

Implications for differences in conservation strategies and reserve networks

Feature	Terrestrial ecosystems	Marine ecosystems
Reserve objectives		
Spatial focus for protection	within reserves	within and outside reserves
Emphasis on propagule export	little	great
State of knowledge		
Taxonomic identification	good	poor
Patterns of species distribution and abundance	good	poor to moderate
Geographic patterns of marine ecosystem diversity	good	poor
Design criteria		
Movement (connectivity) corridors		
Importance of connectivity	less	greater
Type	primarily habitat based	primarily current based
Importance of habitat corridors	greater	lower
Human managed	great	little
Constancy/predictability	high	low
Protection of nonreserve populations	less critical	very critical
Reserve size		
Sufficient for local replenishment (single reserve)	smaller	larger
Habitat diversity necessary for resource requirements	smaller	larger
Reserve location		
Sensitivity to biogeographic transitions	less	greater
Importance of import–export processes (i.e., winds, currents)	less	great

Contribution of ecological theories to marine conservation

Theory of island biogeography

(MPAs can be seen as 'islands' of reduced human influence within a 'sea' subject to several human pressures; the larger the more speciose, high isolation - low diversity)

Supply side ecology

Metapopulation theory

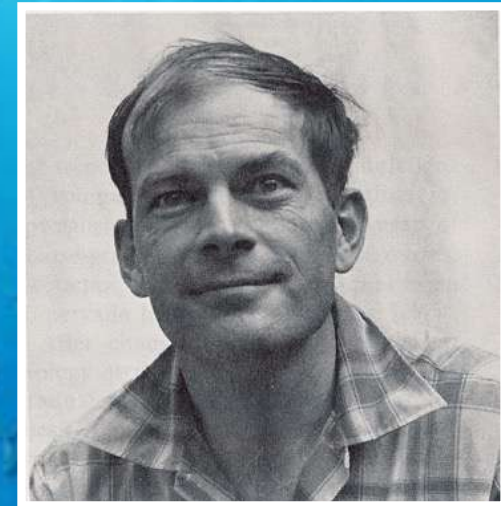
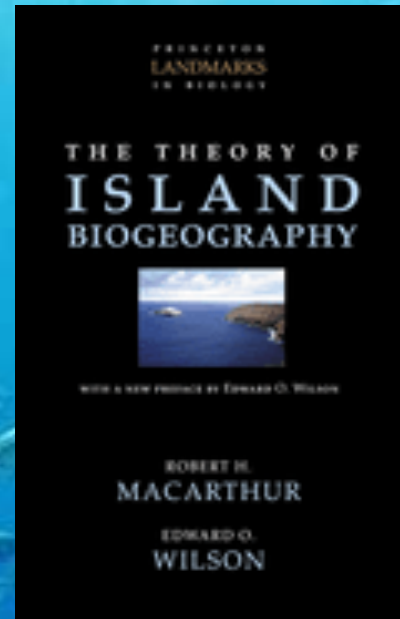
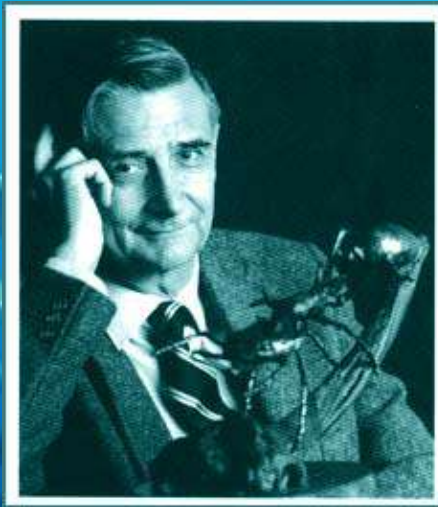
Patch dynamic



Great contribution of experimental marine biology and ecology

The Theory of Island Biogeography

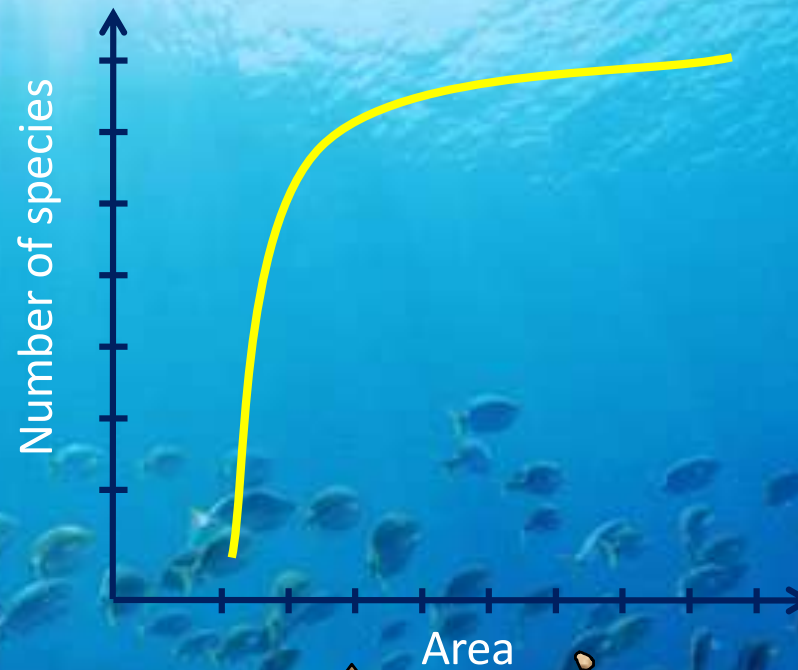
Robert H. MacArthur and Edward O. Wilson (1967)



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.

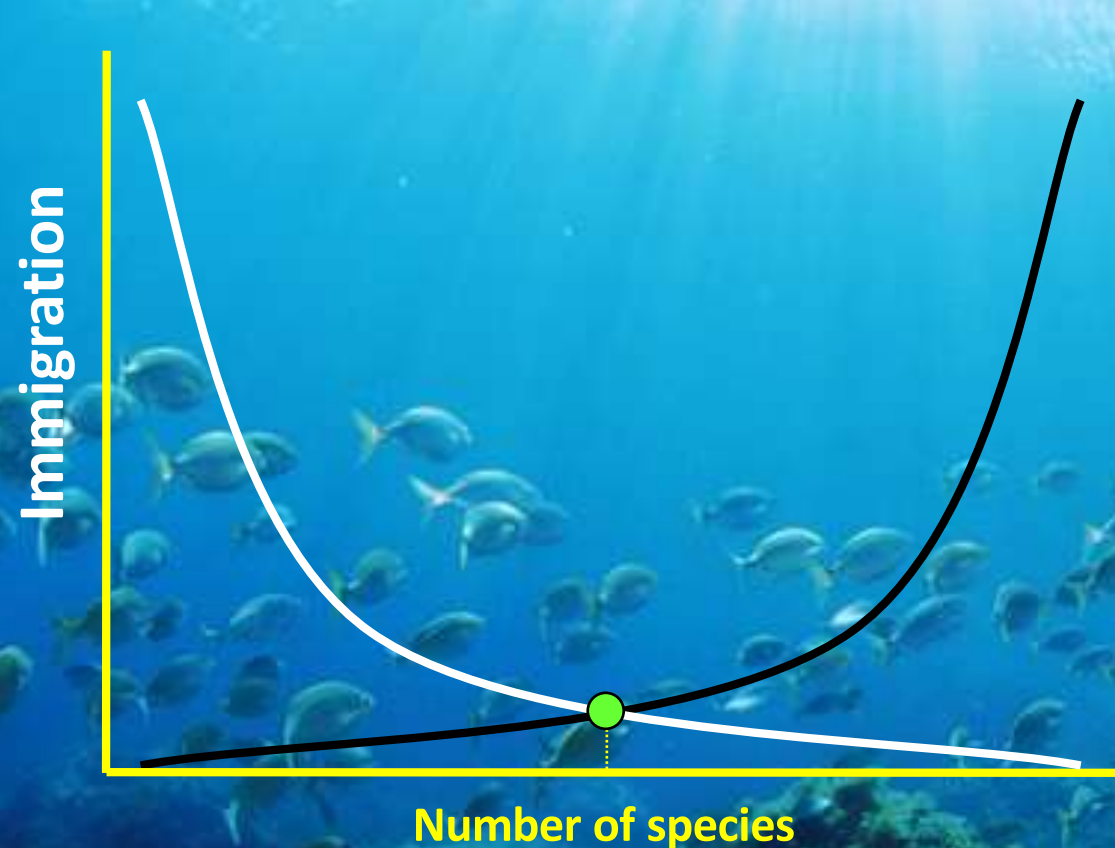
Distance from the “source” and size

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 depend on immigration and extinction rates, and thus also 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 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

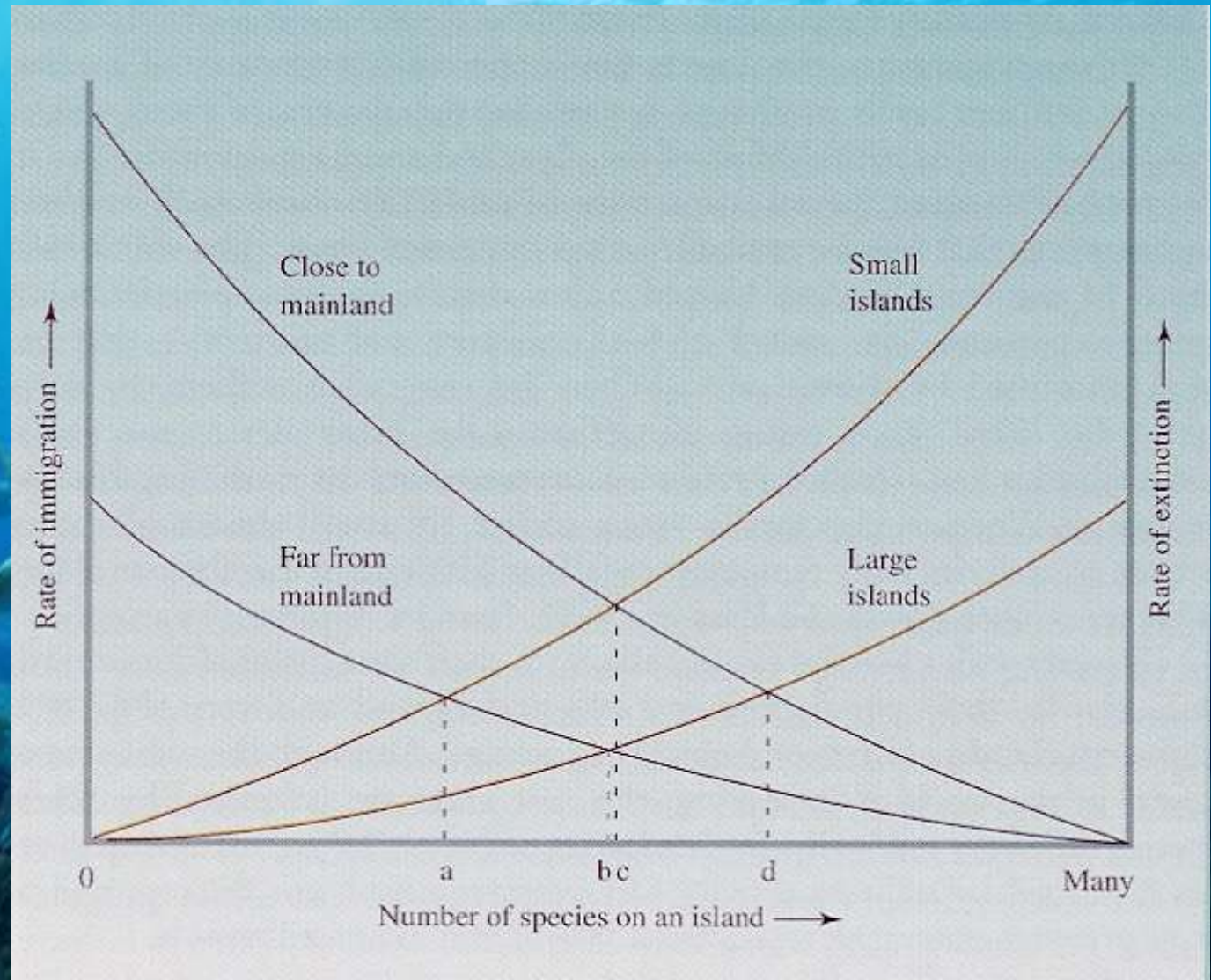
- 1) The number of species is the result of the balance between immigration and extinction
- 2) This balance is dynamic, because species will go extinct and will be replaced by others continuously
- 3) The immigration rate will mostly depend on the distance form the source
- 4) The extinction rate will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

Scenarios

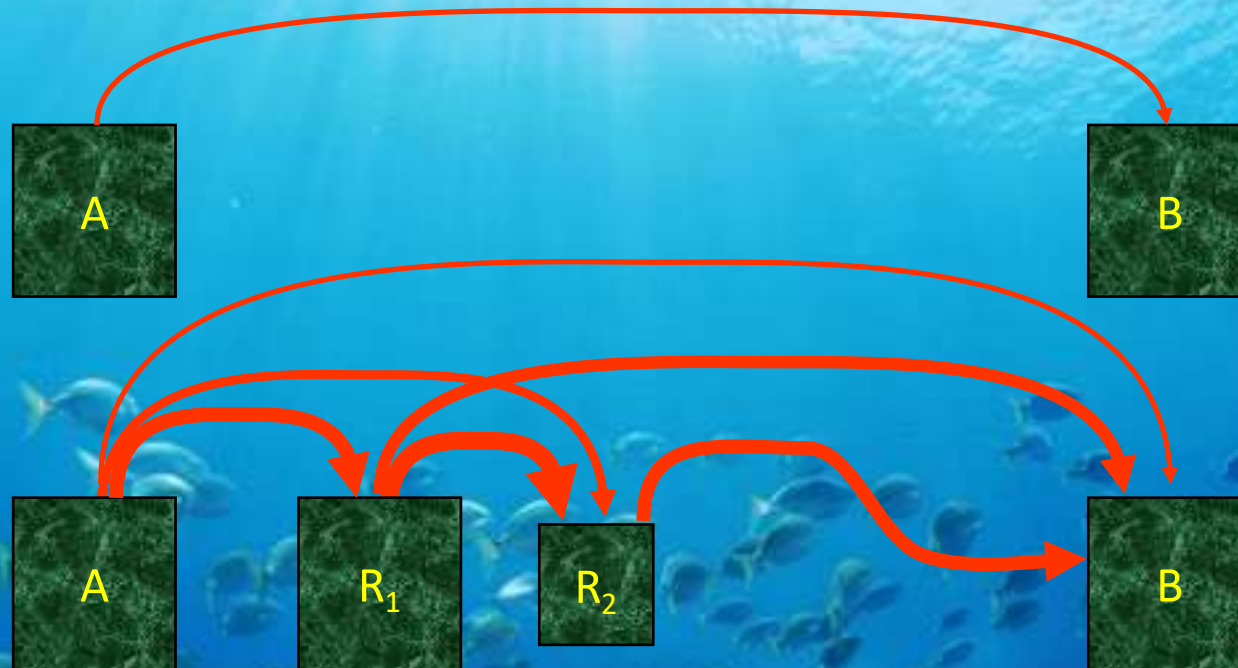
Shape of the immigration curve depends on the distance from the source: the closer the source the higher the immigration rate. The size of island also influence

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 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.

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)

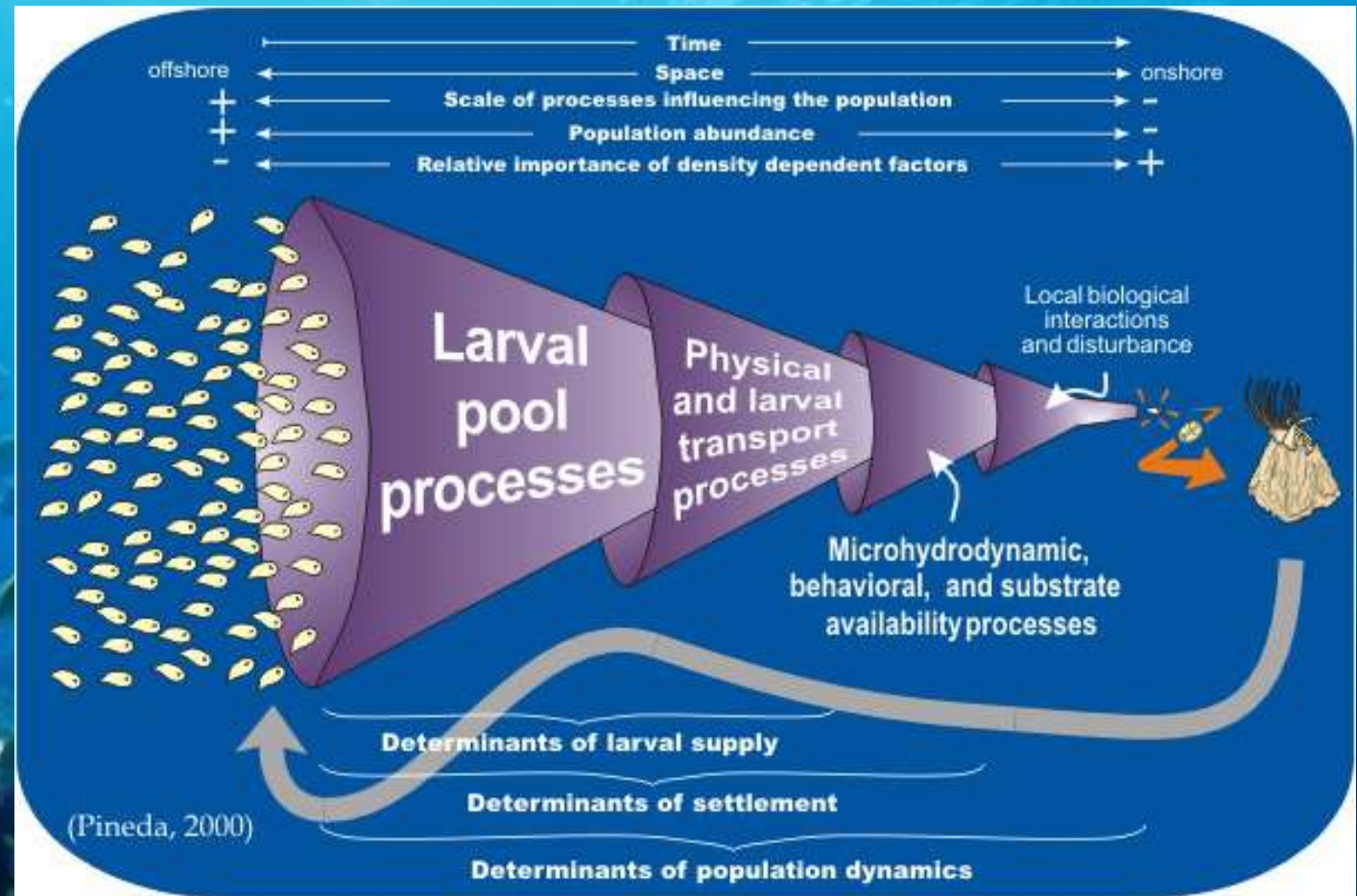
Dispersal ability
(life cycle – planktotrophic, lecithotrophic, adult dispersal; duration of larval stage)

Larval transport
(currents, vectors, isolation)

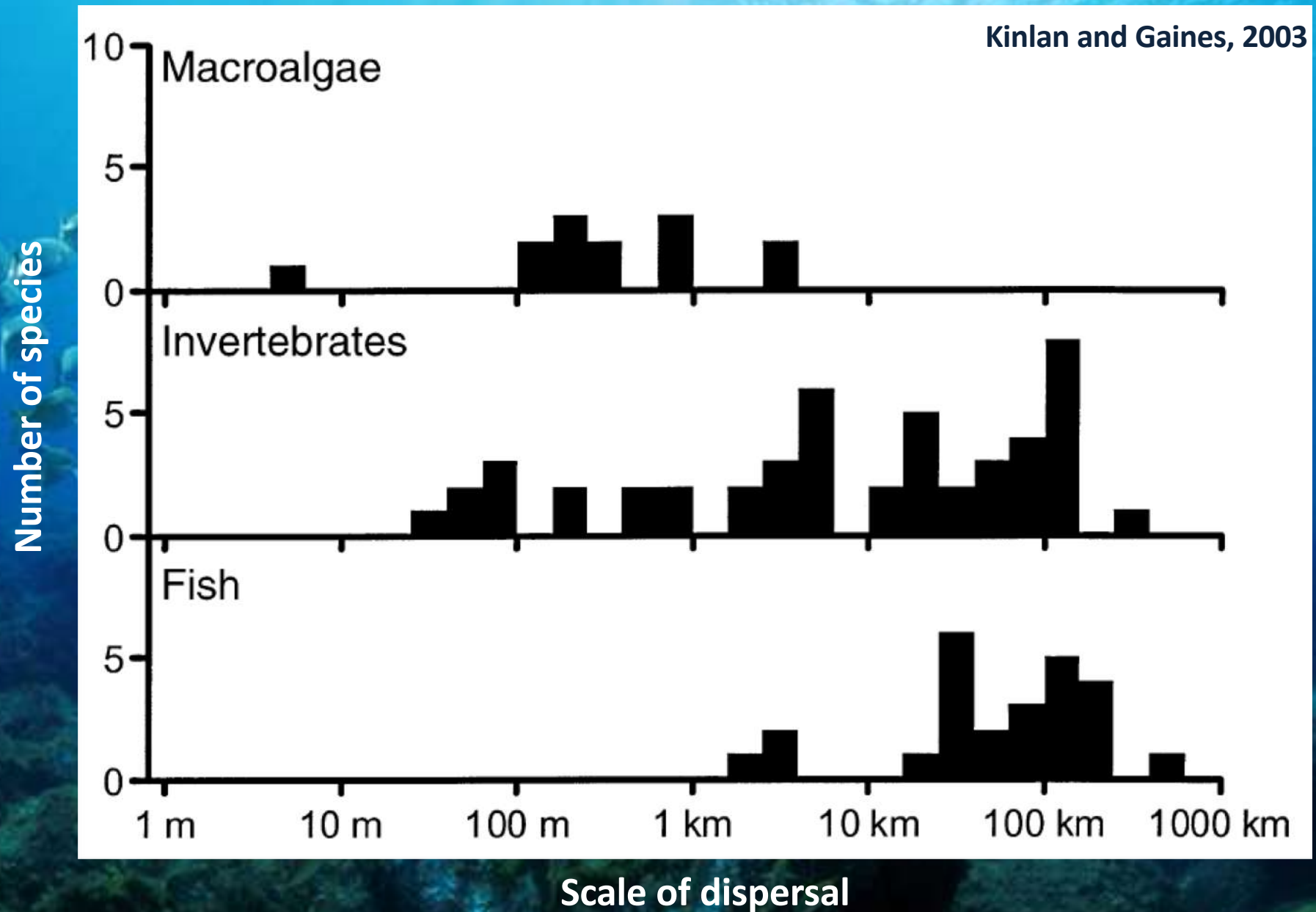
Larval mortality
(predation in the water column, disturbance, limiting food resources, sinking/advection)

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.

birth

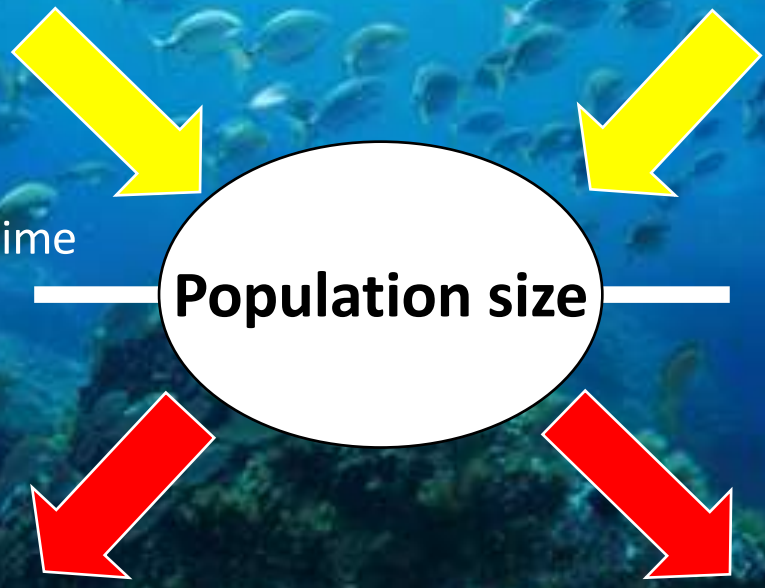
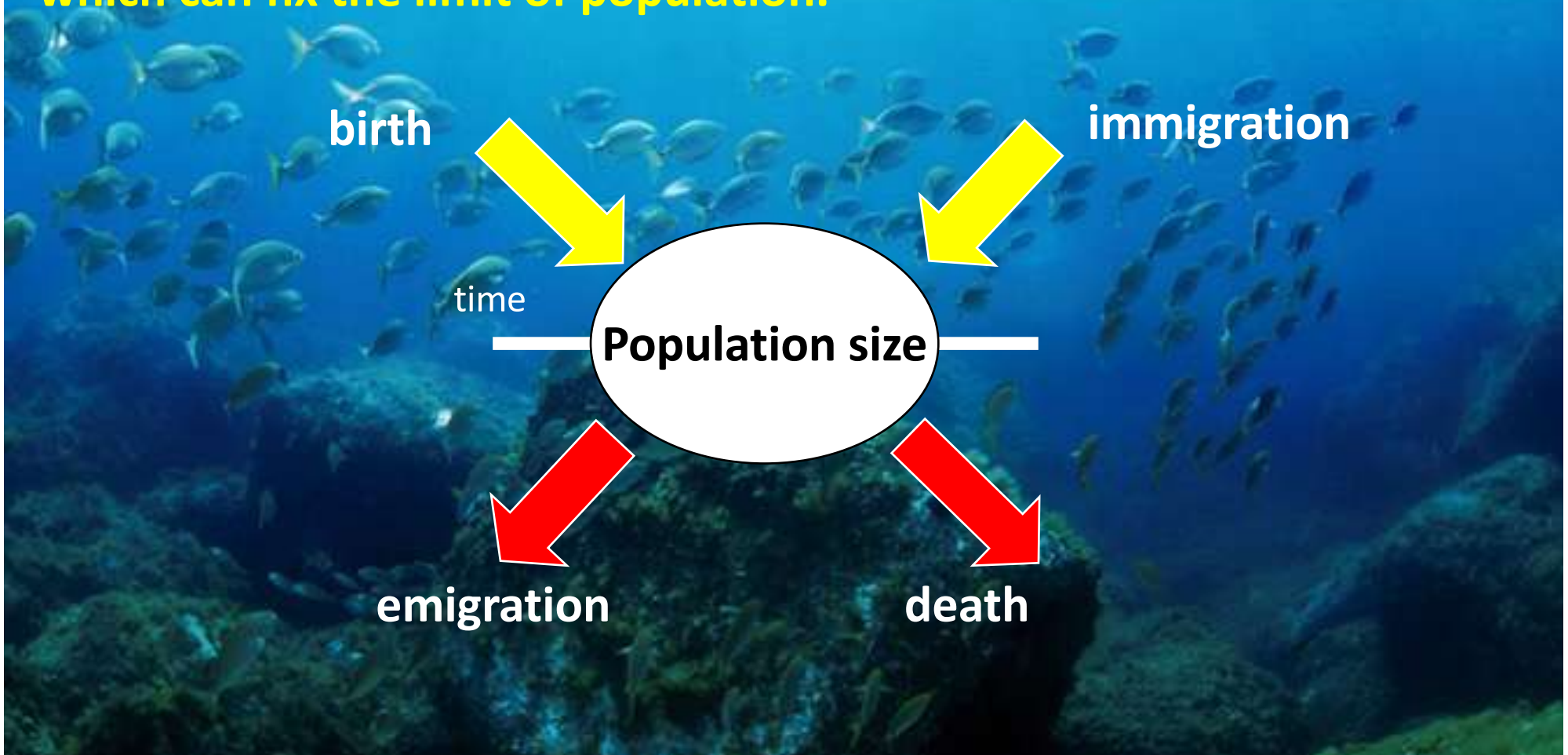
immigration

time

Population size

emigration

death



Metapopulations

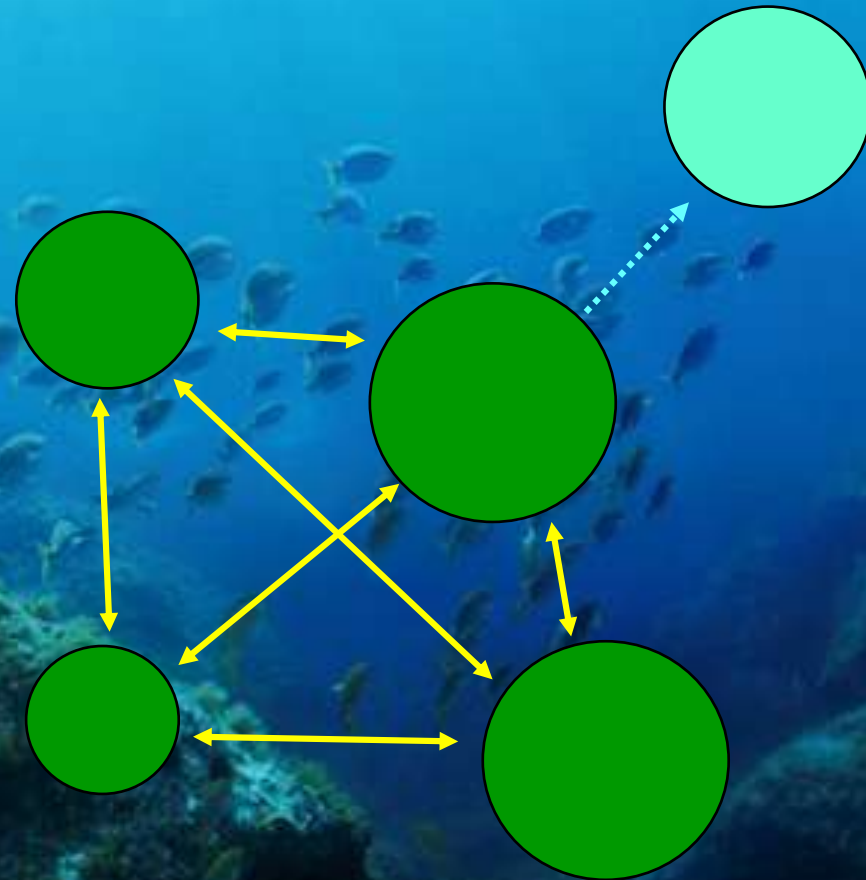
Metapopulations are groups of populations in which there are one or more core populations stable in time, and satellite populations undergoing temporal fluctuations.

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

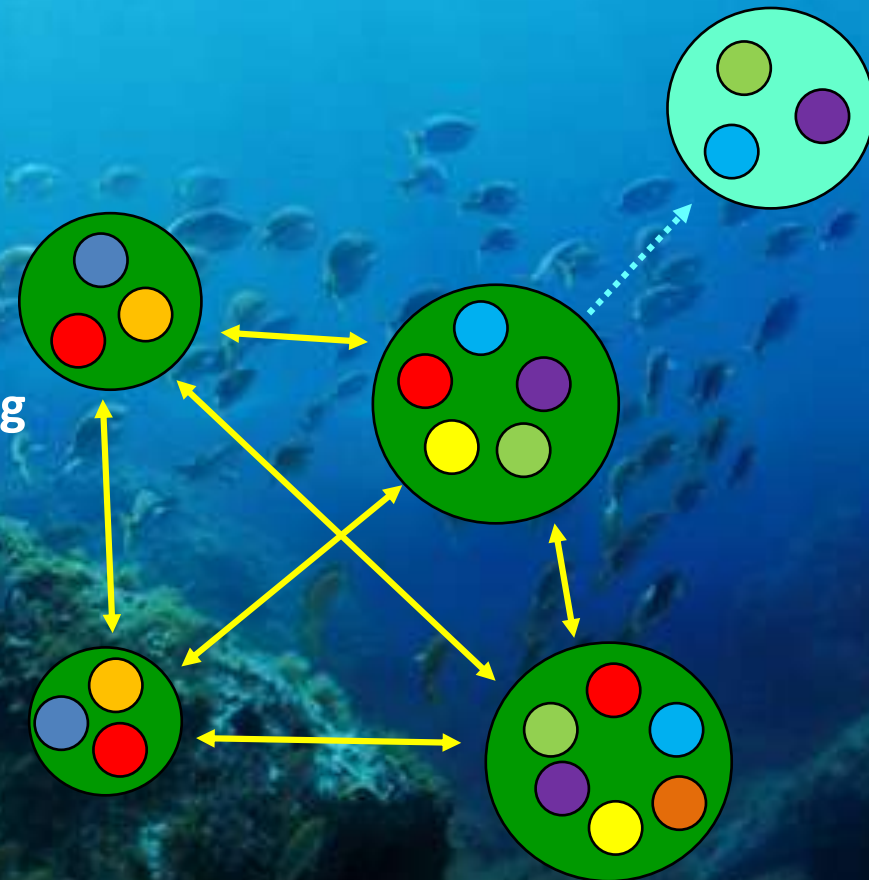


Metacommunities

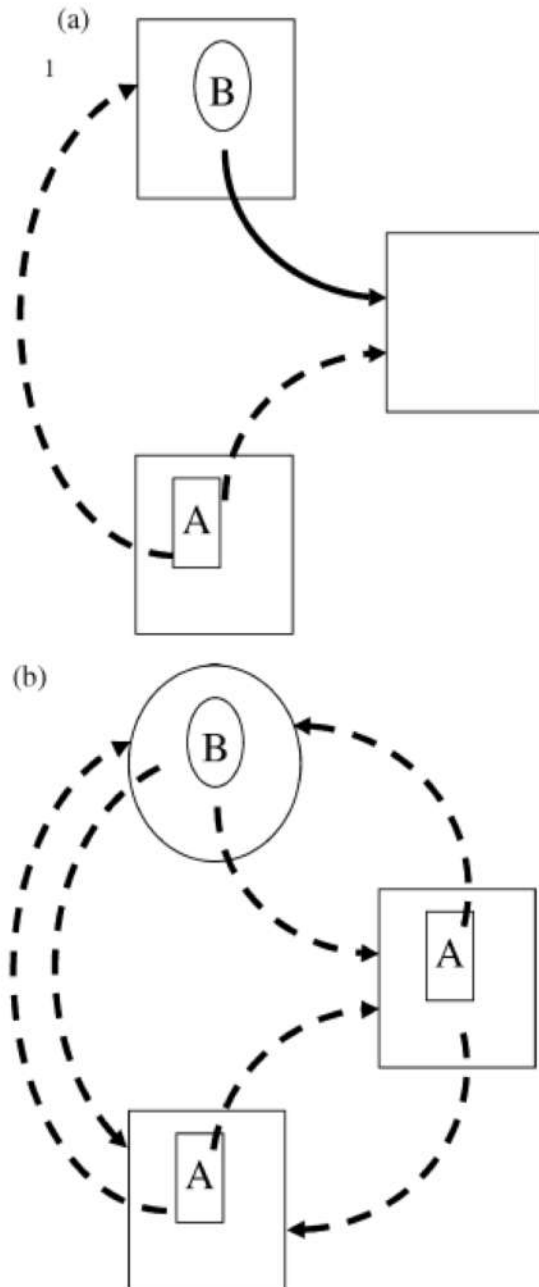
Metacommunities are sets of communities interconnected by dispersal, immigration and/or emigration of multiple (interacting or potentially interacting) species

(Gilpin and Hansky, 1991)

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



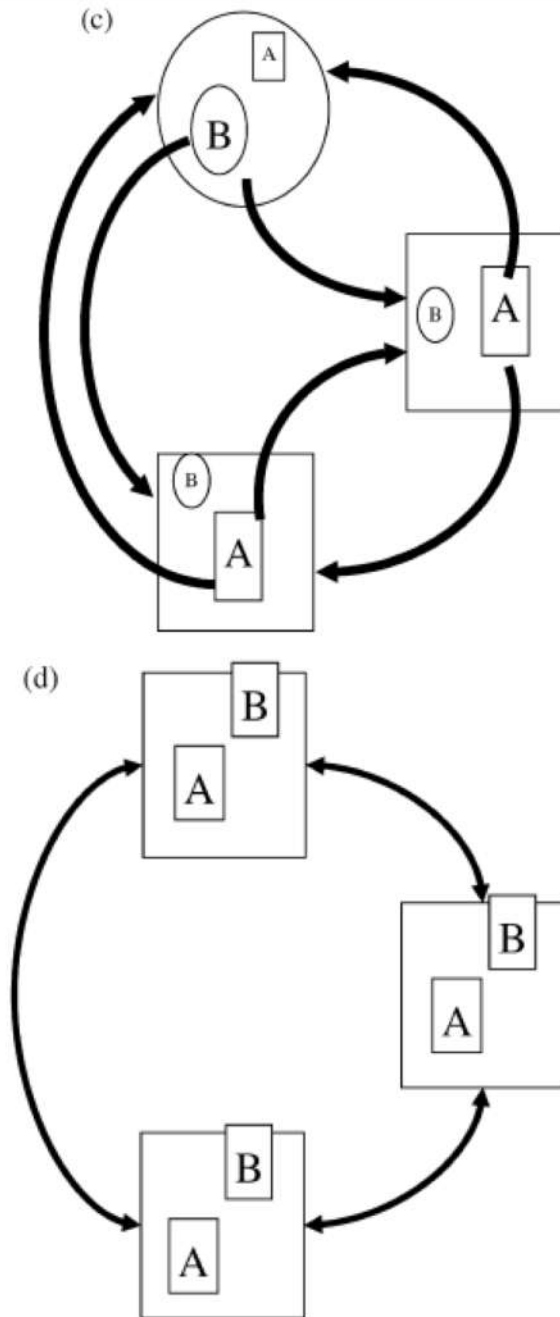
Perspectives in meta-communities



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 where 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.

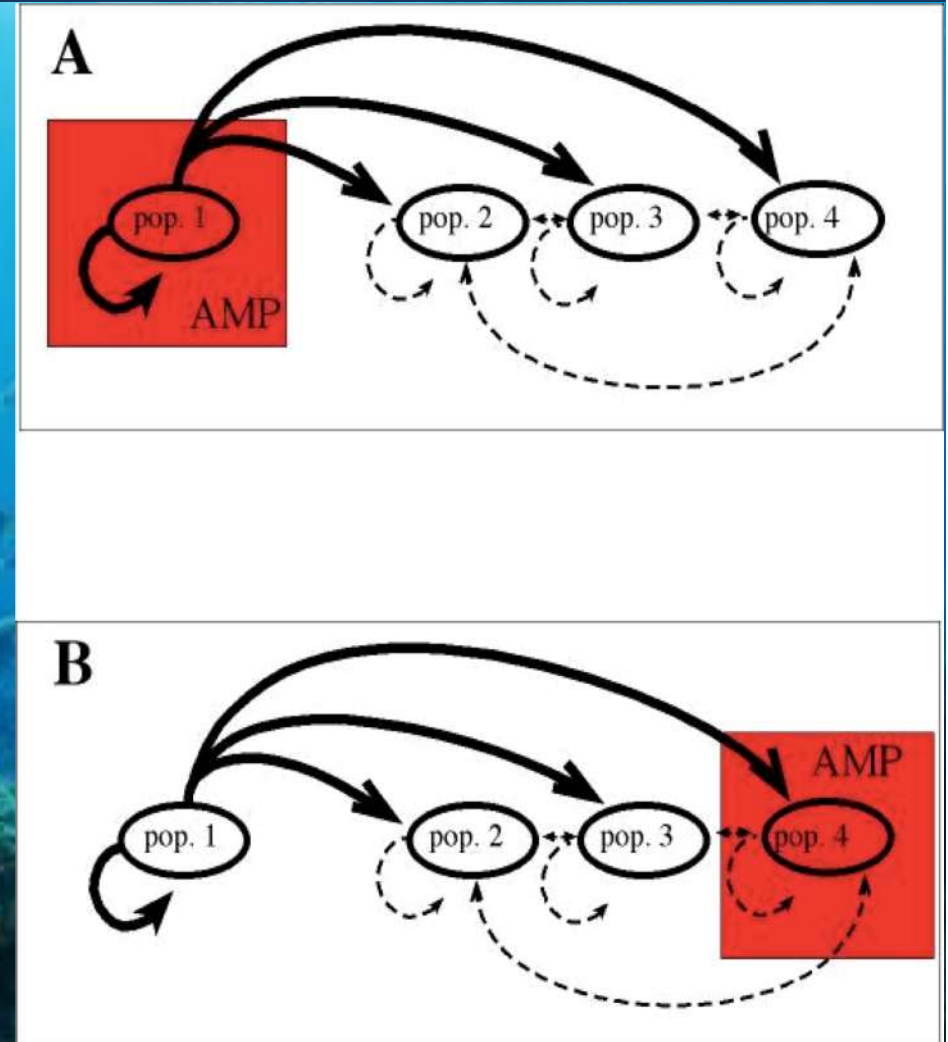
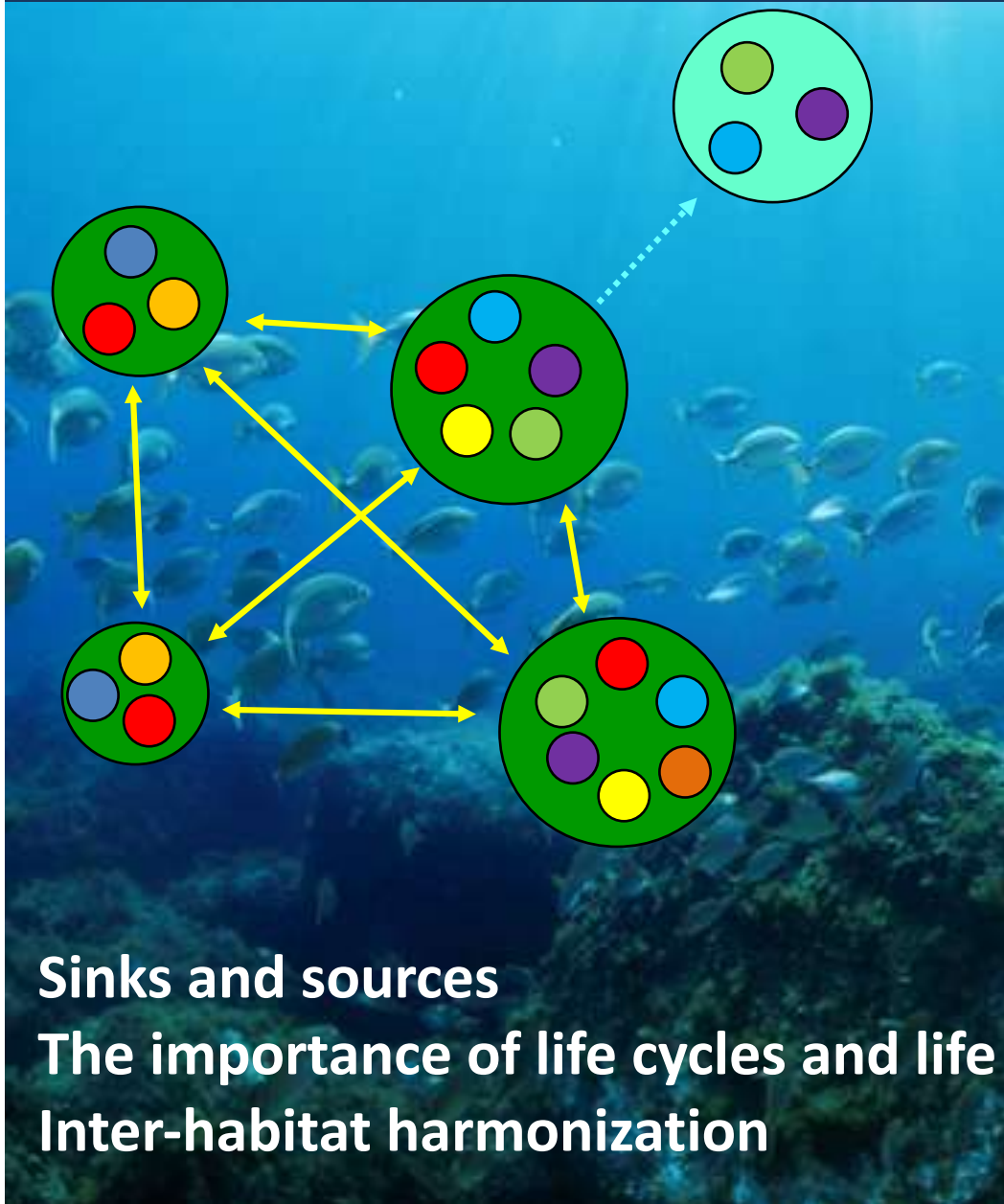
Perspectives in meta-communities



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.

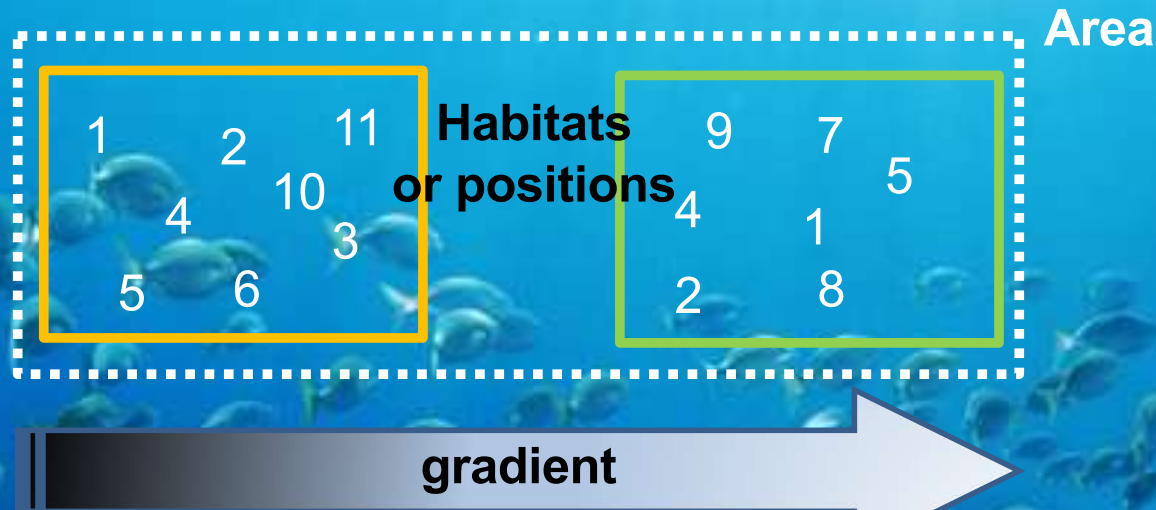
Species are equal in terms of competitive abilities, dispersal and fitness. Community composition depends on stochastic factors related to speciation-immigration and extinction-emigration.

Supply side ecology, metapopulations, and metacommunities



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 the environment (Whittaker 1960).



γ -diversity

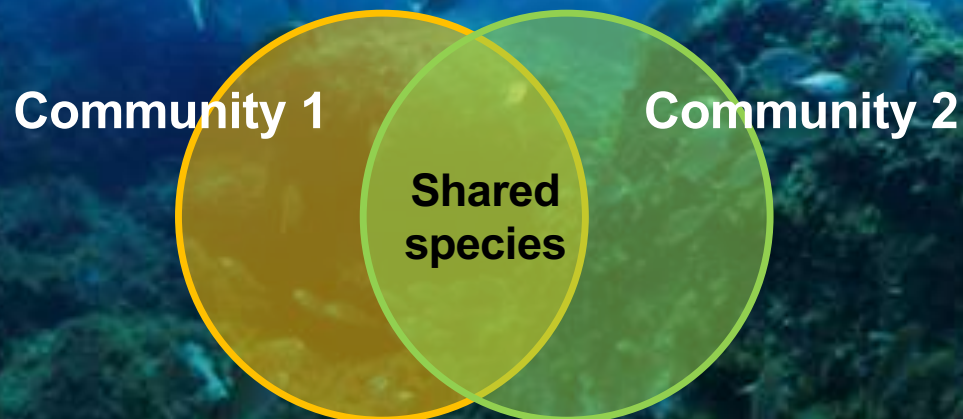
the total diversity in the landscape

α -diversity

the local (site or habitat) diversity

β -diversity

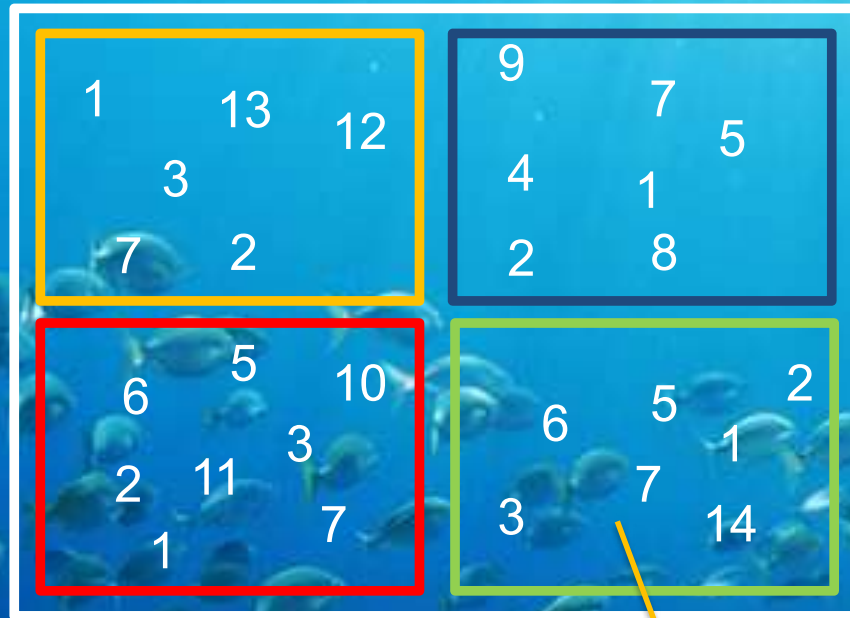
the differentiation diversity between sites or positions



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

Jaccard distance

β -diversity: linking local to regional diversity



Area

Site

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

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

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

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).

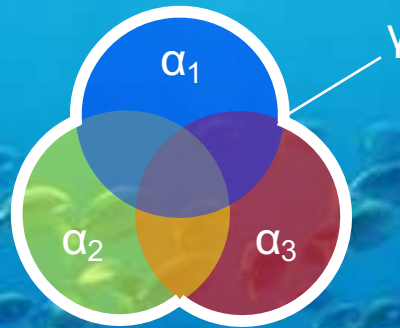
β -diversity and connectivity

β -diversity

Changes in composition among communities within a given spatial extent

→ How local (α) diversity links to regional (γ) diversity →

Siting Spacing
Networking



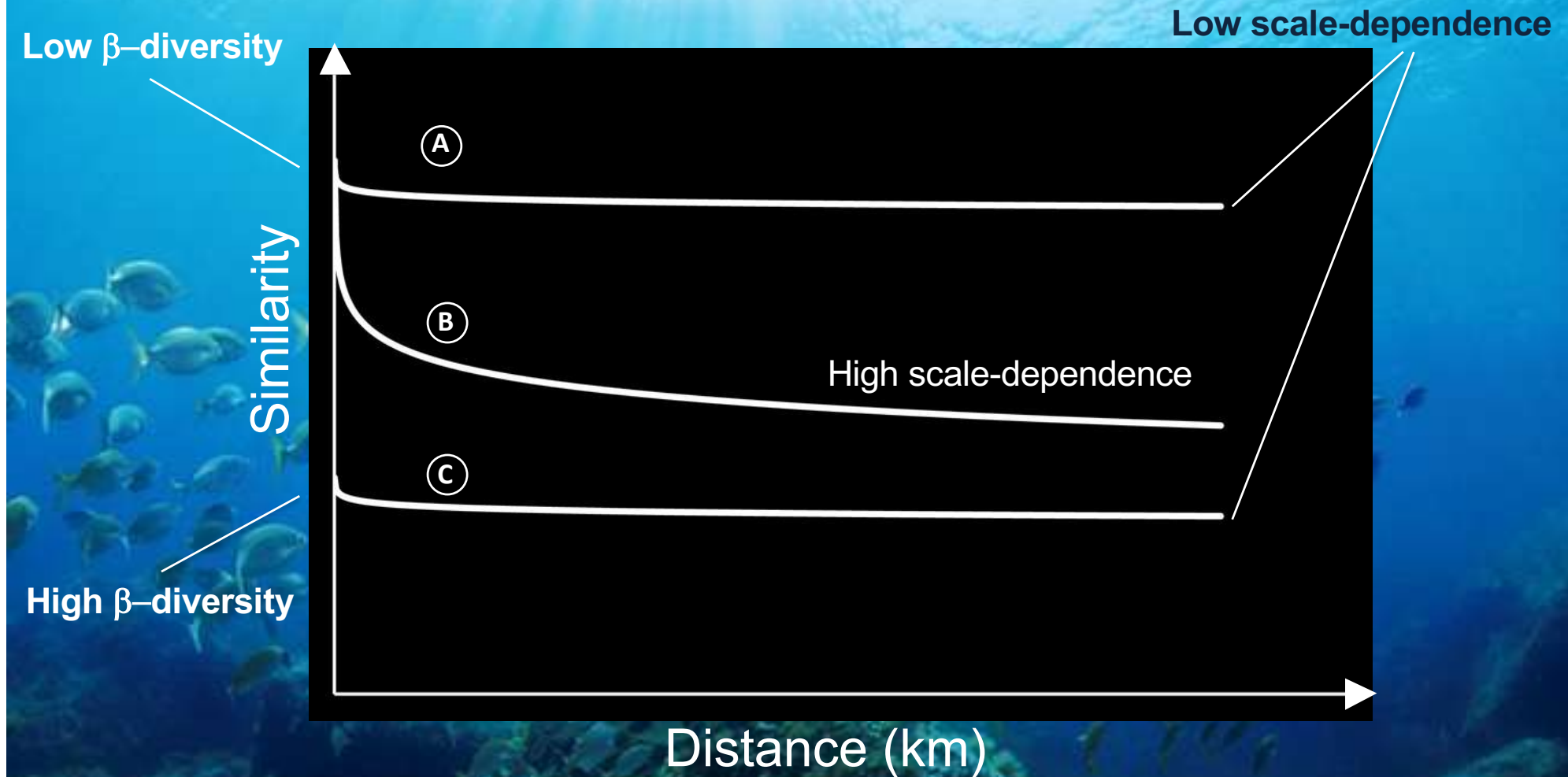
β -diversity

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

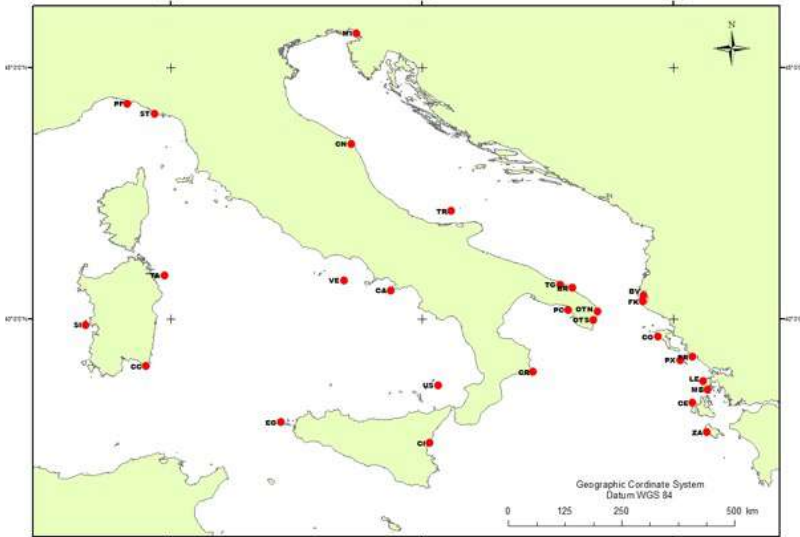
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Homogeneity decrease with scale: high connectivity at local scale that decrease over large scale

Ⓒ

Heterogeneity at local scale, high/low connectivity across the region

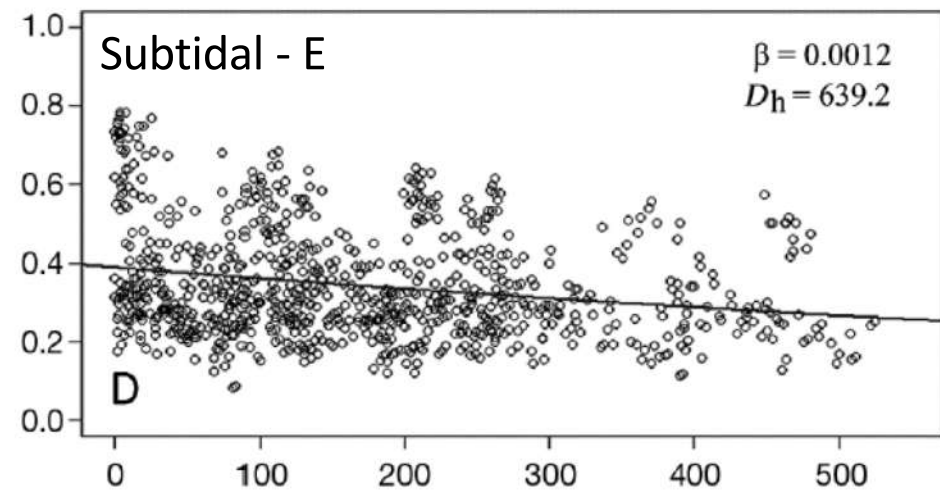
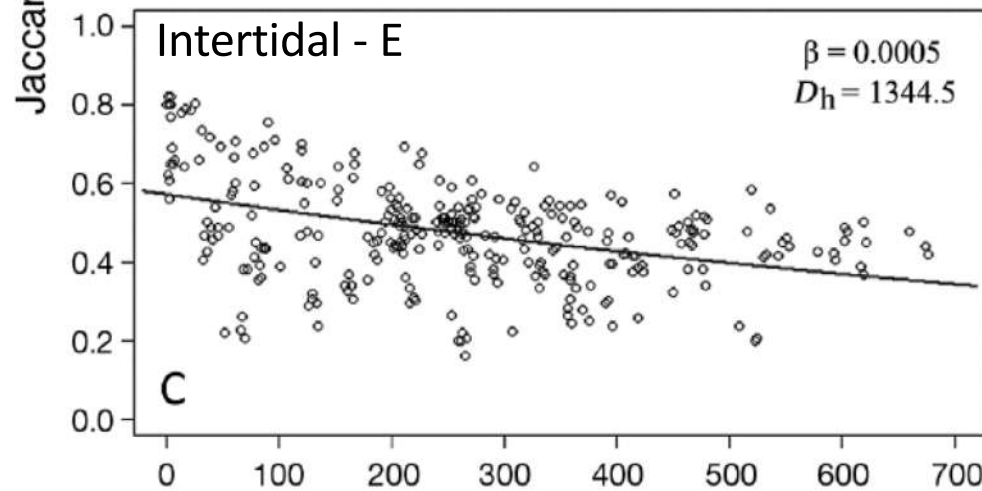
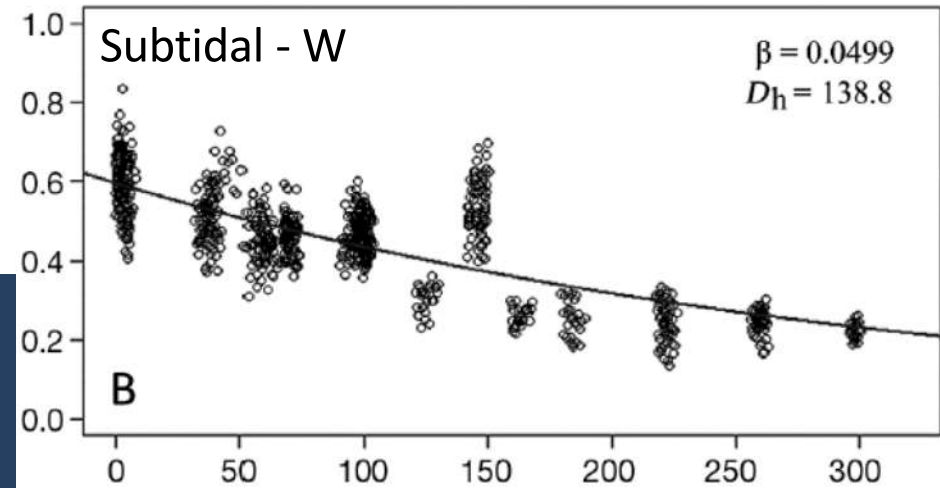
An example in the Mediterranean sea



Distance-decay of similarity in composition

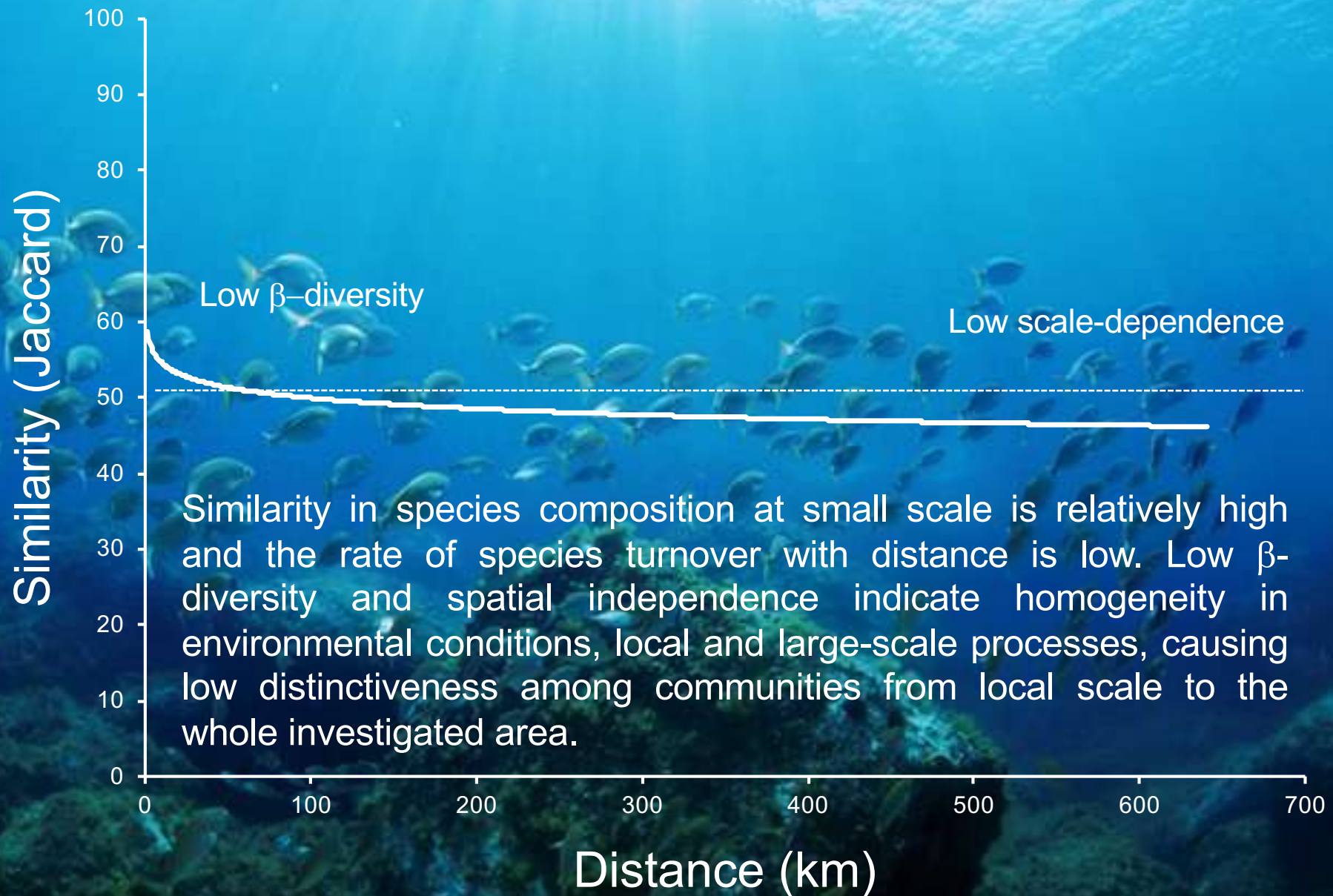
Jaccard similarity

Mediterranean shallow subtidal sessile assemblages



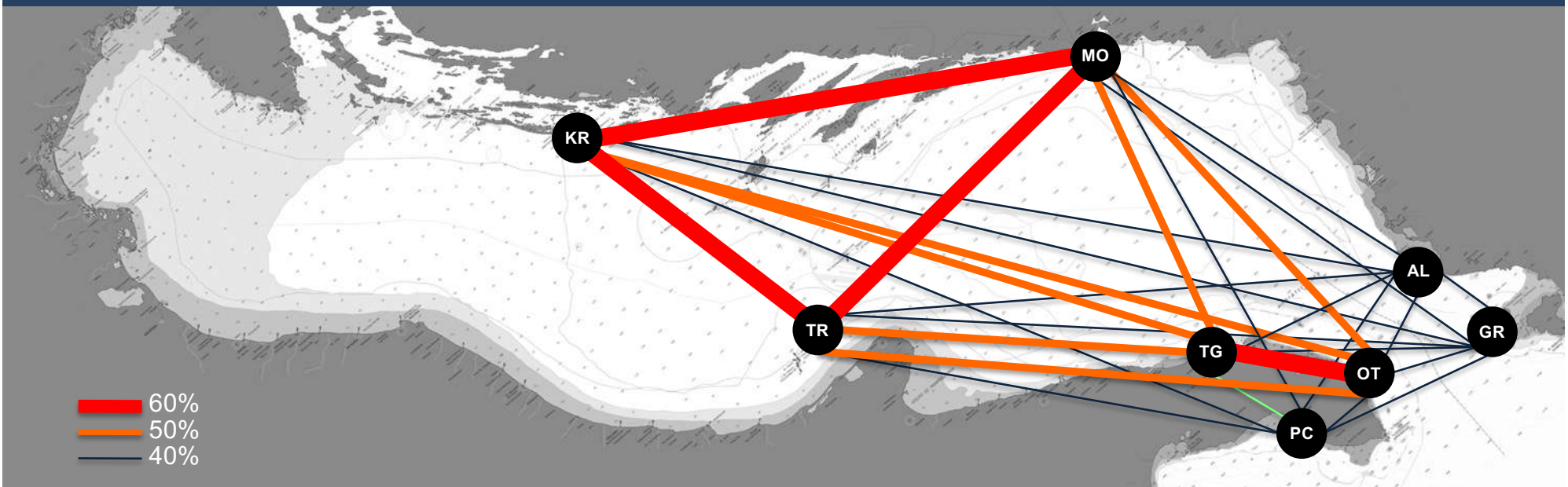
Least-cost paths distance (km)

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



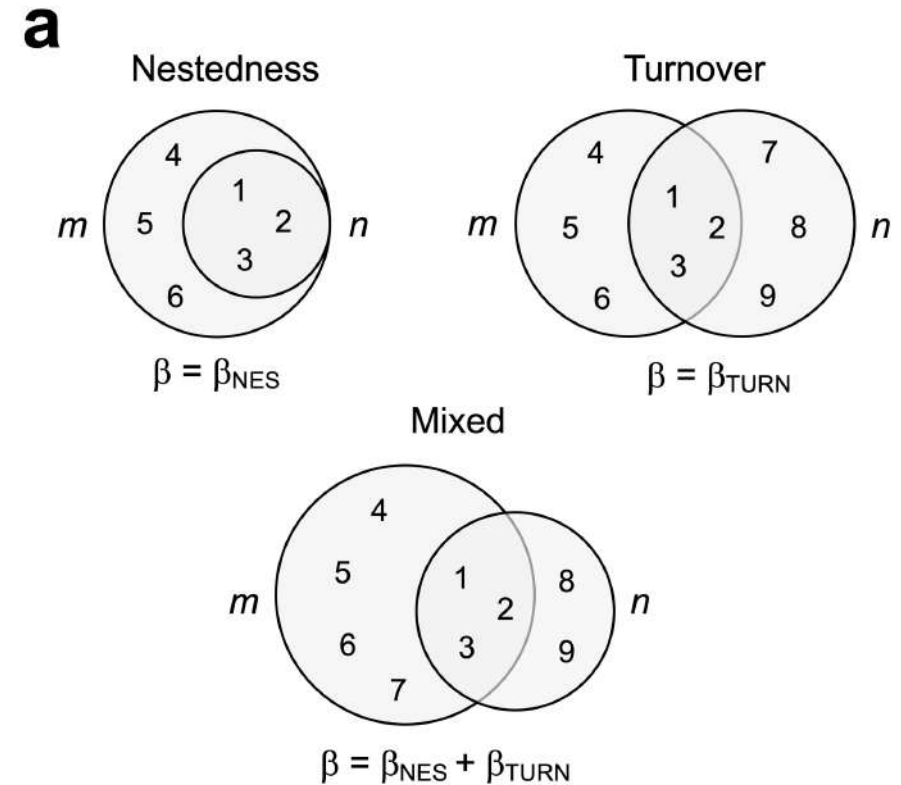
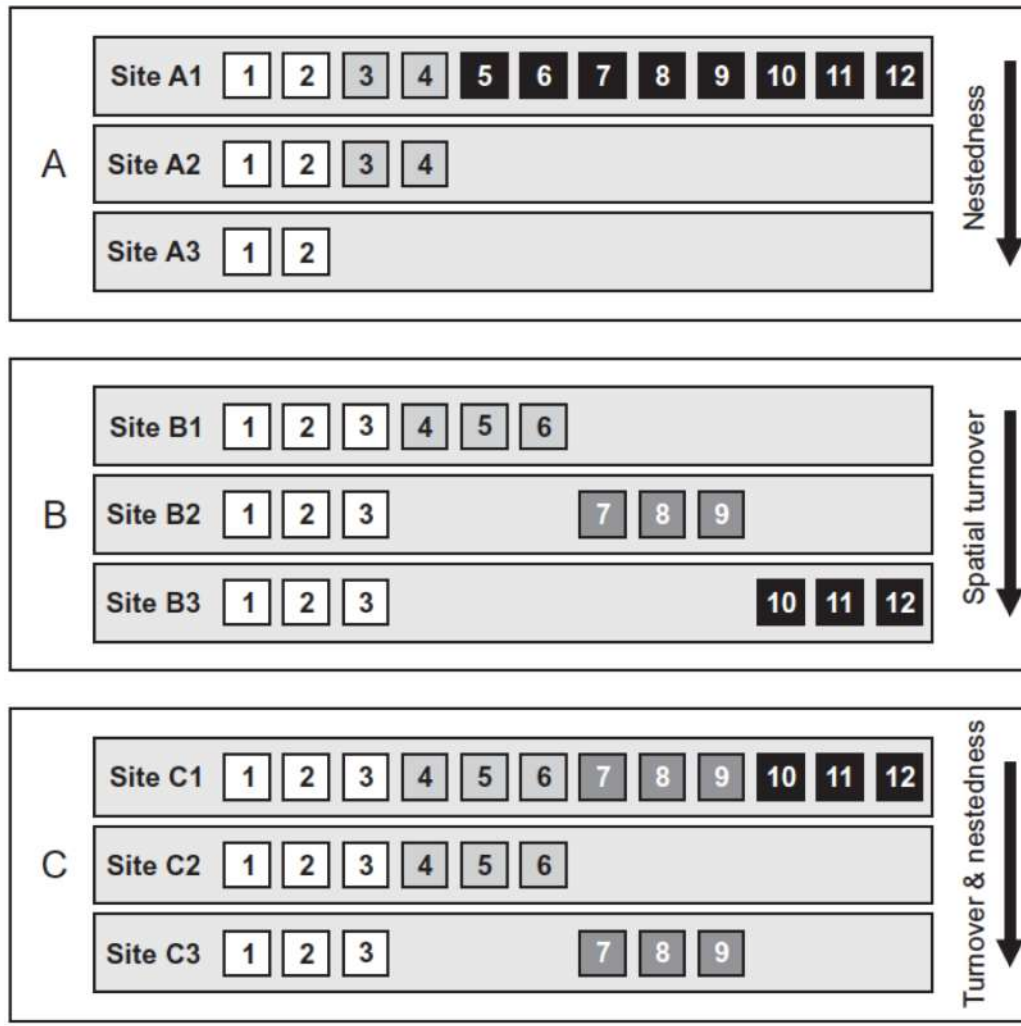
Higher similarity among locations in the central (KR-TR-MO) and southern Adriatic (TG-OT)

Intermediate similarity between these two groups

Discontinuity with locations AL, GR, PC

Sessile assemblages on subtidal rocky reefs

β -diversity: 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.

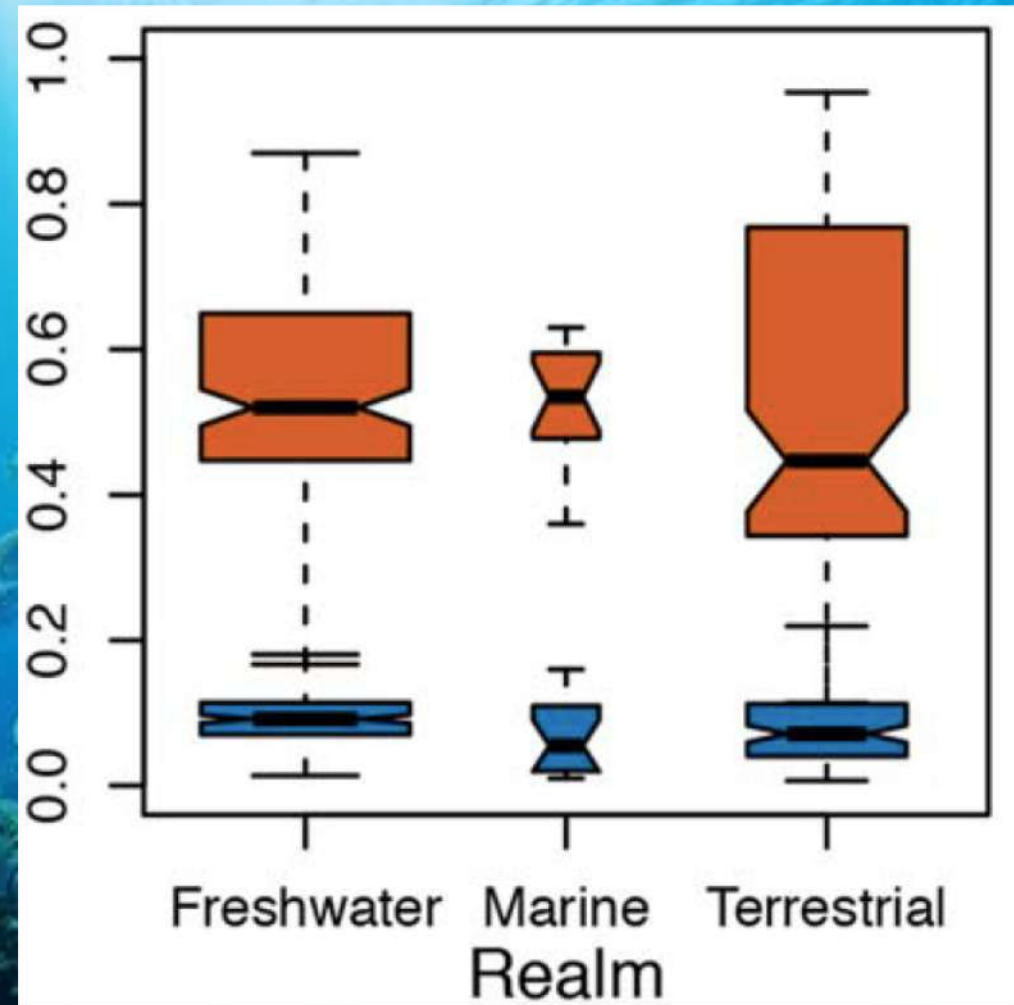
Spatial turnover implies the replacement of some species by others as a consequence of environmental sorting or spatial and historical constraints (Baselga, 2010).

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



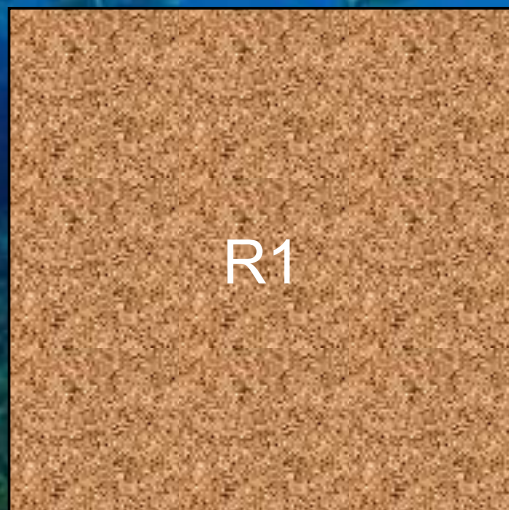
Nestedness and turnover in marine, freshwater and terrestrial environments. (median, quartile, and 95% CI) (269 studies in total)

SLOSS controversy

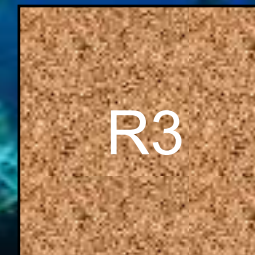
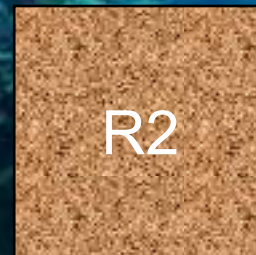
IBT raised concerns about the opportunity to implement single large or several small reserves

Large areas allow protecting more species than smaller ones. However... Large areas are more difficult to manage and control. They are politically difficult to propose and sustain. Large areas have higher probability to create social and economic conflicts. They are also more difficult to monitor. Uncertainty on the result of conservation in terms of amount of species protected...

$$S_{R1} \leq (S_{R2} + S_{R3})$$



=



?

Habitat heterogeneity, species distribution

A question of size

Pelagos Sanctuary (SPAMI)

Year of institution: 1999

Surface: about 90,000 km²

Countries: Italy, France, Monaco

Large reserve for large animals or animals requiring a large surface for movements and foraging



A question of size: distribution

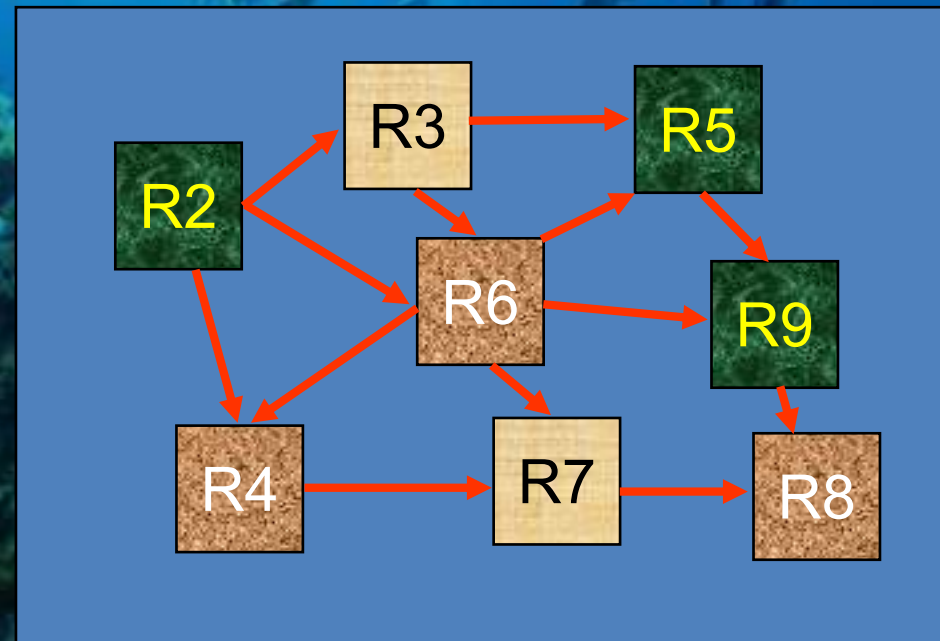
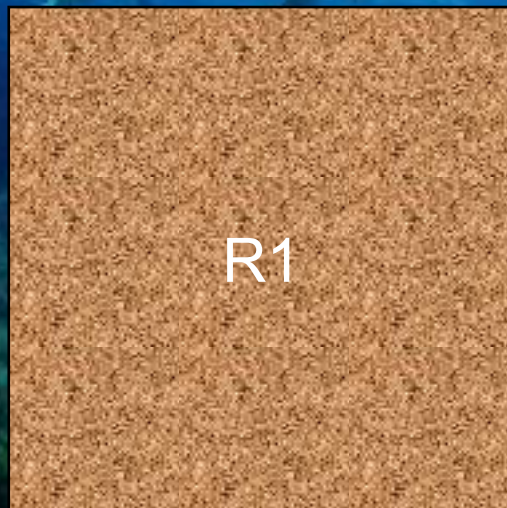


The largest marine park in the Mediterranean Sea is the National Marine Park of Sporadi, in the Aegean Sea. Created in 1992, it is devoted to protection of *Monachus monachus*, the Mediterranean monk seal



Small reserves could increase chance in the face of perturbations

Several small interspersed reserves could provide insurance against perturbations (e.g., catastrophic disturbance or demographic events), with recolonization provided by undisturbed sites, or including higher habitat diversification with respect to larger ones and therefore more species



Notwithstanding, large reserves...

Should....

1 – decrease competition and predation pressure from neighbouring species, with border populations more exposed than those in the centre of the reserve;

2 – provide a better spatial match with the *home-range* of large carnivorous species;

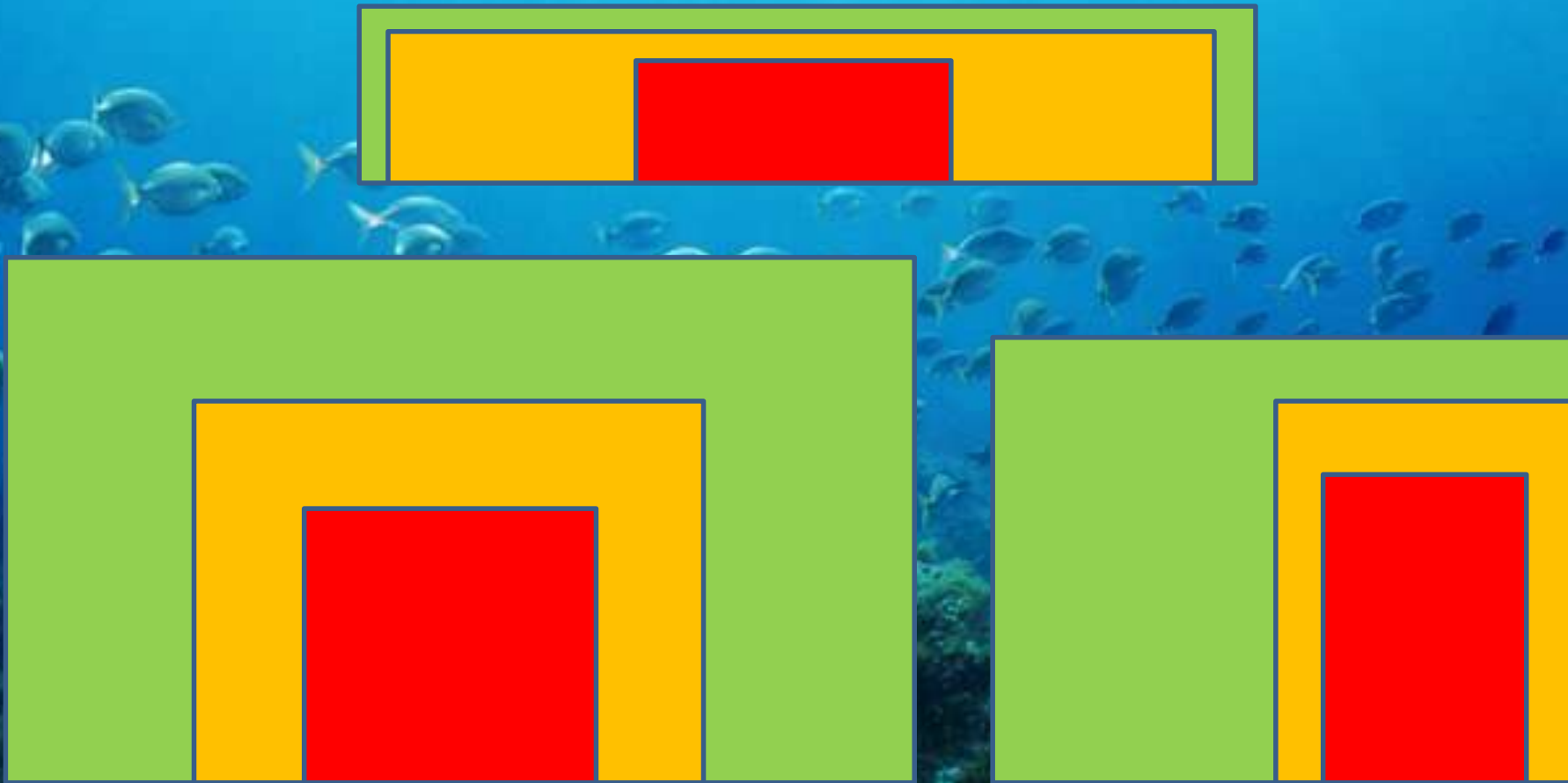
3 – include a larger range of environments to allow persistence of different species populations in the long term;

4 – include different subpopulations and, as a consequence, higher intra-specific genetic diversity;

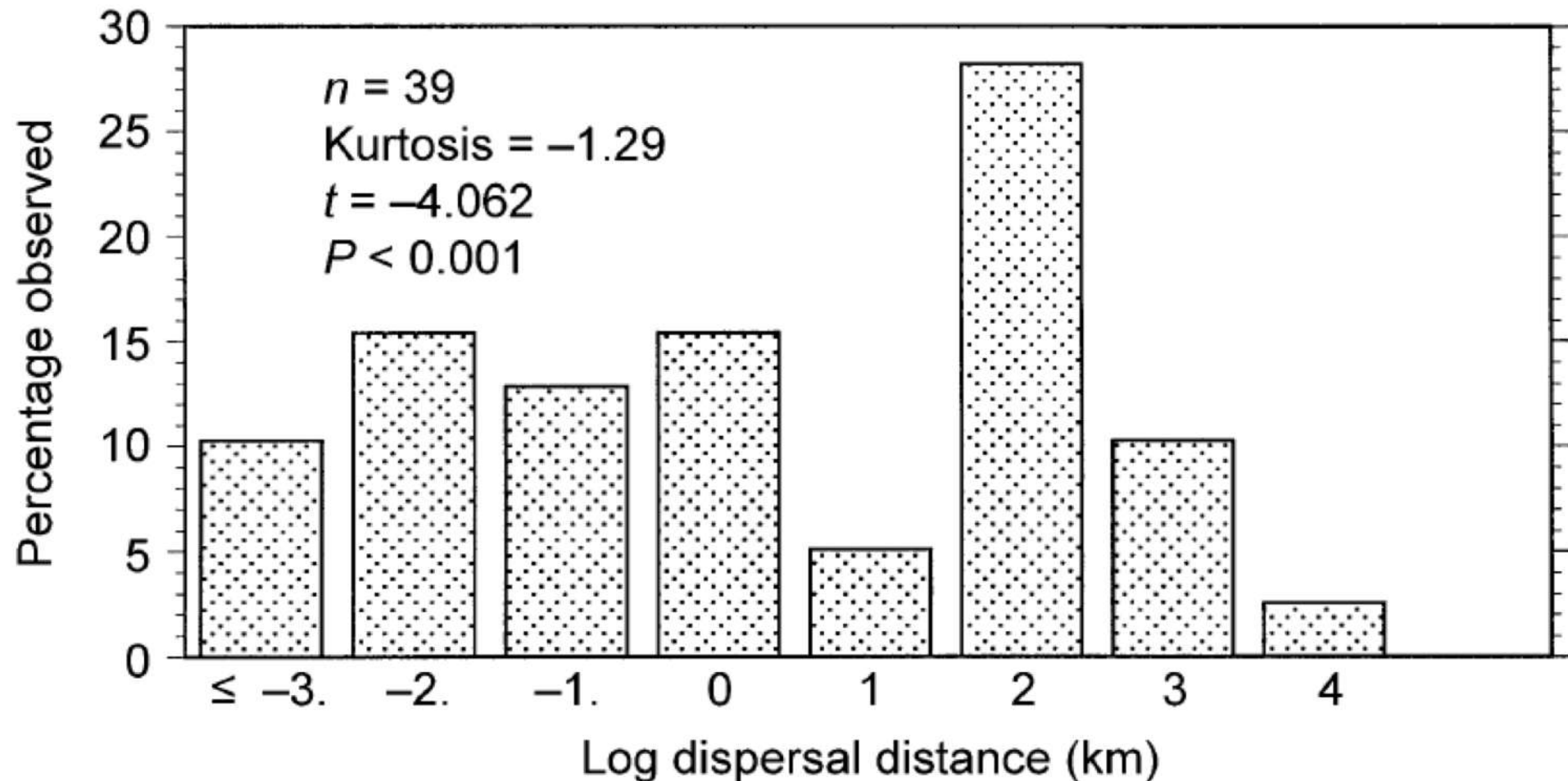
5 – better respond to external disturbance through a buffer effect

Shape

Low area/perimeter ratio could increase exposure of central populations to external influence



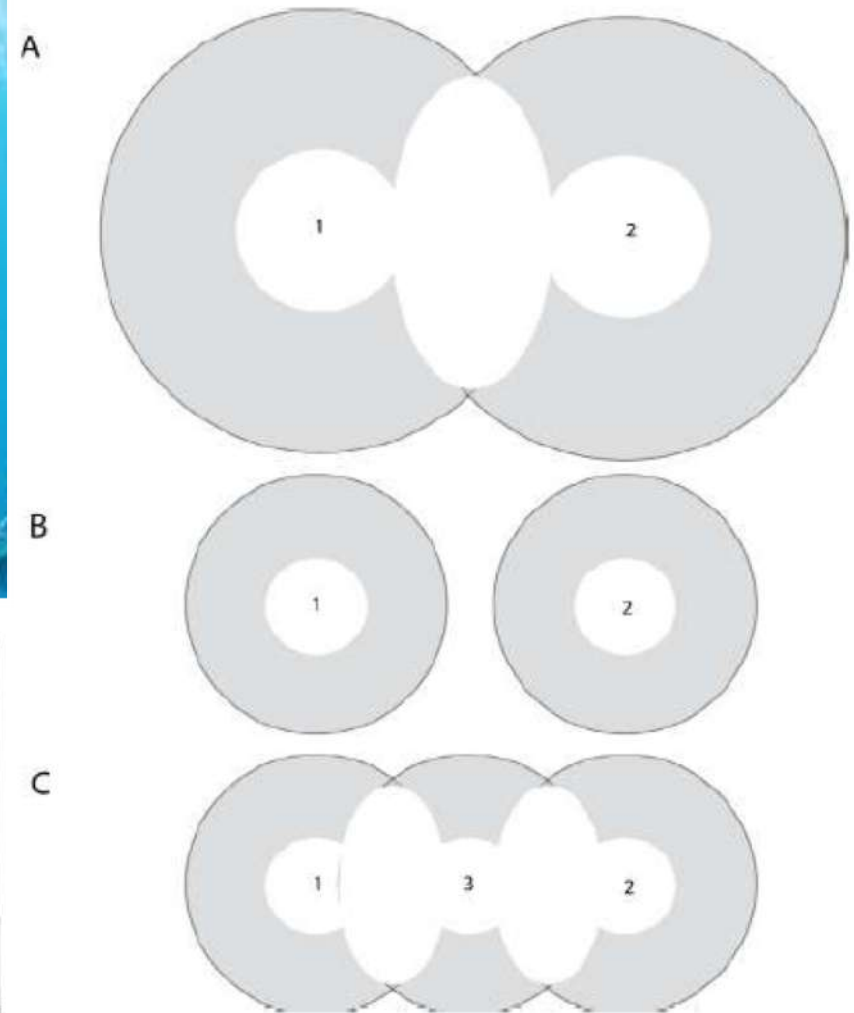
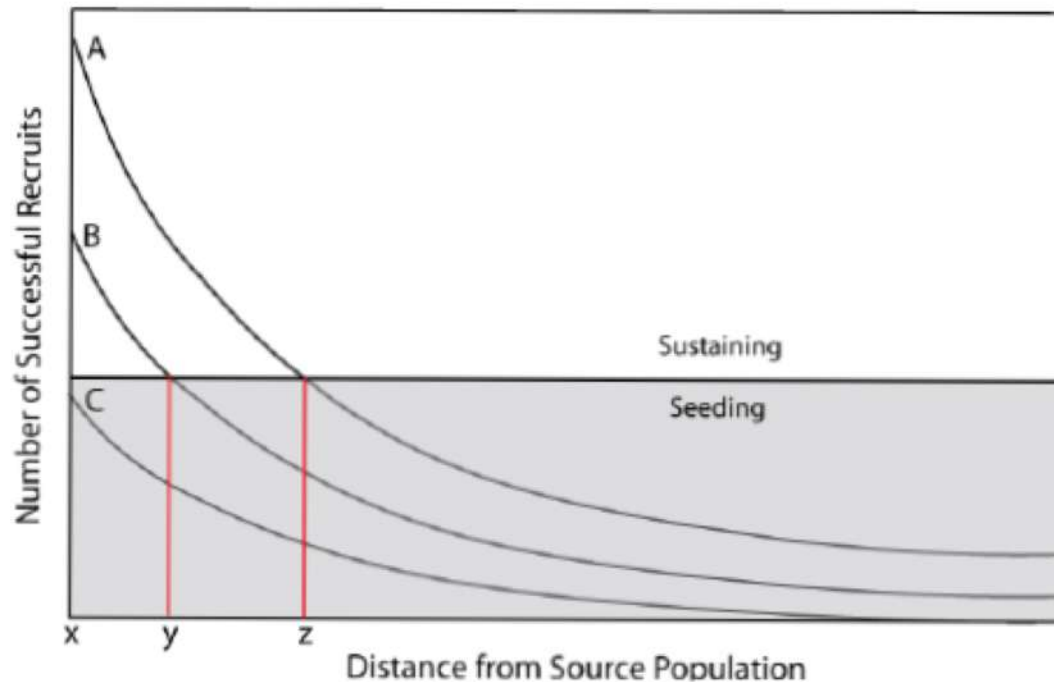
Spacing



- 1) Bimodal trend in dispersal strategies, one short distance and long distance.
 - 2) Reserves with diameter of 4-5 km, 10-20 km apart are wide enough to retain propagules of short-distance dispersers and far enough to allow long-distance dispersers to be captured. However, limited range of organisms.
- Shank et al., 2003

Spacing

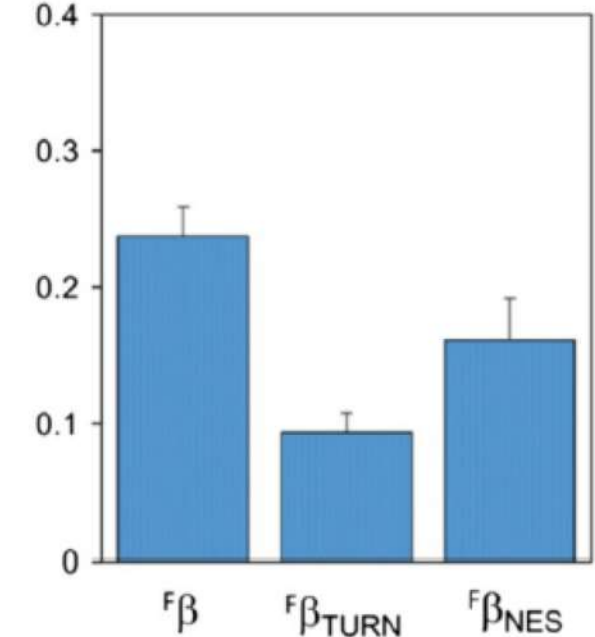
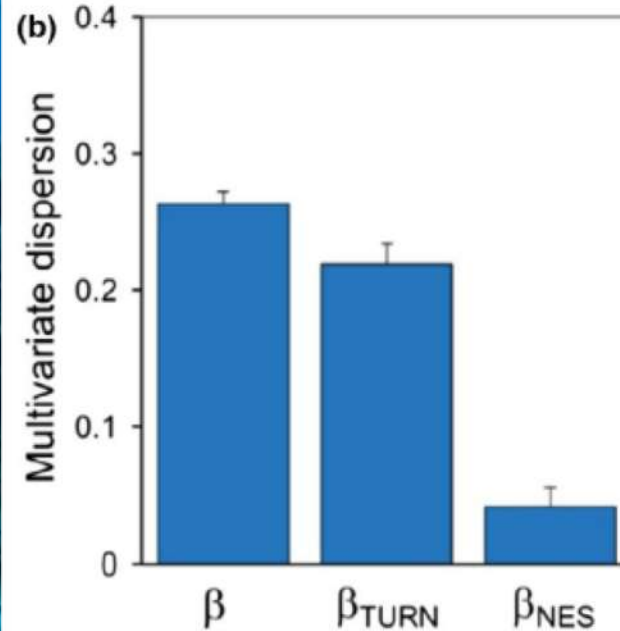
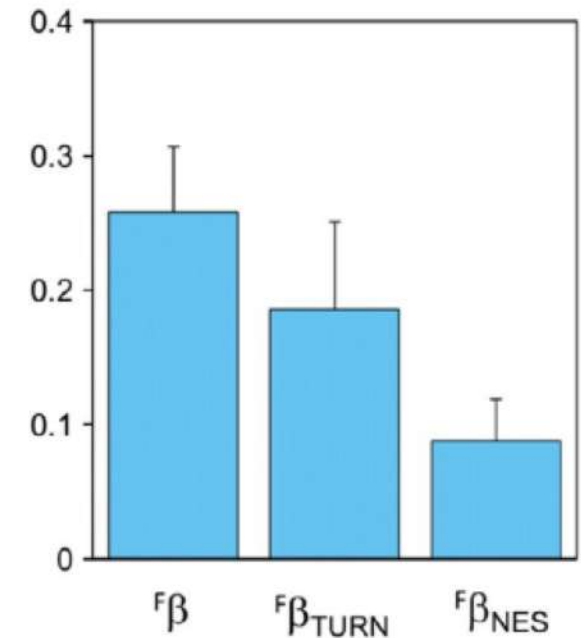
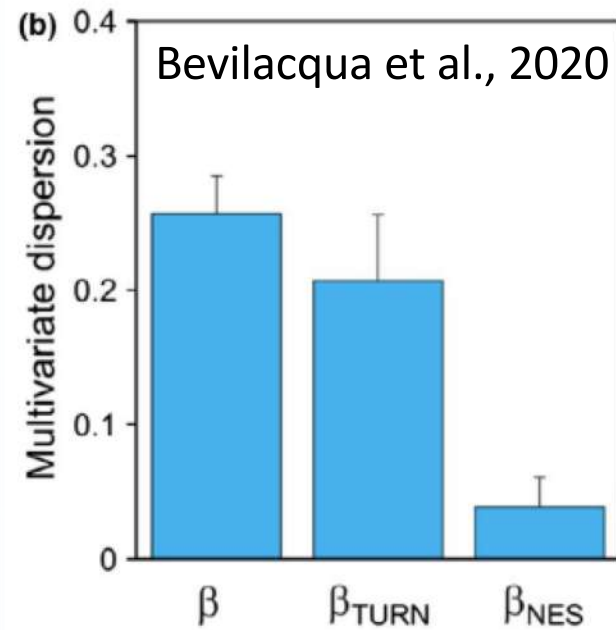
To understand the effects of dispersal on population replenishment and resilience, it is important to differentiate between (1) “sustaining” dispersal: ecologically/ demographically important in maintaining or increasing a local population and (2) “seeding” dispersal: evolutionarily important in maintaining gene flow and decreasing the long-term probability of local extinction. Sustaining dispersal occurs over small spatial scales whereas seeding dispersal occurs over large spatial scales.



Small populations produce fewer propagules than large populations. Thus, as size decrease distance of seeding and sustaining decrease.

Biological heterogeneity

Siting and spacing are strictly related to connectivity. Current transport of propagules, and heterogeneity in distribution of species are main factors to account for ecologically coherent network. Often, the analysis of beta-diversity patterns focuses on taxonomic diversity. However, other aspects of diversity should be considered to implement networks that, beyond representative of species diversity also allow to conserve functional diversity.



Implication for siting and spacing

A $\beta = \beta_{\text{TURN}} = 0.5$ $\beta_{\text{NES}} = 0$

1	2	3	4	5	6	7			
		3	4	5	6	7	8	9	10

S1 (red circle) S2 (blue circle)

Both S1 and S2 should be selected to ensure that all species are protected

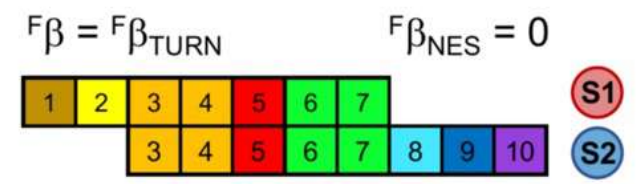
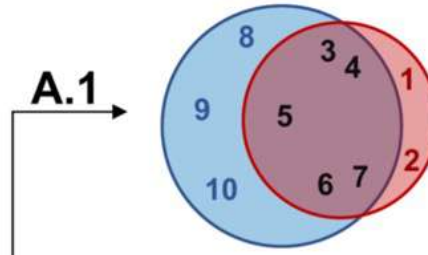
S1 and S2 have 50% of unshared species ($\beta = 0.5$) on their total number of species ($\gamma = 10$). Based on compositional β -diversity, both S1 and S2 should be selected to ensure that all species are protected

B $\beta = \beta_{\text{NES}} = 0.5$ $\beta_{\text{TURN}} = 0$

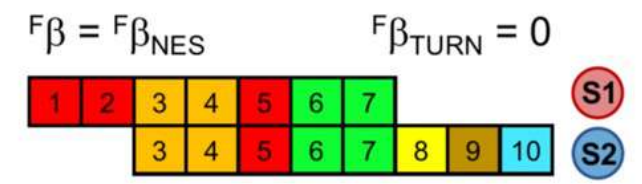
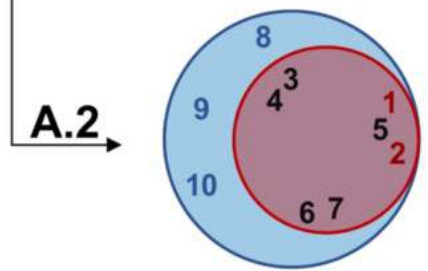
1	2	3	4	5	6	7	8	9	10
1	2	3	4	5					

S1 (red circle) S2 (blue circle)

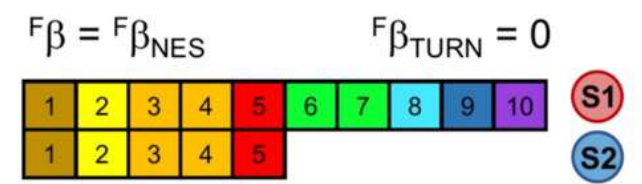
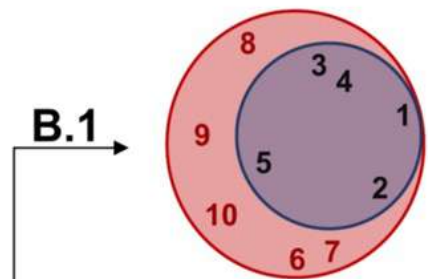
Selecting S1 is sufficient to ensure that all species are protected



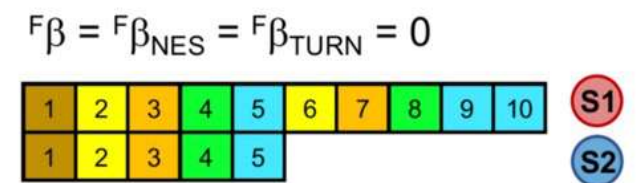
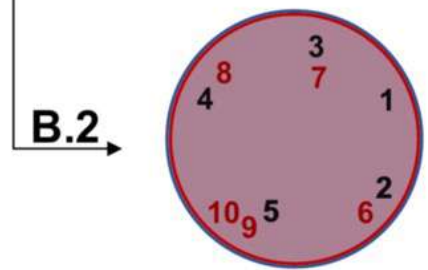
Both S1 and S2 should be selected to ensure that all traits (and all species) are protected



Selecting S2 is sufficient to ensure that all traits (and most of the species) are protected

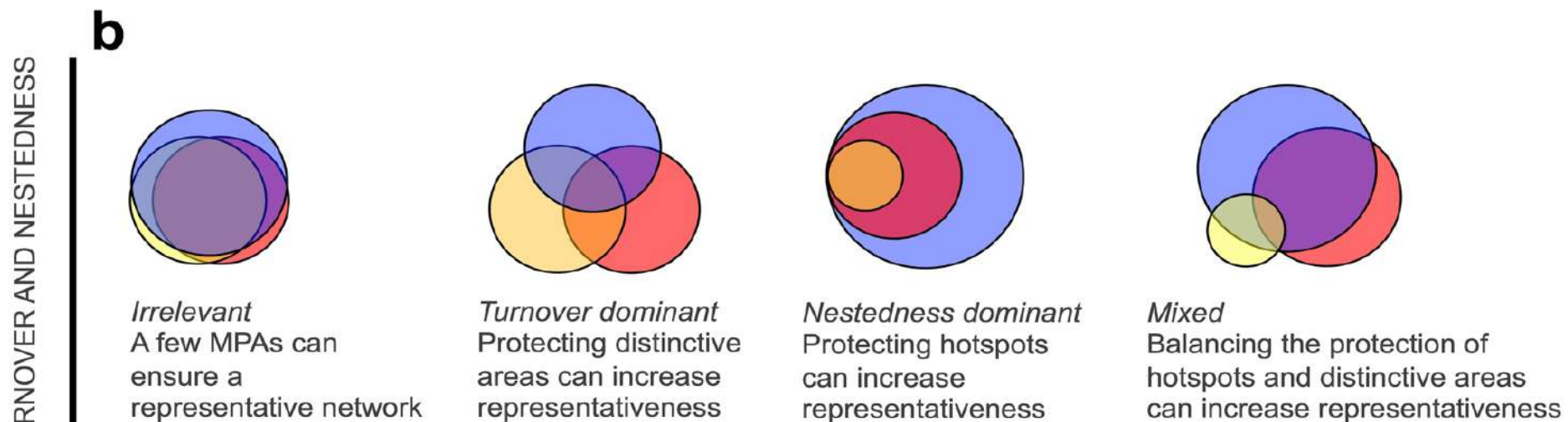
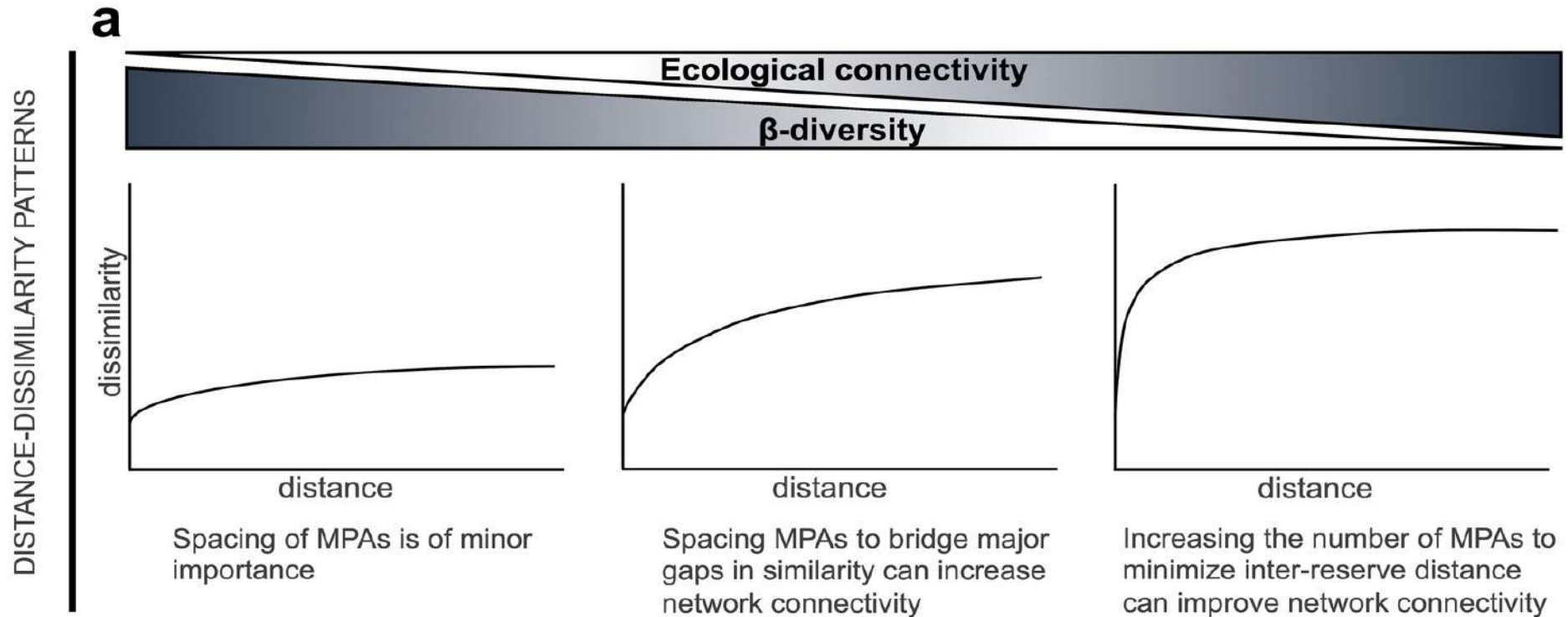


Selecting S1 is sufficient to ensure that all traits (and all species) are protected

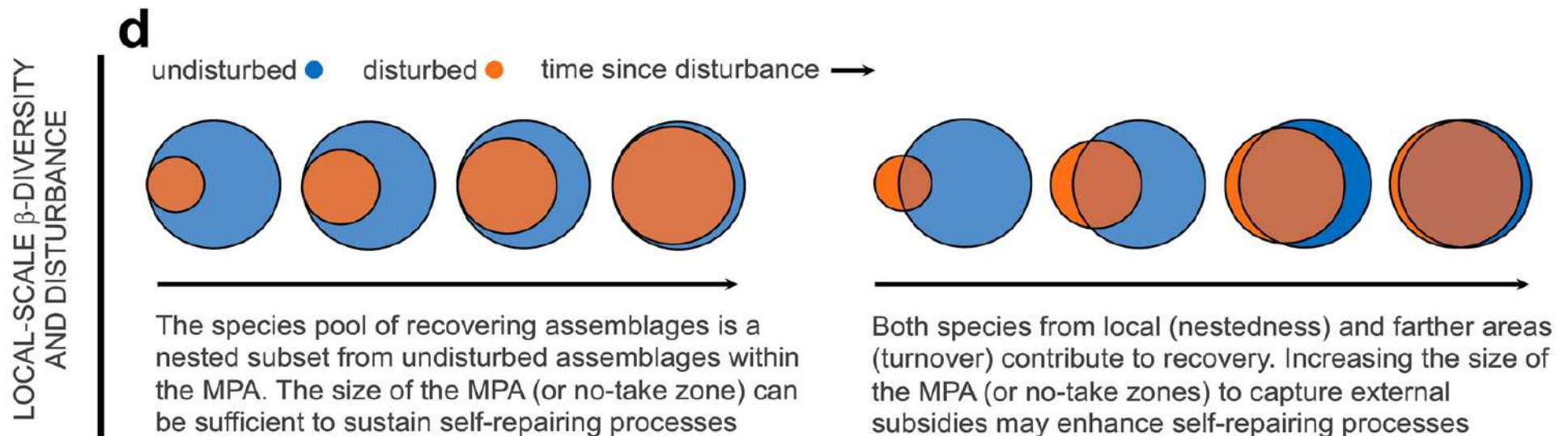
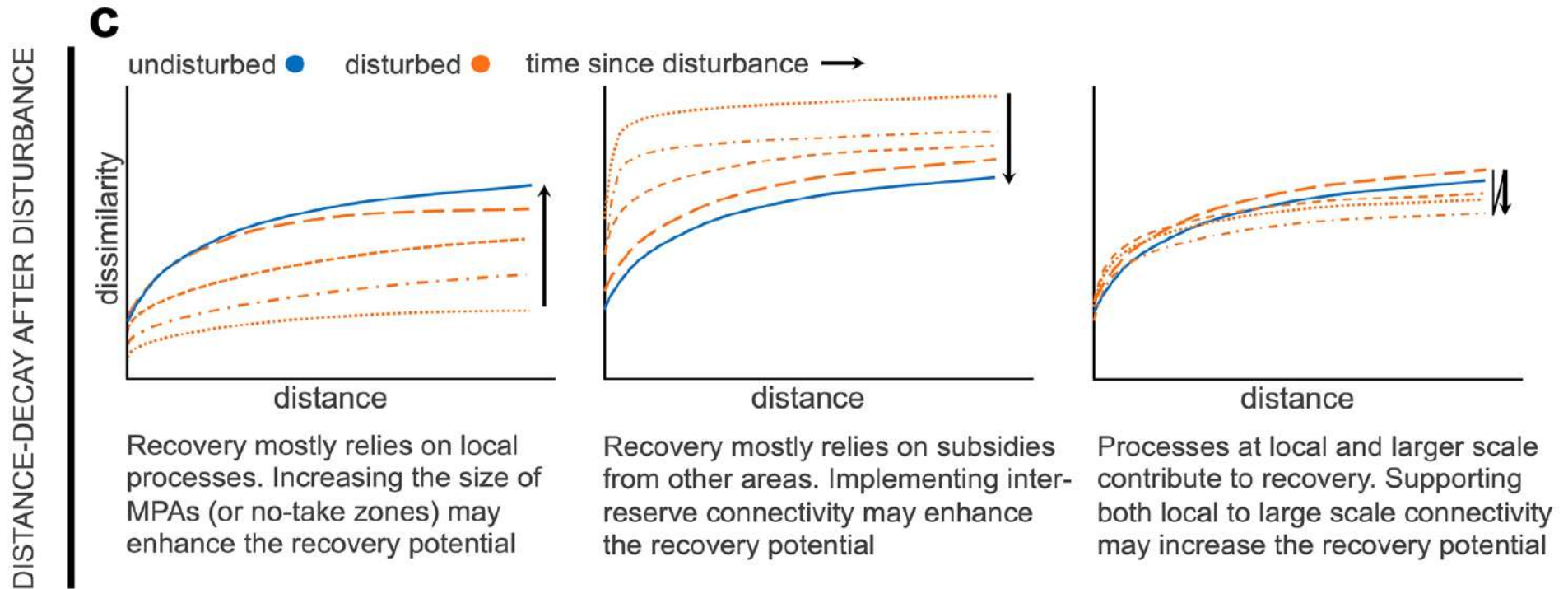


Selecting S1 is sufficient to ensure that all traits (and all species) are protected

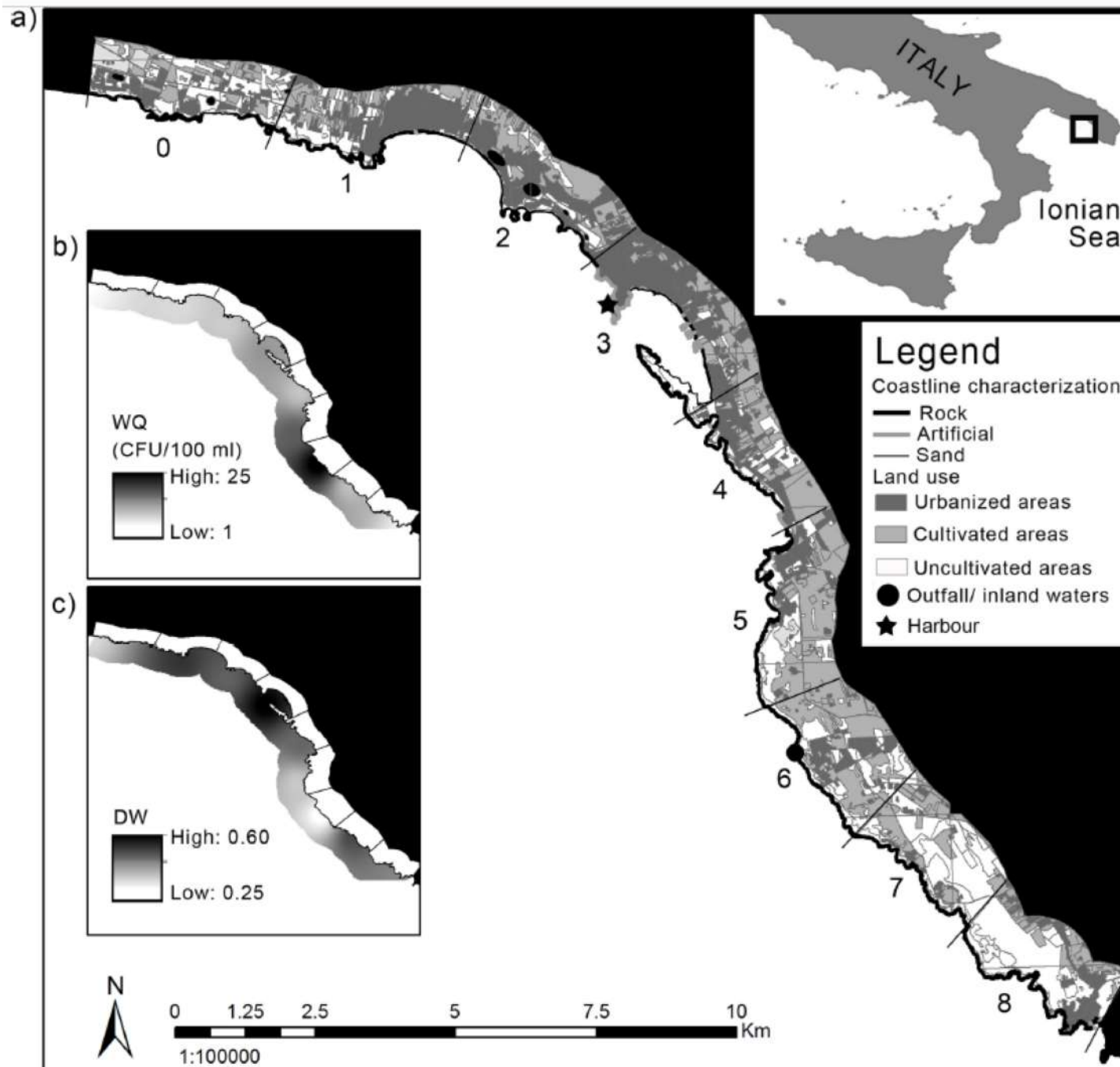
Implication for siting and spacing



Implication for siting and spacing



Environmental context: human threats



Guarnieri et al., 2016

High level of anthropization could increase exposure of protected populations and communities to human pressures or impacts

Should We Protect the Strong or the Weak?

If the conservation objective was to maximize the chance of having at least 1 healthy site, then the best strategy was protection of the site at lowest risk. On the other hand, if the goal was to maximize the expected number of healthy sites, the optimal strategy was more complex. If protected sites are likely to spend a significant amount of time in a degraded state, then it is better to protect low-risk sites. Alternatively, if most areas are generally healthy then it is better to protect sites at higher risk. (Game et al., 2008)

Alternative strategies have been proposed, for instance, to protect areas proportional to the risk of perturbation event to increase insurance that catastrophic events will not affect the core of reserves. (Allison et al., 2003)



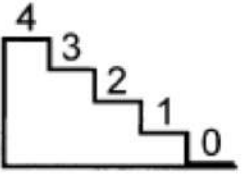
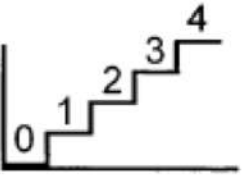
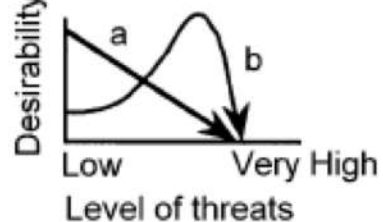
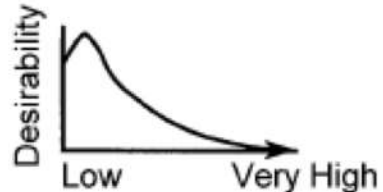
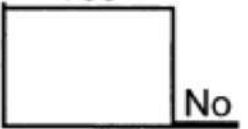
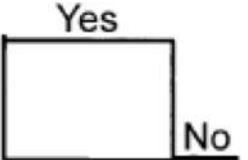
Network of MPAs: general criteria

Roberts et al., 2003

- 1) Define the goals of the network.
- 2) Define area of interest.
- 3) Divide it into possible reserve units. These may be defined in many ways, for example through grids of uniform sized blocks (e.g., 10 km²), stretches of coastline, habitat classification schemes, or other means.
- 4) Select criteria for the evaluation of those units that are appropriate to the goals.
- 5) Decide how to quantify the information needed for determining the level achieved for each criterion.
- 6) Assemble information on those units (e.g., species or habitats present, levels of threat, etc.).
- 7) The evaluation process
 - a) Characterize or “score” sites based on the following characteristics:
 - i) Define biogeographic regions, scoring sites based on what region they occur in. At this stage, sites could be stratified according to region, with site selection decisions made separately for each region. The latter approach would be most useful where a large geographic area is being considered and there are many potential sites from which to choose.
 - ii) Define habitats within each biogeographic region for representation.
 - iii) Exclude sites subject to excessive levels of threat from human or natural sources.
 - iv) Include sites that are already reserves.
 - v) Score potential reserves on the basis of habitat heterogeneity and representation criteria, ensuring that reserve units will be sufficiently large to include viable populations.
 - vi) Rank or score sites within each habitat type according to other modifying criteria.
 - b) Set conservation targets for each of the above criteria (e.g., decide what proportion of the region and of each habitat to protect, what level of replication is required, levels of connectivity desired, etc.).
 - c) Select among sites for inclusion in the network (this can be done with an algorithm, by ranking or scoring, or by delphic methods). Criteria may be given different weightings at this stage in order to meet specific network objectives. Map the various possible biologically adequate reserve networks.
 - d) Ensure that the networks resulting from the above selection process are sufficiently connected.
- 8) Use information on alternative, biologically adequate reserve networks to inform final network selection according to socioeconomic criteria.



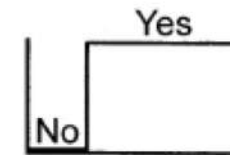
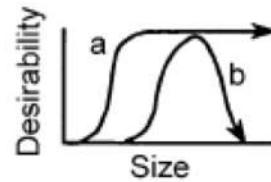
Network of MPAs: general criteria

Criteria	Relationship	Possible ranking
<p>Prerequisite criteria</p> <p>1) Biogeography</p> <p>2) Habitats</p> <p>a) Diversity</p> <p>b) Diversity <i>not</i> protected elsewhere</p>	<p>Desirability</p>  <p>Zero Many</p> <p>Existing reserves in biogeog. region</p> <p>Desirability</p>  <p>Low High</p> <p>Diversity of habitats</p>	 
<p>Excluding criteria</p> <p>3) Human threats</p> <p>a) Non-mitigatable</p> <p>b) Mitigatable</p> <p>4) Natural threats</p> <p>(Boero et al., 2016)</p>	<p>Desirability</p>  <p>Low Very High</p> <p>Level of threats</p> <p>Desirability</p>  <p>Low Very High</p> <p>Level of threats</p>	<p>Yes</p>  <p>No</p> <p>Yes</p>  <p>No</p>

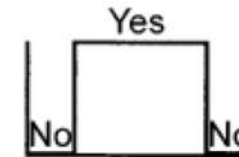
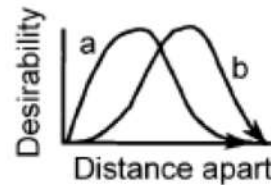
Network of MPAs: general criteria

Modifying criteria

- 5) Adequacy of size
 a) for conservation
 b) for fisheries



- 6) Optimal distance apart
 a) for conservation
 b) for fisheries



- 7) Vulnerable habitats

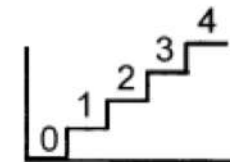
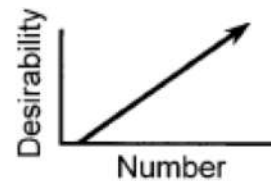
- 8) Vulnerable life stages

- 9) Species of special interest
 (rare, endemic, etc.)

- 10) Inclusion of exploited species

- 11) Linkages (dependencies)
 between systems

- 12) Ecosystem services
 for human needs



(Boero et al., 2016)



Criteria for selection of MPAs

MPA Selection Factor	Attributes
Knowledge	This covers not only information about the present situation (best available scientific knowledge) but also its historical ecology (how the current situation came about). Unfortunately, it is rare to have such knowledge as there is a general lack of long time series data in the marine environment, but it may be possible to undertake comparative studies to help distinguish features which are artefacts of human influence from those which arise naturally.
Scientific justification	This refers to how well the site accords with accepted ecological criteria (CBD, Habitats Directive), as well as the network contribution e.g. replication and resilience.
Risk assessment	The location of the site should be assessed in relation to shipping lanes, actual or potential industrial development including renewable energy, possible accidental pollution events, attraction of tourists/poachers, colonisation by invasive species, aquaculture or other possible impacts. The potential for mitigating such impacts should be elaborated, for example possible contingency measures to respond to incidents where there is major vessel traffic through the area (Lisovsky <i>et al.</i> , 2015).
Political feasibility	Surveys and consultations are needed to confirm stakeholder agreement, from government to civil society at all levels. In particular, any conflict and/or lack of cooperation between environmental and fisheries management agencies will inhibit progress in establishing MPAs.
Legislation applicable and/or available	An audit of the existing local, state and supranational legislation should be undertaken, as well as resource ownership and access, freedom of navigation rights etc. For designation purposes, a check is needed on which littoral states are parties to specific international agreements and how they interpret them in national legislation.
Governance model	The potential governance model (Table 6) should be determined as part of the stakeholder consultation process, and whether and how the site will form part of a network at the international level under the regional agreements.



Criteria for selection of MPAs

Management integrity	The site management plan has to be prepared in full collaboration with the relevant stakeholders. The recruitment of suitable staff, planning competence, effectiveness, monitoring and adaptability are other issues to be taken into account.
Economic sustainability	The need and potential for self-financing of the site administration has to be considered. Sustainable financing needs to be put in place in from the beginning, employing appropriate economic instruments based on assessments, valuations and MCDA.
Communication and outreach	The potential role of the site to provide research, education and public awareness opportunities (forming a part of collaborative networks, Table 1) should be considered.
Secular trends	Natural and political worlds operate as complex systems with characteristics which ensure that they will function unpredictably over time. Therefore, the potential for the site and its management to adopt objectives and policies that are adaptable over short, medium, and long-term timescales is an important factor.

The governance system proposed for a new MPA, or MPA network, is crucial in terms of delivering the benefits expected by the stakeholders during the formation phase. It is important to distinguish between “governance” (which is the strategic, decision making and monitoring process) and “management” (which is the executive role of those responsible for implementing the management plan).

Issues

Effective protection require three main points:

1) as first, MPAs should be sited to fulfil well-defined conservation purposes. This in turn will guide positioning and subsequent conservation strategies. The aims of MPAs should take into account connectivity, population dynamics, diversity distribution and, last but not least, the context to reduce socio-economic conflicts and external human pressures.

2) effective protection cannot fall outside considerations of geopolitical and large scale governance constraints, resources availability to maintain governance of reserves, and therefore enforcement, to avoid creation of 'paper reserves'

3) adaptive management is unavoidable; habitats distribution could change, zonation could require refinements, and monitoring is mandatory to detect changes and implement actions, modifying strategies, or simple to insure that conservation target are being achieved

(Airamè et al., 2003)

Necessary but not sufficient...

Research is demonstrating that marine reserves are powerful management and conservation tools, but they are not a panacea; They cannot alleviate all problems, such as pollution, climate change, or overfishing, that originate outside reserve boundaries. Marine reserves are thus emerging as a powerful tool, but one that should be complemented by other approaches.

The answer to the question, “how much is enough” is the holy grail of conservation in both marine and terrestrial ecosystems. The goal of marine reserves is to ensure the persistence of the full range of marine biodiversity—from gene pools to populations, to species and whole ecosystems—and the full functioning of the ecosystem in providing goods and services for present and future generations. Because there will always be opportunity costs to conservation, there is a limit to how much we can conserve.

(Lubchenco, 2003)