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

BIODIVERSITY AND ECOSYSTEM FUNCTIONING

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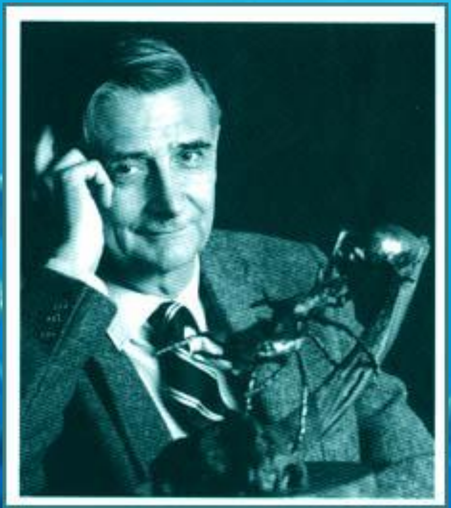
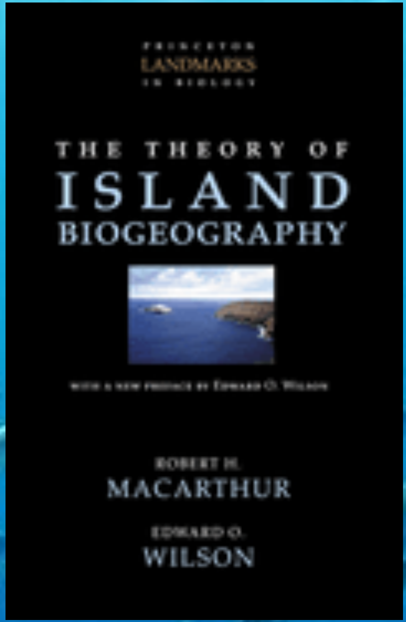
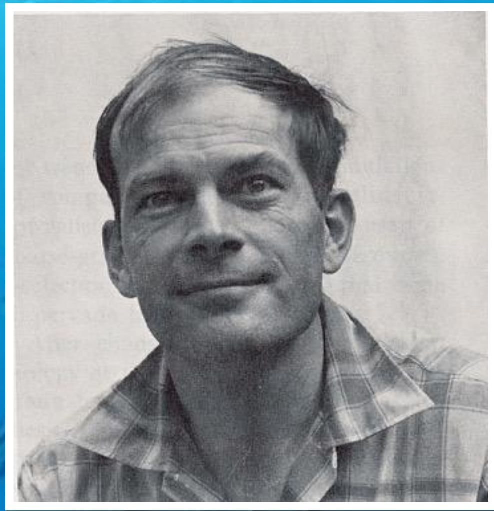
β-diversity and connectivity

The Theory of Island Biogeography

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



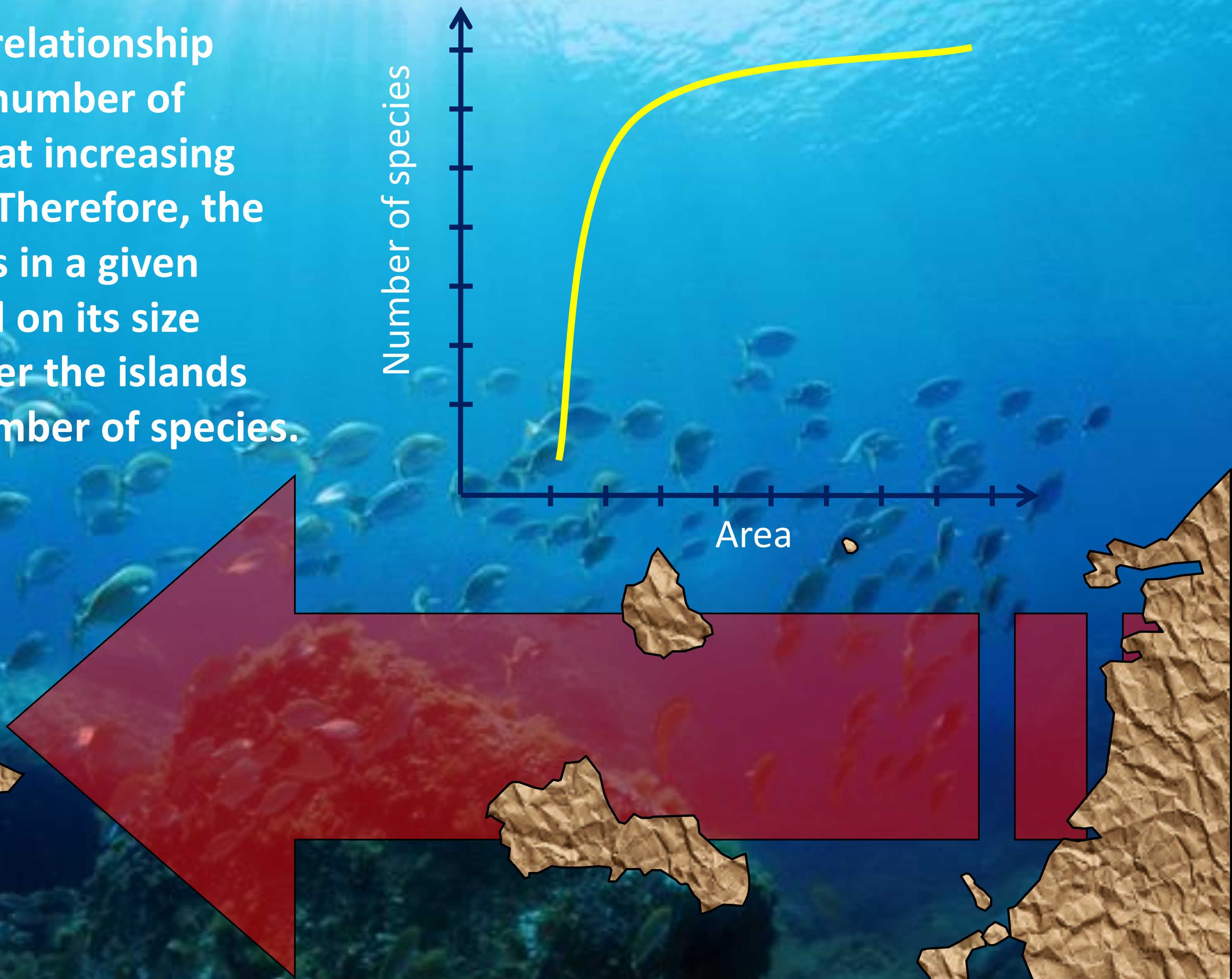




Theory is based on the concept of ‘island’, which true islands (portions of land surrounded by water) are only one representation. Everything ‘isolated’ is an ‘island’. Also, depending on the scale considered, even different portions of continuous environments can be considered as islands.

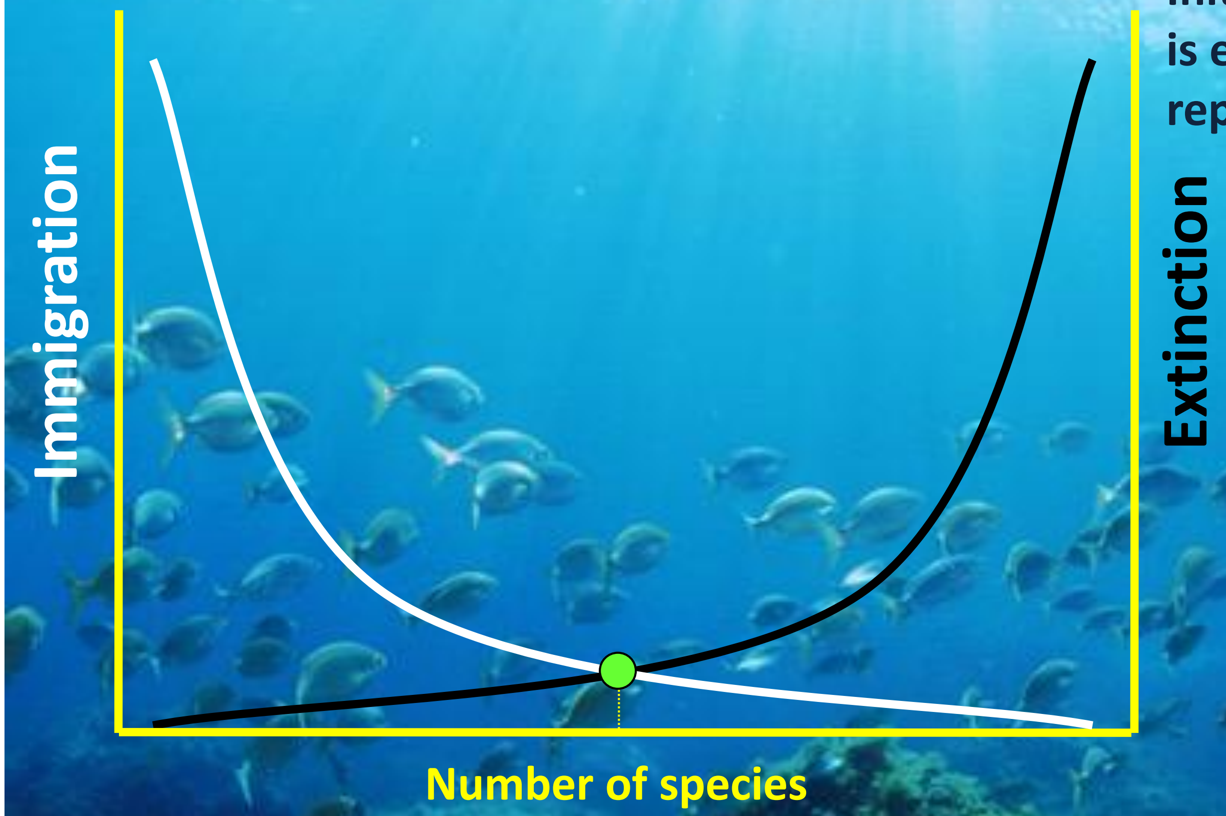
Distance from the “source”

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



In TIB, species richness of islands will also depend on immigraton 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

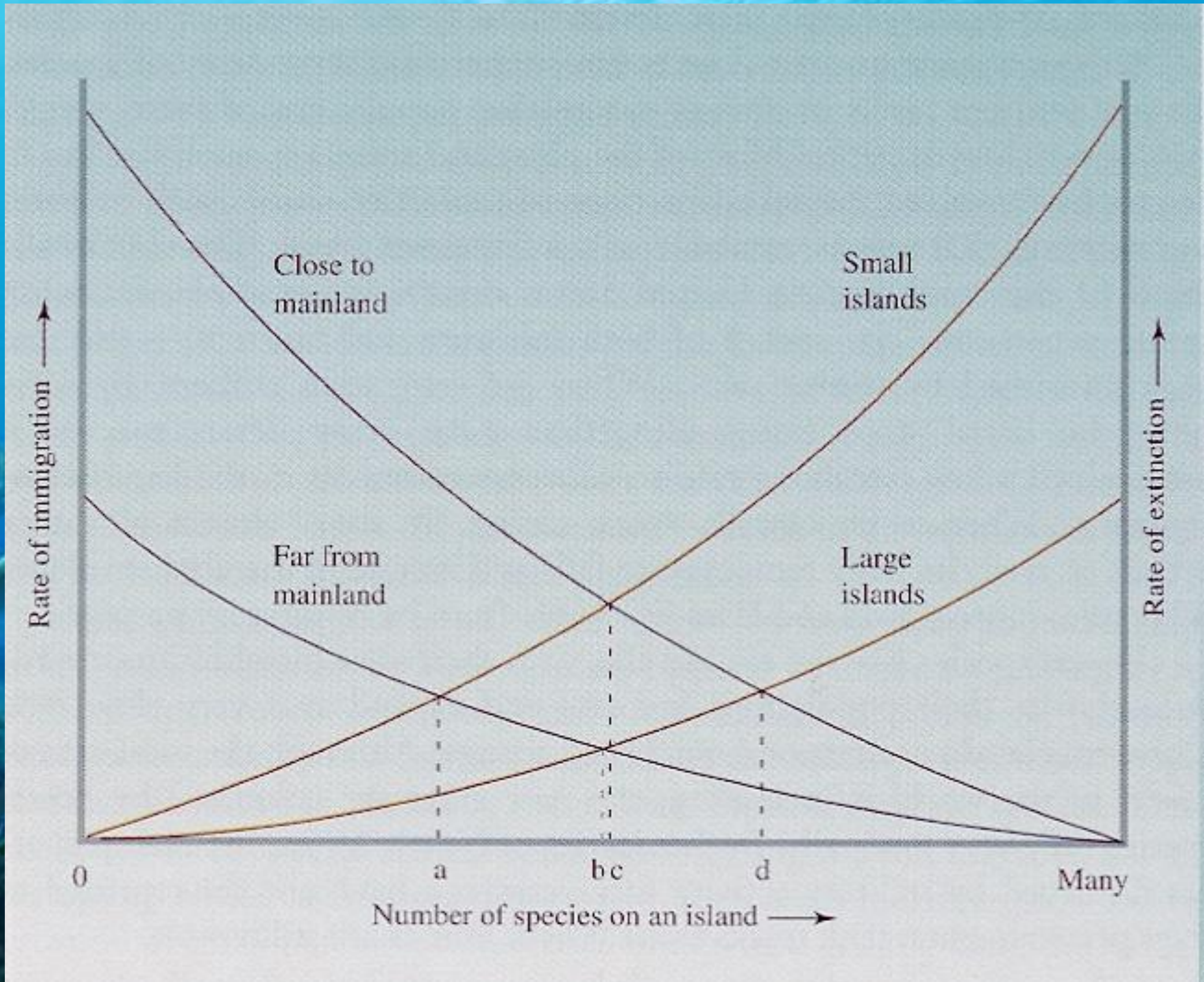
As species number increase, immigration decrease and tends to 0 as the number of species tends to reach that of the source

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

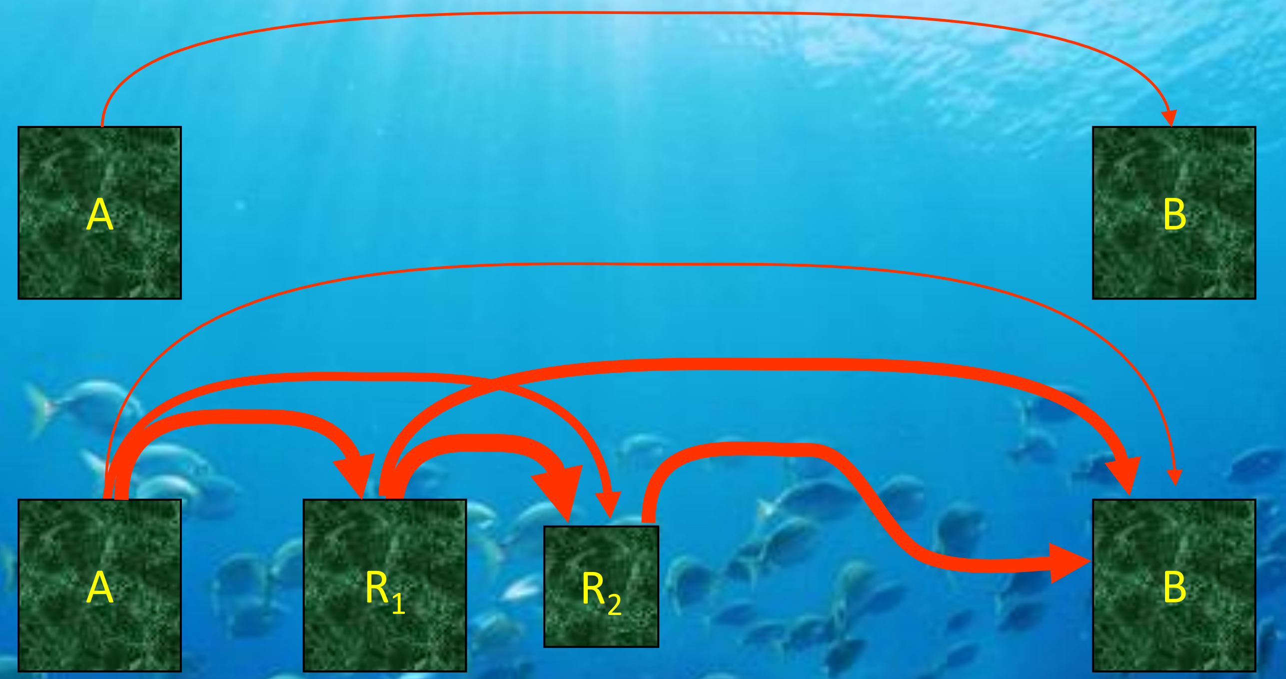
1) The number of species is the result of the balance between immigration and extinction
2) This balance is dynamic, because species will go extinct and will be replaced by others continuously
3) The immigration rate will mostly depend on the distance form the source
4) The extinction rate will mostly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

Stepping stones

Man made fixed structures, ships, litter, could serve as stepping stones for dispersion, or as vectors of invasion

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 focuses 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

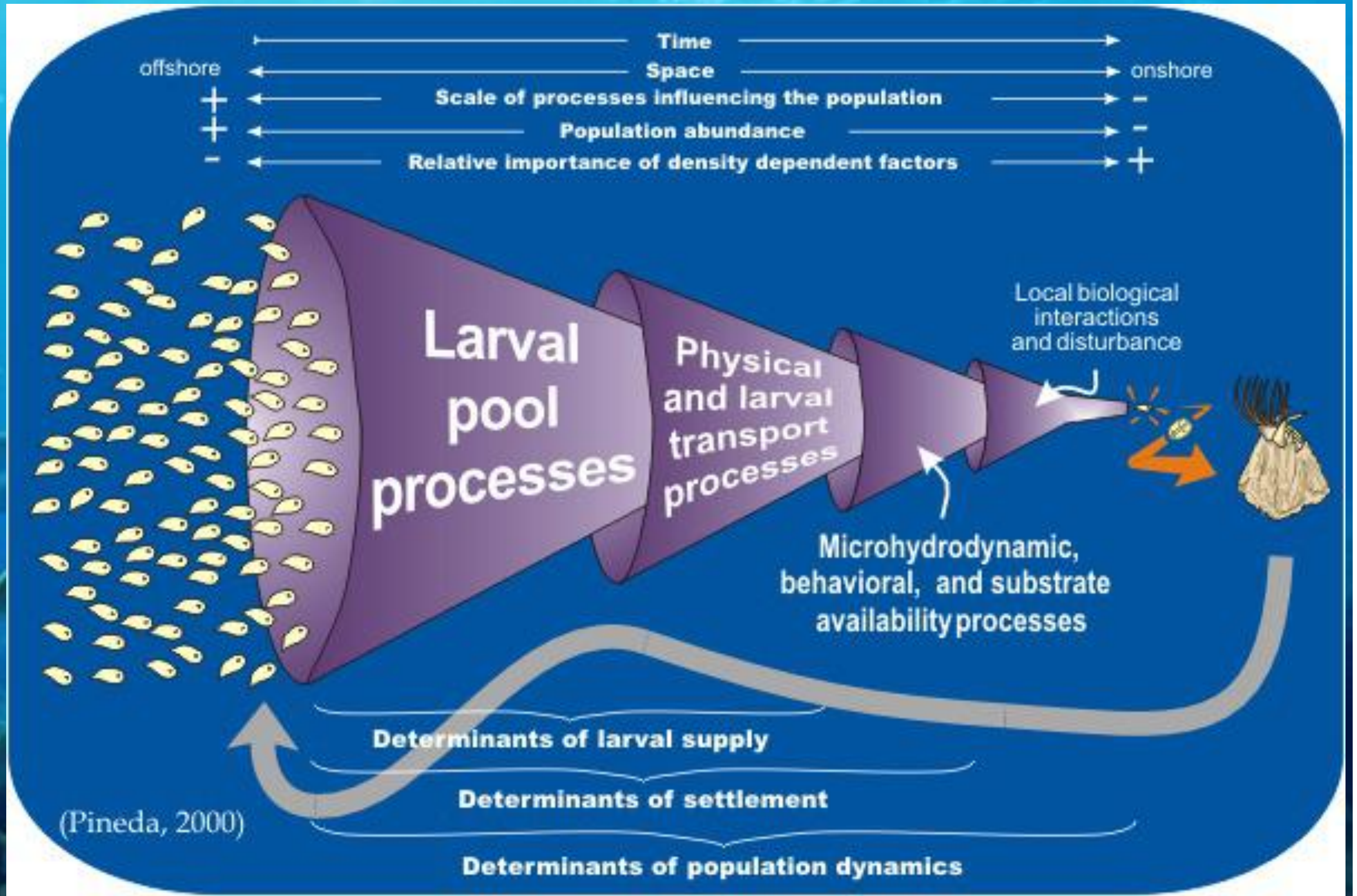
Processes affecting larval supply

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

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

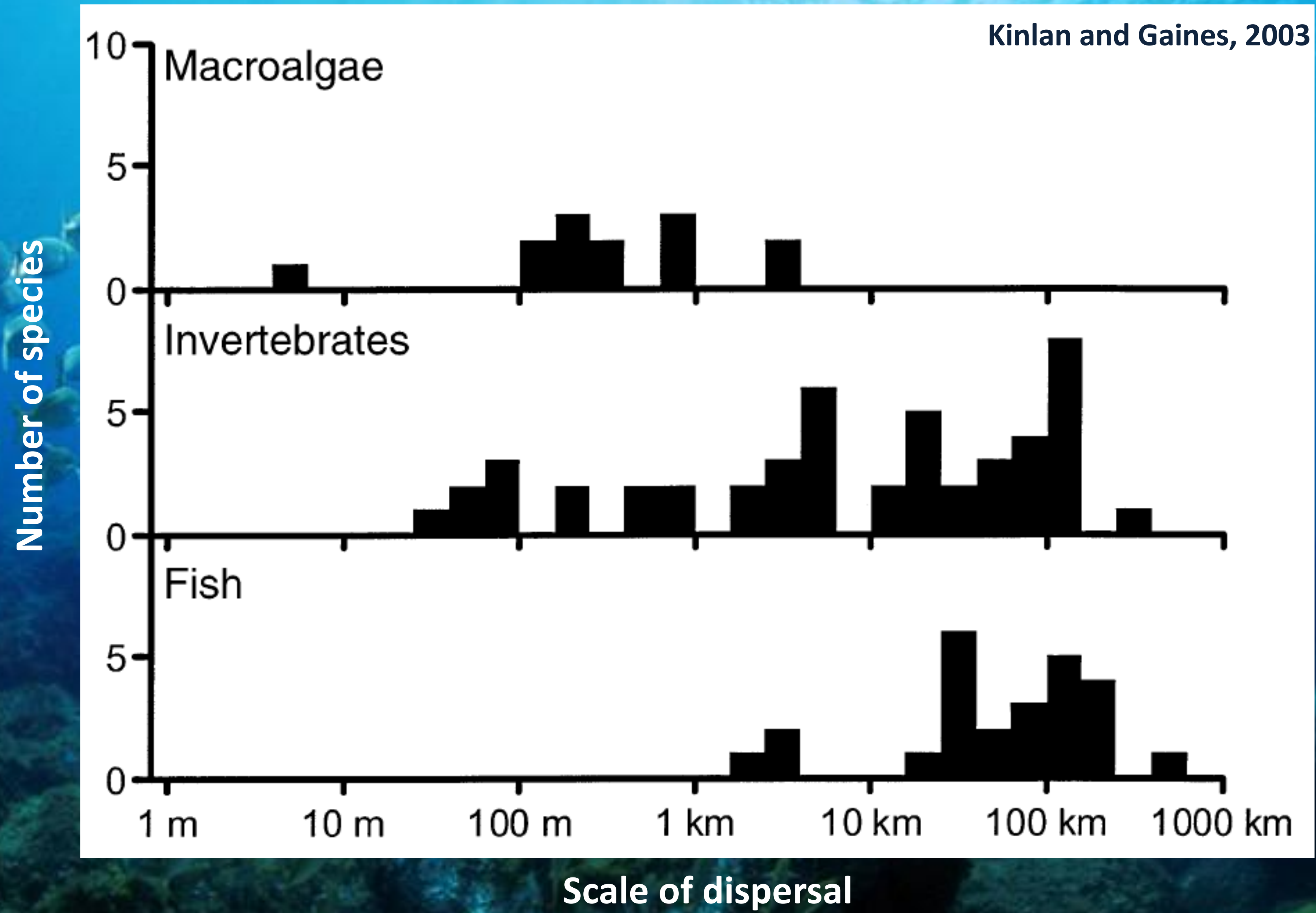
Larval transport
(currents, vectors, isolation)

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



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

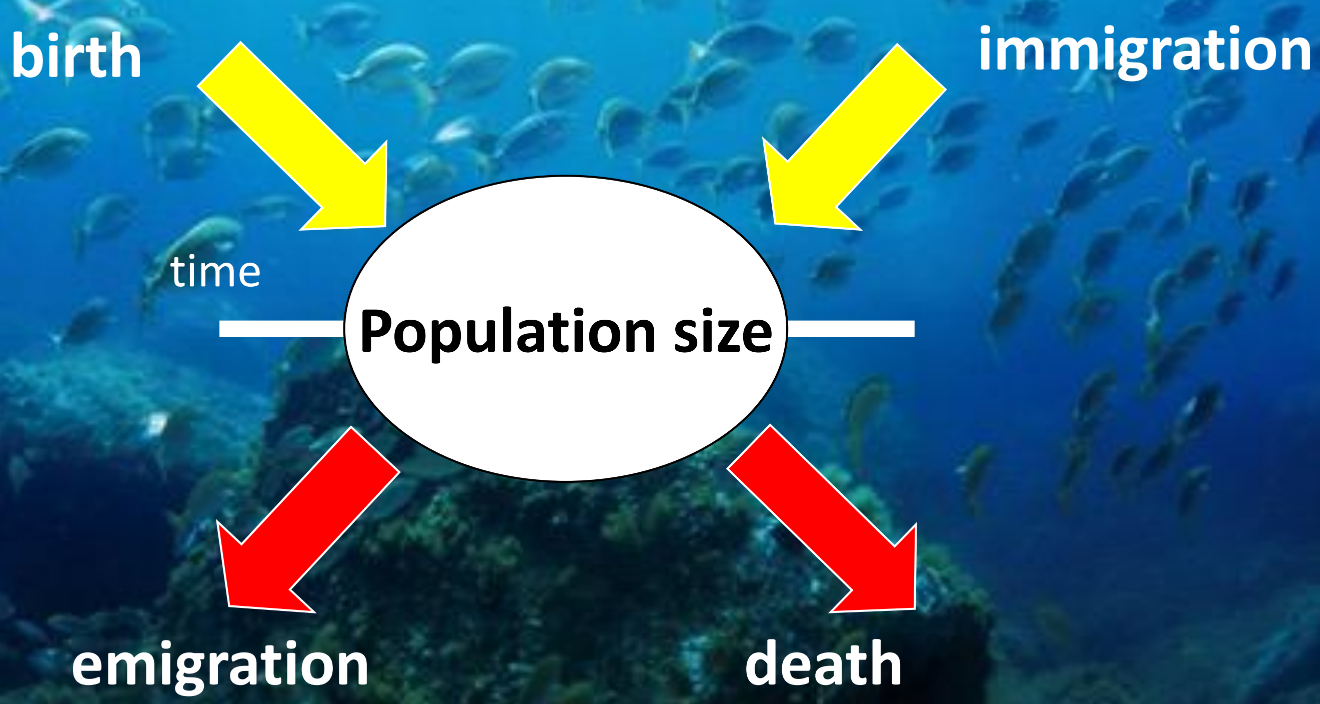
Dispersal potential in marine species



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.

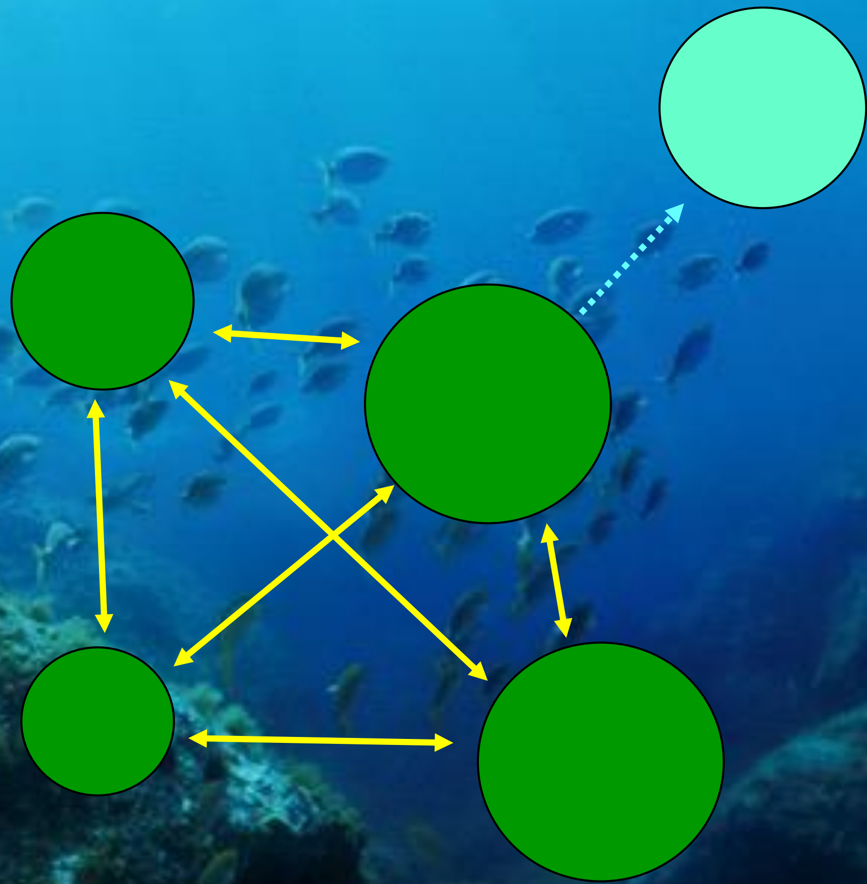


Metapopulations

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.



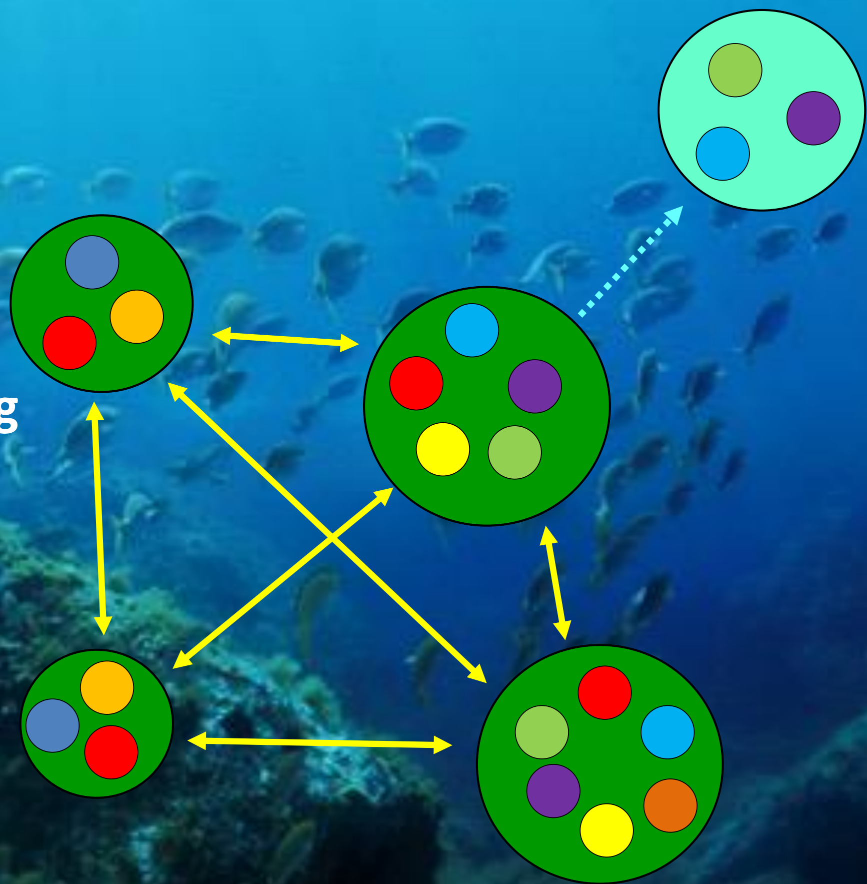
Sinks may experience extinction and subsequent recolonization

Metacommunities

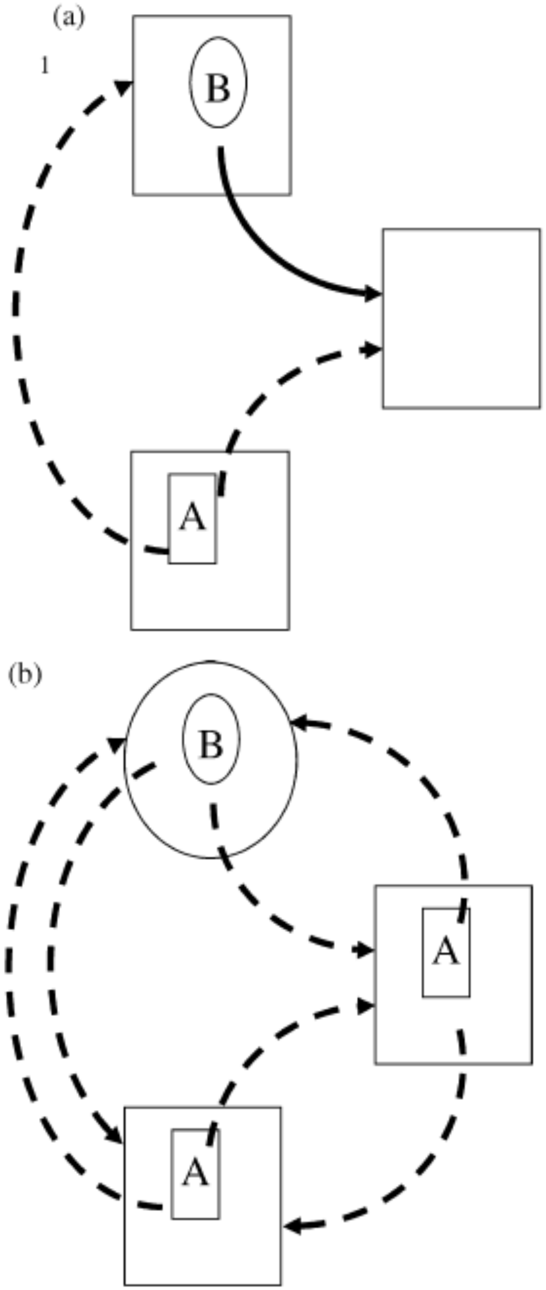
Metacommunities are sets of communities interconnected by dispersal, immigration and/or emigration of multiple (interacting or potentially interacting) species

(Gilpin and Hansky, 1991)

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



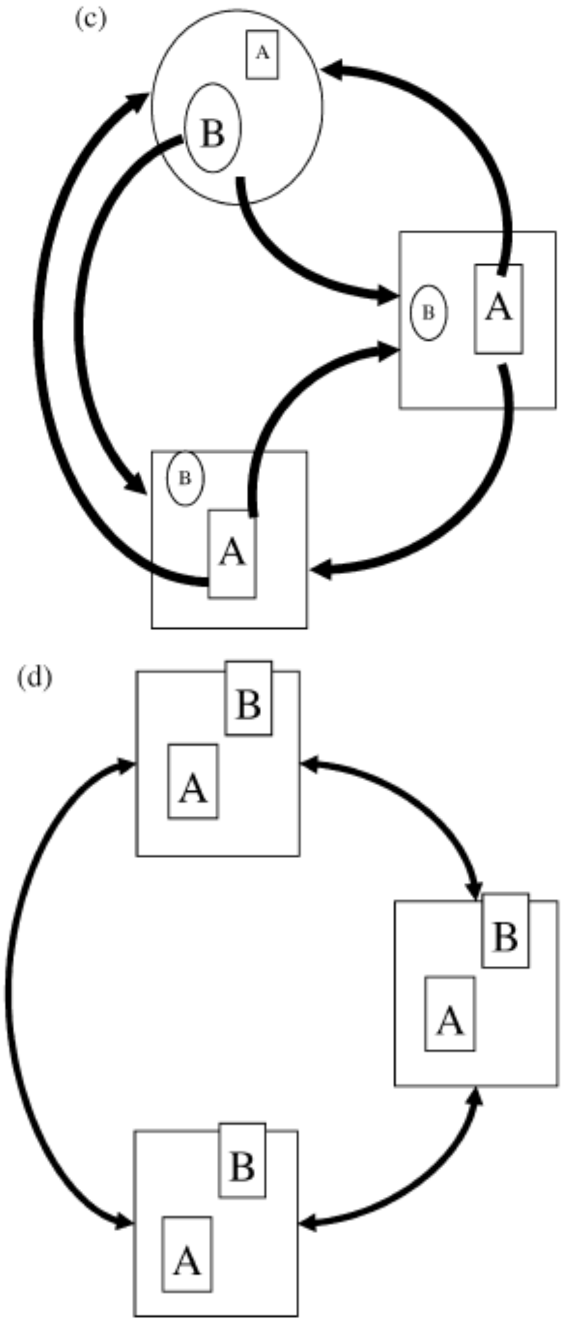
Perspectives in meta-communities



Patch dynamics: competitive model of coexistence in a homogeneous habitat. The habitat is composed by equal patches, which could be empty or occupied. Species coexistence is mediated by competition for resources and dispersal abilities. Local dynamics are not important. There are strong competitors and good dispersers, and trade-offs between these abilities determine the distribution of species in the habitat.

Species sorting: model of coexistence in a heterogeneous habitat. The habitat is composed by unequal patches, because of differences in conditions and resources. Species coexistence is mediated by local conditions. Depending on niche width, species can occupy several patches, or only those were local conditions allow survival. Dispersal is not so important, since good dispersers could reach more patches than poor dispersers, but colonization is mediated by the environment.

Perspectives in meta-communities

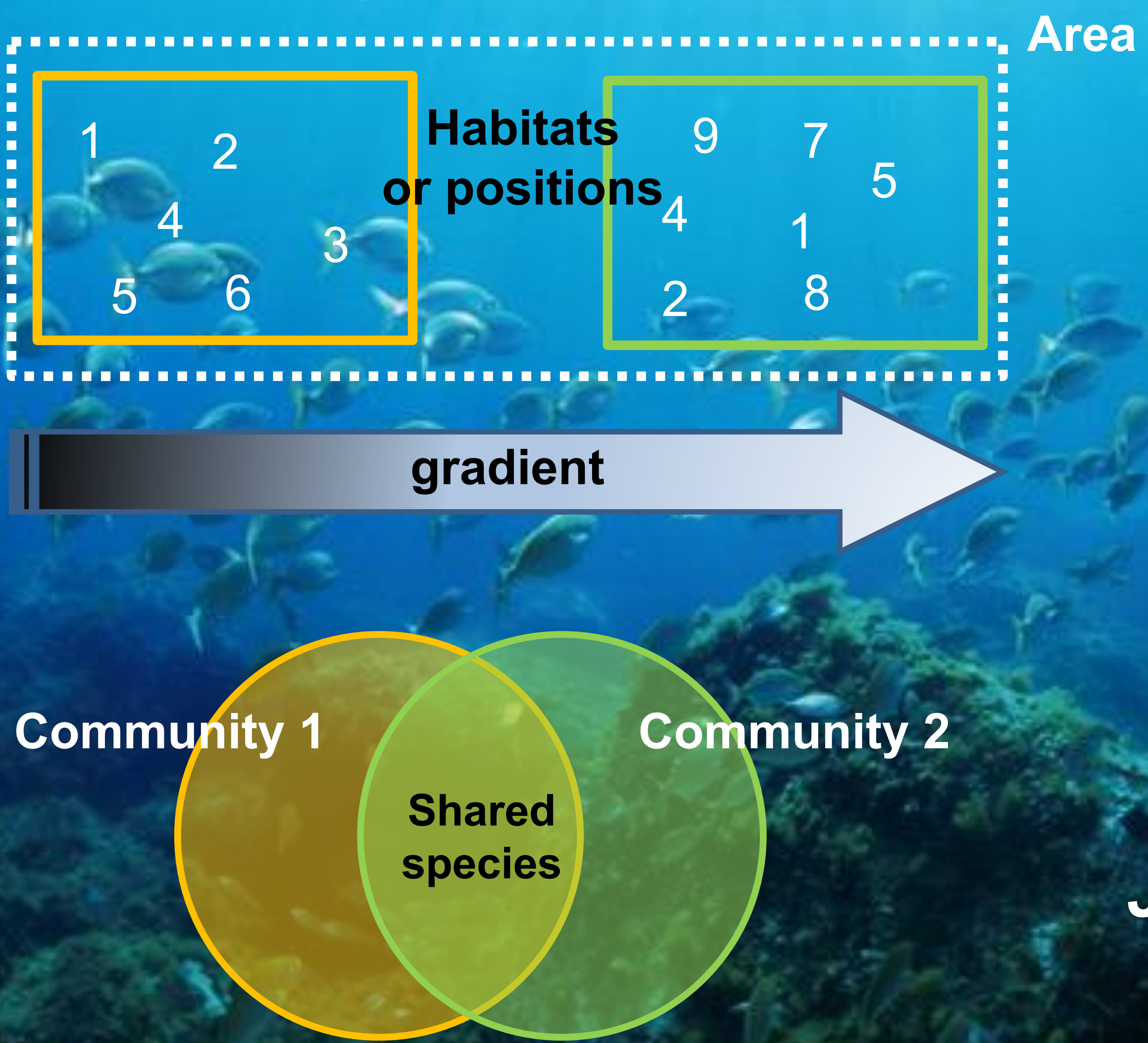


Sink-source (or mass effect): Species coexistence is mediated by immigration and emigration. Local competitive exclusion in patches where species are bad competitors are compensated by immigration from communities where they are good competitors. There are productive patches (sources) and receiving patches (sink), connected by dispersal.

Species are equal in terms of competitive abilities, dispersal and fitness. Community composition depends on stochastic factors related to speciation-immigration and extinction-emigration.

β-diversity: basic concepts

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



γ-diversity

the total diversity in the landscape

α-diversity

the local (site or habitat) diversity

β-diversity

the differention diversity between sites or positions

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

Jaccard distance

β-diversity: linking local to regional diversity

$\overline{\alpha} = 7$

$\gamma = 14$

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

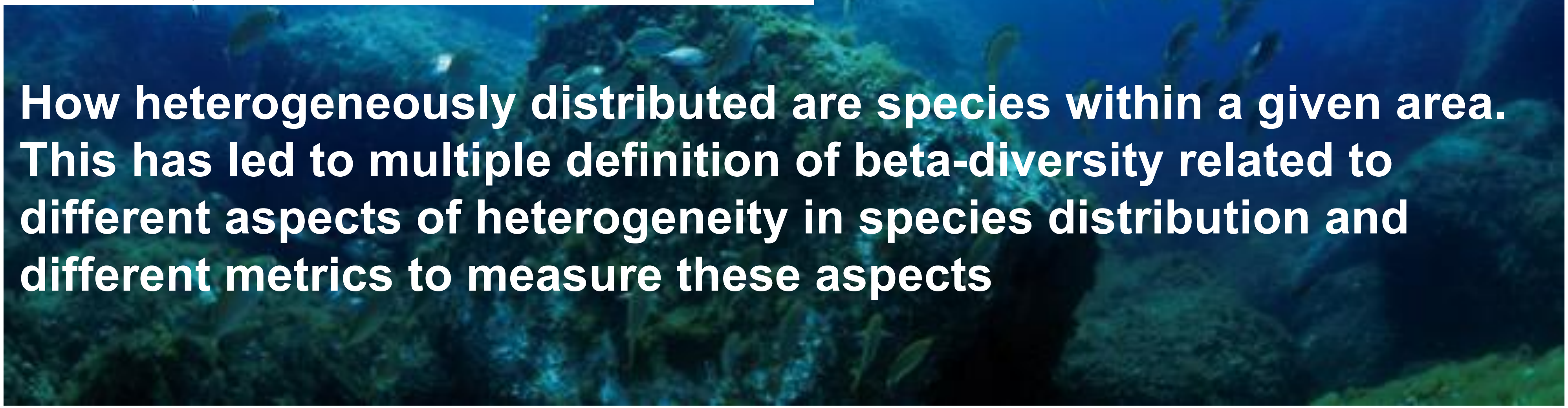
$$\beta = \gamma - \overline{\alpha}$$

β-diversity, generally defined as variation in the identities of species among sites, provides a direct link between biodiversity at local scales (α-diversity) and the broader regional species pool (γ-diversity) (Whittaker 1960, 1972).

A diversity of β-diversities

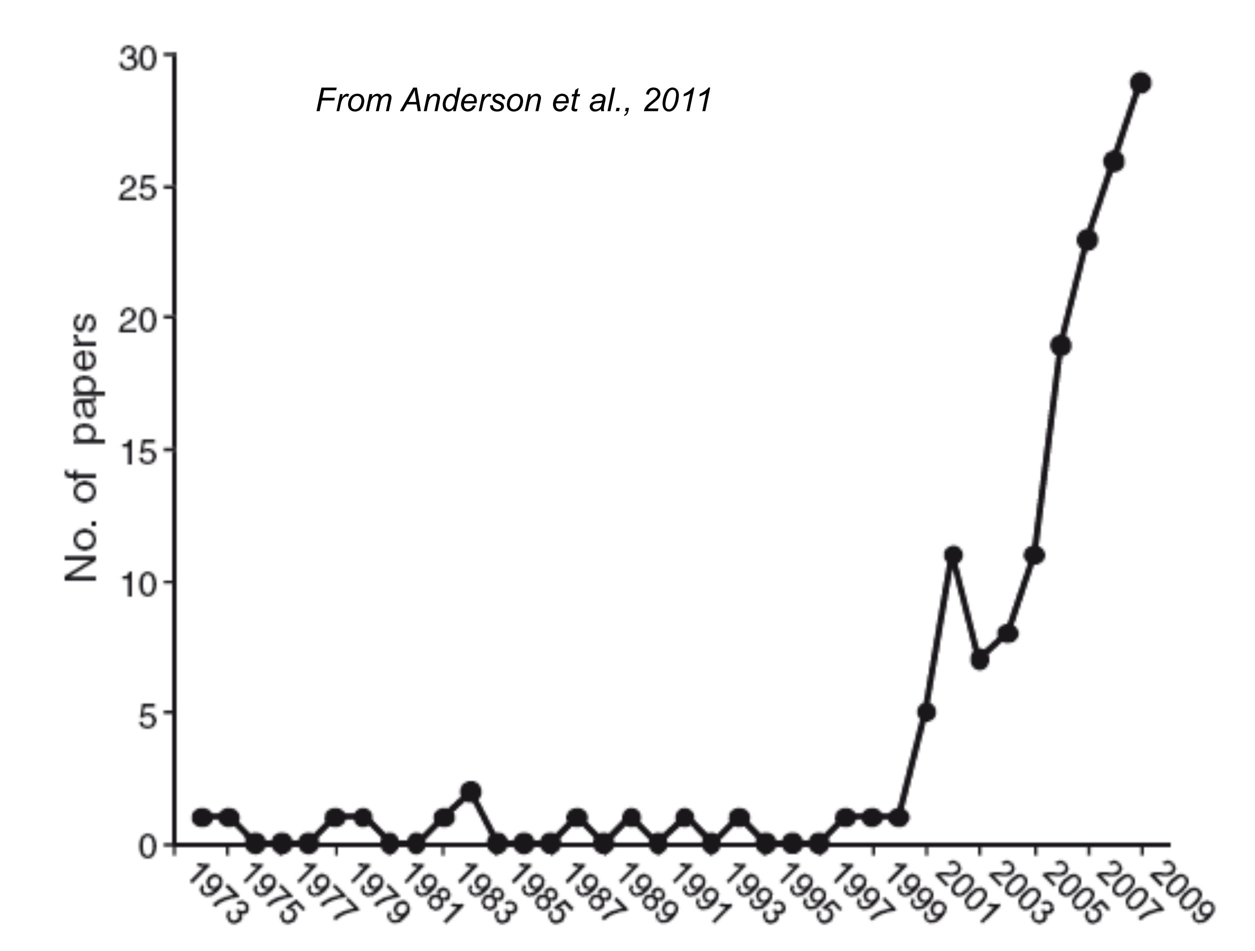
Notation	Definition	Measurement unit [range]
β_{Md}	true beta diversity $= \gamma/\alpha_d$	CU [1 CU to N CU]
β_{Mt}	regional-to-local diversity ratio $= \gamma/\alpha_t$	sp_E/sp_E [1 to N]
β_{At}	absolute effective species turnover $= \gamma - \alpha_t$	sp_E [0 to $(N-1)\alpha_t$]
β_{Mt-1}	Whittaker's effective species turnover $= (\gamma - \alpha_t)/\alpha_t = \gamma/\alpha_t - 1$	sp_E/sp_E [0 to $N-1$]
β_{Pt}	proportional effective species turnover $= (\gamma - \alpha_t)/\gamma = 1 - \alpha_t/\gamma$	sp_E/sp_E [0 to $1 - 1/N$]
Δc	any of the effective species turnover measures, i.e. β_{At}, β_{Mt-1} or β_{Pt}	as in the chosen turnover
β_{Mtot} or Δc_{tot}	a beta component quantified for the entire dataset	as in the chosen beta component
$\beta_{Mj,k}$ 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
$\overline{\Delta c}_{j,k}$	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
$\overline{\Delta c}_{j,centr}$	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
$\Delta c_{j,kmax}$ or $\Delta c'_{max}$	compositional gradient length in the dataset along the compositional dimension with most turnover	as in the chosen turnover
$\Delta c_{(\Delta g)}$	compositional gradient length along a specified section of an external gradient g	as in the chosen turnover
$\Delta g_{(\Delta \log(1-\Delta c))}$	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 α and γ are based on different datasets	as in the chosen beta component
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
$\Delta\gamma/\Delta x$	rate of gamma diversity accumulation with increasing (logarithm of the) number of sampling units	sp_E/SU or sp_E/log(SU)
$\Delta\alpha_t/\Delta x$	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)
$\Delta\log(\gamma)/\Delta x$	rate of gamma entropy accumulation with increasing logarithm of the number of sampling units	log(sp_E)/log(SU)
$\Delta\log(\alpha_t)/\Delta x$	rate of alpha entropy accumulation when sampling unit size increases in multiples of the logarithm of original size	log(sp_E)/log(SU)
$\Delta\beta_M/\Delta x$ 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
$\Delta\beta_M/\Delta x$ 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
$\Delta\beta_{Pt}/\Delta x$	proportional effective species turnover accumulation rate when an increasing proportion of the available sampling units is taken into account	(sp_E/sp_E)/SU
$\Delta\log(^q\beta_M)/\Delta x$	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)
n.n.	species diversity or entropy accumulation rate with alpha and gamma diversities based on different data	as in the chosen accumulation rate
$\Delta c_{(\Delta g)}/\Delta g$	compositional turnover rate along a specified section of an external gradient g	(unit of chosen turnover)/(unit of external gradient)
$\Delta\Delta c_{(\Delta\Delta g)}/\Delta\Delta g$ 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(unit of turnover)/(unit of external gradient)

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 β-diversity in ecology



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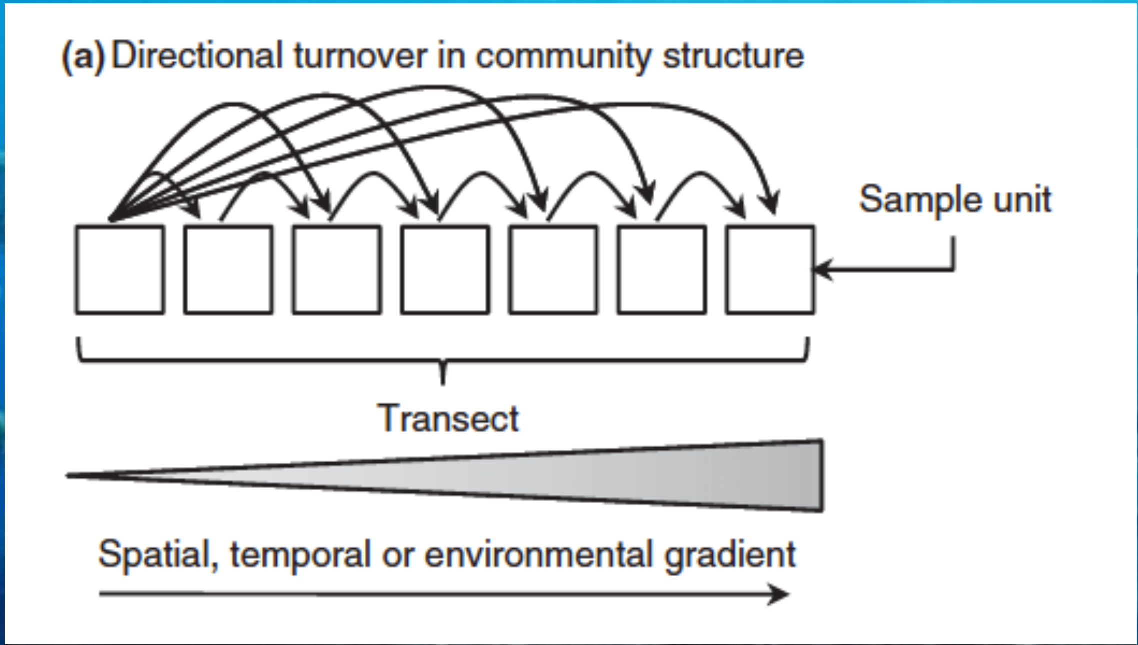
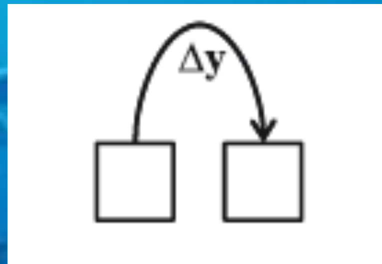
Increasing concern about beta-diversity in ecological and environmental studies

β-diversity: directional change between communities





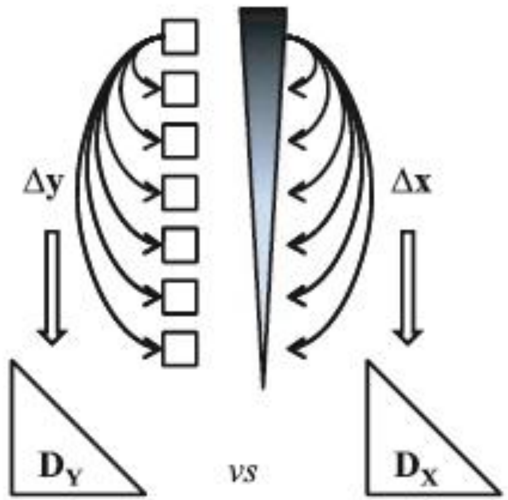
Measure of turnover between communities

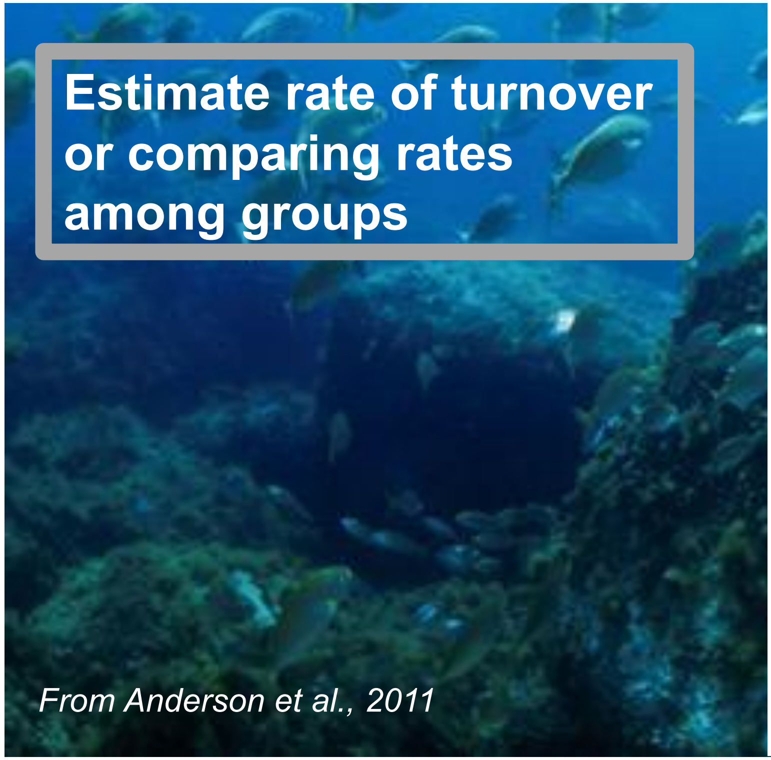
Changes occurring among communities along a gradient

From Anderson et al., 2011

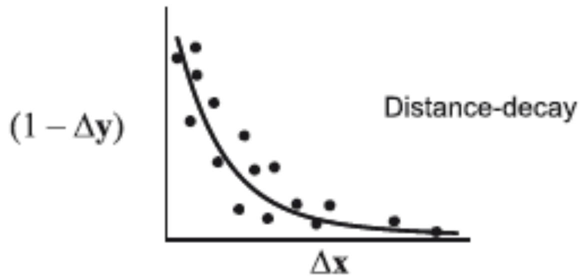
Modelling directional β-diversity

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

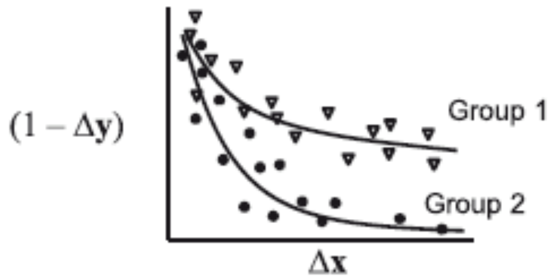




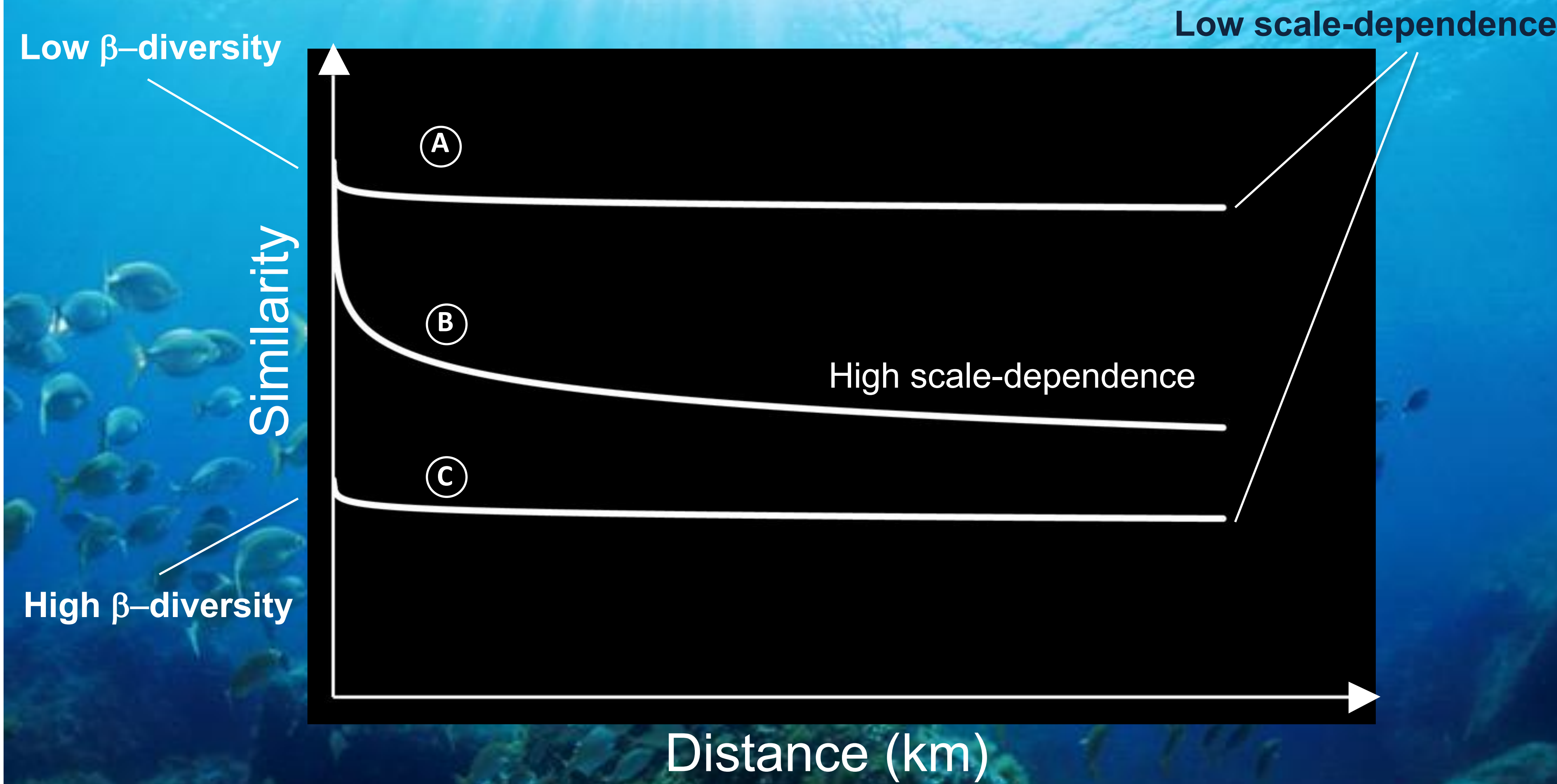
T4. Estimate the rate of turnover along a spatial, temporal or environmental gradient.



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



General patterns of distance-decay



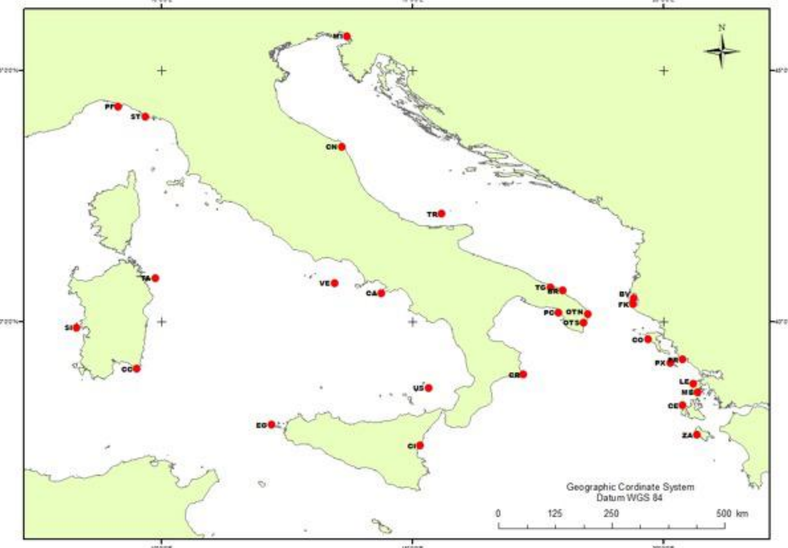
Ⓐ Homogeneity from local to large scale: high connectivity across the region

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

Ⓒ Heterogeneity at local scale, high connectivity across the region

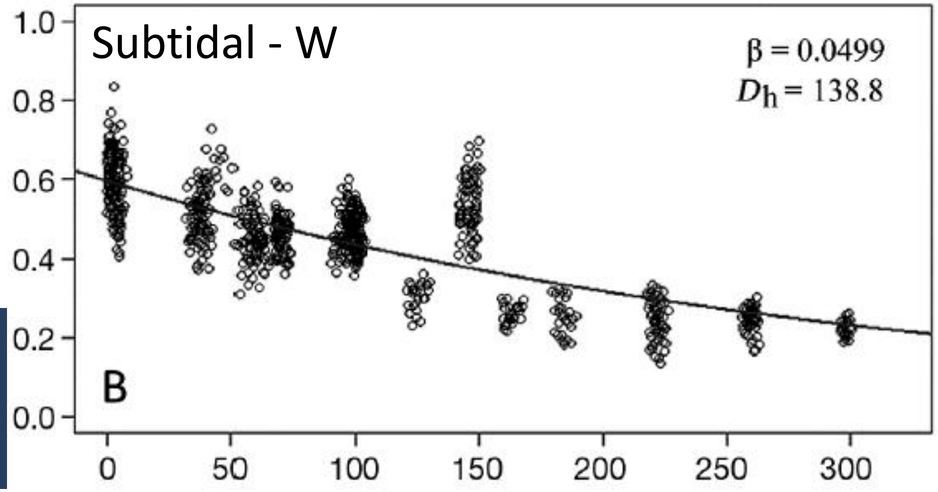
Modified from Soininen et al, 2007

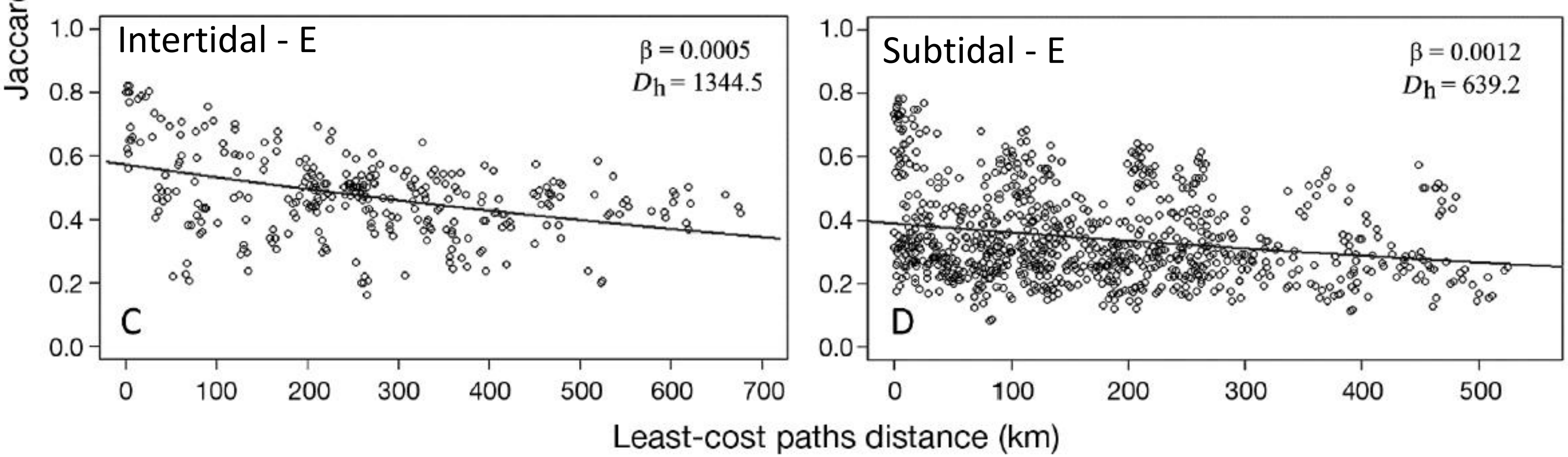
An example in the Mediterranean sea



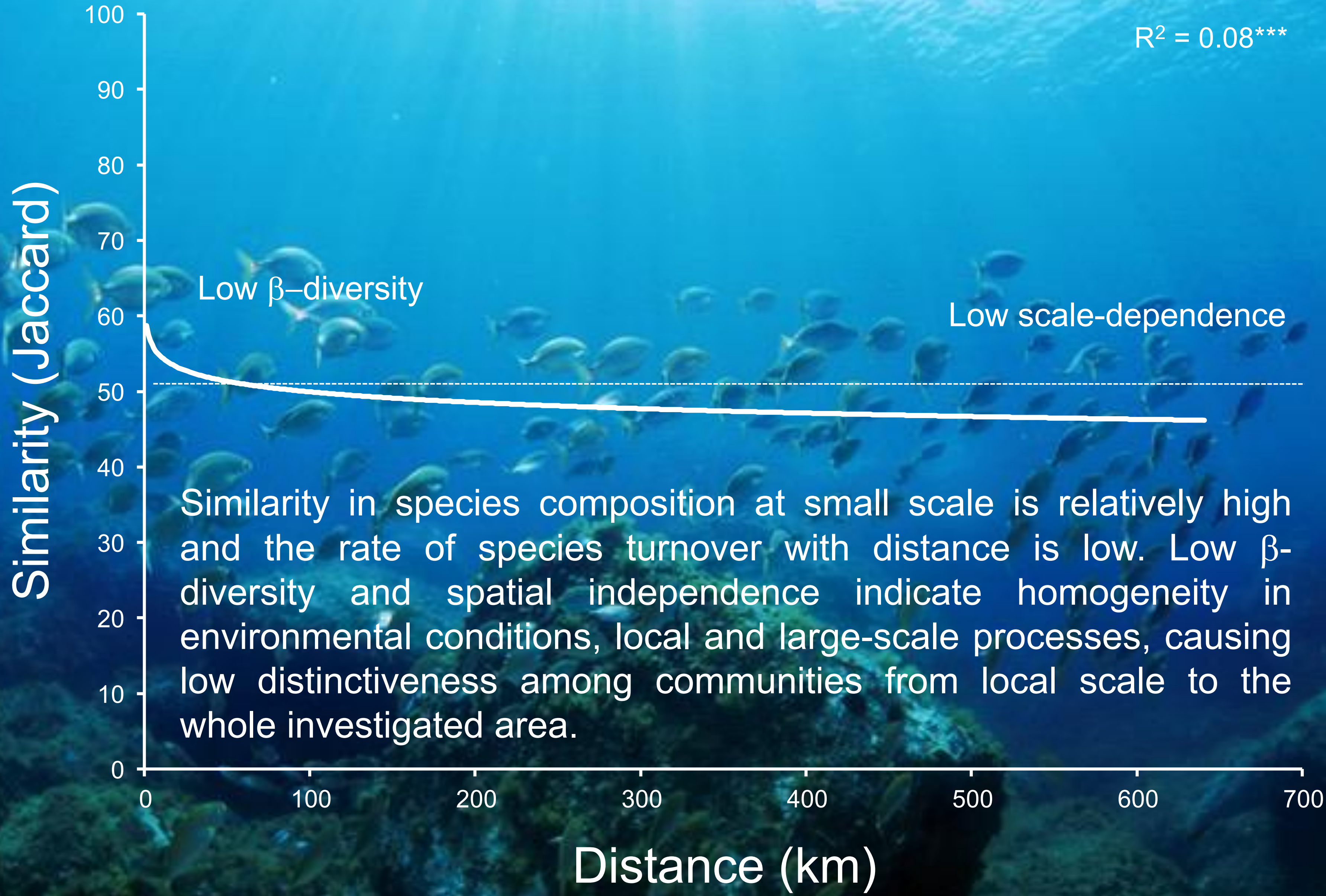
Distance-decay of similarity in composition

Mediterranean shallow subtidal sessile assemblages



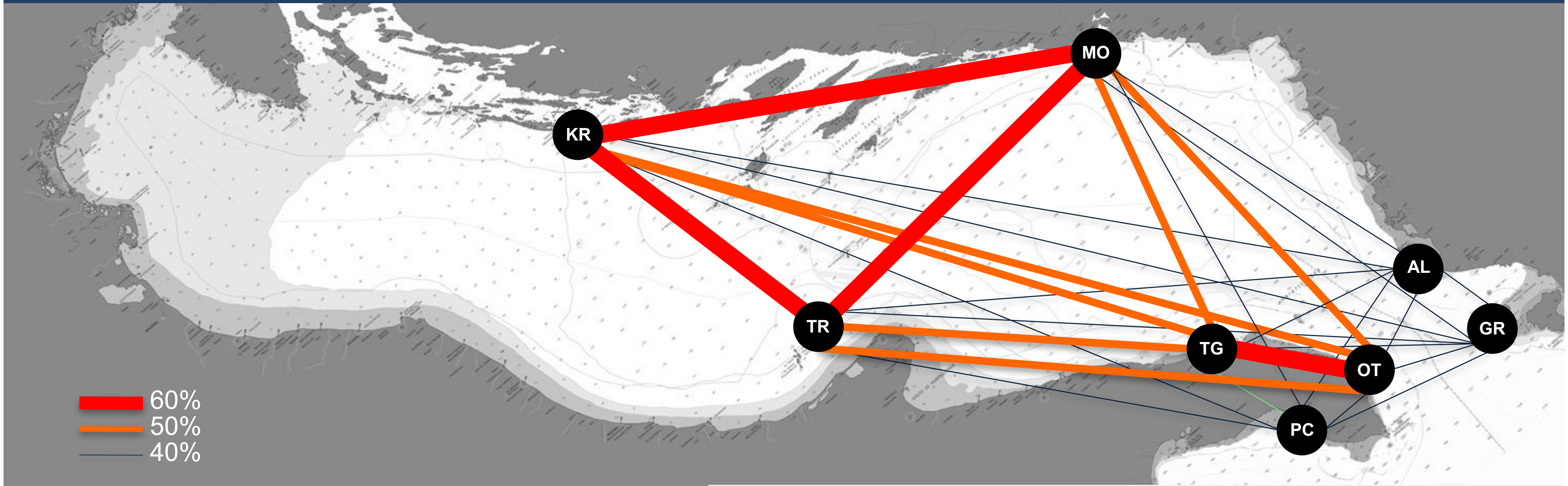


Distance-decay sessile assemblages: Adriatic Sea



Similarity in species composition at small scale is relatively high and the rate of species turnover with distance is low. Low β-diversity and spatial independence indicate homogeneity in environmental conditions, local and large-scale processes, causing low distinctiveness among communities from local scale to the whole investigated area.

Similarity in composition in the Adriatic



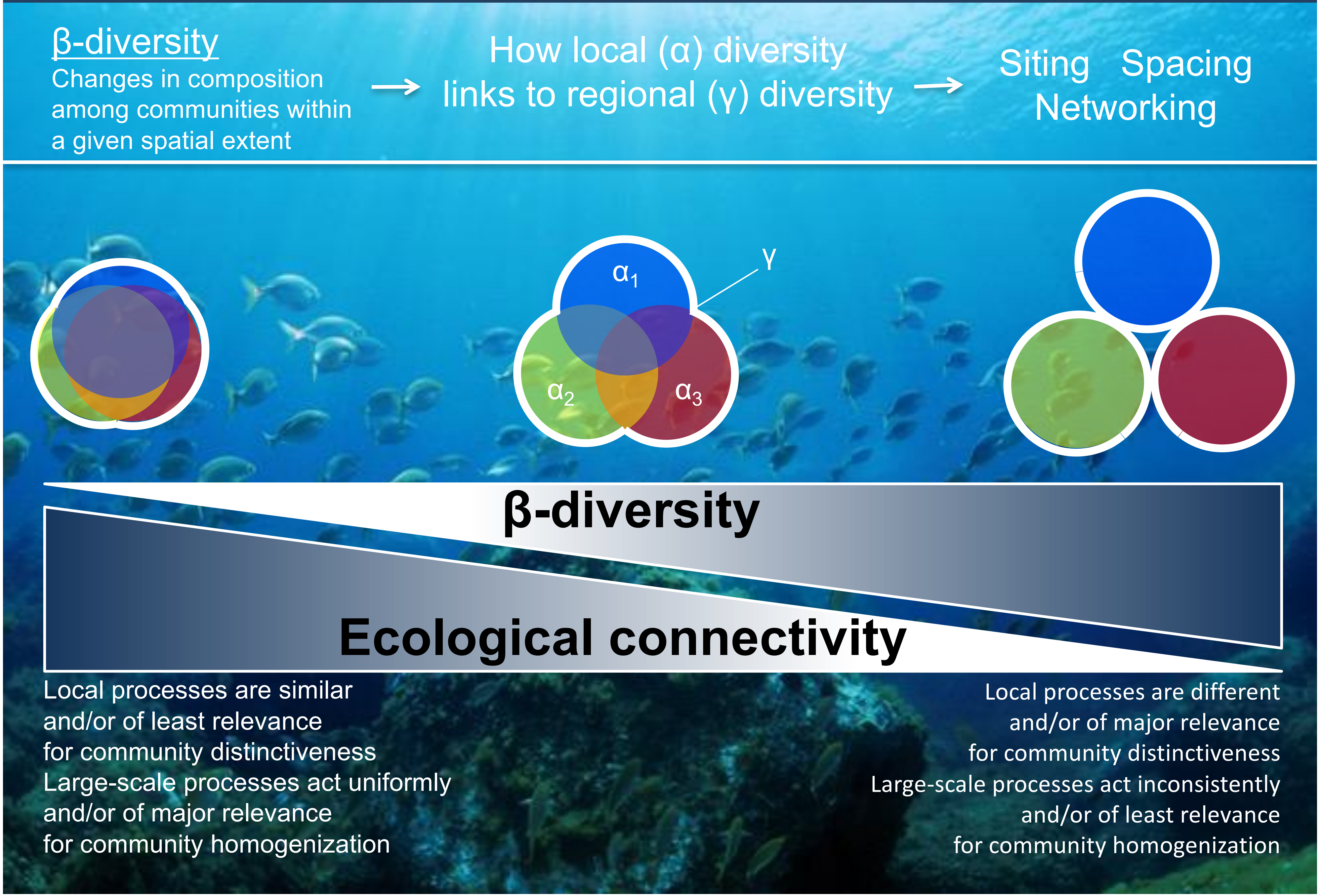
Higher similarity among locations in the central (KR-TR-MO) and southern Adriatic (TG-OT)

Intermediate similarity between these two groups

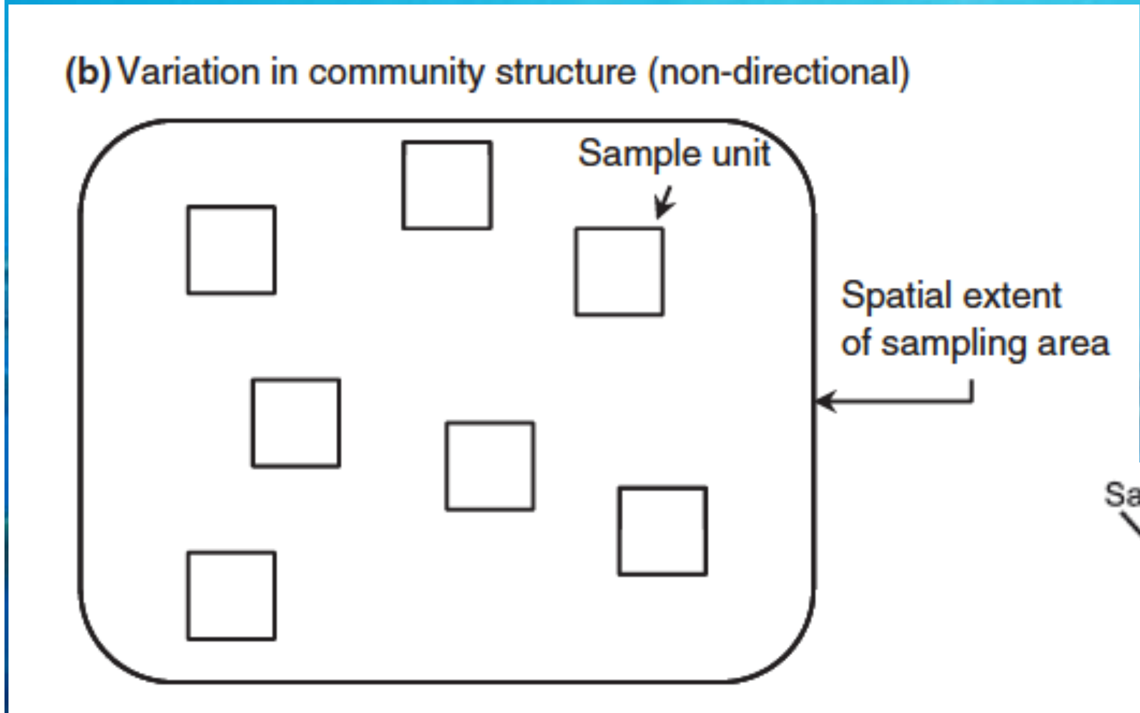
Discontinuity with locations AL, GR, PC

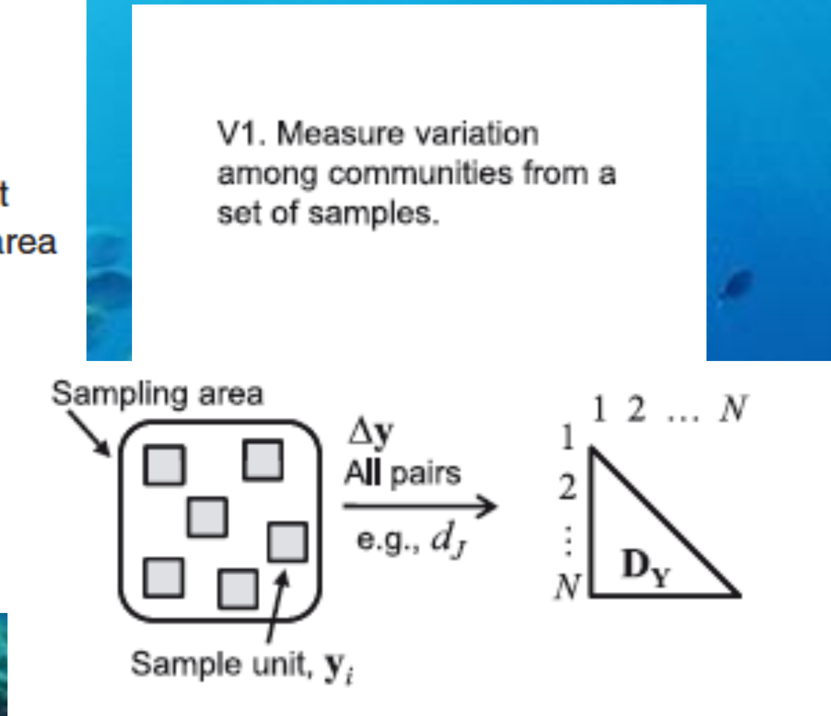
Sessile assemblages on subtidal rocky reefs

β-diversity and connectivity



β-diversities as variation

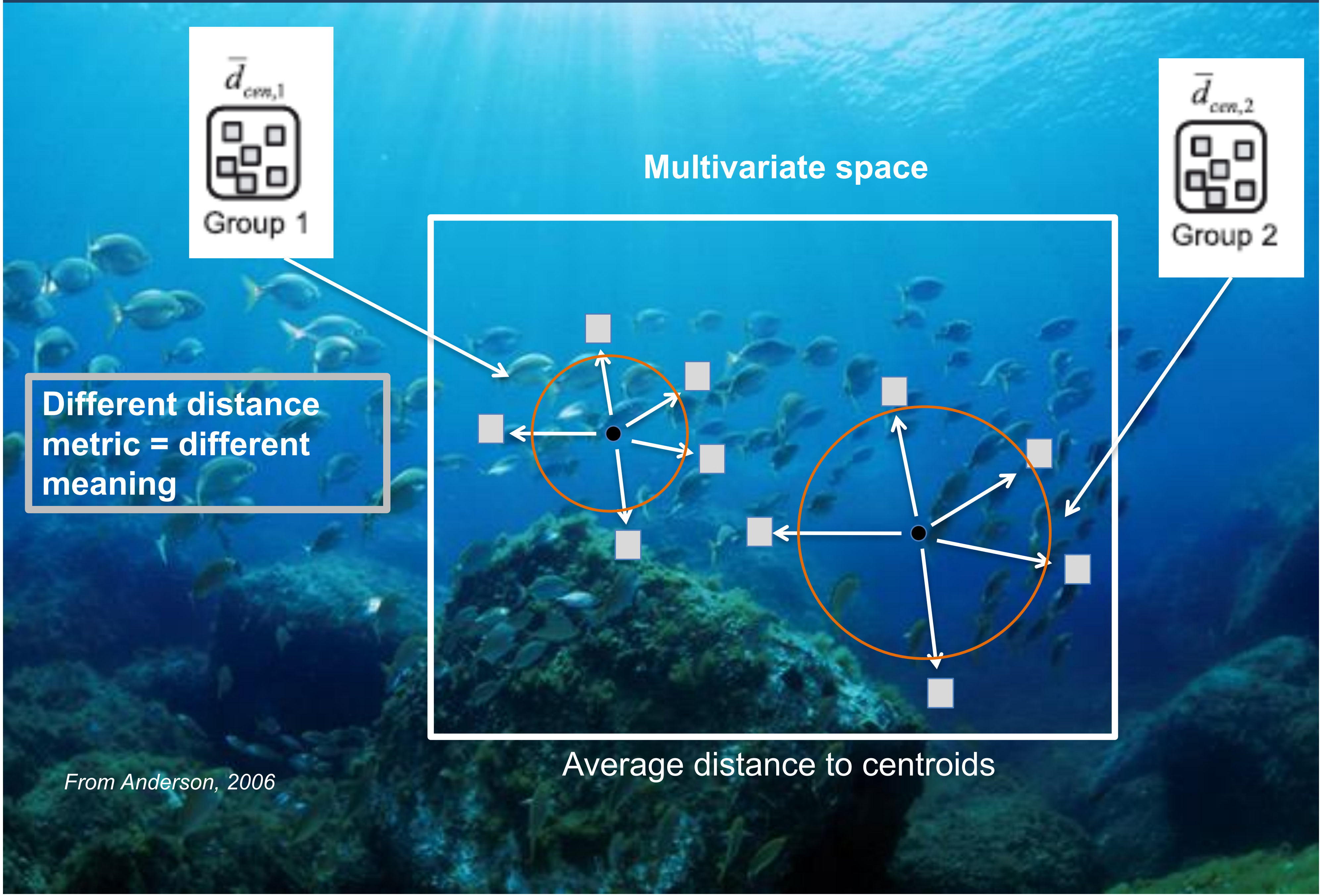




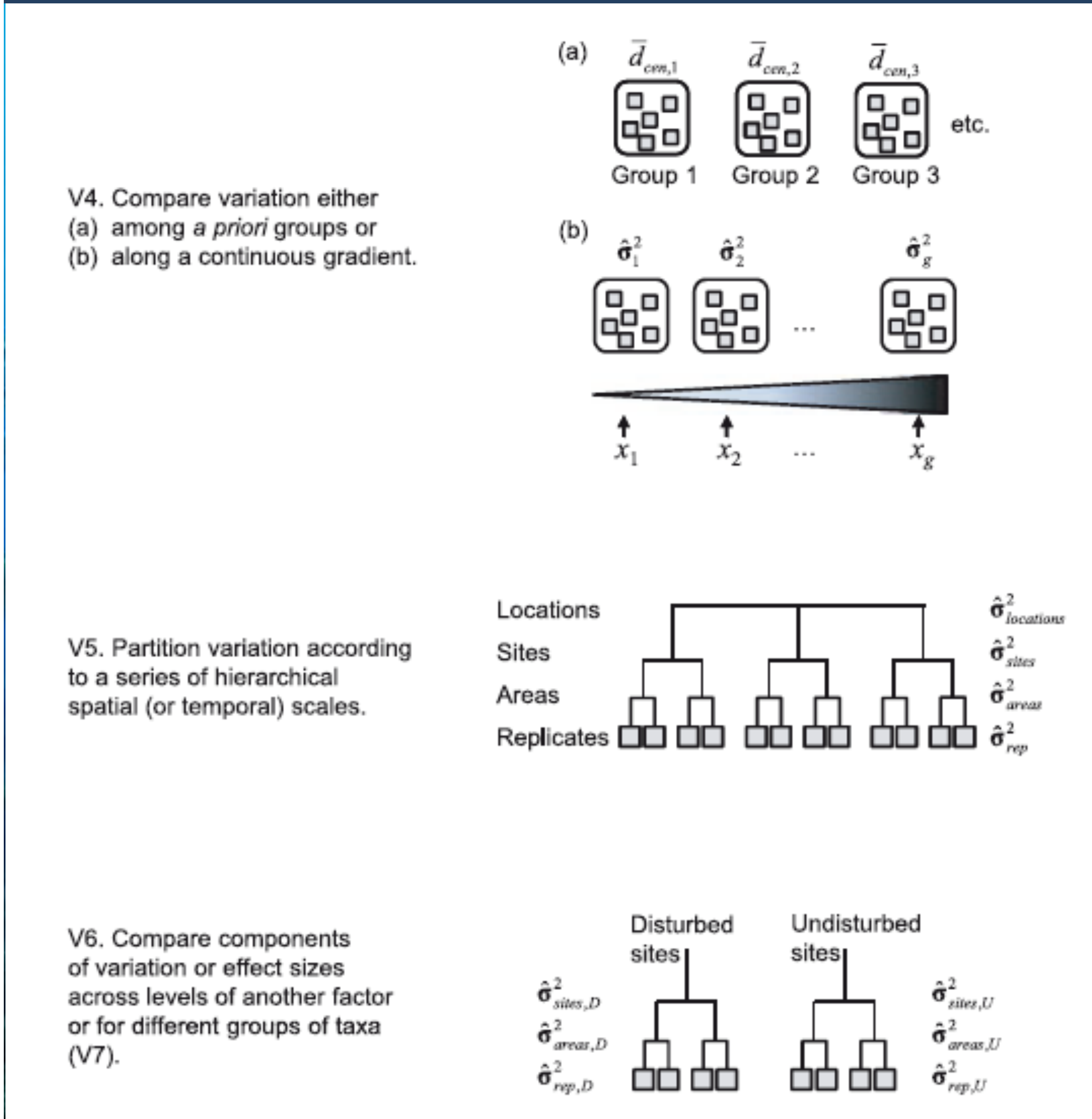
Changes occurring occurring in community composition among a set of sample units within a given spatial, temporal, or environmental extent

From Anderson et al., 2011

Multivariate dispersion as a measure of β-diversity



Modelling β-diversity as variation

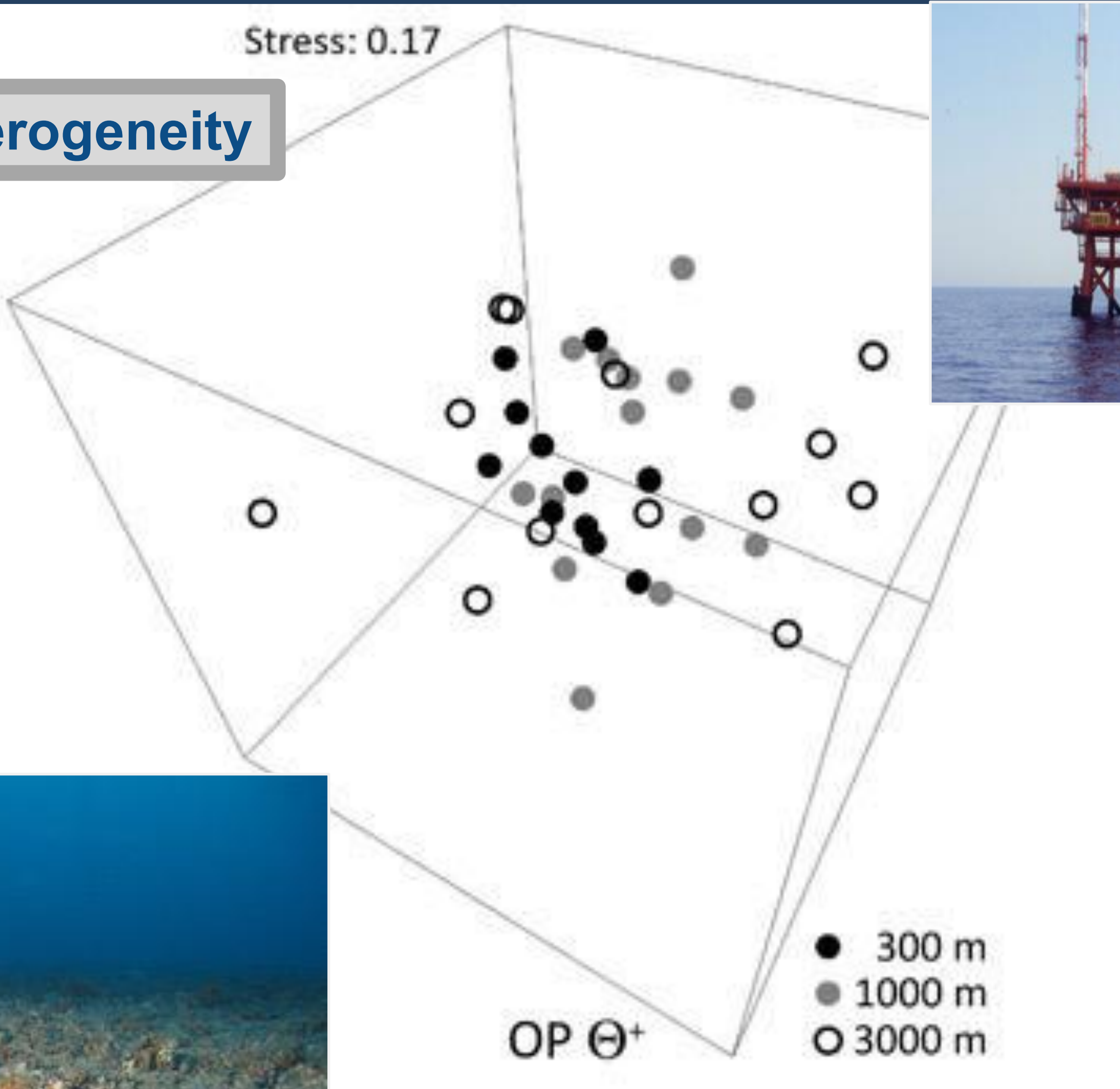


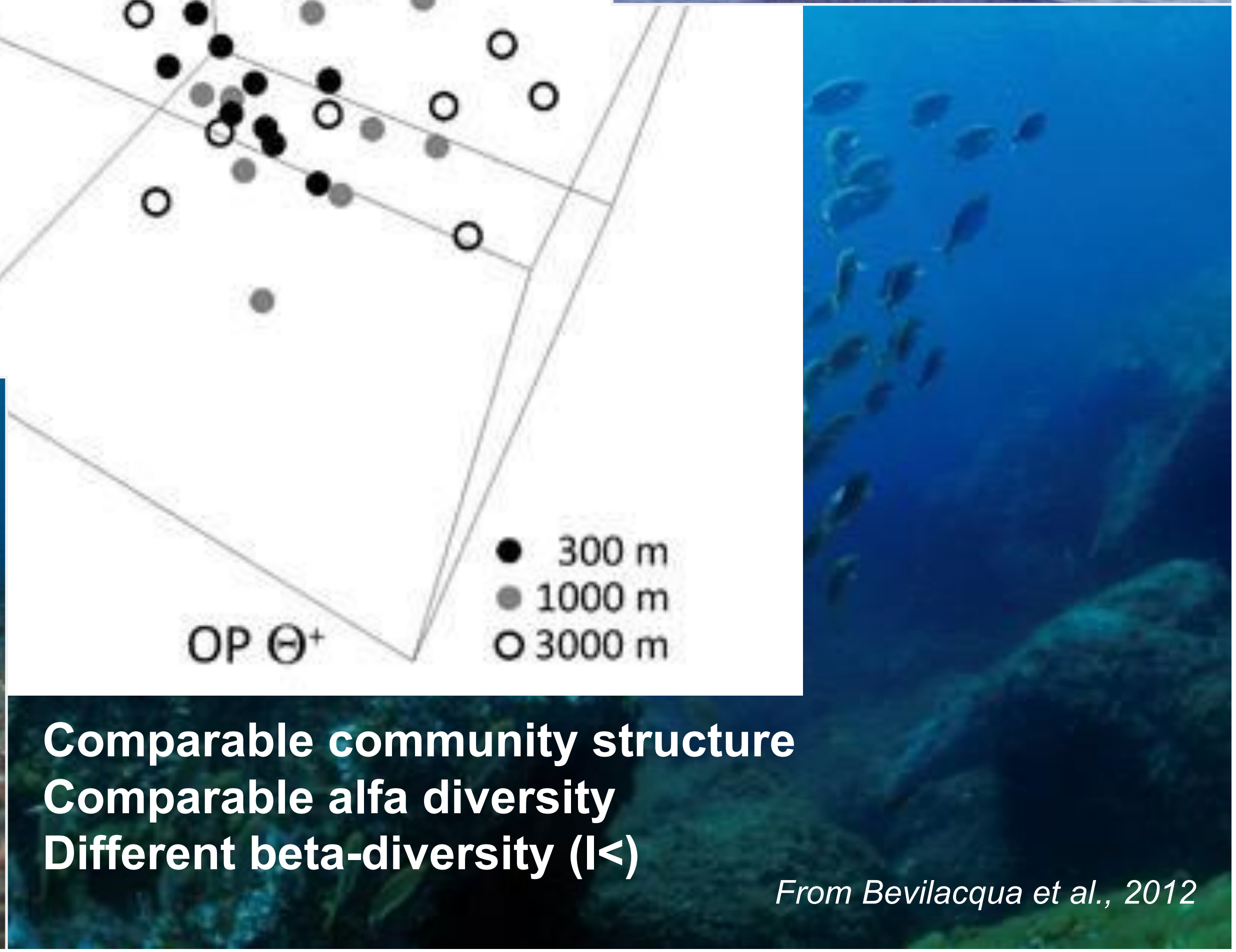
Compare variation among communities, groups of communities, or according to spatial and temporal scales, or other factors

From Anderson et al., 2011

Case studies on impacts and heterogeneity

Decreased heterogeneity



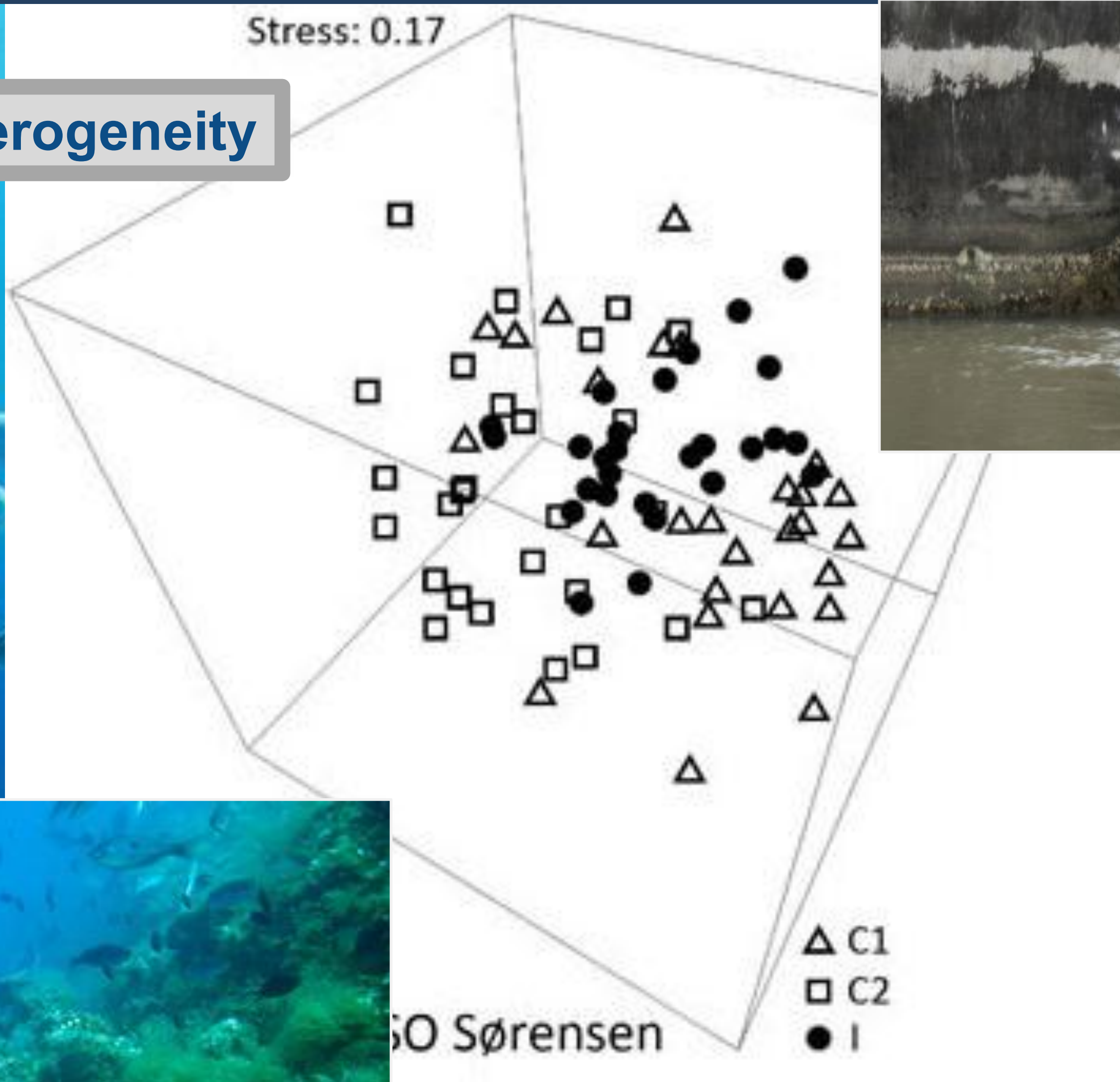


Comparable community structure
Comparable alfa diversity
Different beta-diversity (I<)

From Bevilacqua et al., 2012

Case studies on impacts and heterogeneity

Decreased heterogeneity

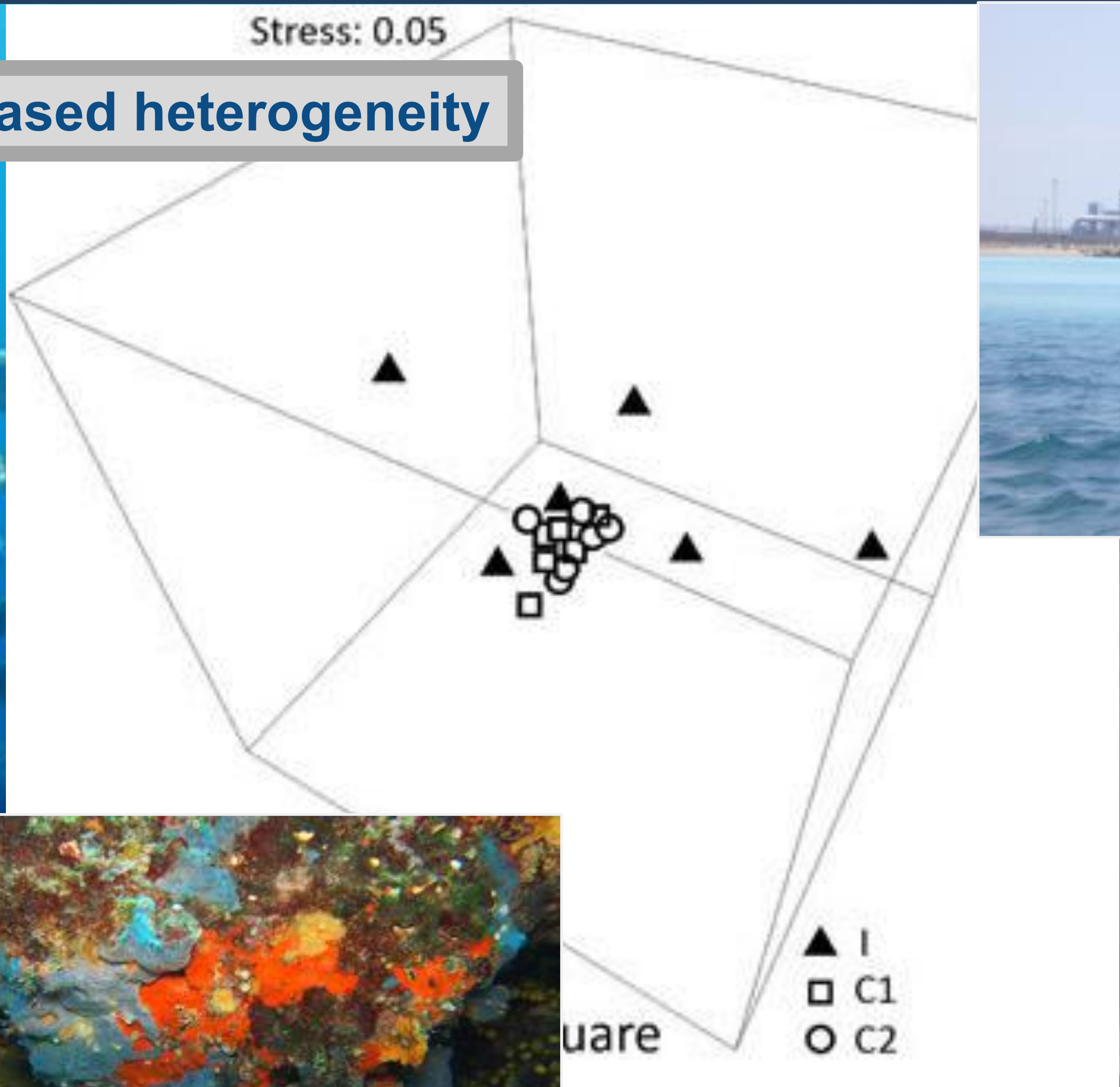


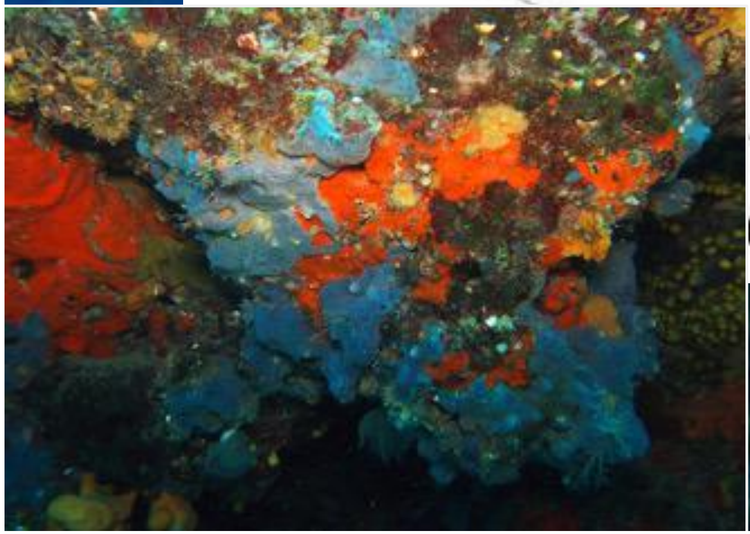
Different community structure
Different alfa diversity (I<)
Different beta (I<)

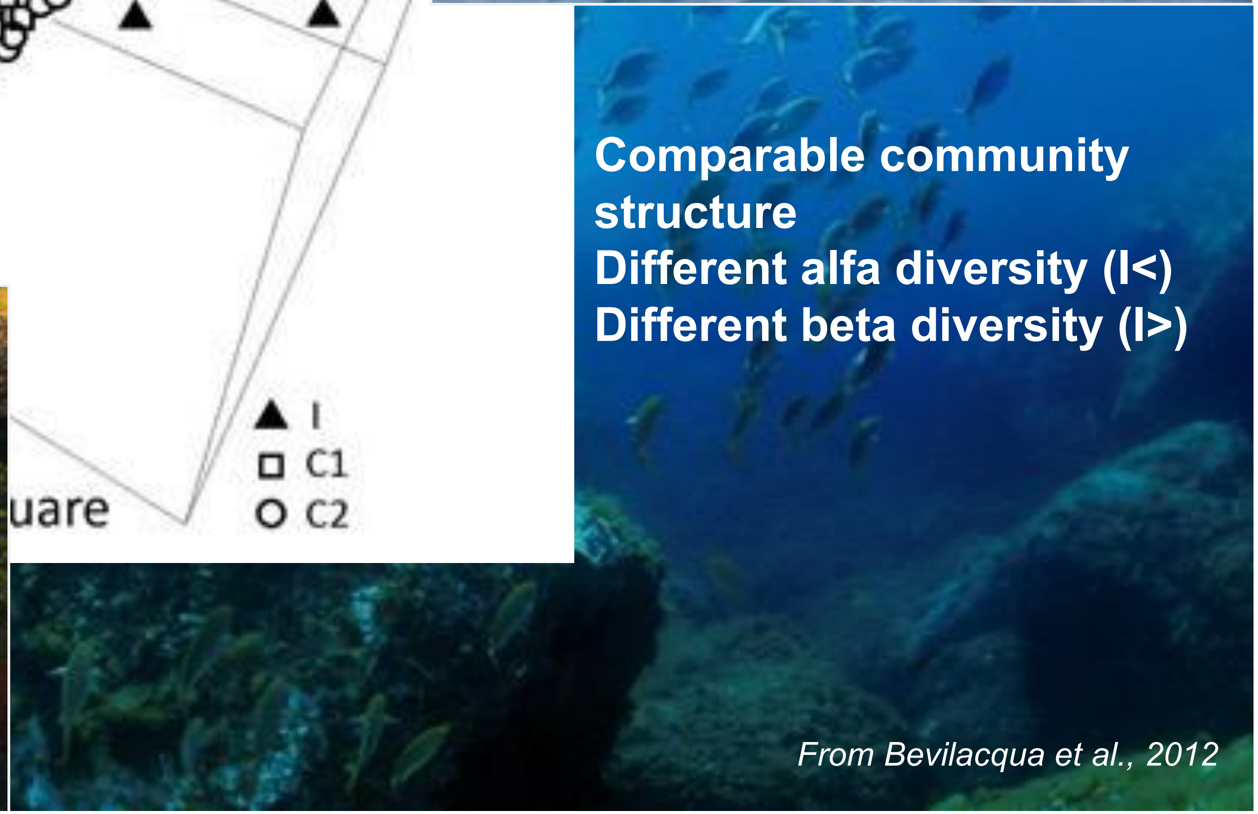
From Bevilacqua et al., 2012

Case studies on impacts and heterogeneity

Increased heterogeneity



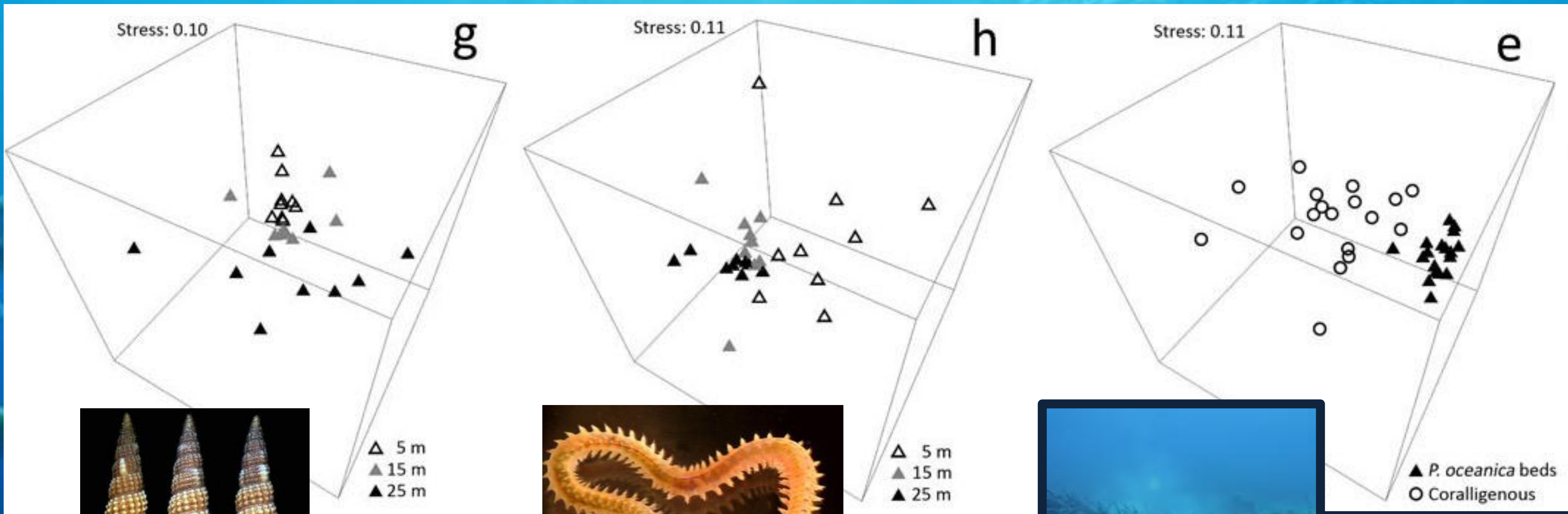


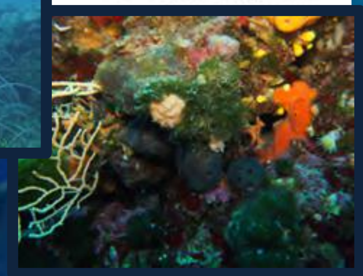


Comparable community structure
Different alfa diversity (I<)
Different beta diversity (I>)

From Bevilacqua et al., 2012

Changes in heterogeneity depends on habitats, geography and taxonomic group





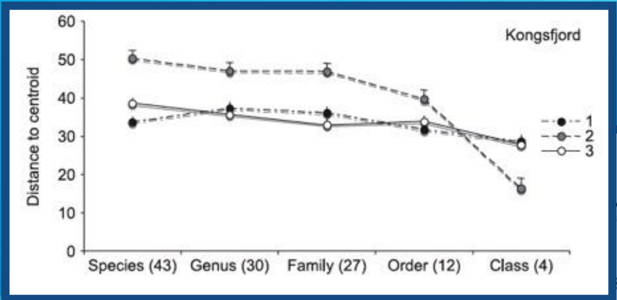
Same gradient
Different groups
Opposite patterns of beta

Same group
Different habitat
Different beta

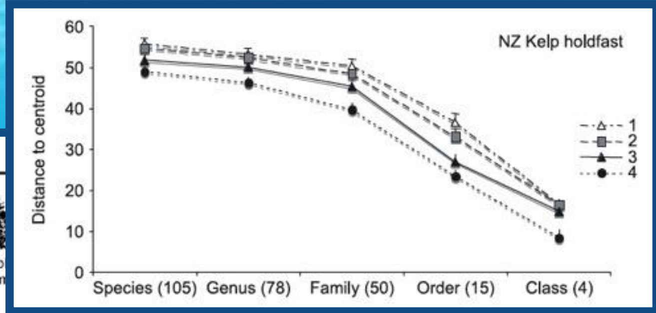
From Bevilacqua et al., 2012

Case studies on impacts and heterogeneity

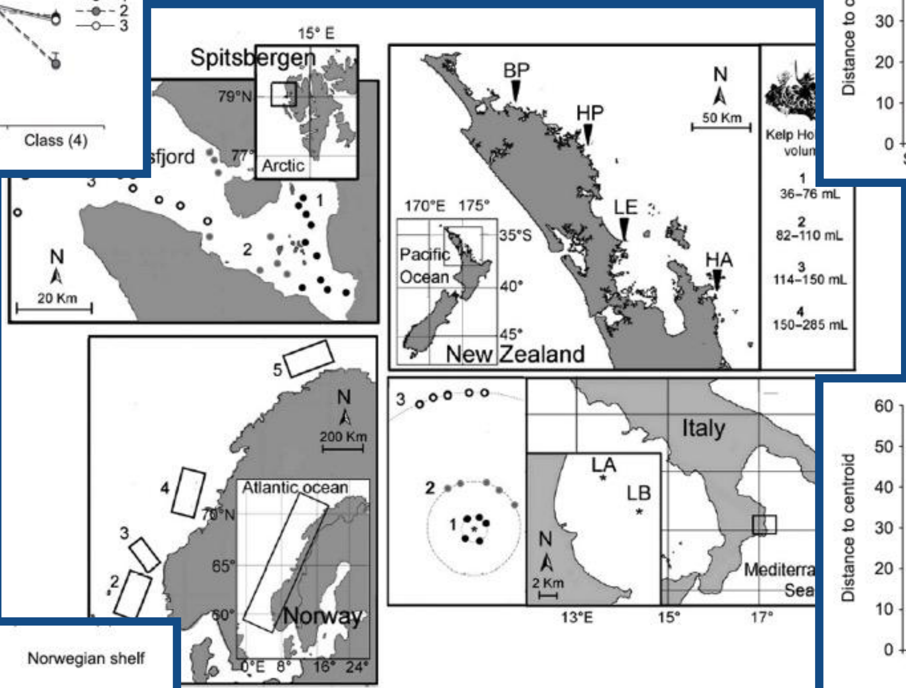
MOLLUSK ASSEMBLAGES



Glacial sedimentation gradient



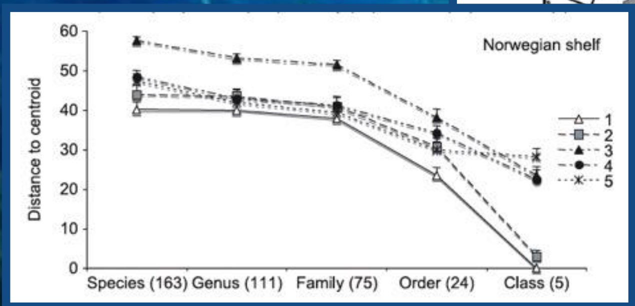
Kelp holdfast size



Distance from offshore platform

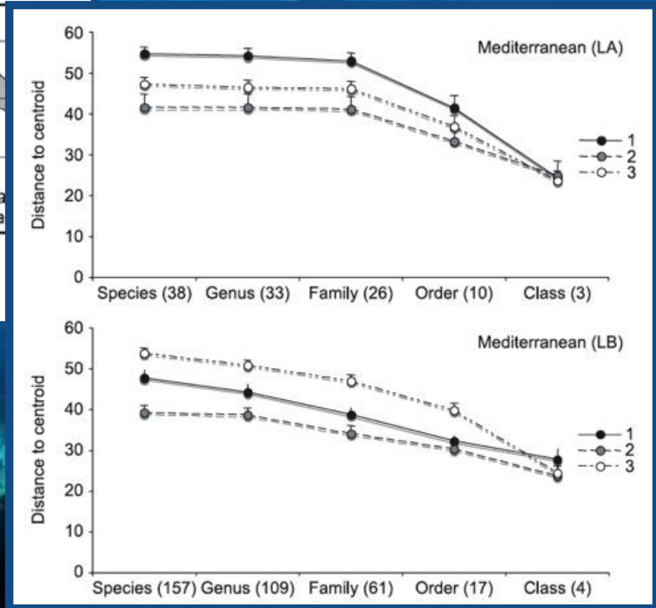
From Terlizzi et al., 2009

Latitudinal gradient

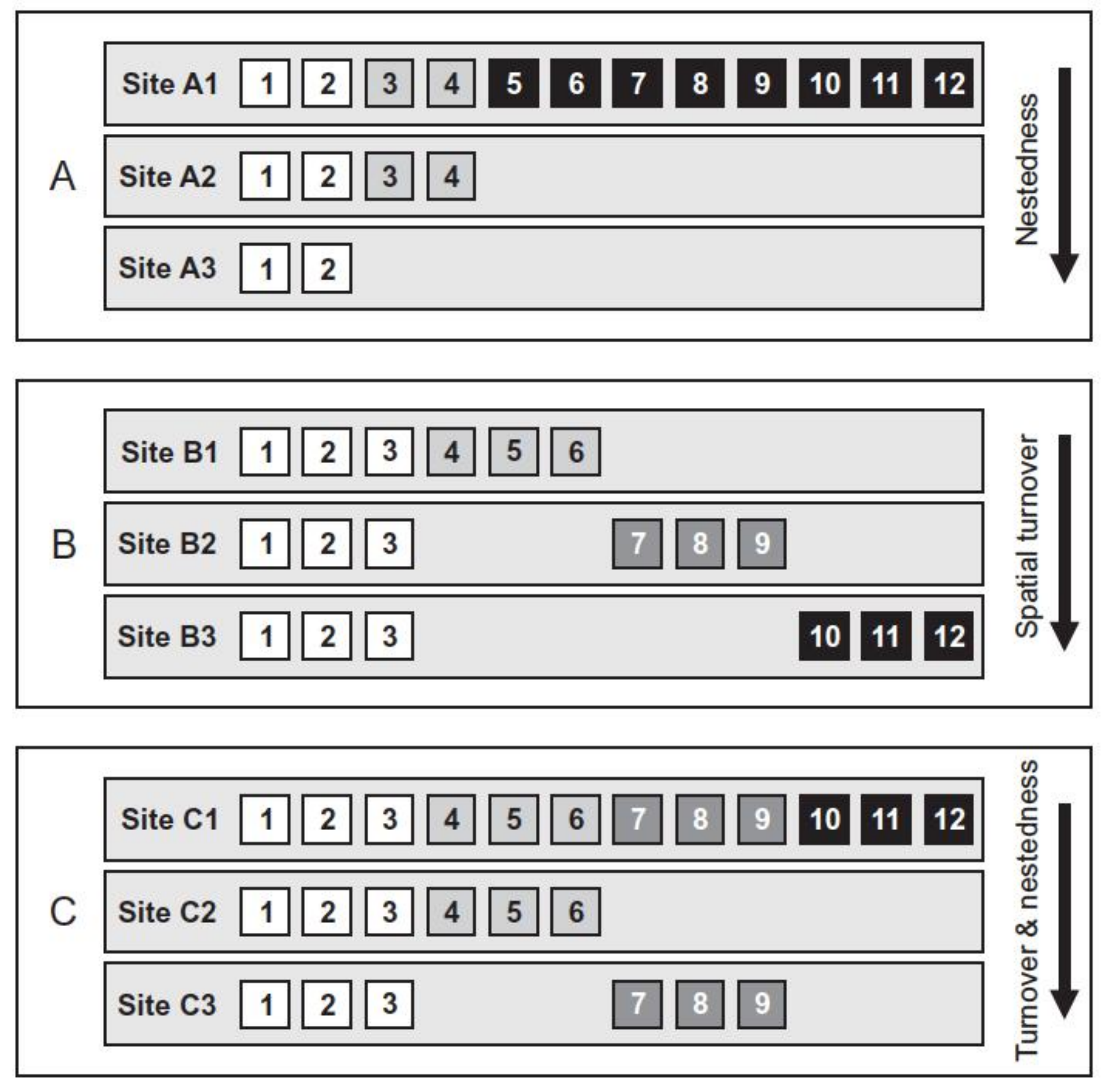


Terlizzi et al. 2009 Divers Distrib

Species level beta-diversity patterns retained up to family level



β-diversity: turnover and nestedness

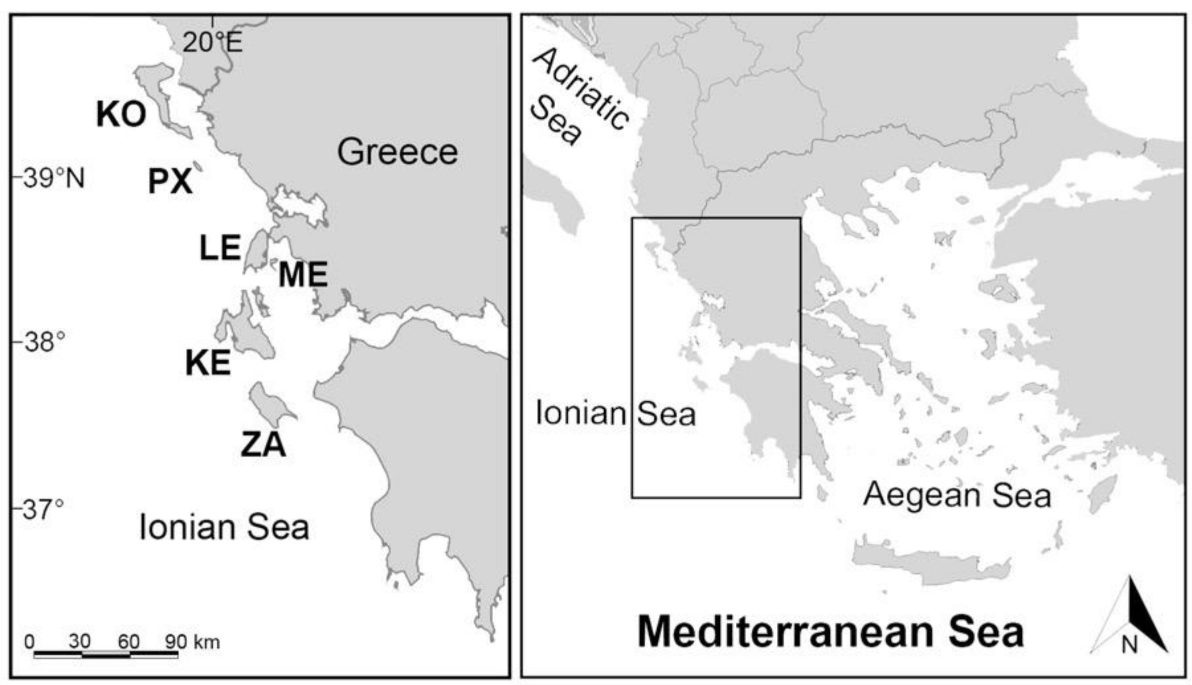


β- diversity may reflect two different phenomena: nestedness and spatial turnover.

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)

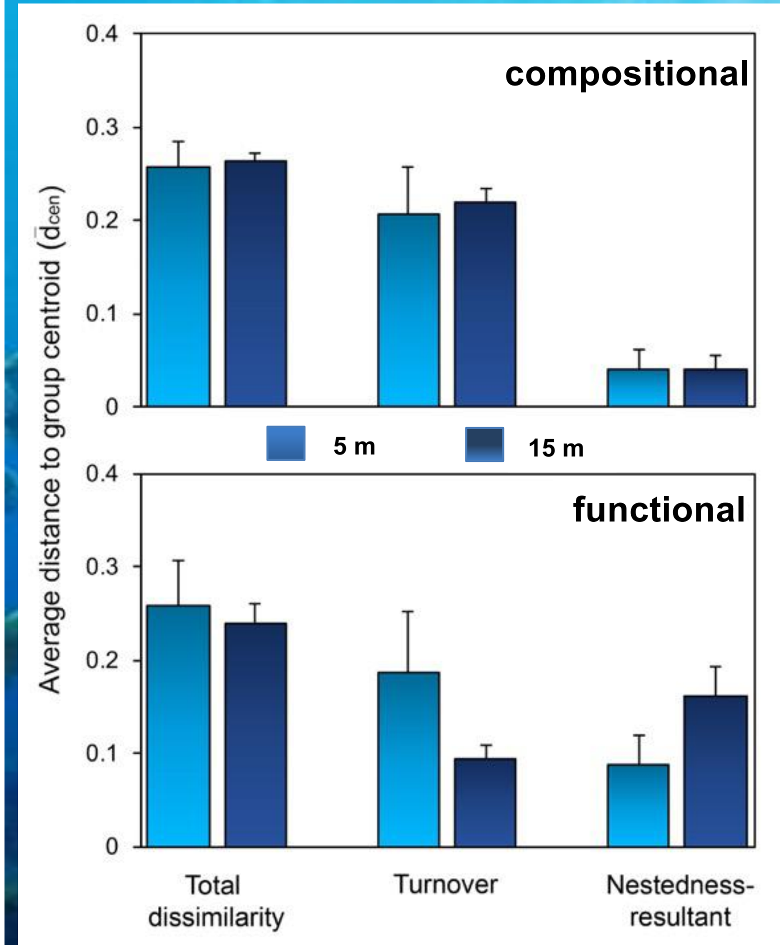
A case study in the Ionian Sea



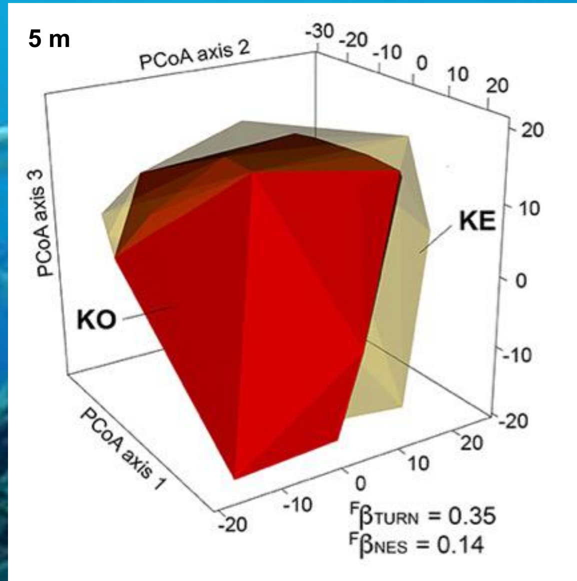
Six islands, four sites in each islands. Sessile assembalges on subtidal reefs at 5 and 15 m depth. Photographic samples with 10 replicates in each sites. Identification of taxa at species level (genus or morphological groups in case of difficult organisms). Identification of funtional traits (48)

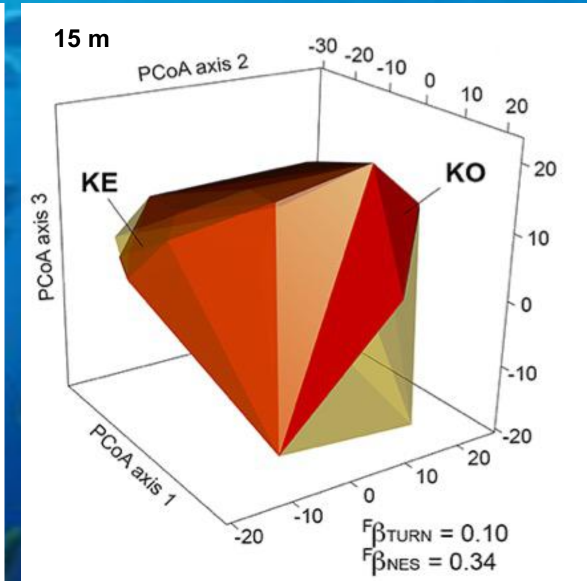
Traits related to functional aspects of organisms (shape, reproduction, dispersal, interaction with the environments, energy flow. Construction of muldimensional functional space for each assemblage in each islands and depth

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 ⟹ functional turnover
15 m: species turnover ⟹ 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.

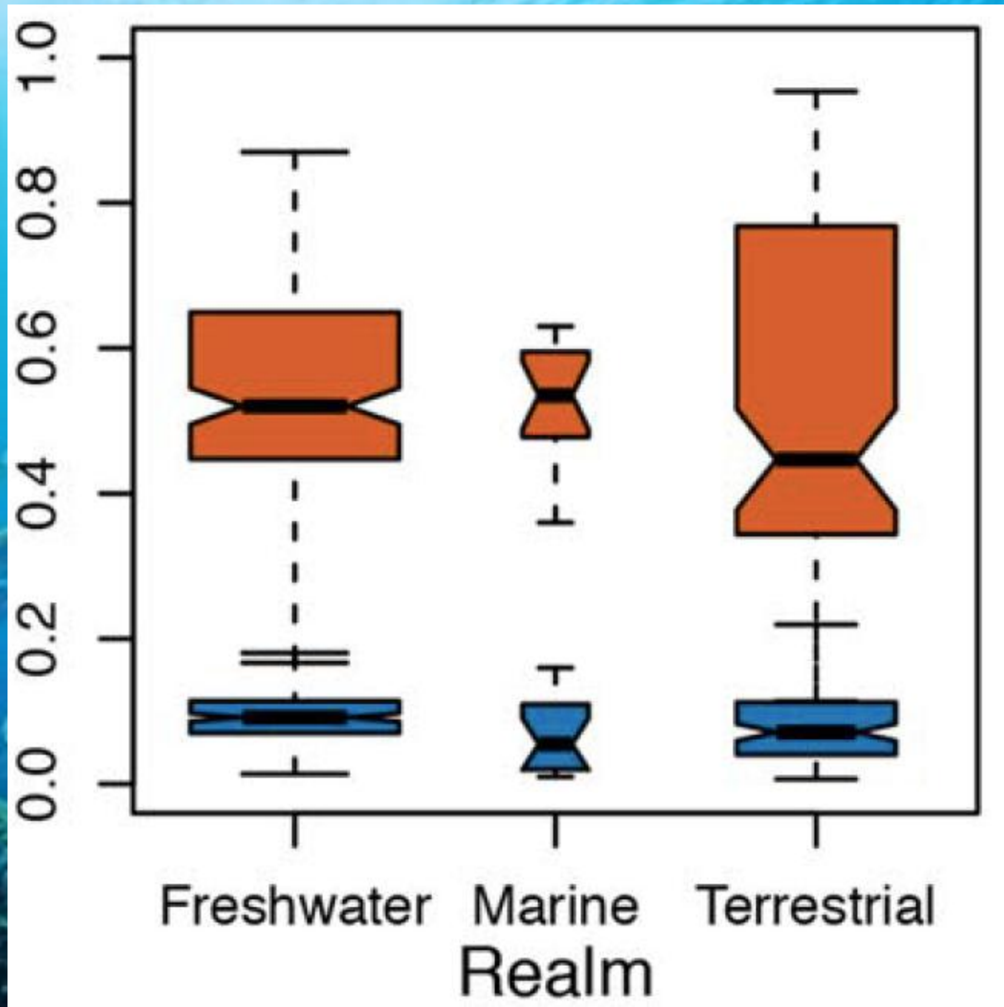
**Understanding whether compositional diversity underlies functional diversity is crucial for conservation strategies.
Reserve networks based on taxonomic beta-diversity, although maximizing protection of species richness, do not necessarily ensure preserving functional representativeness.**

β-diversity in different realms

β-diversity in marine environments is predicted to be lower than in other realms. β-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 β-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)

The importance of β-diversity

β-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 β-diversity in its basic components could help optimizing reserve selection and accounting for functional diversity