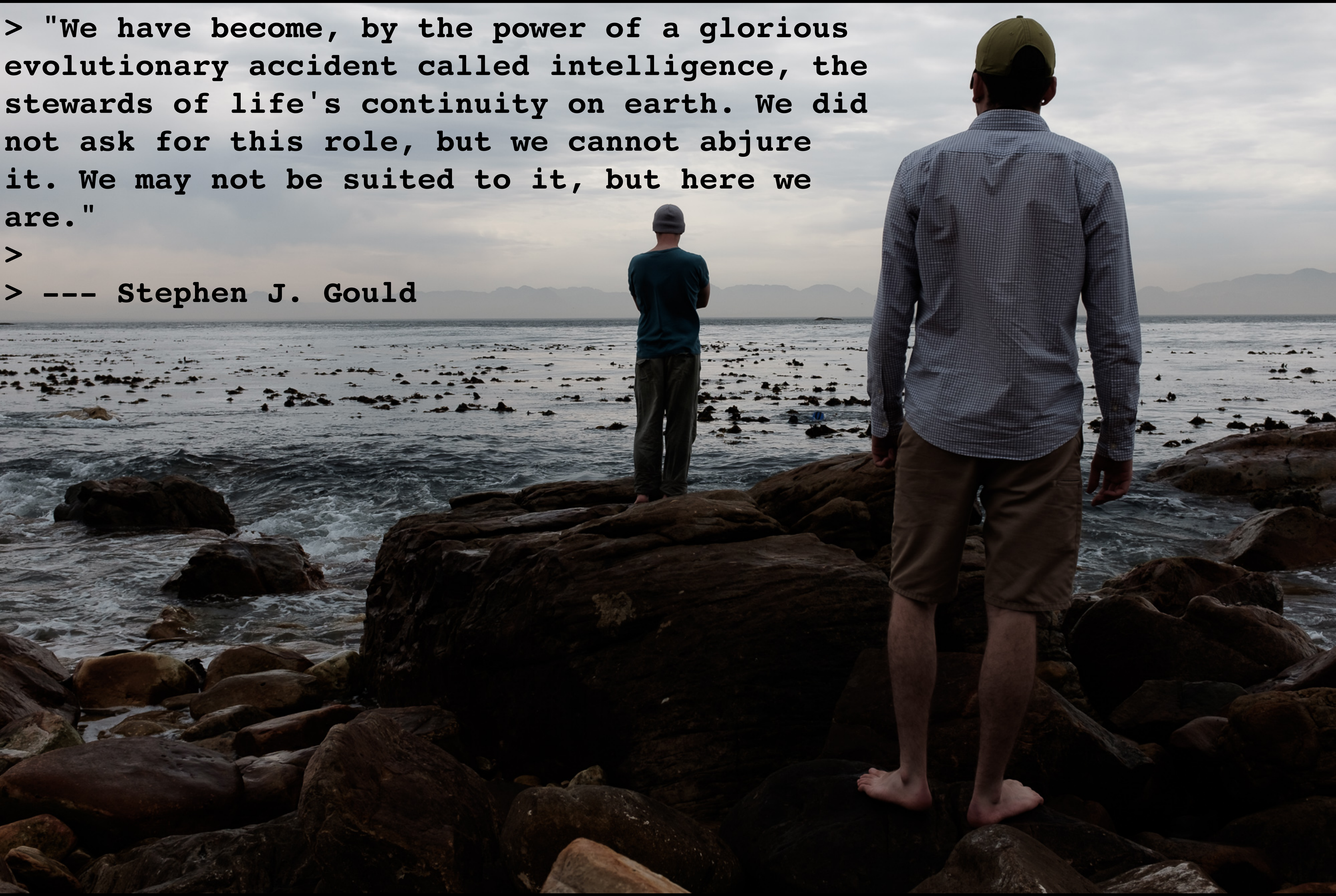
INTRODUCTION

QUANTITATIVE ECOLOGY

AJ Smit


> "We have become, by the power of a glorious evolutionary accident called intelligence, the stewards of life's continuity on earth. We did not ask for this role, but we cannot abjure it. We may not be suited to it, but here we are."
>
> --- Stephen J. Gould

Intent of Day 1

What is ecology?

Ecological questions:

- What kinds of questions have been asked by ecologists?
- What kinds of questions can be asked?
- What has caused the difference is kinds of questions being asked?

What is QE?

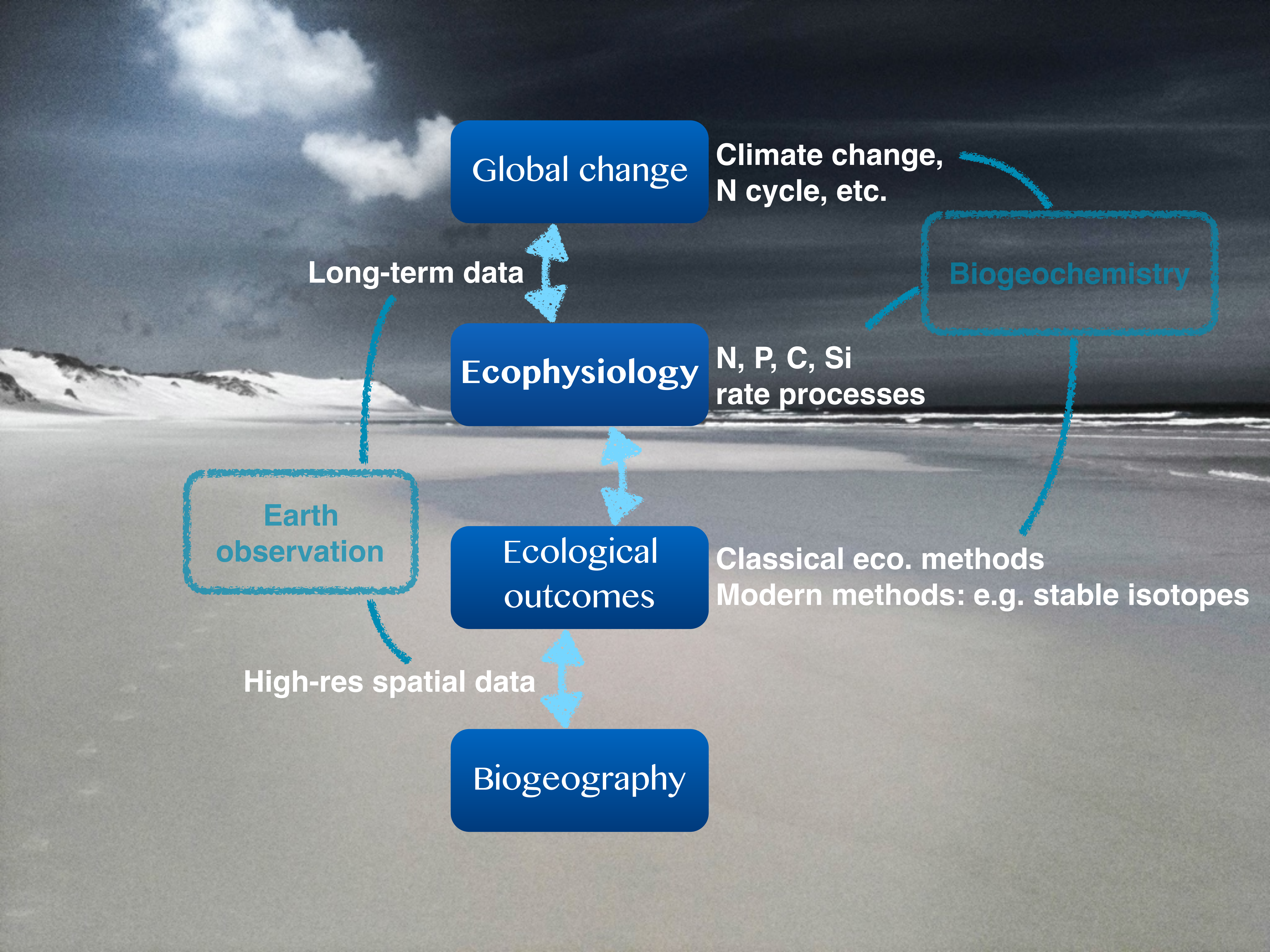
Why not use the biology and statistics knowledge you already have?

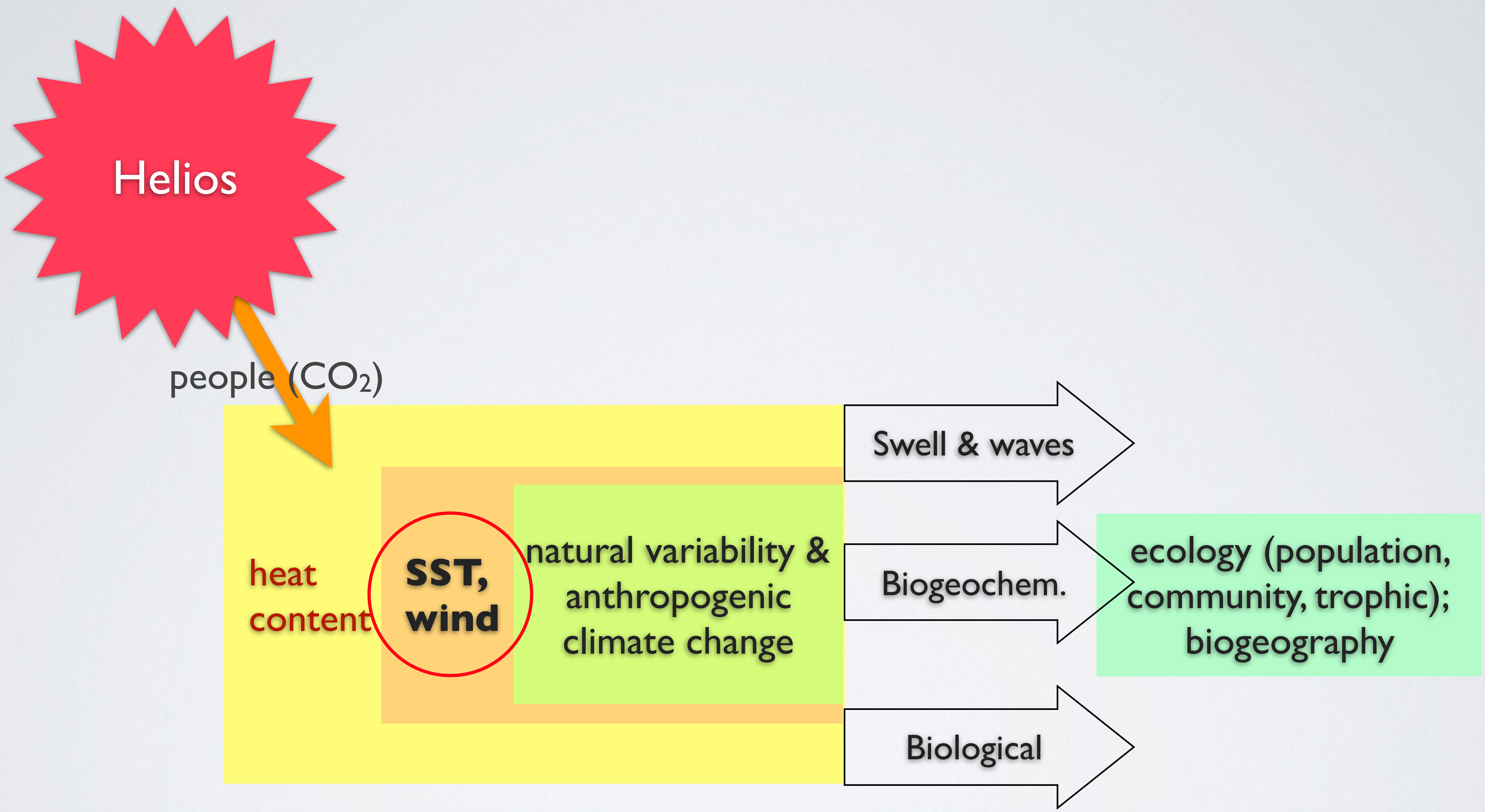
What is ecology?

Community ecology vs. population ecology

What kinds of questions?

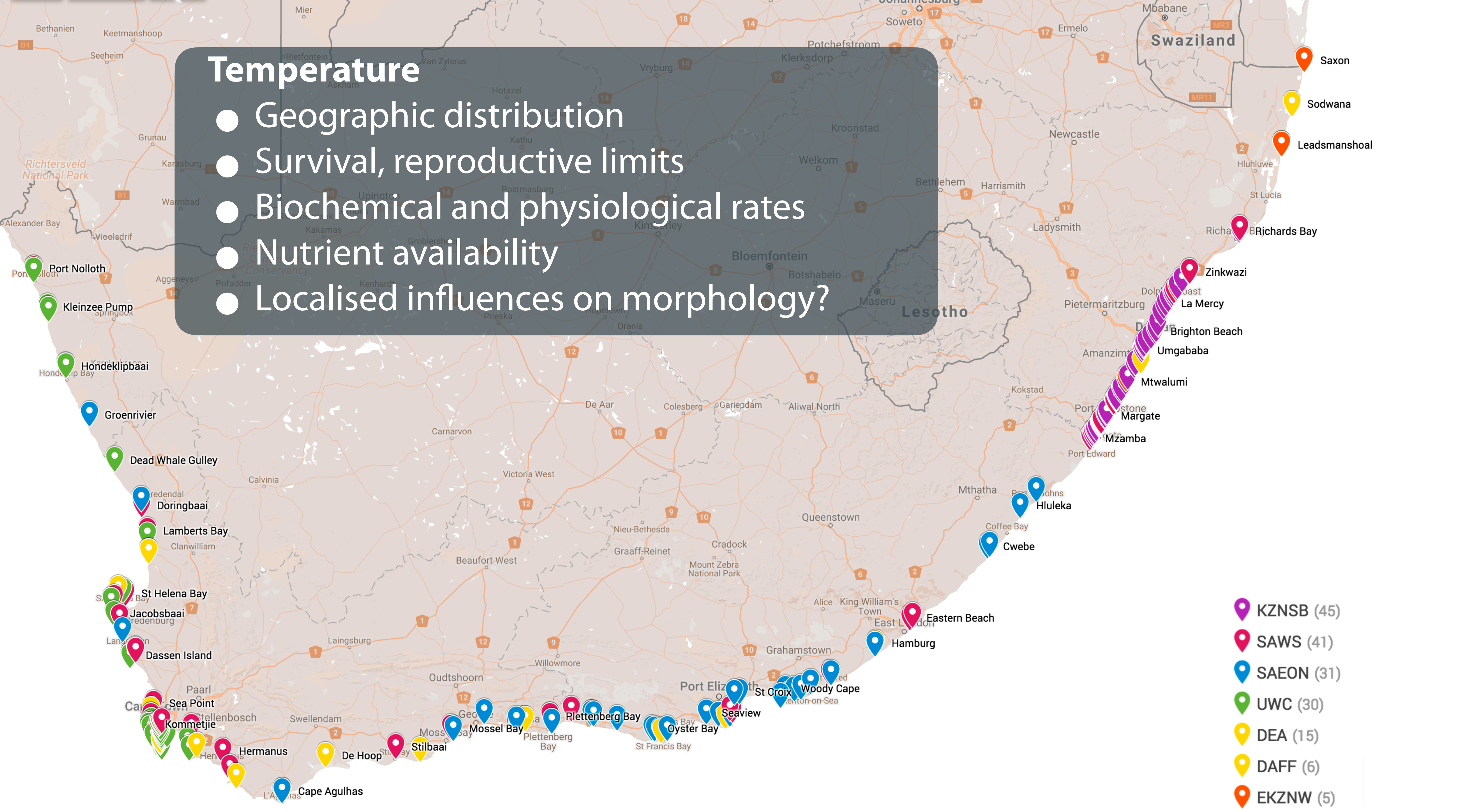
Community ecology underpins the vast fields of biodiversity and biogeography, and concerns spatial scales from squares of meters to all of Earth. We can look at historical, contemporary, and future processes that have been implicated in shaping the distribution of life on our planet.


Global change
Climate change,
N cycle, etc.
Long-term data
Biogeochemistry
Ecophysiology
N, P, C, Si
rate processes
Earth
observation
Ecological
outcomes
Classical eco. methods
Modern methods: e.g. stable isotopes
High-res spatial data
Biogeography

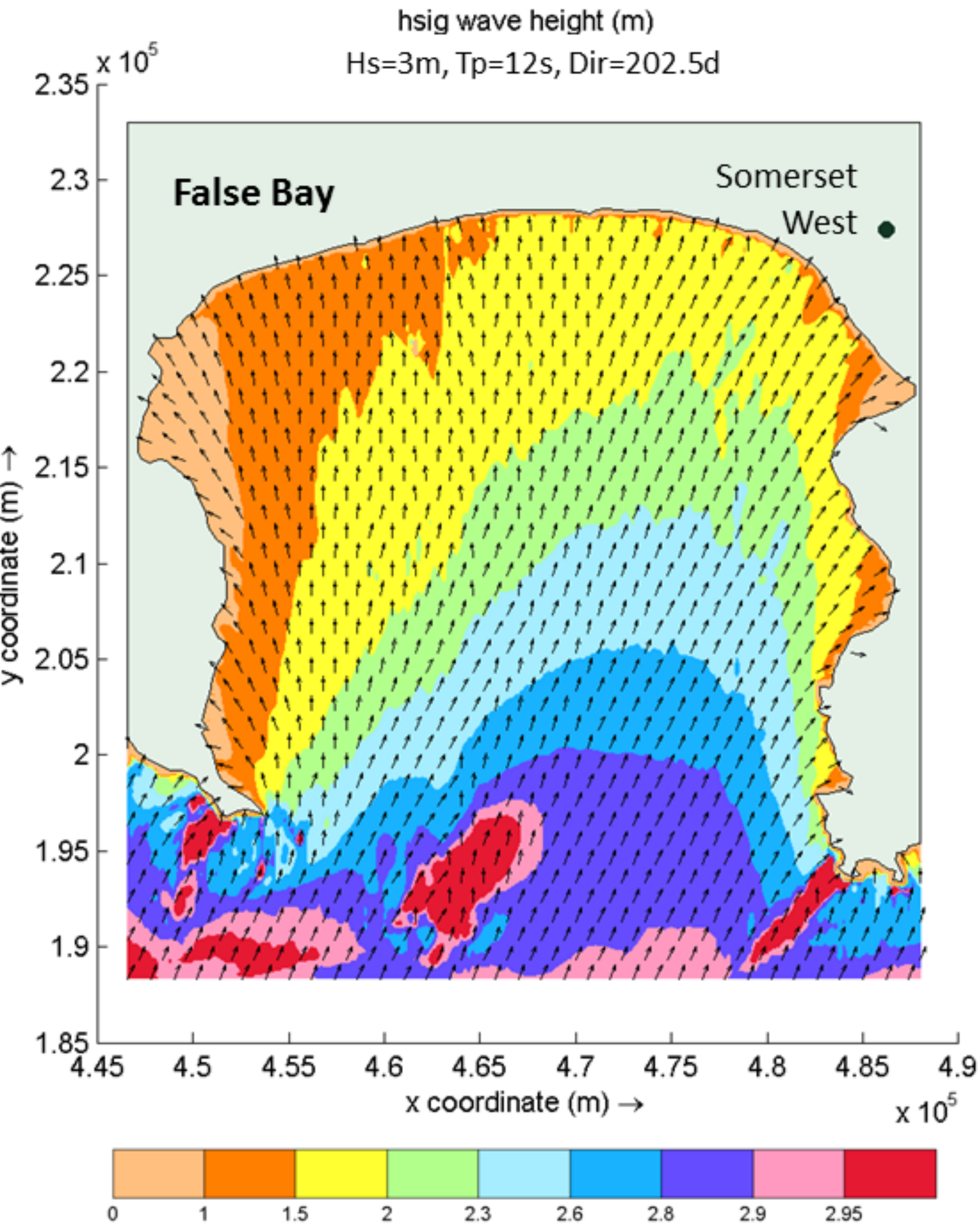

Helios
people (CO_2)
heat content
SST, wind
natural variability & anthropogenic climate change
Swell & waves
Biogeochem.
Biological
ecology (population, community, trophic); biogeography

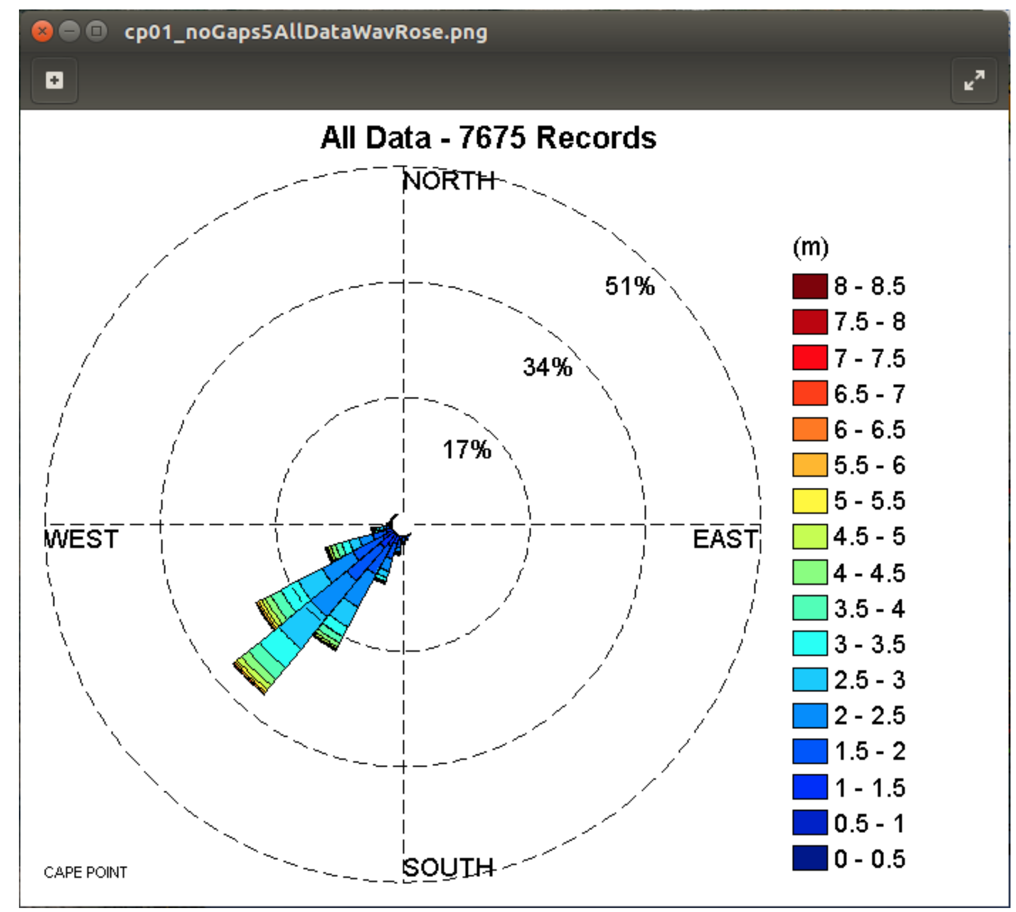
Temperature

- Geographic distribution
- Survival, reproductive limits
- Biochemical and physiological rates
- Nutrient availability
- Localised influences on morphology?



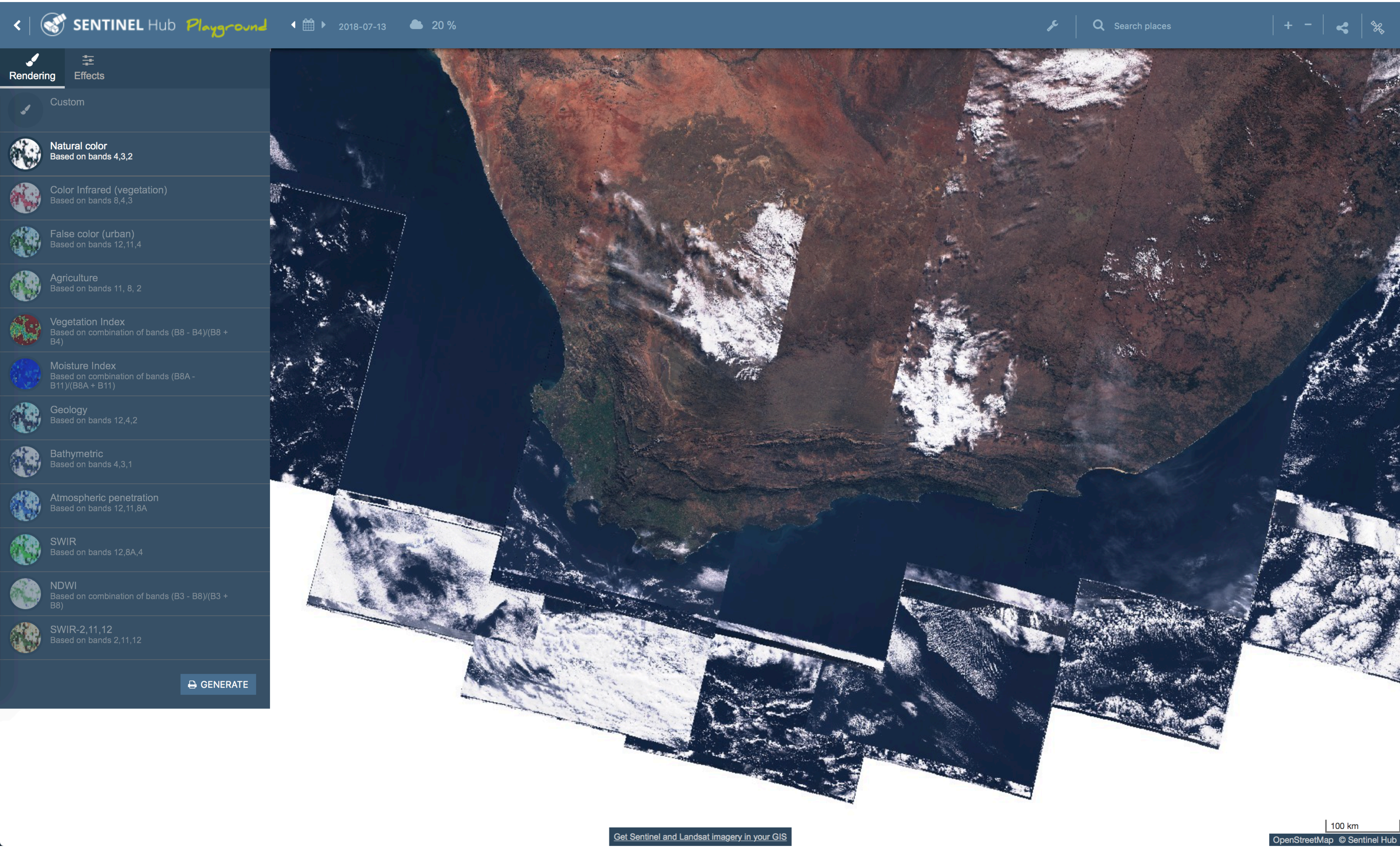
UNIVERSITY of the WESTERN CAPE
SAEON
EZEMVELO KZN WILDLIFE
South African Weather Service
KWAZULU-NATAL SHARKS BOARD
National Research Foundation
environmental affairs
Department: Environmental Affairs
REPUBLIC OF SOUTH AFRICA
agriculture, forestry & fisheries
Department: Agriculture, Forestry and Fisheries
REPUBLIC OF SOUTH AFRICA





Numerical wave model

- **Wave Watch III** forced by **NCEP** winds at 3hr resolution, hindcast from 1994-2013
- Wave parameters modelled using **SWAN**
- 200m alongshore resolution


SENTINEL Hub Playground
2018-07-13
20 %
Search places
Rendering
Effects
Custom
Natural color
Based on bands 4,3,2
Color Infrared (vegetation)
Based on bands 8,4,3
False color (urban)
Based on bands 12,11,4
Agriculture
Based on bands 11, 8, 2
Vegetation Index
Based on combination of bands (B8 - B4)/(B8 + B4)
Moisture Index
Based on combination of bands (B8A - B11)/(B8A + B11)
Geology
Based on bands 12,4,2
Bathymetric
Based on bands 4,3,1
Atmospheric penetration
Based on bands 12,11,8A
SWIR
Based on bands 12,8A,4
NDWI
Based on combination of bands (B3 - B8)/(B3 + B8)
SWIR-2,11,12
Based on bands 2,11,12
GENERATE
Get Sentinel and Landsat imagery in your GIS
100 km
OpenStreetMap © Sentinel Hub

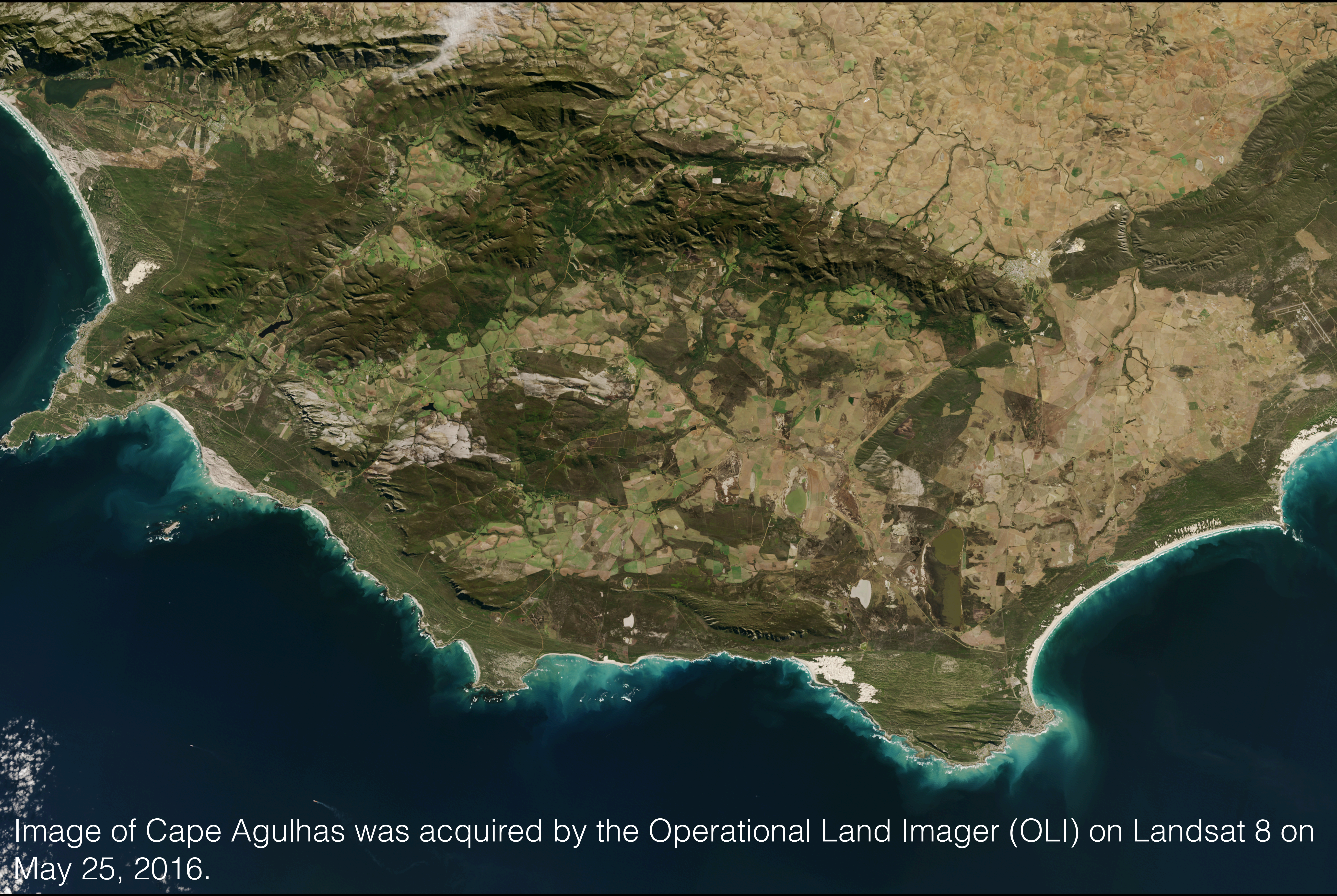
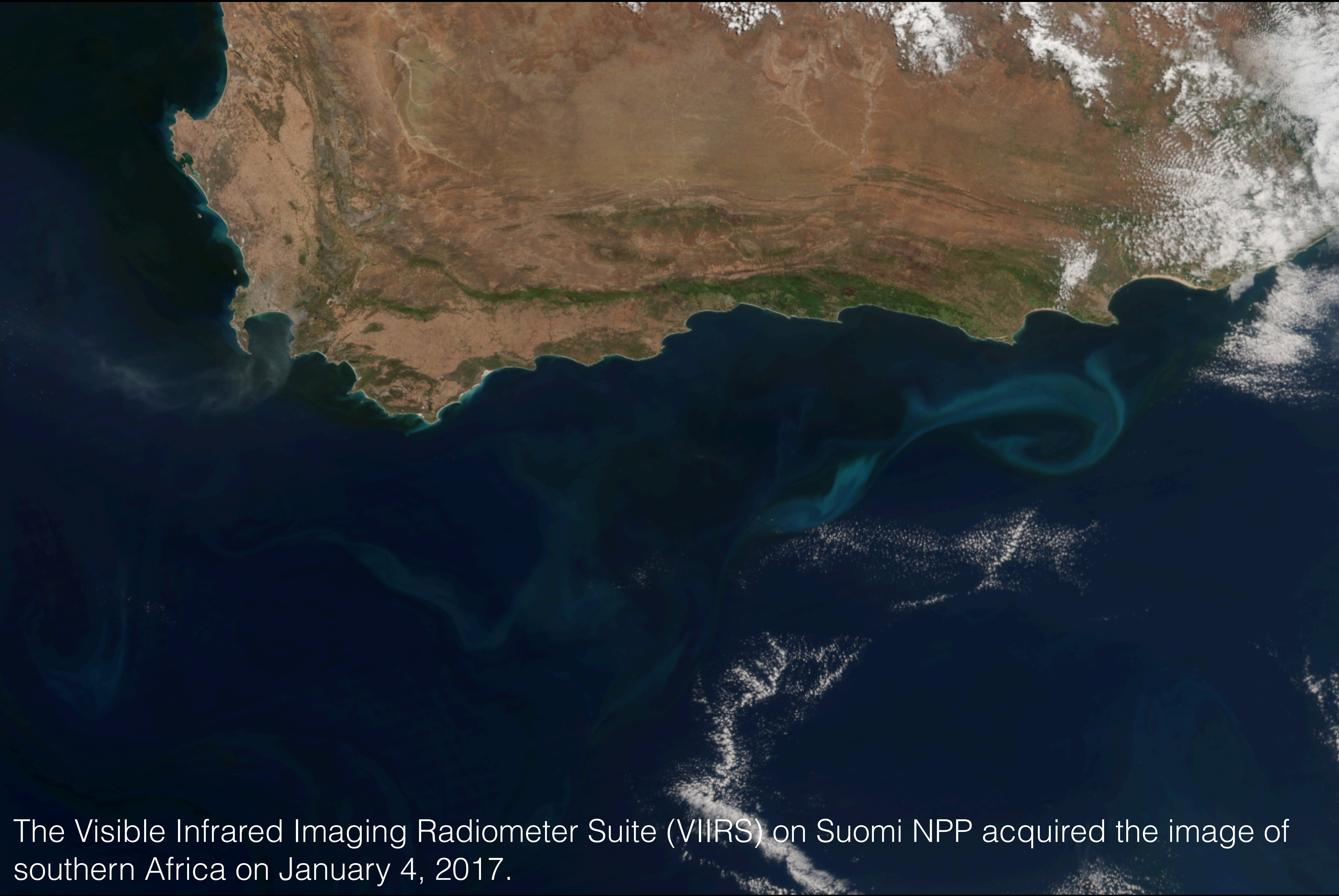


Image of Cape Agulhas was acquired by the Operational Land Imager (OLI) on Landsat 8 on May 25, 2016.



The Visible Infrared Imaging Radiometer Suite (VIIRS) on Suomi NPP acquired the image of southern Africa on January 4, 2017.

What is QE?

- Community ecologists tend to analyse how multiple environmental factors act as drivers that influence the distribution of tens or hundreds of species.
- These data tend to often be messy (not in the sense of untidy data as per the 'tidyverse' definition of tidy data, but it can be that too!) and statistical considerations need to be understood within the context of the data available to us.

- This translates to errors of measurement and errors due to extreme values, the presence of a few very rare or very abundant species, autocorrelated residuals (due to repeated sampling, for example), colinearity, issues of scaling, etc.
- These challenges make to application of 'basic' statistical approaches problematic, and a new branch of inferential and exploratory statistical needs to be followed.

- These approaches involve techniques that allow us to work with all the data at once, and because it can simultaneously analyse all the variables (multiple environmental drivers acting on multiple species at multiple places and across multiple times), this group of statistics is called 'multivariate statistics.' There are two main groups of multivariate statistics: '**classifications**' and '**ordinations**.'

- Classification generally concerns placing samples (species or environments) into groups or hierarchies of groups.
- Ordination is best suited for analyses that involve arranging samples along gradients.
- Often they complement each other, but we shall see later that each approach has its own strengths. Irrespective of the analysis, the data share a few characteristics.

TOPIC 2

DIVERSITY

Some more important reading…

Ordination Methods for Ecologists

http://ordination.okstate.edu

GUide to STatistical Analysis in Microbial Ecology (GUSTA ME)

https://sites.google.com/site/mb3gustame/

Alpha, beta, and gamma diversity

- *alpha (α) diversity* is the diversity of a community, and it captures the diversity within a site, plot, transect, or quadrat
- often used to represent the diversity of the smallest sampling unit
- can be seen as representing the local scale
- usually represented as a **synthetic diversity index** (a.k.a. *dissimilarity index*, e.g. Bray-Curtis, Sørensen, Jaccard, etc.) or simply as species richness

Alpha, beta, and gamma diversity

- *beta (β) diversity* is also known as '**species turnover**', and represents is the rate of change in species composition from one community to another
- usually applied along **gradients**

Alpha, beta, and gamma diversity

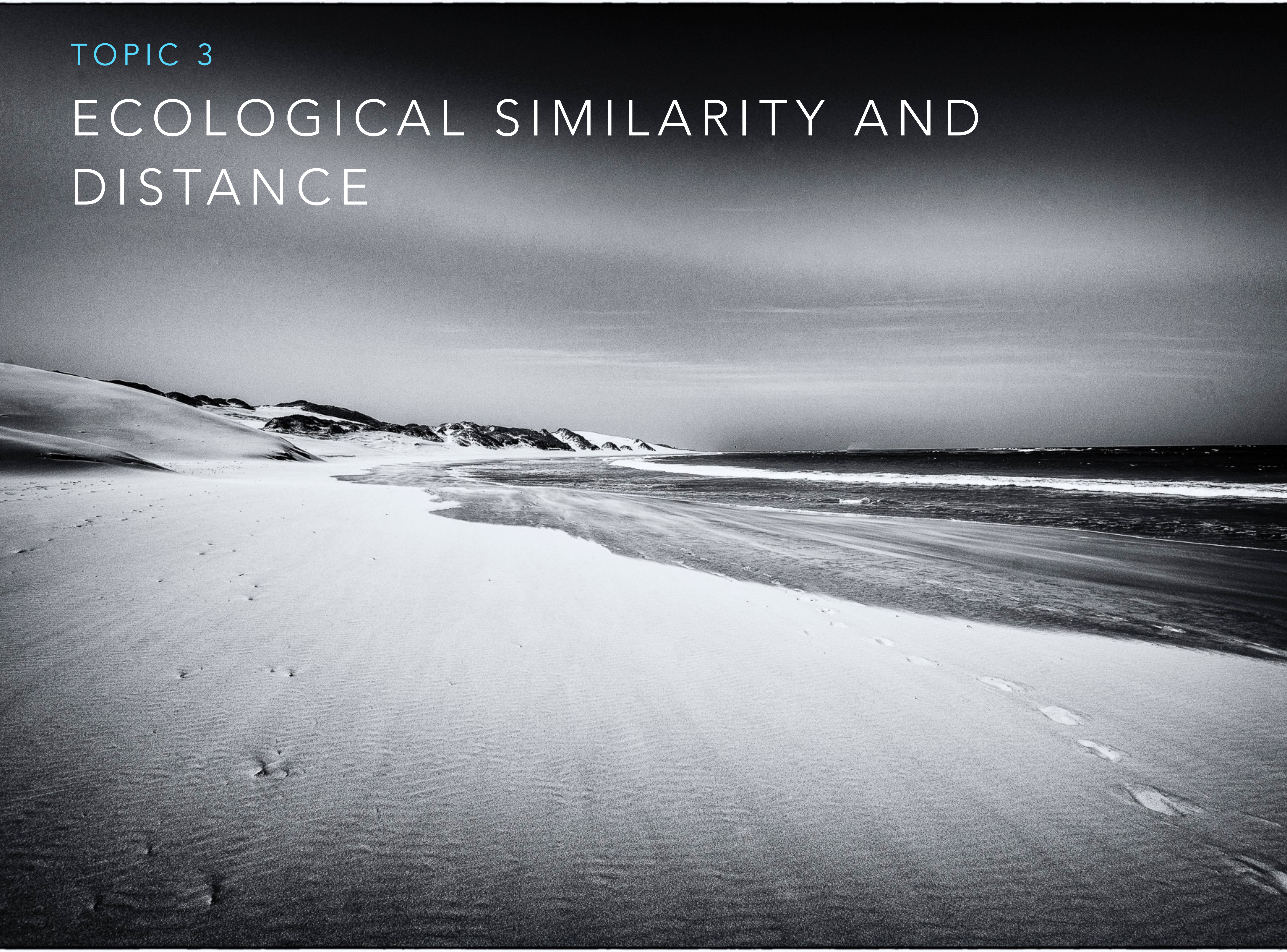
- *gamma (γ) diversity* is the **total diversity** of a region or landscape
- can represent the diversity of all samples combined
- same metric as alpha diversity (i.e. one of the dissimilarity indices)

Alpha, beta, and gamma diversity

- which diversity measure to use depends on the ecological question being asked
- it depends on considerations of the spatial scales of the landscape being studied
- here we shall primarily be concerned with alpha diversity as captured by some of the dissimilarity indices

TOPIC 3

ECOLOGICAL SIMILARITY AND DISTANCE



Similarity and dissimilarity

- sites sharing a similar species composition are ecologically similar
    - i.e. high similarity / low dissimilarity
- how similar sites are depends on measurable environmental differences that influence species composition, or it can be due to unmeasured influences; it can also simply be noise
- it is the ecologist's role to figure out what influences the similarity/dissimilarity among sites

Distance matrices

- a **distance matrix** is produced from the data matrix (**species table** or **environment table**) by calculating one of several dissimilarity indices
- also called **association** or **resemblance** matrices
- see `vegdist {vegan}` for a list of dissimilarity indices
- the result is a matrix of **pairwise differences** in community composition (as synthesised by the chosen index) or ecological distance between all sites

Distance matrices

- the matrices are **square** and **symmetrical**, and it will have as many rows and columns as the number of sites present in the original species or environment table
- the **diagonals are zero** (a site is the same as itself, so it has zero dissimilarity)
- the table can be read directly, and each cell represents the species or ecological difference between a pair of sites
- all information of the species ID (and maybe also abundance) of a site is lost, as this info is condensed into one metric

Distance matrix for environmental data

- Euclidian distance is "*the 'ordinary' straight-line distance between two points in Euclidean space*" calculated using the Pythagorean theorem
- conforms to our physical concept of distance
- in 2D and 3D, gives distance in cartesian units between points on a plane (x, y) or in a volume (x, y, z)
    - e.g. short geographic distances between points on a map
    - (loses accuracy over large distances, as Earth's surface is not on a plane but on a sphere… correct by using great circle distances, e.g. use the Haversine formula)

Two dimensions [edit]

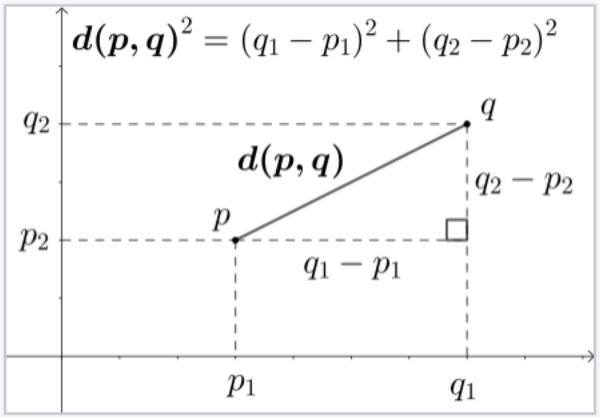
In the Euclidean plane, if **p** = (p_1, p_2) and **q** = (q_1, q_2) then the distance is given by

$$d(\mathbf{p},\mathbf{q}) = \sqrt{(q_1-p_1)^2 + (q_2-p_2)^2}.$$

This is equivalent to the Pythagorean theorem.

Alternatively, it follows from (2) that if the polar coordinates of the point **p** are (r_1, θ_1) and those of **q** are (r_2, θ_2), then the distance between the points is

$$\sqrt{r_1^2 + r_2^2 - 2r_1r_2\cos(\theta_1-\theta_2)}.$$



Euclidean distance in R^2

Three dimensions [edit]

In three-dimensional Euclidean space, the distance is

$$d(\mathbf{p},\mathbf{q}) = \sqrt{(p_1-q_1)^2 + (p_2-q_2)^2 + (p_3-q_3)^2}.$$

n dimensions [edit]

In general, for an *n*-dimensional space, the distance is

$$d(\mathbf{p},\mathbf{q}) = \sqrt{(p_1-q_1)^2 + (p_2-q_2)^2 + \cdots + (p_i-q_i)^2 + \cdots + (p_n-q_n)^2}.$$

https://en.wikipedia.org/wiki/Euclidean_distance

Euclidian distance

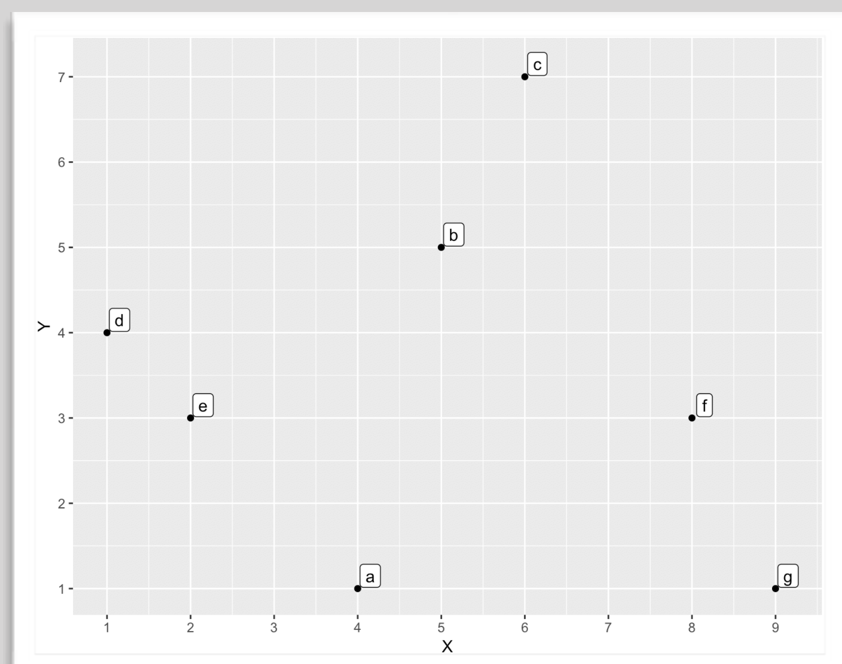
- where x_{ij} x_{ik} refer to the quantity in (column) i, at sites (rows) j and k
- $d_{jk} = \sqrt{\sum(x_{ij} - x_{ik})^2}$

e.g. example with position (such as geographic) coordinates…

use **vegan**'s `vegdist()` function

Raw data

	x	y
a	4	1
b	5	5
c	6	7
d	1	4
e	2	3
f	8	3
g	9	1



Euclidian distances

```
> ex.xy.euc ← vegdist(ex.xy, method = "euclidian")
> ex.xy.euc
         a        b        c        d        e        f
b 4.123106
c 6.324555 2.236068
d 4.242641 4.123106 5.830952
e 2.828427 3.605551 5.656854 1.414214
f 4.472136 3.605551 4.472136 7.071068 6.000000
g 5.000000 5.656854 6.708204 8.544004 7.280110 2.236068
```

e.g. example with higher dimension environmental data…

Raw data

	pH	O2	temp	depth
a	7.1	6.5	12.1	1.1
b	7.5	5.5	12.3	1.3
c	7.6	5.7	11.9	1.5
d	7.0	5.4	11.8	1.6
e	7.1	6.3	12.0	1.8
f	7.2	6.3	12.1	1.9
g	6.9	6.1	12.2	2.2

(transformation)

Standarised data

```
> ex.env.std ← decostand(xy.env, method = "standardize")
> ex.env.std
          pH         O2       temp       depth
a -0.3872983  1.2156767  0.2494233 -1.41749621
b  1.1618950 -1.0842522  1.4133987 -0.88114629
c  1.5491933 -0.6242664 -0.9145521 -0.34479637
d -0.7745967 -1.3142450 -1.4965398 -0.07662142
e -0.3872983  0.7556909 -0.3325644  0.45972850
f  0.0000000  0.7556909  0.2494233  0.72790346
g -1.1618950  0.2957051  0.8314110  1.53242833
```

Euclidian distances

```
                          ex.env.std
> ex.env.euc ← vegdist(xy.dat, method = "euclidian")
> ex.env.euc
         a        b        c        d        e        f
b 4.123106
c 6.324555 2.236068
d 4.242641 4.123106 5.830952
e 2.828427 3.605551 5.656854 1.414214
f 4.472136 3.605551 4.472136 7.071068 6.000000
g 5.000000 5.656854 6.708204 8.544004 7.280110 2.236068
```

Distance matrix for species data

- use Bray-Curtis for the case where data are abundances
- use Jaccard (with `binary = TRUE`) for presence/absence data
- many more in **vegan**; see `?vegdist`

Bray-Curtis

- again, where x_{ij} x_{ik} refer to the quantity in (column) i, at sites (rows) j and k
- $d_{jk} = \frac{\sum(|x_{ij} - x_{ik}|)}{\sum(x_{ij} + x_{ik})}$

Distance matrix for species data

- using the Doubs species data:
… look at the data
… would we use Bray-Curtis or Jaccard dissimilarities?
… apply the calculation
… explain the meaning of the data in broad terms
… examine it more closely: what general pattern comes out?
… plot this pattern (*hint, it is best seen in the 1st column of the resemblance matrix*)
… what explanation can you offer for this pattern?
… using the `decostand()` function, create presence/absence data, and apply the appropriate `vegdist()` function to obtain a suitable dissimilarity matrix

Distance matrices: some old, some new

- recap
    - **Euclidian distance** for environmental data
    - **Bray-Curtis** for species **abundances** (but also many others in `vegdist()`) and elsewhere
    - **Jaccard** for **presence-absence** (binary) species data

- …also **Gower's distance** for **categorical** (factor; must be declared) data, i.e. use `daisy()` in the **cluster** package or `gowdis()` in the **FD** package

Correlations and associations

- e.g. **associations between species** (info on co-varying species) based on dissimilarities, or **correlations between environmental variables**
- associations are usually found on a **transposed** species table

Associations: species presence-absence

Species table

```
> spe[1:10, 1:10]
# A tibble: 10 x 10
    Cogo  Satr  Phph  Babl  Thth  Teso  Chna  Pato  Lele  Sqce
   <int> <int> <int> <int> <int> <int> <int> <int> <int> <int>
 1     0     3     0     0     0     0     0     0     0     0
 2     0     5     4     3     0     0     0     0     0     0
 3     0     5     5     5     0     0     0     0     0     0
 4     0     4     5     5     0     0     0     0     0     1
 5     0     2     3     2     0     0     0     0     5     2
 6     0     3     4     5     0     0     0     0     1     2
 7     0     5     4     5     0     0     0     0     1     1
 8     0     0     1     3     0     0     0     0     0     5
 9     0     1     4     4     0     0     0     0     2     2
10     1     3     4     1     1     0     0     0     0     1
```

Transposed

```
> spe.t <- t(spe)
> spe.t[1:10, 1:10]
     [,1] [,2] [,3] [,4] [,5] [,6] [,7] [,8] [,9] [,10]
Cogo    0    0    0    0    0    0    0    0    0     1
Satr    3    5    5    4    2    3    5    0    1     3
Phph    0    4    5    5    3    4    4    1    4     4
Babl    0    3    5    5    2    5    5    3    4     1
Thth    0    0    0    0    0    0    0    0    0     1
Teso    0    0    0    0    0    0    0    0    0     0
Chna    0    0    0    0    0    0    0    0    0     0
Pato    0    0    0    0    0    0    0    0    0     0
Lele    0    0    0    0    5    1    1    0    2     0
Sqce    0    0    0    1    2    2    1    5    2     1
```

Jaccard coefficient

```
> spe.t.S7 <- vegdist(spe.t, "jaccard", binary = TRUE)
> round(as.matrix(spe.t.S7)[1:10, 1:10], 2)
     Cogo Satr Phph Babl Thth Teso Chna Pato Lele Sqce
Cogo 0.00 0.53 0.60 0.67 0.22 0.40 0.89 0.81 0.82 0.73
Satr 0.53 0.00 0.24 0.36 0.53 0.61 0.88 0.83 0.65 0.55
Phph 0.60 0.24 0.00 0.17 0.60 0.60 0.77 0.71 0.54 0.39
Babl 0.67 0.36 0.17 0.00 0.67 0.67 0.62 0.60 0.38 0.25
Thth 0.22 0.53 0.60 0.67 0.00 0.40 0.82 0.81 0.82 0.73
Teso 0.40 0.61 0.60 0.67 0.40 0.00 0.75 0.64 0.70 0.73
Chna 0.89 0.88 0.77 0.62 0.82 0.75 0.00 0.23 0.42 0.52
Pato 0.81 0.83 0.71 0.60 0.81 0.64 0.23 0.00 0.39 0.56
Lele 0.82 0.65 0.54 0.38 0.82 0.70 0.42 0.39 0.00 0.28
Sqce 0.73 0.55 0.39 0.25 0.73 0.73 0.52 0.56 0.28 0.00
```

also available are the Sørensen and Ochiai coefficients

Correlation: environmental variables

Environment table

```
> env
# A tibble: 30 x 11
     dfs   alt   slo   flo    pH   har   pho   nit   amm   oxy   bod
 * <dbl> <int> <dbl> <dbl> <dbl> <int> <dbl> <dbl> <dbl> <dbl> <dbl>
 1   0.3   934  48    0.84   7.9    45  0.01  0.2   0     12.2   2.7
 2   2.2   932   3    1      8      40  0.02  0.2   0.1   10.3   1.9
 3  10.2   914   3.7  1.8    8.3    52  0.05  0.22  0.05  10.5   3.5
 4  18.5   854   3.2  2.53   8      72  0.1   0.21  0     11     1.3
 5  21.5   849   2.3  2.64   8.1    84  0.38  0.52  0.2    8     6.2
 6  32.4   846   3.2  2.86   7.9    60  0.2   0.15  0     10.2   5.3
 7  36.8   841   6.6  4      8.1    88  0.07  0.15  0     11.1   2.2
 8  49.1   792   2.5  1.3    8.1    94  0.2   0.41  0.12   7     8.1
 9  70.5   752   1.2  4.8    8      90  0.3   0.82  0.12   7.2   5.2
10  99     617   9.9 10      7.7    82  0.06  0.75  0.01  10     4.3
# ... with 20 more rows
```

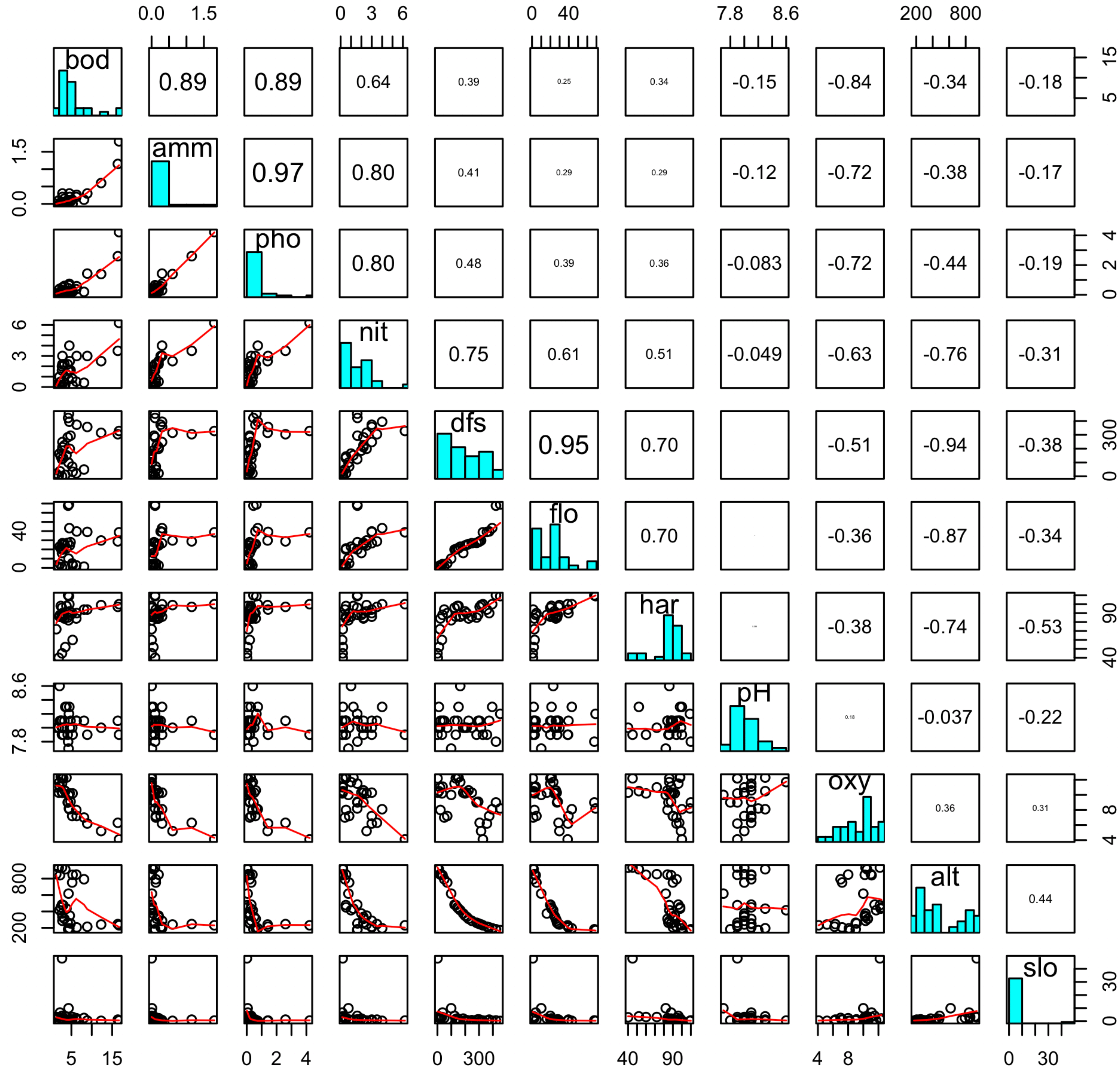
Pearson correlation coefficients

```
> env.pearson <- cor(env)        # default method = "pearson"
> round(env.pearson, 2)
      dfs   alt   slo   flo    pH   har   pho   nit   amm   oxy   bod
dfs  1.00 -0.94 -0.39  0.95  0.02  0.73  0.47  0.74  0.41 -0.57  0.43
alt -0.94  1.00  0.46 -0.86 -0.05 -0.79 -0.44 -0.75 -0.38  0.42 -0.38
slo -0.39  0.46  1.00 -0.36 -0.22 -0.53 -0.20 -0.31 -0.17  0.31 -0.17
flo  0.95 -0.86 -0.36  1.00  0.03  0.74  0.38  0.59  0.29 -0.42  0.30
pH   0.02 -0.05 -0.22  0.03  1.00  0.08 -0.08 -0.04 -0.12  0.19 -0.16
har  0.73 -0.79 -0.53  0.74  0.08  1.00  0.37  0.53  0.30 -0.37  0.34
pho  0.47 -0.44 -0.20  0.38 -0.08  0.37  1.00  0.80  0.97 -0.76  0.91
nit  0.74 -0.75 -0.31  0.59 -0.04  0.53  0.80  1.00  0.80 -0.69  0.68
amm  0.41 -0.38 -0.17  0.29 -0.12  0.30  0.97  0.80  1.00 -0.75  0.90
oxy -0.57  0.42  0.31 -0.42  0.19 -0.37 -0.76 -0.69 -0.75  1.00 -0.84
bod  0.43 -0.38 -0.17  0.30 -0.16  0.34  0.91  0.68  0.90 -0.84  1.00
```

no need to transpose or standardise as the `cor()` function does this internally

“comparison among ordinal variables, or among quantitative variables that may be monotonically but not linearly related, can be achieved using rank correlation coefficients like Spearman’s ρ (rho) or Kendall’s τ (tau)”

Pearson Correlation Matrix



Associations: species tables

- we do not derive Euclidian distances from species data, nor do we determine pairwise covariances or correlations (this is fine with the environmental data)
- it may be necessary to apply various transformations to the species data, e.g. when there are a few rare species
- transformation options are provided by `decostand()`; see section 3.5 in *Numerical Ecology with R*

Table 3.1 Commonly-used distance and dissimilarity functions in Q mode available in R packages. The symbol ⇒ means that applying the function designed for quantitative data to presence–absence data produces the same result as computing the corresponding function designed for presence–absence data

Quantitative data		Presence–absence data
Community composition data		
Ruzicka dissimilarity `vegdist(.,"jac")`	⇒	Jaccard dissimilarity `vegdist(.,"jac", binary=TRUE)` `dist.binary(.,method=1)`
Hellinger distance `decostand(.,"hel")` followed by `vegdist(.,"euc")`	⇒	Ochiai dissimilarity `dist.binary(.,method=7)`
Chord distance `decostand(.,"norm")` followed by `vegdist(.,"euc")`	⇒	Ochiai dissimilarity `dist.binary(.,method=7)`
Bray–Curtis dissimilarity `vegdist(.,"bray")`	⇒	Sørensen dissimilarity `dist.binary(.,method=5)`
Chi-square distance `decostand(.,"chi.square")`		Chi-square distance (idem)
Canberra distance `vegdist(.,"canberra")`		
Other variables, mixed physical units		
Standardized variables: Euclidean distance `vegdist(.,"euc")`		Standardized variables: Simple matching coefficient `dist.binary(.,method=2)`
Non-standardized variables: Gower distance `daisy(.,"gower")`		

Correlations and associations

- the square association and correlation matrices are generally only used as intermediate steps in our workflow, and are not usually scrutinised directly
- however, meaningful information is already present in these matrices, and it is beneficial to be able to read them
- it is definitely necessary to understand how they are calculated
- the next step in the workflow takes the association and/or correlation matrices and applies the multivariate analyses on them

TOPIC 4

CLUSTERING

TOPIC 5

UNCONSTRAINED ORDINATION

Ordinations

- clustering find discontinuities, but **ordinations highlight gradients**
- gradients are particularly present in ecological communities
- suited to multivariate data, which represent…
    - …a **space** (*e.g.* the landscape) comprised of many **sites** (*i.e.* the samples forming the rows), each one occupied by many **variables** (*i.e.* species or environmental variables in the columns)
    - there are as many dimensions as variables
    - it would be a silly and not very revealing to analyse it all using a series of univariate or bivariate analyses;
    - (27x26)/2=351 in the Doubs data set to be precise

Ordinations

- ordinations represent the data along a reduced number of **orthogonal axes** (linearly independent, uncorrelated), constructed in such a way that they represent, in decreasing order, the main trends of the data
- interpretation is aided by visualisations, regressions, and clustering
- **unconstrained** ordinations are not statistical (no inference testing); they are purely descriptive
  - *also called indirect gradient analysis*
- **constrained** ordination adds a level of statistical testing (next topic)
  - *also called direct gradient analysis*

According to Gauch (1982): "**Ordination primarily endeavors to represent sample and species relationships as faithfully as possible in a low-dimensional space**". But why is this objective desirable? There are a number of answers, but most are derived from the 'properties of community' data as described above:

- It is **impossible to visualize multiple dimensions simultaneously** […] ecologists typically grapple with dozens of dimensions (species and/or samples).
- A single **multivariate analysis saves time**, in contrast to a separate univariate analysis for each species.
- Ideally and typically, **dimensions of this 'low dimensional space' will represent important and interpretable environmental gradients**.
- If statistical tests are desired, **problems of multiple comparisons are diminished** when species composition is studied in its entirety.
- **Statistical power is enhanced** when species are considered in aggregate, because of redundancy.
- **By focusing on 'important dimensions', we avoid interpreting (and misinterpreting) noise**. Thus, ordination is a 'noise reduction technique' (Gauch 1982).
- We can **determine the relative importance of different gradients**; this is virtually impossible with univariate techniques.
- **Community patterns may differ from population patterns**.
- Some techniques provide a measure of beta diversity.
- The **graphical results from most techniques often lead to ready and intuitive interpretations** of species-environment relationships.

Taken verbatim from http://ordination.okstate.edu/overview.htm

Ordinations

- **Principal component analysis (PCA):** the main eigenvector-based method. Works on raw, quantitative data. Preserves the Euclidean distance among sites.
- **Correspondence analysis (CA):** works on data that must be frequencies or frequency-like, dimensionally homogeneous, and non-negative. Preserves the χ^2 distance among rows or columns. Mainly used in ecology to analyse species data tables.
- **Principal coordinate analysis (PCoA):** devoted to the ordination of distance matrices, most often in the Q mode, instead of site-by-variables tables. Hence, great flexibility in the choice of association measures.
- **Nonmetric multidimensional scaling (NMDS):** unlike the three others, this is not an eigenvector-based method. NMDS tries to represent the set of objects along a predetermined number of axes while preserving the ordering relation- ships among them.
- PCoA and NMDS can produce ordinations from any square distance matrix.

Taken verbatim from 5.2.2 in Numerical Ecology with R

Interpretation of ordination plots

- The **direction of the axes** (*e.g.* left vs. right; up vs. down) **is arbitrary** and should not affect the interpretation.
- The **numeric scale on the axis is not very useful for the interpretation** (an exception for this is DCA, in which the scales are in units of beta diversity).
- In most techniques (but not NMDS), **the order of the axes is important**. Thus, axis 1 is more important than axis 2, *etc*. The meaning of 'importance' depends on the technique employed, but ideally **related to the relative influence of environmental gradients**.
- **Third and higher axes can be constructed**. The choice of 'when to stop' interpreting new axes is largely a matter of taste, the quantity and quality of the data, and the ability to interpret the results. Fortunately, most of the techniques presented later provide supplemental statistics that can assist in the task.
- It is desirable that axes not be correlated, because you would like them to represent different gradients. **Most techniques automatically result in uncorrelated** (or orthogonal) axes.
- **A biologist's insight, experience, and knowledge of the literature are the most important tools for interpreting indirect gradient analysis**.

Taken verbatim from http://ordination.okstate.edu/overview.htm