An operational framework for biome boundary research

Fynbos Forum, Montagu, 2016

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Botany Department
Nelson Mandela Metropolitan University

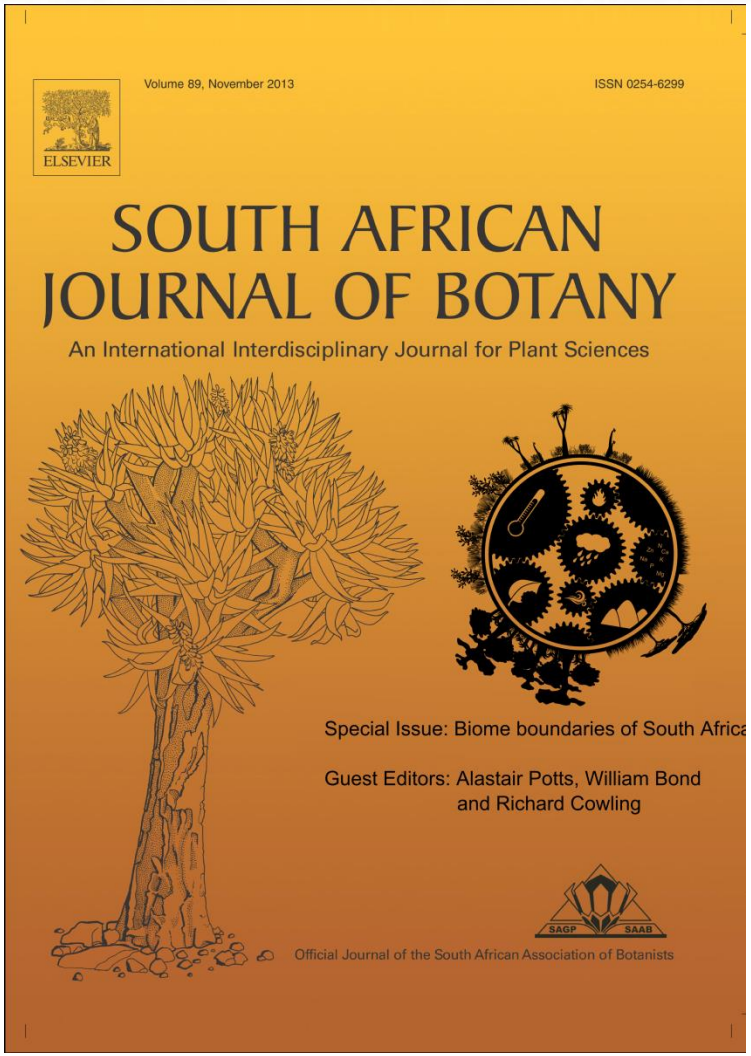
Contents lists available at ScienceDirect

South African Journal of Botany

journal homepage: www.elsevier.com/locate/sajb

An operational framework for biome boundary research with examples from South Africa

A.J. Potts [a], G.R. Moncrieff [b,c], W. Bond [c], R. Cowling [a]



Special Issue on South African Biome Boundaries

November 2015 issue

How do we study biome boundaries?

Aim?

Outline

- Approaches (with many examples)
  - Adv/disadv
  - Spatial/Temporal aspects
  - Links

Approaches

Approaches

Category	Sub-category
Field observations	
Correlative approach	Tightly-linked
	Loosely-linked
Experimental approach	Field-based: *ad hoc*
	Field-based: manipulation
	Common garden
	Greenhouse
	Laboratory
Mechanistic modelling	
Phylogenetic approach	

Approaches

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	Loosely-linked
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Mechanistic modelling	
Phylogenetic approach	

Field Observations

Field Observations

- Foundation of ecology.
- Perceived importance of field observations & natural history: ↓
- Foundation for more analytically rigorous, hypothesis-testing approaches.

Langeberg, Marloth Reserve

Image courtesy of Coert Geldenhuys

Langeberg, Marloth Reserve

Image courtesy of Coert Geldenhuys

Langeberg, Marloth Reserve

Image courtesy of Coert Geldenhuys

Langeberg, Marloth Reserve

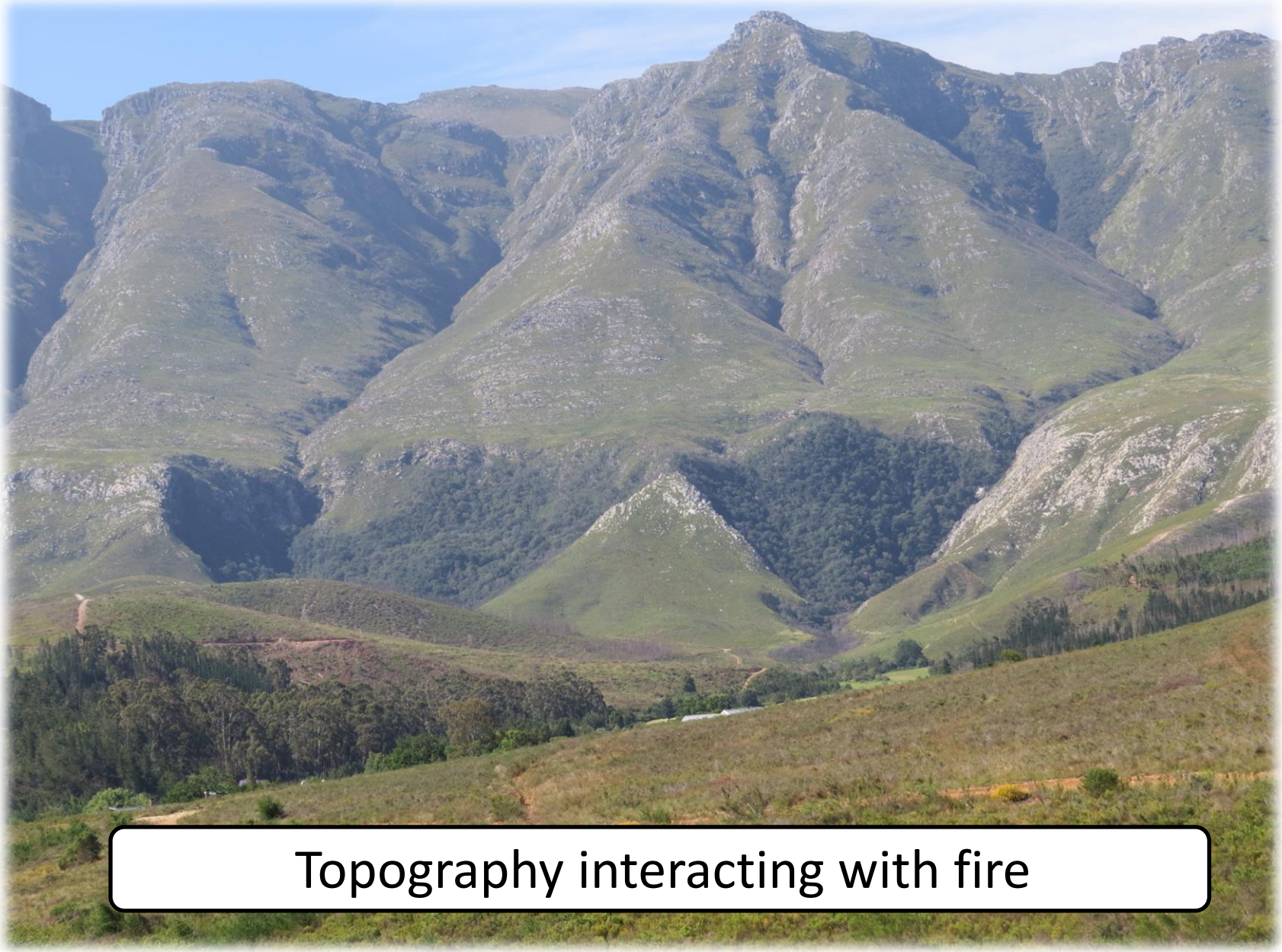


Image courtesy of Coert Geldenhuys

Journal of Biogeography (1994) **21**, 49–62

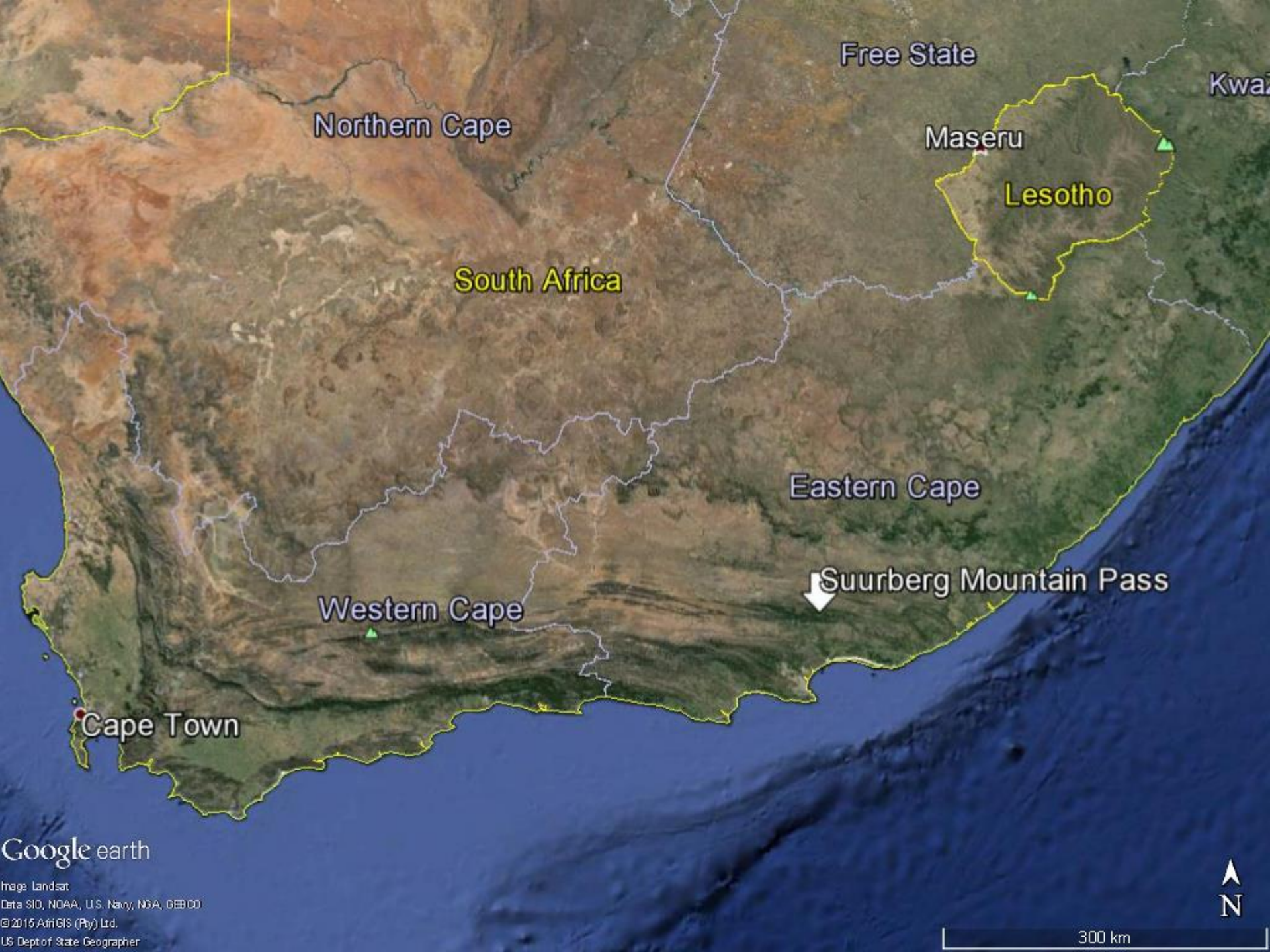
Bergwind fires and the location pattern of forest patches in the southern Cape landscape, South Africa

C. J. GELDENHUYS *CSIR Division of Forest Science and Technology, P.O. Box 395, Pretoria 0001, Republic of South Africa*

Field Observations

Another example:

Fynbos – Thicket boundary
(in the Suurberg, Eastern Cape)


Free State
Northern Cape
Maseru
Lesotho
South Africa
Eastern Cape
Suurberg Mountain Pass
Western Cape
Cape Town
Google earth
Image Landsat
Data SIO, NOAA, U.S. Navy, NGA, GEBCO
© 2015 AfriGIS (Pty) Ltd.
US Dept of State Geographer
N
300 km


Google earth
Image © 2013 DigitalGlobe
N
500 m


Thicket
Google earth
Image © 2013 DigitalGlobe
N
500 m


Grassland
Thicket
Google earth
Image © 2013 DigitalGlobe
N
500 m


Grassland
Fynbos
Thicket
Google earth
Image © 2013 DigitalGlobe
N
500 m


Grassland
Fynbos
Thicket
Google earth
Image © 2013 DigitalGlobe
N
300 m


Fynbos
Grassland
Thicket
Google earth
Image © 2015 DigitalGlobe
© 2015 Cnes/Spot Image
Image NASA
200 m

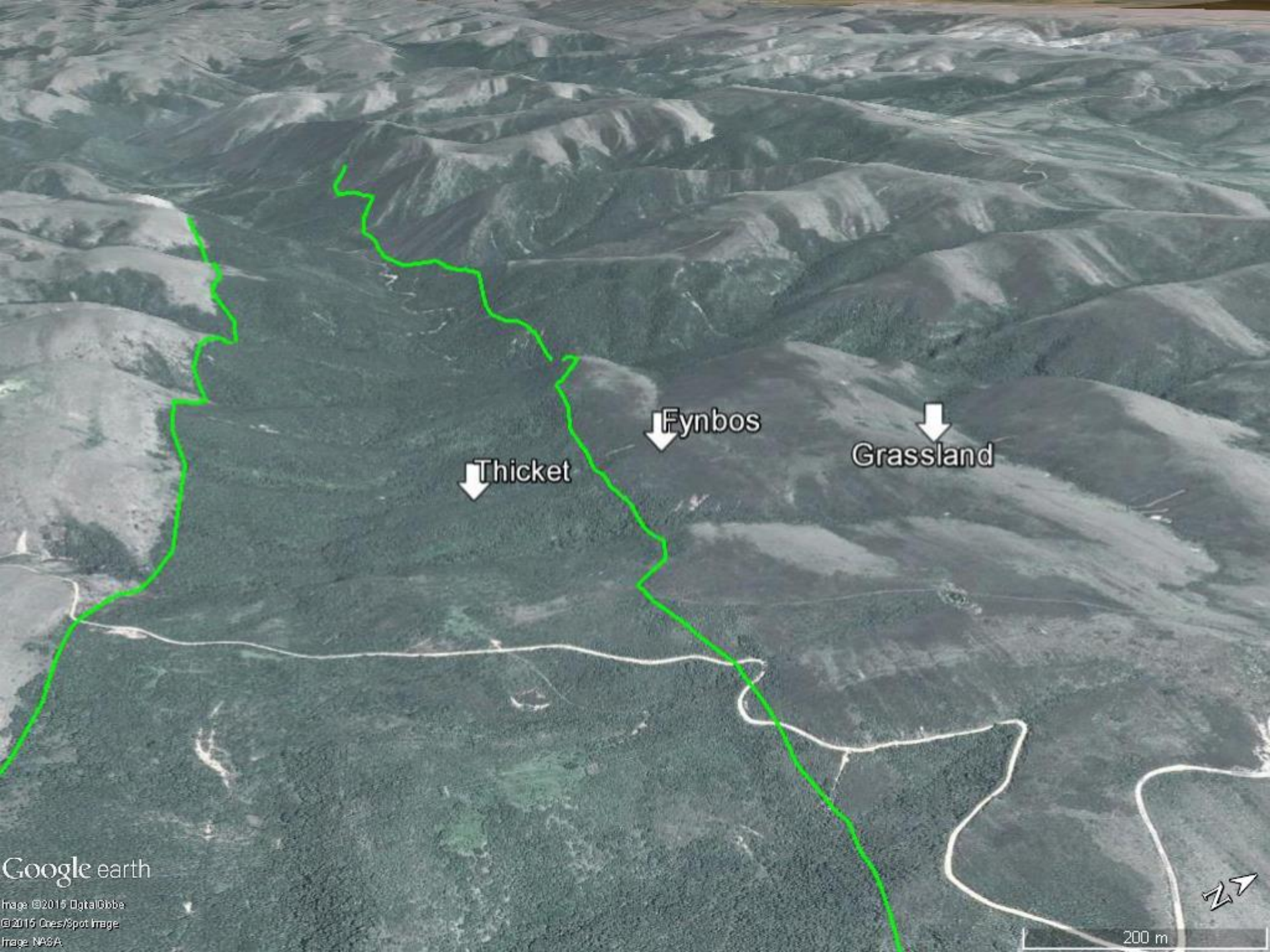

Fynbos
Grassland
Thicket
Google earth
Image © 2015 DigitalGlobe
© 2015 Cnes/Spot Image
Image NASA
200 m

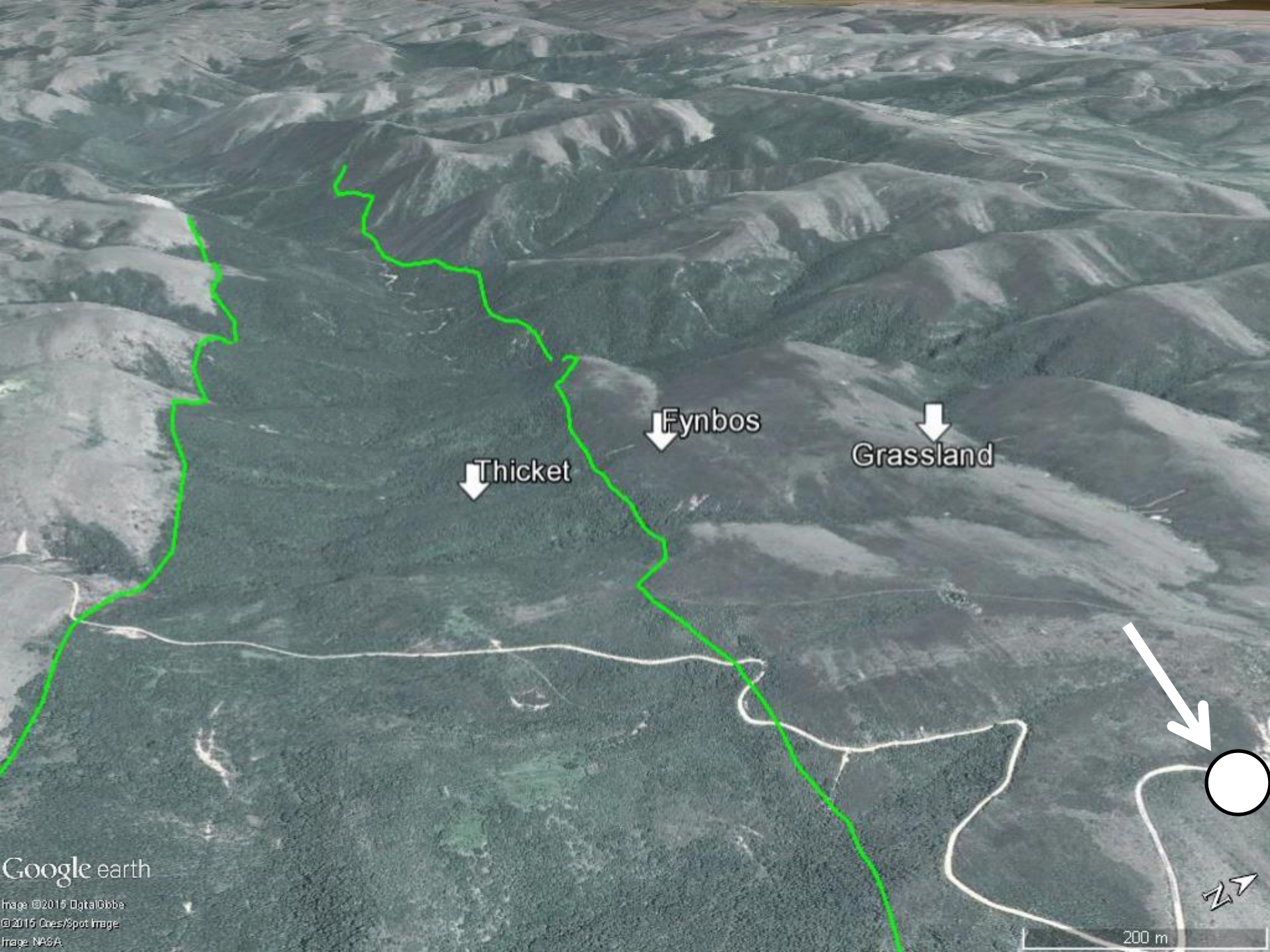

Google earth
©2016 Google
N
1.82 m


Fynbos
Thicket
Google earth
©2016 Google
N
1.82 m

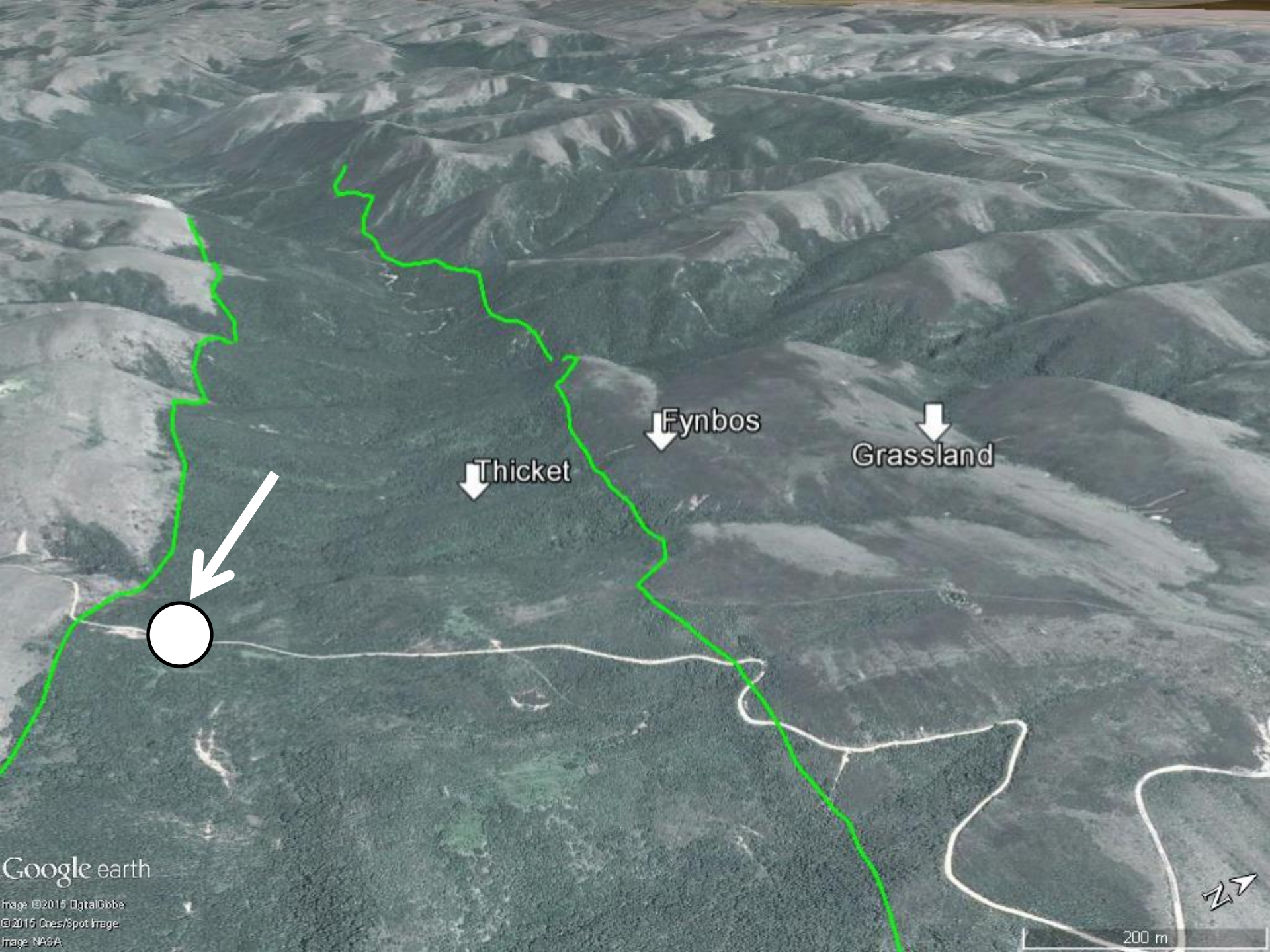

Fynbos
Grassland
Thicket
Google earth
Image © 2015 DigitalGlobe
© 2015 Cnes/Spot Image
Image NASA
200 m


Fynbos
Grassland
Thicket
Google earth
Image © 2015 DigitalGlobe
© 2015 Cnes/Spot Image
Image NASA
200 m

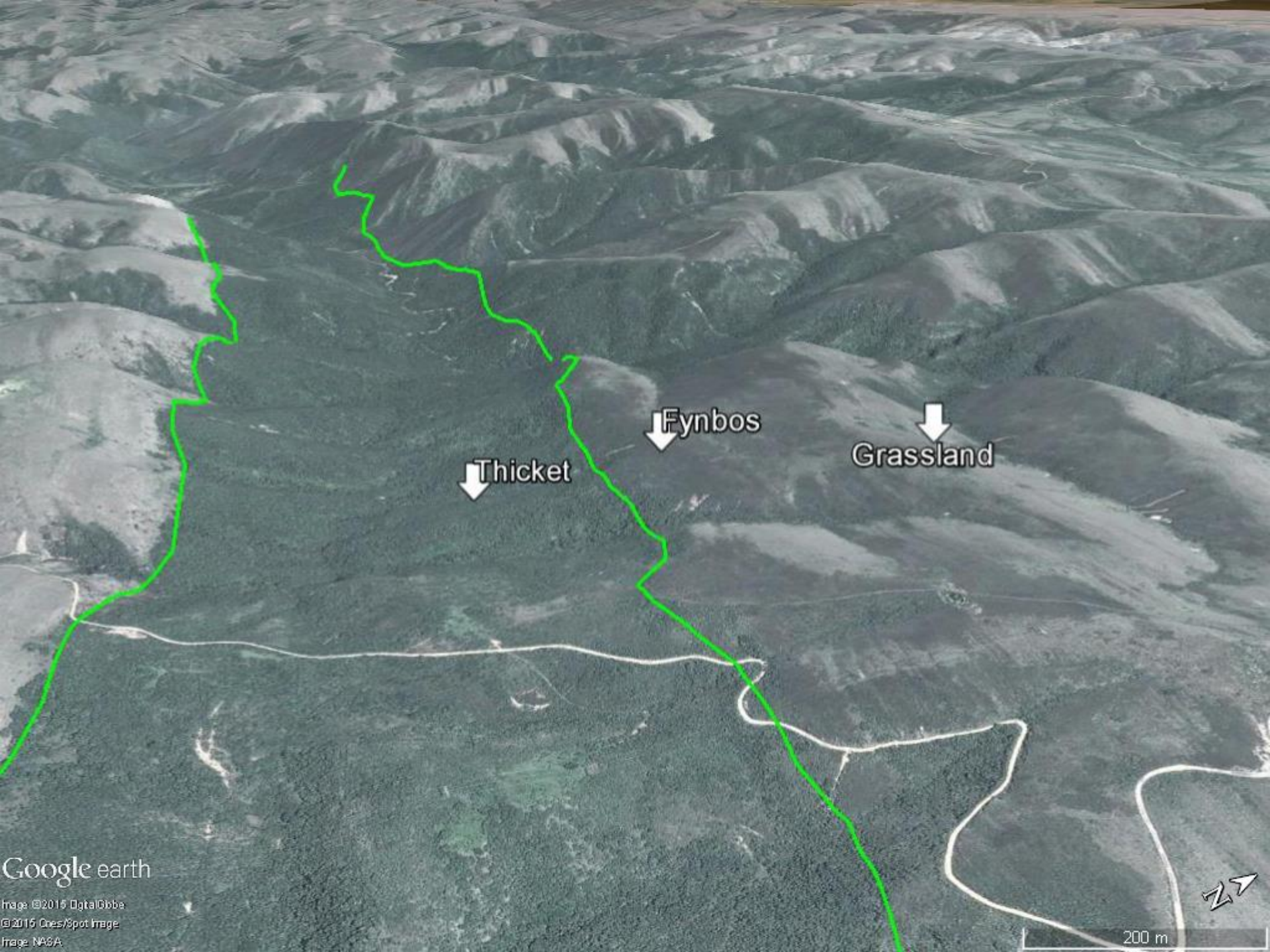

Fynbos
Grassland
Thicket
Google earth
Image © 2015 DigitalGlobe
© 2015 Cnes/Spot Image
Image NASA
200 m

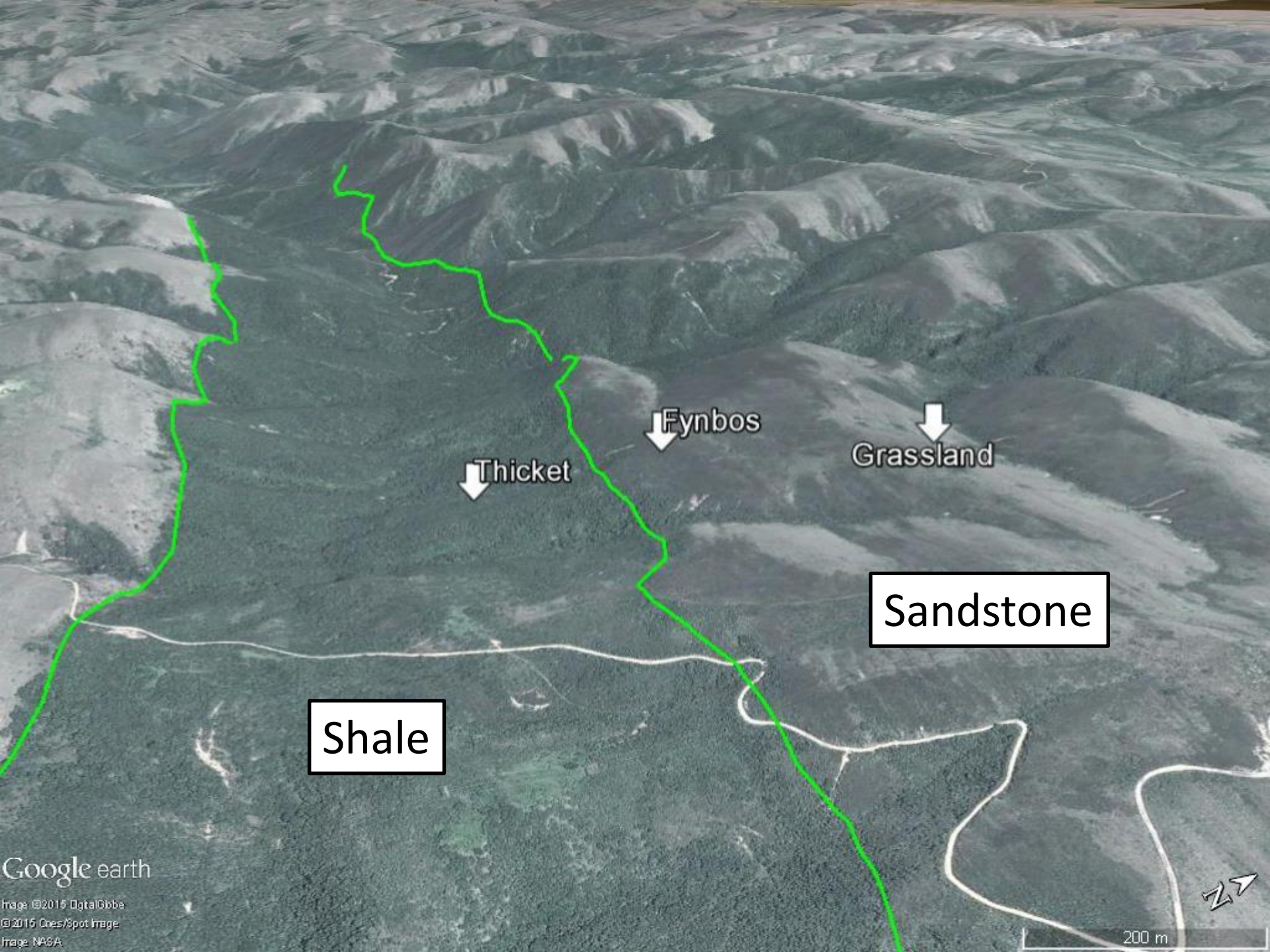

Fynbos
Grassland
Thicket
Google earth
Image © 2015 DigitalGlobe
© 2015 Cnes/Spot Image
Image NASA
200 m


Google earth
©2015 Google
1.19 m


Fynbos
Grassland
Thicket
Google earth
200 m


Google earth
© 2016 Google
1.40 m


Fynbos
Grassland
Thicket
Google earth
Image © 2015 DigitalGlobe
© 2015 Cnes/Spot Image
Image NASA
200 m


Fynbos
Grassland
Thicket
Sandstone
Shale
Google earth
200 m


Fynbos
Grassland
Thicket
Geology, not topography, interacting with fire
Google earth
200 m

Field Observations

Field observations are not restricted to researcher-based observations.

Field Observations

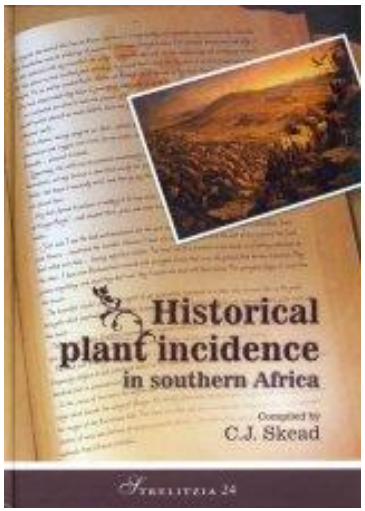
Field observations are not restricted to researcher-based observations.

- Old travellers records

Field Observations

Field observations are not restricted to researcher-based observations.

"At the foot of the mountains [of the Cape Peninsula] towards the West they **found forests of tall trees**, as thick as apple trees without any fruit on them and of a very hard wood". De Beulieu 1620



Field Observations

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- Old travellers records

Field Observations

Field observations are not restricted to researcher-based observations.

- Old travellers records
- Newspaper archives
- Old photos or paintings

Field Observations

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- Old travellers records
- Newspaper archives
- Old photos or paintings

Field Observations

Advantages:

- Large ‘sample sizes’ over varying conditions, including rare events.
- Early detection of biome shifts.

Field Observations

Disadvantages:

- Lack certainty…
- Difficult to assess interactions.
- “Unseen” drivers.

Approaches

Category	Sub-category
Field observations	
Correlative approach	Tightly-linked
	Loosely-linked
Experimental approach	Field-based: *ad hoc*
	Field-based: manipulation
	Common garden
	Greenhouse
	Laboratory
Mechanistic modelling	
Phylogenetic approach	

Correlative Approach

Correlative Approach

Vegetation (response variables)	Environment (explanatory variables)

Correlative Approach

Two subcategories

Correlative Approach

Two subcategories

- Tightly-linked
- Loosely-linked

Correlative Approach

Tightly-linked

Correlative Approach

Tightly-linked

Vegetation
(response variables)

Environment
(explanatory variables)

Correlative Approach

Tightly-linked

Vegetation
(response variables)

Environment
(explanatory variables)

Measurements are sampled together
(e.g. floristic composition and soil samples for a site)

Correlative Approach

Loosely-linked

Correlative Approach

Loosely-linked

Vegetation
(response variables)

Environment
(explanatory variables)

Correlative Approach

Loosely-linked

Vegetation
(response variables)

↔

Environment
(explanatory variables)

Measurements are made up of different datasets
(e.g. aerial photographs, stocking records and weather station data)

Example:
Tightly-linked correlative approach

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Forest and fynbos are alternative states on the same nutrient poor geological substrate

C. Coetsee [a,*], W.J. Bond [b], B.J. Wigley [a]

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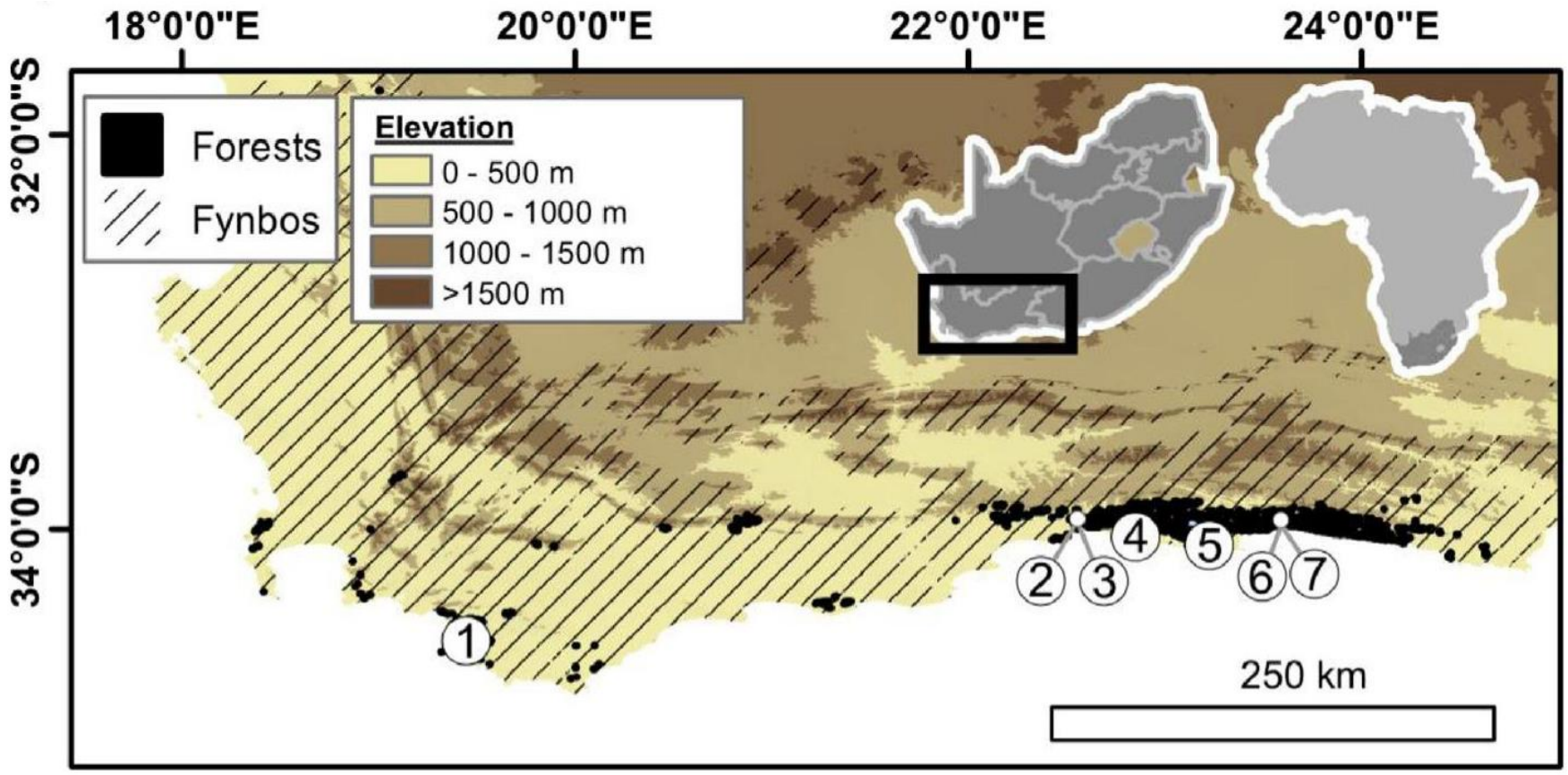
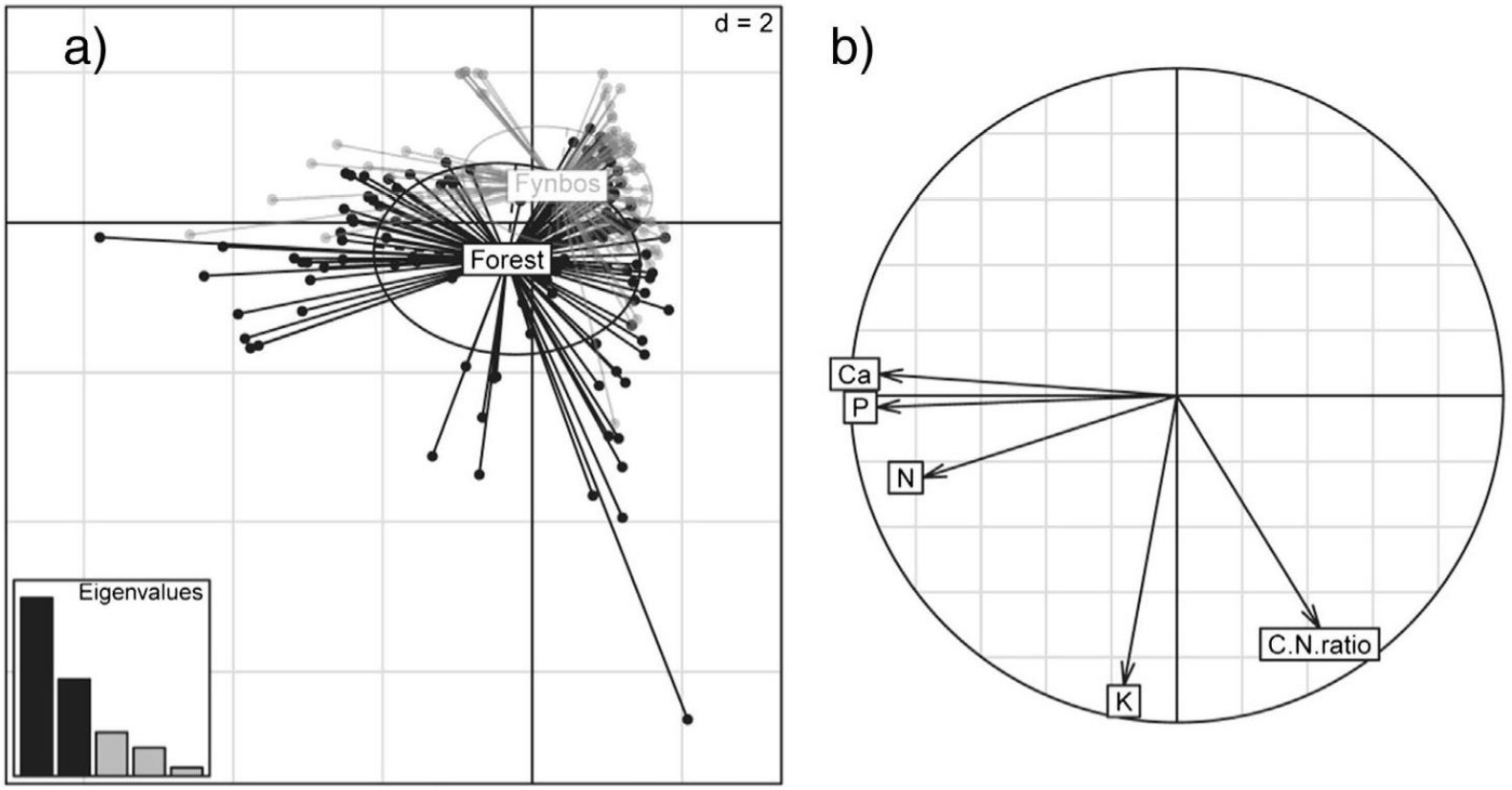
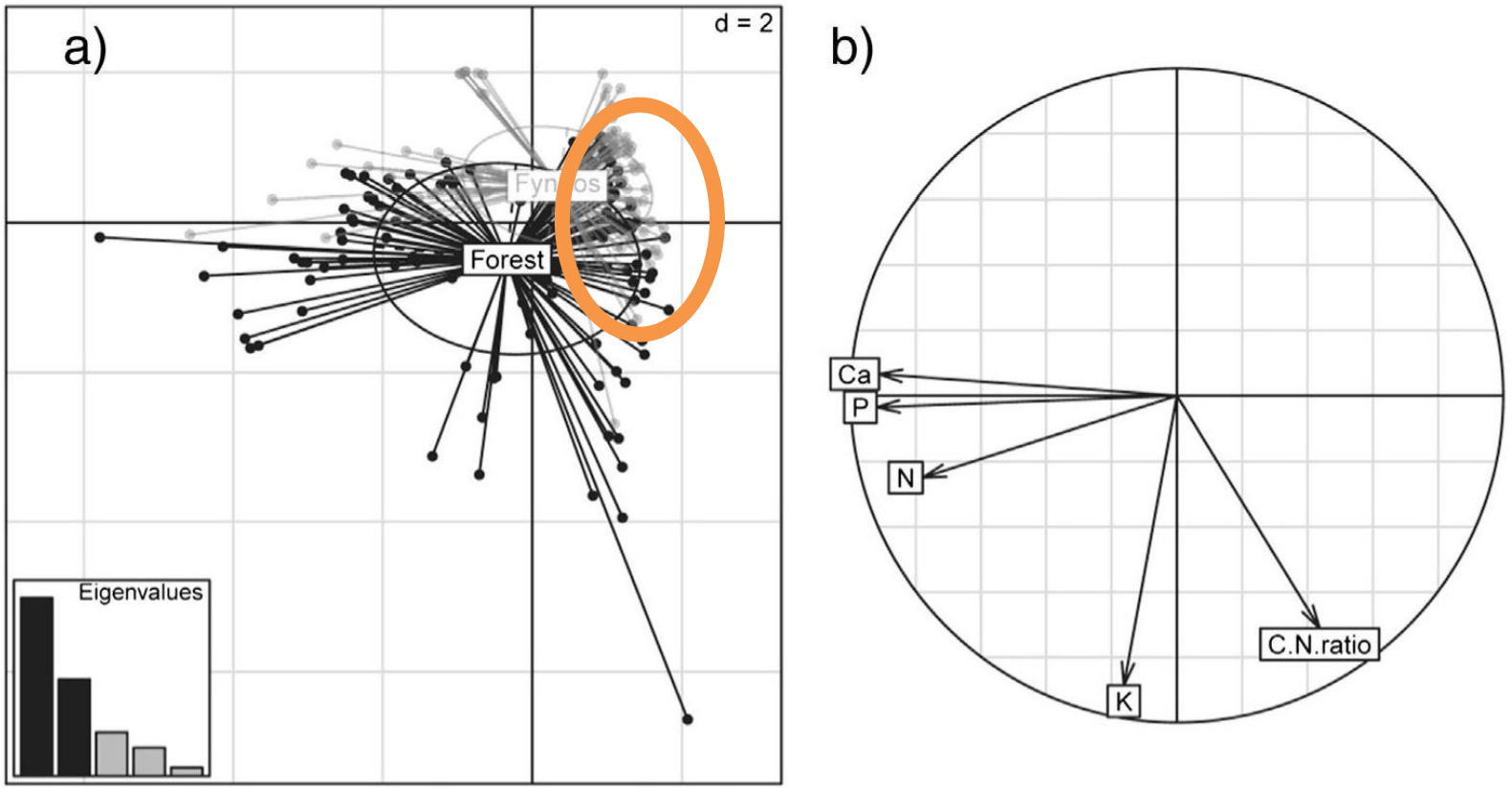
Are soil properties (nutrients) responsible for the limiting the distribution of Fynbos or Forest?


18°0'0"E
20°0'0"E
22°0'0"E
24°0'0"E
32°0'0"S
34°0'0"S
Forests
Fynbos
Elevation
0 - 500 m
500 - 1000 m
1000 - 1500 m
>1500 m
1
2
3
4
5
6
7
250 km


1
2
1
3



PCA ordination showing **soil variables** for plots with Forest or Fynbos biomes



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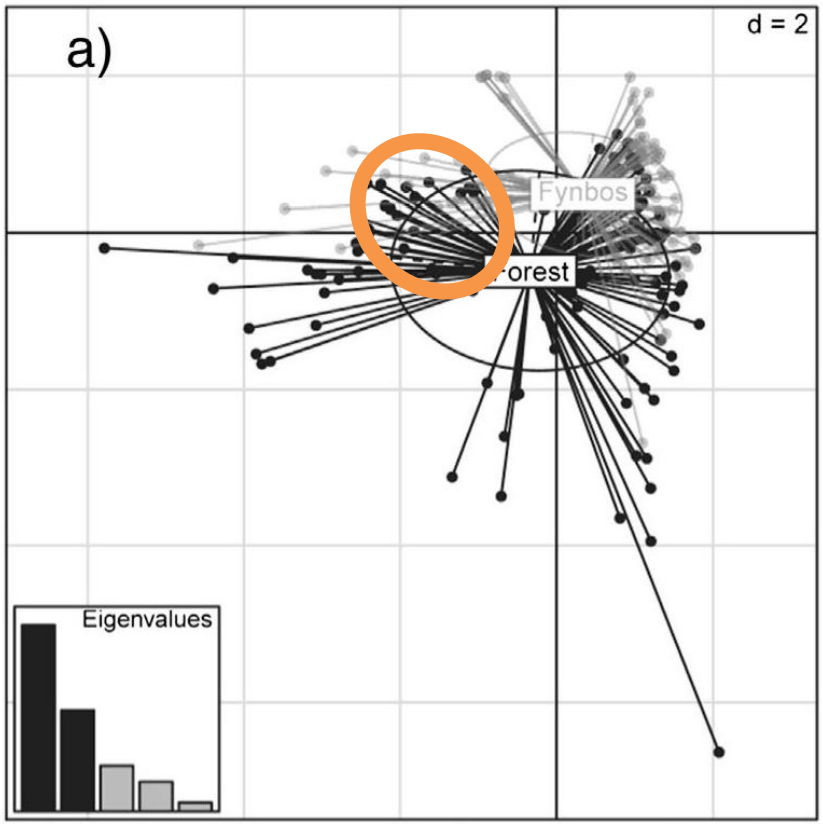
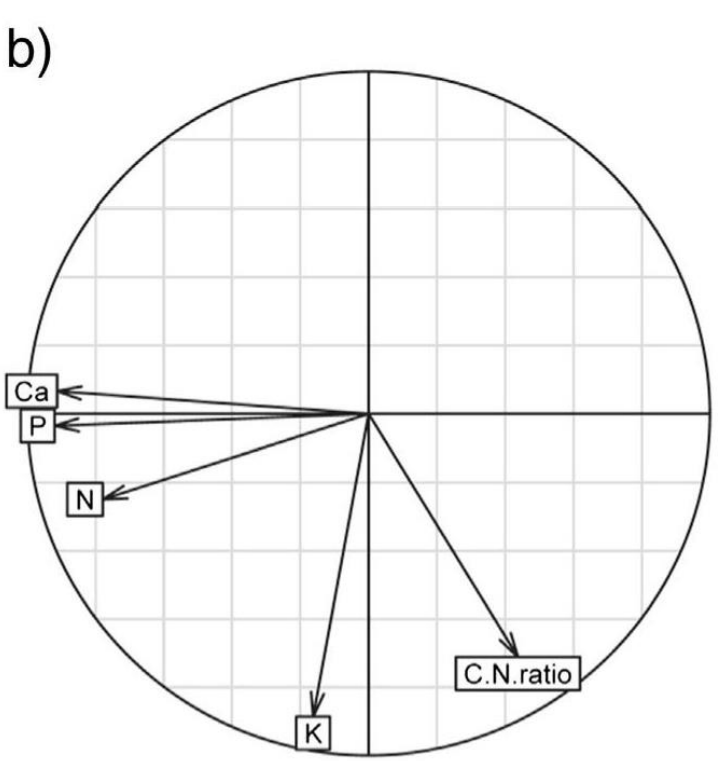




PCA ordination showing **soil variables** for plots with Forest or Fynbos biomes

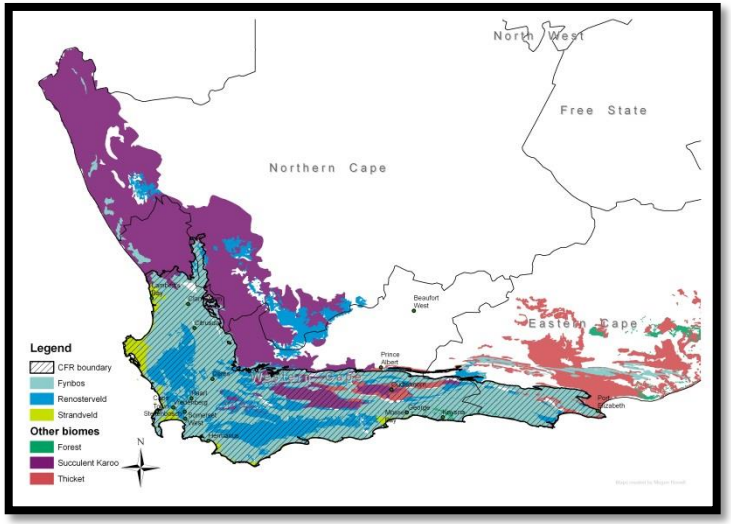
Are soil properties (nutrients) responsible for the limiting the distribution of Fynbos or Forest?

NO

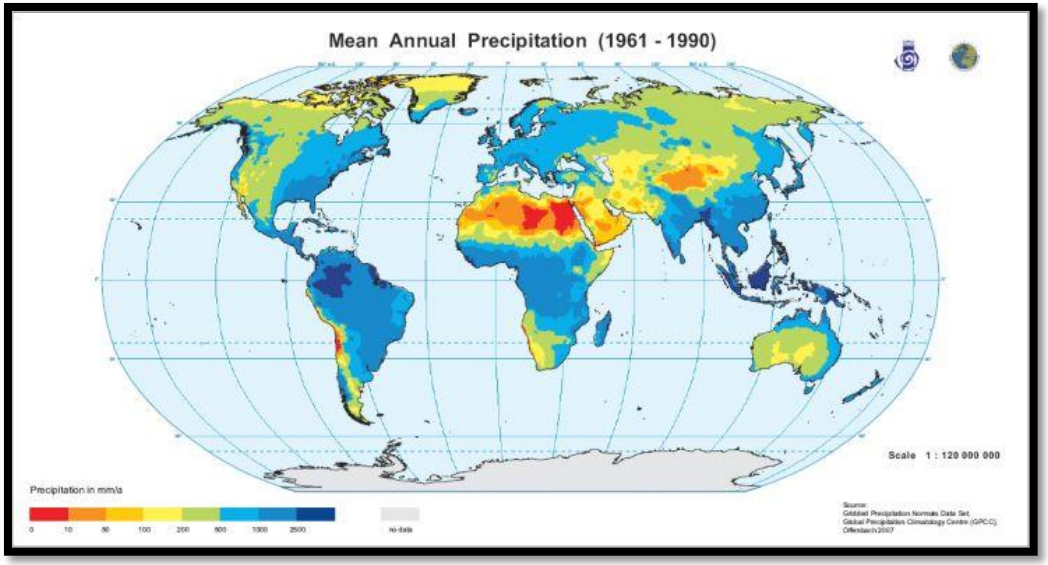
Loosely-linked

Loosely-linked

Vegetation map

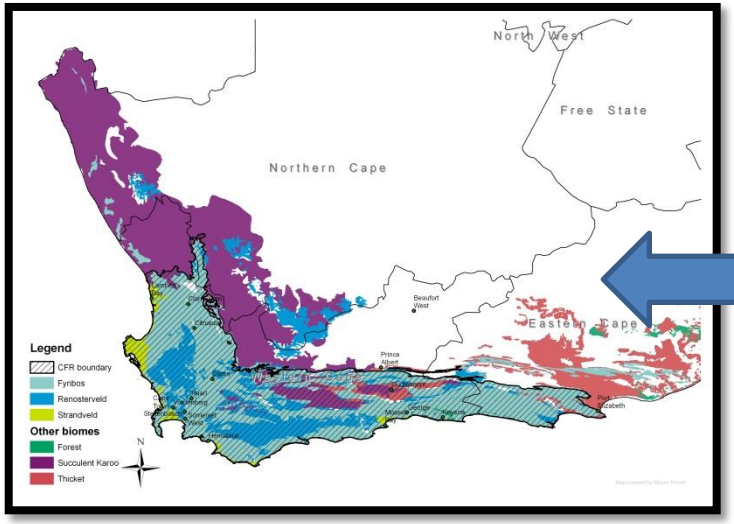


Interpolated rainfall map

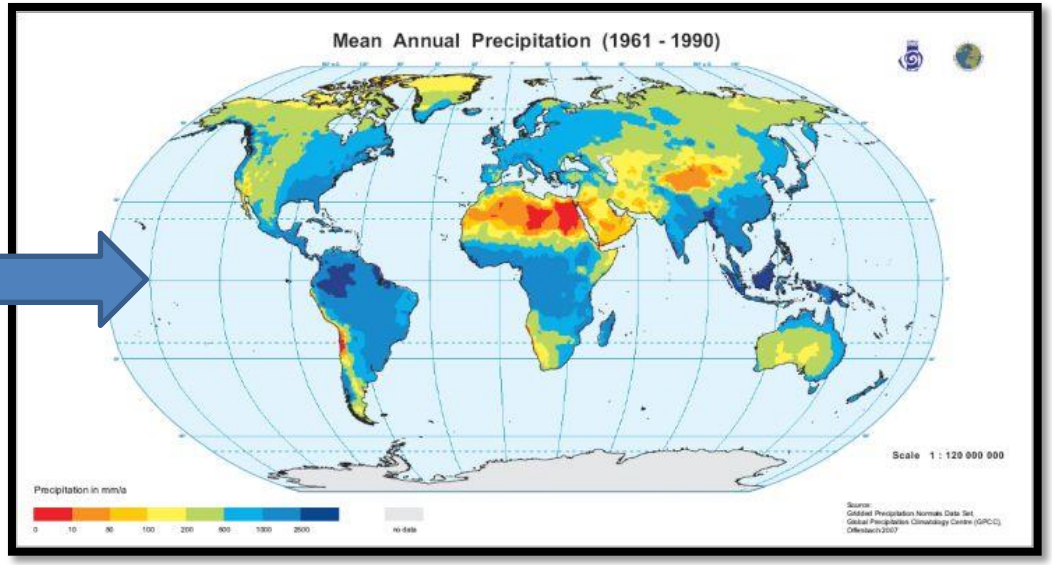


Loosely-linked

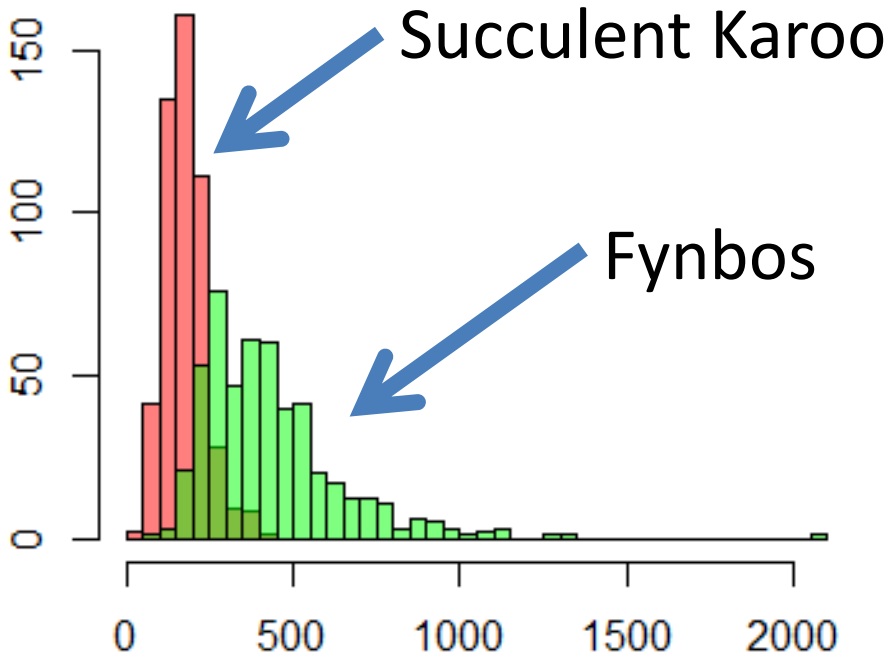
Vegetation map



Interpolated rainfall map



Loosely-linked



Correlative Approach

Advantages:

- Include many variables.
- Identify potential thresholds and interactions.

Correlative Approach

Disadvantages:

- Correlation does not imply causation.
- Often cannot unequivocally identify a causal factor.
- Often lacks a causal mechanism.
- Cannot extrapolate beyond recorded measurements.

Correlative Approach

Disadvantages:

Atmospheric [CO_2]

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	Field-based: manipulation
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	Greenhouse
	Laboratory
Mechanistic modelling	
Phylogenetic approach	

Experimental Approach

Experimental Approach

Manipulation of the environment

Experimental Approach

Categorised along a continuum based on how many factors are controlled

Experimental Approach

Field experiments: *ad hoc*
Field experiments: *a priori*
Common garden experiment
Greenhouse experiments
Laboratory experiments

Experimental Approach

Field experiment: *ad hoc*

Journal of Biogeography (1994) **21**, 49–62

Bergwind fires and the location pattern of forest patches in the southern Cape landscape, South Africa

C. J. GELDENHUYS *CSIR Division of Forest Science and Technology, P.O. Box 395, Pretoria 0001, Republic of South Africa*

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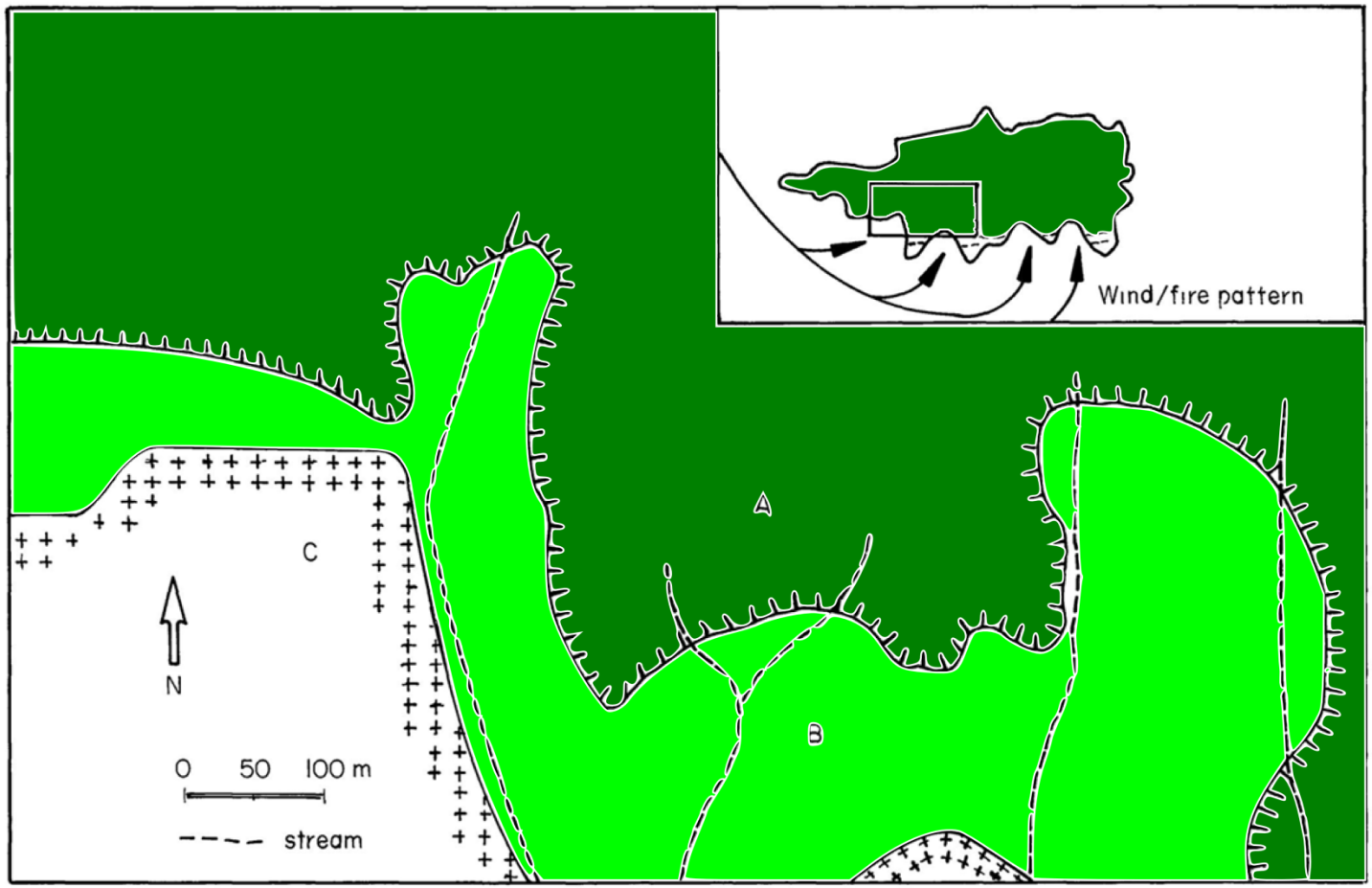
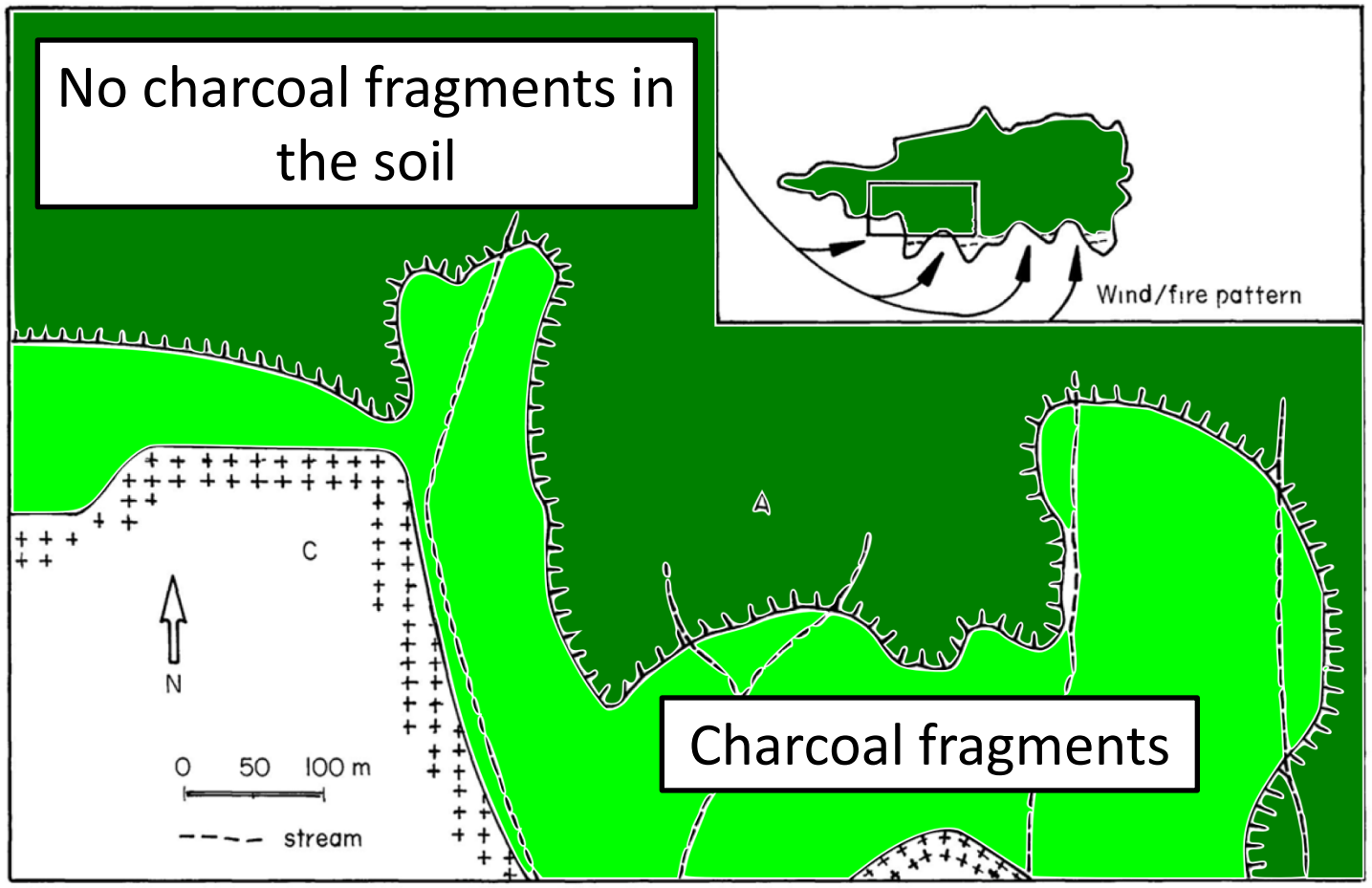
How does post-fire forest succession occur?



Witelsbos Forest in the southern Cape



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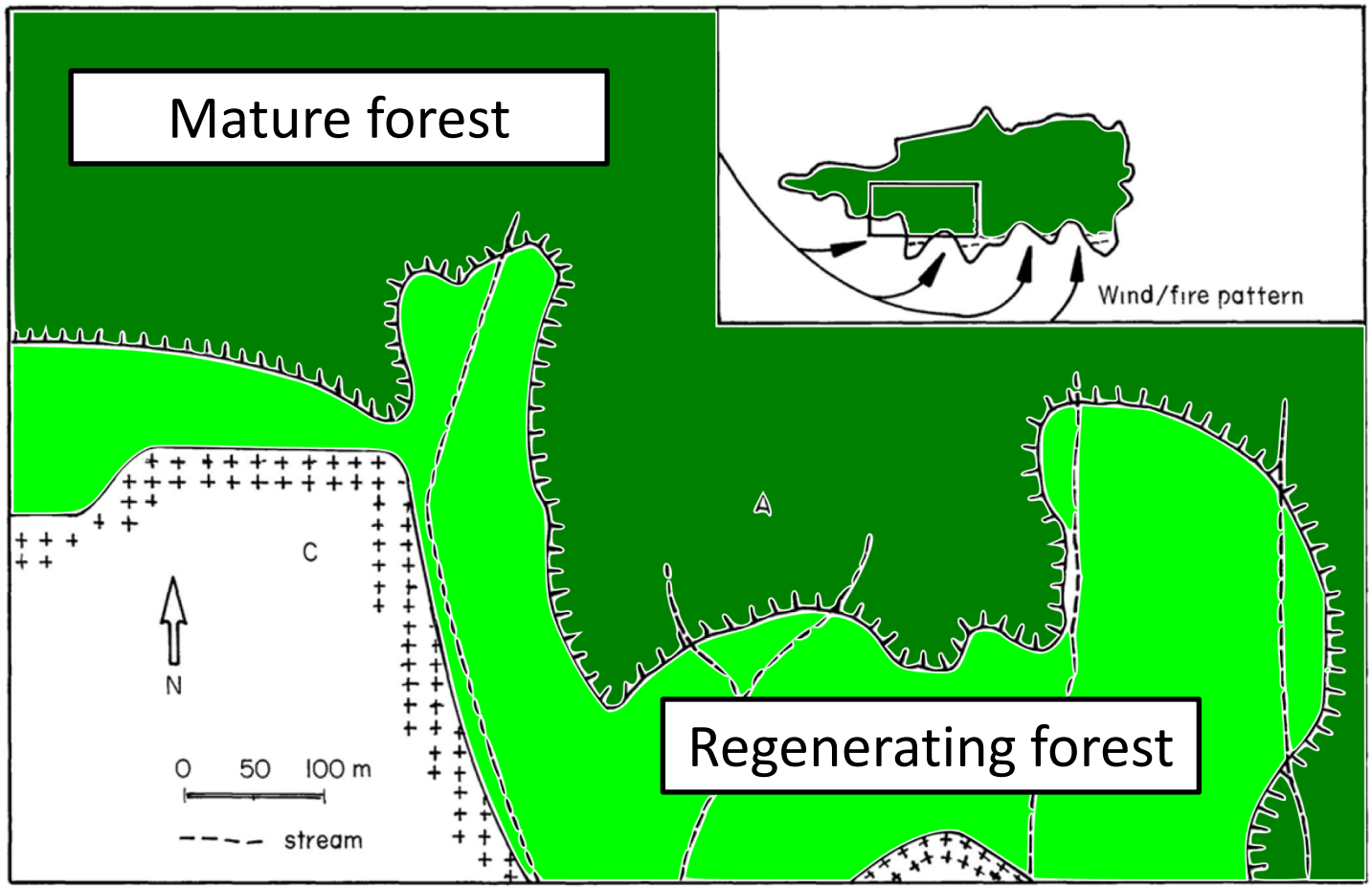
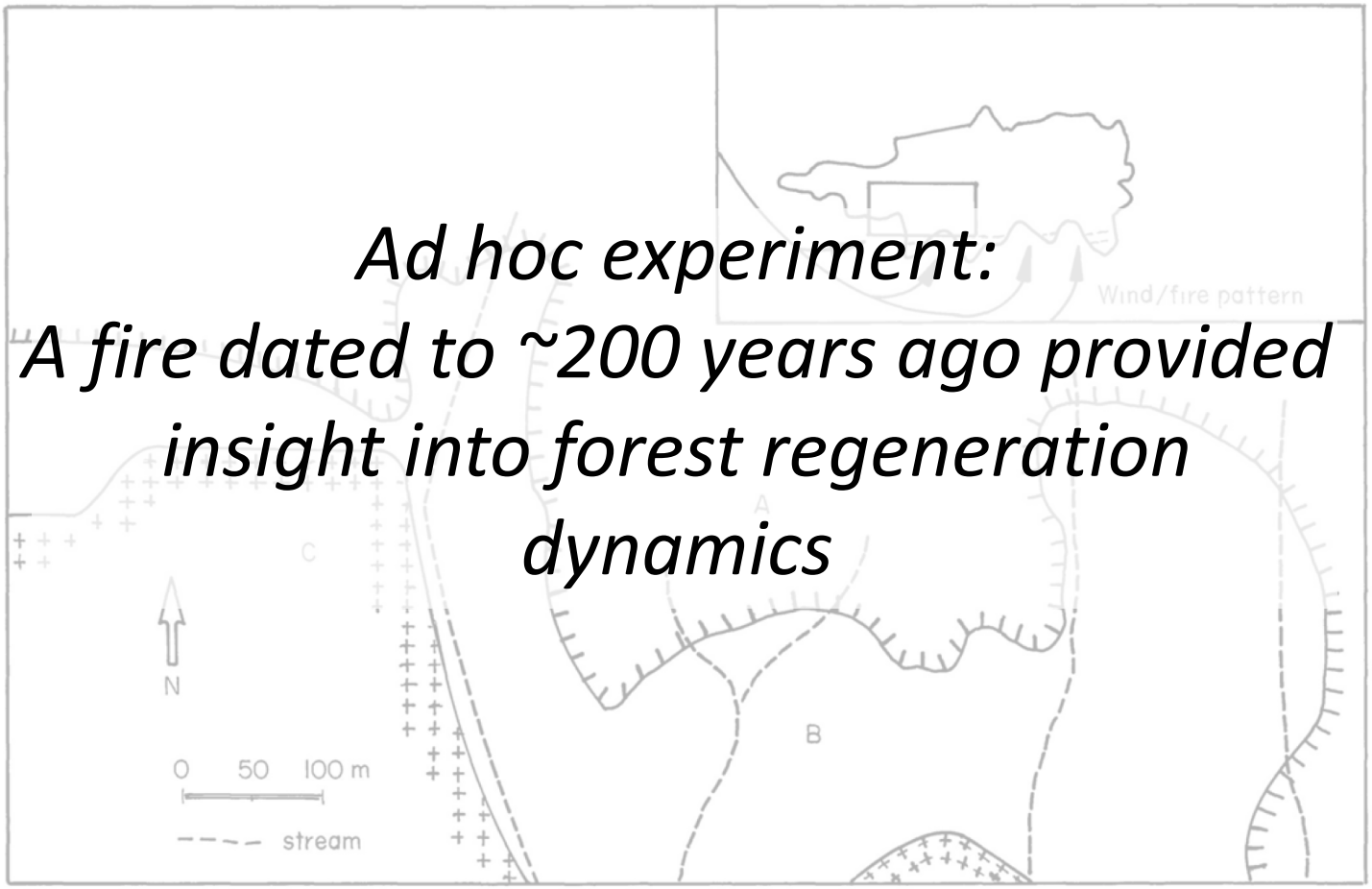


Witelsbos Forest in the southern Cape



Ad hoc experiment:
A fire dated to ~200 years ago provided insight into forest regeneration dynamics

Witelsbos Forest in the southern Cape

Experimental Approach

Field experiment: *a priori*

Transplant

APPROACHES: OBSERVATIONS CORRELATIVE EXPERIMENTAL MECH. MODELLING PHYLOGENETIC

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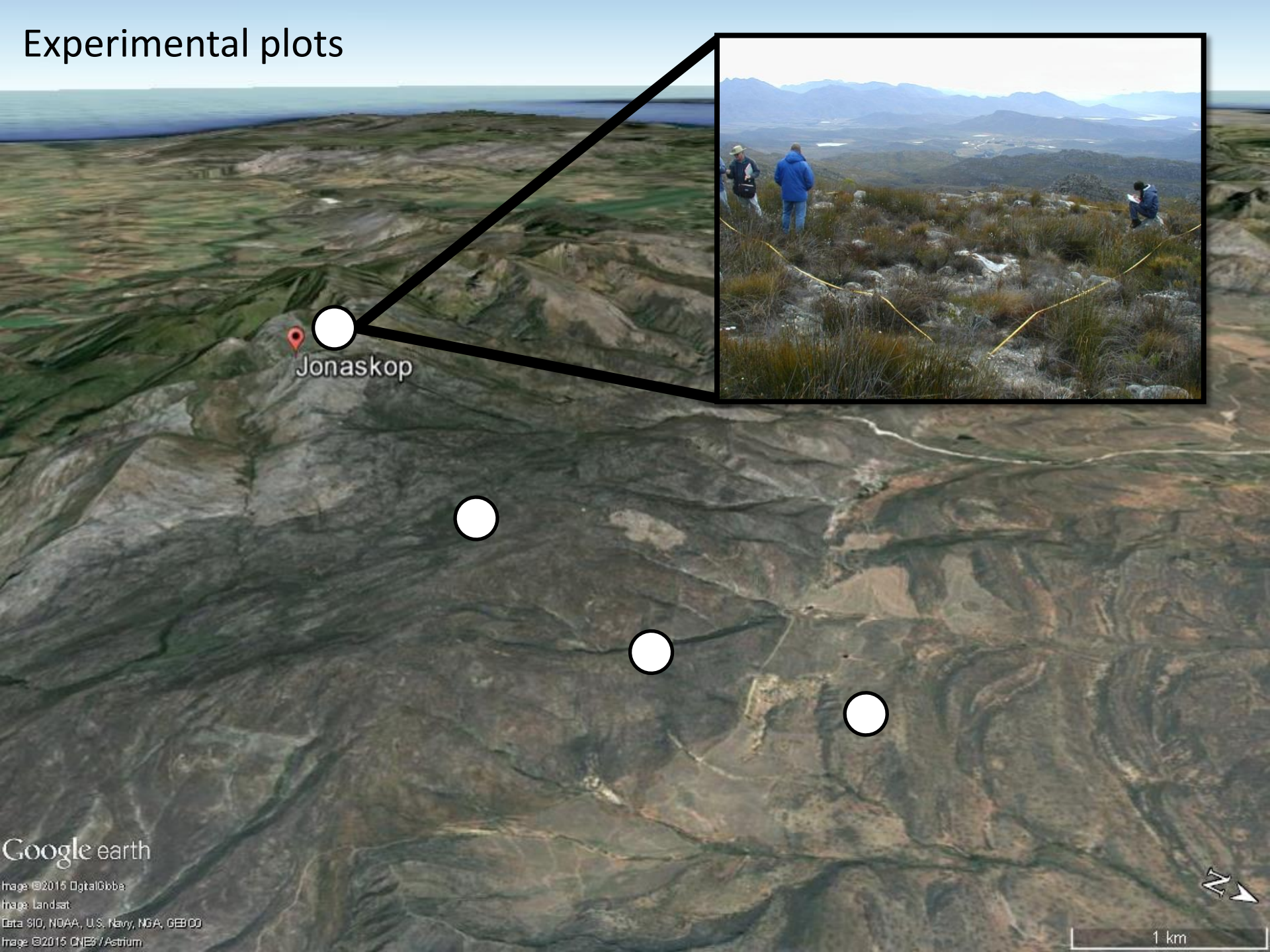
Determinants of the Fynbos/Succulent Karoo biome boundary: Insights from a reciprocal transplant experiment

K.J. Esler [a,*], L. von Staden [b], G.F. Midgley [b,c]

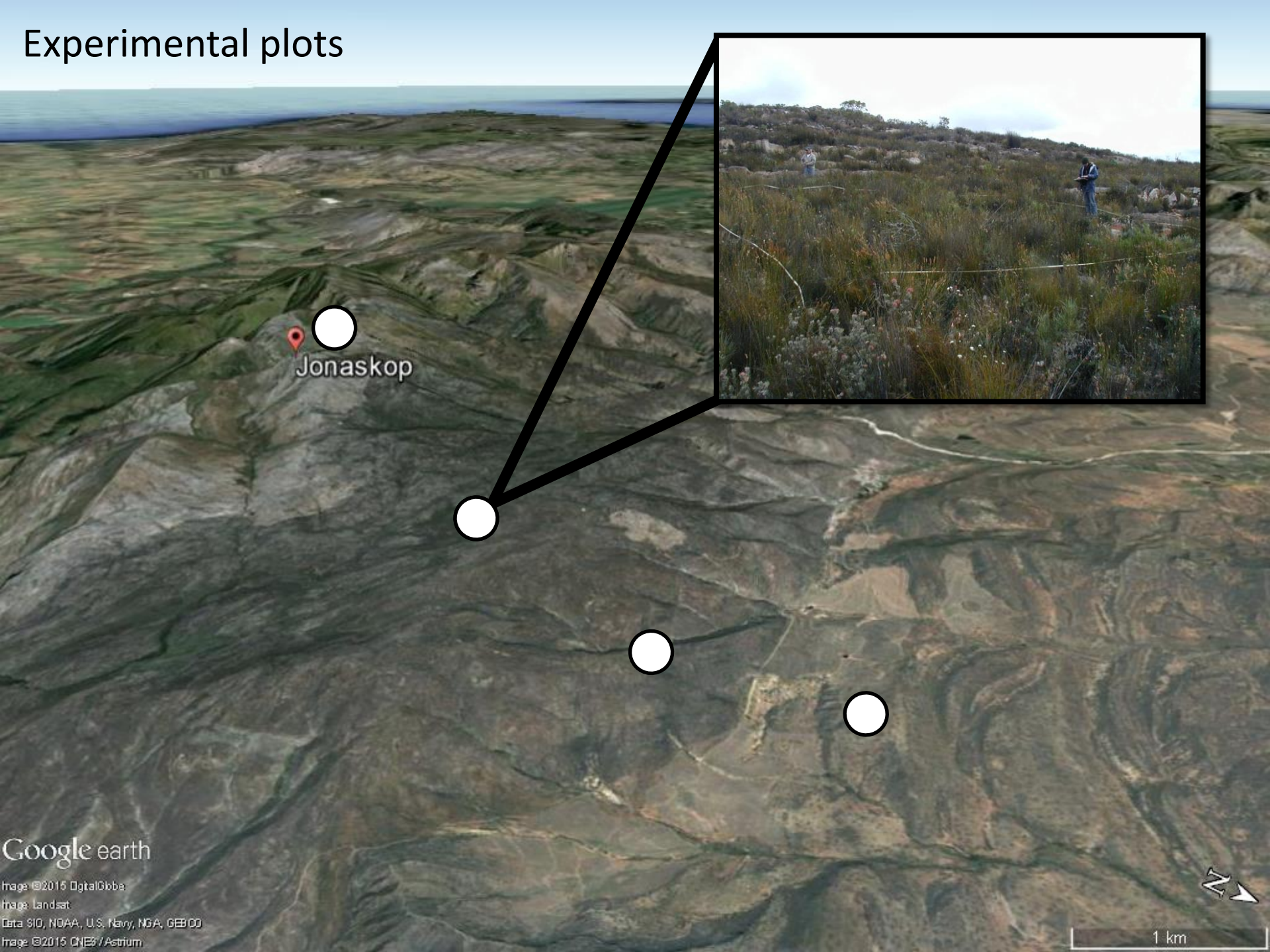

Jonaskop
Google earth
Image © 2015 DigitalGlobe
Image Landsat
Data SIO, NOAA, U.S. Navy, NGA, GEBCO
Image © 2015 CNES / Astrium
N
1 km

Experimental plots

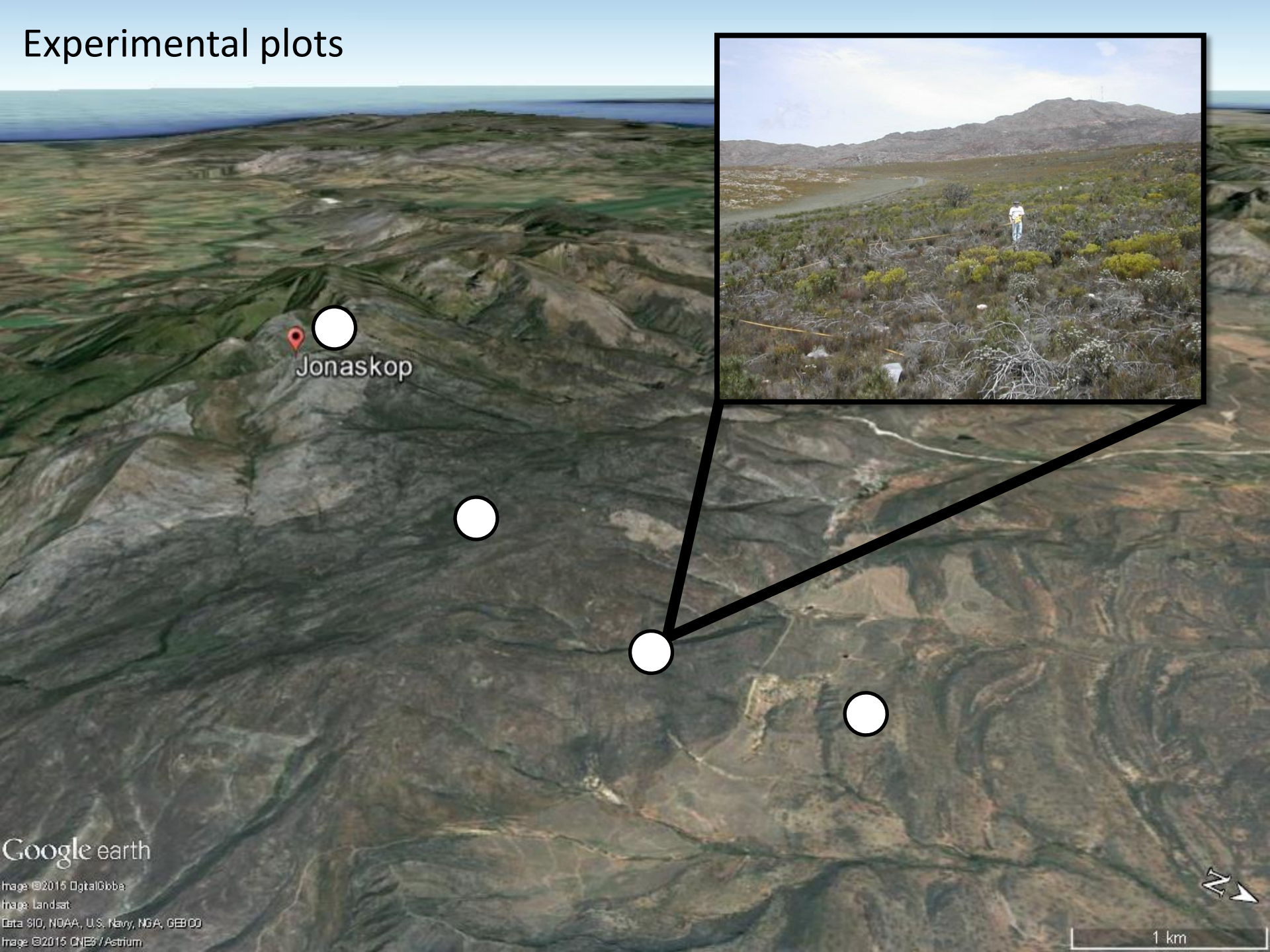
Experimental plots



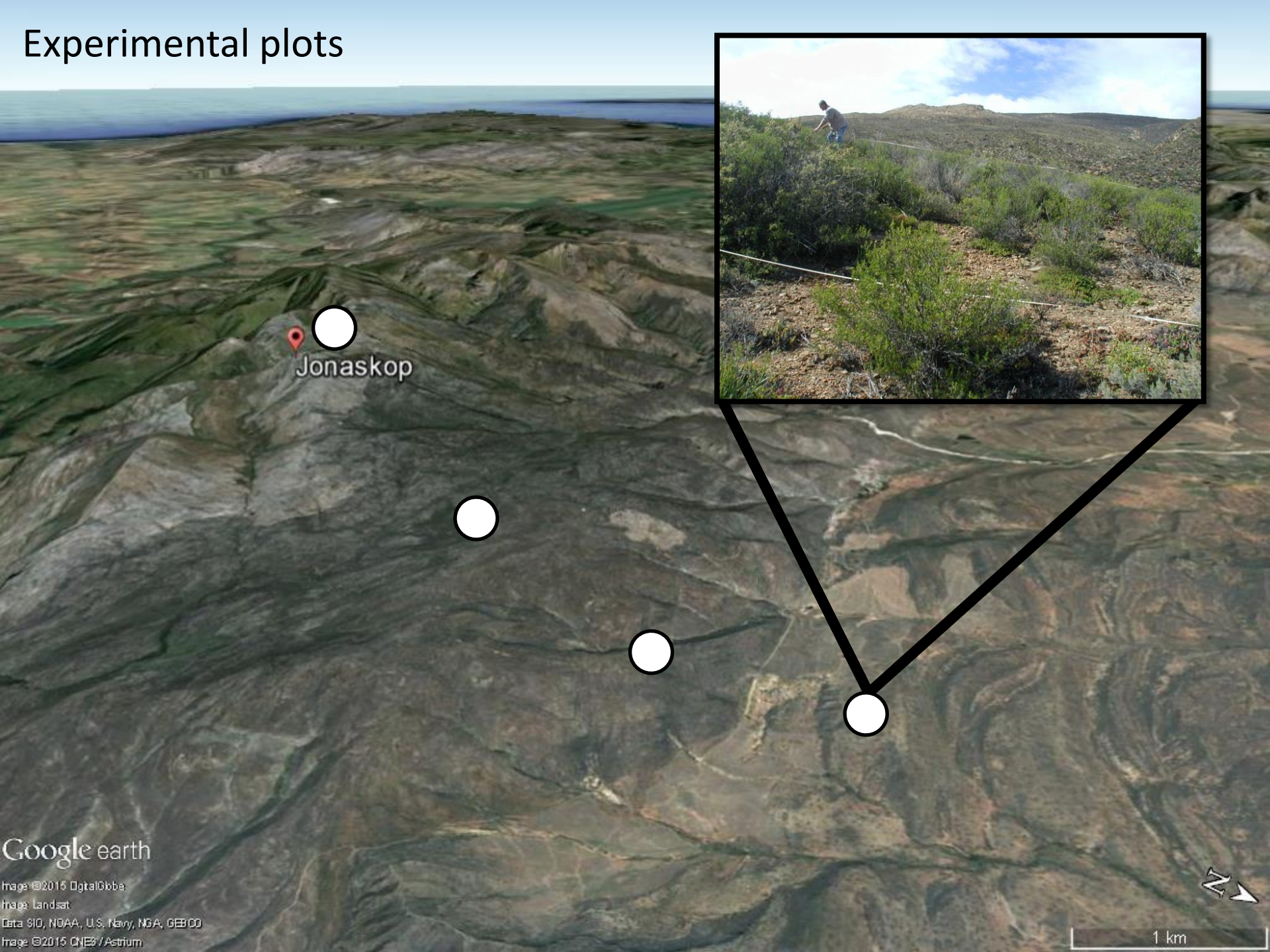
Experimental plots



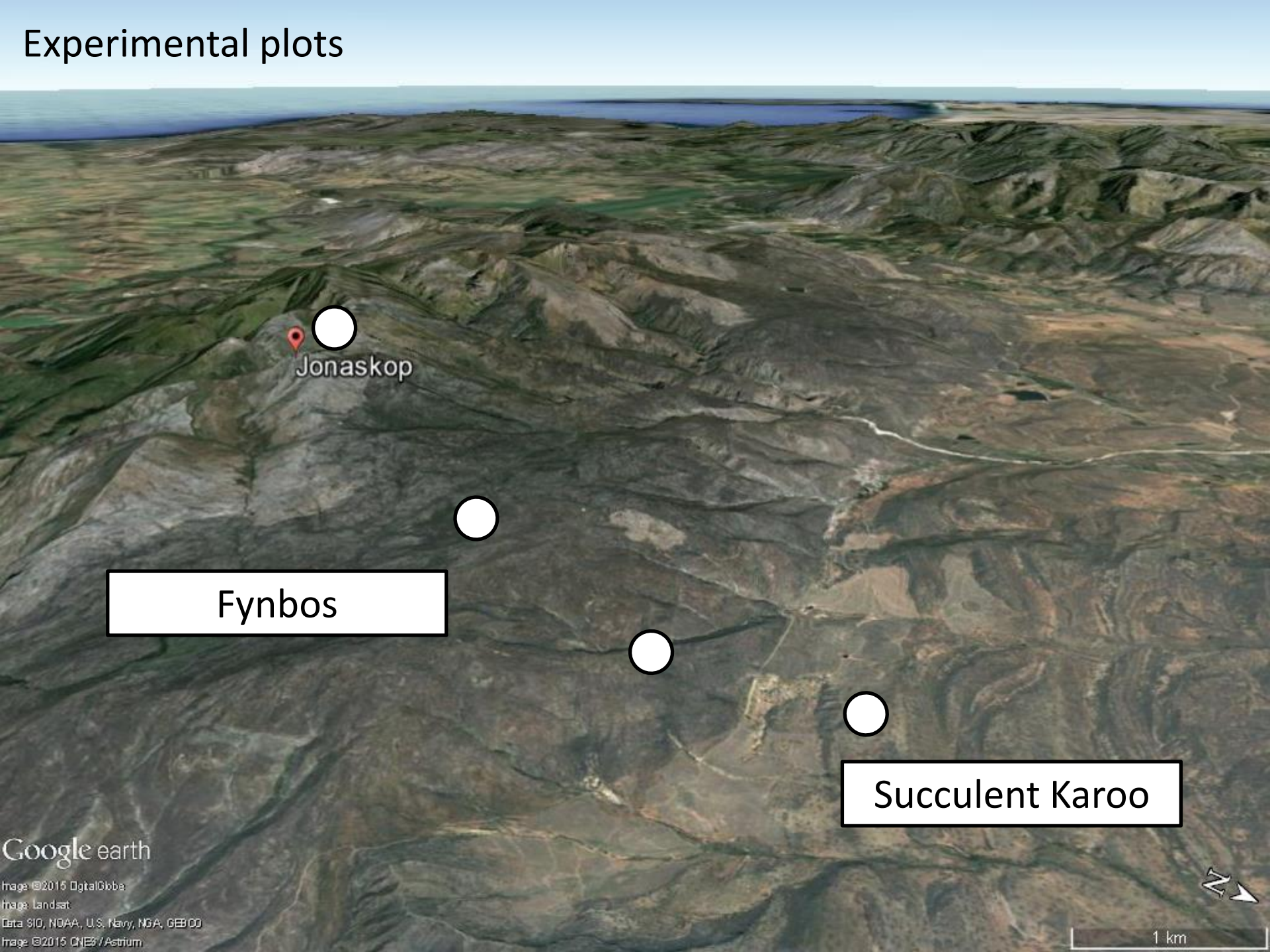
Experimental plots



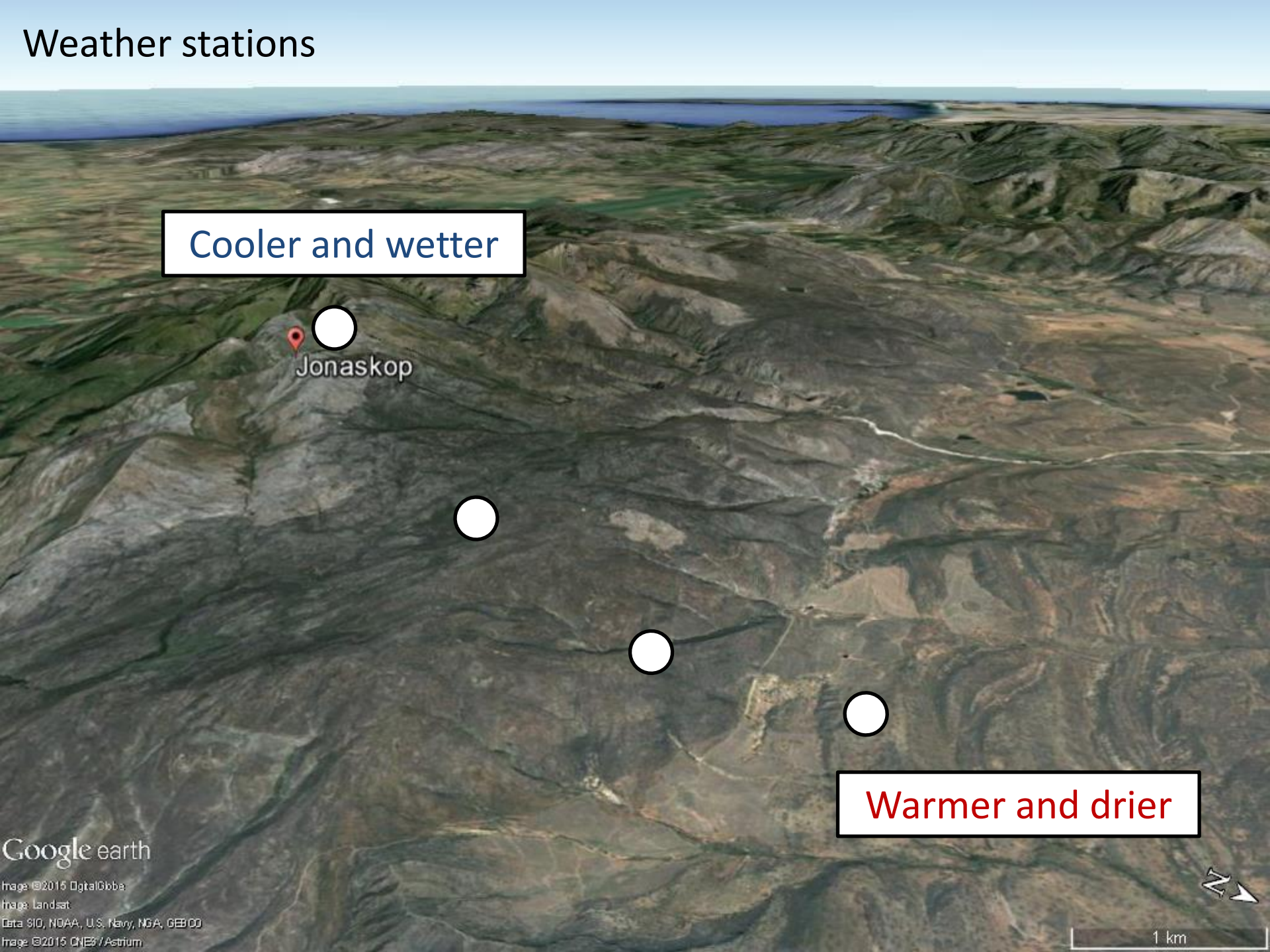
Experimental plots



Experimental plots

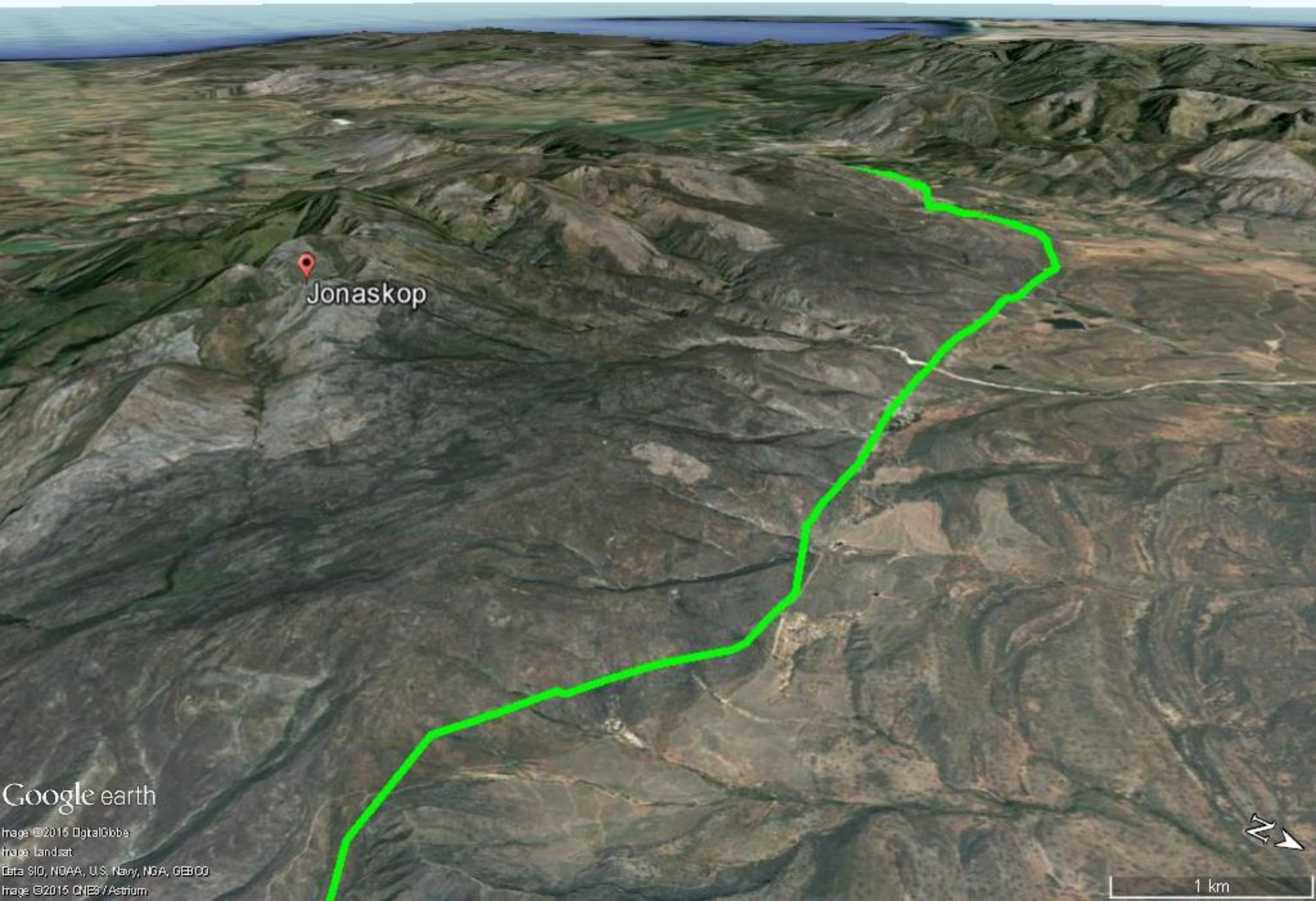


Weather stations

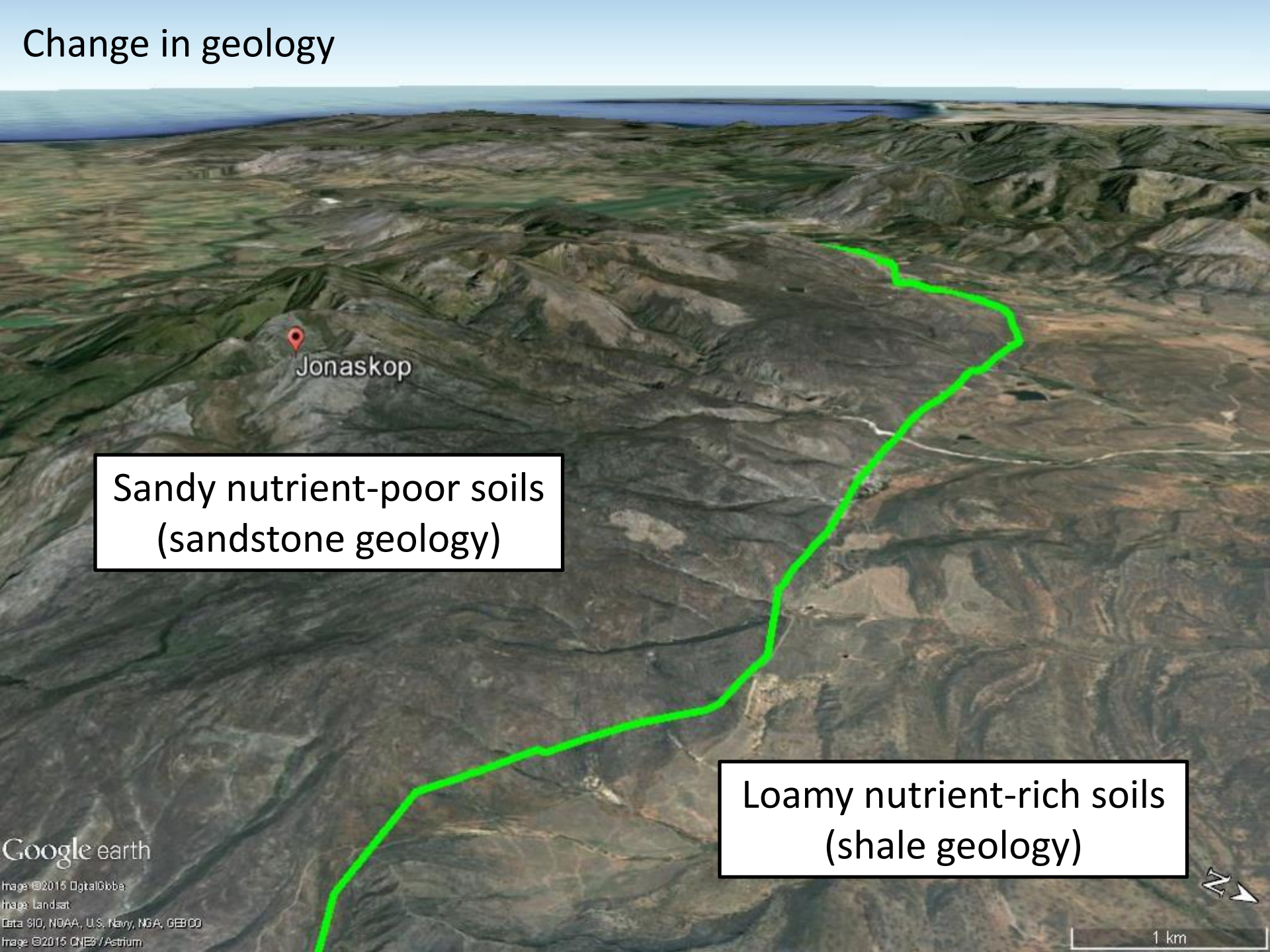



Jonaskop
Google earth
Image © 2015 DigitalGlobe
Image Landsat
Data SIO, NOAA, U.S. Navy, NGA, GEBCO
Image © 2015 CNES / Astrium
N
1 km

Change in geology



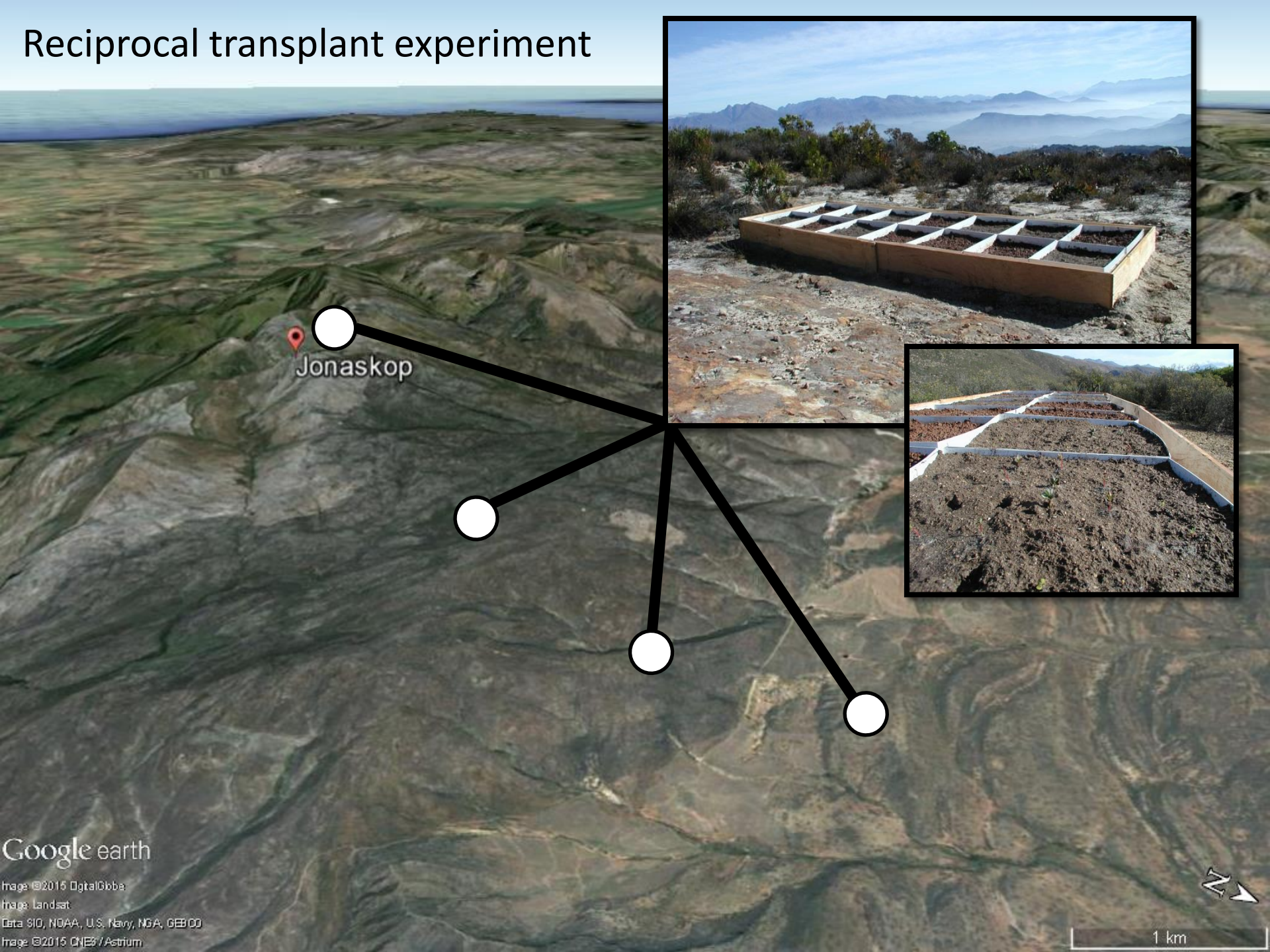
Change in geology




Jonaskop
Google earth
Image © 2015 DigitalGlobe
Image Landsat
Data SIO, NOAA, U.S. Navy, NGA, GEBCO
Image © 2015 CNES / Astrium
N
1 km

Experimental plots

Reciprocal transplant experiment



FYNBOS spp.

Protea amplexicaulis

Protea humiflora

Protea magnifica

S.K. spp.

Ruschia lineolata

Drosanthemum speciosum

Pteronia incana

Reciprocal transplant experiment

- Across T & PPT gradient
- 2 soil types: sandstone & shale
- 3 spp. per biome
- 7 Months

Jonaskop

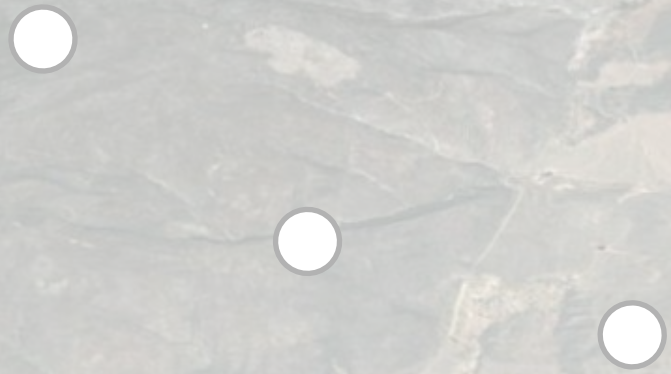
N

1 km

Findings

Fynbos

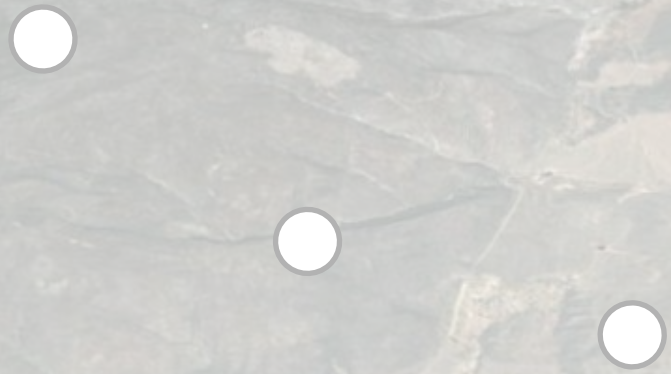
	Cool & Wet	Warm & Dry
Sandy Soils	✓	
Loamy soils		



Findings

Fynbos

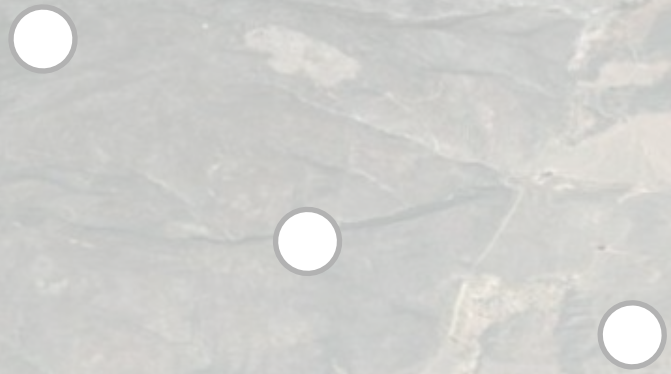
	Cool & Wet	Warm & Dry
Sandy Soils	✓	✗
Loamy soils		



Findings

Fynbos

	Cool & Wet	Warm & Dry
Sandy Soils	✓	✗
Loamy soils	✗	✗



Findings

Fynbos

	Cool & Wet	Warm & Dry
Sandy Soils	✓	✘
Loamy soils	✘	✘

Succulent Karoo

	Cool & Wet	Warm & Dry
Sandy Soils		✓
Loamy soils		✓

Findings

Fynbos

	Cool & Wet	Warm & Dry
Sandy Soils	✓	✘
Loamy soils	✘	✘

Succulent Karoo

	Cool & Wet	Warm & Dry
Sandy Soils	✓	✓
Loamy soils	✓	✓

Fynbos

Jonaskop

Google earth

Image © 2015 DigitalGlobe
Image Landsat
Data SIO, NOAA, U.S. Navy, NGA, GEBCO
Image © 2015 CNES / Astrium

N

1 km

Fynbos

Jonaskop

Wrong geology + too dry/warm

1 km

Succulent Karoo

Jonaskop

Higher growth rates at higher elevations

1 km

Succulent Karoo

Succulent Karoo

Jonaskop

Competition and/or fire

1 km

Experimental Approach

Field experiments: *ad hoc*
Field experiments: *a priori*
Common garden experiment
Greenhouse experiments
Laboratory experiments

Experimental Approach

Greenhouse experiment

Journal of Vegetation Science 12: 75-80, 2001

Abiotic determinants of the fynbos / succulent karoo boundary, South Africa

Lechmere-Oertel, Richard G[1,2*] & Cowling, Richard M.[1]

Established seedlings transplanted into pots:

- Fynbos or Succulent Karoo species
- Sandstone-derived soils or shale-derived soils
- No water vs daily water
- Greenhouse setting

Similar story to Esler et al. (2015)

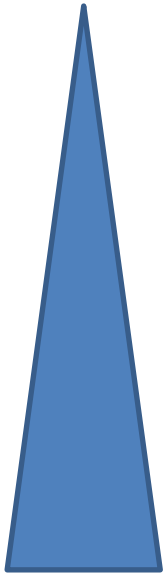
- Field experiments: *ad hoc*
- Field experiments: *a priori*
- Common garden experiment
- Greenhouse experiments
- Laboratory experiments

Control of environmental variables

Field experiments: *ad hoc*
Field experiments: *a priori*
Common garden experiment
Greenhouse experiments
Laboratory experiments

Control of environmental variables

Field experiments: *ad hoc*
Field experiments: *a priori*
Common garden experiment
Greenhouse experiments
Laboratory experiments

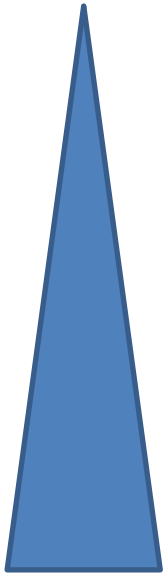


Number of treatments

Field experiments: *ad hoc*
Field experiments: *a priori*
Common garden experiment
Greenhouse experiments
Laboratory experiments

Number of treatments

Field experiments: *ad hoc*
Field experiments: *a priori*
Common garden experiment
Greenhouse experiments
Laboratory experiments



Application to broader context

Field experiments: *ad hoc*
Field experiments: *a priori*
Common garden experiment
Greenhouse experiments
Laboratory experiments

Application to broader context

Field experiments: *ad hoc*
Field experiments: *a priori*
Common garden experiment
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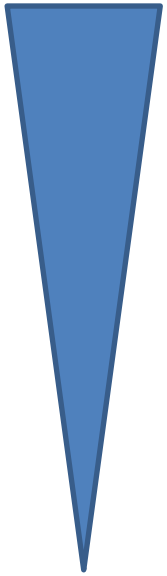
Laboratory experiments



Experimental Approach

Advantages:

- Explicitly test variable importance and interactions.

Experimental Approach

Disadvantages:

- Practical limits on the # of variables/treatments.
- Extrapolation beyond experimental conditions ~problematic.
- Not practical if lots of *time* is required to observed results

Approaches

Category	Sub-category
Field observations	
Correlative approach	Tightly-linked
	Loosely-linked
Experimental approach	Field-based: *ad hoc*
	Field-based: manipulation
	Common garden
	Greenhouse
	Laboratory
Mechanistic modelling	
Phylogenetic approach	

Mechanistic Modelling

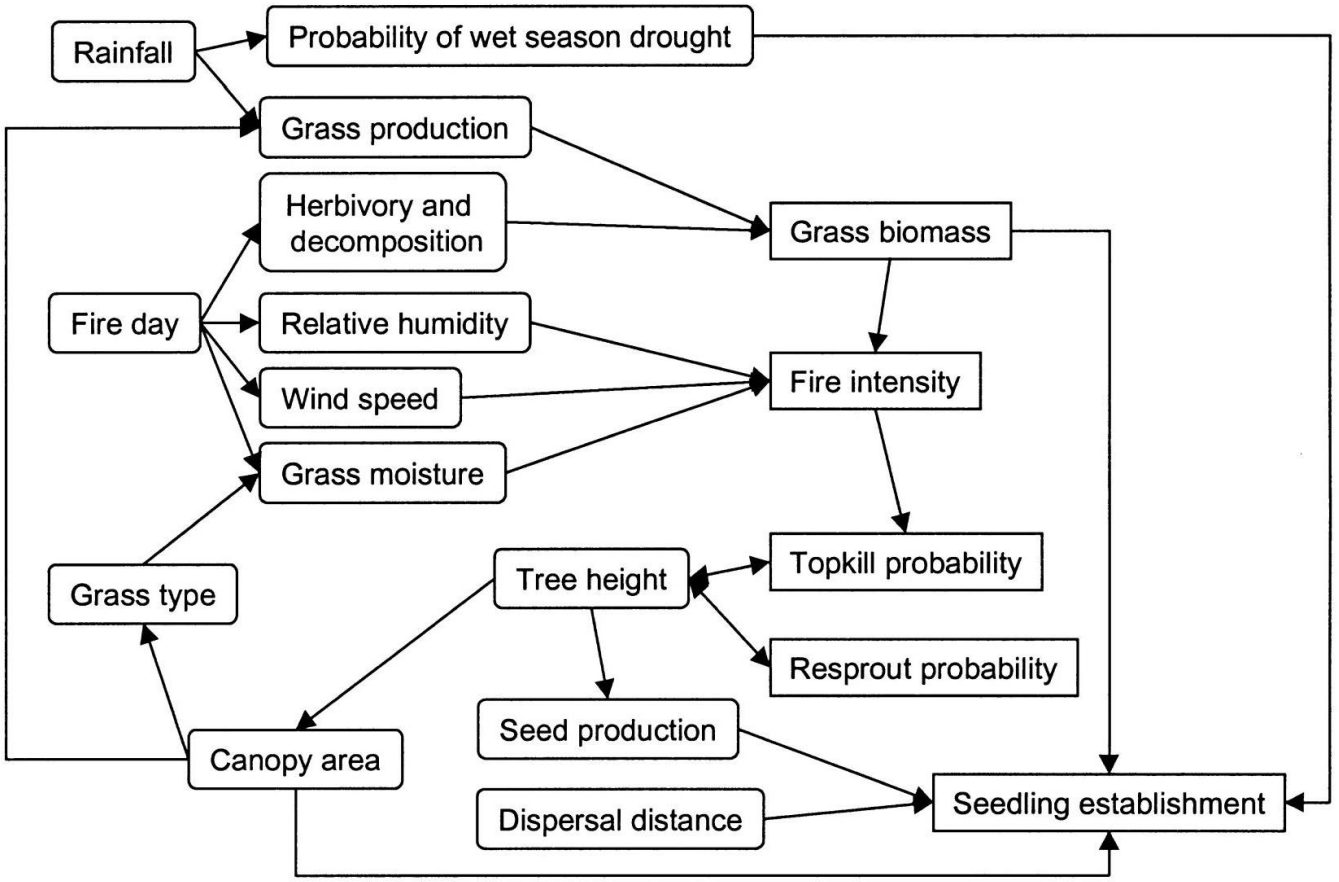
Mechanistic Modelling Approach

11h00
Glenn Moncrieff

Improving projections of the future distribution of the Fynbos and Succulent Karoo Biomes using ***Dynamic Vegetation Models***

Mechanistic Modelling Approach

- Examine a complex system by combining different parts (modules/cogs).
- Each cog is a process-based representation of a system component.
- Usually requires a lot of mathematical and programming skills.



Higgins et al. (2000) J. Ecol

Global Change Biology

Global Change Biology (2009) **15**, 2224–2246, doi: 10.1111/j.1365-2486.2008.01838.x

Impacts of climate change on the vegetation of Africa: an adaptive dynamic vegetation modelling approach

SIMON SCHEITER* and STEVEN I. HIGGINS†

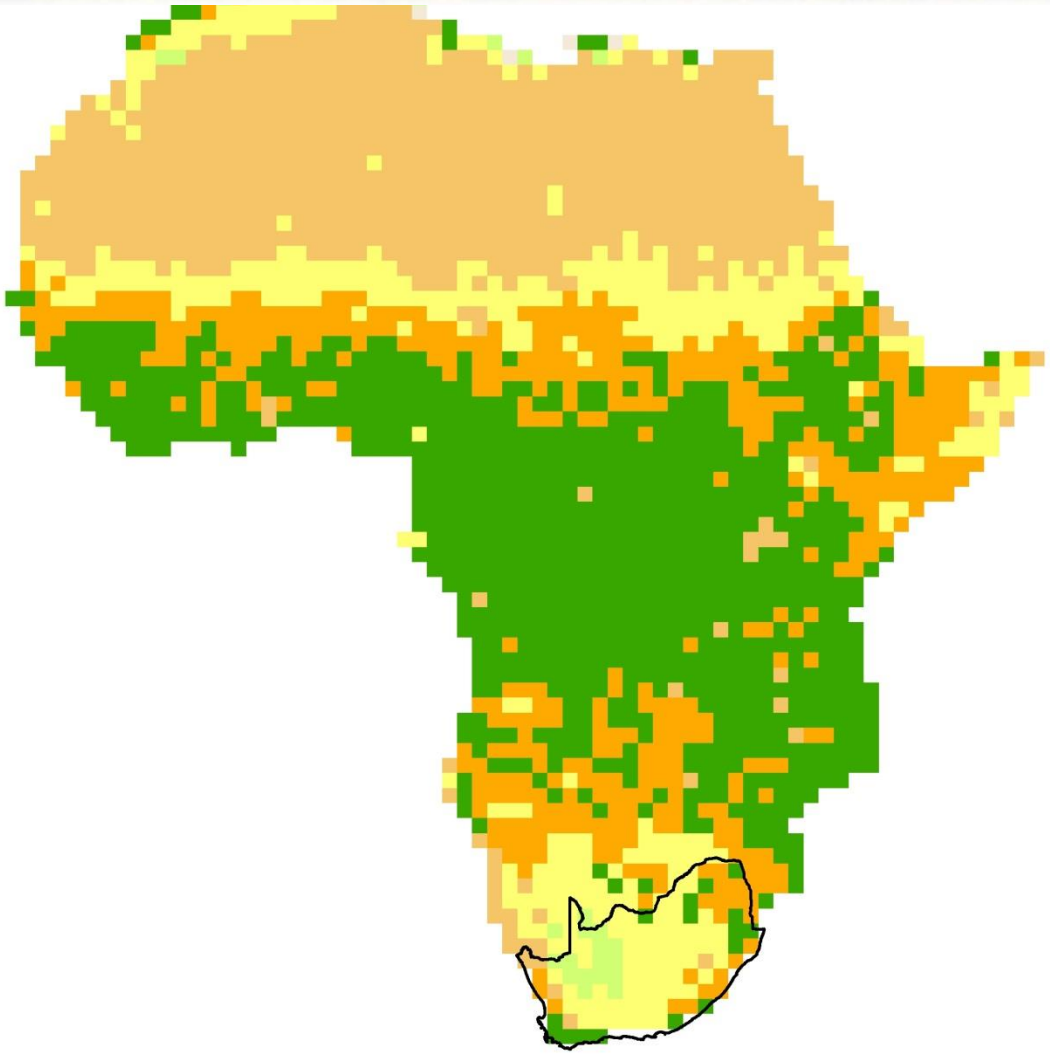
aDGVM

Scheiter &Higgins (2009) GCB

C4 Grassland

C4 Savannah

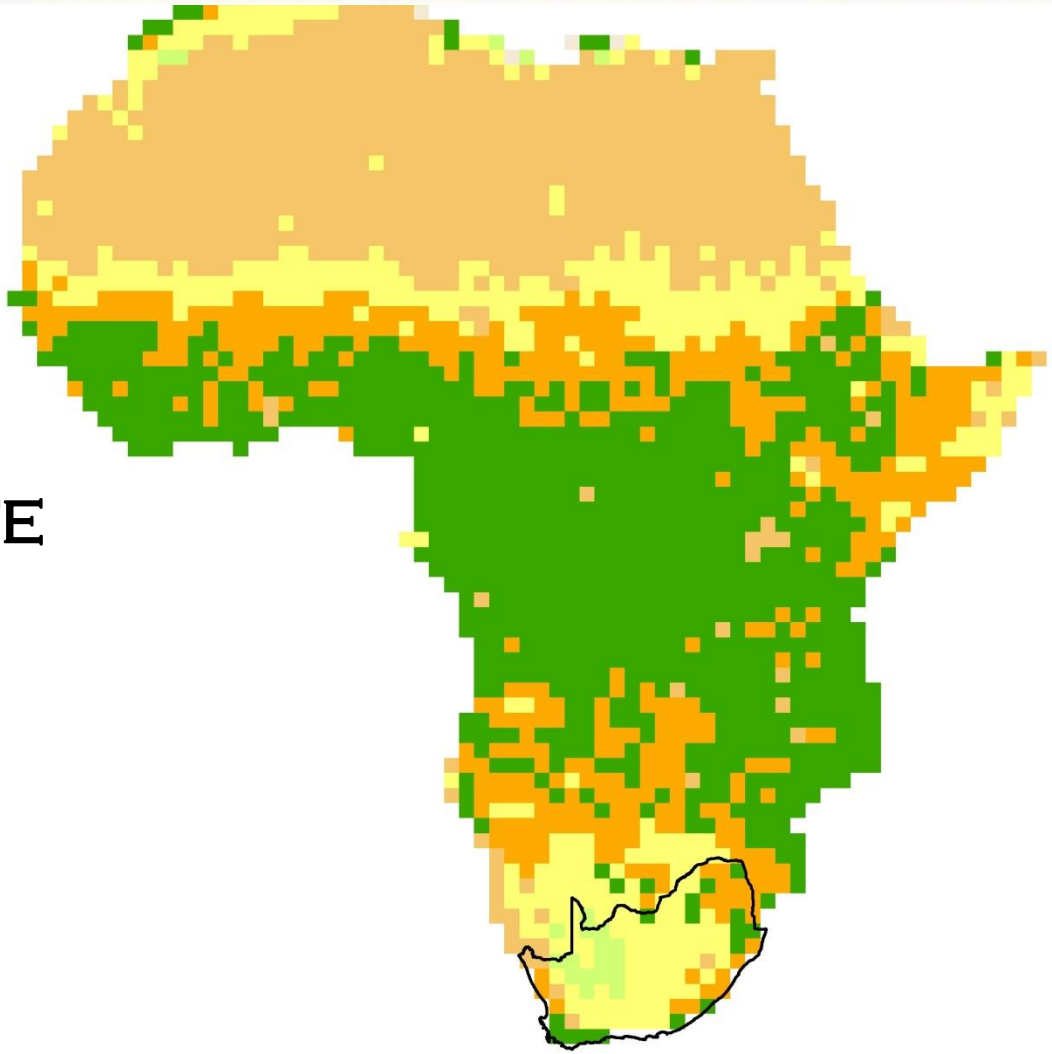
Forest and closed woodland



aDGVM

Scheiter &Higgins (2009) GCB

- C4 Grassland
- C4 Savannah
- Forest and closed woodland

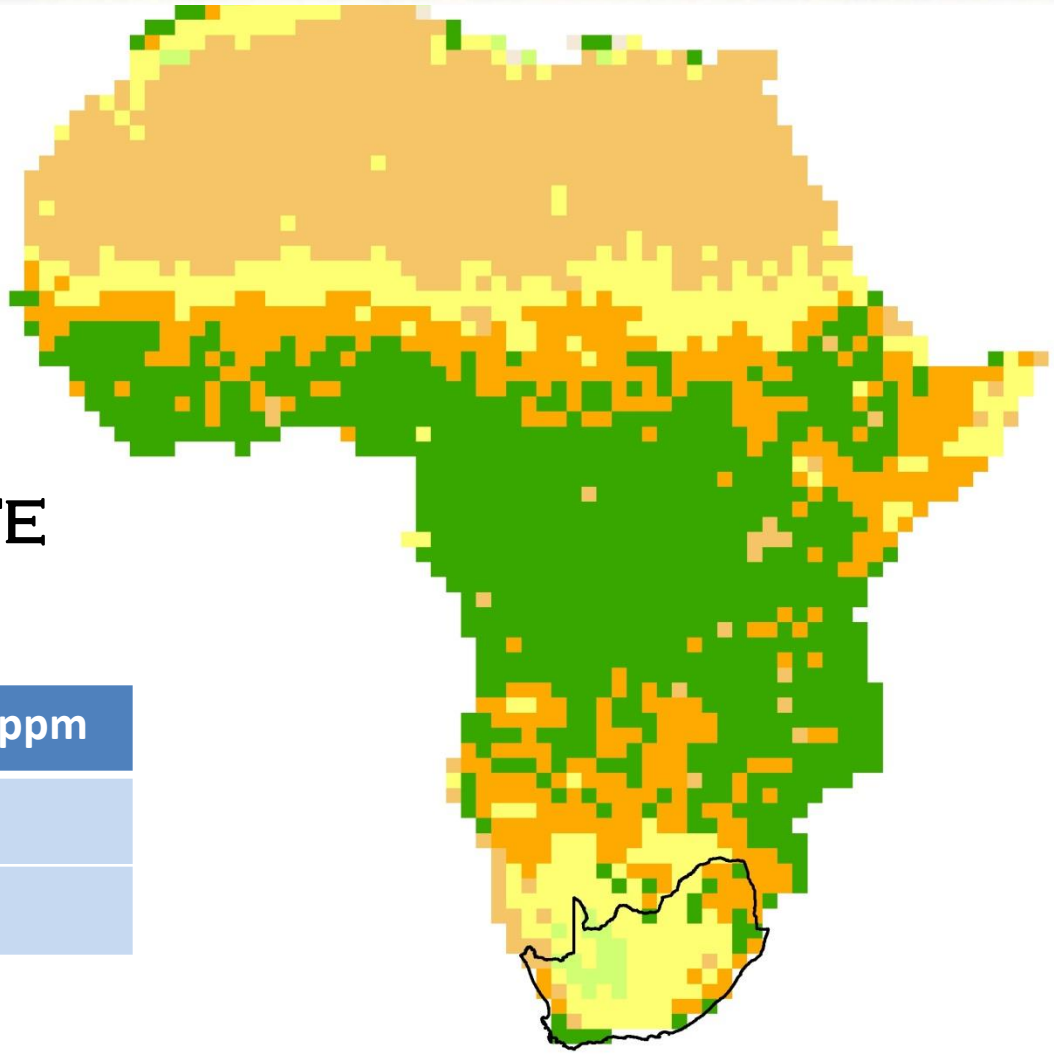


Present day climate

aDGVM

Scheiter &Higgins (2009) GCB

- C4 Grassland
- C4 Savannah
- Forest and closed woodland



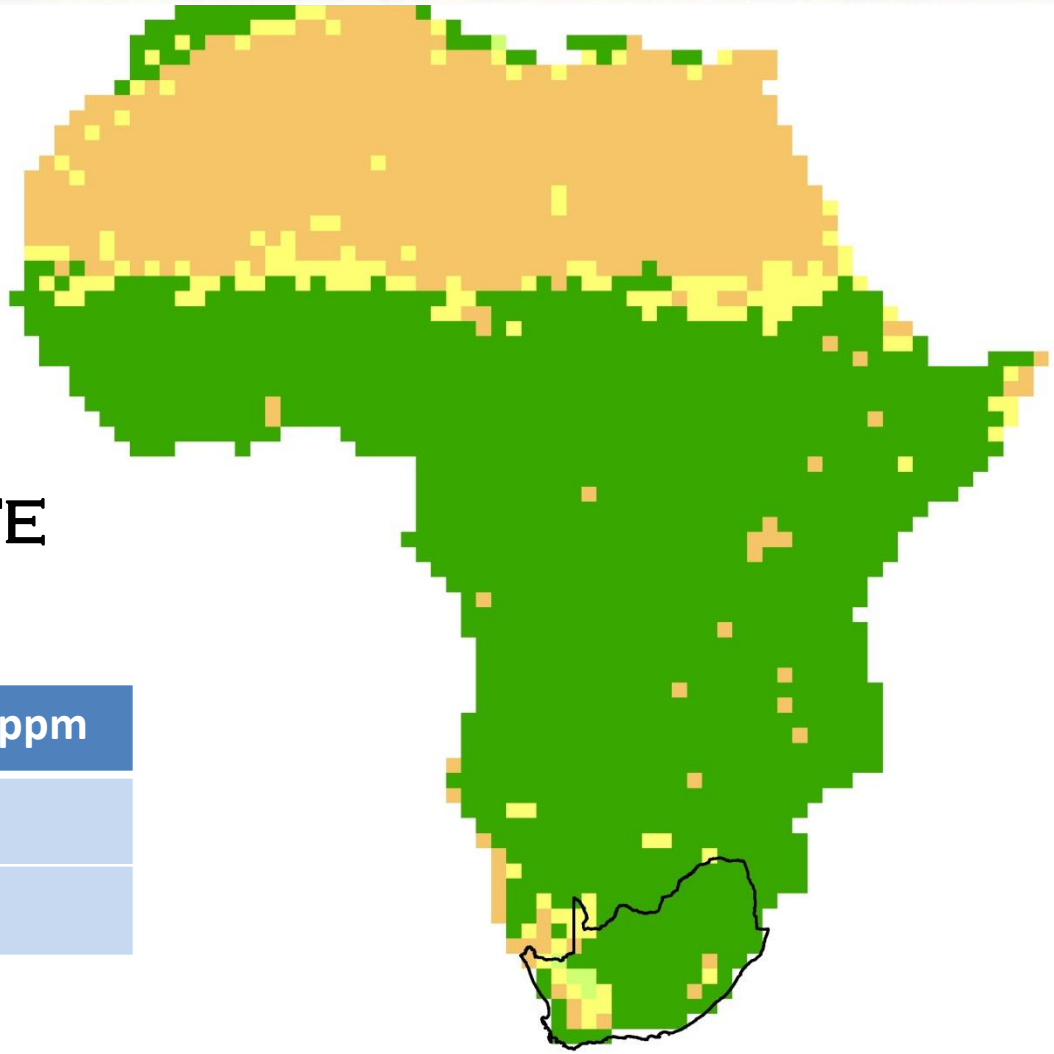
Present day climate

	350 ppm	150 ppm
Fire	●	
No fire		

aDGVM

Scheiter &Higgins (2009) GCB

- C4 Grassland
- C4 Savannah
- Forest and closed woodland



Present day climate

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Fire		
No fire	•	

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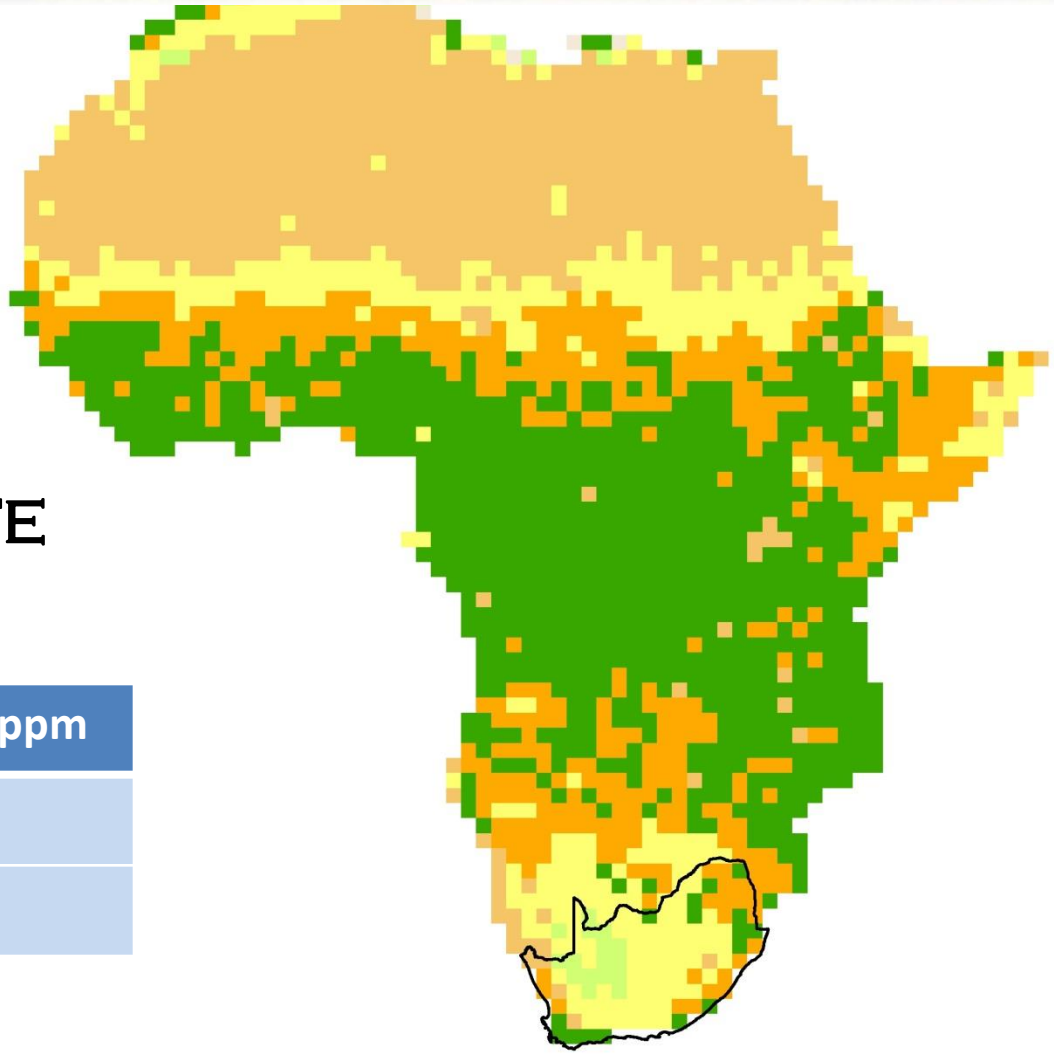

Present day climate

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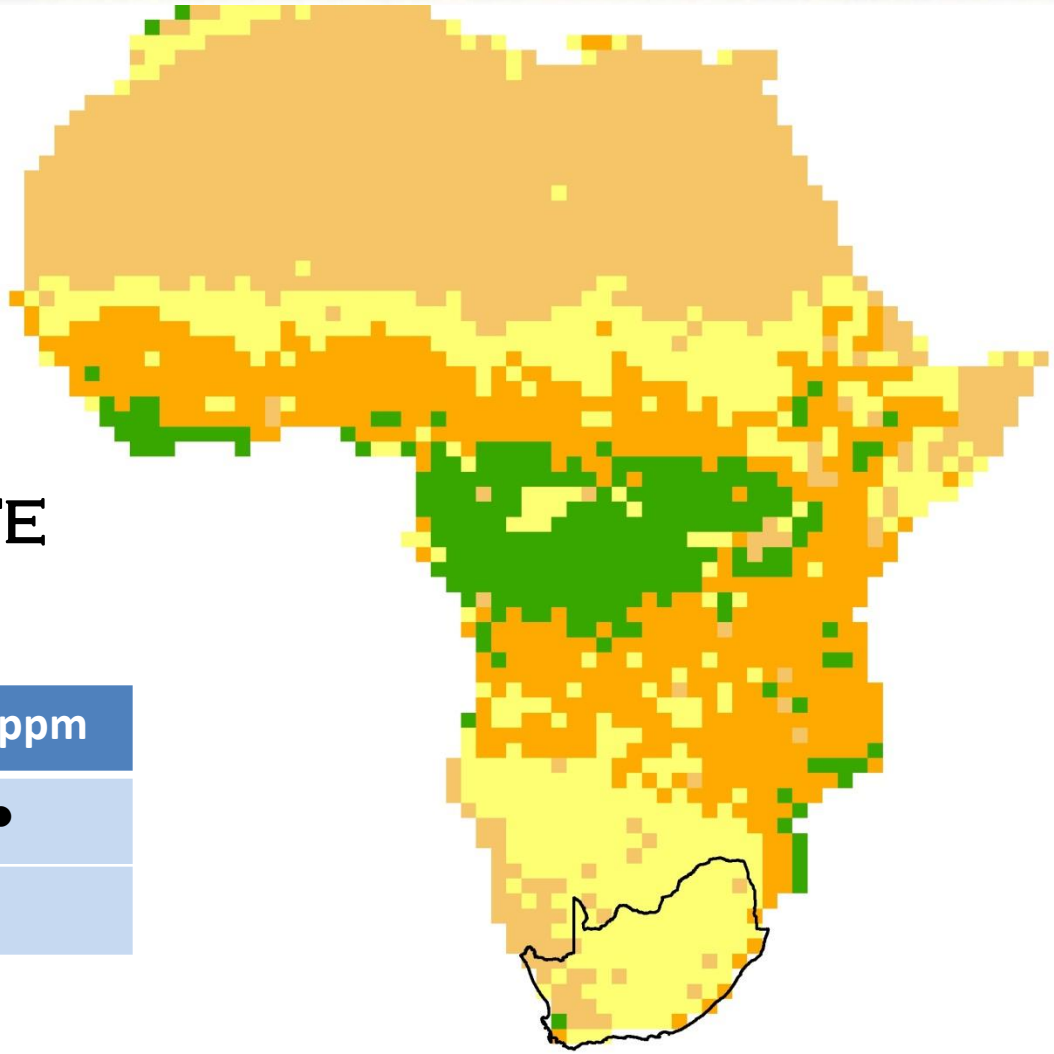

Present day climate

	350 ppm	150 ppm
Fire		•
No fire		

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Scheiter &Higgins (2009) GCB

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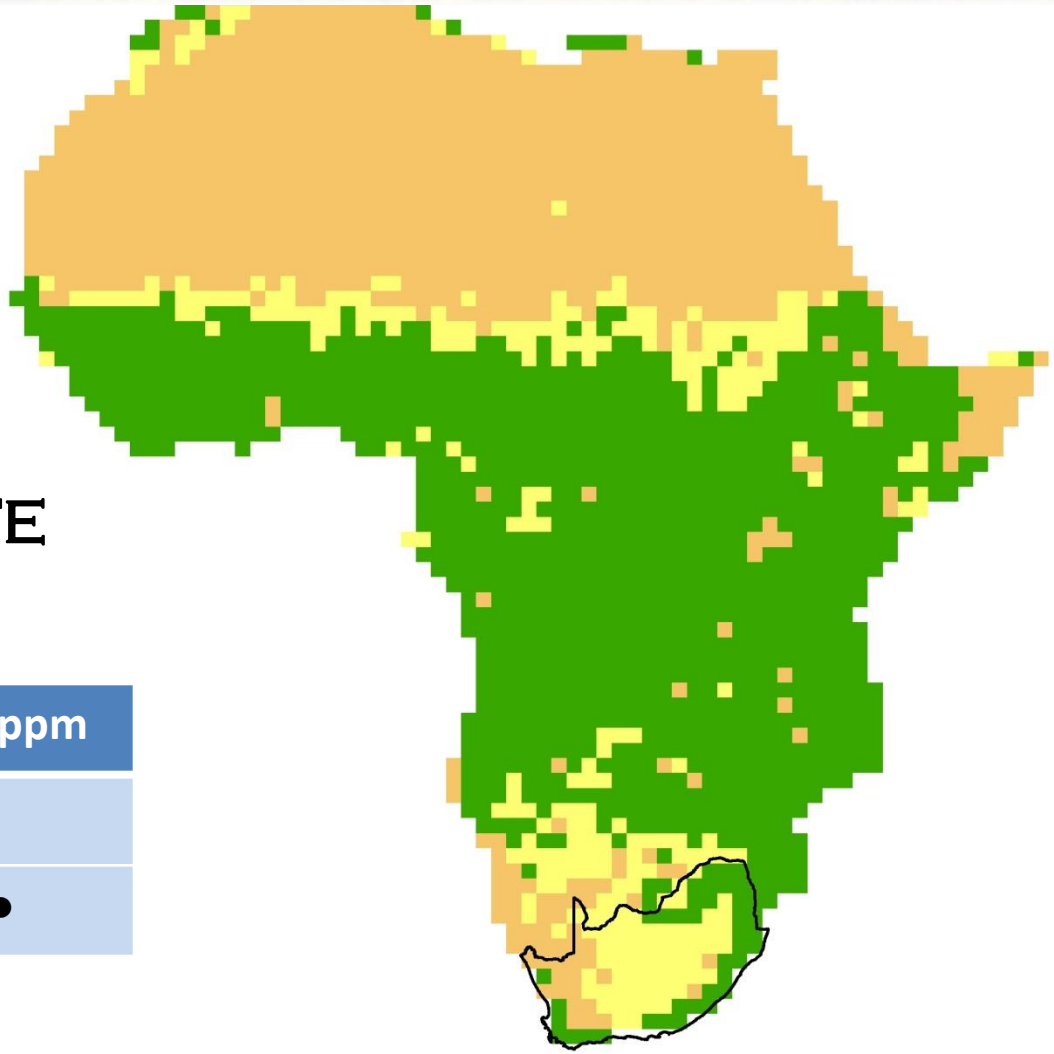


Present day climate

	350 ppm	150 ppm
Fire		
No fire		•

Mechanistic Modelling Approach

Advantages:

- Wide range of variables and processes.
- Predictions under novel conditions.
- Enables complex interactions.
- Ask questions at spatial and temporal scales not feasible in the real world.

Mechanistic Modelling Approach

Disadvantages:

- Challenging to obtain data to test model accuracy.
- Difficult to model unexpected evolutionary scenarios (e.g. effects of keystone species).
- Limited plant growth forms (e.g. no succulents).
- Many parameters, some poorly estimated or constrained.

Approaches

Category	Sub-category
Field observations	
Correlative approach	Tightly-linked
	Loosely-linked
Experimental approach	Field-based: *ad hoc*
	Field-based: manipulation
	Common garden
	Greenhouse
	Laboratory
Mechanistic modelling	
Phylogenetic approach	

Phylogenetic Approach

- Recent addition to the biome boundary toolbox.
- Well-sampled and dated molecular phylogenies.

Phylogenetic Approach

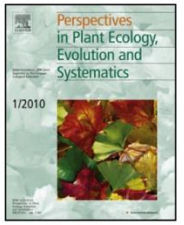
- Origins of biomes
- Phylogenetic niche conservatism
- Evolution of traits and diversification across boundaries
- Phylogenetically-controlled comparisons

PHYLOGENETIC APPROACH

Contents lists available at ScienceDirect

Perspectives in Plant Ecology, Evolution and Systematics

journal homepage: www.elsevier.com/locate/ppees



Research article

Diversification rate shifts in the Cape Floristic Region: The right traits in the right place at the right time

Renske E. Onstein*, Richard J. Carter, Yaowu Xing, H. Peter Linder

PHYLOGENETIC APPROACH

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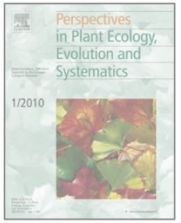
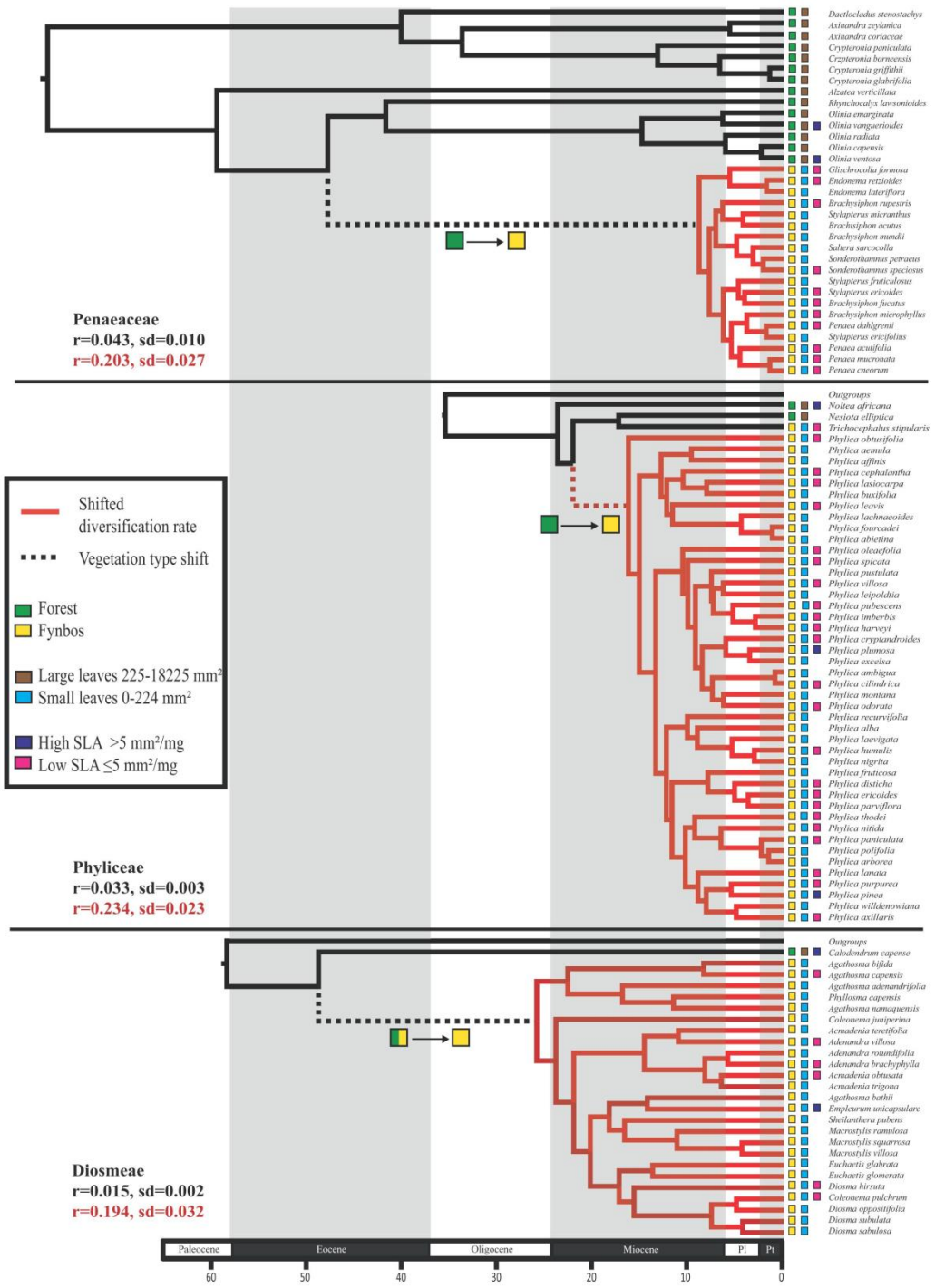


Research article

Diversification rate shifts in the Cape Floristic Region: The right traits in the right place at the right time

Renske E. Onstein*, Richard J. Carter, Yaowu Xing, H. Peter Linder

What happens to lineages when they shift between biomes?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r=0.234, sd=0.023
Diosmeae
r=0.015, sd=0.002
r=0.194, sd=0.032
Shifted diversification rate
Vegetation type shift
Forest
Fynbos
Large leaves 225-18225 mm²
Small leaves 0-224 mm²
High SLA >5 mm²/mg
Low SLA ≤5 mm²/mg
Paleocene
Eocene
Oligocene
Miocene
Pl
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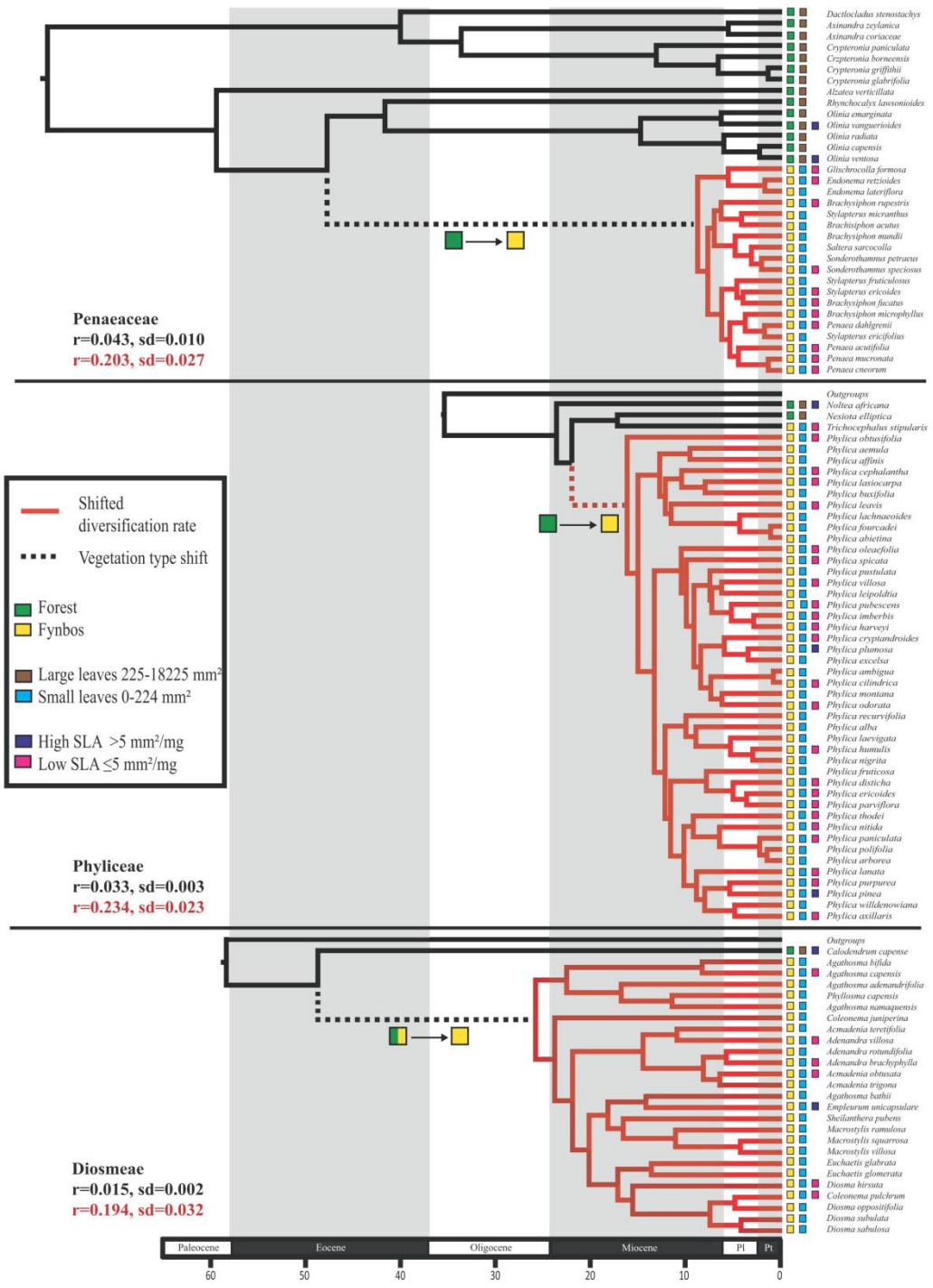
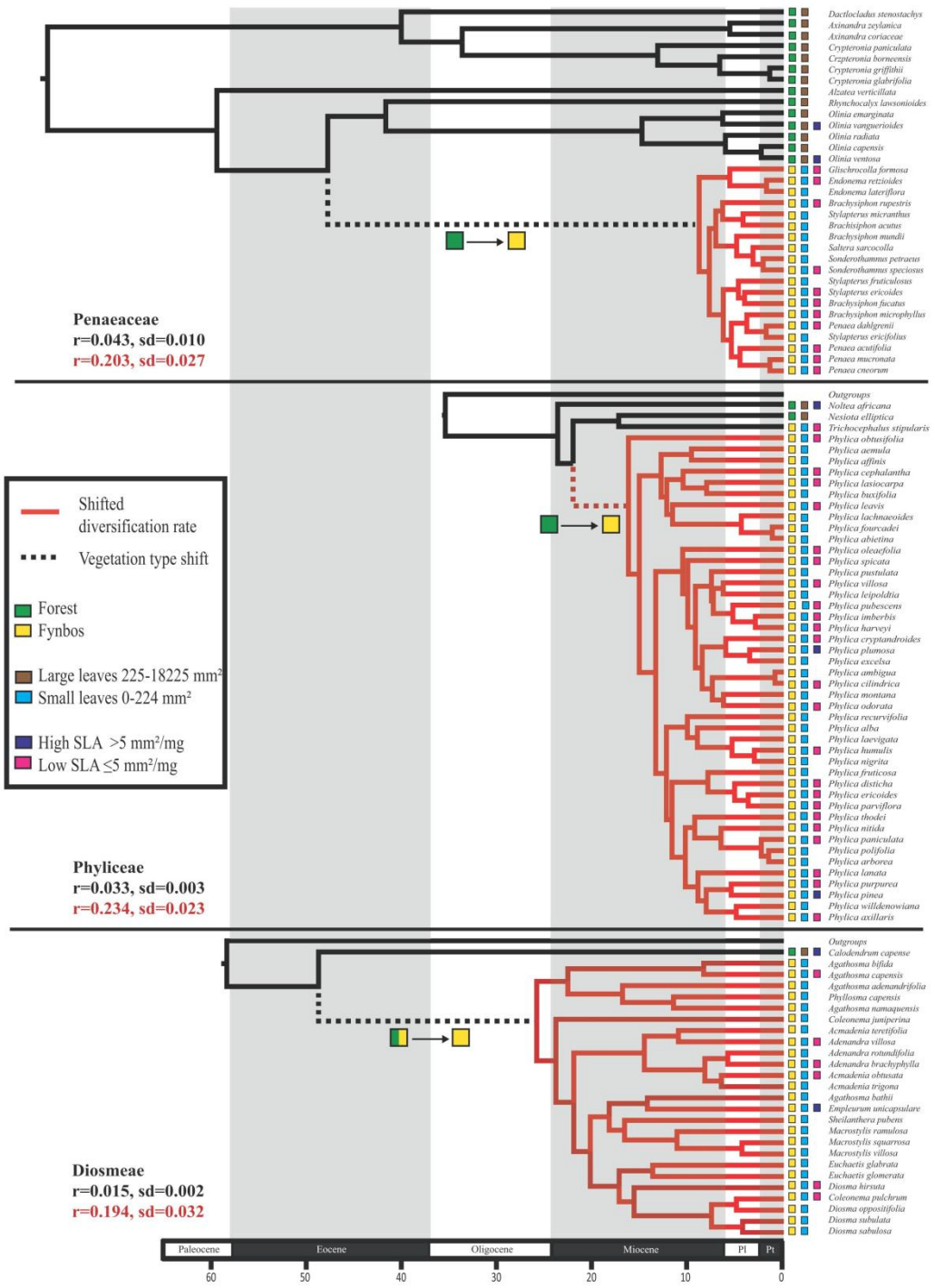
Constructed dated phylogenies of three clades that have species in Forest and Fynbos.



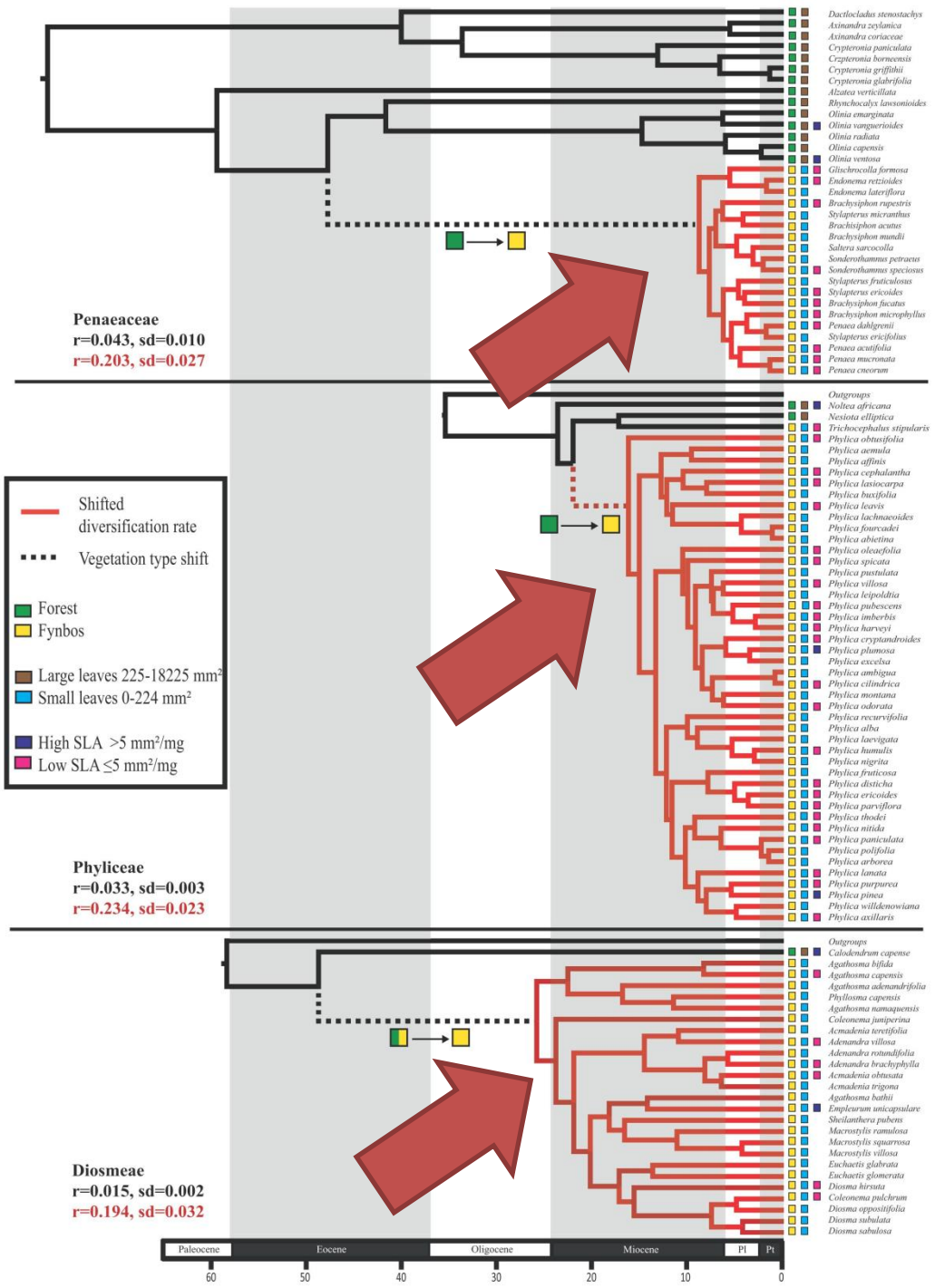
Penaeaceae

Phyliceae

Diosmeae



Fynbos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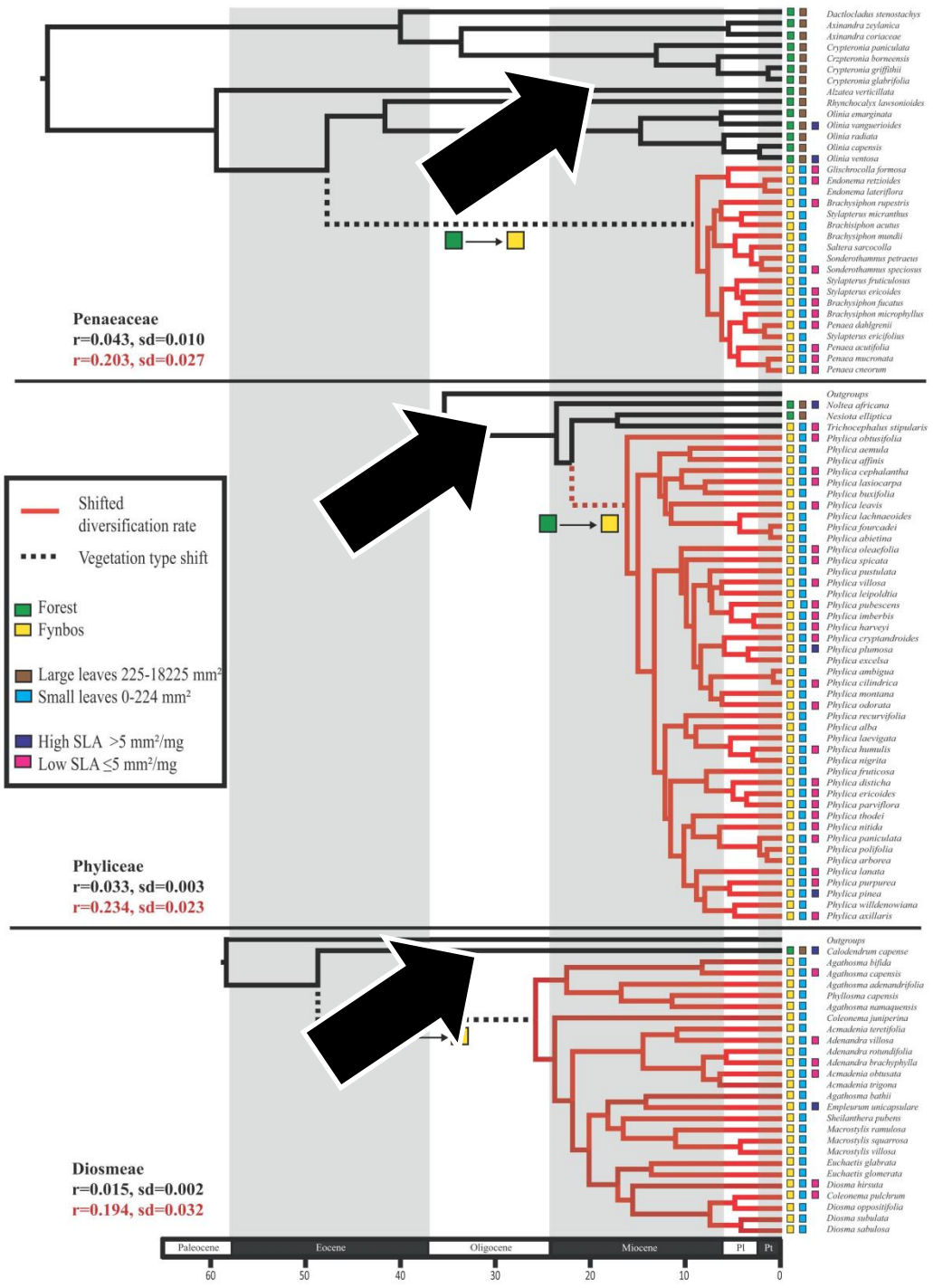
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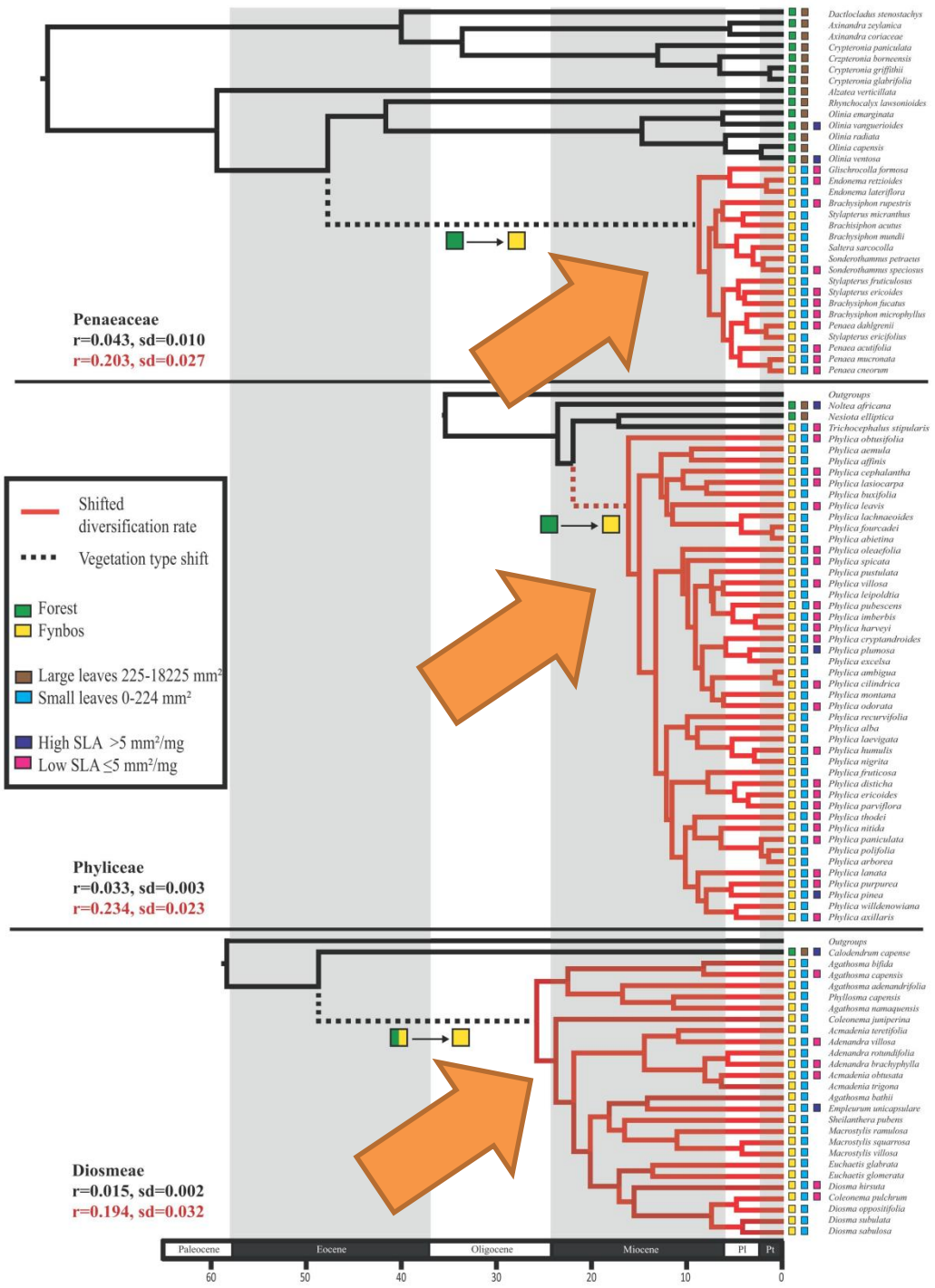
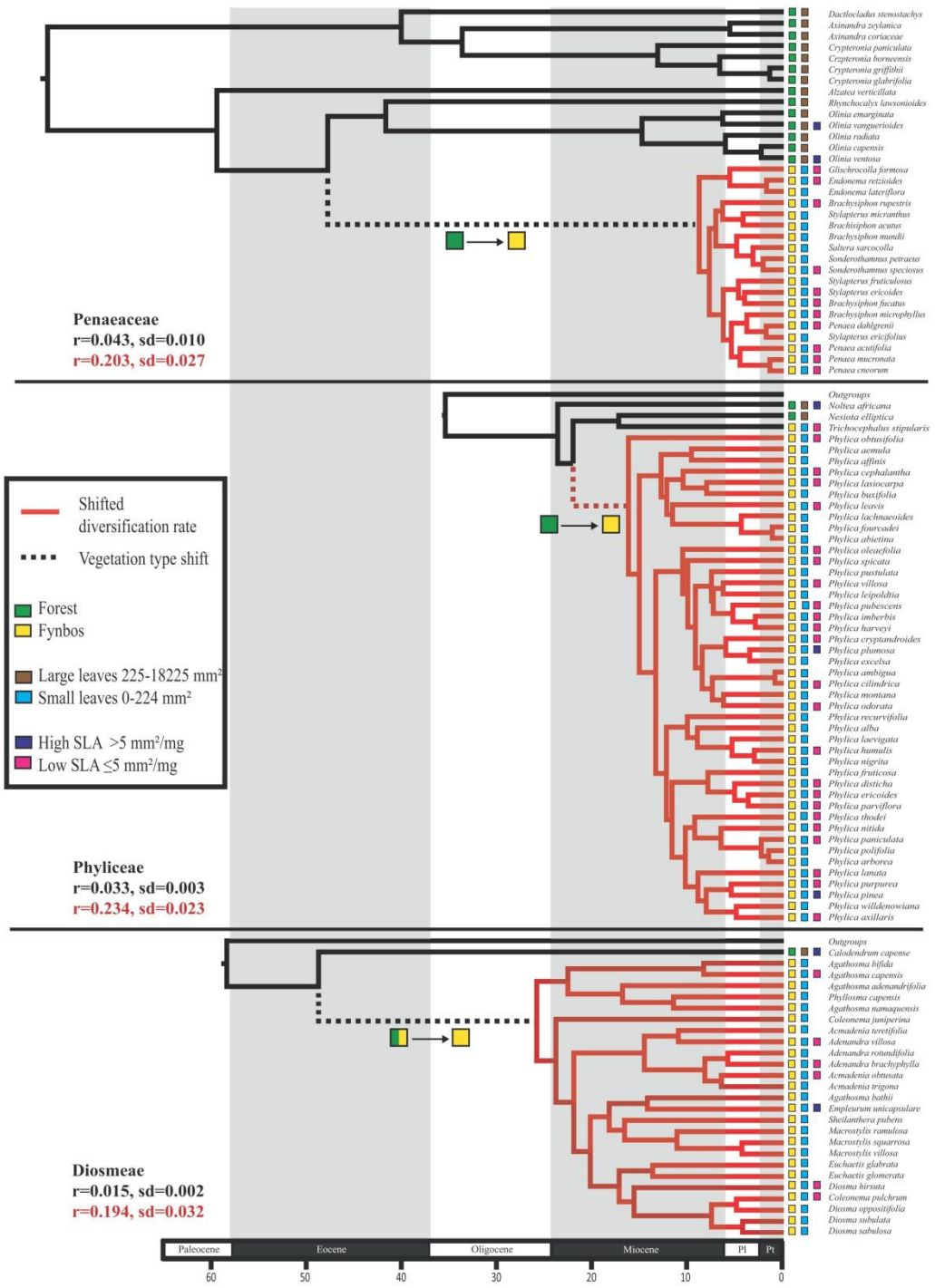
Higher diversification rate in Fynbos

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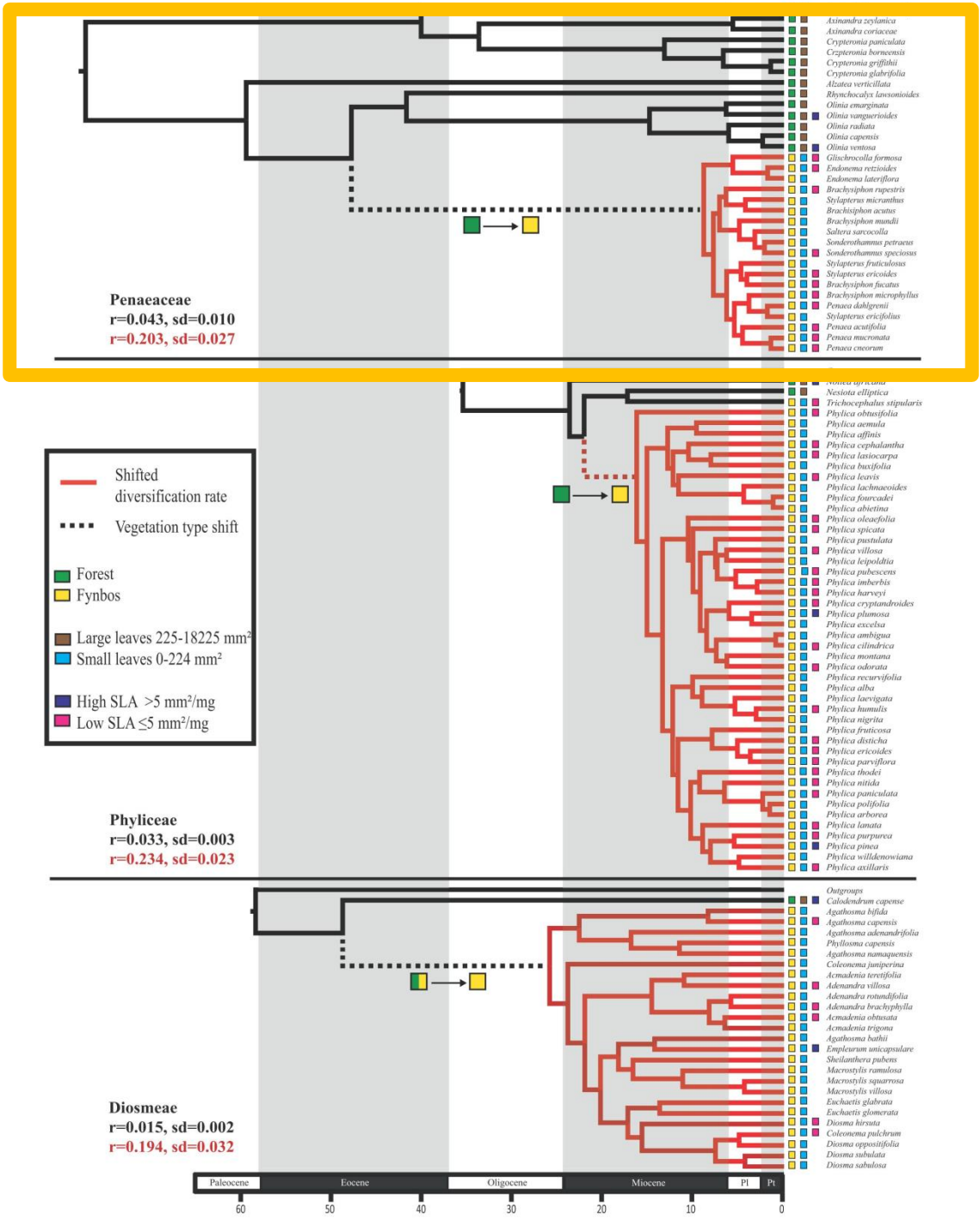
Penaeaceae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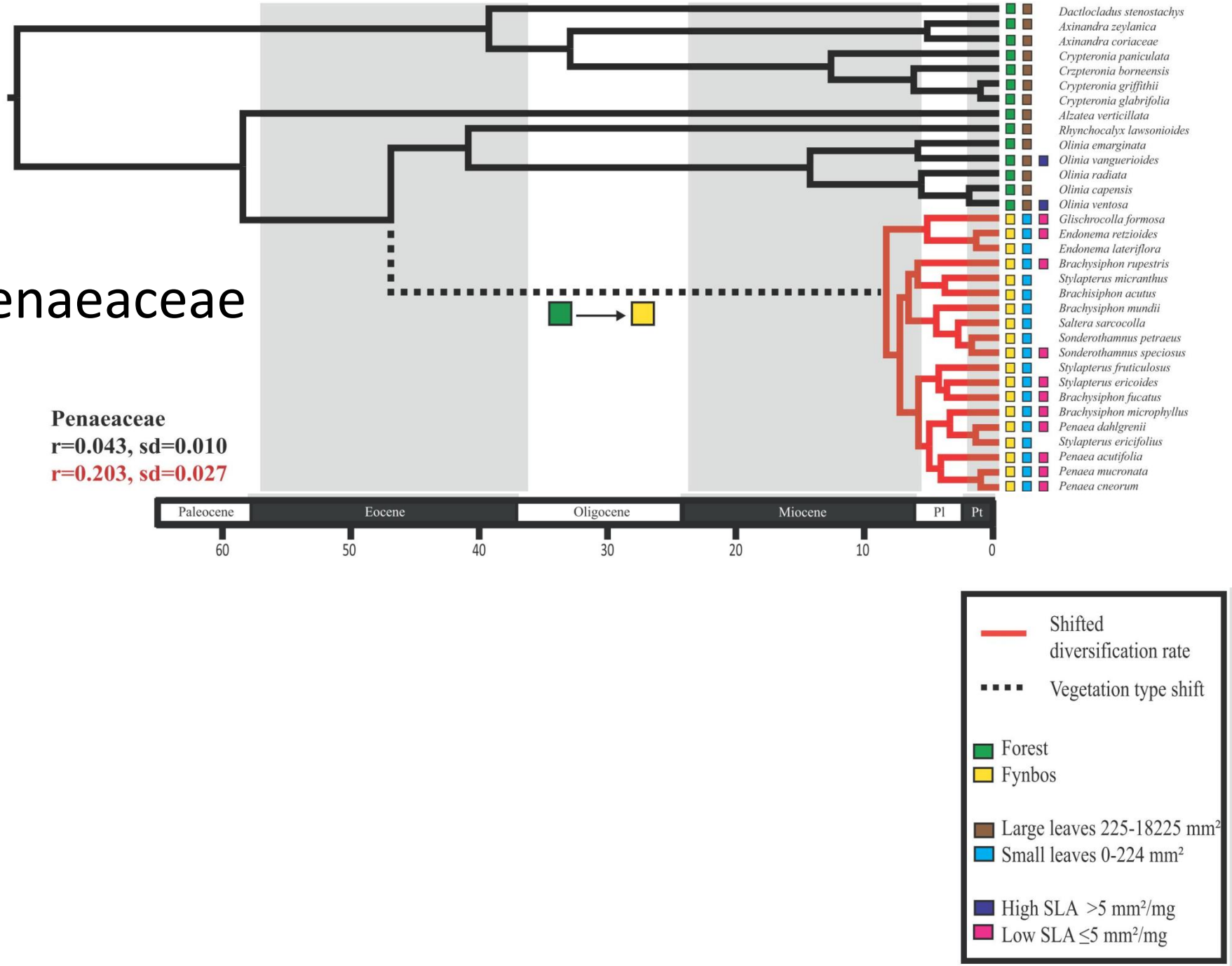
Penaeaceae



Shifted diversification rate

Vegetation type shift

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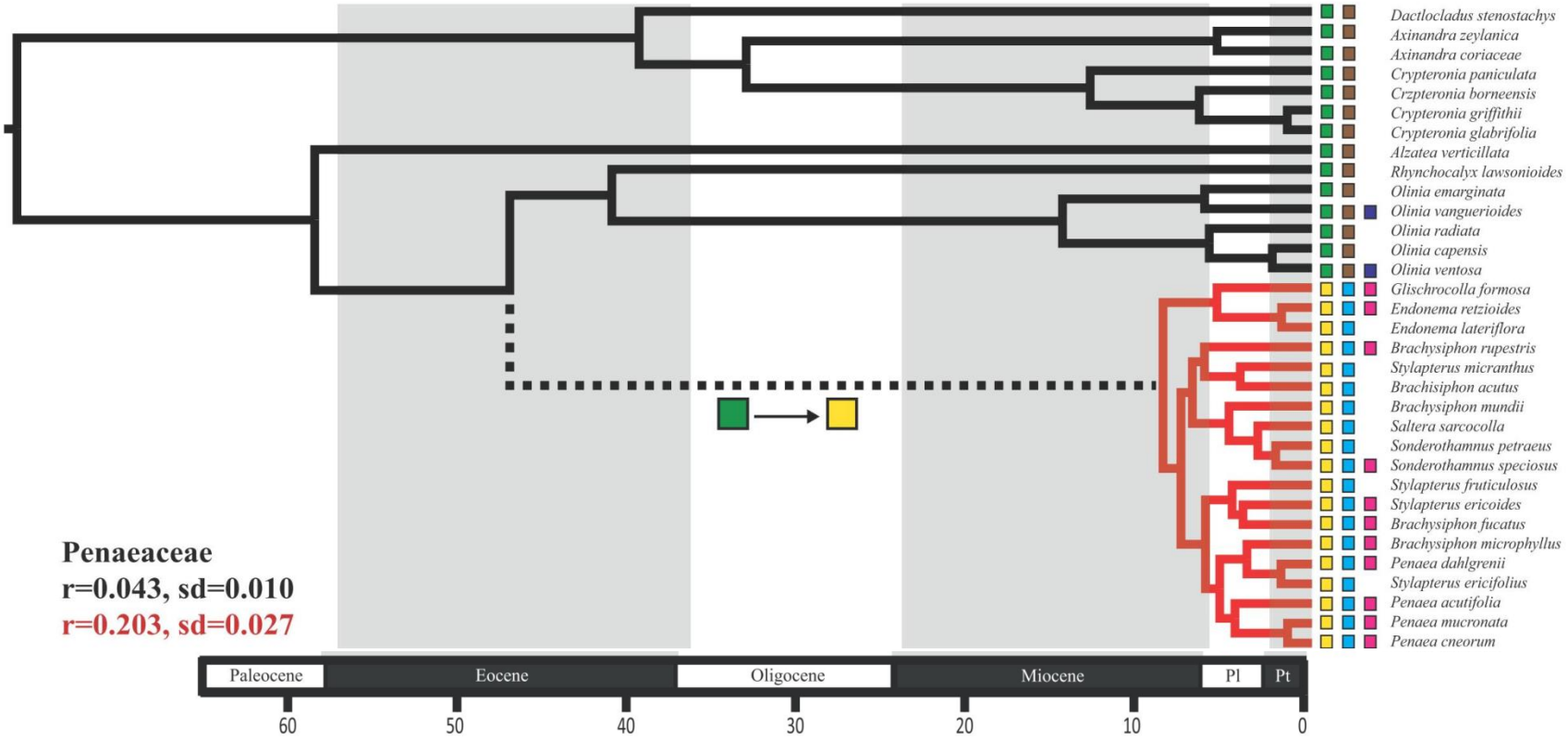
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Axinandra coriaceae
Crypteronia paniculata
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Crypteronia griffithii
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Alzatea verticillata
Rhynchocalyx lawsonioides
Olinia emarginata
Olinia vanguerioides
Olinia radiata
Olinia capensis
Olinia ventosa
Glischrocolla formosa
Endonema retzioides
Endonema lateriflora
Brachysiphon rupestris
Stylapterus micranthus
Brachisiphon acutus
Brachysiphon mundii
Saltera sarcocolla
Sonderothamnus petraeus
Sonderothamnus speciosus
Stylapterus fruticulosus
Stylapterus ericoides
Brachysiphon fucatus
Brachysiphon microphyllus
Penaea dahlgrenii
Stylapterus ericifolius
Penaea acutifolia
Penaea mucronata
Penaea cneorum
Penaeaceae
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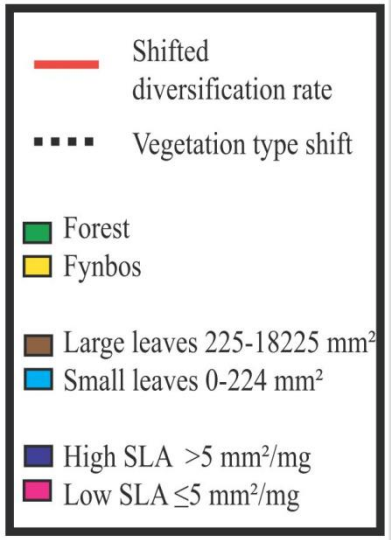
Leaf size?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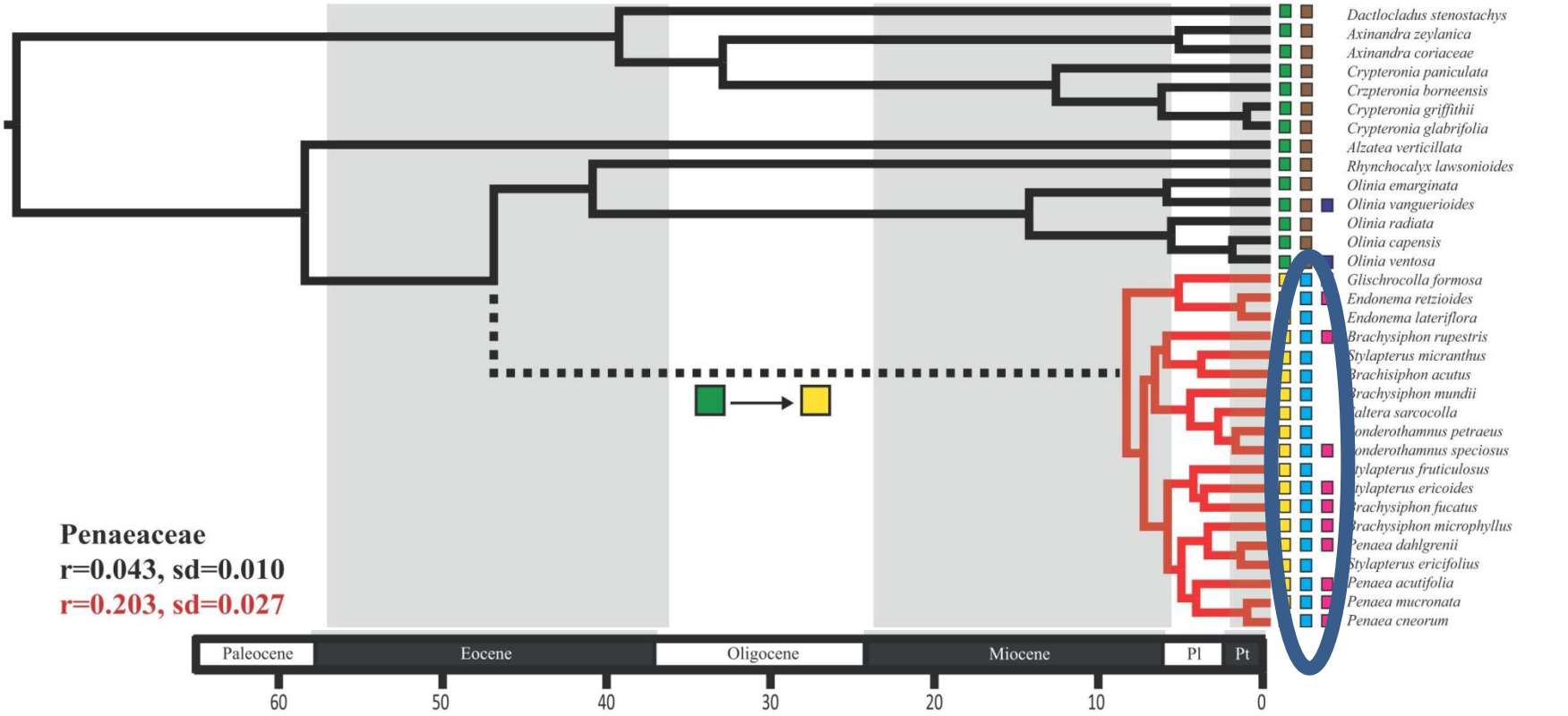
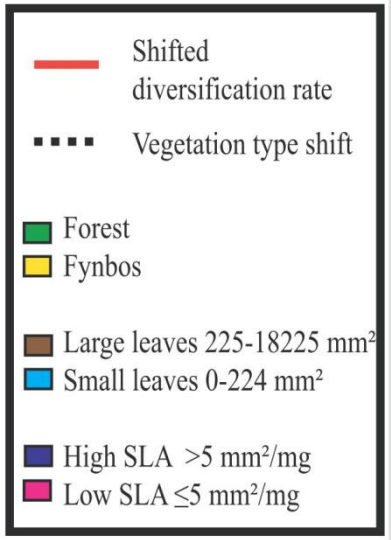
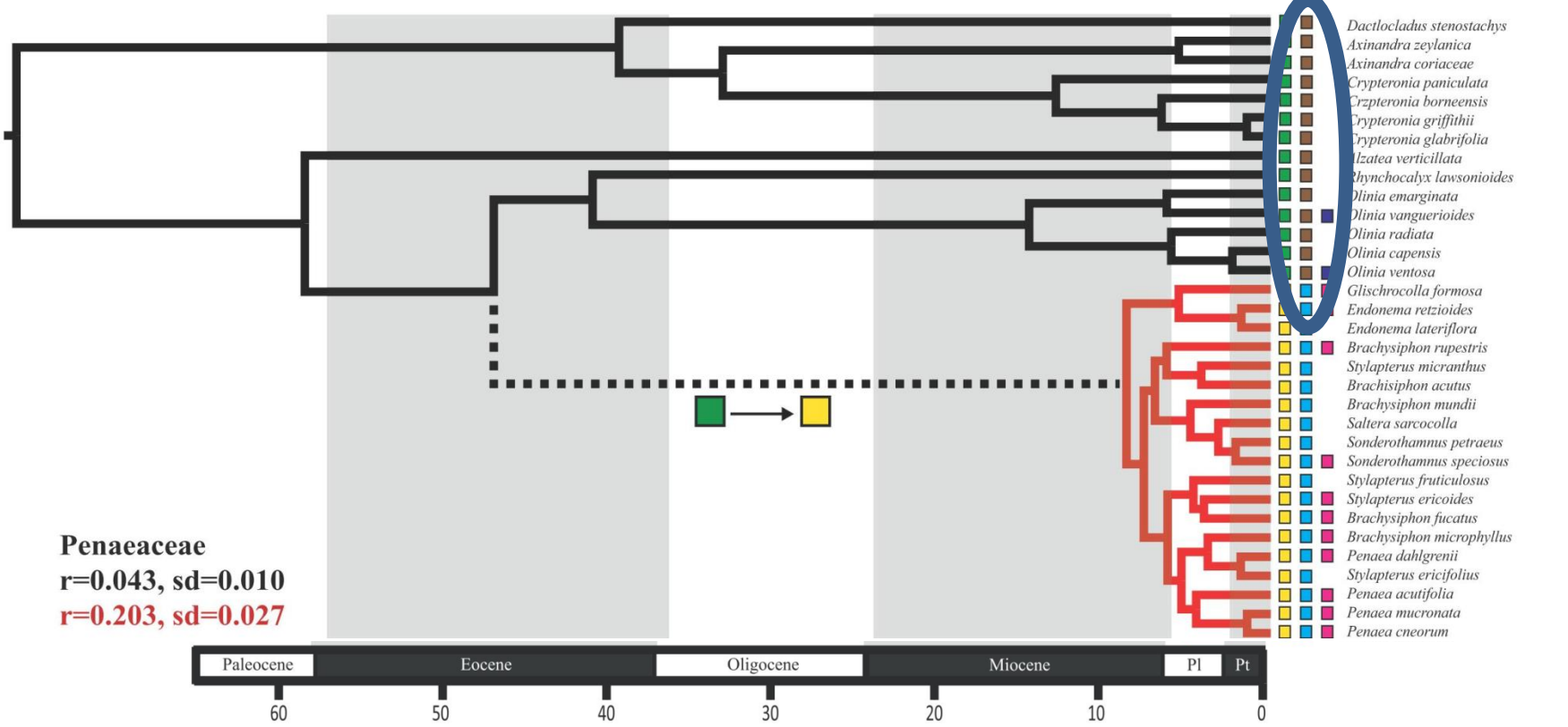


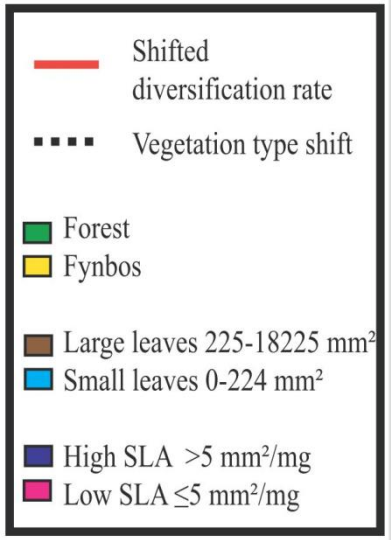
Small leaves in Fynbos species



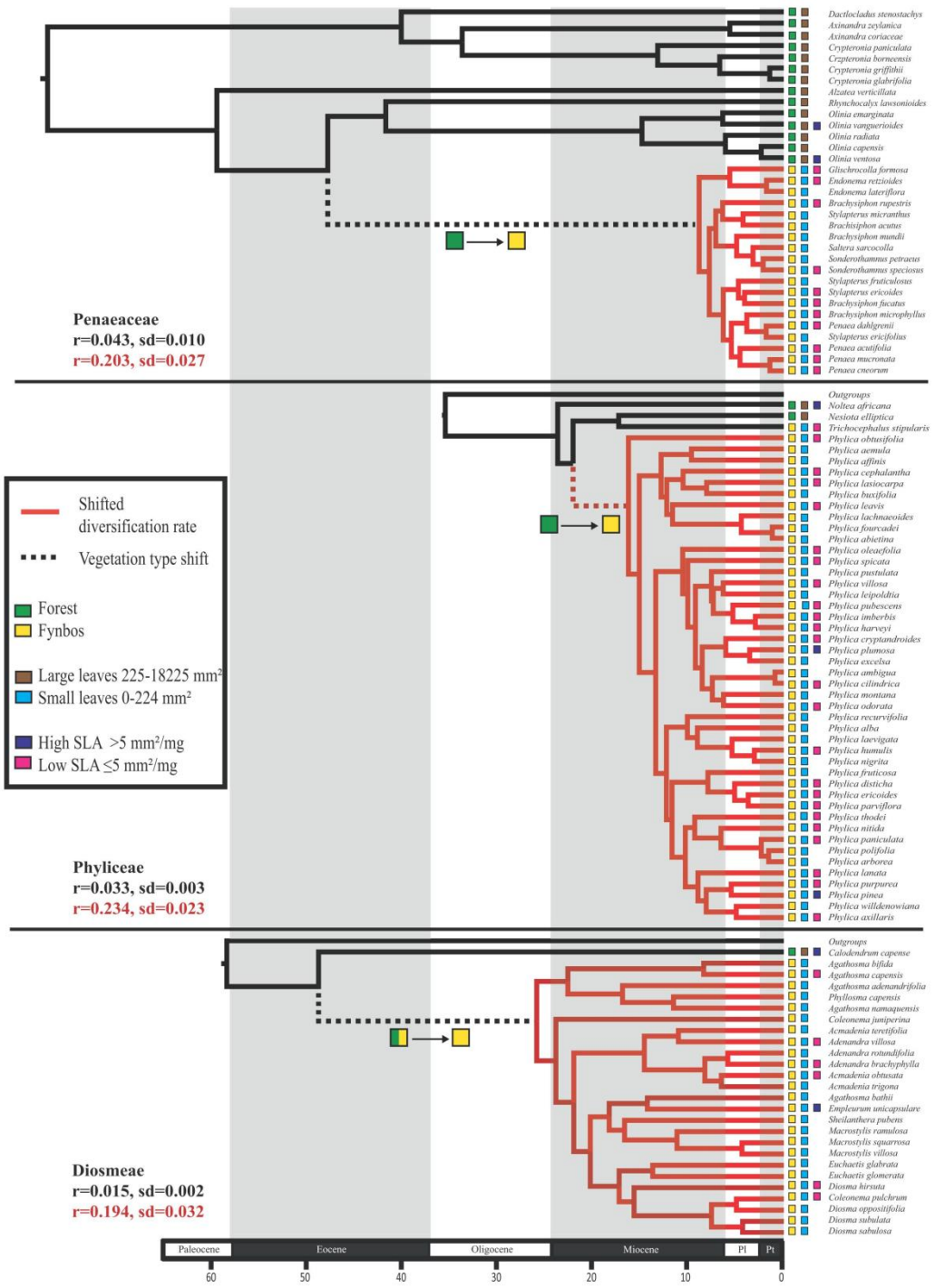


Small leaves in Fynbos species

Large leaves in Forest species



Shift in leaf size across all clades



Phylogenetic Approach

09h45
Nasiphi Ntshanga

Transitions of southern African plant lineages between biomes

Phylogenetic Approach

Advantages:

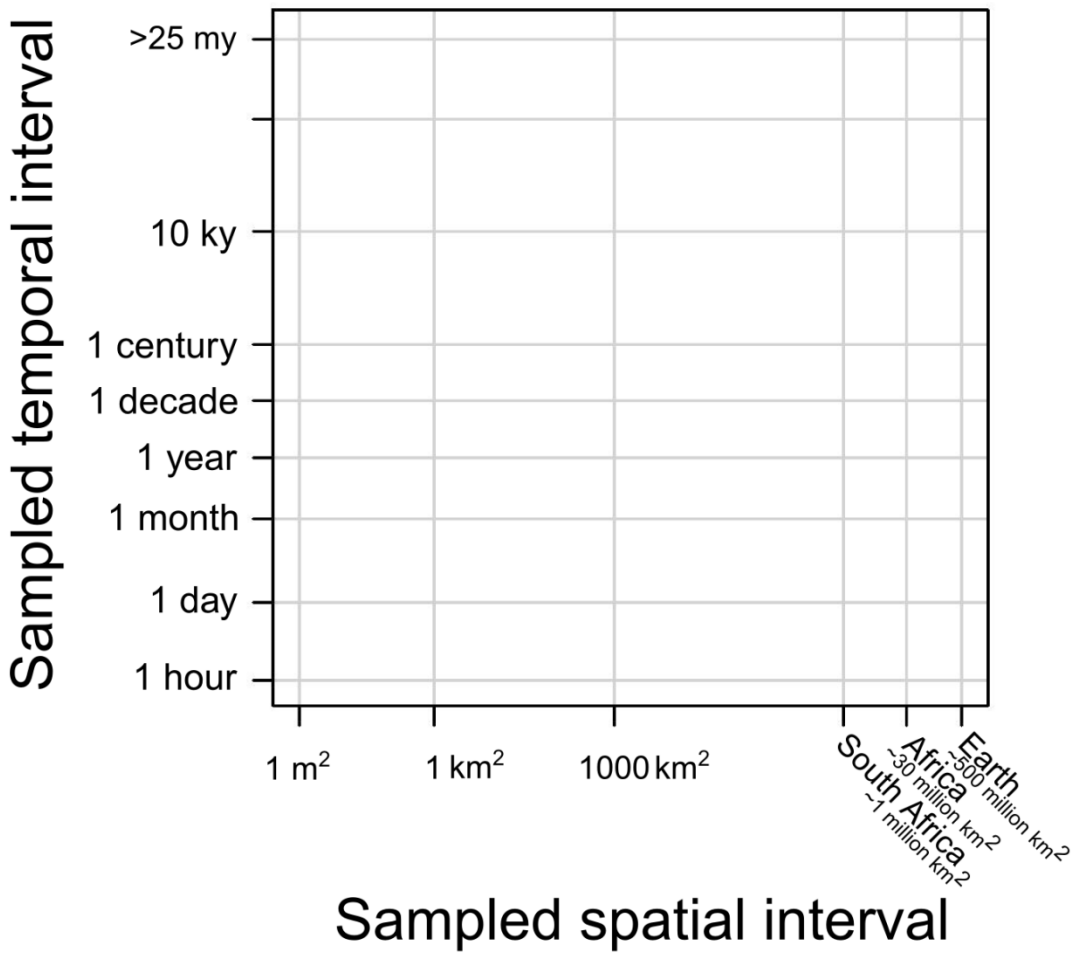
- Evolutionary and deep-time perspectives on biome:
  - Origins, assembly, trait evolution.
- Determine the strength of boundaries over evolutionary time (i.e. biome conservatism)
- Incorporate evolutionary relationships into analyses (e.g. phylogenetically independent contrasts)

Phylogenetic Approach

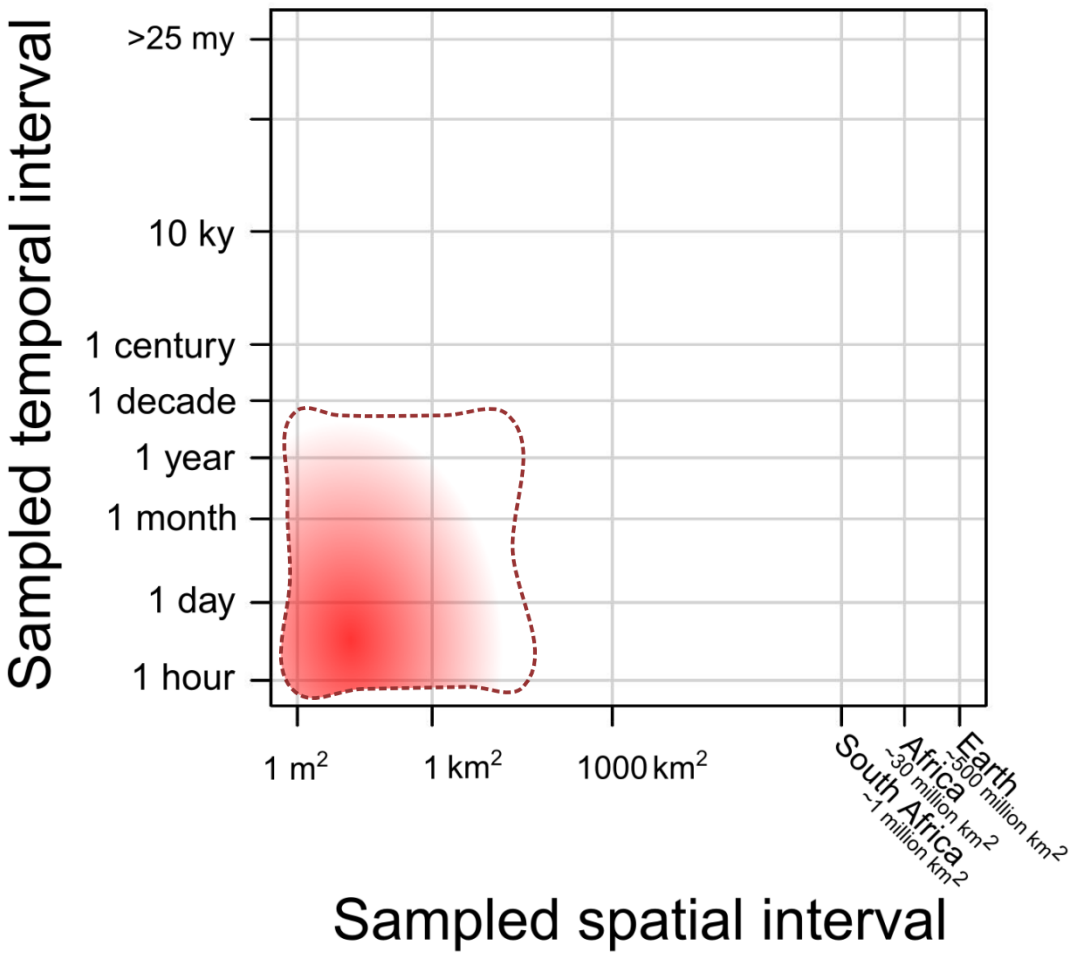
Disadvantages:

- Requires ***well-sampled*** phylogenies
- Unlikely to identify the causal driver/s of the boundary.

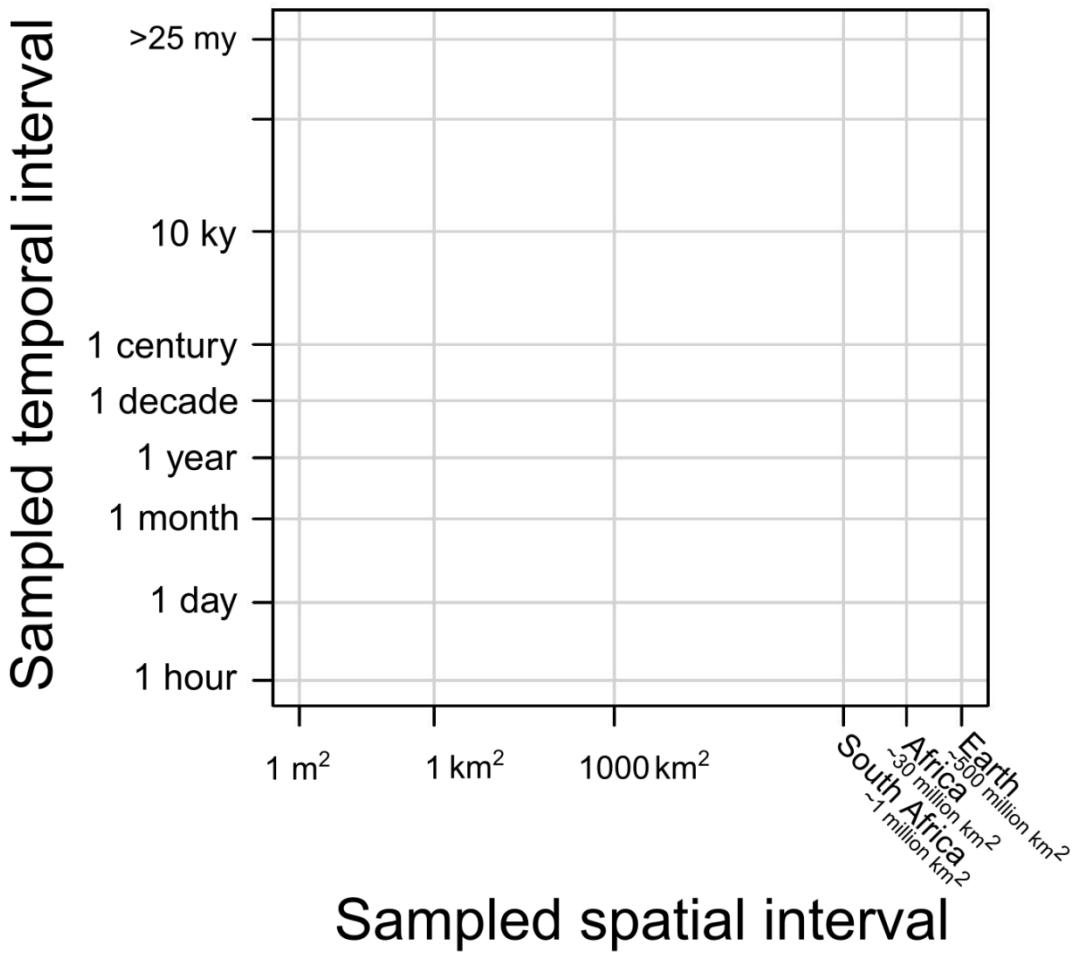
Approaches in Space & Time


Sampled temporal interval
>25 my
10 ky
1 century
1 decade
1 year
1 month
1 day
1 hour
1 m2
1 km2
1000 km2
South Africa ~1 million km2
Africa ~30 million km2
Earth ~500 million km2
Sampled spatial interval

Field Observations

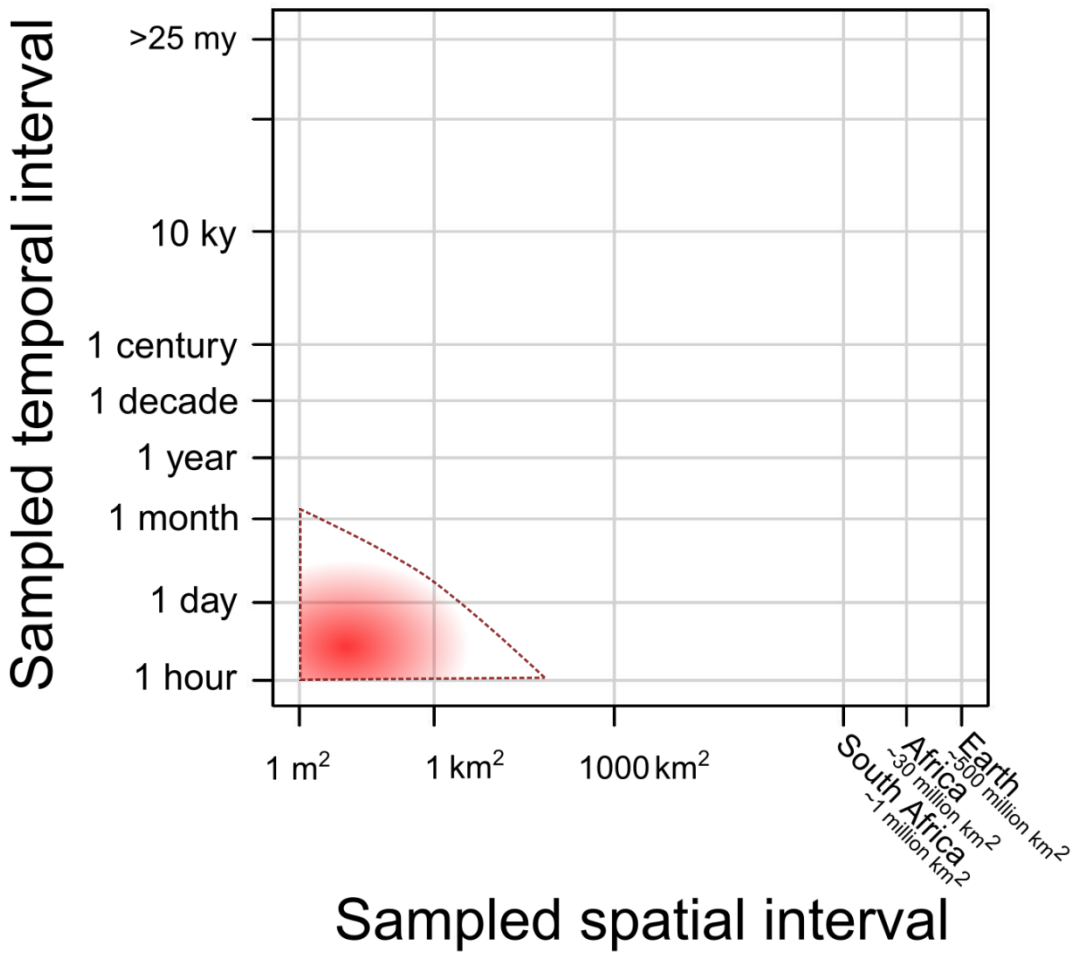


Correlative Approach



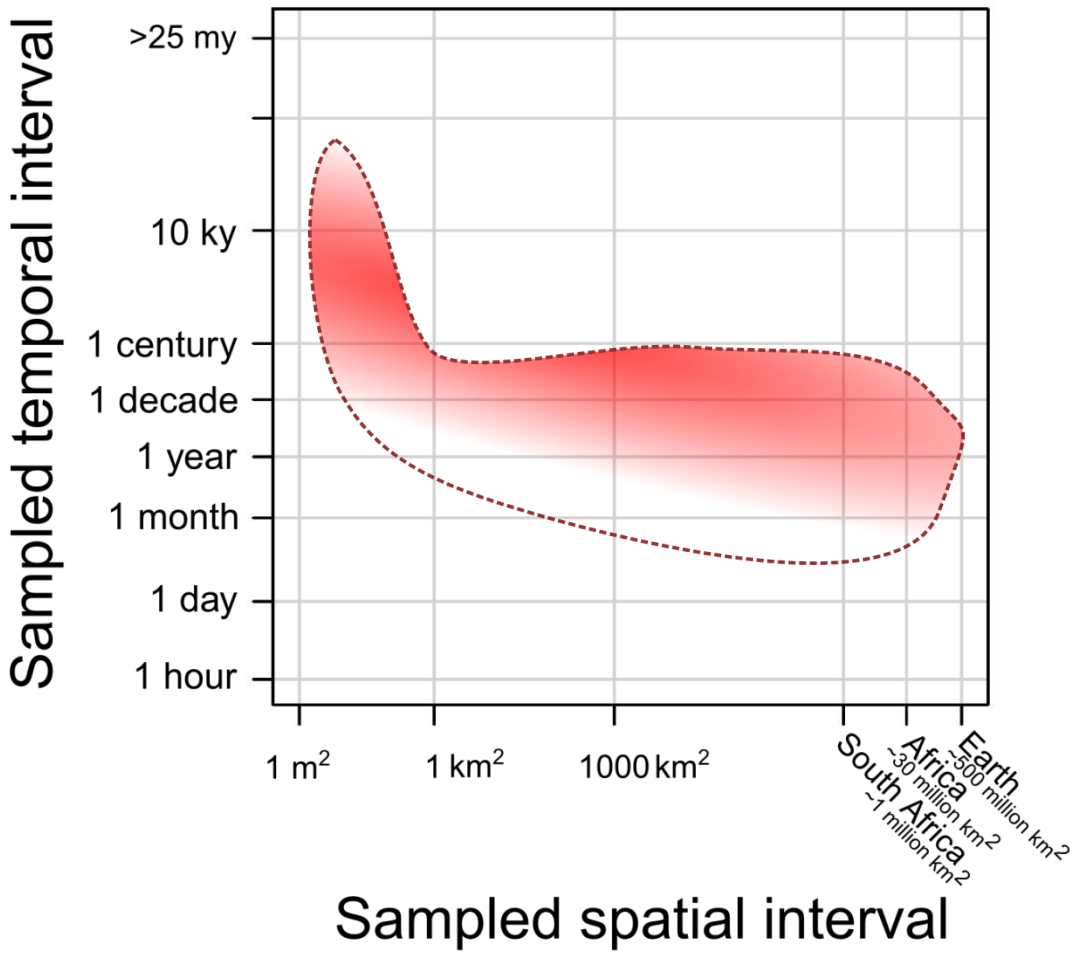
Correlative Approach

Tightly-Linked

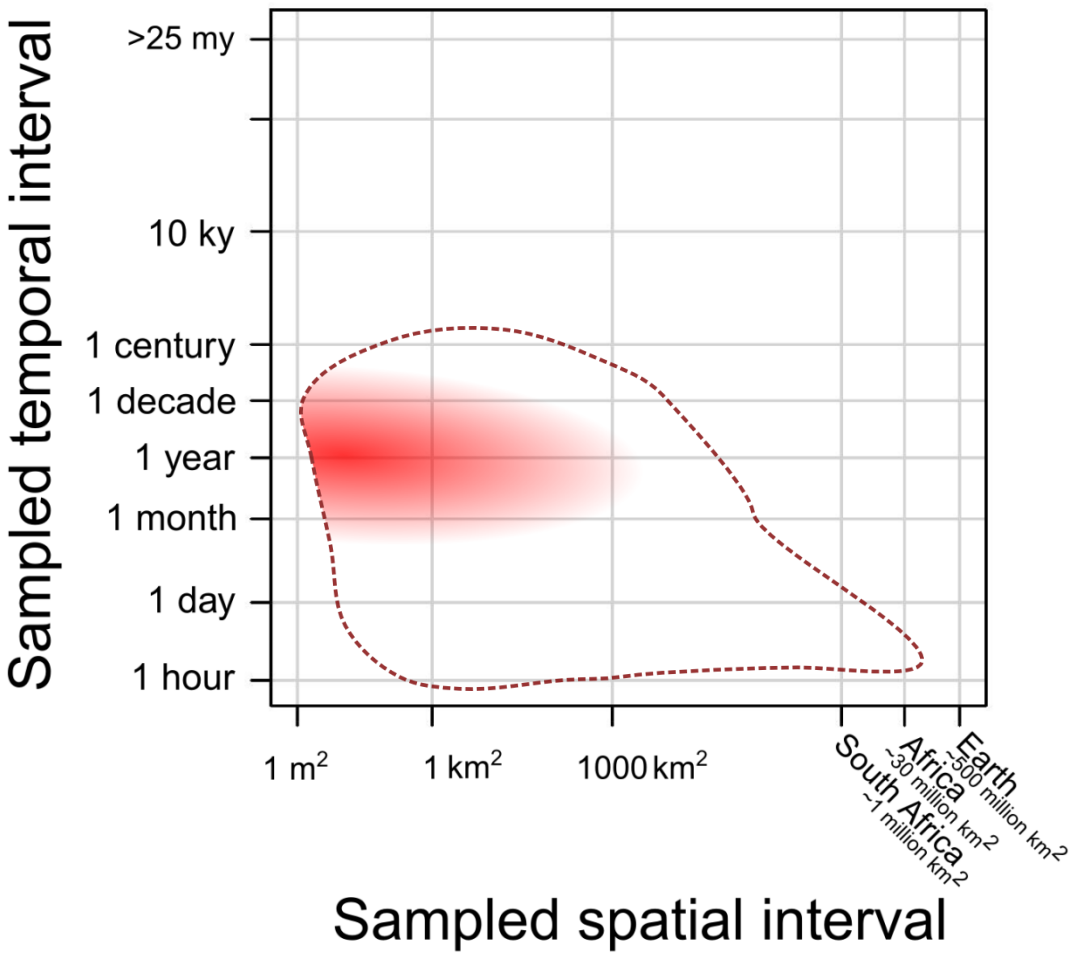


Correlative Approach

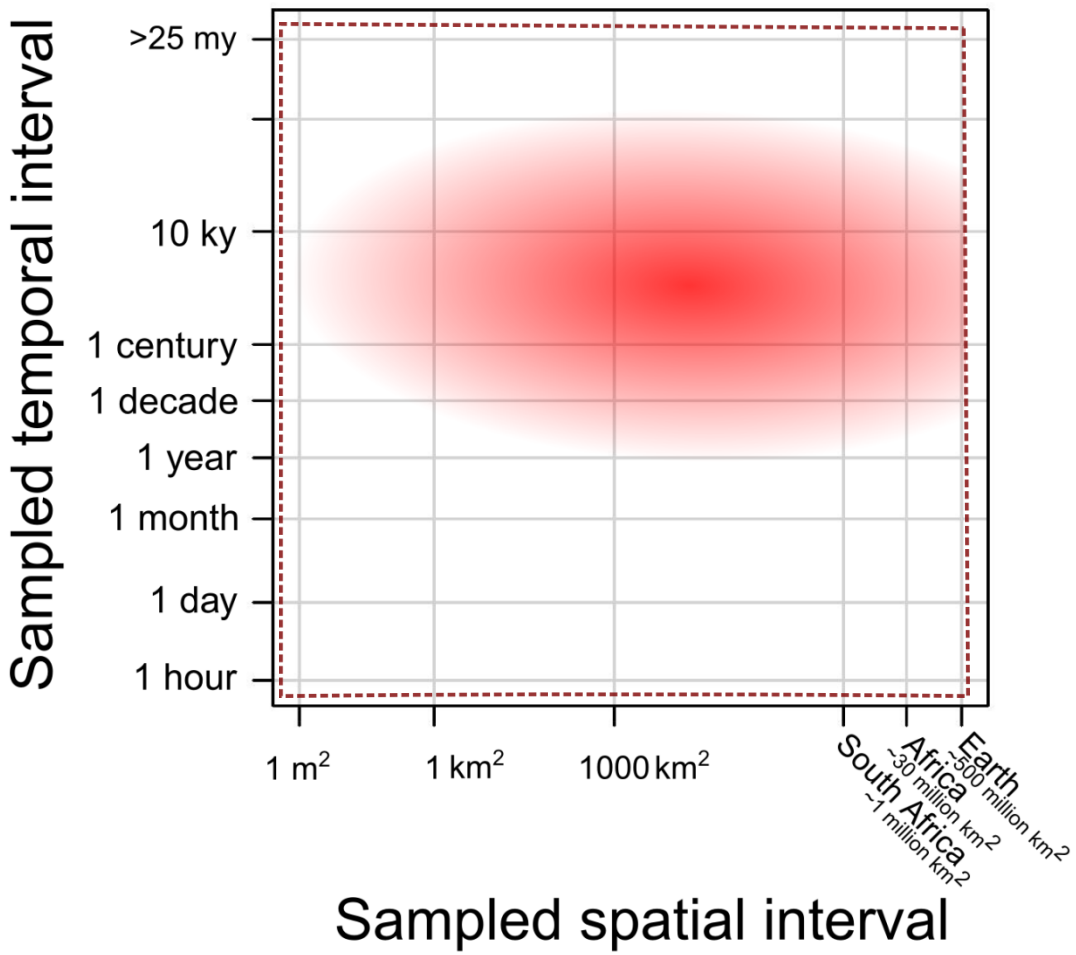
Loosely-Linked



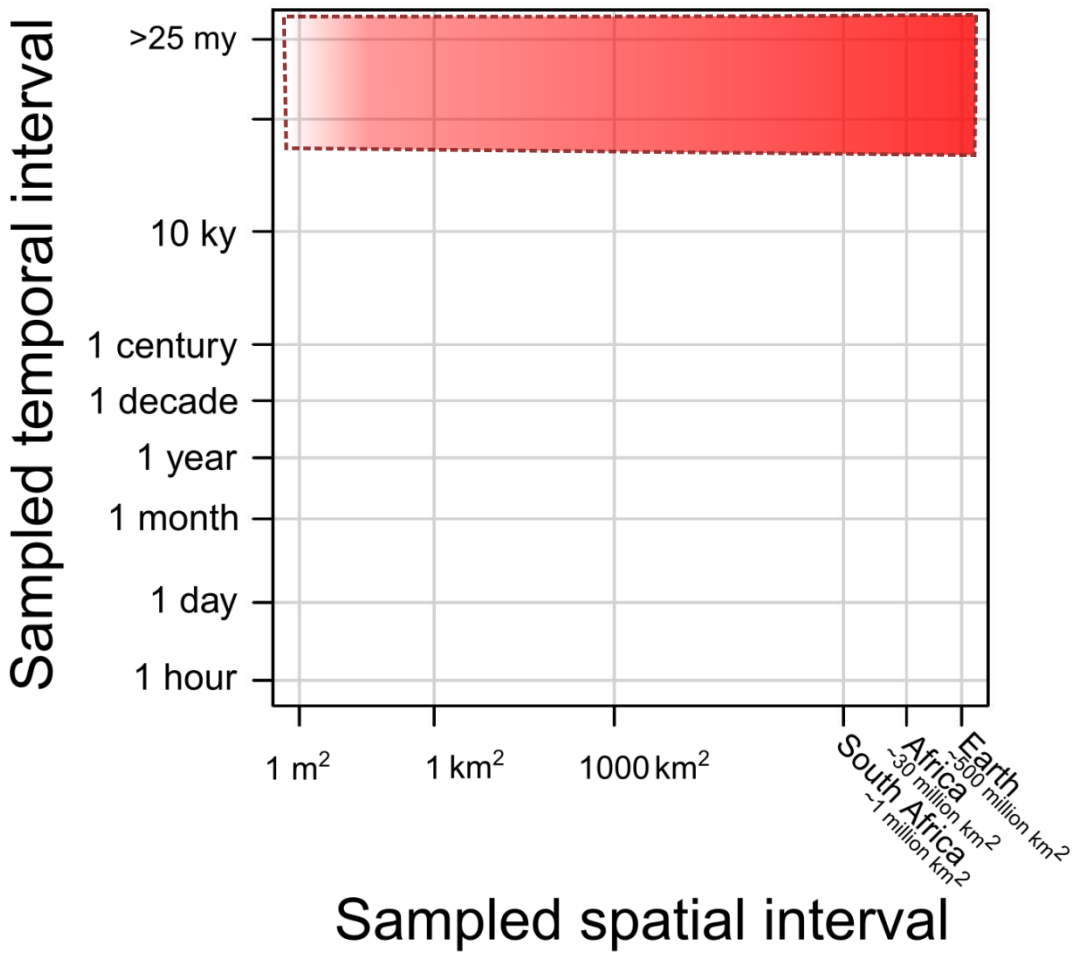
Experimental Approach



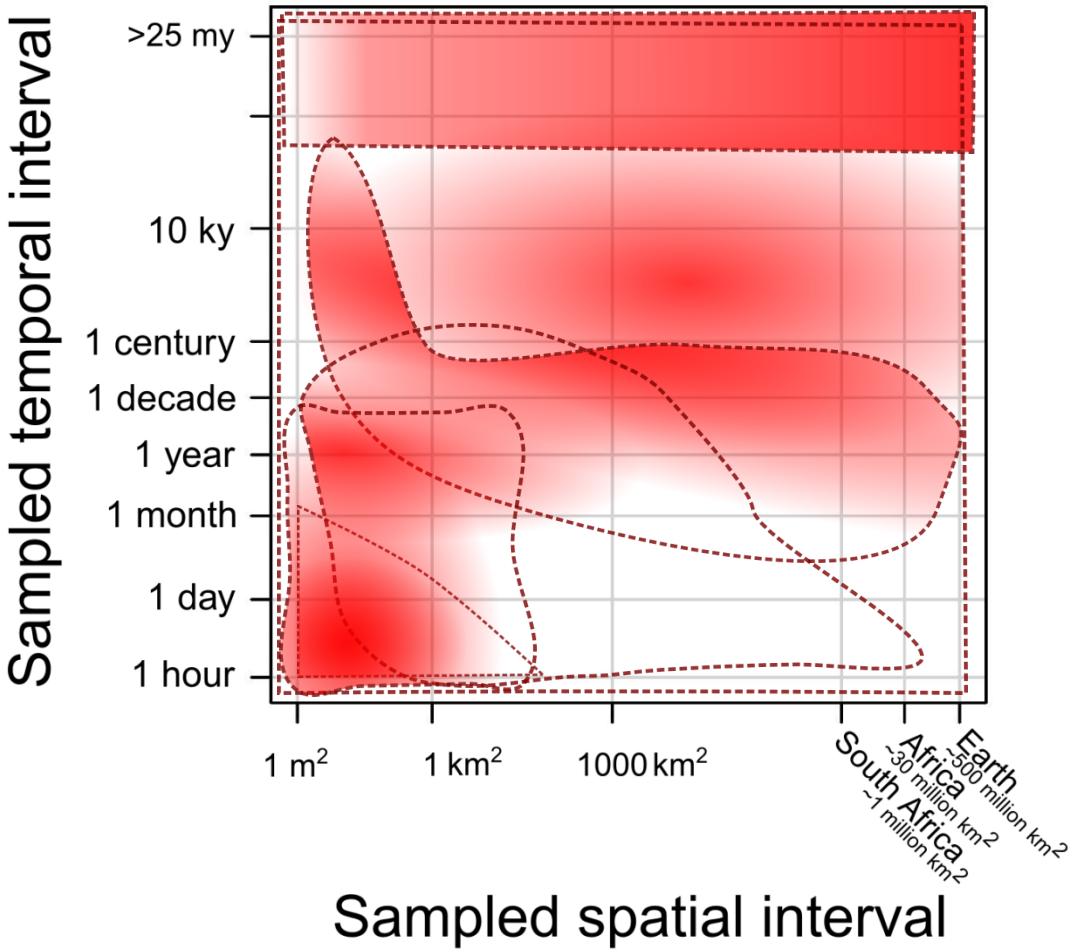
Mechanistic Modelling



Phylogenetic Approach



All Approaches



Links

between

Approaches

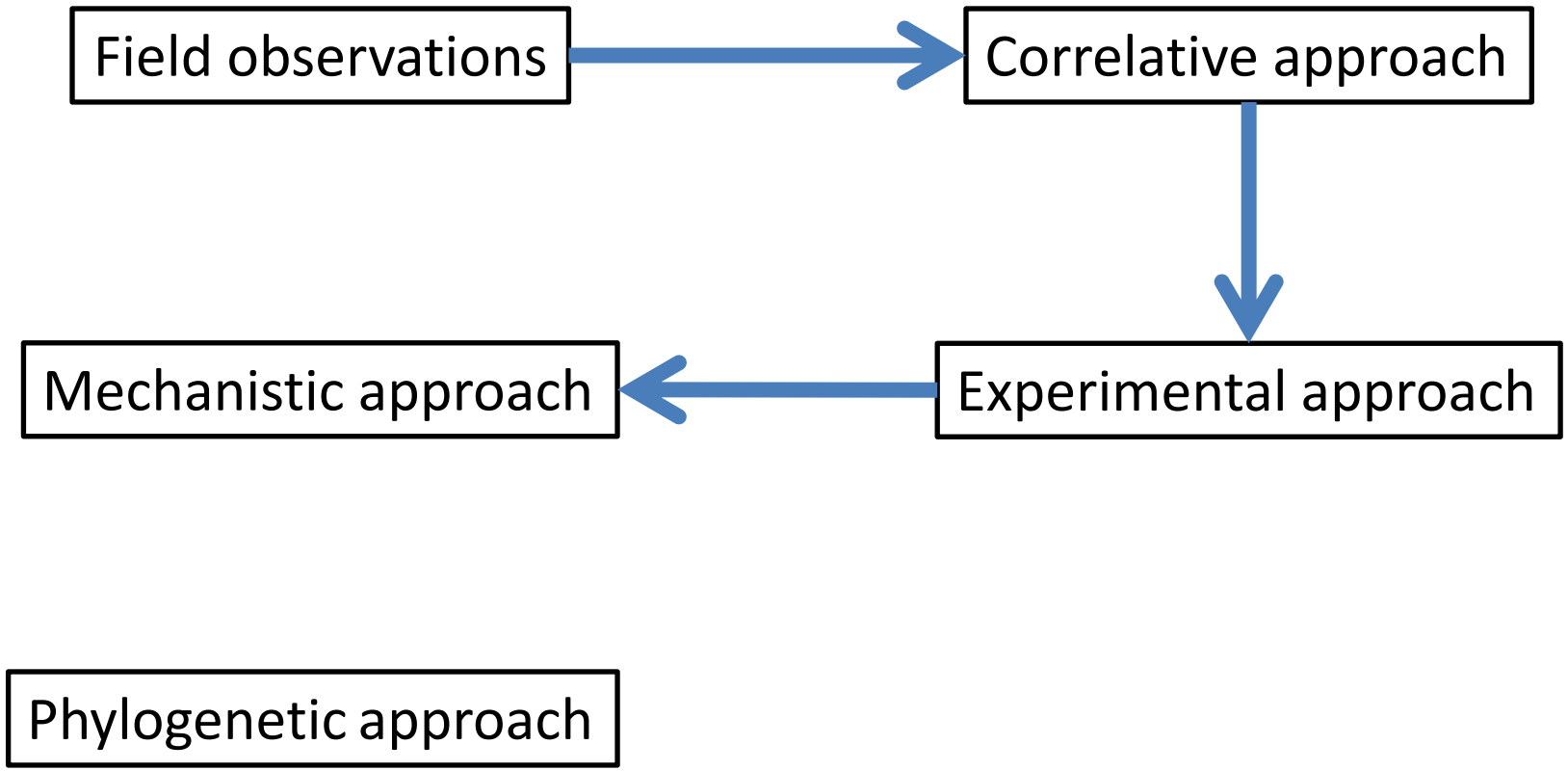
Field observations

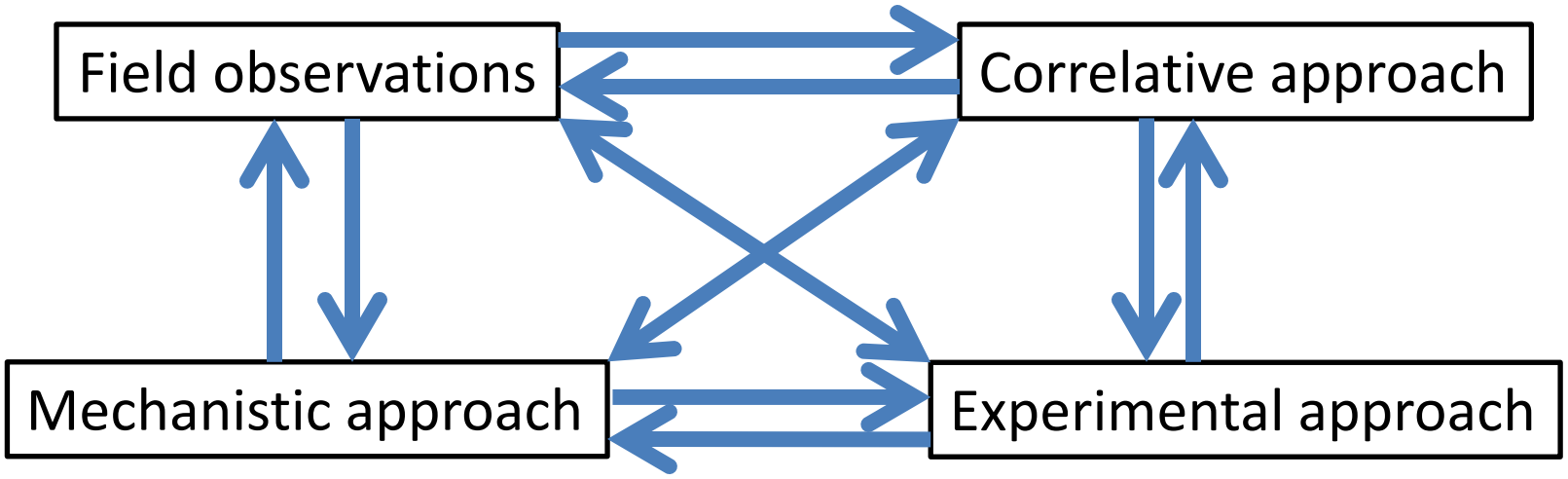
Correlative approach

Mechanistic approach

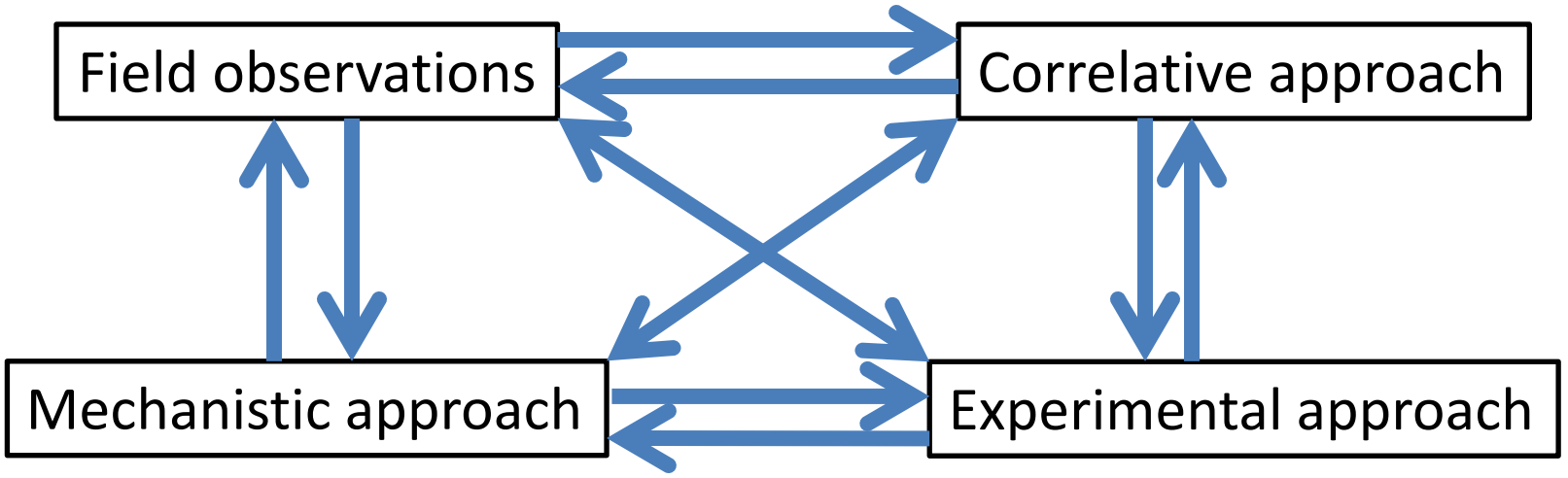
Experimental approach

Phylogenetic approach

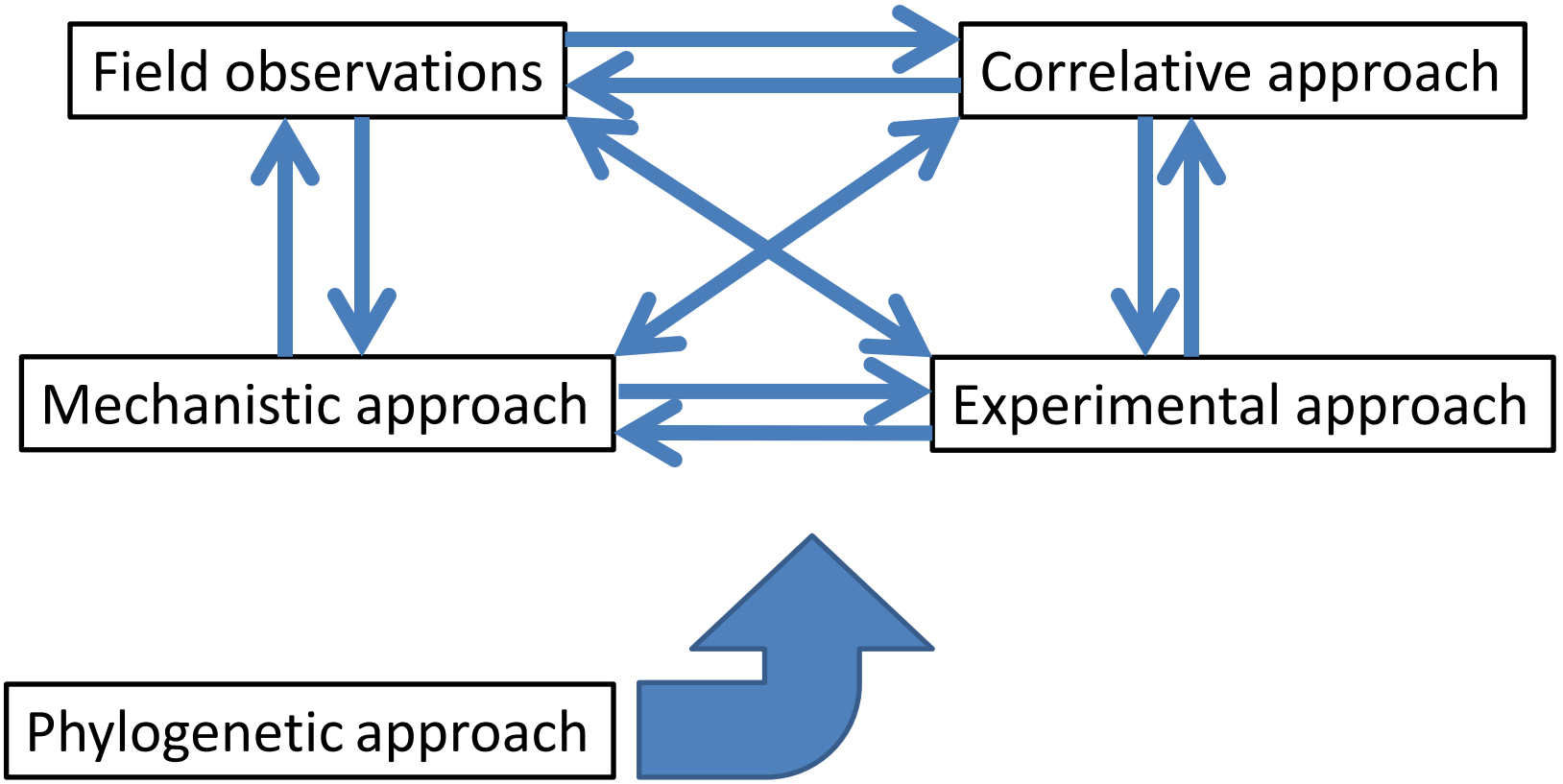

Field observations
Correlative approach
Experimental approach
Mechanistic approach
Phylogenetic approach

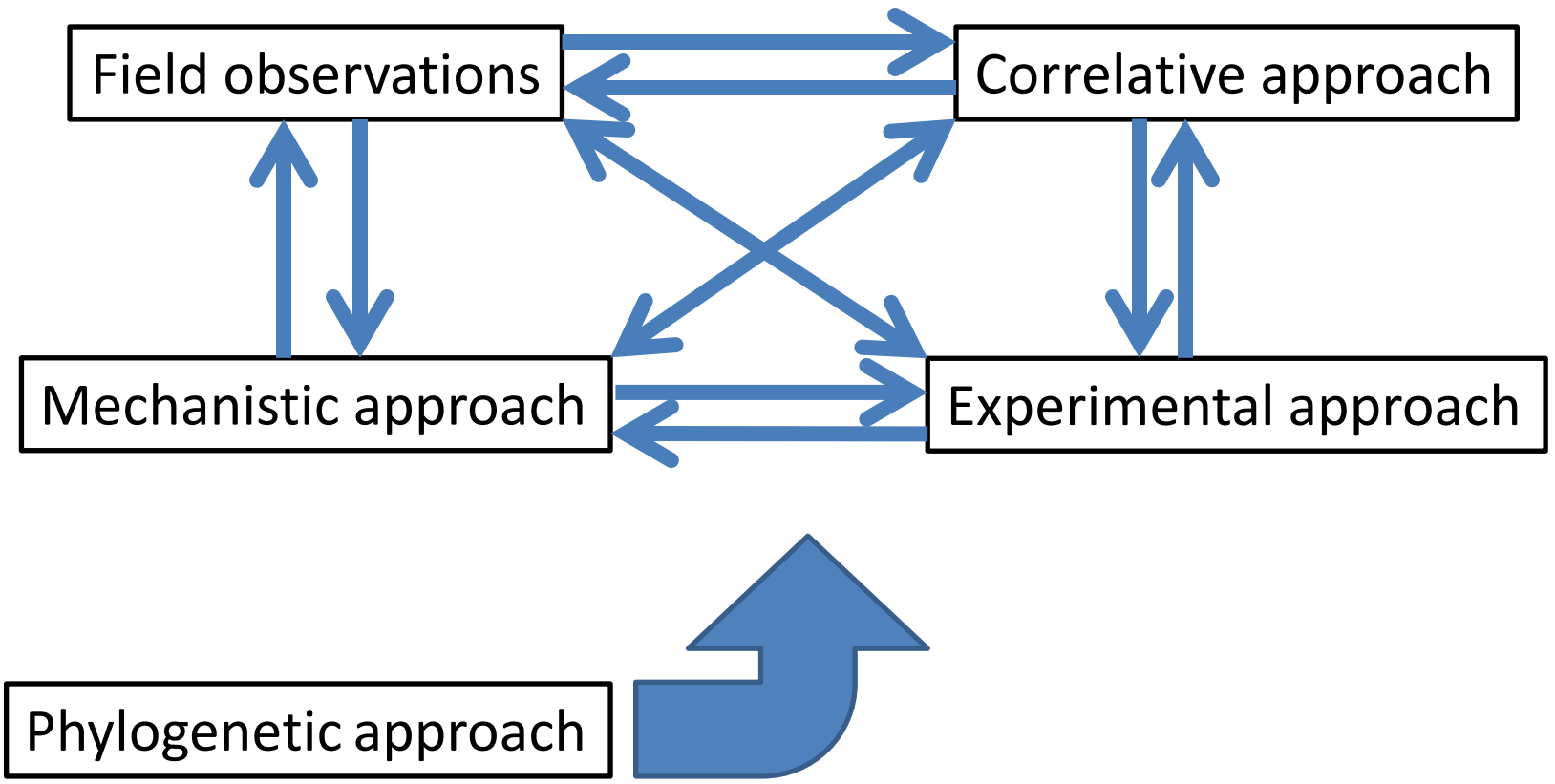


Phylogenetic approach



Phylogenetic approach ?


Field observations
Correlative approach
Mechanistic approach
Experimental approach
Phylogenetic approach


Field observations
Correlative approach
Mechanistic approach
Experimental approach
Phylogenetic approach

The End

"There is scarcely any biological task more attractive than that of determining the nature of the weapons by which plants oust each other from habitats"
(Warming, 1895)