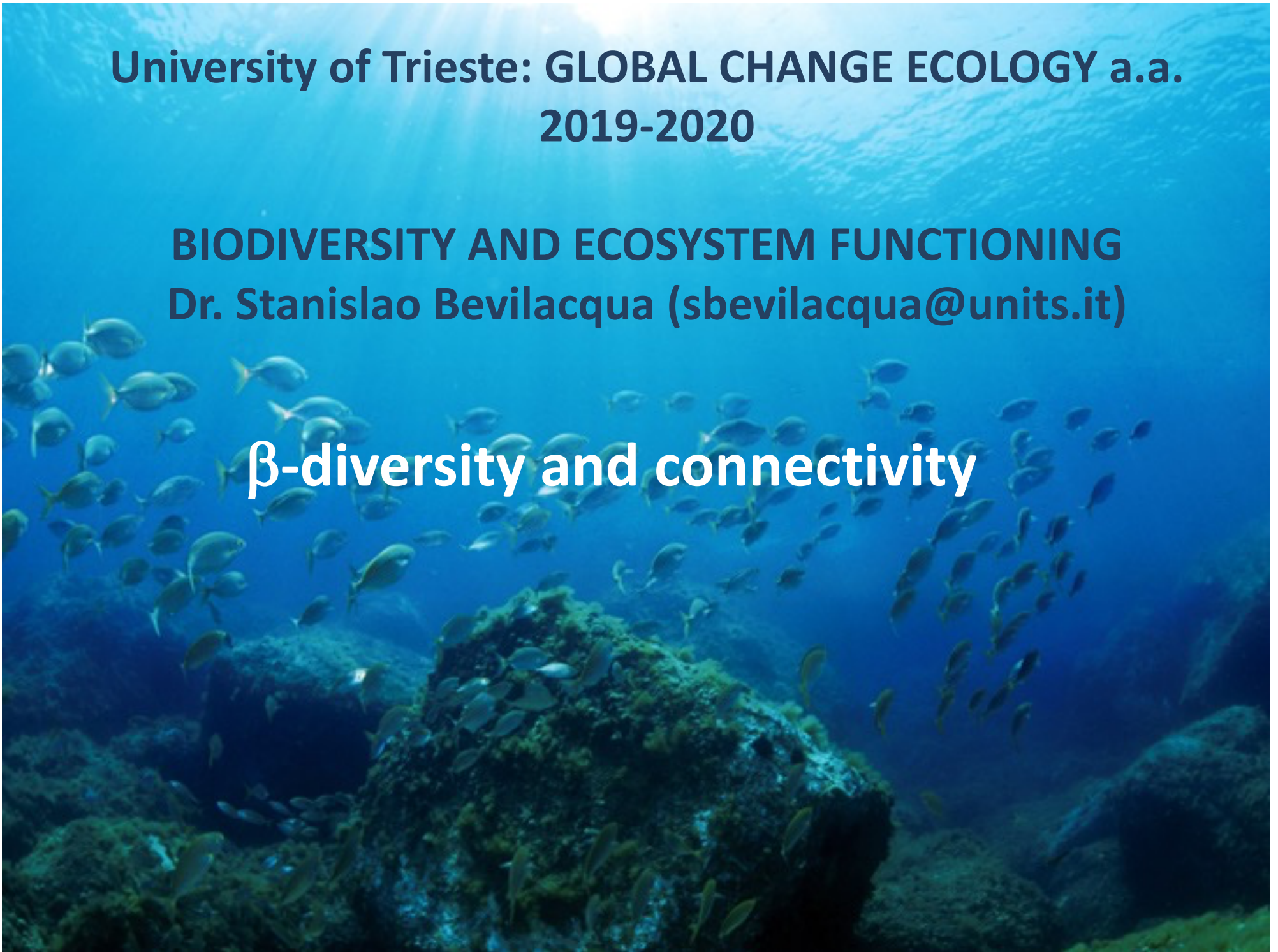


**University of Trieste: GLOBAL CHANGE ECOLOGY a.a.  
2019-2020**

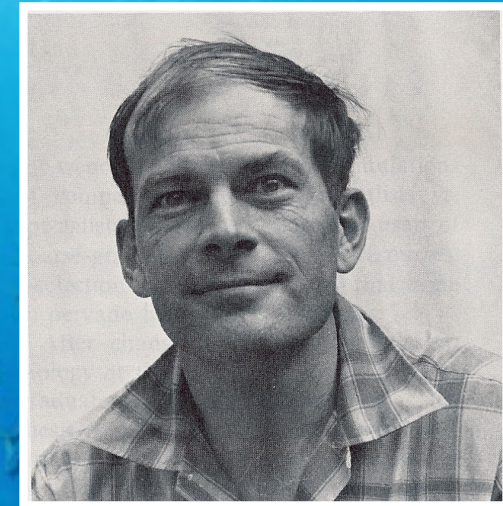
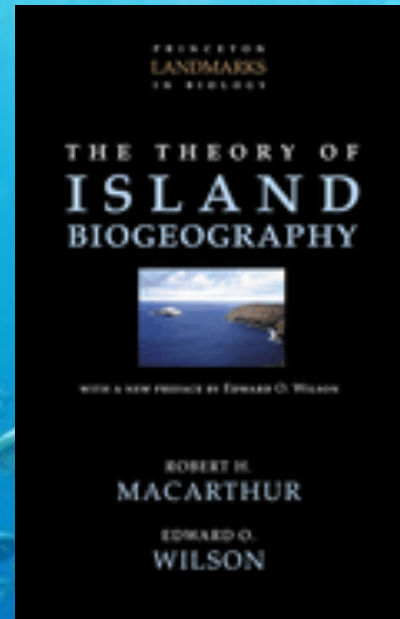
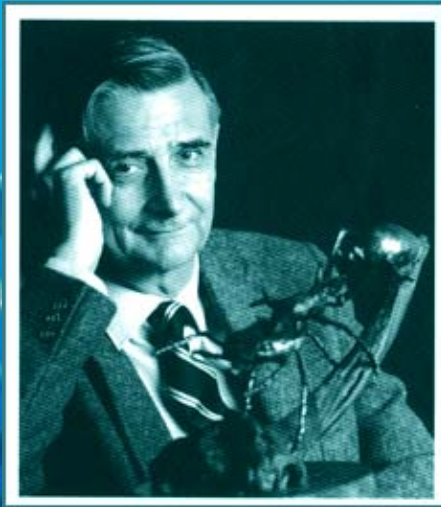
**BIODIVERSITY AND ECOSYSTEM FUNCTIONING**  
**Dr. Stanislao Bevilacqua (sbevilacqua@units.it)**

**$\beta$ -diversity and connectivity**



# The Theory of Island Biogeography

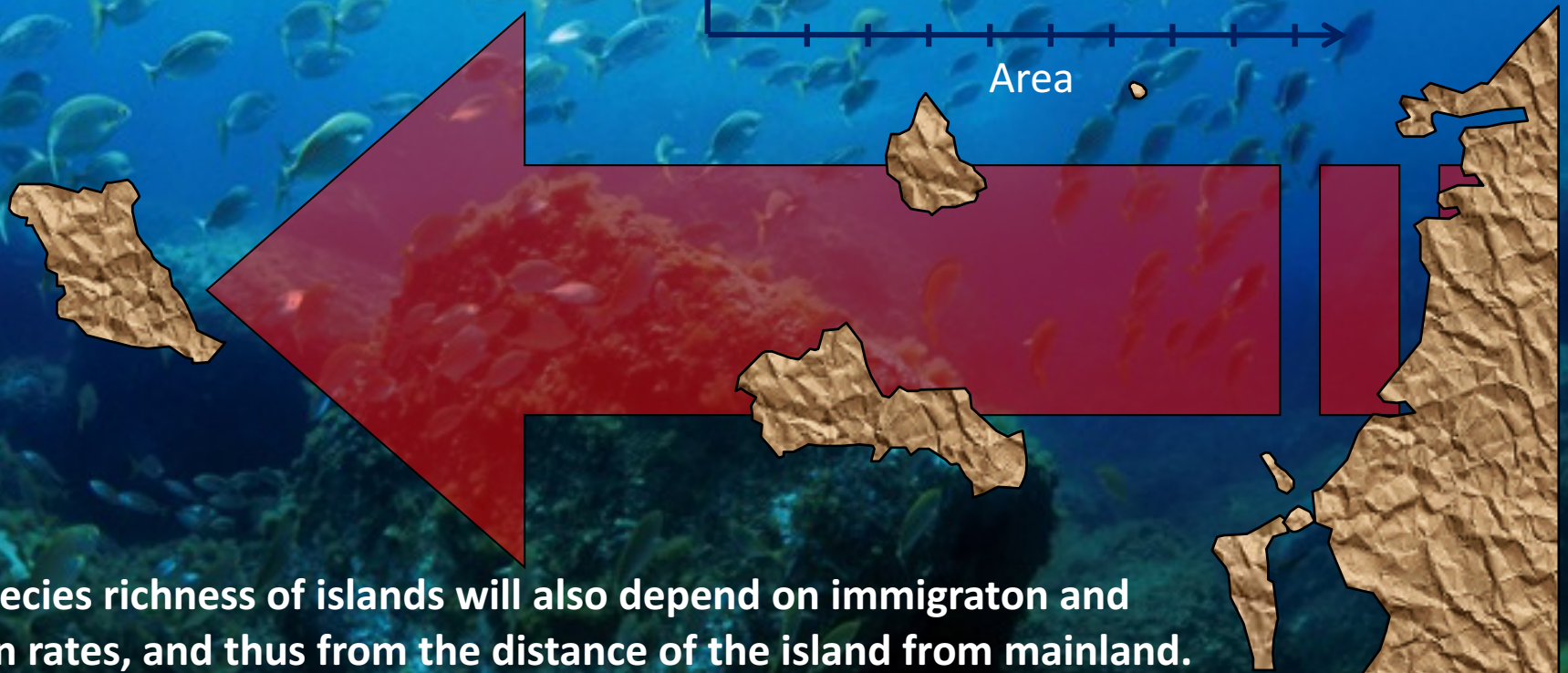
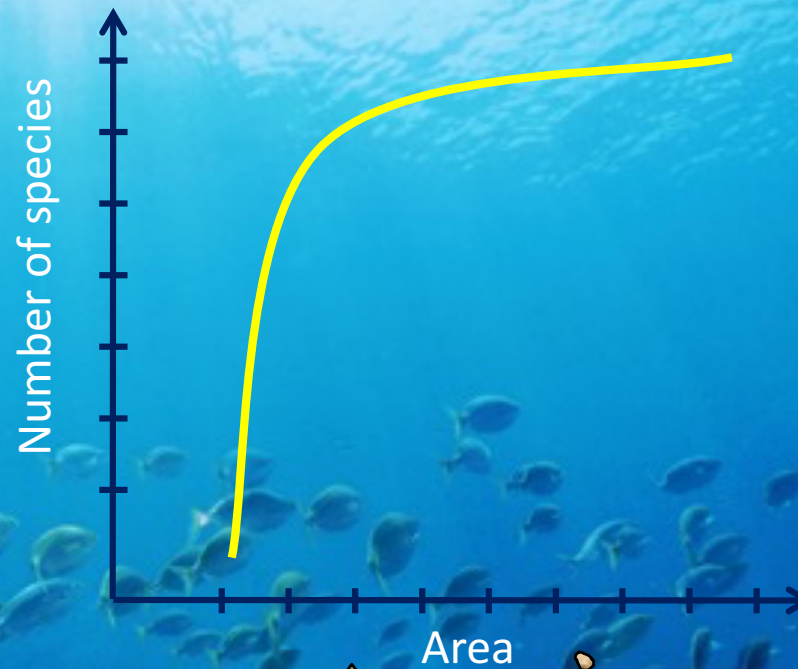
Robert H. MacArthur and Edward O. Wilson (1967)



Theory is based on the concept of 'island', which true islands (portions of land surrounded by water) are only one representation. Everything 'isolated' is an 'island'. Also, depending on the scale considered, even different portions of continuous environments can be considered as islands.

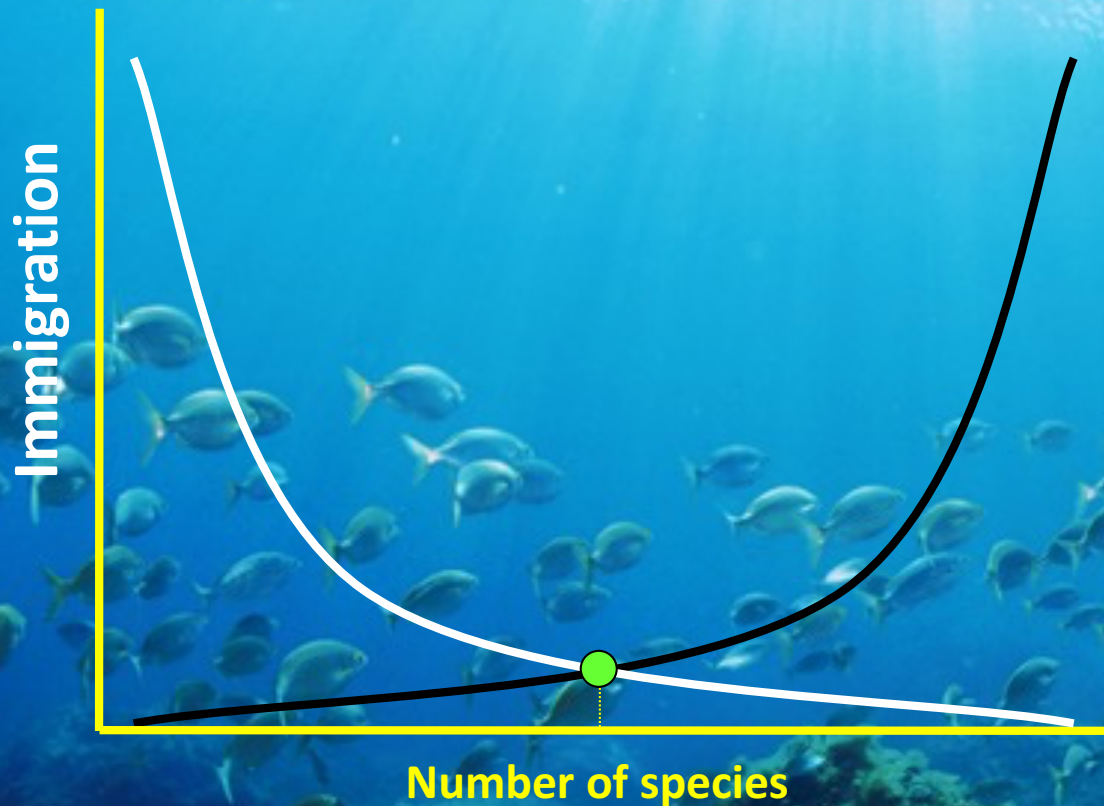
# Distance form the “source”

The species-area relationship predicts that the number of species increases at increasing sampled surface. Therefore, the number of species in a give island will depend on it size (surface), the larger the islands the higher the number of species.



In TIB, species richness of islands will also depend on immigration and extinction rates, and thus from the distance of the island from mainland.

# Immigration and extinction



**Initial rate of immigration is high (island is empty and each new arrival likely represent a new species)**

**Extinction**  
As species number increase, immigration decrease, because of biotic interactions and saturation, and tends to 0 as the number of species tends to reach that of the source

Extinction is 0 at the beginning, when no species are on the island, and is low when few species reach the island. Then it rapidly increase because of competitive exclusion and predation. Densities are lower than before and population more prone to casual extinction (e.g. diseases).

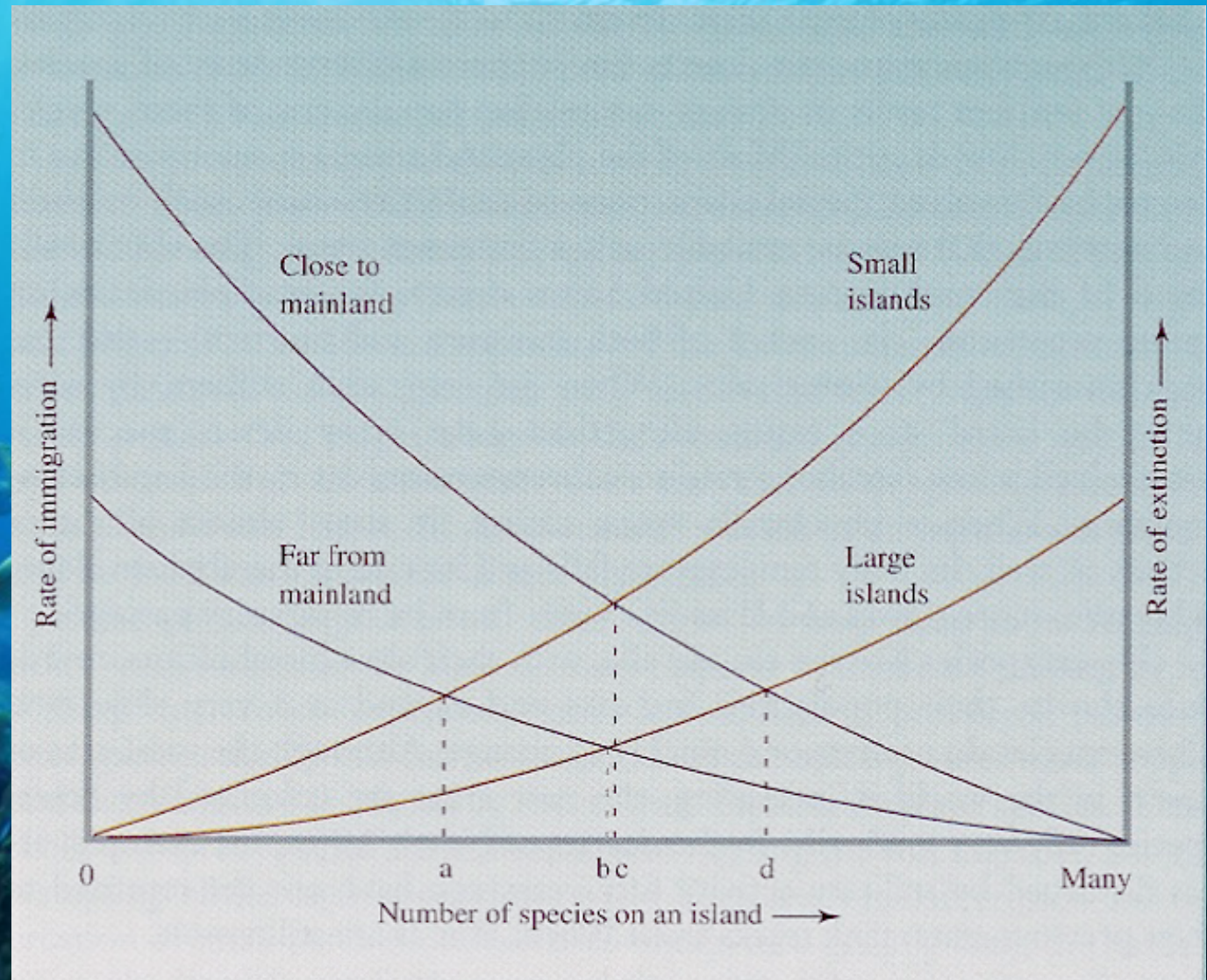
- 1) The number of species is the result of the balance between immigration and extinction
- 2) This balance is dynamic, because species will go extinct and will be replaced by others continuously
- 3) The immigration rate will depend mostly on distance form the source
- 4) The extinction rate will depend mostly on the size of the island

# Scenarios

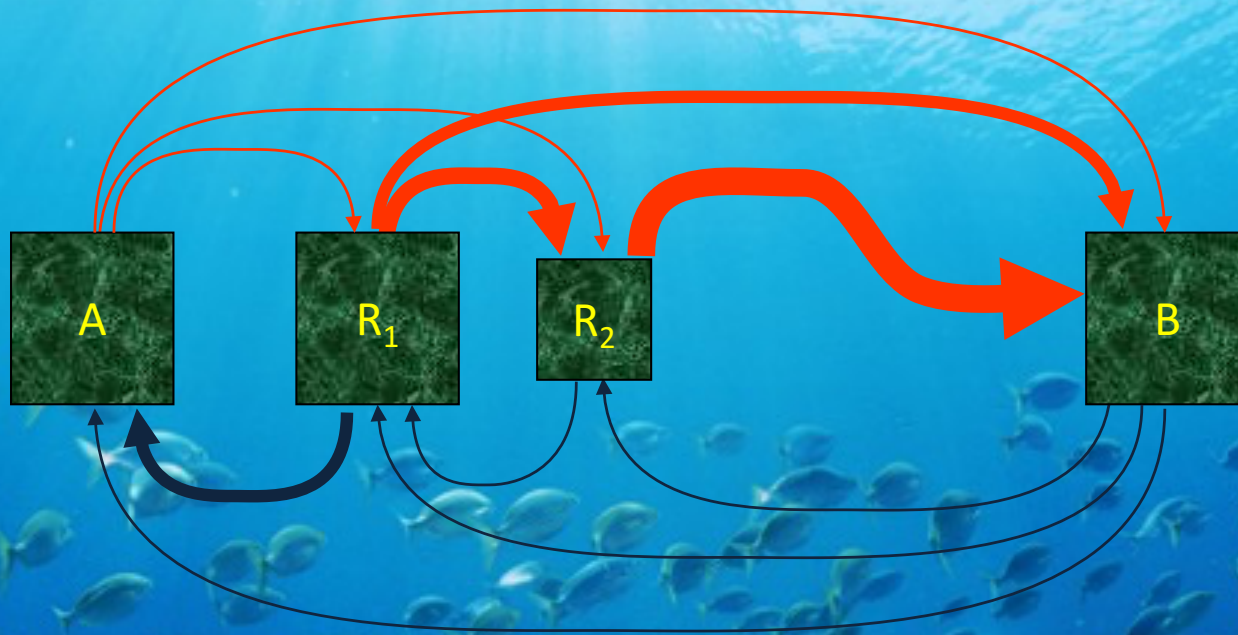
Shape of the immigration curve depends on the distance from the source: the closer the source the higher the immigration rate. The size of island also influence

Immigration, because larger islands are more likely to intercept propagules than smaller ones, and offer more habitats.

Extinction is strongly influenced by island size, because of reduced resources, habitat availability, and higher probability to compete with other species in smaller islands with respect to larger ones



# Stepping stones



Stepping stones are islands (or patches) that may help connection between the source of species and the receiving island (or patch). If too close to the source or too small they do not contribute substantially to connection. The same occurs if they are too far from the receiving islands. They may help weak dispersers to reach the island that is too far from the source to allow a direct colonization of such species.

# Populations

A population is a group of individuals of the same species that live in a given area, this group being spatially, genetically or demographically disjointed from other groups.

Populations can be also defined on the basis of research interests, which can fix the limit of population.

birth

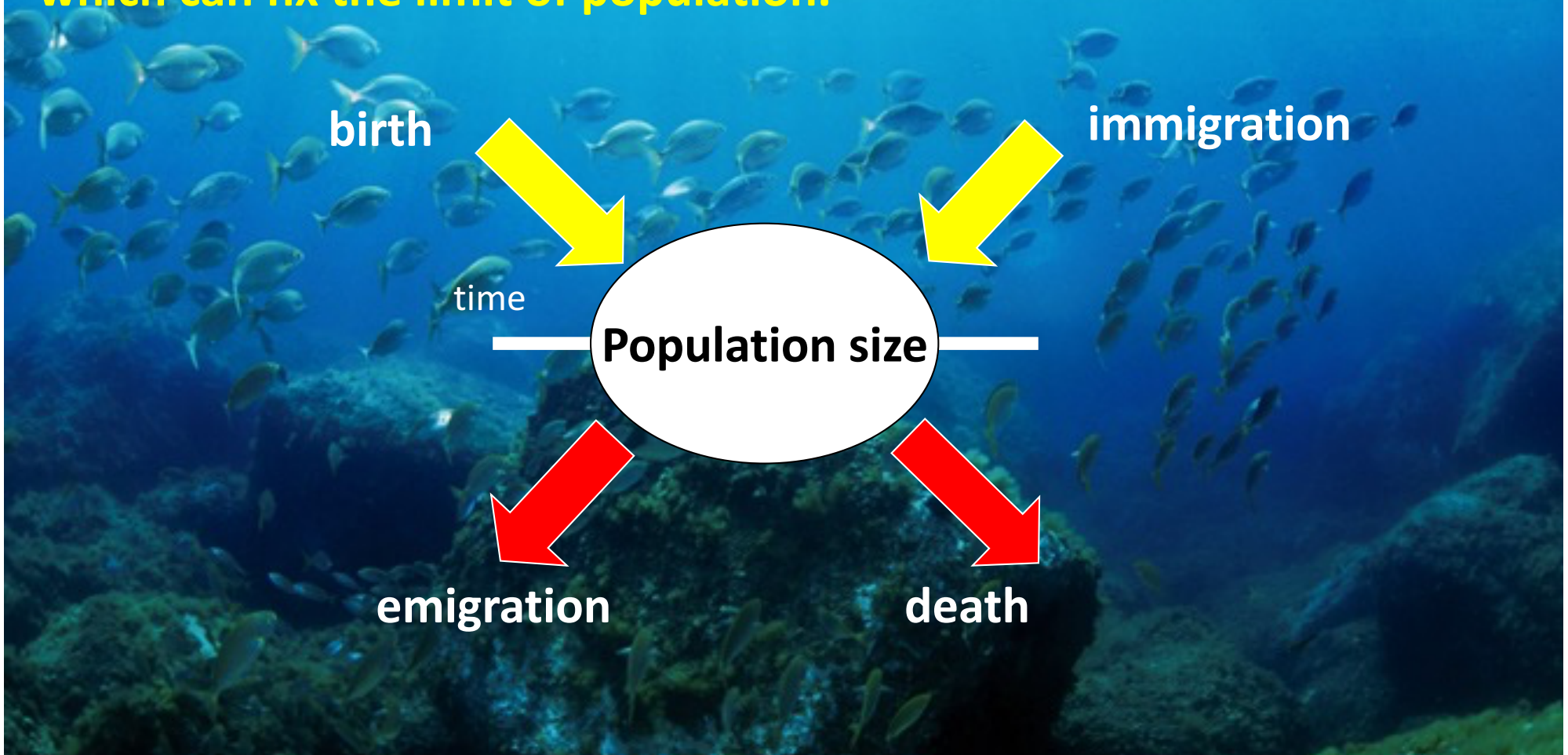
immigration

time

Population size

emigration

death

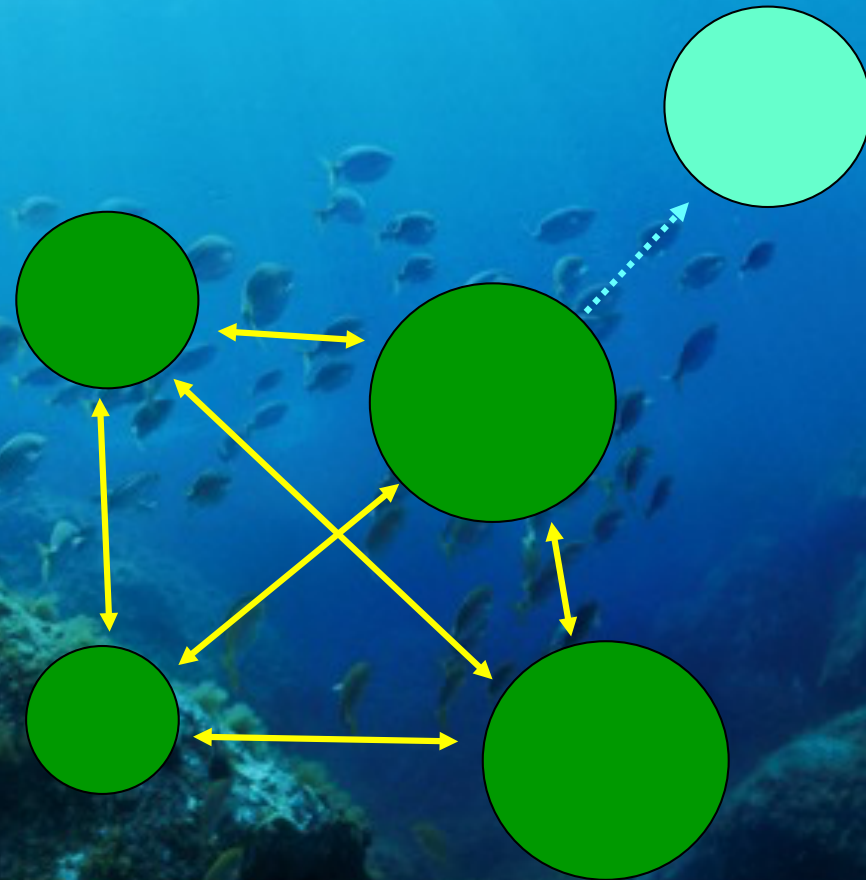


# Metapopulations

**Metapopulations are groups of populations in which there are one or more core populations stable in time, and satellite populations undergoing temporal fluctuations.**

Levins, 1969

The habitat can be modelled as a set of patches. Some of which productive, due to favourable environmental conditions for the species to thrive, and other unproductive. Productive patches produce emigrants that can colonize satellite patches. This model identifies productive patches as 'sources', and receiving patches as 'sink'. Sinks are unproductive patches where mortality exceed birth, due to unfavourable conditions. Their persistence depend on immigration from sources.



**Sinks may experience extinction and subsequent recolonization**

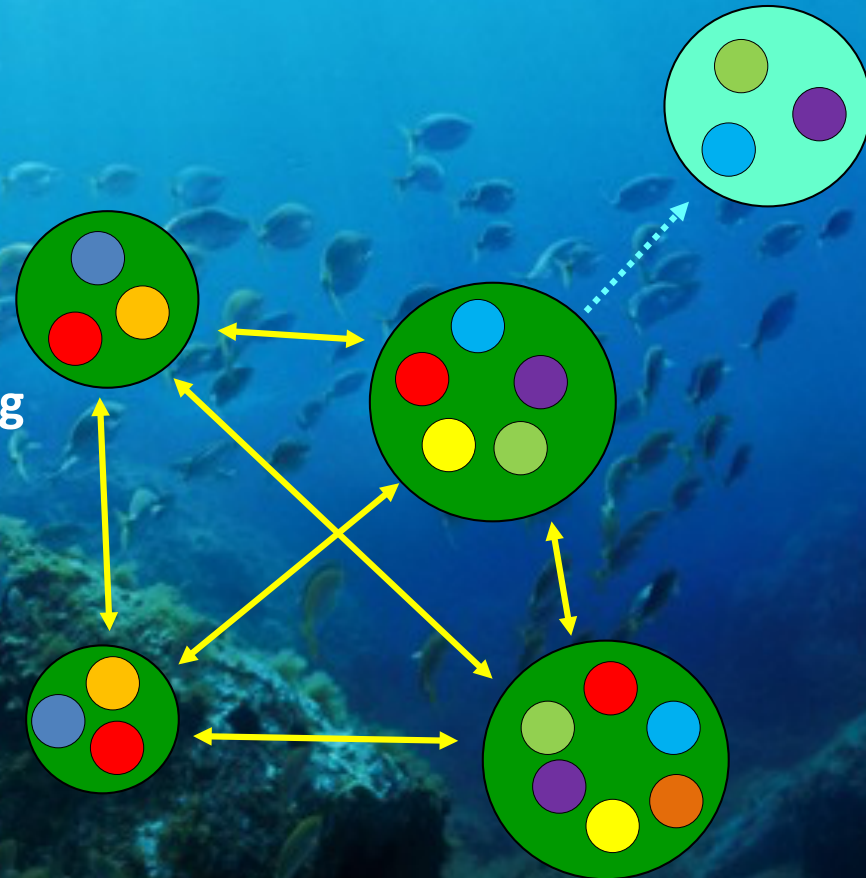


# Metacommunities

Metacommunities are sets of communities interconnected by dispersal, immigration and/or emigration of multiple (interacting or potentially interacting) species

(Gilpin and Hansky, 1991)

Sink-source  
Species sorting (environmental filtering and biotic interactions)  
Patch dynamic  
Stochasticity (neutral theory)



# Supply-side ecology

Supply-side ecology relates to the consequence to structure and dynamics of assemblages due to variations in numbers and timing of offspring arriving into any portion of habitat. (Lewin 1986)

More generally, includes the arrival of individuals from any planktonic stage of life cycle.

It focus on the role of larval (and more generally of propagules) supply in shaping the structure of marine assemblages, besides biological interactions that may have a role only *after* colonization (settlement and/or recruitment) of patches.

This because the first step in community formation is that colonizers reach the empty patch. Predators have to reach the area in sufficient number to exert their influence in structuring the community. The same is true for dominant competitors

# Processes affecting larval supply

## Larval production

(life histories – production of eggs, sperms; asexual propagules; fertilization success)

## Dispersal ability

(life cycle – planktotrophic, lecithotrophic, adult dispersal; duration of larval stage)

## Larval transport

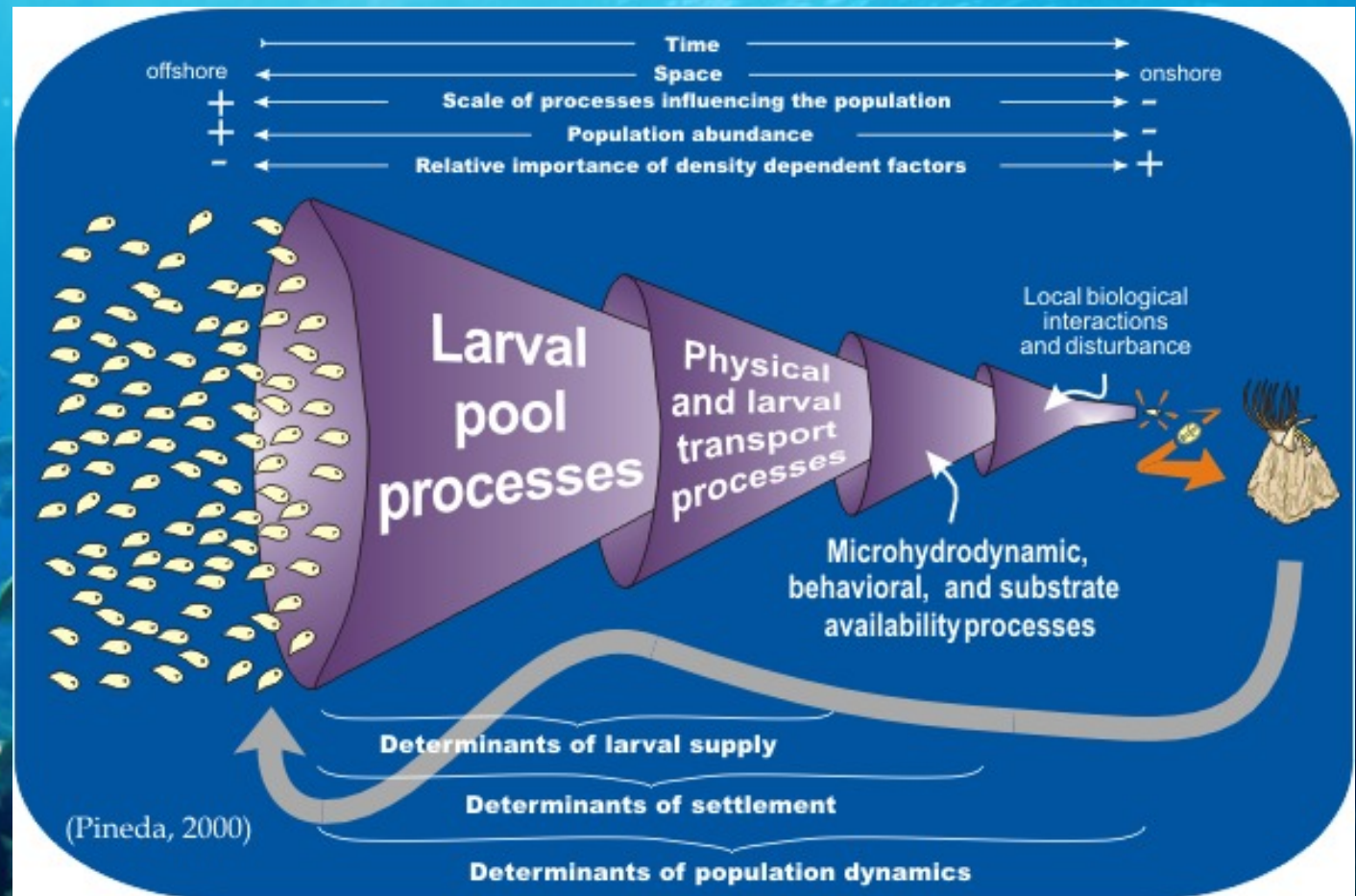
(currents, vectors, isolation)

## Larval mortality

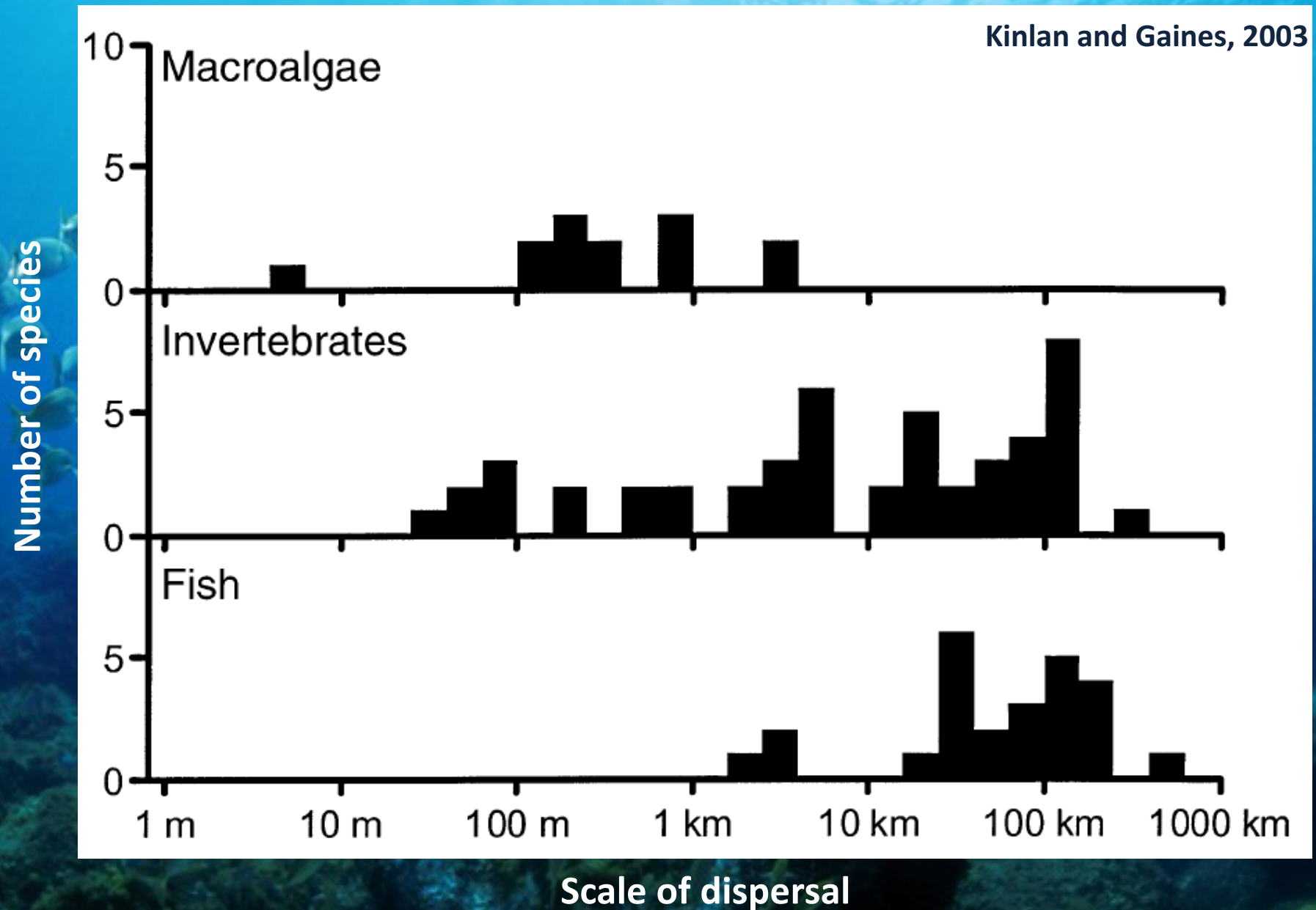
(predation in the water column, disturbance, limiting food resources, sinking/advection)

## Settlement

Predation, biological disturbance (e.g. whiplash, bulldozing, overgrowth), environmental disturbance.

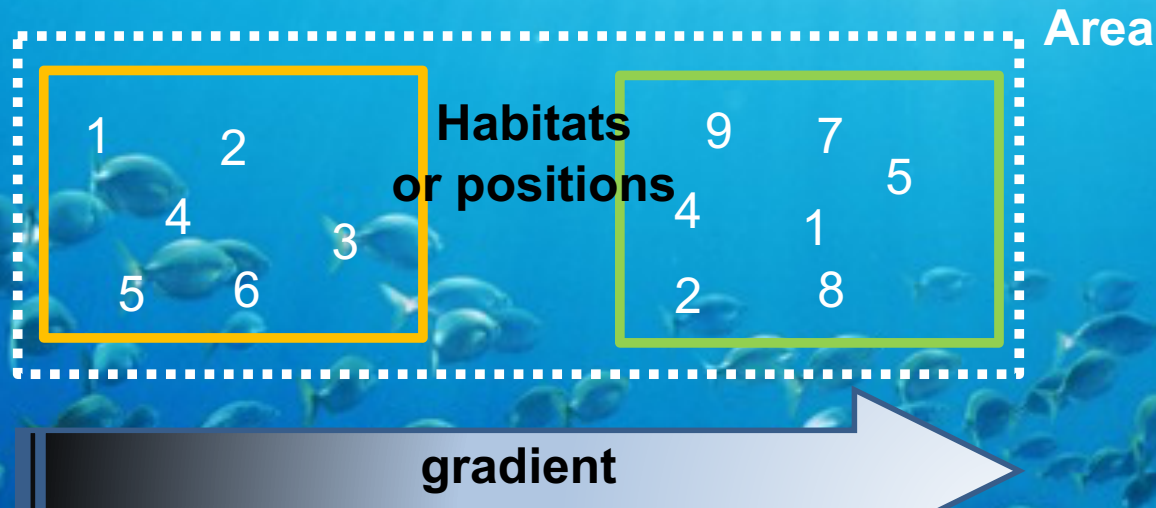


# Dispersal potential in marine species



# $\beta$ -diversity: basic concepts

The extent of change in community composition, or degree of community differentiation, in relation to a complex-gradient of environment, or a pattern of environments (Whittaker 1960).



## $\gamma$ -diversity

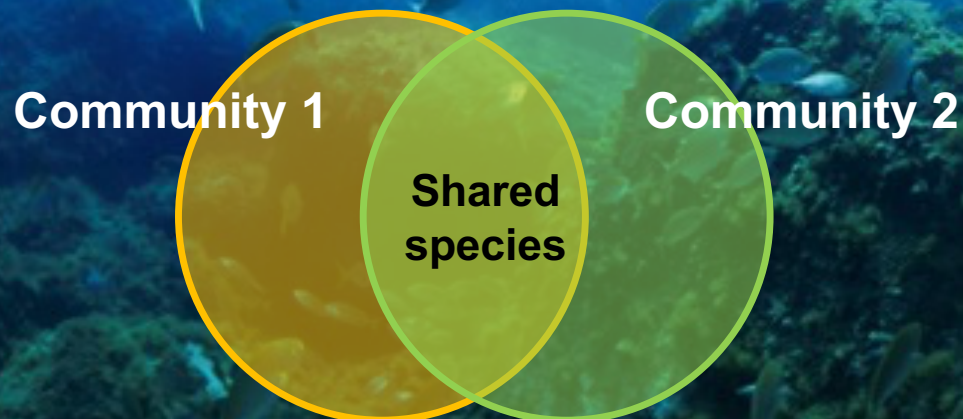
the total diversity in the landscape

## $\alpha$ -diversity

the local (site or habitat) diversity

## $\beta$ -diversity

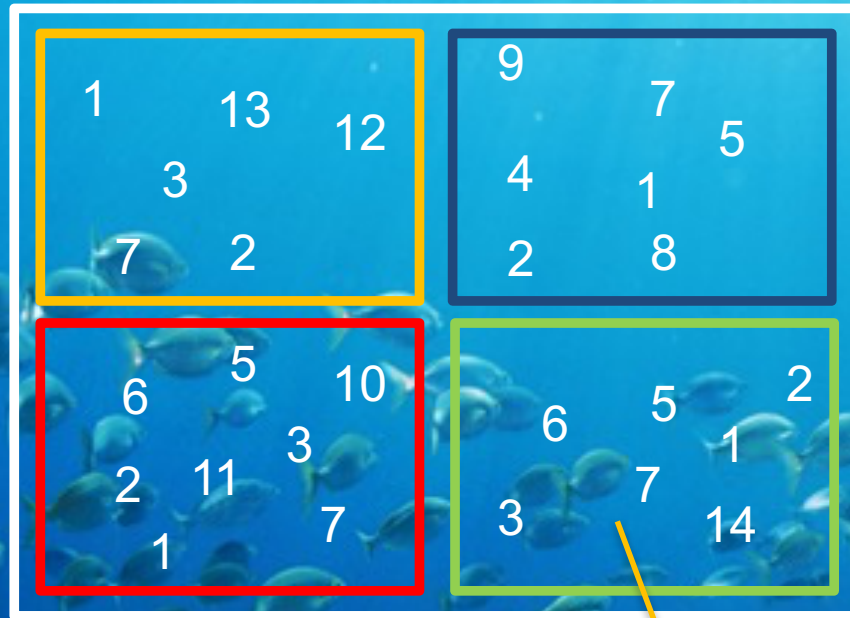
the differentiation diversity between sites or positions



$$\beta = \frac{b+c}{a+b+c}$$

Jaccard distance

# $\beta$ -diversity: linking local to regional diversity



$$\bar{\alpha} = 7$$
$$\gamma = 14$$

$$\beta = \gamma / \bar{\alpha}$$

Area

Site

$\beta$ -diversity, generally defined as variation in the identities of species among sites, provides a direct link between biodiversity at local scales ( $\alpha$ -diversity) and the broader regional species pool ( $\gamma$ -diversity) (Whittaker 1960, 1972).  
Species turnover (replacement in species composition)

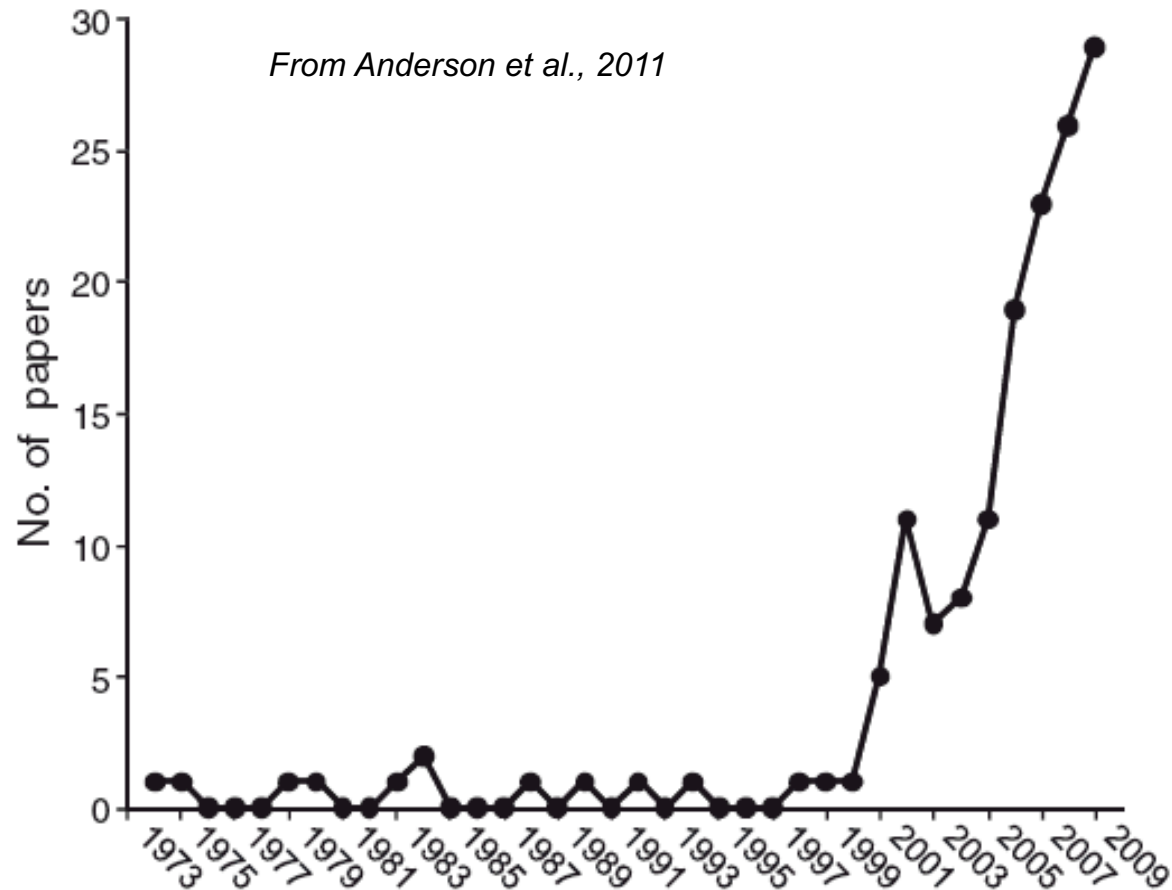
# A diversity of $\beta$ -diversities

Notation	Definition	Measurement unit [range]			
$\beta_{Md}$	true beta diversity = $\gamma/\alpha_d$	CU [1 CU to $N$ CU]	n.n.	average of all pairwise beta component values with compositional data taken from outside the sampling units of interest	as in the chosen beta component
$\beta_{Mt}$	regional-to-local diversity ratio = $\gamma/\alpha_t$	$sp_E/sp_E$ [1 to $N$ ]	$\Delta\gamma/\Delta x$	rate of gamma diversity accumulation with increasing (logarithm of the) number of sampling units	$sp_E/SU$ or $sp_E/\log(SU)$
$\beta_{At}$	absolute effective species turnover = $\gamma - \alpha_t$	$sp_E$ [0 to $(N-1)\alpha_t$ ]	$\Delta\alpha_t/\Delta x$	rate of alpha diversity accumulation when sampling unit size increases in multiples of (logarithm of the) original size	$sp_E/SU$ or $sp_E/\log(SU)$
$\beta_{Mt-1}$	Whittaker's effective species turnover = $(\gamma - \alpha_t)/\alpha_t = \gamma/\alpha_t - 1$	$sp_E/sp_E$ [0 to $N-1$ ]	$\Delta\log(\gamma)/\Delta x$	rate of gamma entropy accumulation with increasing logarithm of the number of sampling units	$\log(sp_E)/\log(SU)$
$\beta_{Pt}$	proportional effective species turnover = $(\gamma - \alpha_t)/\gamma = 1 - \alpha_t/\gamma$	$sp_E/sp_E$ [0 to $1 - 1/N$ ]	$\Delta\log(\alpha_t)/\Delta x$	rate of alpha entropy accumulation when sampling unit size increases in multiples of the logarithm of original size	$\log(sp_E)/\log(SU)$
$\Delta c$	any of the effective species turnover measures, i.e. $\beta_{At}$ , $\beta_{Mt-1}$ or $\beta_{Pt}$	as in the chosen turnover	$\Delta\beta_M/\Delta x$ or $\Delta\Delta c/\Delta x$	rate of change in a beta component of diversity with increasing number of sampling units	(unit of the beta component)/SU
$\beta_{Mtot}$ or $\Delta c_{tot}$	a beta component quantified for the entire dataset	as in the chosen beta component	$\Delta\beta_M/\Delta x$ or $\Delta\Delta c/\Delta x$	decay rate of a beta component of diversity when sampling unit size increases in multiples of original size	(unit of the beta component)/SU
$\beta_{Mj,k}$ or $\Delta c_{j,k}$	a beta component quantified for a subset of the dataset that consists of the sampling units $j$ and $k$	as in the chosen beta component	$\Delta\beta_{Pt}/\Delta x$	proportional effective species turnover accumulation rate when an increasing proportion of the available sampling units is taken into account	$(sp_E/sp_E)/SU$
$\overline{\Delta c}_{j,k}$	average of all the species turnover values that can be calculated for different sampling unit pairs in the dataset (with $j \neq k$ )	as in the chosen turnover	$\Delta\log({}^q\beta_M)/\Delta x$	rate of change in beta entropy or regional entropy excess with increasing logarithm of the number of sampling units	(unit of entropy)/ $\log(SU)$ , e.g. bits/ $\log(SU)$
$\overline{\Delta c}_{j,centr}$	average of all the species turnover values that can be calculated between a real sampling unit and a regional compositional centroid in the dataset	as in the chosen turnover	n.n.	species diversity or entropy accumulation rate with alpha and gamma diversities based on different data	as in the chosen accumulation rate
$\Delta c_{j,kmax}$ or $\Delta c'_{kmax}$	compositional gradient length in the dataset along the compositional dimension with most turnover	as in the chosen turnover	$\Delta c_{(\Delta g)}/\Delta g$	compositional turnover rate along a specified section of an external gradient $g$	(unit of chosen turnover)/(unit of external gradient)
$\Delta c_{(\Delta g)}$	compositional gradient length along a specified section of an external gradient $g$	as in the chosen turnover	$\Delta\Delta c_{(\Delta\Delta g)}/\Delta\Delta g$ or $\Delta\log(1 - \Delta c_{(\Delta\Delta g)}/\Delta\Delta g)$	rate of change in (the logarithm of the one-complement of) pairwise effective species turnover with increasing distance along an explanatory gradient $g$ (slope of a distance decay regression)	(unit of chosen turnover)/(unit of external gradient) or $\log(\text{unit of turnover})/(\text{unit of external gradient})$
$\Delta\Delta g_{(\Delta\log(1-\Delta c))}$	number of half-change units, i.e. observed amount of change in differences in explanatory gradient $g$ expressed in terms of decrease in compositional similarity	(unit of $g$ )/(unit of $g$ )			
$\overline{\Delta c}_{j,F}$	compositional distinctness of the focal sampling unit F	as in the chosen turnover			
n.n.	compositional nestedness of a species-poor sampling unit in a more species-rich one	sp/sp			
n.n.	logically inconsistent beta components in which $\alpha$ and $\gamma$ are based on different datasets	as in the chosen beta component			

*From Tuomisto, 2010*

**How heterogeneously distributed are species within a given area. This has led to multiple definition of beta-diversity related to different aspects of heterogeneity in species distribution and different metrics to measure these aspects**

# The role of $\beta$ -diversity in ecology

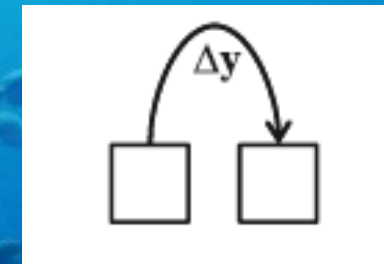
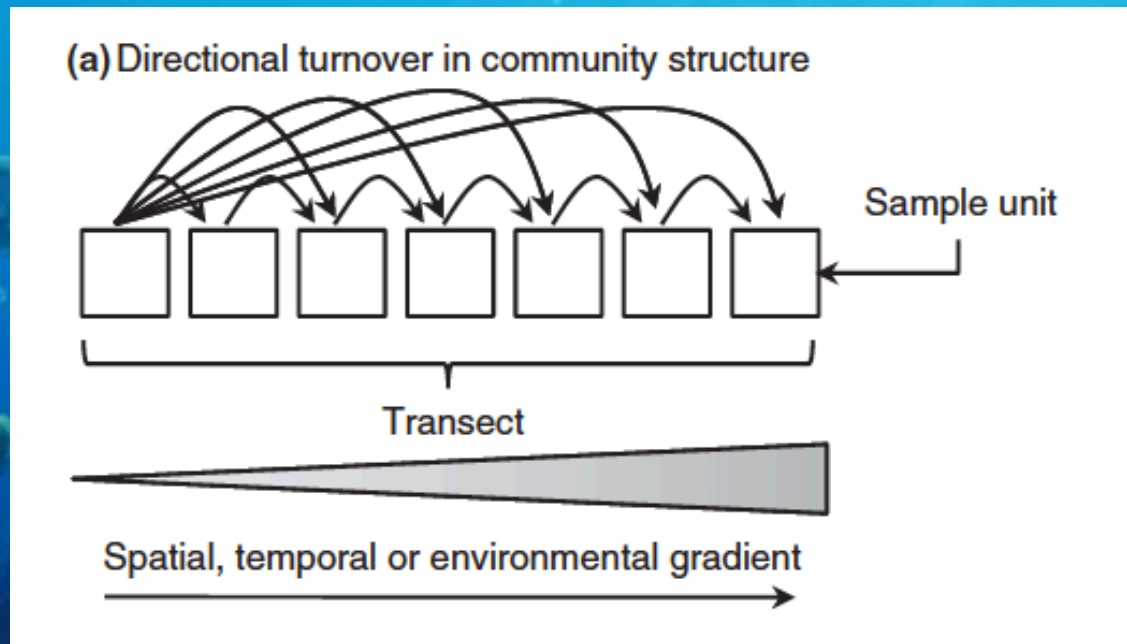


ENVIRONMENTAL SCIENCES  
ECOLOGY  
BIODIVERSITY CONSERVATION  
ZOOLOGY  
MICROBIOLOGY  
MARINE FRESHWATER BIOLOGY  
ENTOMOLOGY  
PLANT SCIENCES  
EVOLUTIONARY BIOLOGY  
WATER RESOURCES  
MYCOLOGY  
FORESTRY  
OCEANOGRAPHY  
FISHERIES

Increasing concern about beta-diversity in ecological and environmental studies



# $\beta$ -diversity: directional change between communities

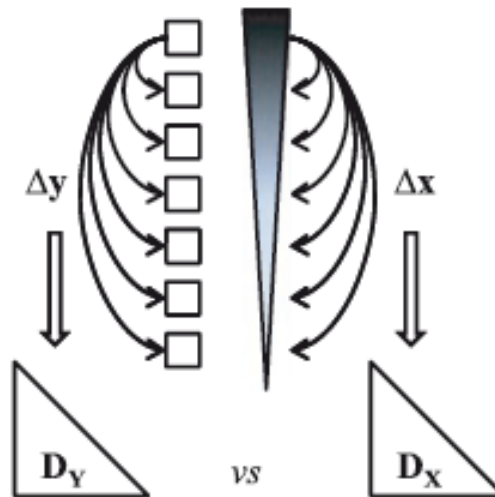


Measure of turnover between communities

Changes occurring among communities along a gradient

# Modelling directional $\beta$ -diversity

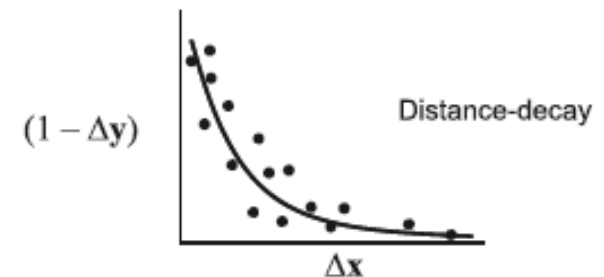
T3. Model pair-wise dissimilarities in communities as a function of pair-wise spatial, temporal or environmental distances.



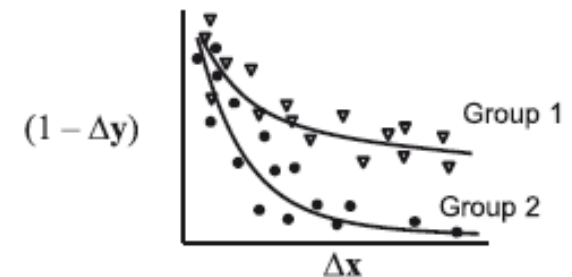
Find correlation between turnover and changes along a gradient

Estimate rate of turnover or comparing rates among groups

T4. Estimate the rate of turnover along a spatial, temporal or environmental gradient.

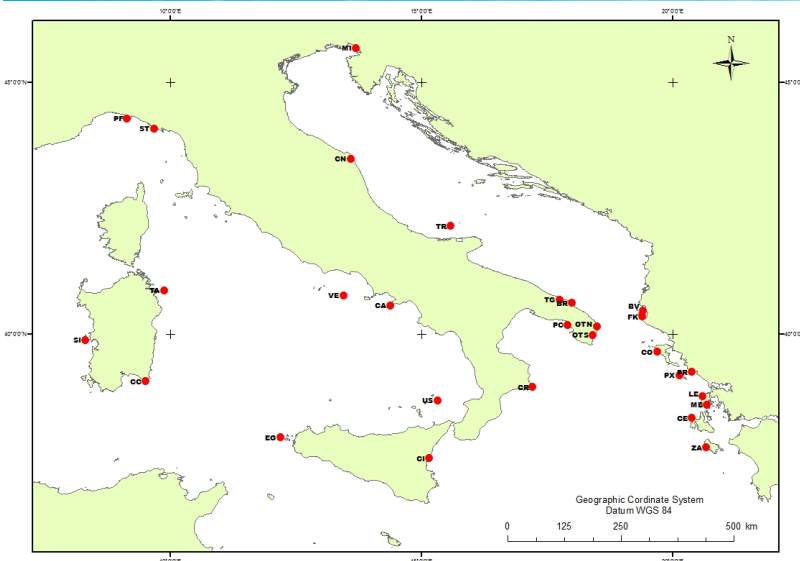


T5. Compare rates of turnover along one gradient for different groups of species or taxa.

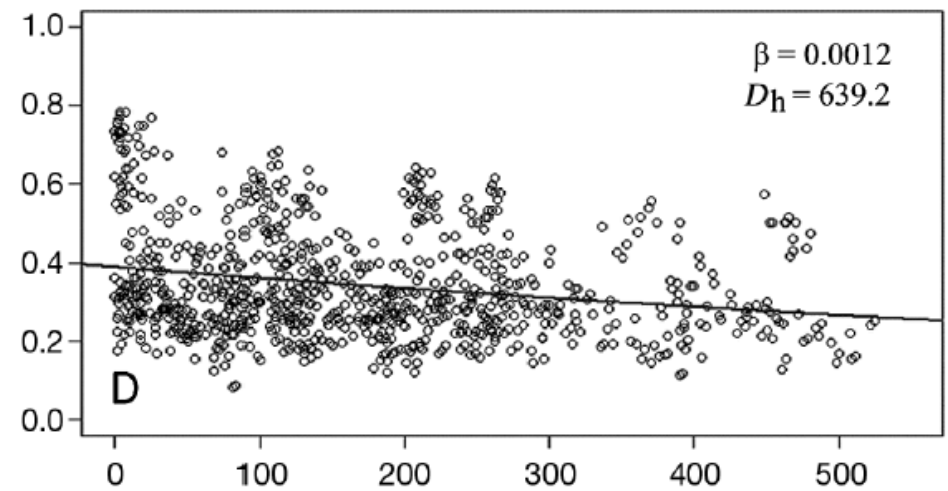
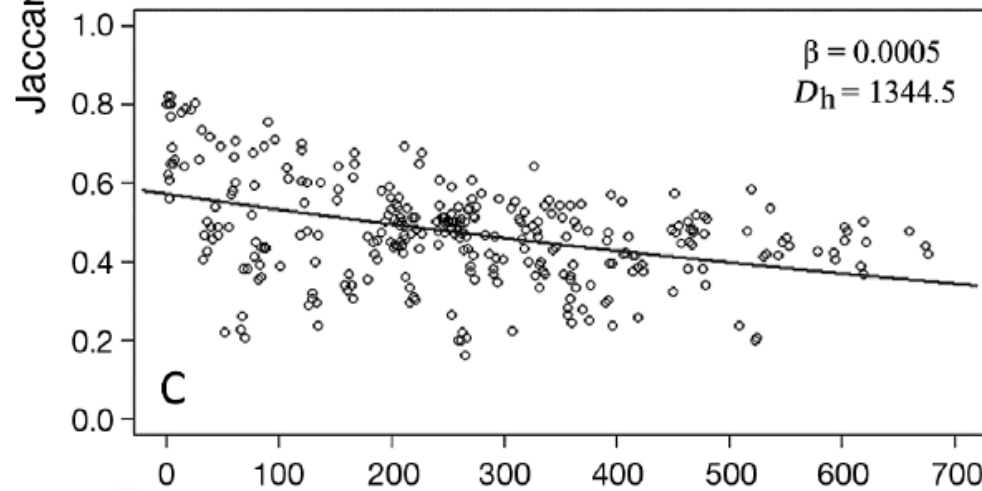
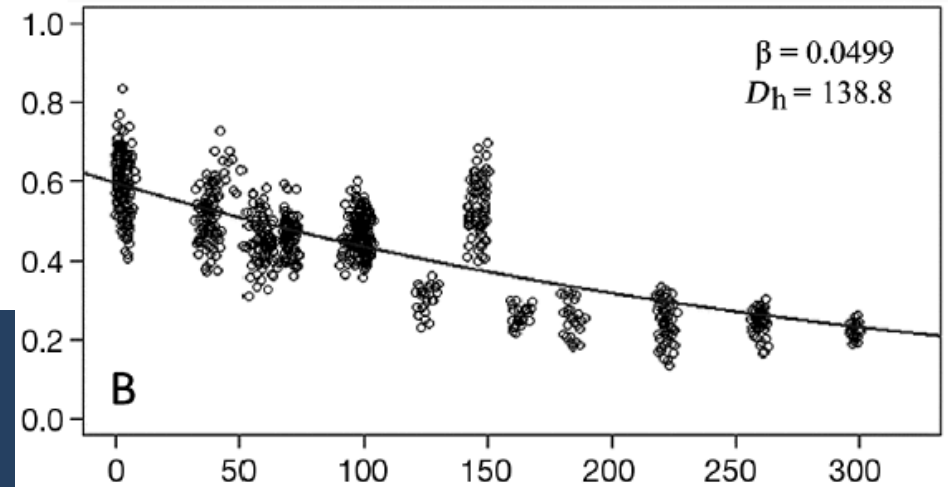


# An example in the Mediterranean sea

## Distance-decay of similarity in composition



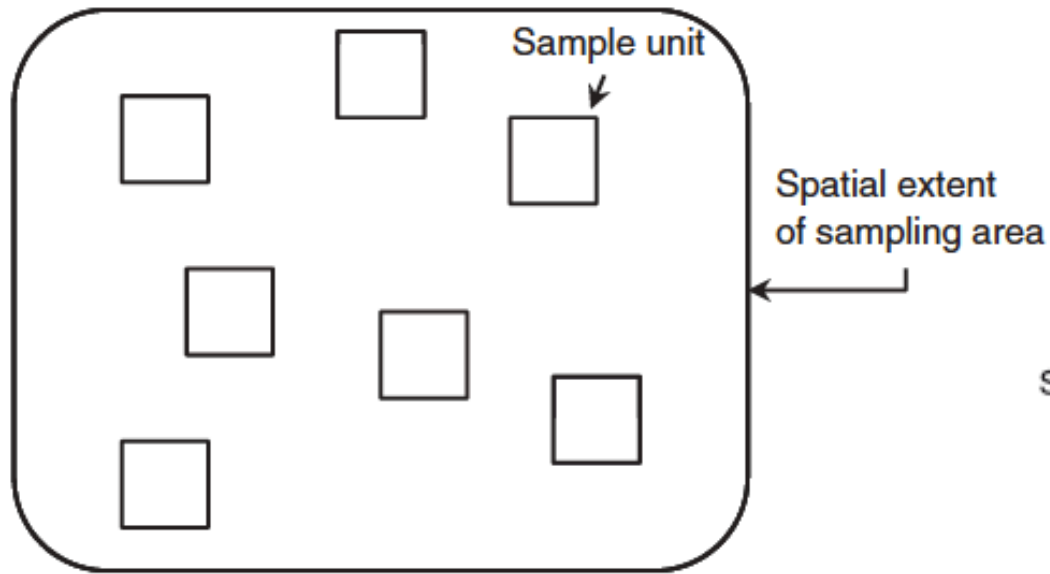
### Mediterranean shallow subtidal sessile assemblages



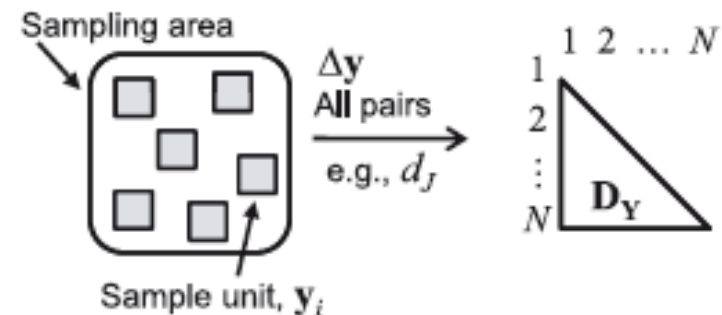
Least-cost paths distance (km)

# $\beta$ -diversities as variation

(b) Variation in community structure (non-directional)

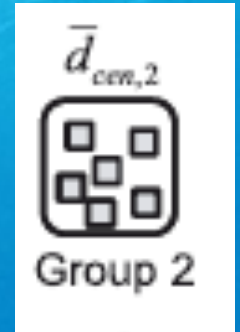
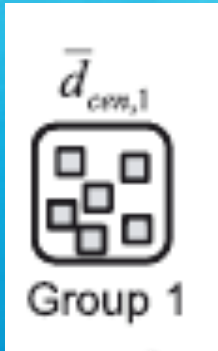


V1. Measure variation among communities from a set of samples.



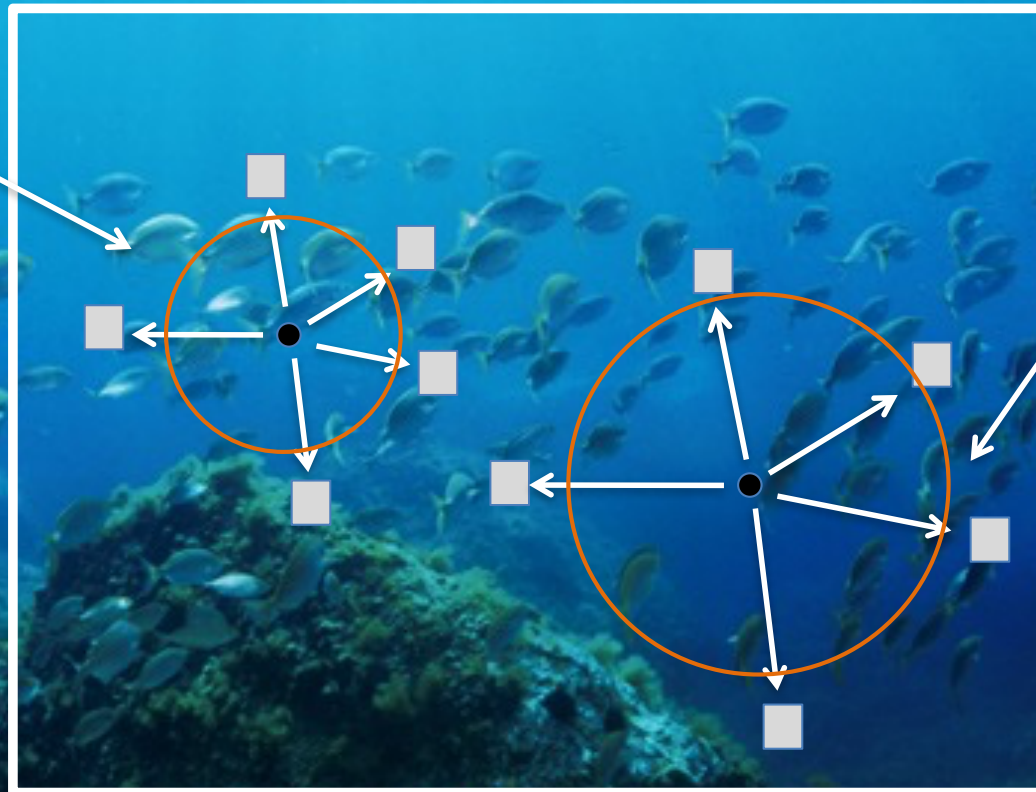
Changes occurring occurring in community composition among a set of sample units within a given spatial, temporal, or environmental extent

# Multivariate dispersion as a measure of $\beta$ -diversity



Multivariate space

Different distance  
metric = different  
meaning

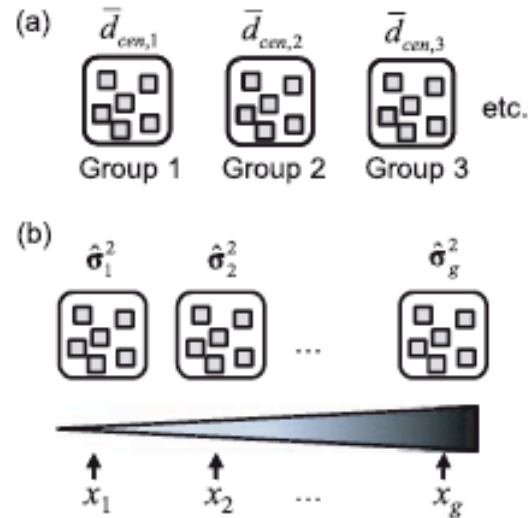


Average distance to centroids

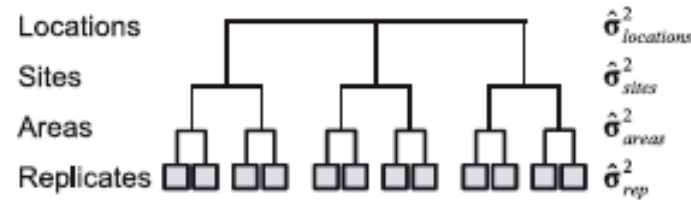
From Anderson, 2006

# Modelling $\beta$ -diversity as variation

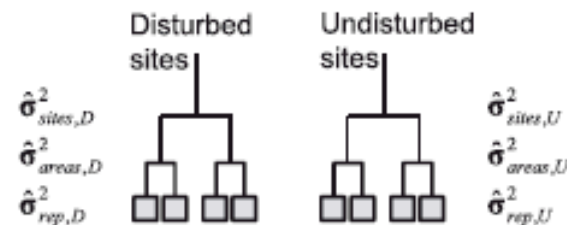
V4. Compare variation either  
 (a) among *a priori* groups or  
 (b) along a continuous gradient.



V5. Partition variation according to a series of hierarchical spatial (or temporal) scales.



V6. Compare components of variation or effect sizes across levels of another factor or for different groups of taxa (V7).



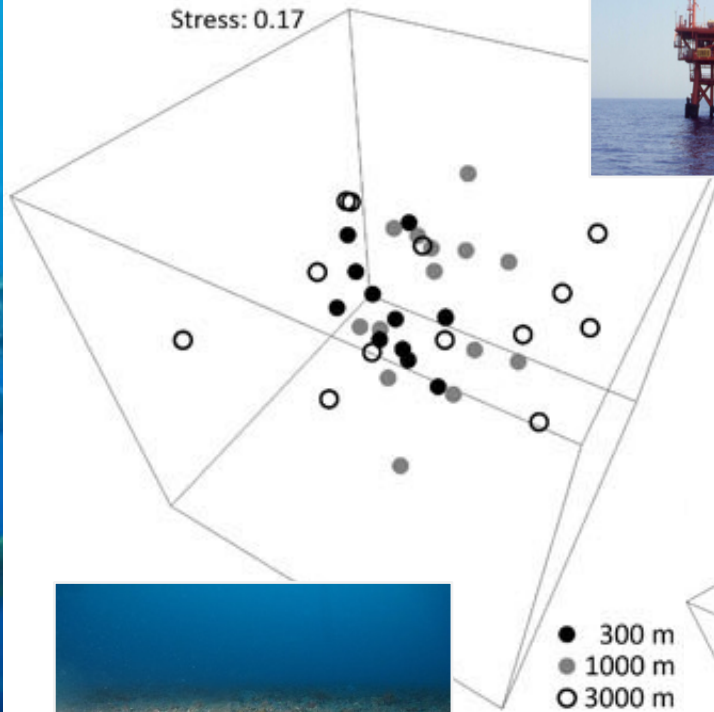
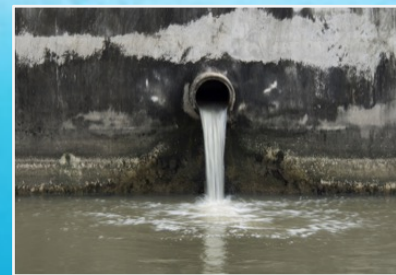
Compare variation among communities, groups of communities, or according to spatial and temporal scales, or other factors

From Anderson et al., 2011

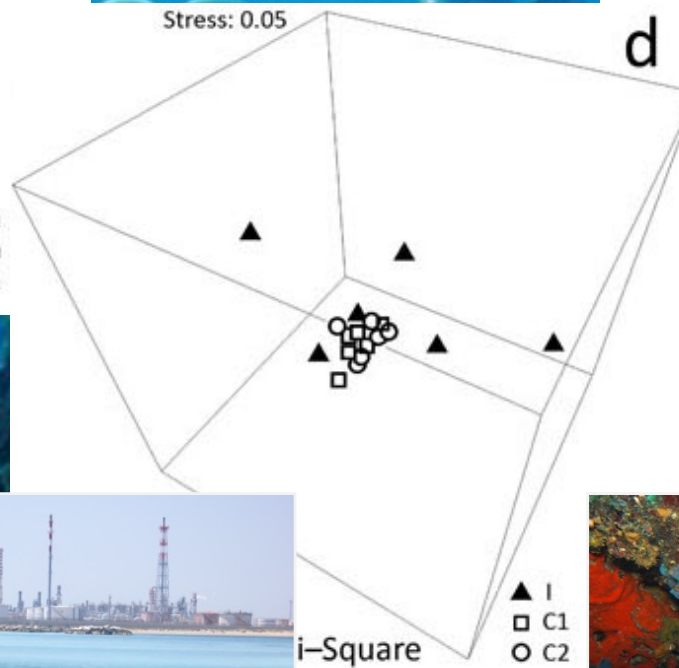
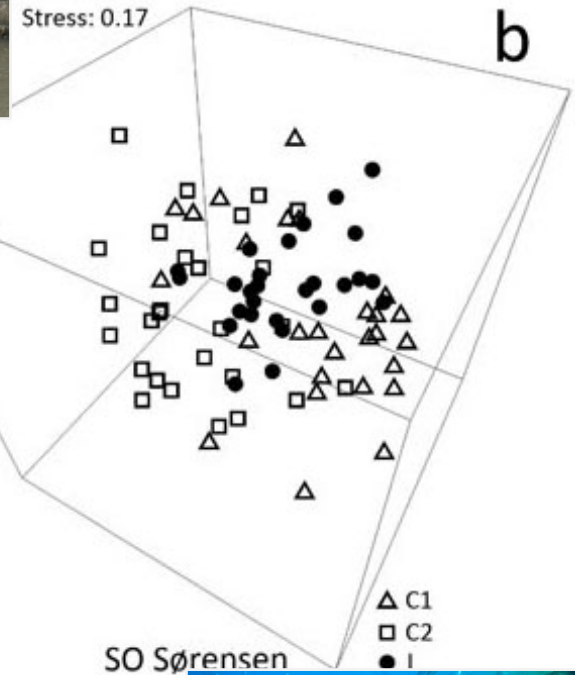
# Case studies on impacts and heterogeneity

Homogenization?

Different structure  
Different  $\alpha$  ( $I <$ )  
Different  $\beta$  ( $I <$ )

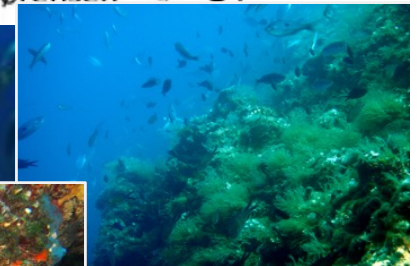


Same structure  
Same  $\alpha$   
Different  $\beta$  ( $I <$ )



SO Sørensen

i-Square

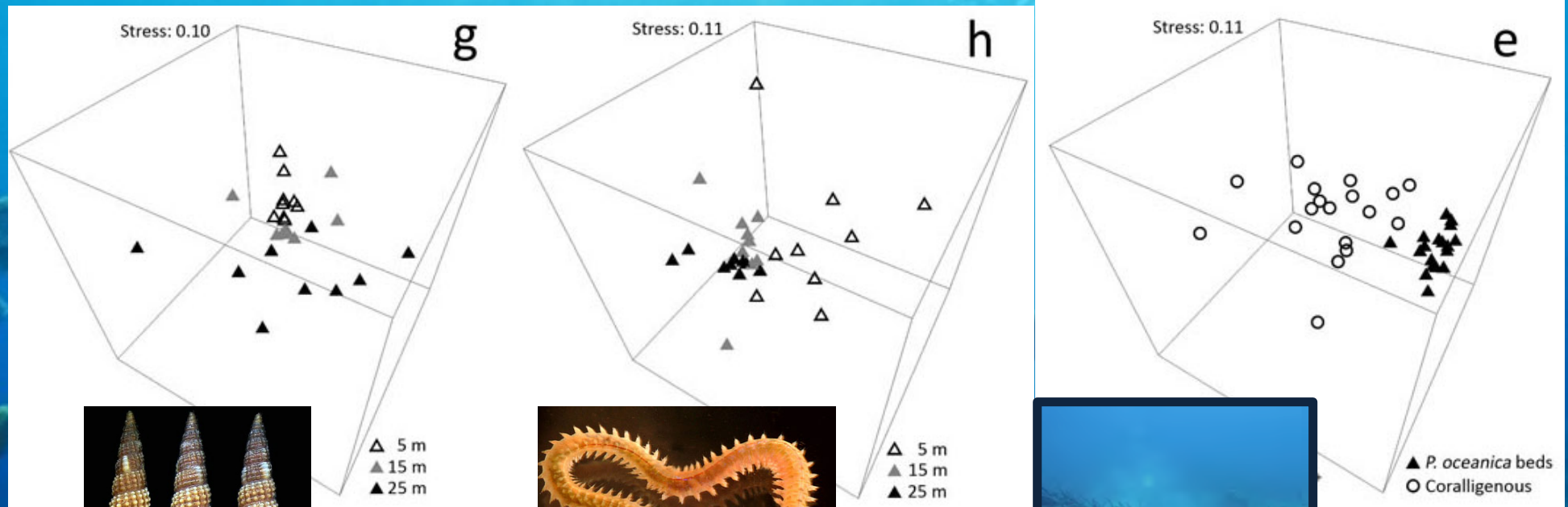


Different structure  
Different  $\alpha$  ( $I <$ )  
Different  $\beta$  ( $>I$ )



From Bevilacqua et al., 2012

# Changes in heterogeneity depends on habitats, geography and taxonomic group



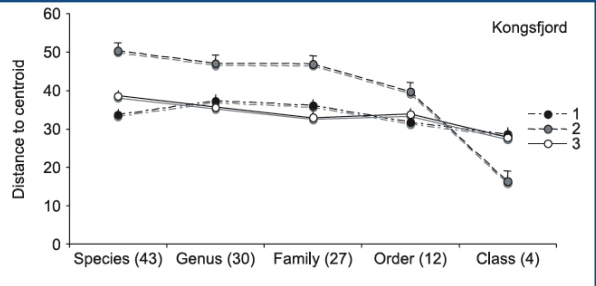
Same gradient  
Different groups  
Opposite patterns of beta

Same group  
Different habitat  
Different beta

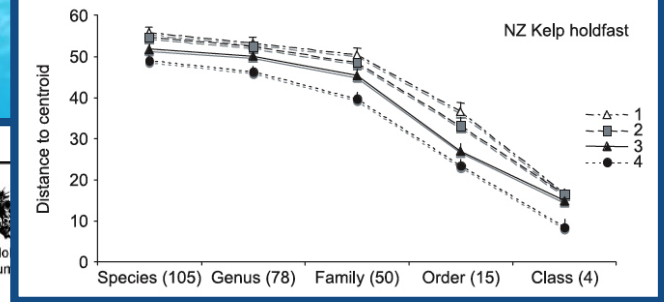


# Case studies on impacts and heterogeneity

## MOLLUSK ASSEMBLAGES



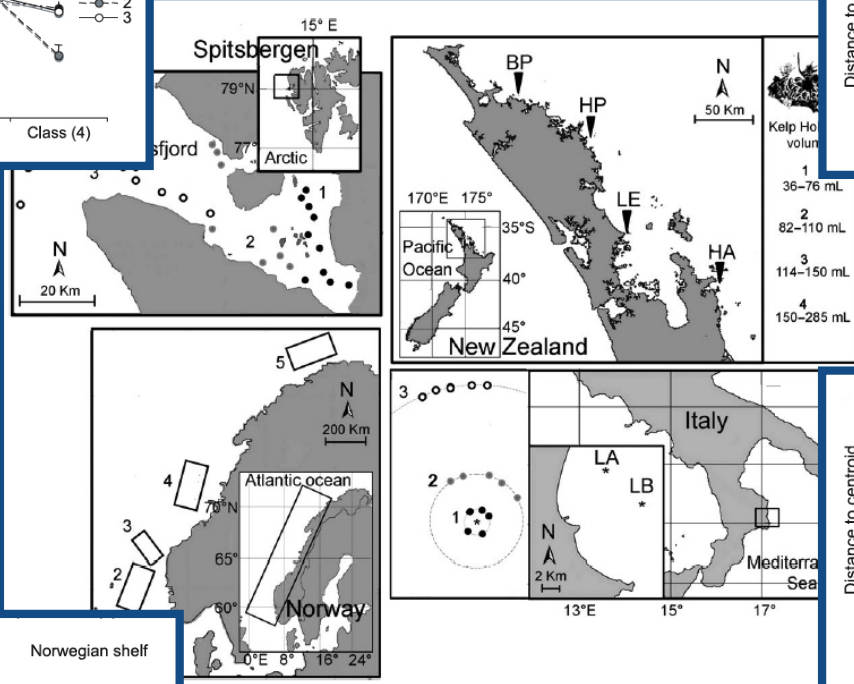
Glacial sedimentation gradient



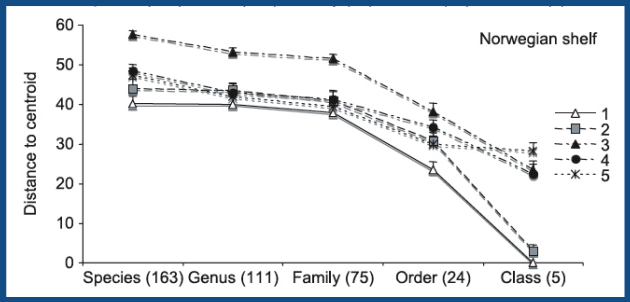
Kelp holdfast size

Distance from offshore platform

From Terlizzi et al., 2009

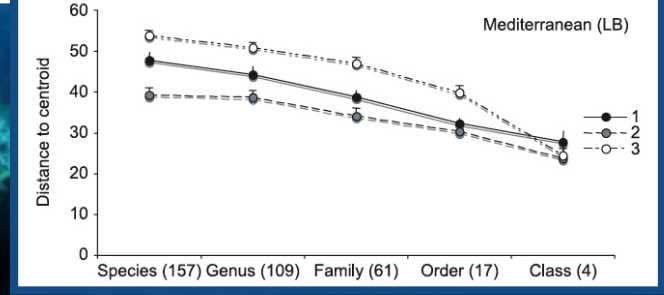
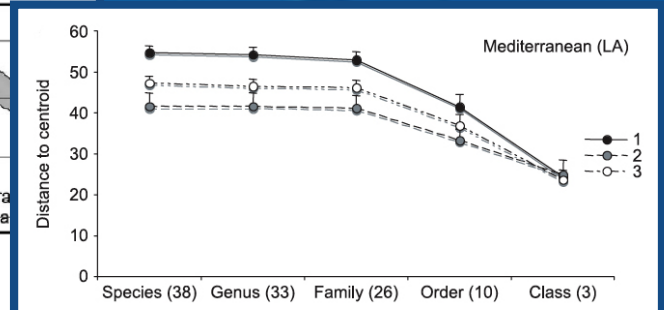


Latitudinal gradient

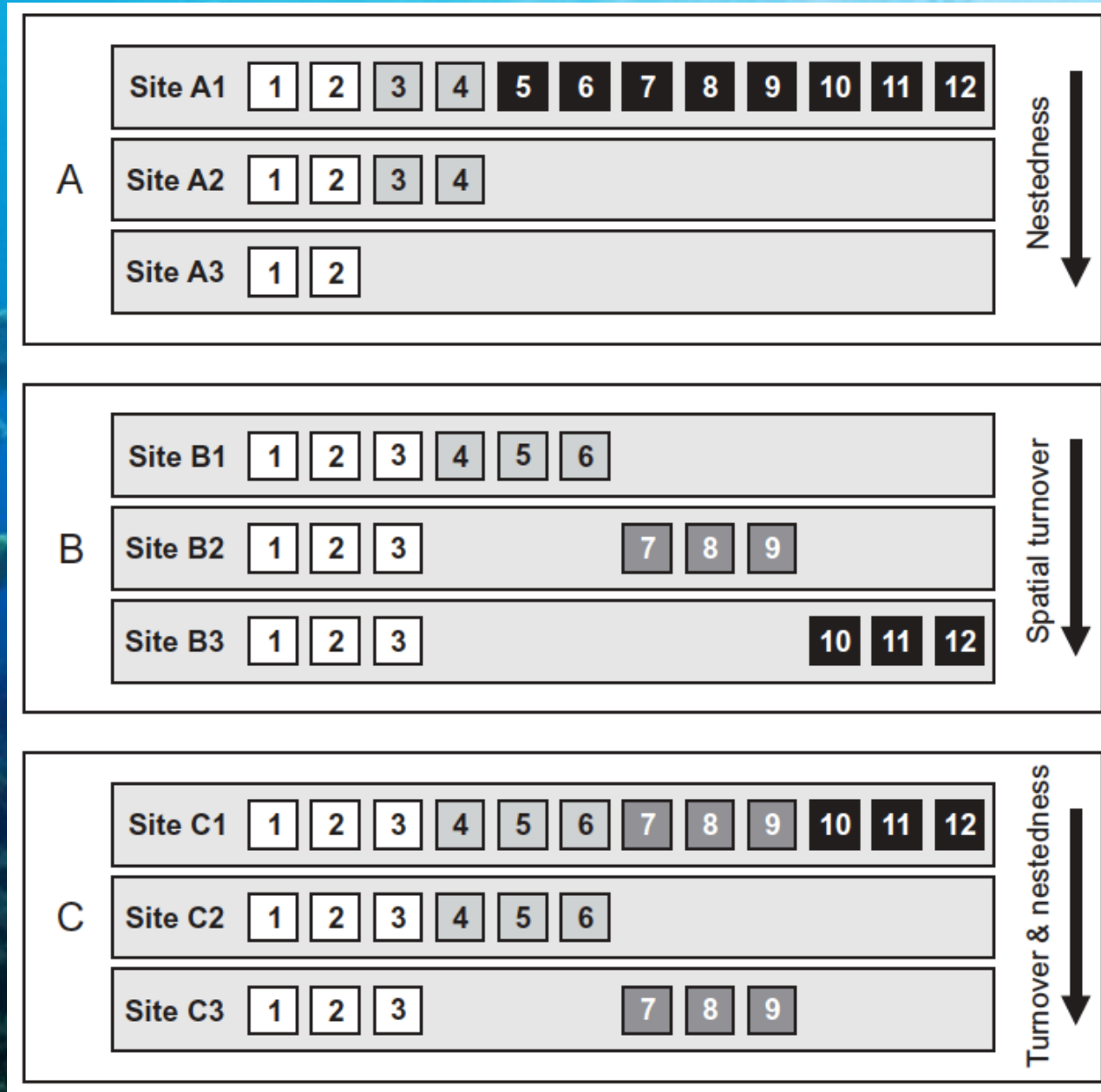


Terlizzi et al., 2009 Divers Distrib

**Species level beta-diversity patterns retained up to family level**



# $\beta$ -diversity: turnover and nestedness



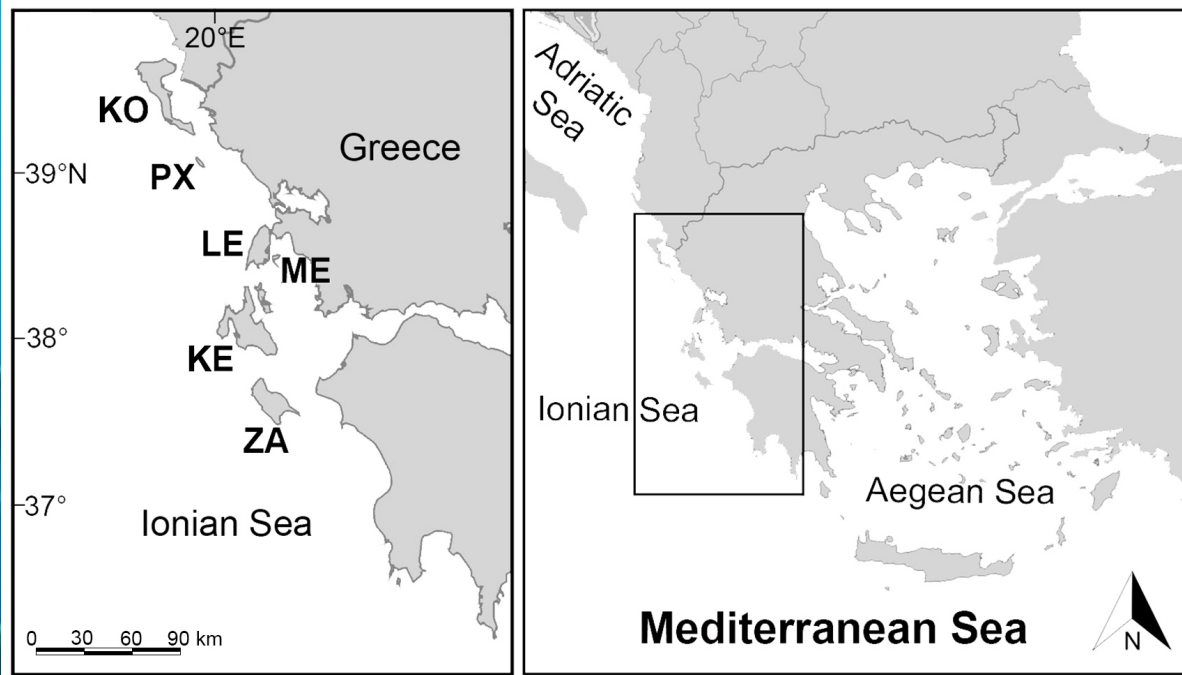
$\beta$ -diversity may reflect two different phenomena: nestedness and spatial turnover.

Nestedness of species assemblages occurs when the biotas of sites with smaller numbers of species are subsets of the biotas at richer sites, reflecting a non-random process of species loss.

Spatial turnover implies the replacement of some species by others as a consequence of environmental sorting or spatial and historical constraints.

(Baselga, 2010)

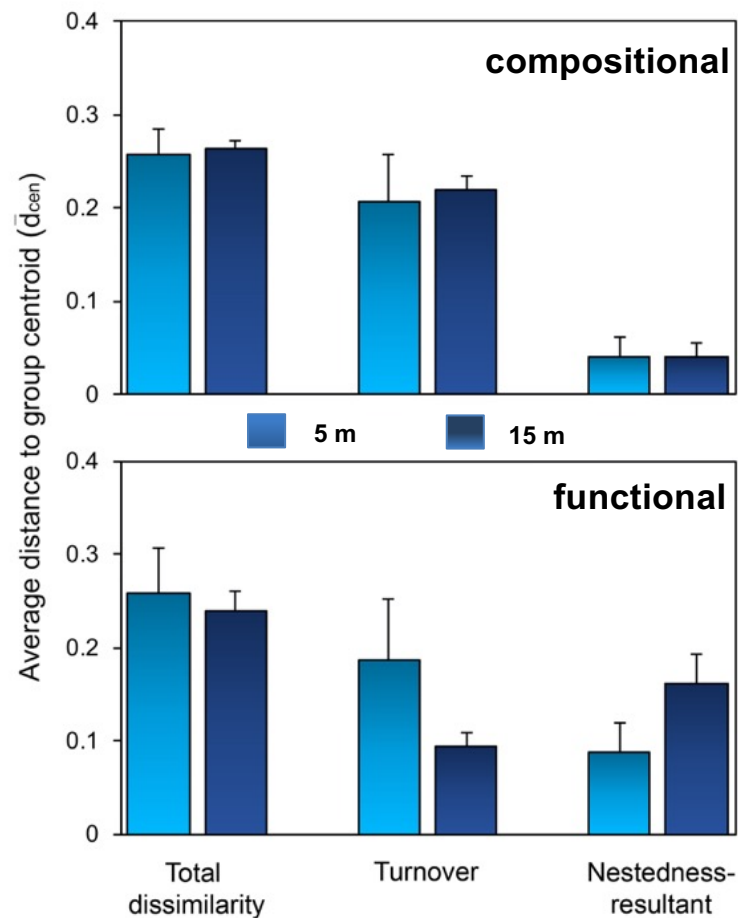
# A case study in the Ionian Sea



Six islands, four sites in each islands. Sessile assemblages on subtidal reefs at 5 and 15 m depth. Photographic samples with 10 replicates in each sites. Identification of taxa at species level (genus or morphological groups in case of difficult organisms). Identification of functional traits (48)

Traits related to functional aspects of organisms (shape, reproduction, dispersal, interaction with the environments, energy flow. Construction of multidimensional functional space for each assemblage in each islands and depth

# Results



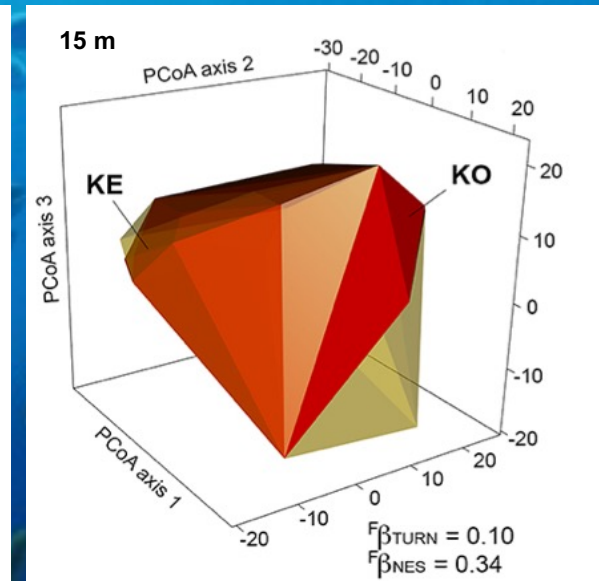
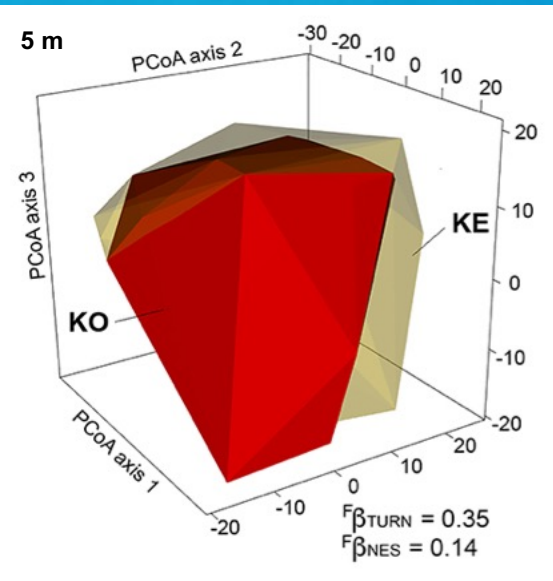
Compositional beta-diversity of assemblages at both depths was mainly due to species turnover (replacement), whereas nestedness component was negligible.

However:

5 m: species turnover  $\Rightarrow$  functional turnover

15 m: species turnover  $\Rightarrow$  functional nestedness

This means that at 15 m there were islands representing hotspots of functional diversity, and islands that were functional subsets of these hotspots.



Partitioning nestedness and turnover unveils contrasting relationships between compositional and functional beta-diversity in subtidal rocky reef assemblages at varying depth.

Understanding whether compositional diversity underlies functional diversity is crucial for conservation strategies.

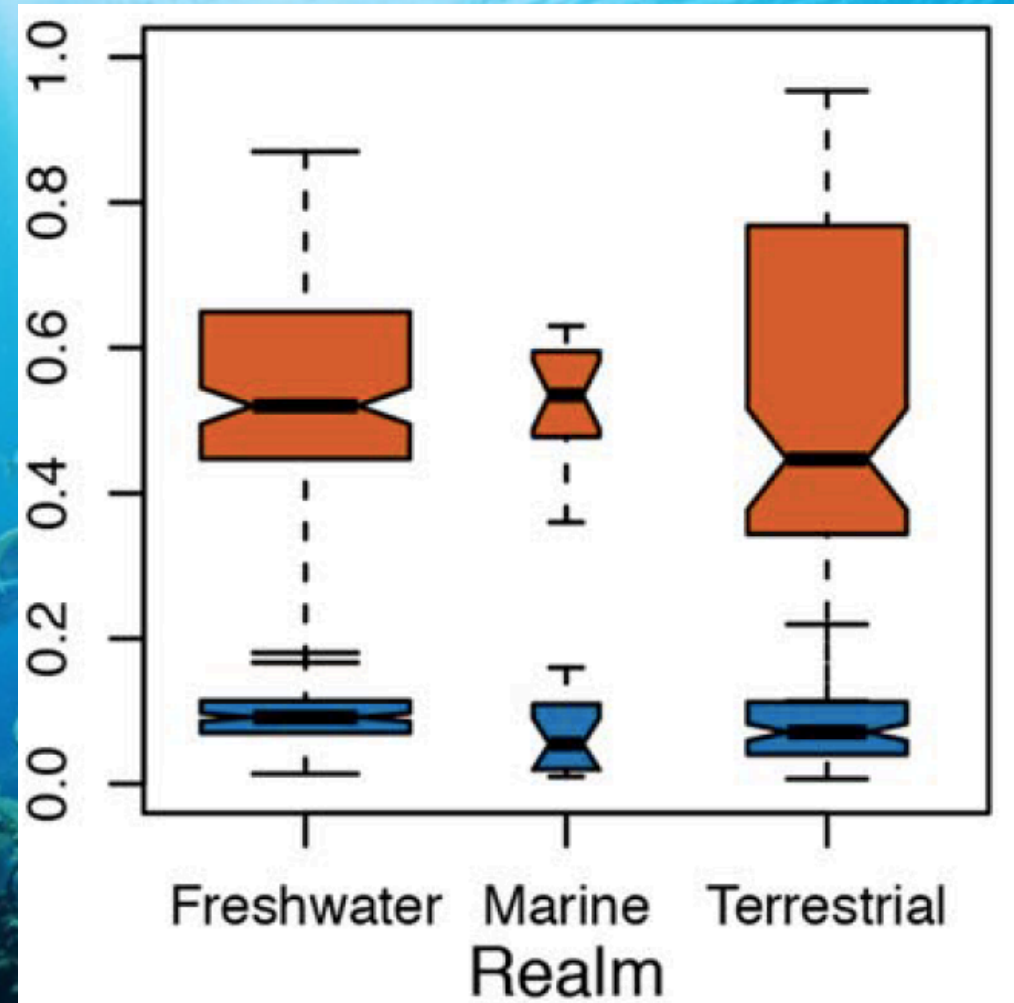
Reserve networks based on taxonomic beta-diversity, although maximizing protection of species richness, do not necessarily ensure preserving functional representativeness.

# $\beta$ -diversity in different realms

$\beta$ -diversity in marine environments is predicted to be lower than in other realms.  $\beta$ -diversity would be less pronounced in seas and oceans than on land or freshwaters, due to the lower variability of the marine environment, and the higher potential of connectivity of marine communities

However, though there is evidence supporting this assumption differences in patterns of  $\beta$ -diversity among realms are still not so clear

Soininen et al. 2017



Nestedness and turnover in marine, freshwater and terrestrial environments. (median, quartile, and 95% CI) (269 studies in total)

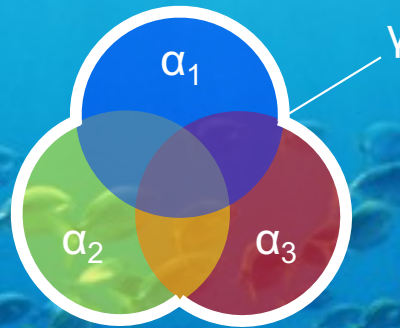
# $\beta$ -diversity and connectivity

## $\beta$ -diversity

Changes in composition among communities within a given spatial extent

→ How local ( $\alpha$ ) diversity links to regional ( $\gamma$ ) diversity →

Siting Spacing  
Networking



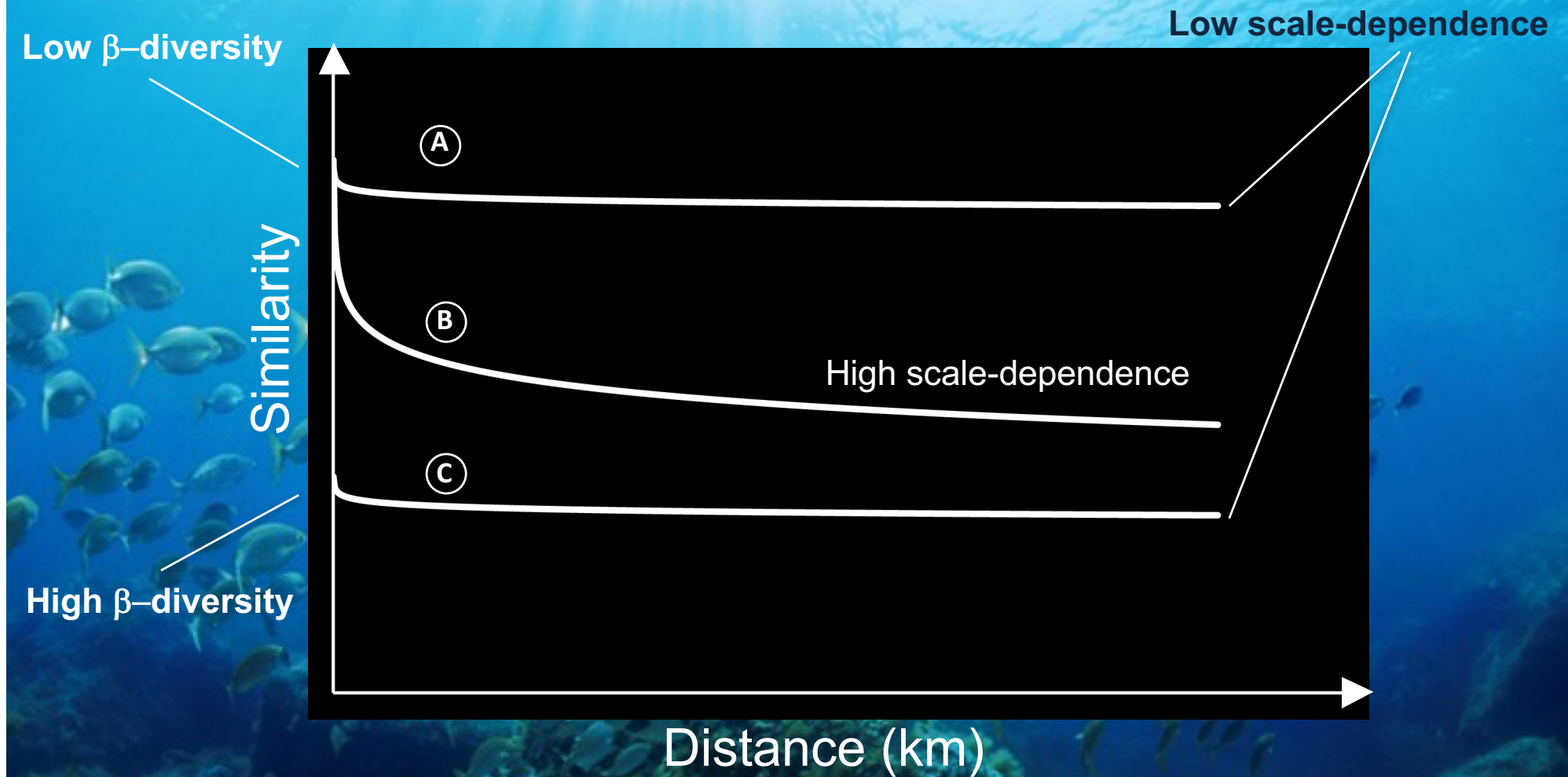
**$\beta$ -diversity**

**Ecological connectivity**

Local processes are similar and/or of least relevance for community distinctiveness  
Large-scale processes act uniformly and/or of major relevance for community homogenization

Local processes are different and/or of major relevance for community distinctiveness  
Large-scale processes act inconsistently and/or of least relevance for community homogenization

# General patterns of distance-decay



Ⓐ

Homogeneity from local to large scale: high connectivity across the region

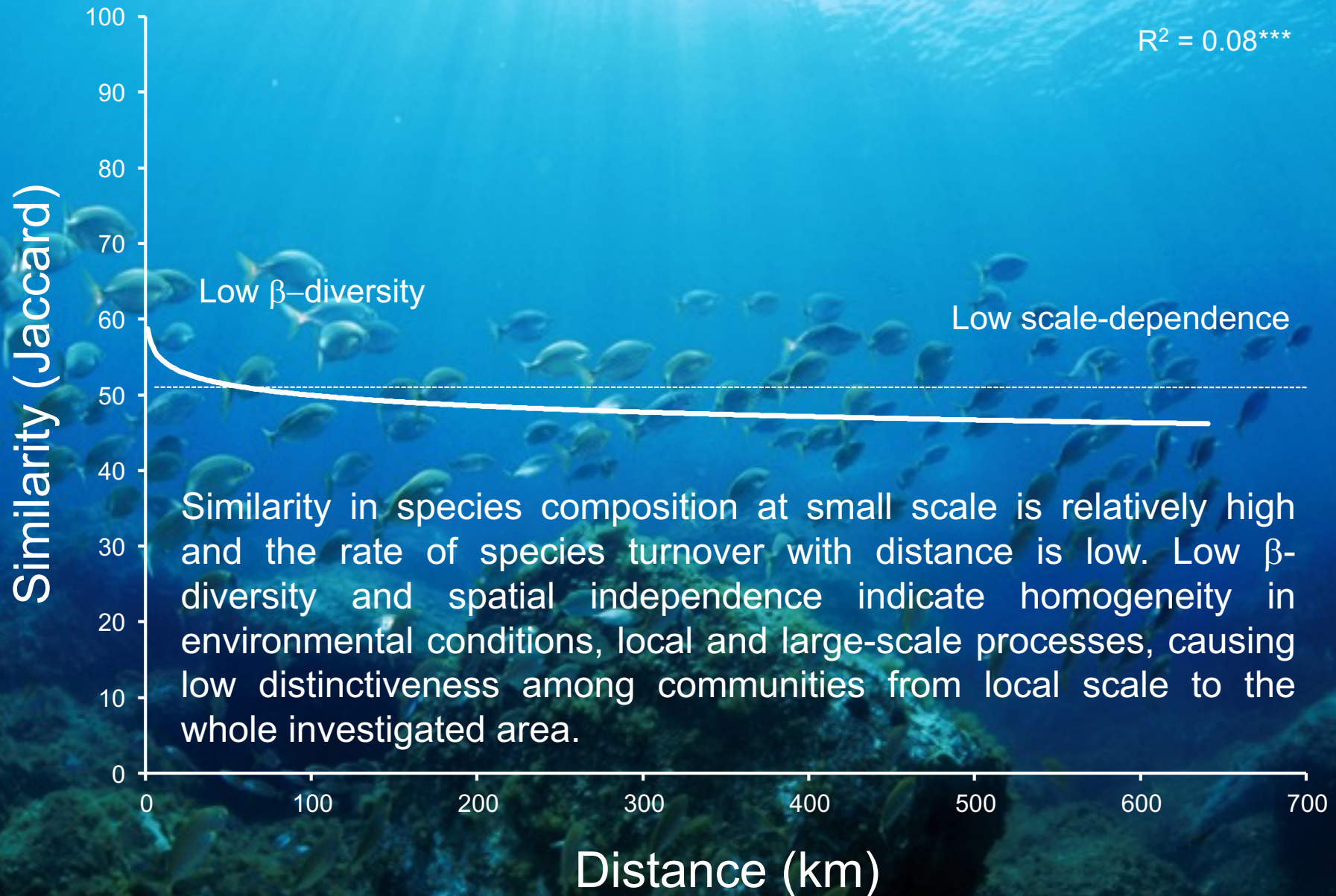
Ⓑ

Homogeneity decrease with scale: high connectivity at local scale that decrease over large scale

Ⓒ

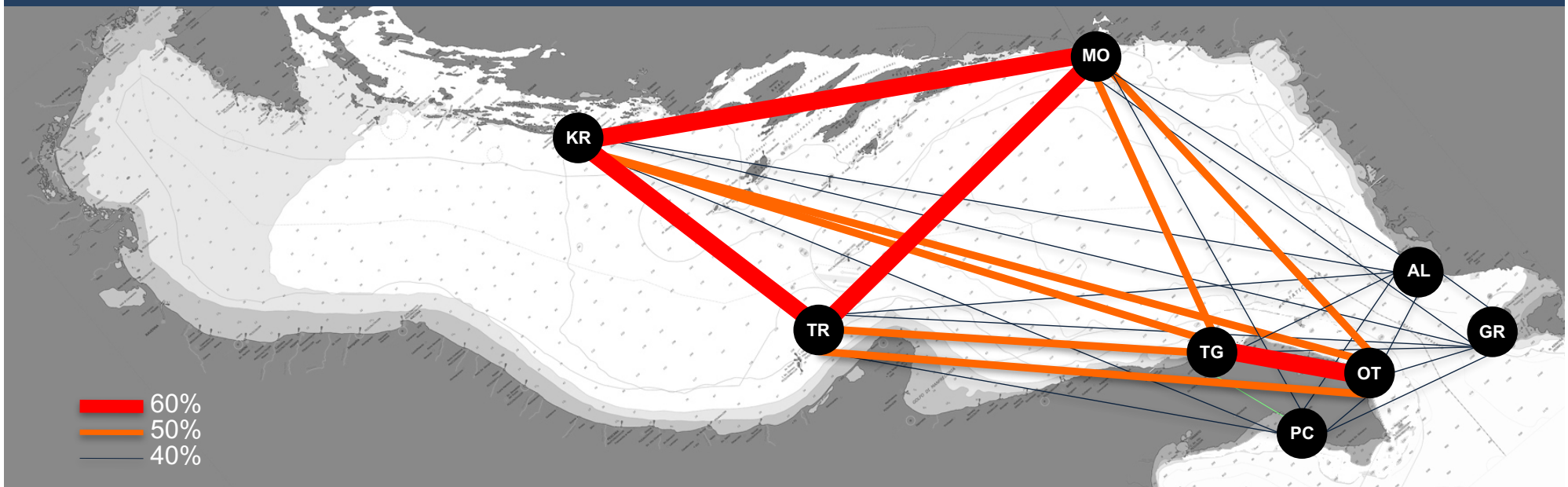
Heterogeneity from local to large scale: low connectivity across the region

# Distance-decay sessile assemblages: Adriatic Sea





# Similarity in composition in the Adriatic



Higher similarity among locations in the central (KR-TR-MO) and southern Adriatic (TG-OT)

Intermediate similarity between these two groups


Discontinuity with locations AL, GR, PC

**Sessile assemblages on subtidal rocky reefs**

# The importance of $\beta$ -diversity

$\beta$ -diversity is influenced by extrinsic factors such as geography and environmental changes, and by intrinsic factors related to ecological and biological traits of species (dispersal ability, trophic position, structural features, life cycles).

Central role in linking local and regional diversity, exploring variations across environmental and biogeographical gradients, understanding ecological processes (e.g. connectivity)

- 
- Estimating and mapping diversity
  - Identifying its relevant scales of variation and biogeographical regions
  - Understanding processes underlying the formation and evolution of biological systems
  - Reserve siting, number and spacing so to achieve representativeness and complementarity
  - Assessing processes of ecological homogenization related to anthropogenic impacts
  - Functional aspects and partitioning  $\beta$ -diversity in its basic components could help optimizing reserve selection and accounting for functional diversity