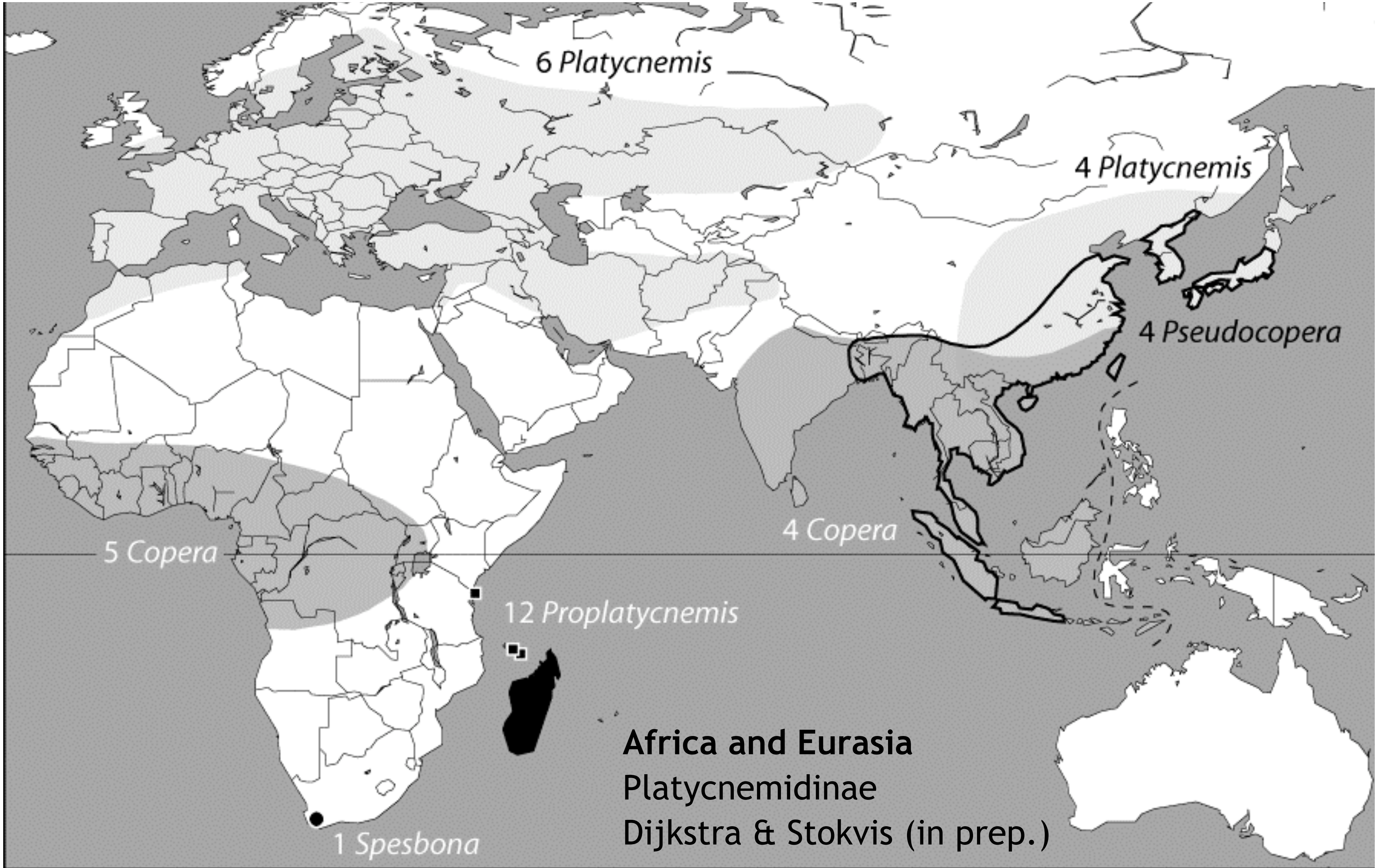


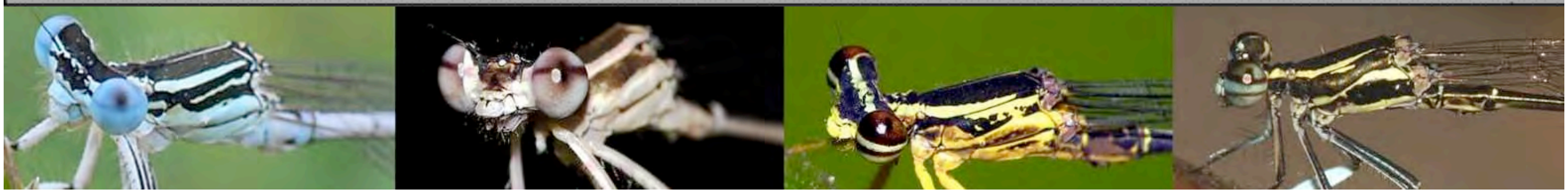
featherlegs (Platycnemidinae):
about 35 species in two debated genera
Copera in Asia only, *Platycnemis* in Africa, Eurasia and Madagascar



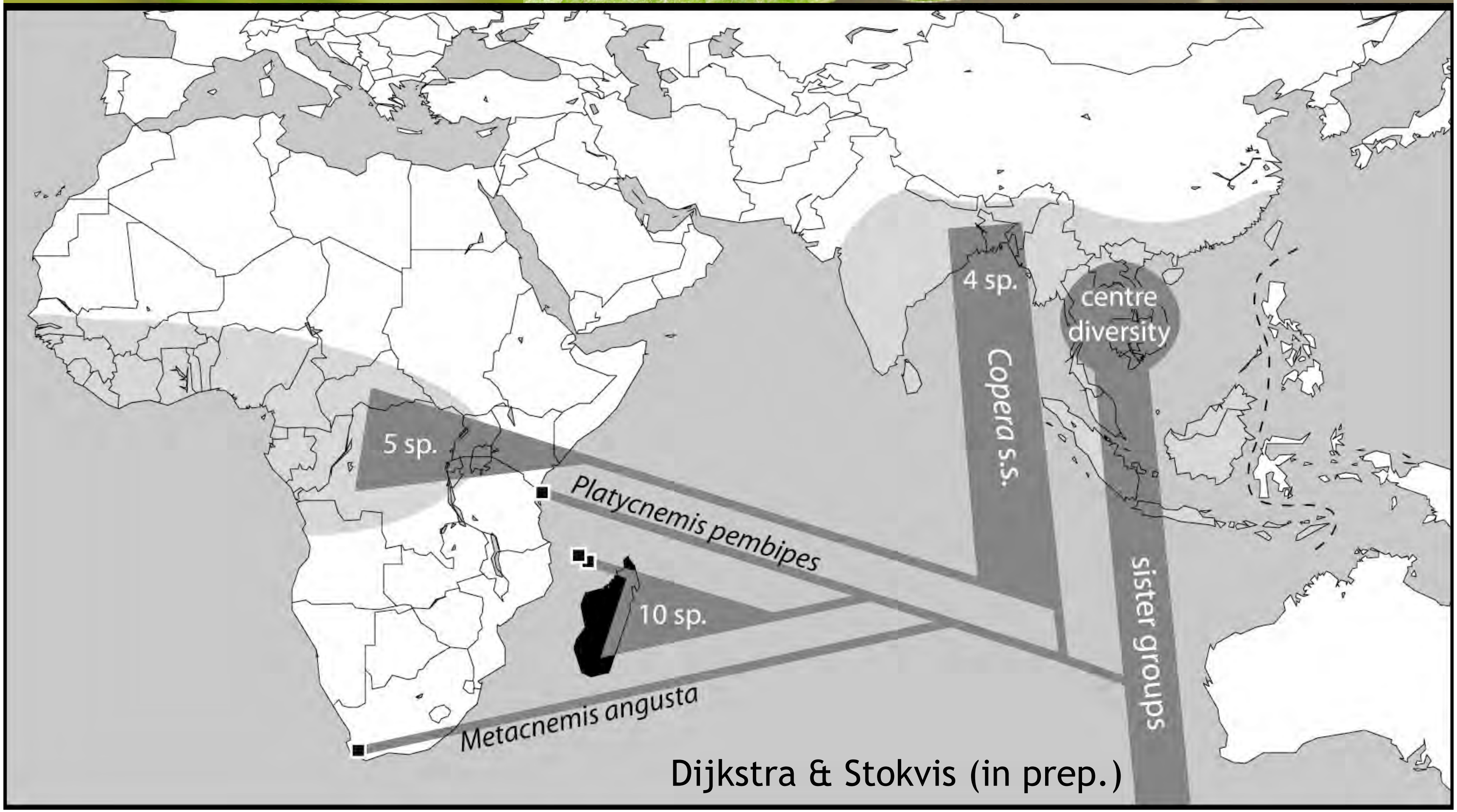




Copera ciliata
Copera ciliata
Copera tokyoensis
Copera annulata
Platycnemis foliacea
Platycnemis echigoana
Platycnemis acutipennis
Platycnemis acutipennis
Platycnemis latipes
Platycnemis pennipes
Platycnemis pennipes
Metacnemis angusta
Metacnemis angusta
Platycnemis pembipes
Platycnemis spec
Platycnemis sanguinipes
Platycnemis sanguinipes
Platycnemis malgassica
Platycnemis hova
Platycnemis hova
Copera vittata
Copera vittata
Copera marginipes
Copera marginipes
Platycnemis nyansana
Platycnemis nyansana
Platycnemis sikassoensis
Platycnemis sikassoensis
Platycnemis guttifera
Platycnemis guttifera
1
0.98
0.99
1
1
0.93
0.91
0.89
1
0.57
1
1
0.95
1
0.91
0.92
1
0.67
Copera
Pseudocopera
Palaearctic Platycnemis
Platycnemis
Metacnemis
new genus
Madagascan Platycnemis
Proplatycnemis
Copera
cont. African Platycnemis
Copera


6 Platycnemis
4 Platycnemis
4 Pseudocopera
4 Copera
5 Copera
12 Proplatycnemis
1 Spesbona
Africa and Eurasia
Platycnemidinae
Dijkstra & Stokvis (in prep.)

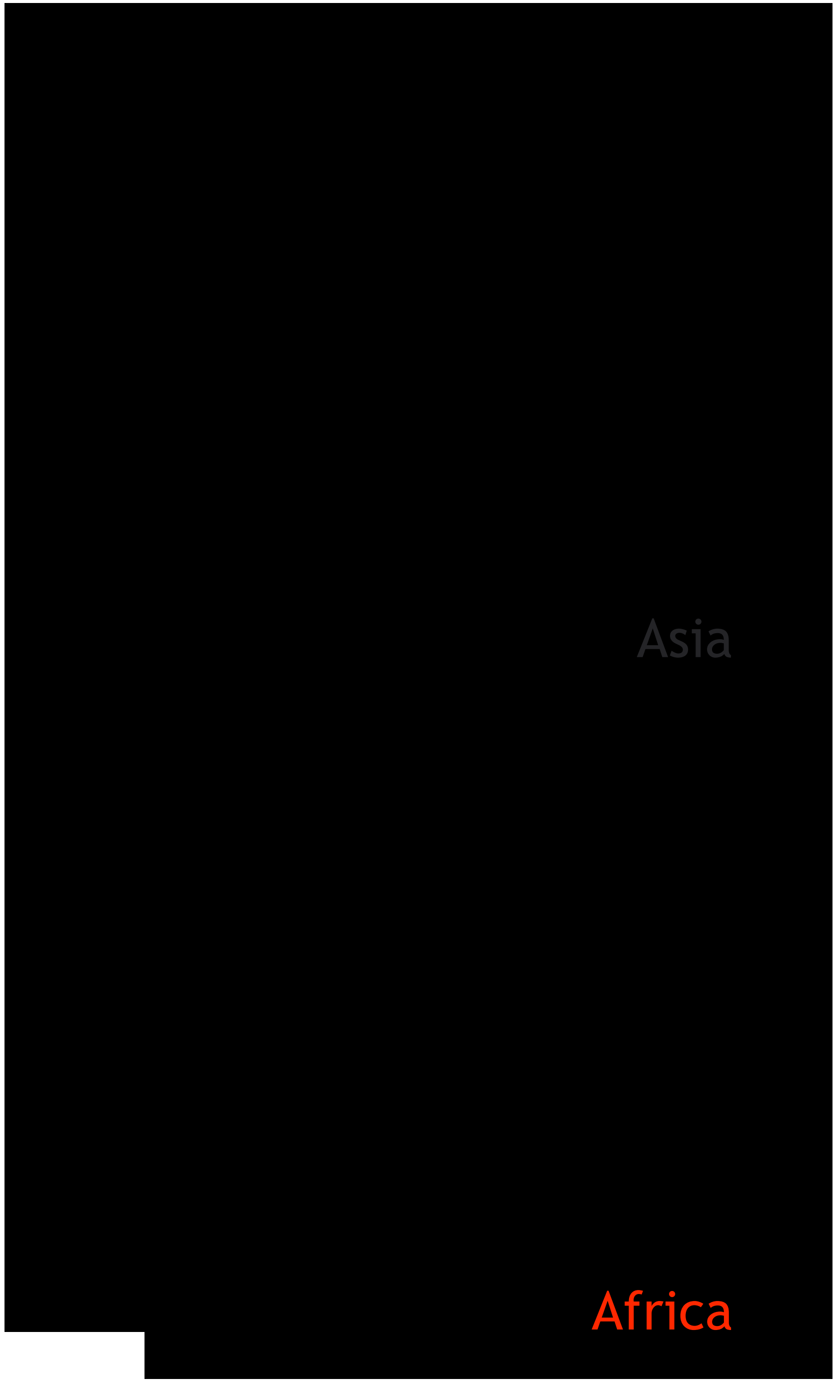



‘Metacnemis’
angusta

‘Platycnemis’ nyansana

4 sp.
centre
diversity
Copera s.s.
5 sp.
Platycnemis pembipes
sister groups
10 sp.
Metacnemis angusta
Dijkstra & Stokvis (in prep.)

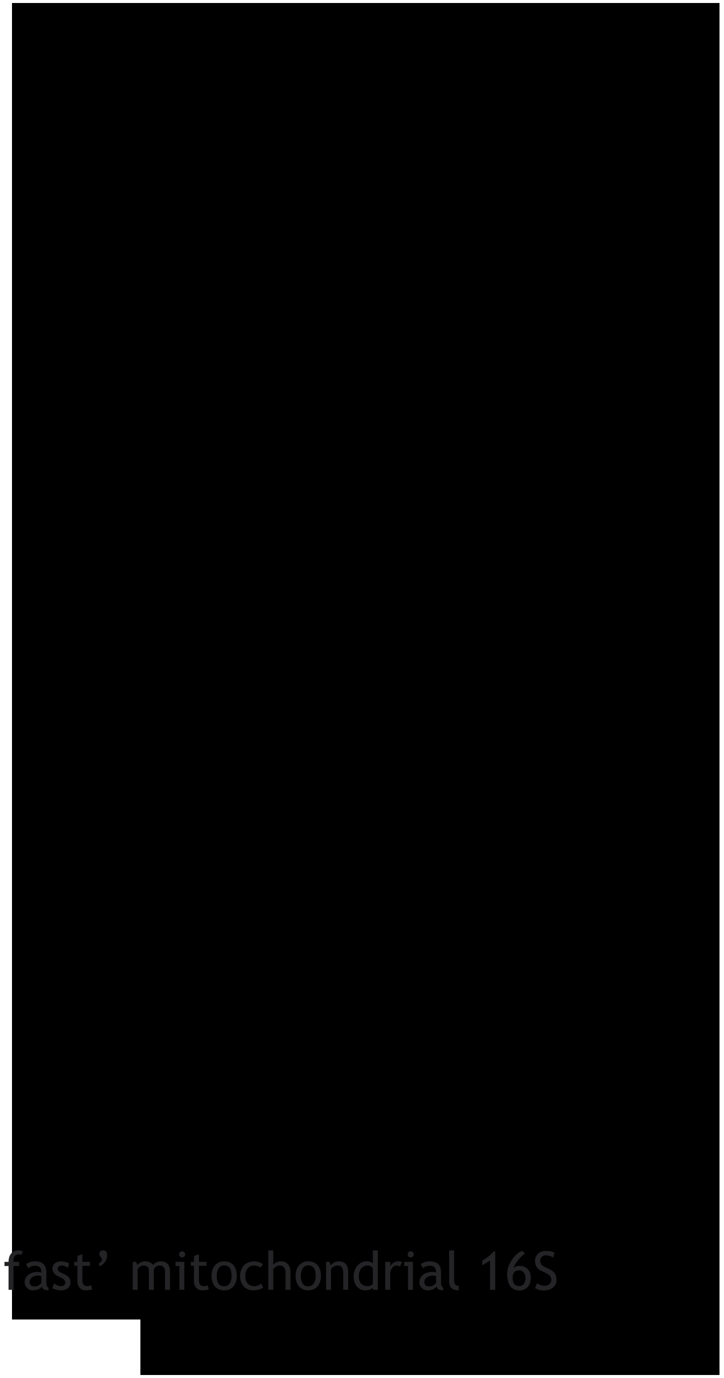
Africa vs. Asia: Chlorocyphidae

dancing jewels of rainforest streams



16S + 28S Bayesian inference

Dijkstra & van den Heuvel (in prep.)



‘fast’ mitochondrial 16S

‘slow’ nuclear 28S

dropwings *Trithemis*

40 African species,
2 Madagascan and
5 Asian

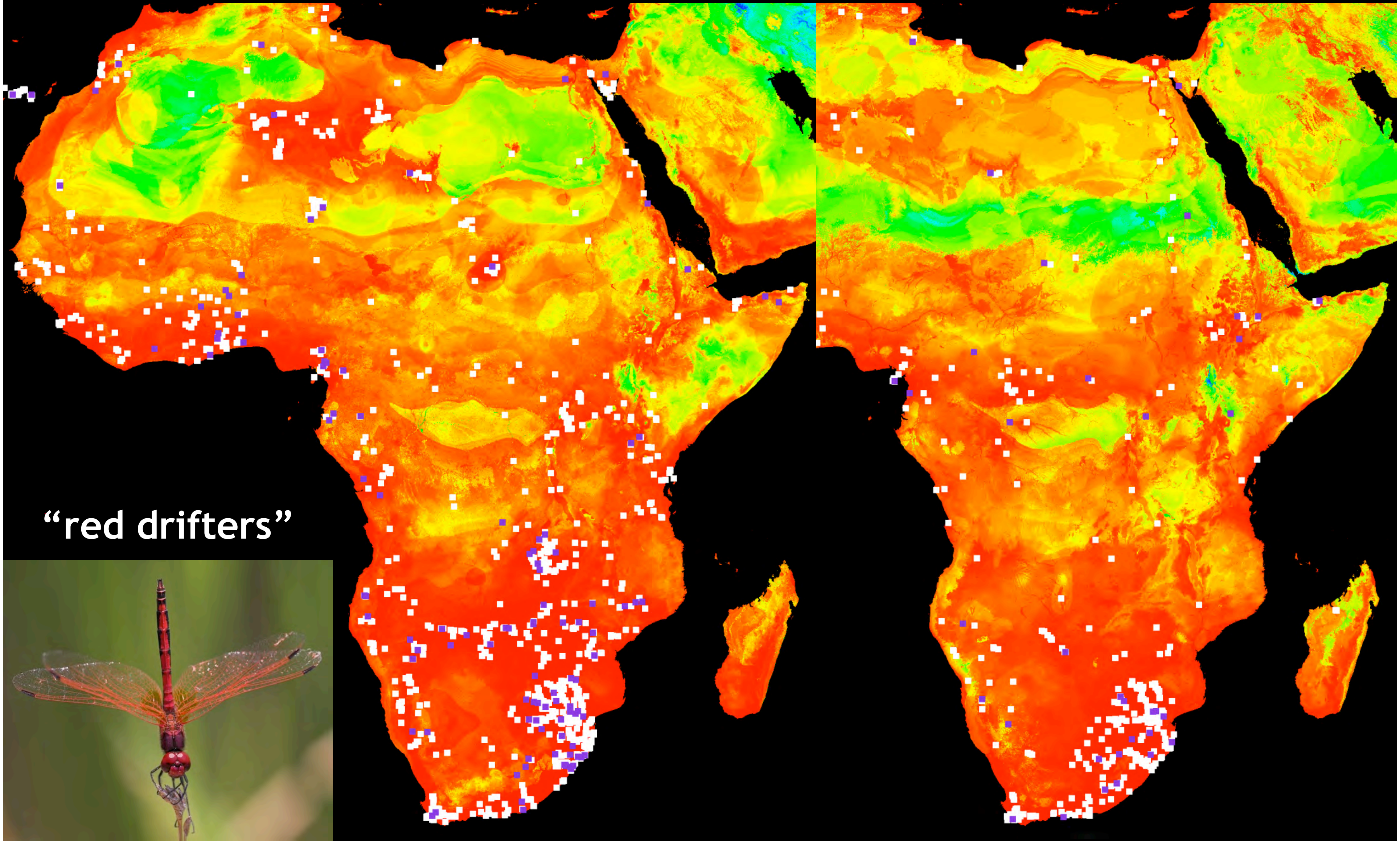
dominant across Africa,
warm temporary pools to
cool permanent streams,
deserts to rainforests,
lowlands to highlands

molecular data for
81% of species

Damm, Dijkstra & Hadrys, 2010

“red drifters” and “dark residents”

Trithemis ecological niche modelling with MaxEnt (Urrutia in prep.)

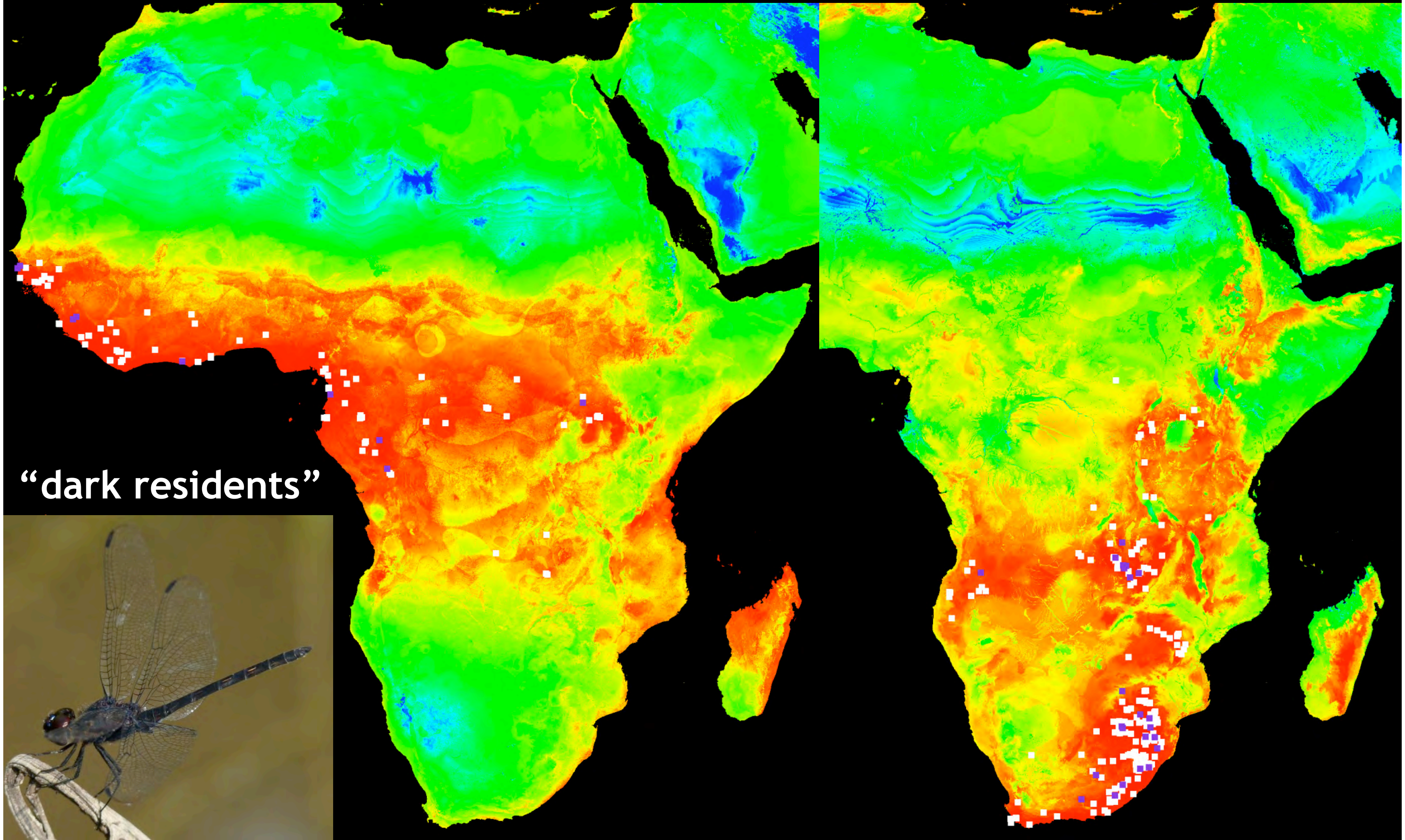


“red drifters”

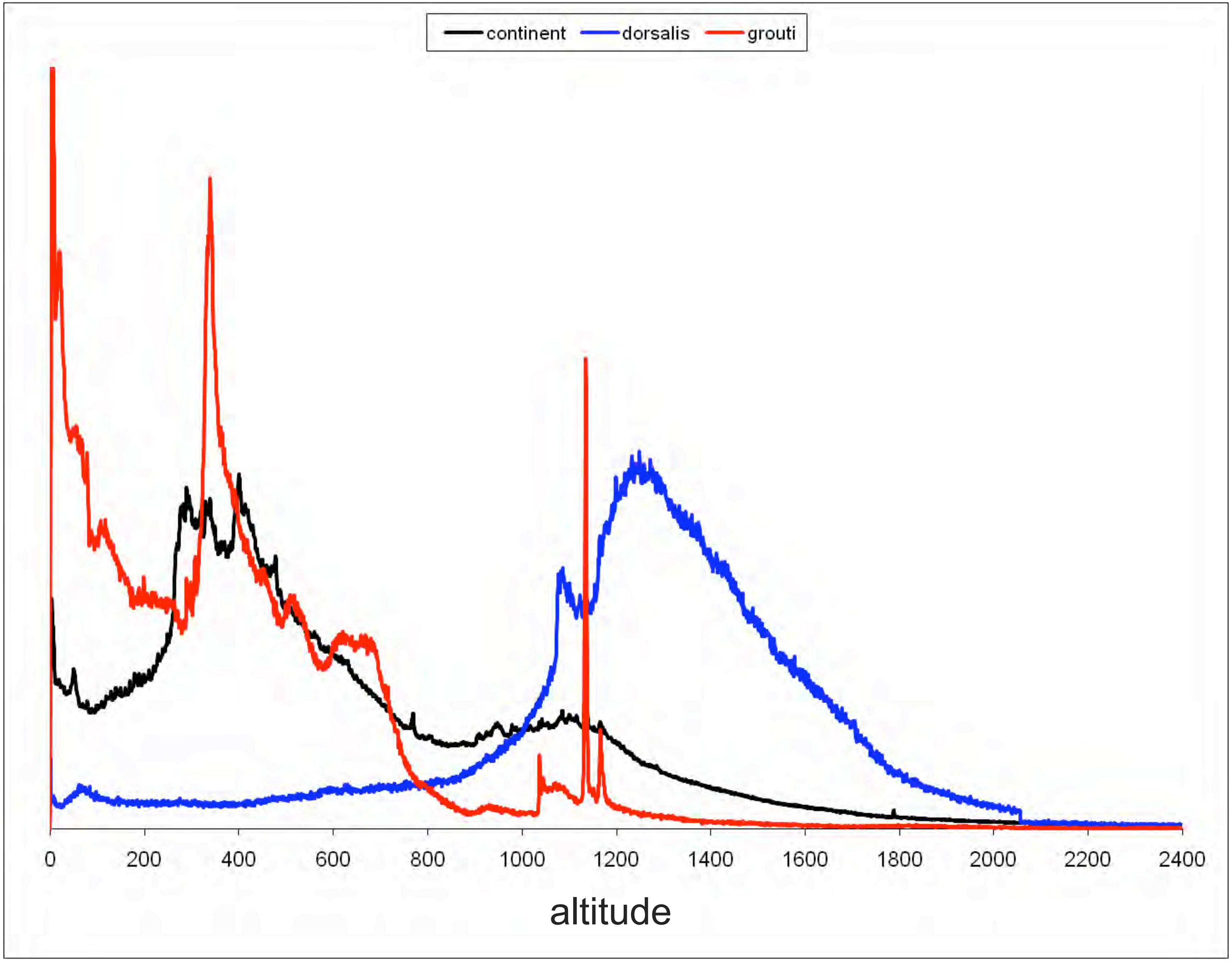
Trithemis arteriosa

T. annulata

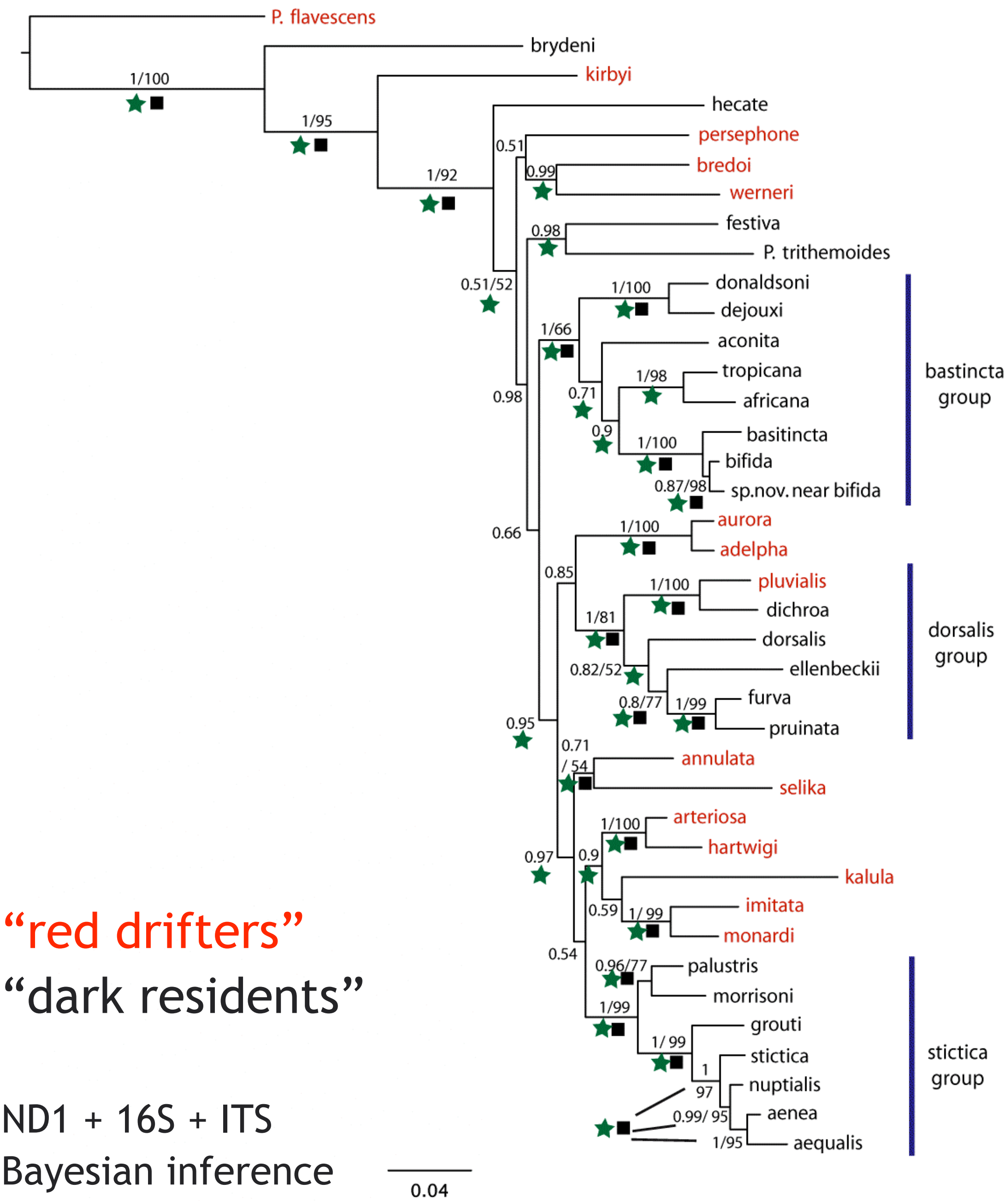
Trithemis ecological niche modelling with MaxEnt (Urrutia in prep.)



Trithemis grouti *T. dorsalis*



continent
dorsalis
grouti
0
200
400
600
800
1000
1200
1400
1600
1800
2000
2200
2400
altitude



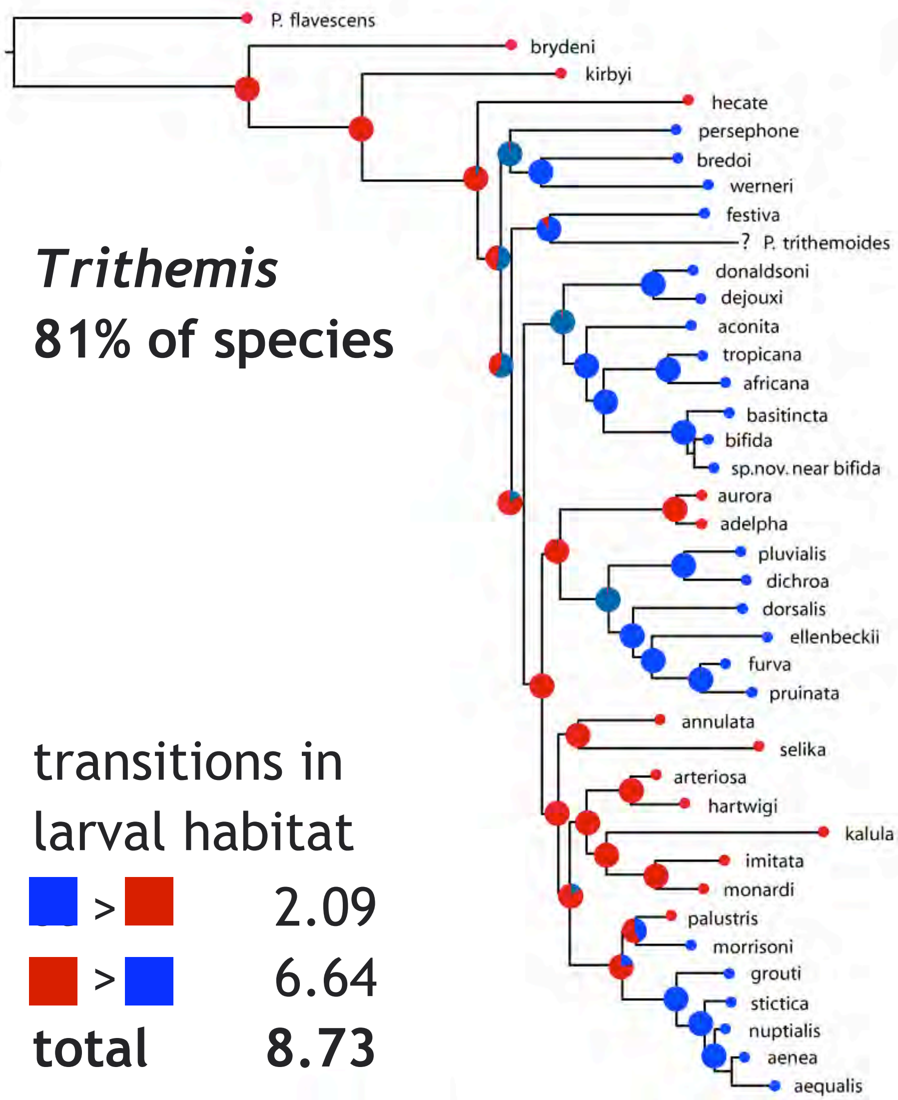
“red drifters”

“dark residents”

ND1 + 16S + ITS

Bayesian inference

evolution of ecology



Trithemis
81% of species

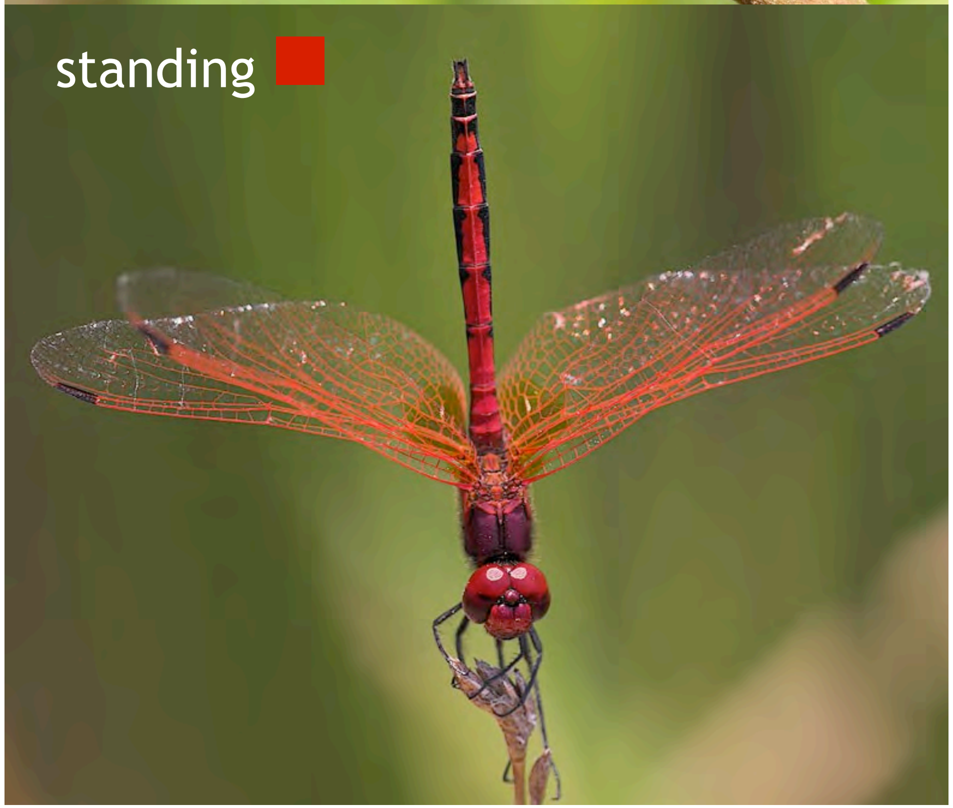
transitions in
larval habitat

■ > ■ 2.09

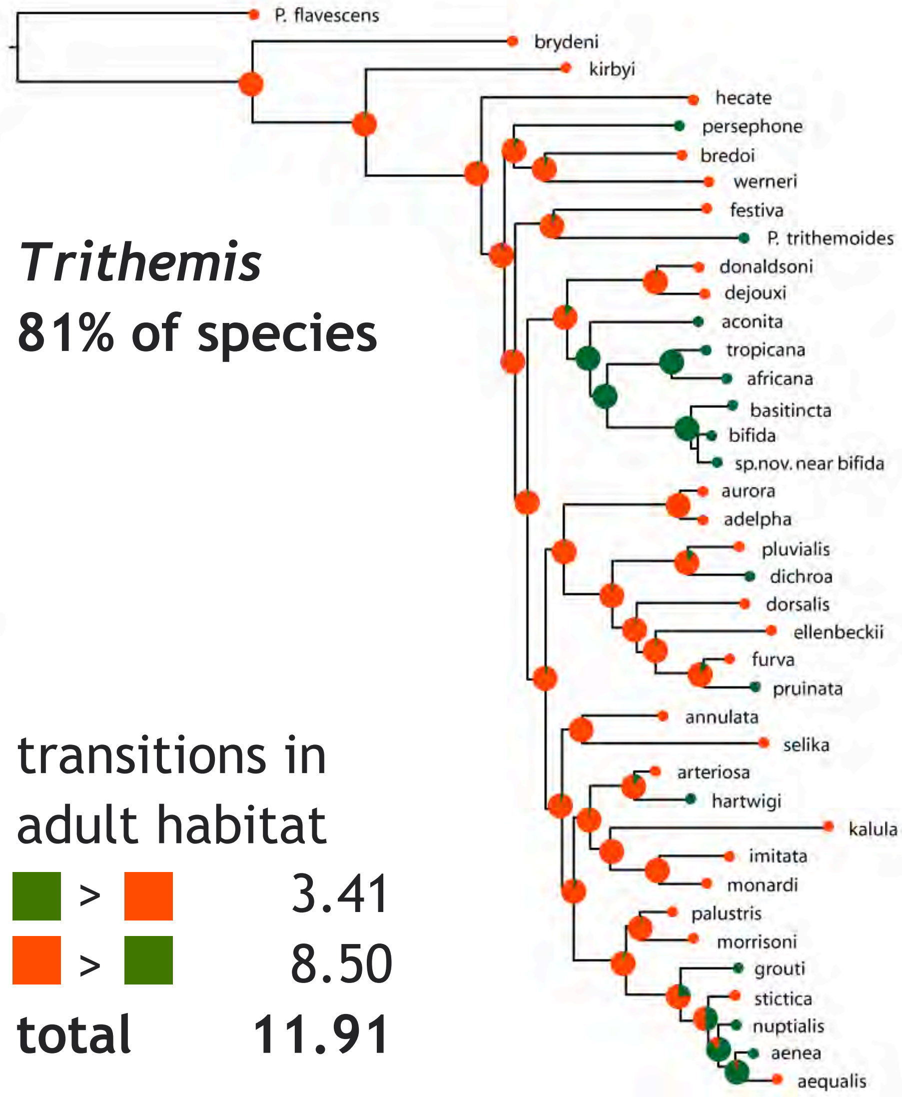
■ > ■ 6.64

total 8.73

ND1 + 16S + ITS Bayesian inference
Damm, Dijkstra & Hadrys (2010)



evolution of ecology

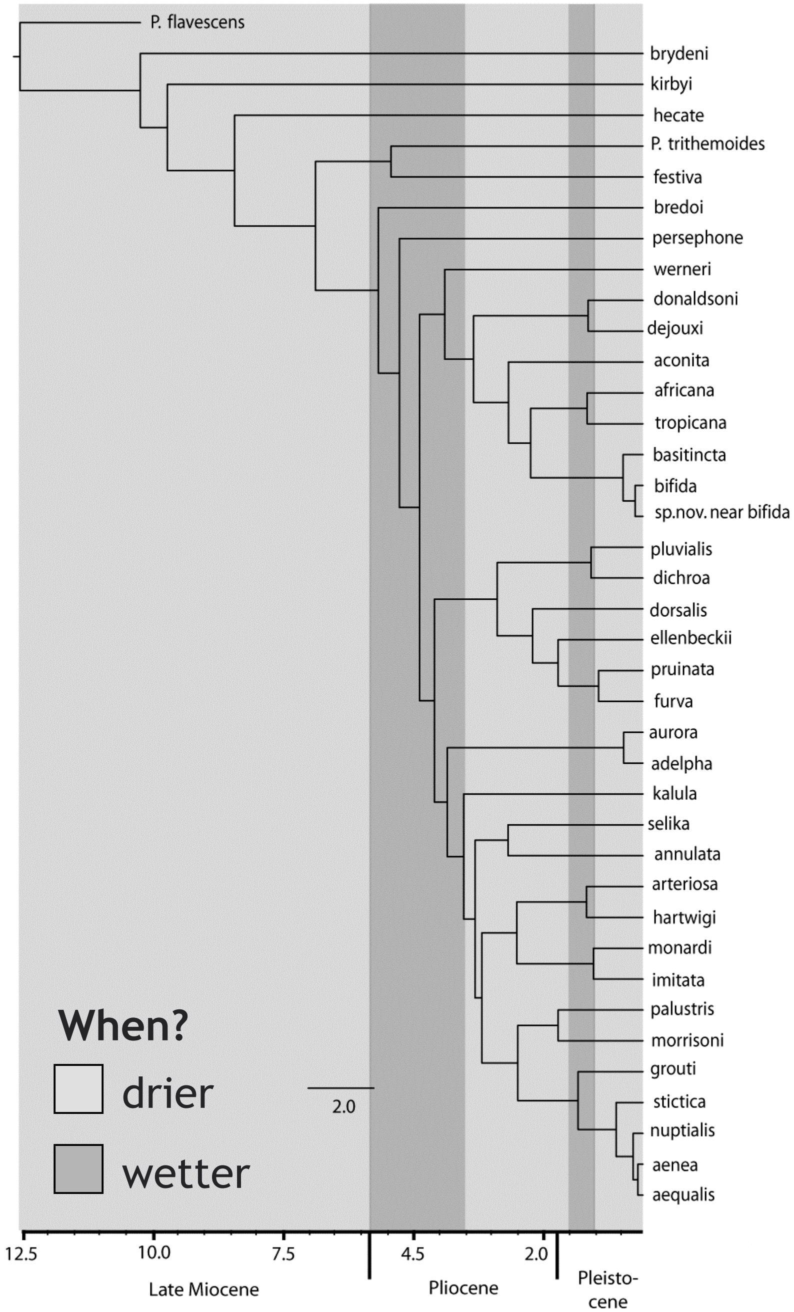


Trithemis
81% of species

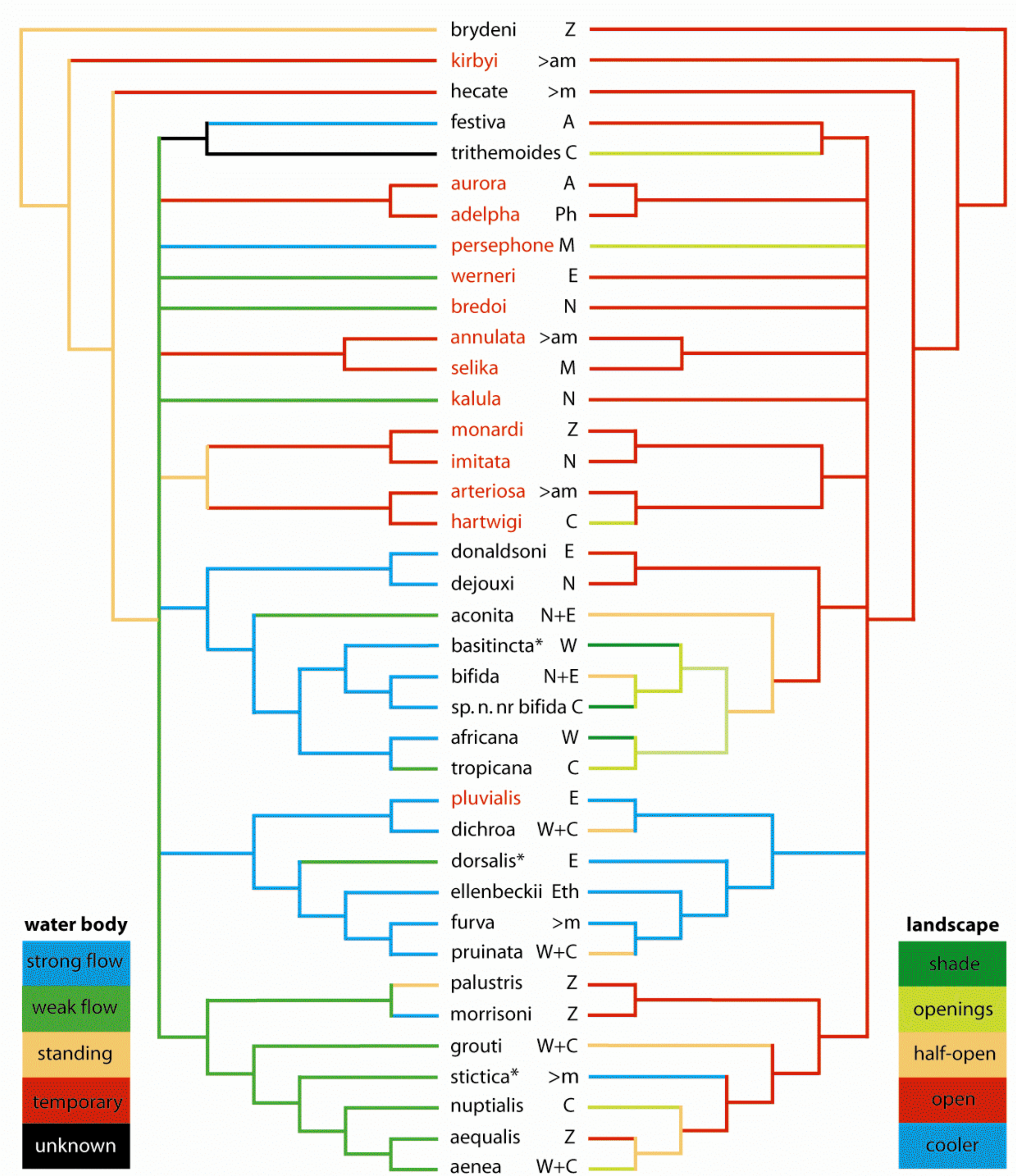
transitions in adult habitat

green > orange	3.41
orange > green	8.50
total	**11.91**

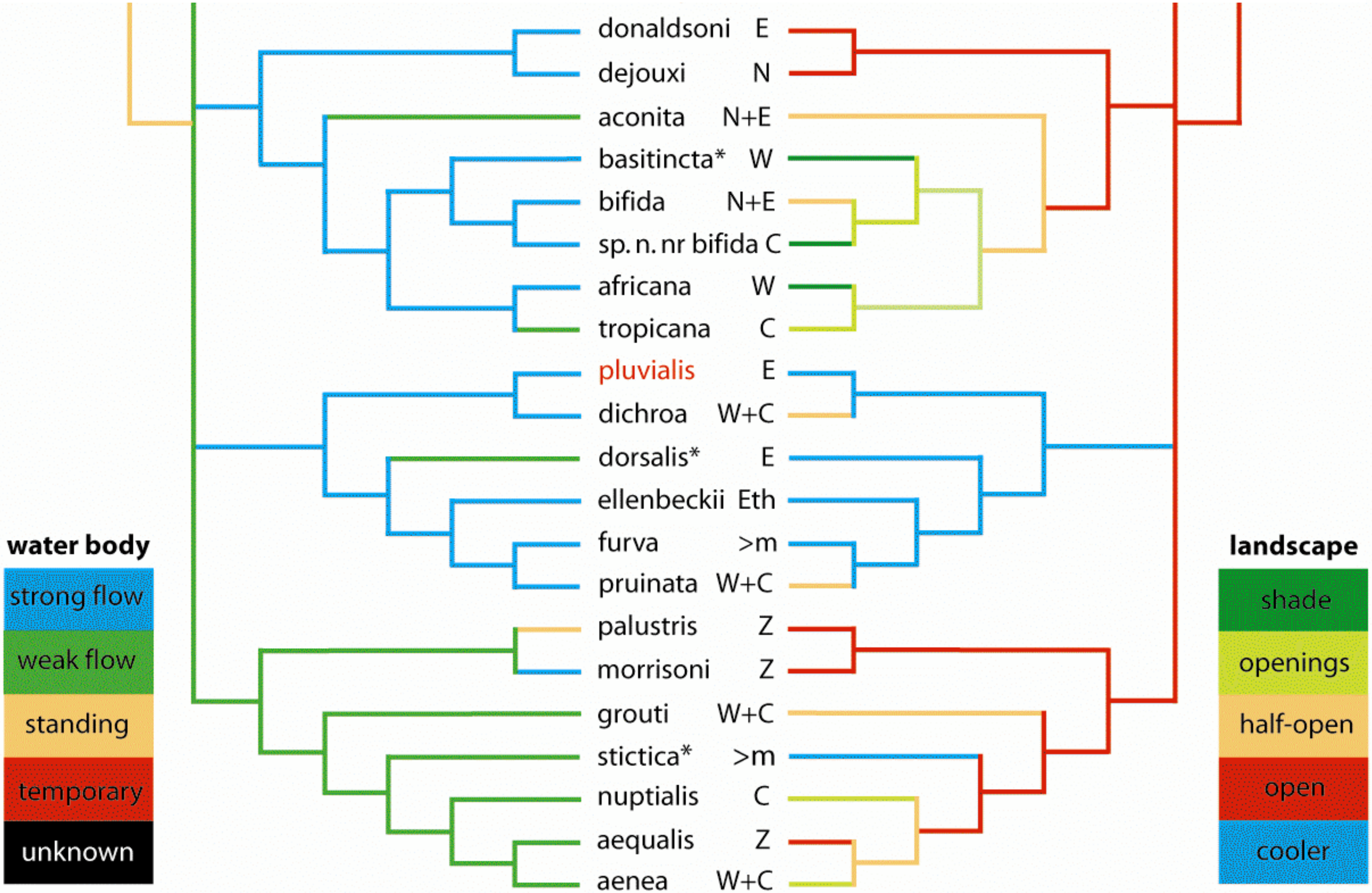
ND1 + 16S + ITS Bayesian inference
Damm, Dijkstra & Hadrys (2010)



ND1 + 16S Maximum Likelihood Ultrametric Tree



Strict consensus (internal nodes with low support collapsed)


donaldsoni E
dejouxi N
aconita N+E
basitincta* W
bifida N+E
sp. n. nr bifida C
africana W
tropicana C
pluvialis E
dichroa W+C
dorsalis* E
ellenbeckii Eth
furva >m
pruinata W+C
palustris Z
morrisoni Z
grouti W+C
stictica* >m
nuptialis C
aequalis Z
aenea W+C
water body
strong flow
weak flow
standing
temporary
unknown
landscape
shade
openings
half-open
open
cooler

Trithemis hypotheses

Origin 6-9 Mya, multiple lineages arising suddenly around 4 Mya.

Most of basal species favour open and stagnant (even temporary) habitats.

Origin and initial diversification could coincide with savannah expansion in late Miocene, followed by its fragmentation in early Pliocene.

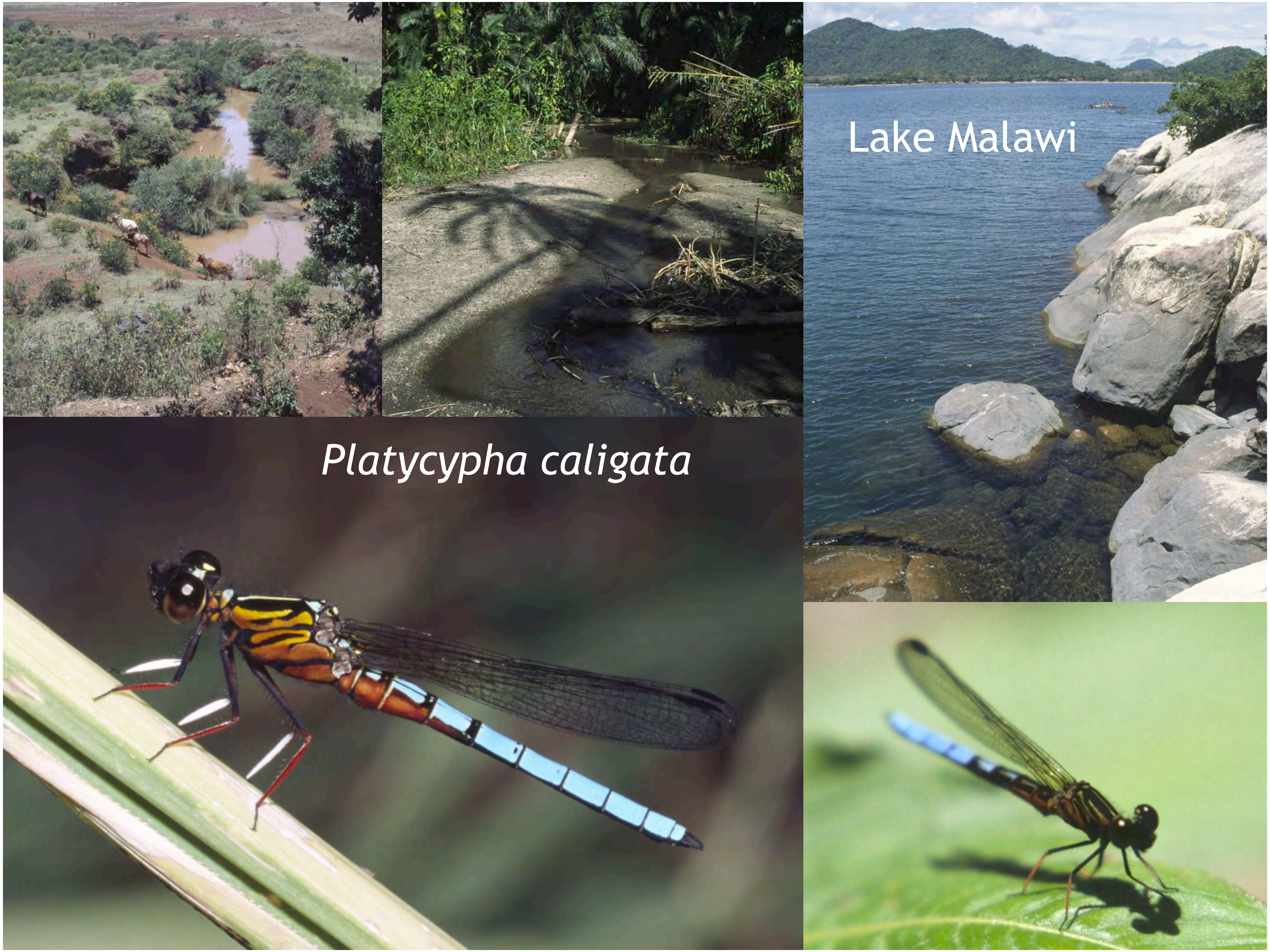
Most red species adapted to more ephemeral conditions and disperse well, limiting potential genetic isolation and radiation.

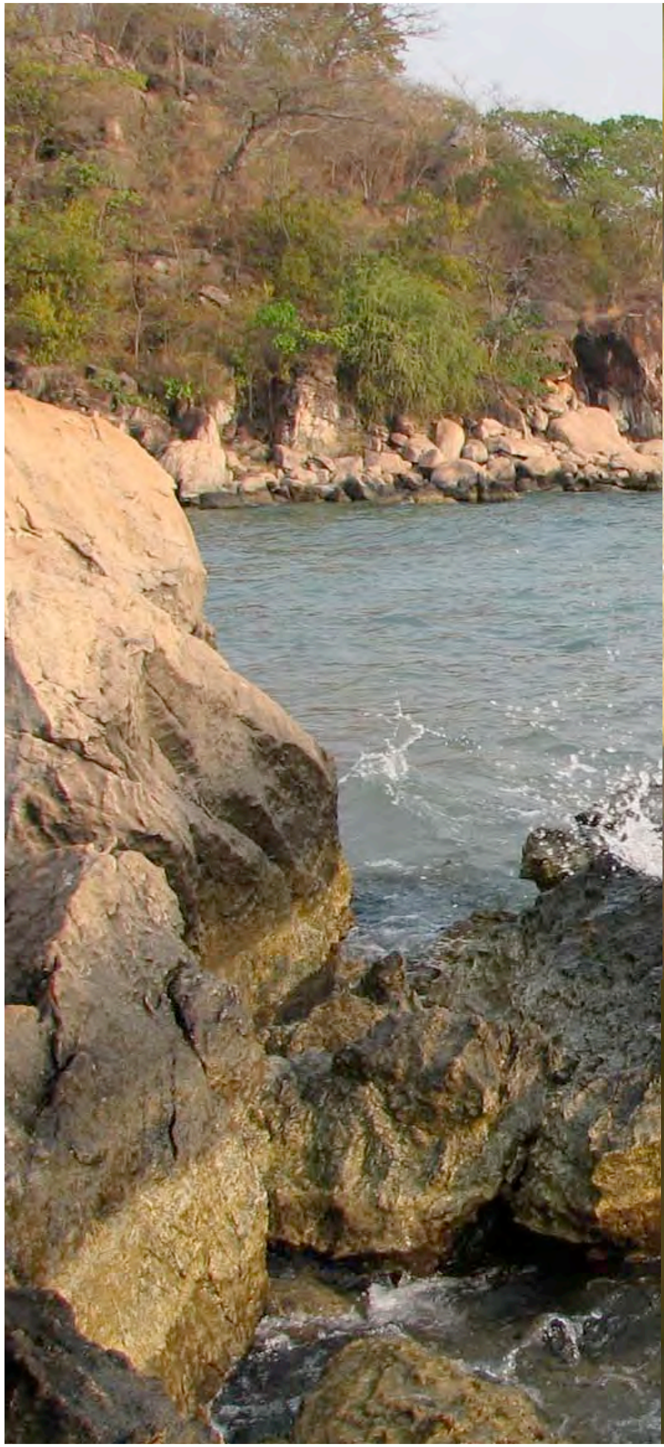
Trithemis hypotheses

Three ‘dark’ clades radiated in the Plio-Pleistocene, within distinct ecological confines (highland and lowland streams, swamps), giving rise to bulk of species.

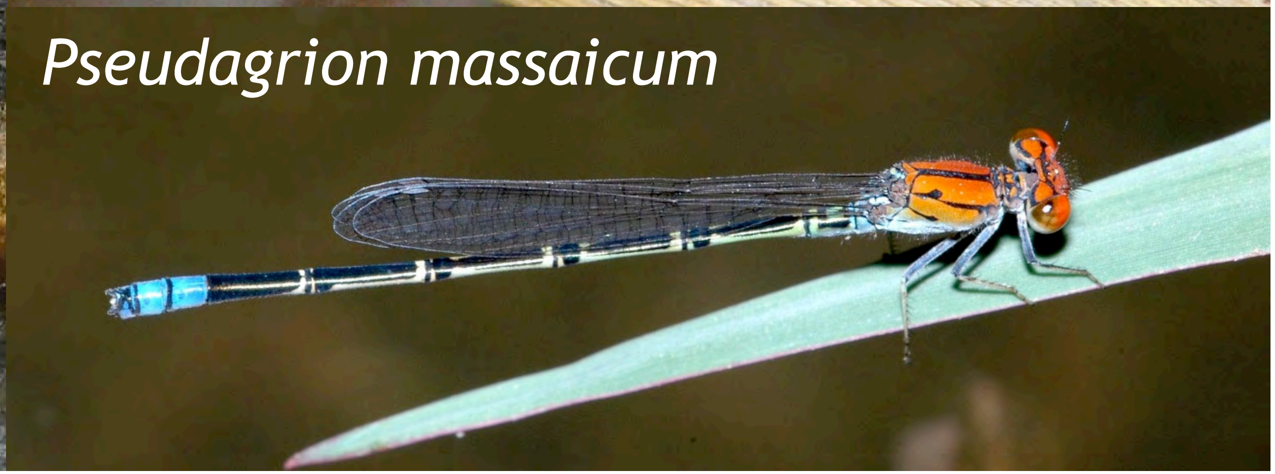
Multiple shifts from open to forested habitats and from standing to running waters.

Further analysis of phylogenetic, geographic, ecological and morphological data needed, but allopatry by habitat fragmentation appears the dominant force in speciation.


Lake Malawi
Platycypha caligata




Pseudagrion
new species?


Pseudagrion massaicum

parapatric speciation?

Africa's Great Lakes

- 'explosive' endemism fish and mollusks
- 'freshwater sea' endemics rare in Odonata

flying adults linked to land

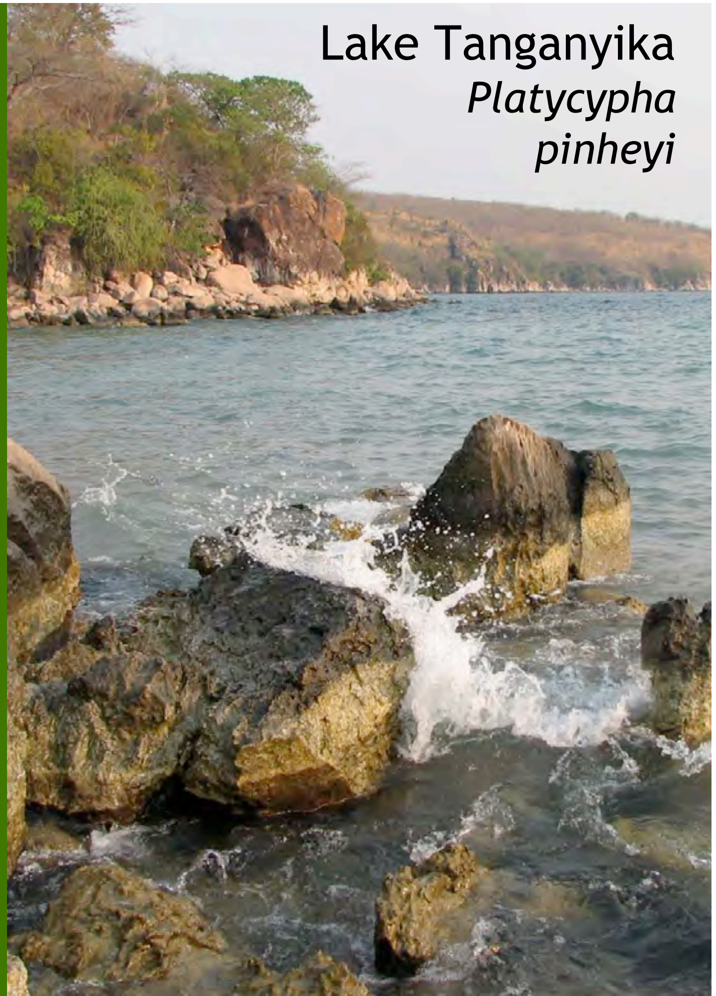
- lake niches inaccessible for reproduction
- dispersal inhibits isolation on lakeshores

known lake odonates

- structurally like riverine congeners
- but coloured distinctly

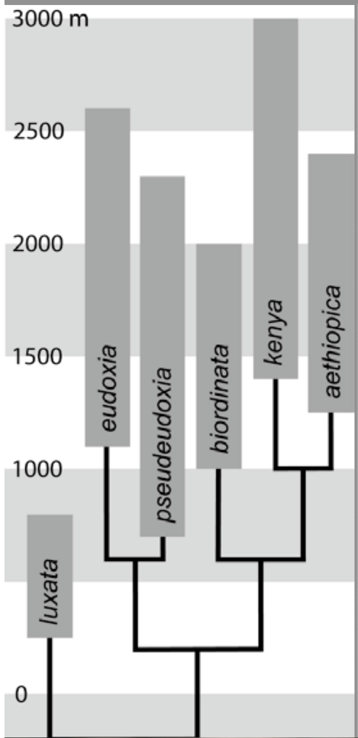
speciation hypothesis

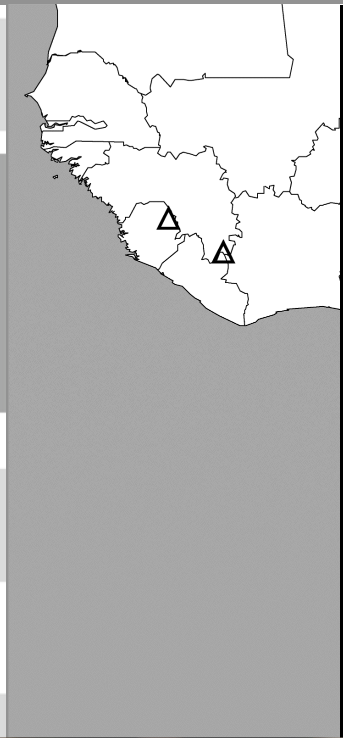
- lake populated by riverine founders
- followed by divergence in coloration
- reinforced by sexual selection

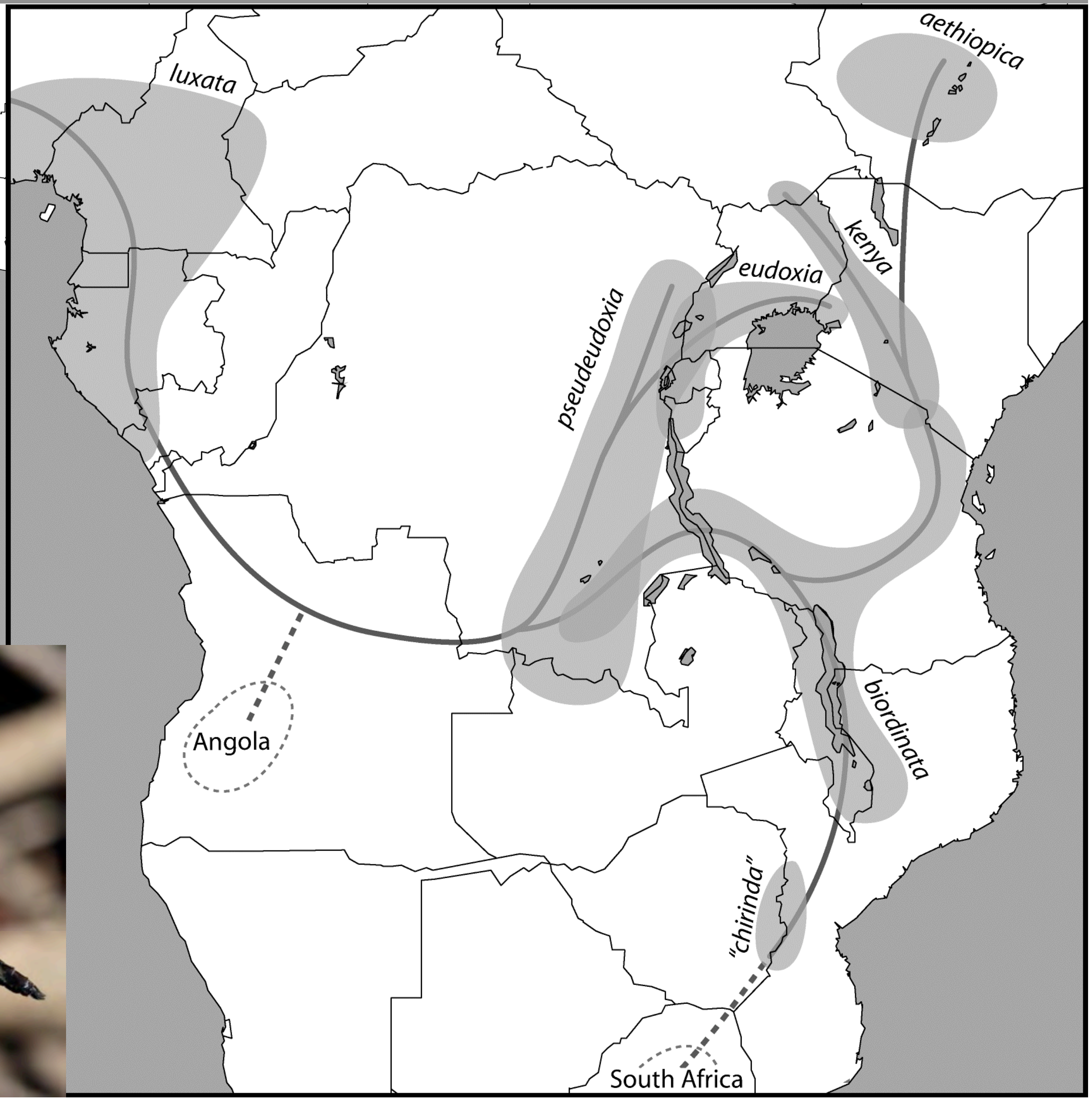


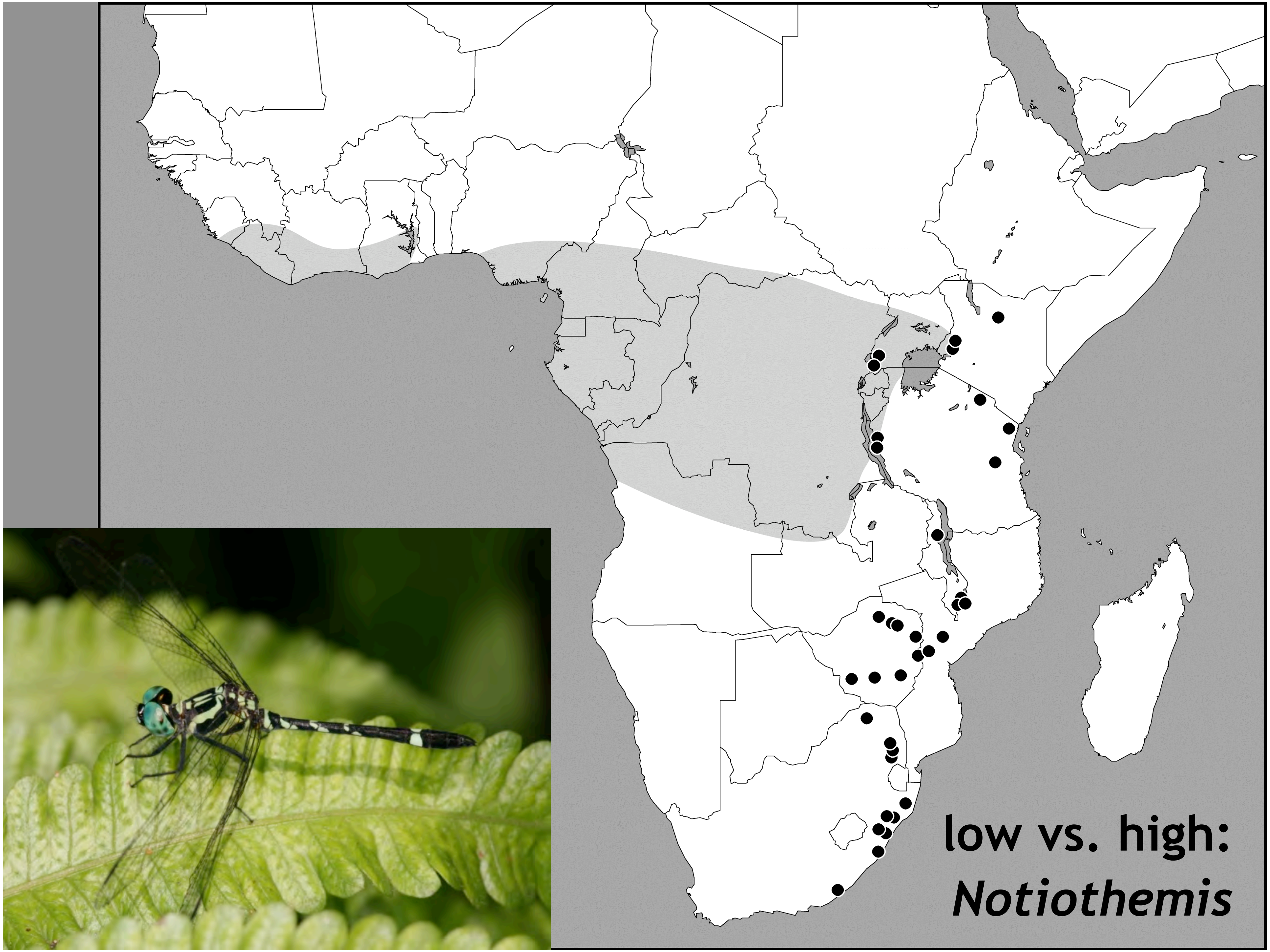
Lake Tanganyika
Platycypha pinheyi

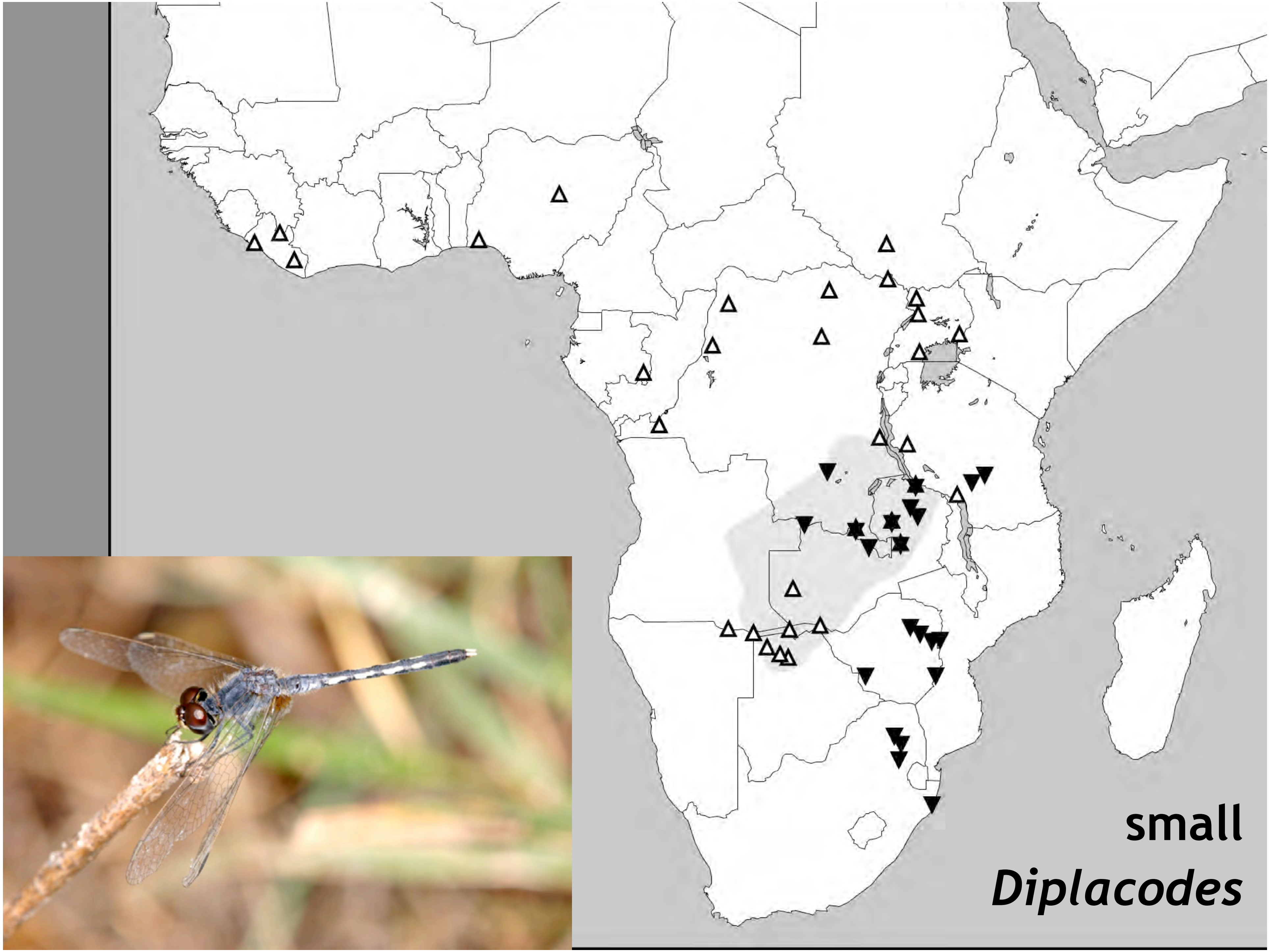
highlands: *Atoconeura*








low vs. high:
Notiothemis



small
Diplacodes

Paleo-Chambeshi system: model for speciation centre?

- transition zone between biomes, also historically
- adjoining Congolian and Albertine forests are huge genetic reservoirs
- montane taxa dispersed along the region’s rather high relief
- complex history of river recombination
- swamps are transient feature of river ‘piracy’

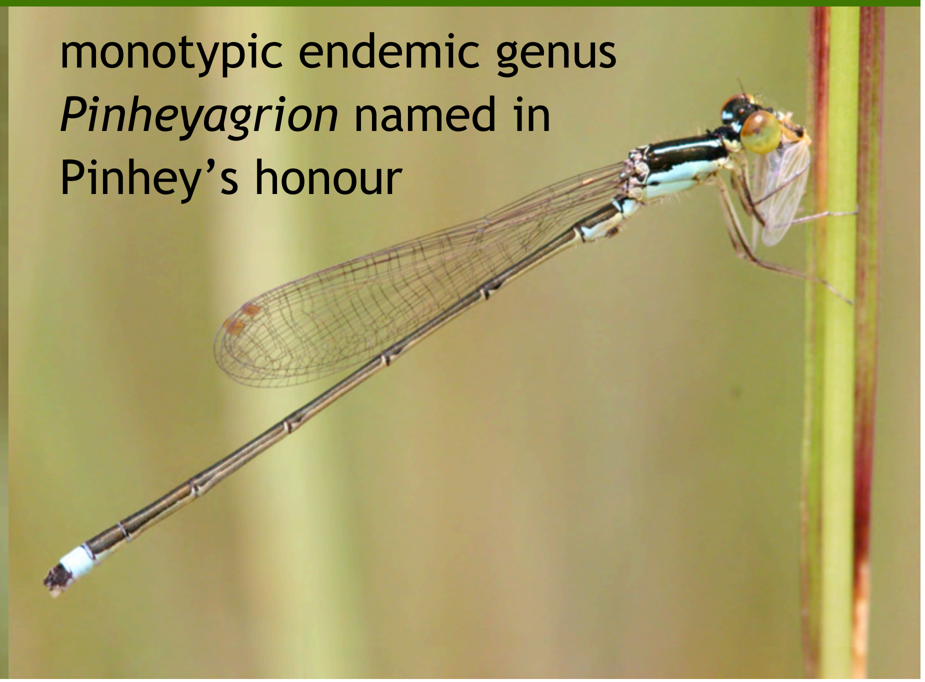
historic equivalents?

- in Congo Basin now ‘drowned’ in forest
- along Great Rift Valley now ‘dried up’ or ‘cooled down’

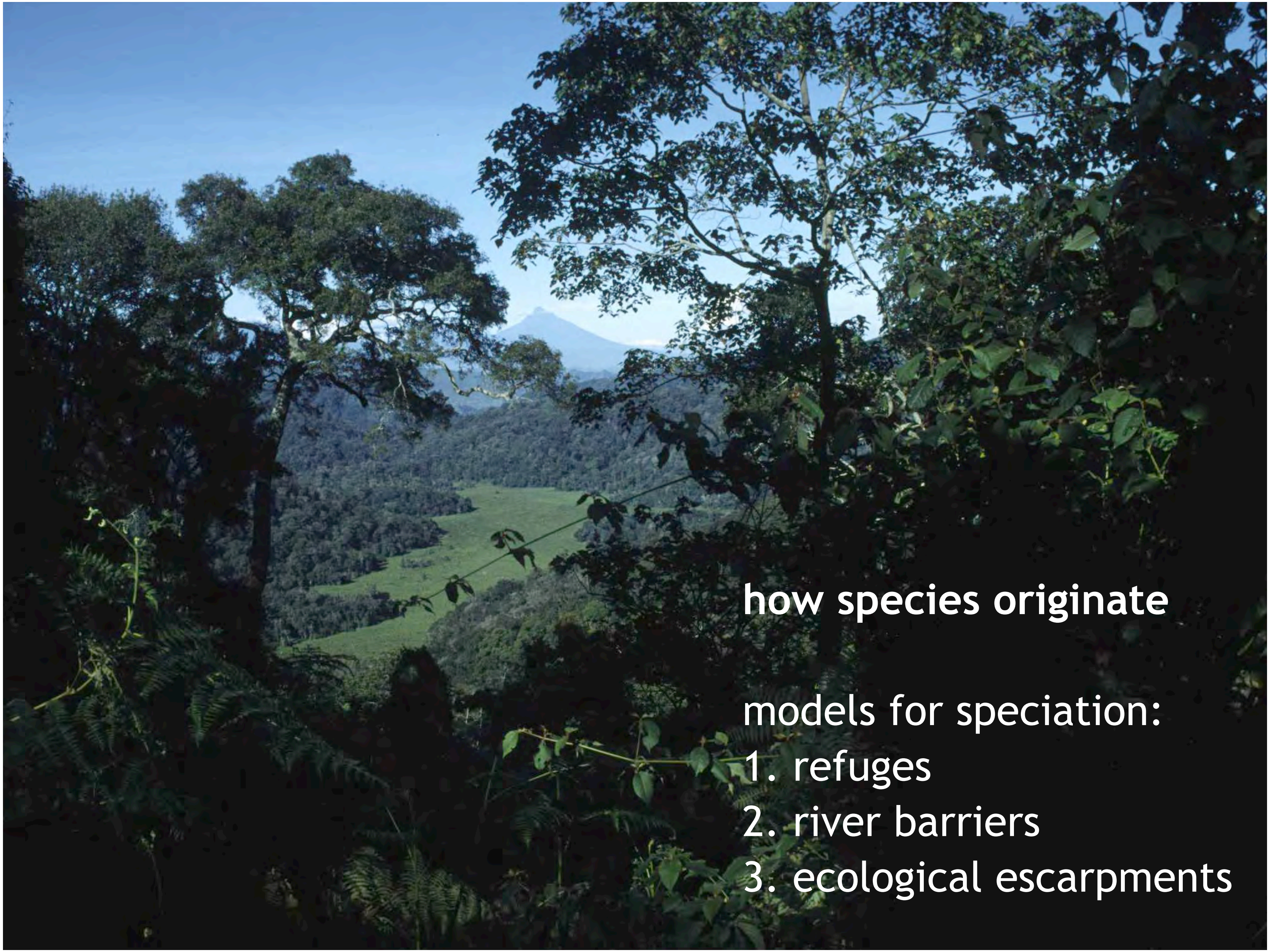
Paleo-Chambeshi system: endemics in two habitat categories

litu, *muhulu*, *mushitu*; swampy streams with thick gallery forest
- galleries allow rainforest species to penetrate well beyond their main range
- genetic divergence possible towards the end of these forest ‘tendrils’

wetland habitats, from numerous *dambos* to huge swamps
- only restricted-range odonate fauna of open swamps in Africa
- most African range-restricted species in running waters (forests, highlands)
- most African swamp-dwellers are widespread



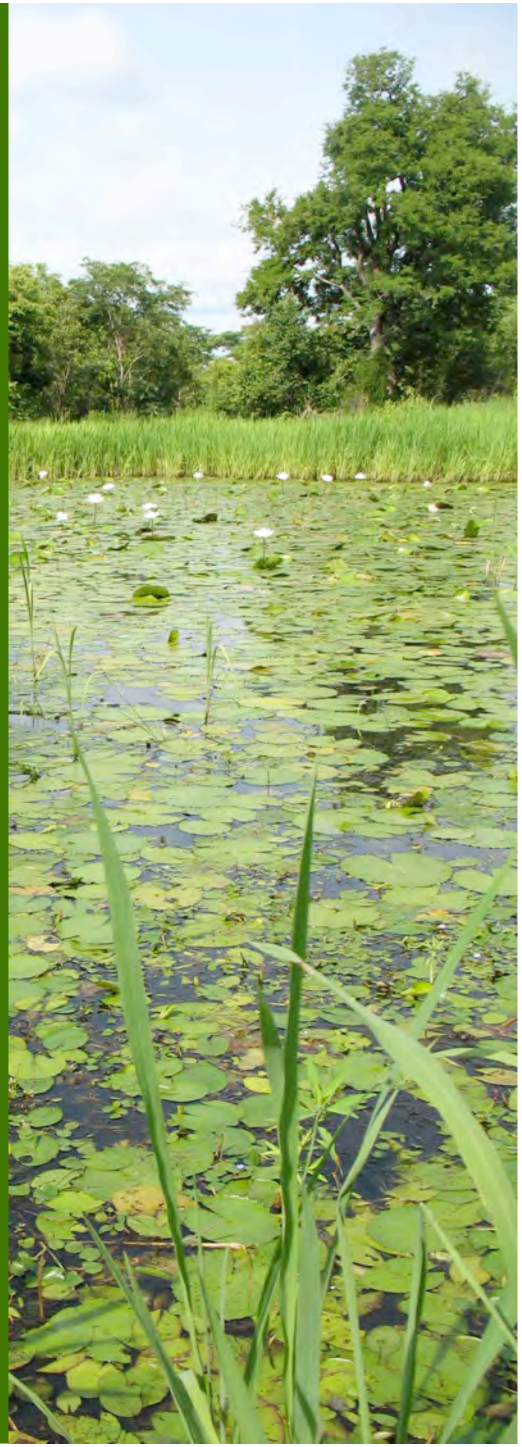
monotypic endemic genus *Pinheyagrion* named in Pinhey’s honour

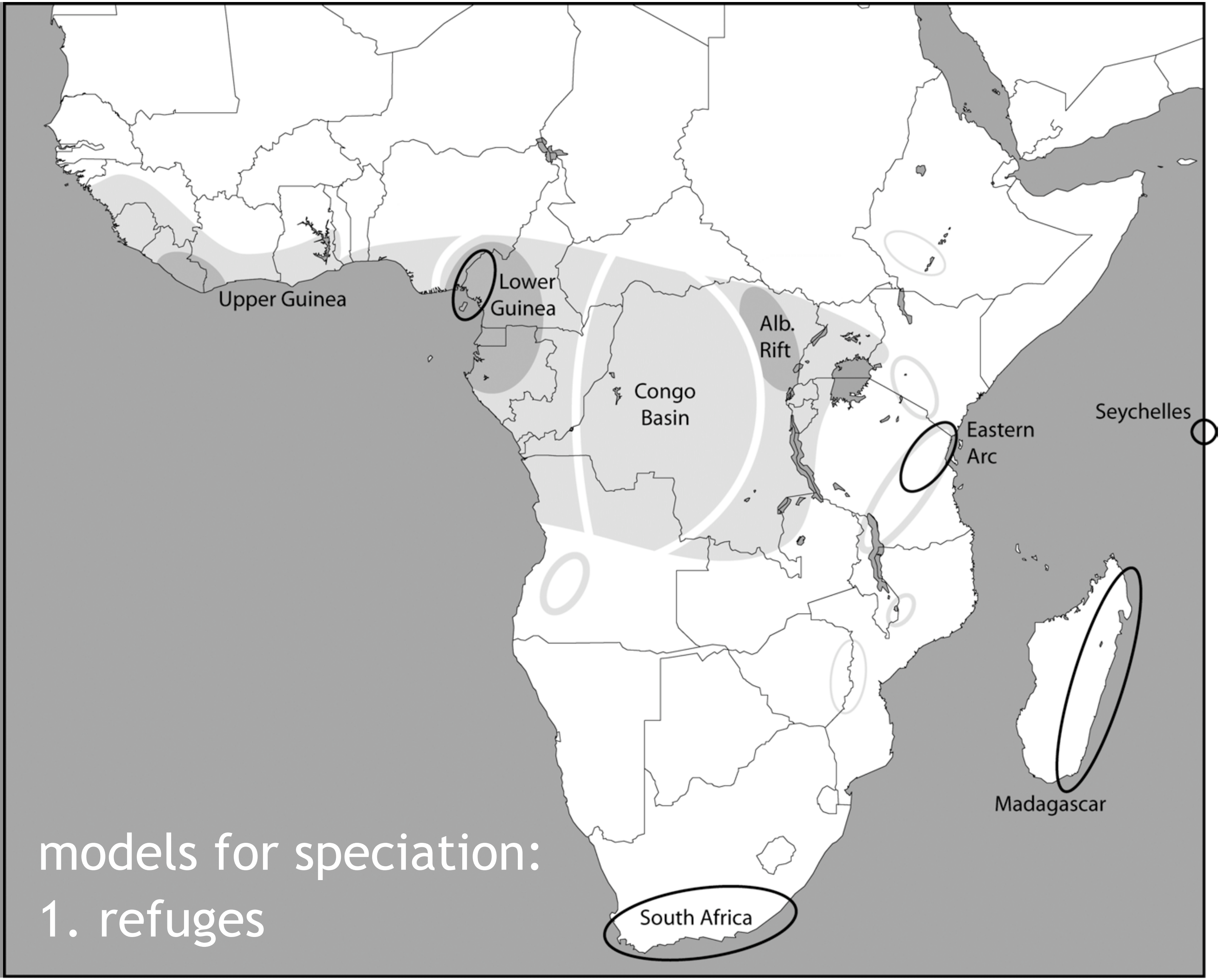

how species originate
models for speciation:
1. refuges
2. river barriers
3. ecological escarpments

models for speciation:
1. refuges

"Forests of highlands would have been preserved during forest retreat in the arid interpluvials and speciation resulted from this isolation. Small forest patches have more chance for mutation than the huge, overcrowded rain forest belt. The reverse effect occurred during pluvial extensions which encouraged uniformity."

Elliot C.G. Pinhey (1978)
'Godfather of African Odonatology'





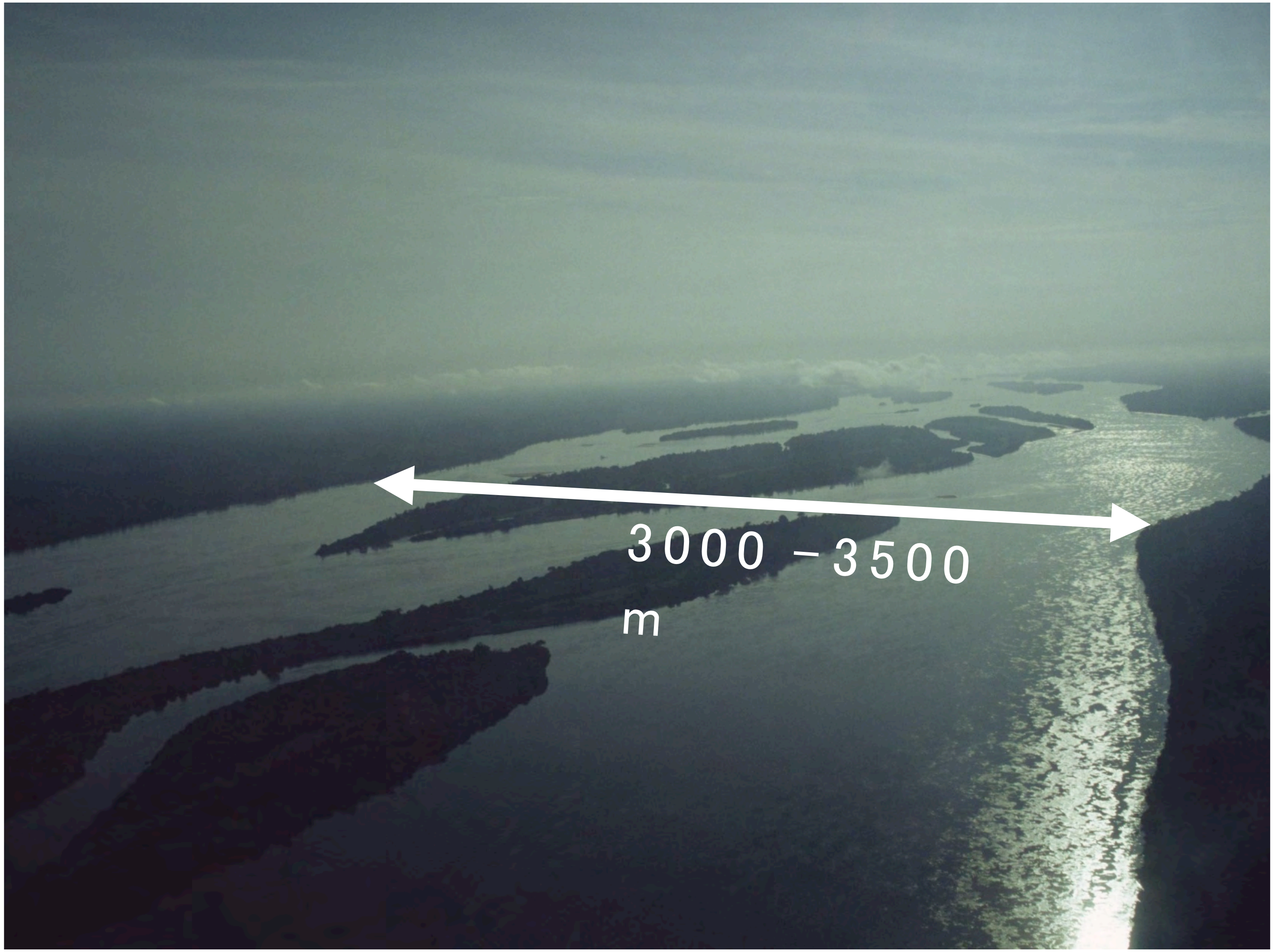
models for speciation:
1. refuges

models for speciation:

2. river barriers

Congo River

Congo River



models for speciation:

3. ecological escarpments

doubts on the role of habitat refuges in speciation

“areas with high habitat heterogeneity and recent climatic or geological instability appear to harbor more species of recent origin” — Moritz et al. (2000)

‘old’ species quite uniformly distributed, peaks in lowland forest (‘refuges’); ‘young’ species in savanna, within forests in highlands: refuges are ‘museums’ rather than ‘pumps’ of species, functioning as genetic reservoirs for speciation processes on their periphery
— Fjeldså (1994), Fjeldså & Lovett (1997)

genetic isolation occurs along ‘ecological escarpments’, rather than in habitat refuges — Endler (1982)

forest-savanna transition plays foremost role in speciation — Fjeldså (1994)

contrasting selective environments across ecotones lead to morphological differentiation in birds — Smith et al. (1997)