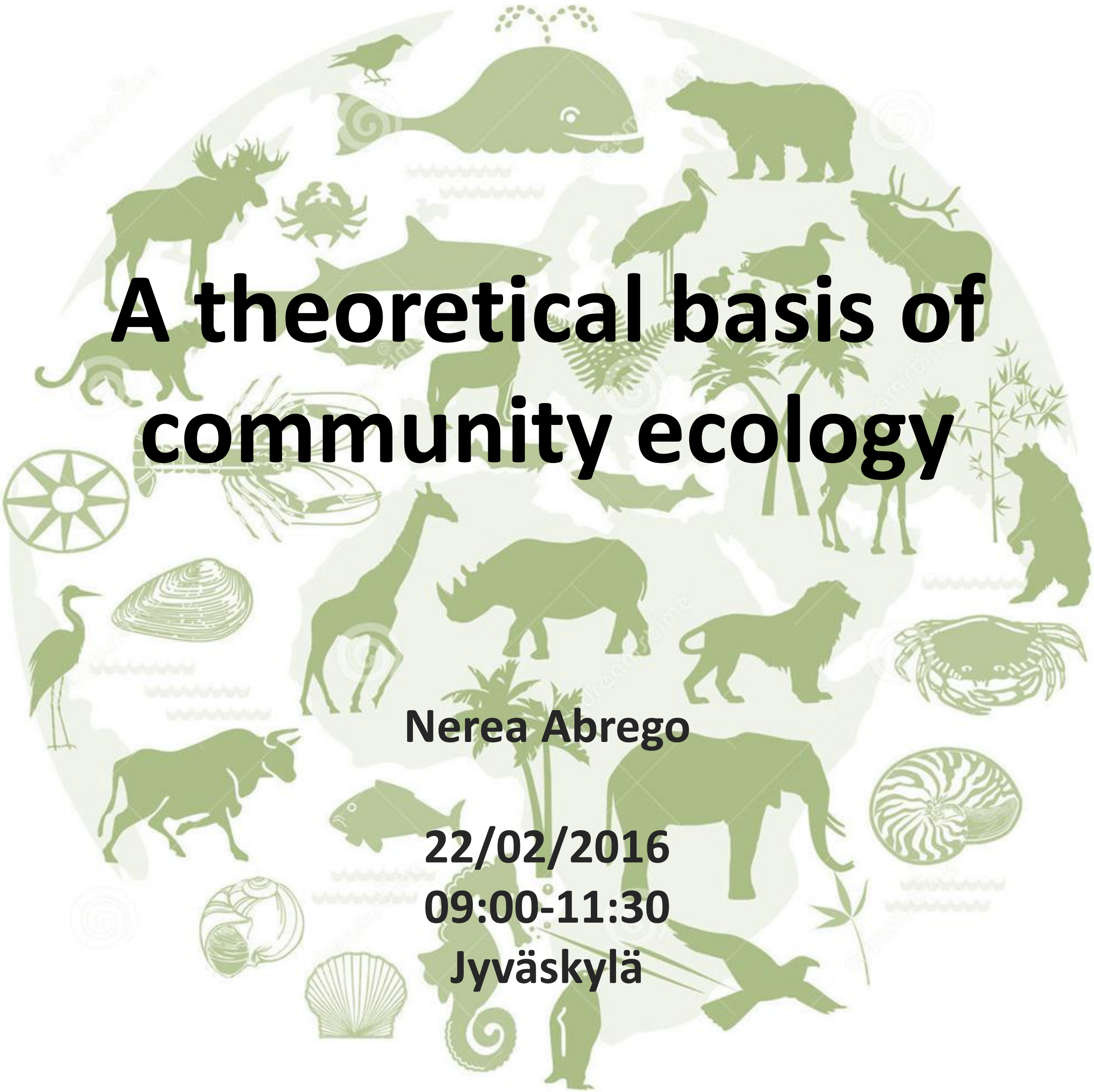

A theoretical basis of community ecology

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09:00-11:30
Jyväskylä

Outline of the lecture

1. What is Community Ecology (CE)?
2. The beginning of CE
   1. Classifying communities
3. First theories in CE
   1. Niche theory
   2. Neutral theory
4. CE nowadays
   1. Metacommunity paradigms
   2. Assembly processes
5. CE from an applied perspective

What is an ecological community?

Robert Whittaker (1975):

“ . . . an assemblage of populations of plants, animals, bacteria and fungi that live in an environment and interact with one another, forming together a distinctive living system with its own composition, structure, environmental relations, development, and function. ”

Robert Ricklefs (1990):

“ . . . the term has often been tacked on to associations of plants and animals that are spatially delimited and that are dominated by one or more prominent species or by a physical characteristic. ”

Peter Price (1984):

“ . . . the organisms that interact in a given area. ”

John Emlen (1977):

“ A biological community is a collection of organisms in their environment. ”

. . .

What is an ecological community?

Interacting assemblage of at least two species at a given time and location

What do we study in community ecology?

The processes influencing the assembly and dynamics of species communities

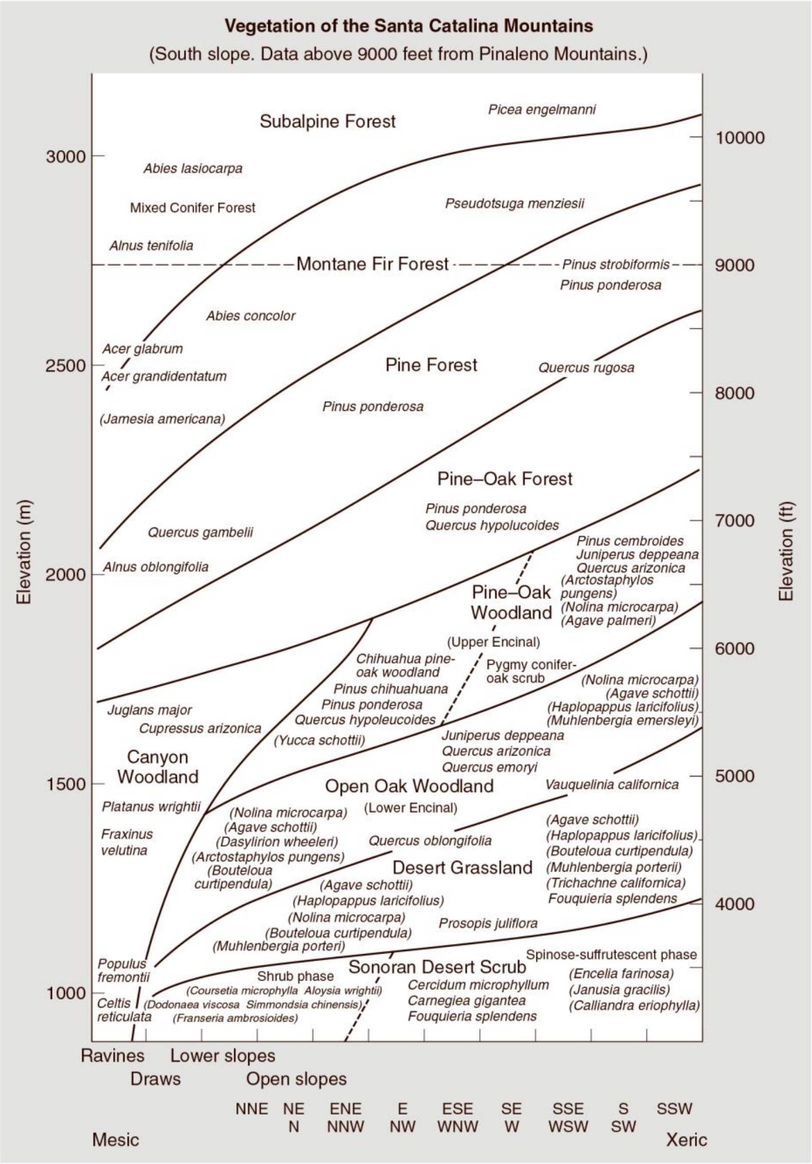
The beginning of community ecology

- CE began as a descriptive science, in which the species from given localities were identified and listed

- Then started to describe some patterns such as differences in the numbers and abundances of the species (i.e. species composition)

- Communities were classified according to their species composition and the environmental variation

The beginning of community ecology



Examples of classifications of communities

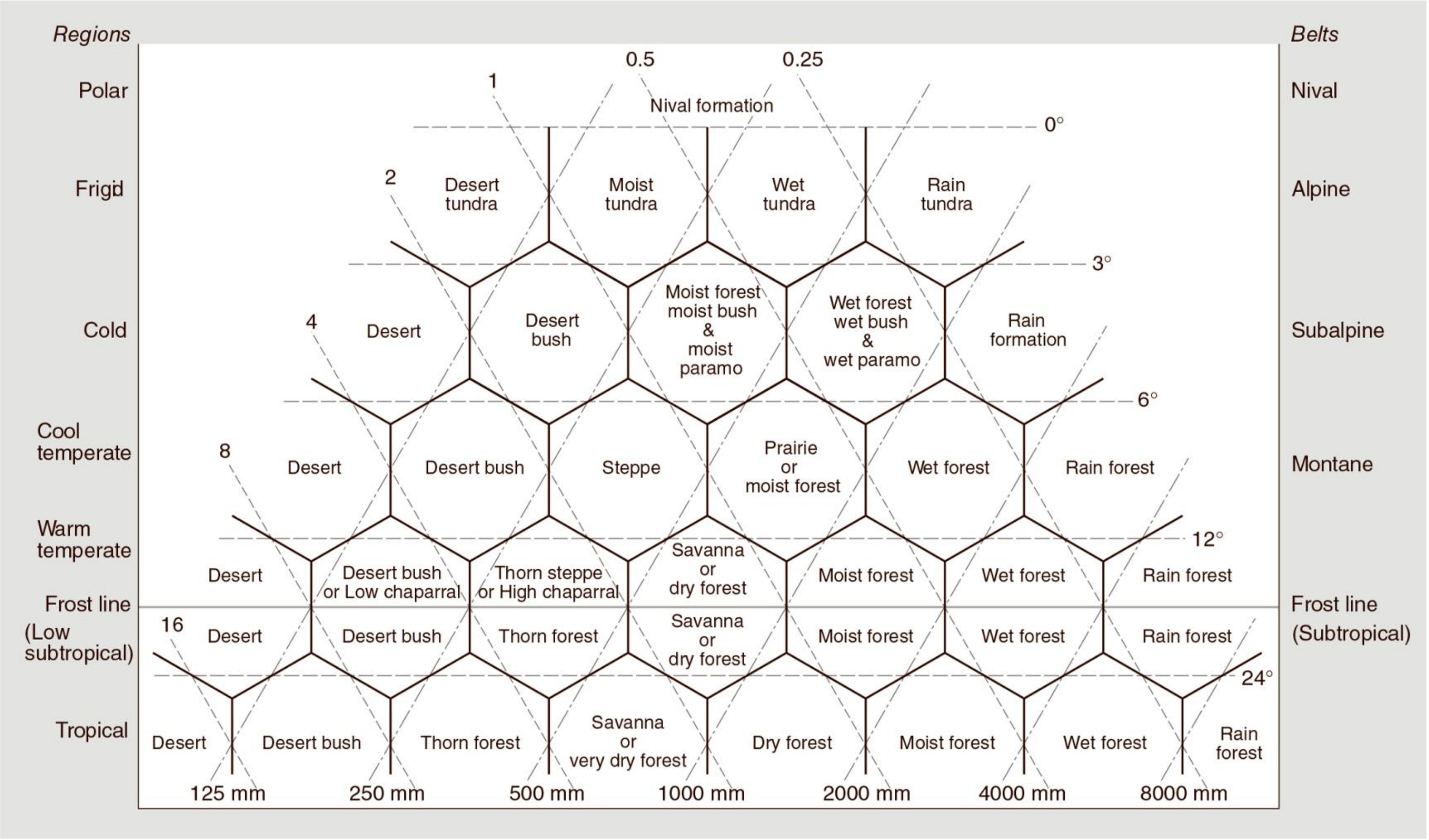
Whittaker and Niering (1965)

Changes in plant species composition along an elevational gradient in the Santa Catalina Mountains of Southeastern Arizona. Changes in elevation result in changes in both temperature and rainfall, which lead to differences in the identity of predominant plant species.

The beginning of community ecology

Examples of classifications of communities

The terrestrial biomes



Relation between average annual temperature, rainfall, and the presence of particular terrestrial biomes characterized by different kinds of vegetation, Holdridge (1947)

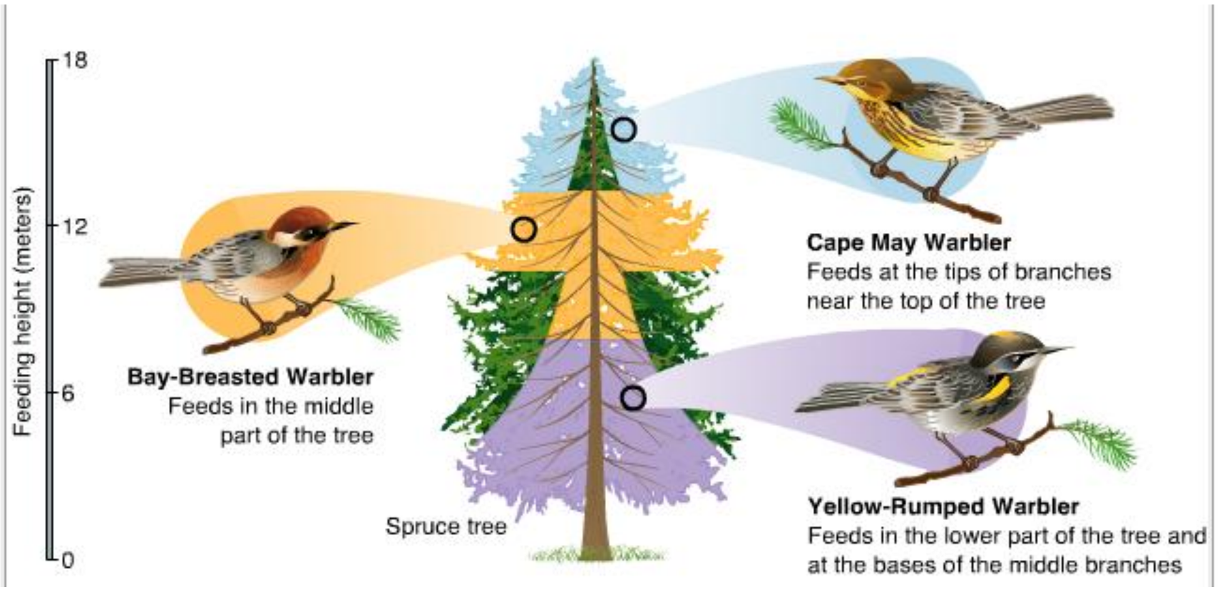
From description of patterns to a more mchanistic undertanding of processes: First theories in community ecology

In the end of the twentieth century, two controversial theories were formalized:

- **Niche theory** (Hutchinson 1959; Macarthur & Levins 1967...)
- **Neutral theory** (Hubbell 2001)

Niche theory

- **Niche:** The place that a species occupies in a community. The range of physical and biological conditions including limiting resources needed for maintaining a stable or icreasing population size.



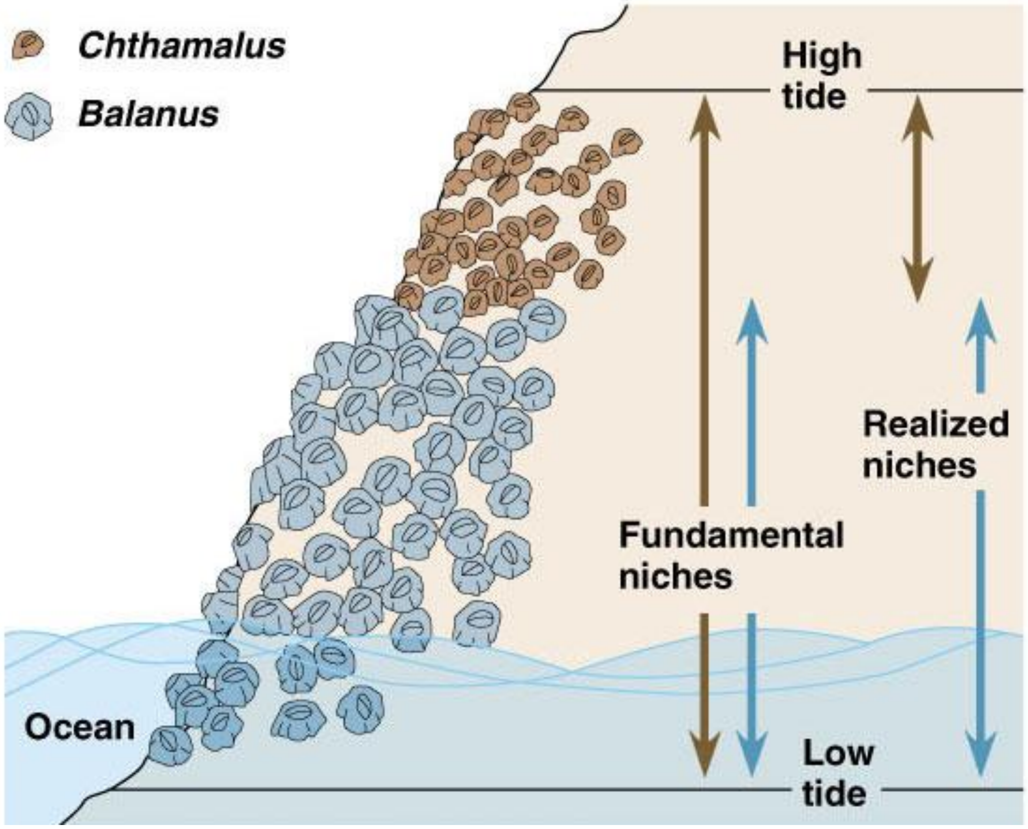
Warbler niches in a spruce tree: each species has a different niche in the spruce by feeding in different parts of the tree, so they coexist without competing with each other.

Niche theory

Connell's (1961) Barnacles example:

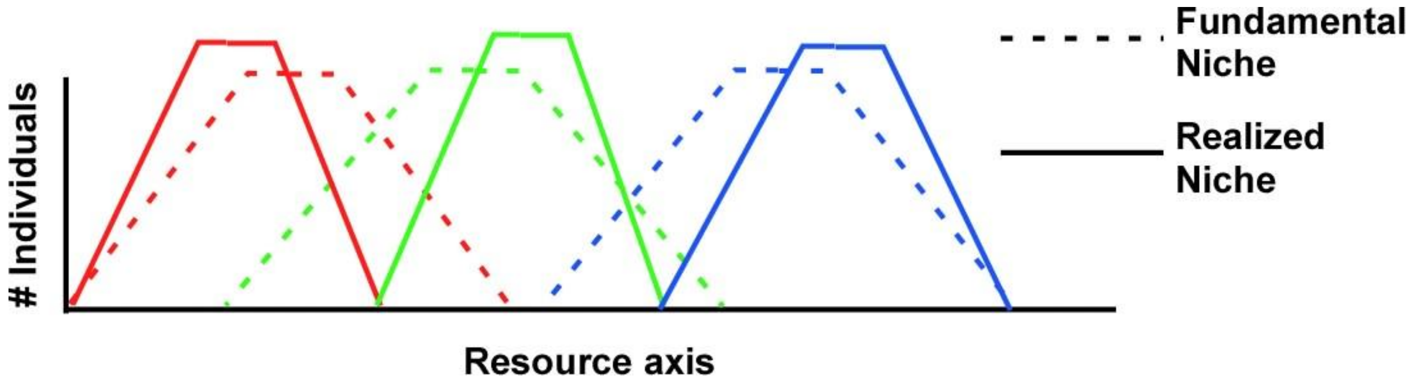
- **Fundamental niche:** The full range of biotic and abiotic conditions that a species could use without interference of other competing species

- **Realized niche:** The niche that a species is forced to use as a result of inter-specific competition effects



Niche theory

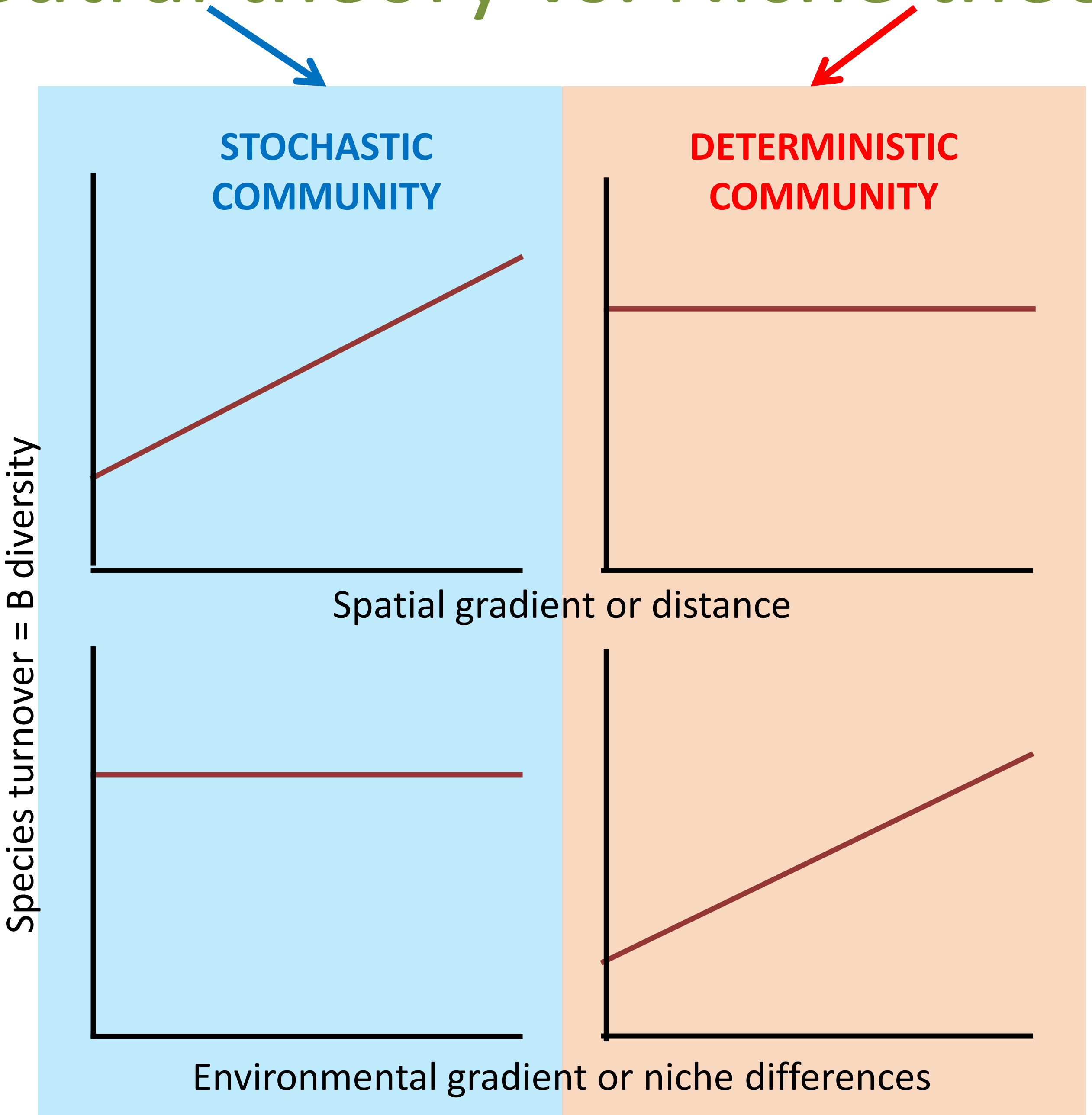
- Deterministic processes such as interspecific competition and differences in resource use are the main mechanisms allowing species coexistence



Neutral theory

- All individuals are ecologically identical and niche differences are not needed to explain biodiversity patterns.
- Highly diverse communities of equivalent species (i.e. species with identical niches) arise because chance extinctions are balanced by speciation. Specifically, stochastic or random processes that include death, immigration from a regional pool of species, and speciation can lead to species-rich communities.

Neutral theory vs. Niche theory



Adapted from Chase & Myers 2011

Theories for community ecology nowadays: Metacommunity paradigms

Leibold et al (2004) identified four theoretical paradigms for explaining the processes shaping metacommunities

- These paradigms emphasize on the importance of the spatial scales and the interactions among the scales
- The differences among the four paradigms derive from differences in relative dispersal rates and the level of heterogeneity among habitat units

1. The patch-dynamic paradigm
2. The species-sorting paradigm
3. The mass effects paradigm
4. The neutral paradigm

Theories for community ecology nowadays: Metacommunity paradigms

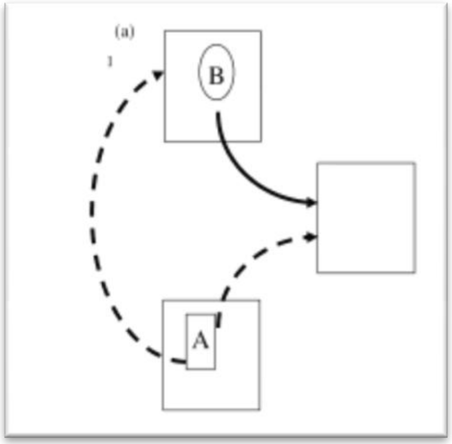
What is a metacommunity?

A set of local communities that are linked by dispersal of multiple potentially interacting species

Theories for community ecology nowadays: Metacommunity paradigms

1. The patch-dynamic paradigm

There are multiple identical patches that undergo both stochastic and deterministic extinctions that can be affected by interspecific interactions, and that are counteracted by dispersal.



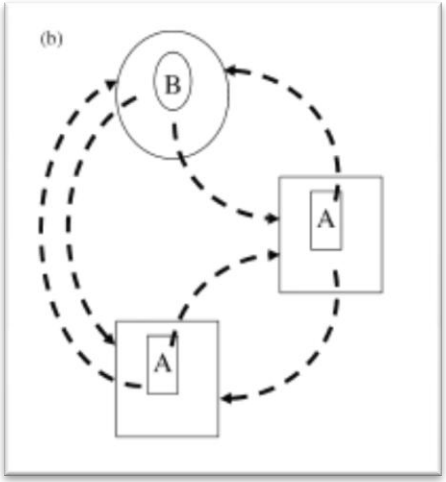
A and B are populations of two competing species
The squares are habitat patches
Solid arrows represent more dispersal
Squares are potential colonization patches

In this case A is a superior competitor but B is better colonists, thus the third patch can be colonized by either species

Theories for community ecology nowadays: Metacommunity paradigms

2. The species-sorting paradigm

Local patches are heterogeneous in environmental conditions and the outcome of species interactions depends on the effects of the environmental conditions.

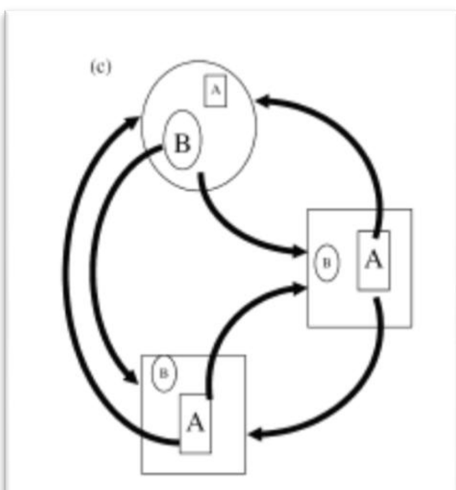


Species are separated into spatial niches and dispersal is not sufficient to alter their distribution.

Theories for community ecology nowadays: Metacommunity paradigms

3. The mass-effects paradigm

Differences in dispersal can result in source sink relations among habitat patches.

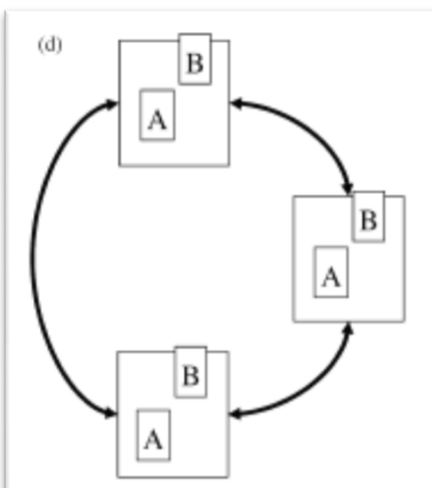


Mass-effects causes species to be present in both source and sink habitat patches

Theories for community ecology nowadays: Metacommunity paradigms

4. The neutral paradigm

Species do not differ in their dispersal abilities.



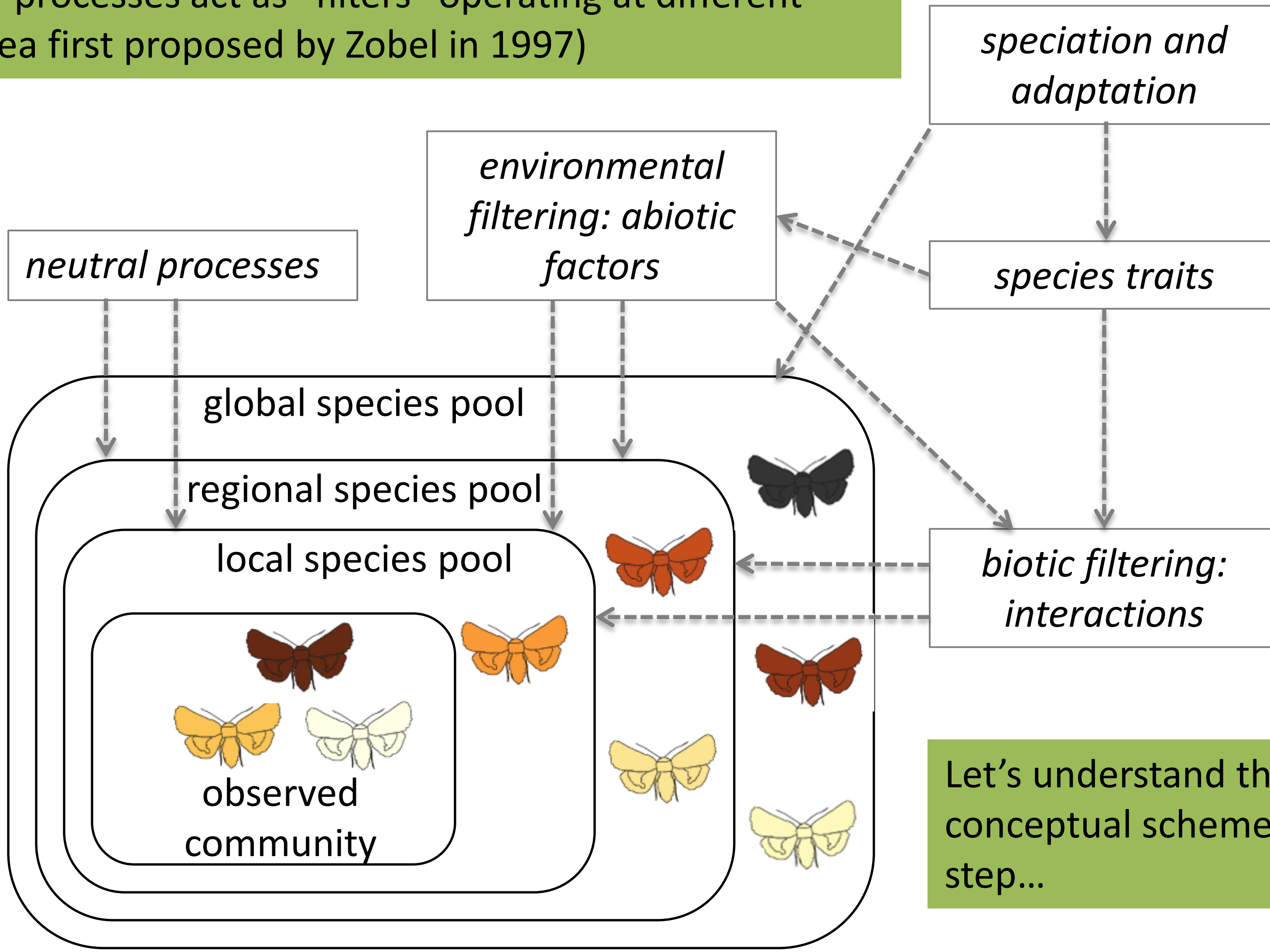
All species are present in all patches; species would gradually be lost from the region and would be replaced by speciation

Theories for community ecology nowadays

- Although there is not a general theory that entirely explains how communities are assembled across space and time, community ecologists nowadays acknowledge that local species communities are a result of the combination of both stochastic and deterministic processes, which are called assembly processes

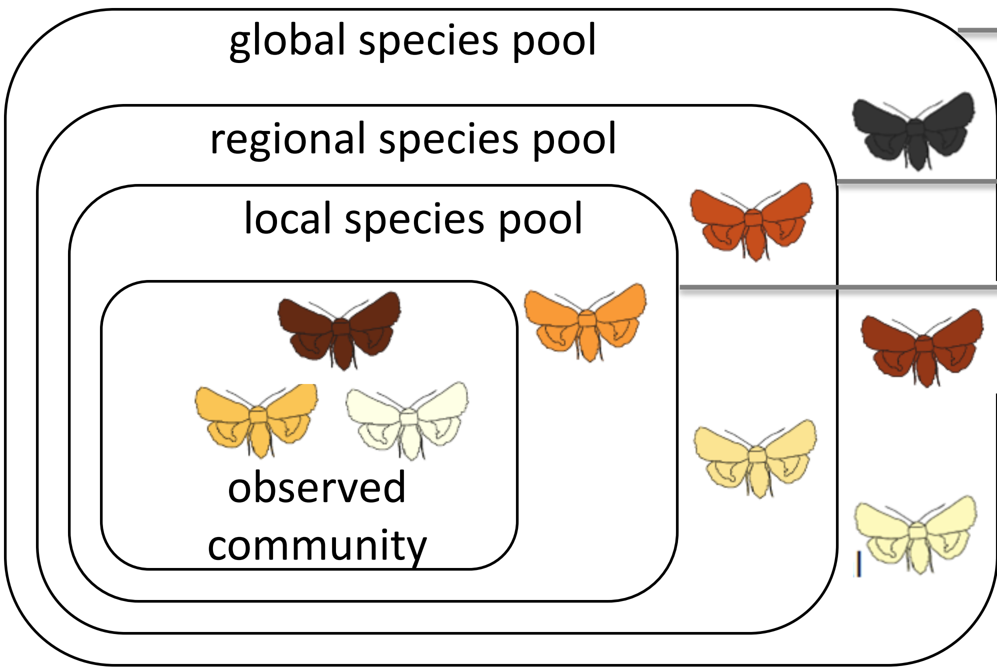
Community ecology nowadays: assembly processes

Assembly processes act as “filters” operating at different scales (idea first proposed by Zobel in 1997)



Let’s understand this conceptual scheme step by step…

Understanding assembly processes: global, regional and local species pools



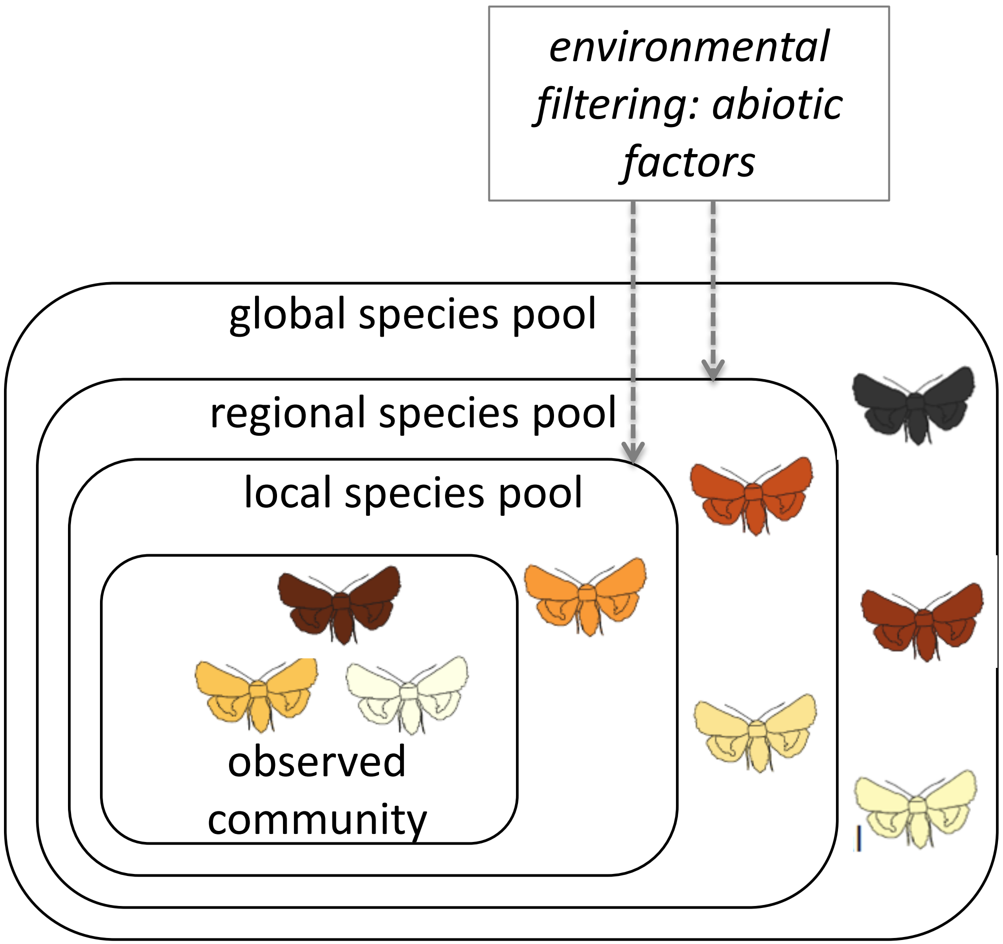
All existing species

All species able to colonize a given area = regional community

species found at smallest scales = local community

The species pools found at smaller scales are the result of the assembly processes acting as filters at higher scales

Understanding assembly processes: environmental filters

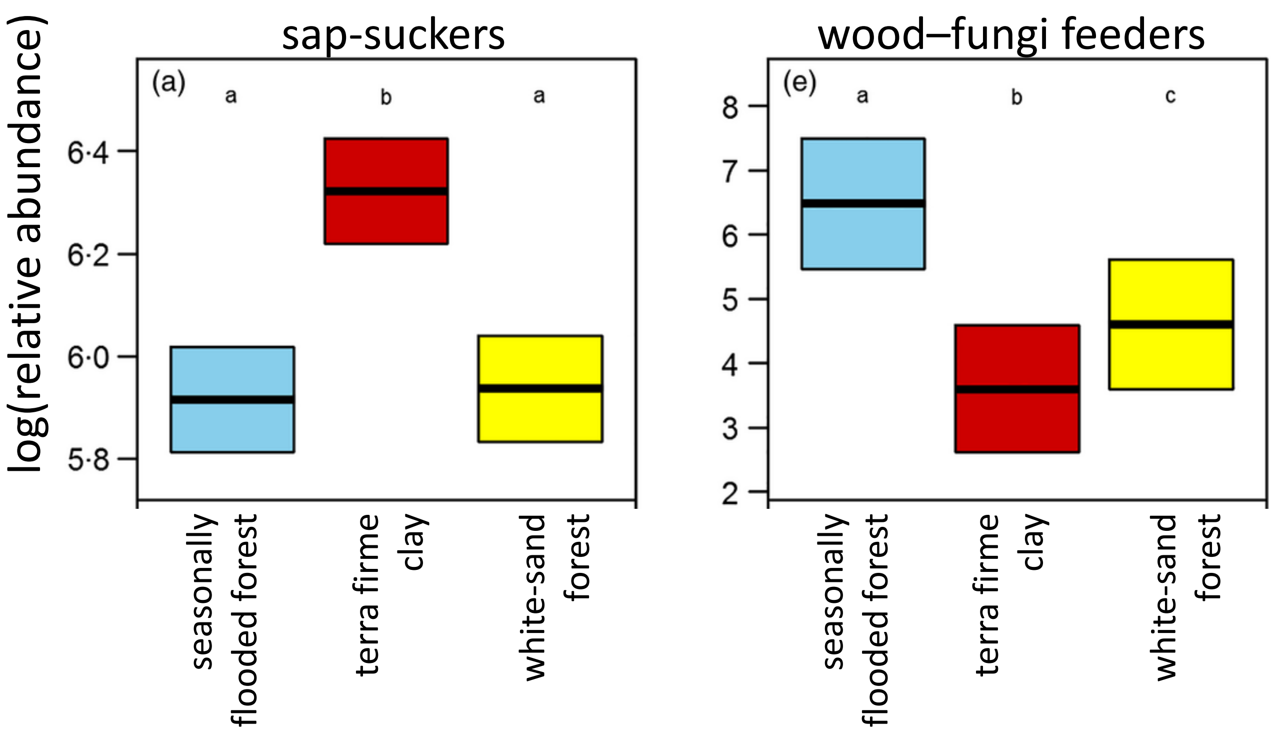


Environmental filters are those abiotic factors that prevent the establishment or persistence of species in local communities. They are deterministic processes.

Understanding assembly processes: environmental filters

Example: Arthropod communities across Amazonian habitat types (Lamarre et al 2016):

Arthropod community composition varied markedly across contrasting tropical forest habitats: shifts in environmental conditions can strongly influence spatial patterns in arthropod communities (geography and environment explained most variation) .



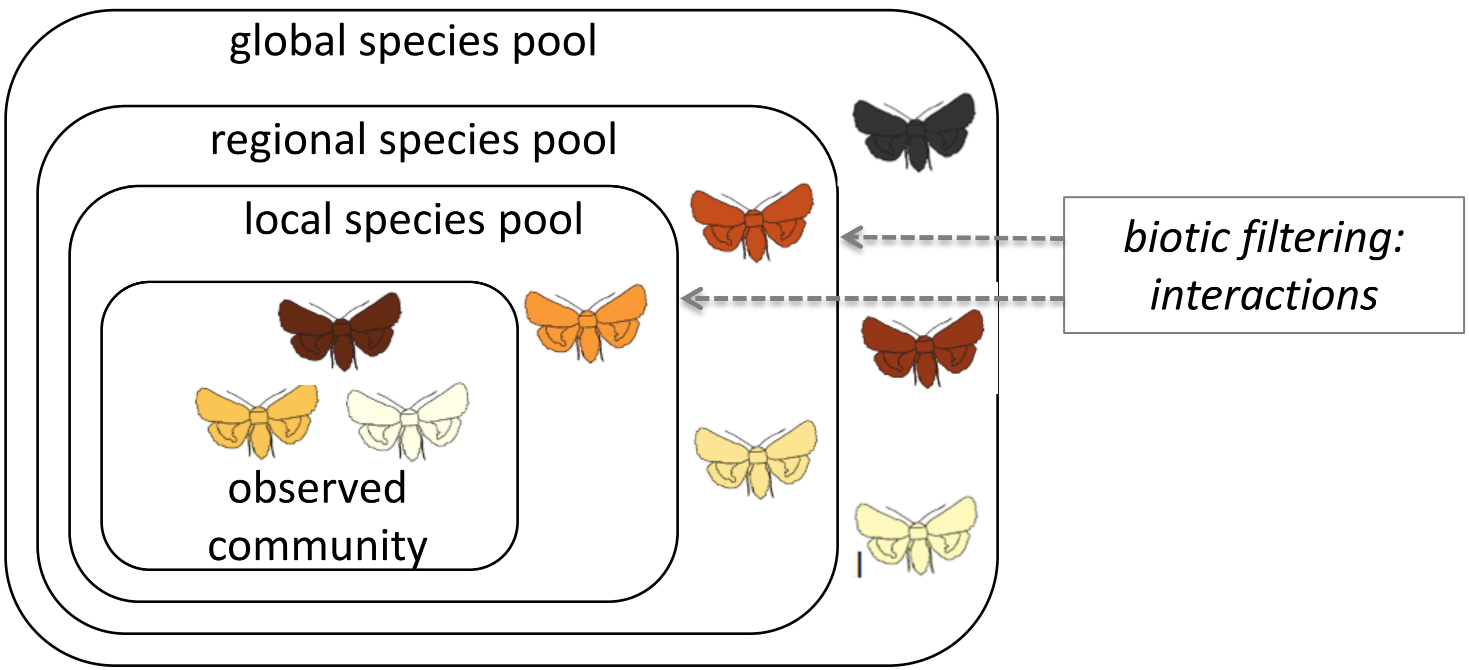
Understanding assembly processes: environmental filters

Example: Tropical plant communities in an altitudinal gradient (Lieberman et al 1996)

Site	Dicot trees	Palms	Tree ferns	Lianas	Hemi-epiphytes	Total
Number of species						
La Selva	241	7	1	20	0	269
100 m	103	5	0	7	0	115
300 m	138	4	0	7	0	149
500 m	118	3	2	7	1	131
750 m	116	3	1	2	3	125
1000 m	88	1	6	1	4	100
1250 m	75	0	7	0	0	82
1500 m	66	0	5	0	3	74
1750 m	58	1	4	0	1	64
2000 m	49	1	2	0	3	55
2300 m	38	1	4	0	1	44
2600 m	27	0	2	0	0	29

Understanding assembly processes: biotic filters

Interspecific and intraspecific competitive and facilitative interactions that determine the set of species in local communities. They are deterministic processes as well.



Understanding assembly processes: biotic filters

Example: Plant communities in dessert systems (Valiente-Banuet & Verdú 2008)

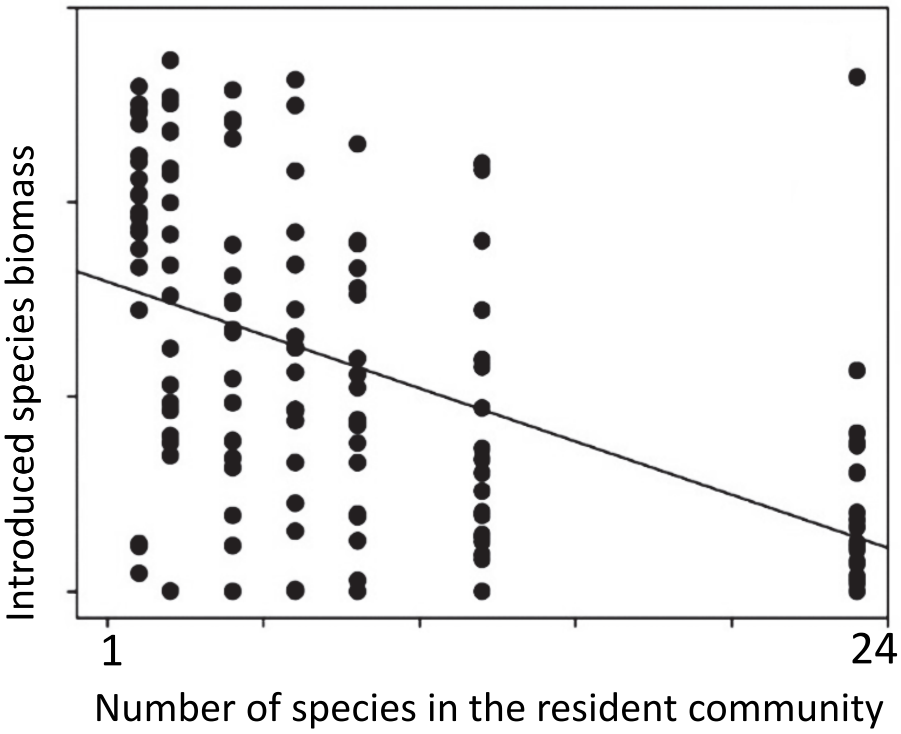
They analyzed 102 woody species in three Mexican semi-arid communities in order to quantify the balance between competition and facilitation at the community level

In the Mexican desert system, facilitation dominates species interactions in young communities as nurse plants allow seedlings to grow and vegetation clumps to develop, and competitive interactions become more important as plants mature.

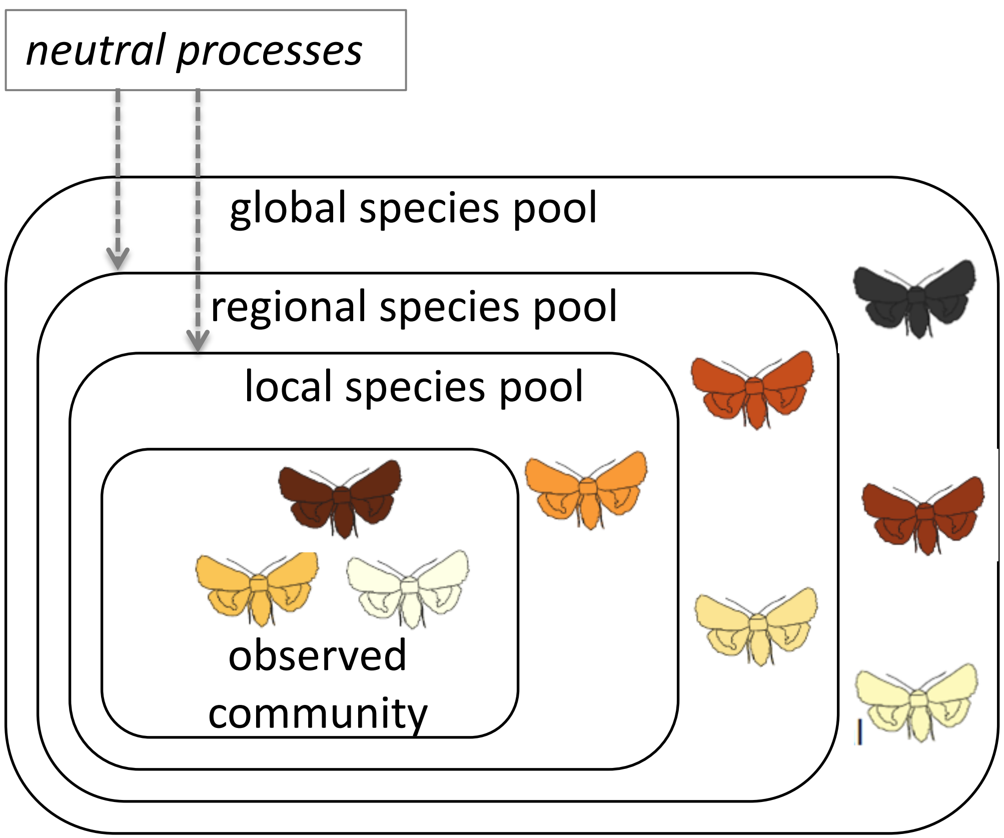
Understanding assembly processes: biotic filters

Example: Competition as a filter structuring plant communities (Fargione et al. 2003)

Fargione et al. (2003) established a set of experimental plots by sowing seeds of 24 species of perennial grassland plants. 3 years later, seeds of 27 other perennial grassland plant species were introduced to the plots. After 2 more years, the plots were surveyed to examine whether the newly introduced species had established.
The results of this experiment demonstrated that the success of the newly introduced species declined with the number of species originally sowed to the plots. This was the case because the resident species communities had depleted resources (e.g. soil nitrate and water, and availability of bare ground and light) to a level that prevented the establishment of many of the newly introduced species.



Understanding assembly processes: neutral processes



Neutral processes refer to stochastic processes related to colonization, extinction and ecological drift that generate additional variation in the local communities, thus making environmentally identical communities diverge in their species compositions.

Understanding assembly processes: neutral processes

Example: Damselfly species in eastern North America (McPeek & Brown 2000)

They investigated differences between competing damselfly species and found rather little difference among some species, leaving the neutral processes as a potential explanation for high species diversity in this groups of insects.

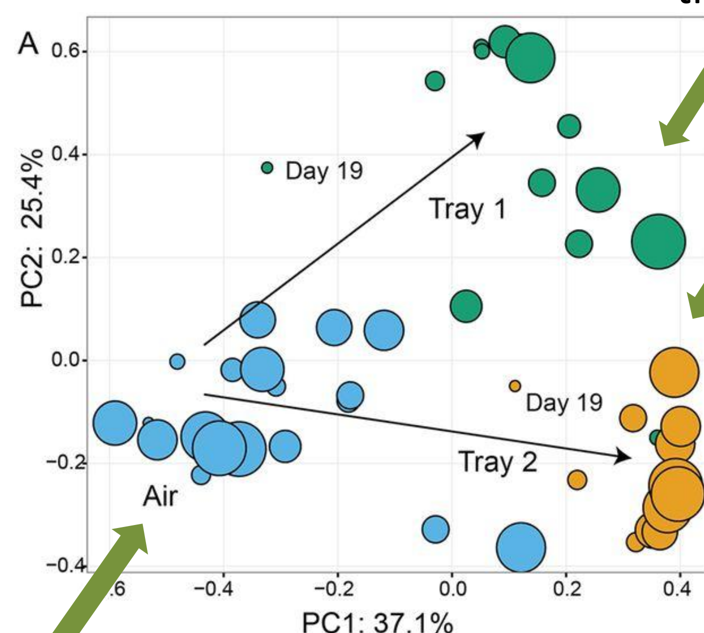
Understanding assembly processes: stochastic processes

Example: Stochastic variation in the bacterial communities associated with *Arabidopsis* plants (Maignien et al 2014)

They used a large number of replicate plants to identify repeatable dynamics in bacterial community assembly and reconstructed assembly history by measuring the composition of the airborne community immigrating to plant leaves.

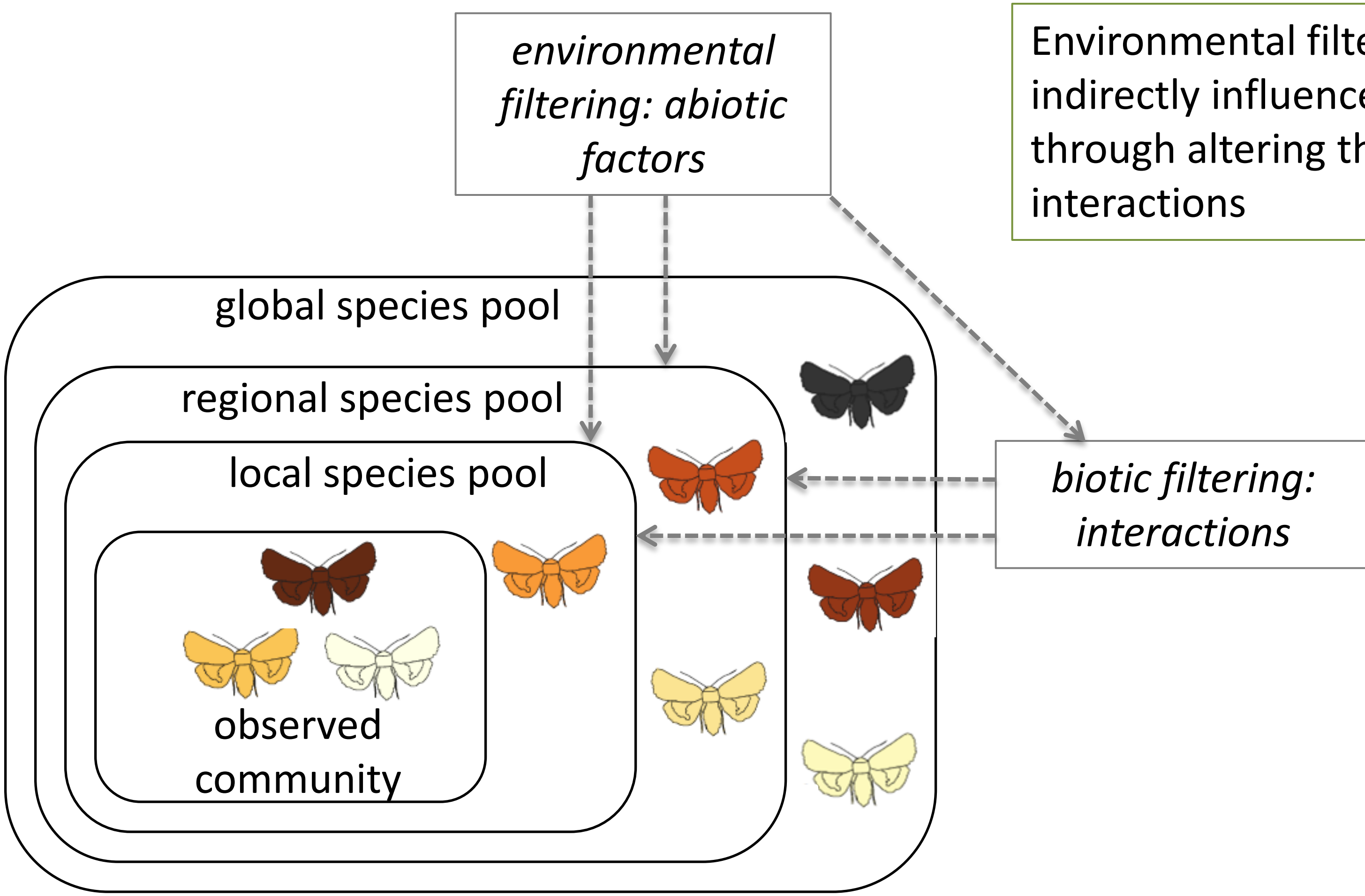
Stochastic events in early colonization, coupled with dispersal limitation, generated alternate trajectories of bacterial community assembly.

Different trajectories



Initial community

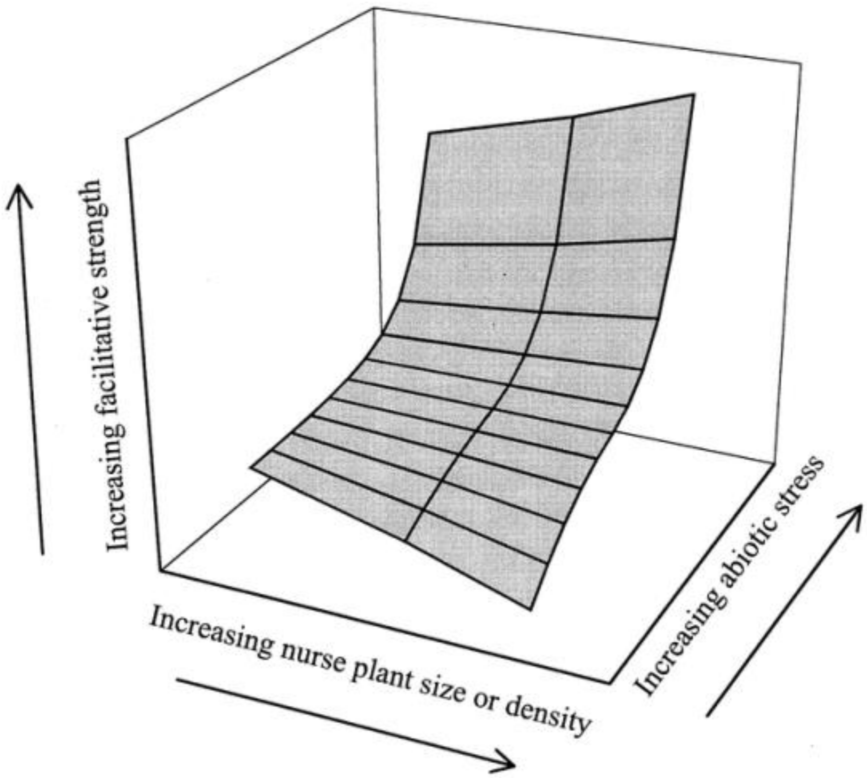
Understanding assembly processes: effects of abiotic factors on biotic interactions



Environmental filters can also indirectly influence communities through altering the outcome of interactions

Understanding assembly processes: effects of abiotic factors on biotic interactions

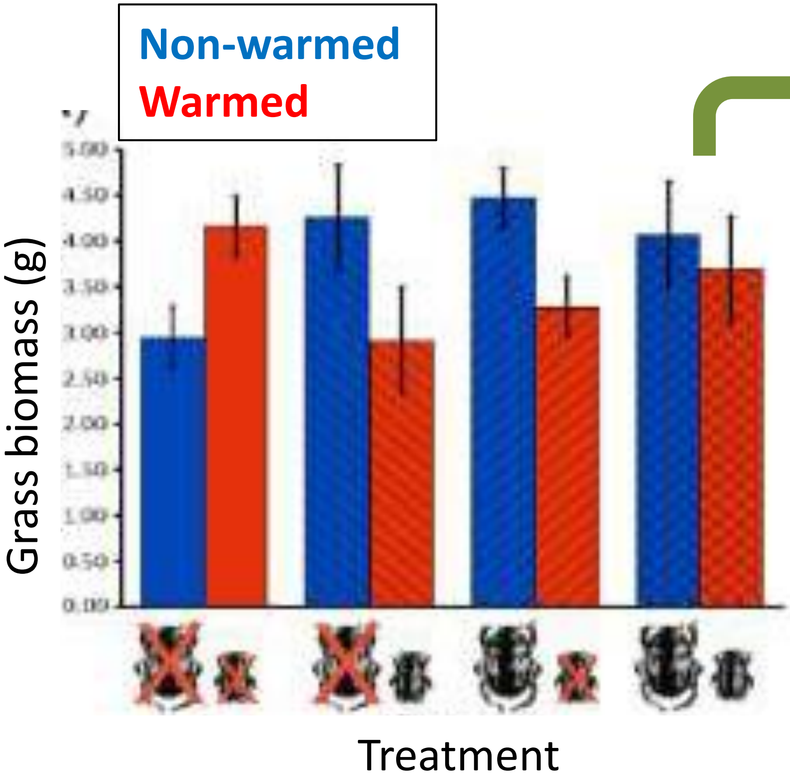
Example: Interactions in plant communities (Callaway & Walker 1997)



Under harsh physical conditions, increasing benefactor age, size, or density increases the relative strength of facilitation. Under benign physical conditions, increased benefactor age, size, or density increases the relative strength of the competitive effect.

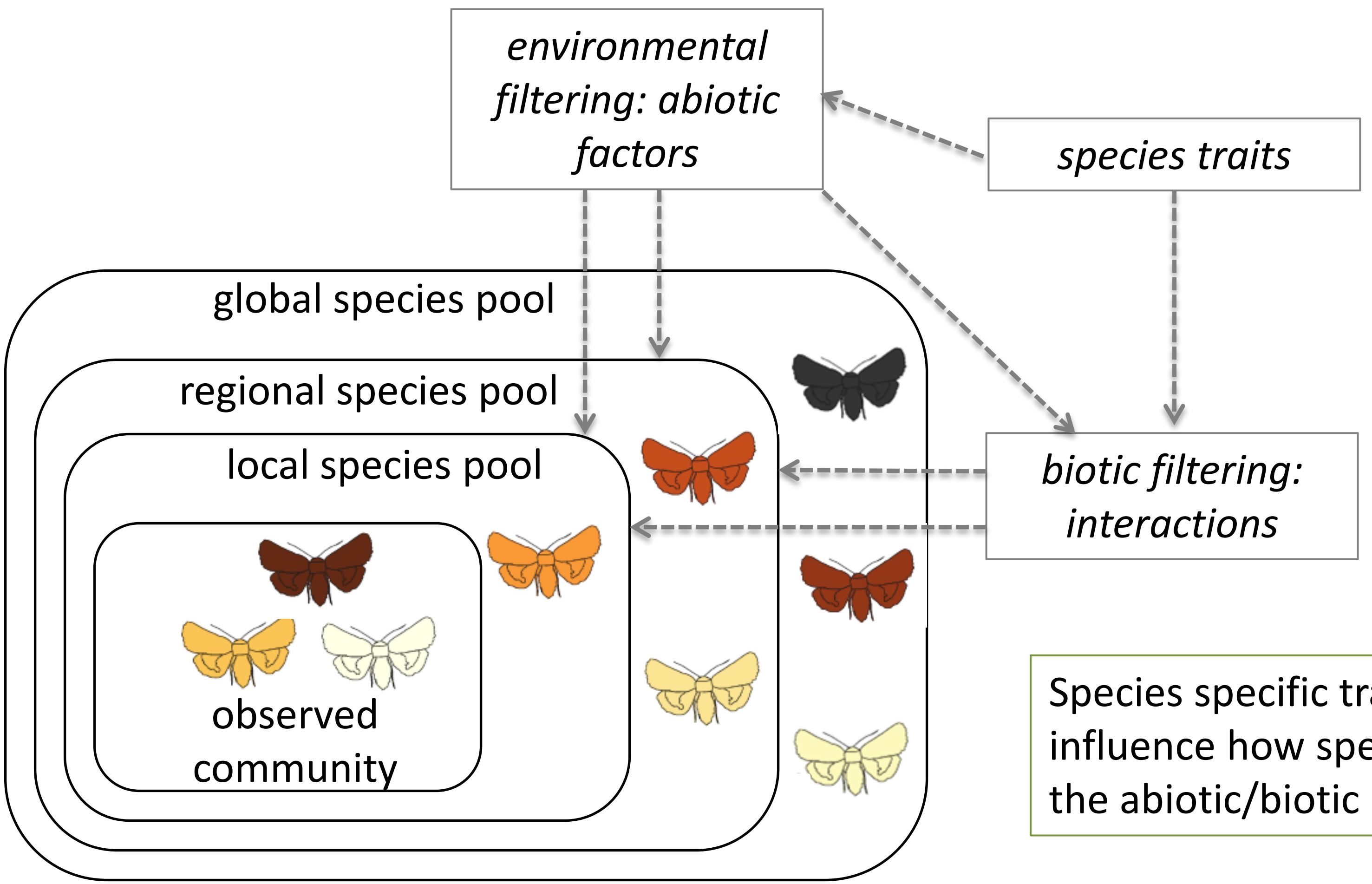
Understanding assembly processes: effects of abiotic factors on biotic interactions

Example: Dung beetle species interactions and multifunctionality are affected by an experimentally warmed climate (Slade and Roslin 2016)



They observed positive interactions between *Geotrupes stercolarius* and *Aphoditus fossor* dung beetles only when temperature was warmer (and this increased plant productivity)

Understanding assembly processes: effects of traits on the responses of species to abiotic factors and inter-specific interactions



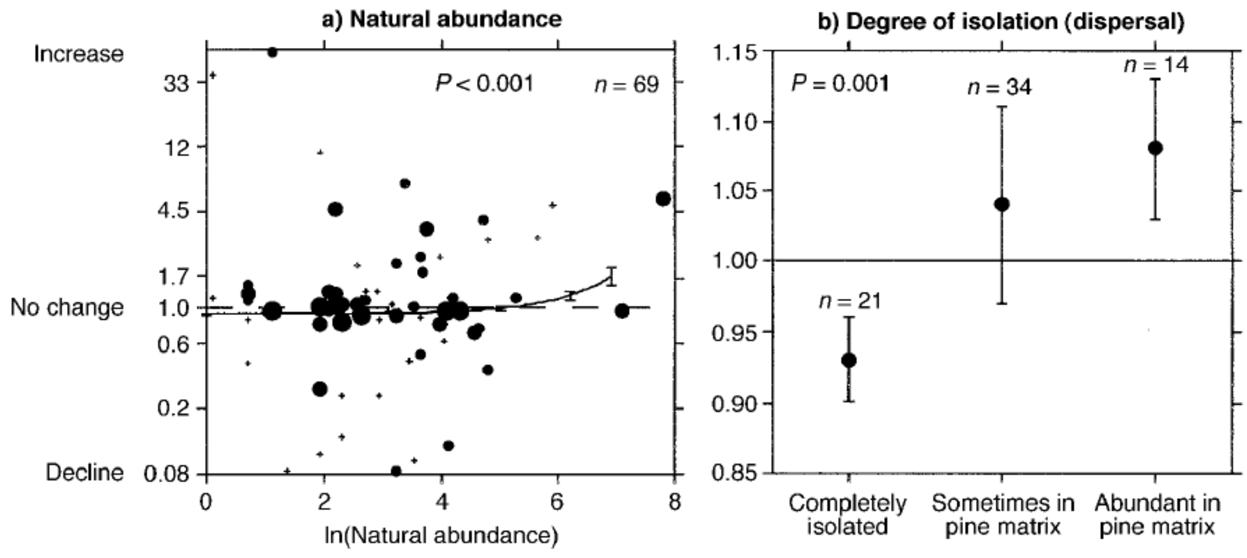
Species specific traits can influence how species respond to the abiotic/biotic environment.

Understanding assembly processes: effects of traits on the responses of species to abiotic factors

Example: Davies et al (2000) studied which are the traits that characterize those species that negatively respond to forest fragmentation

They tested the relationships between five traits of species and decline in abundance for 69 beetle species in an experimentally fragmented forest landscape in Australia.

Rare, dispersal limited and predator species are more vulnerable to the effects of forest fragmentation



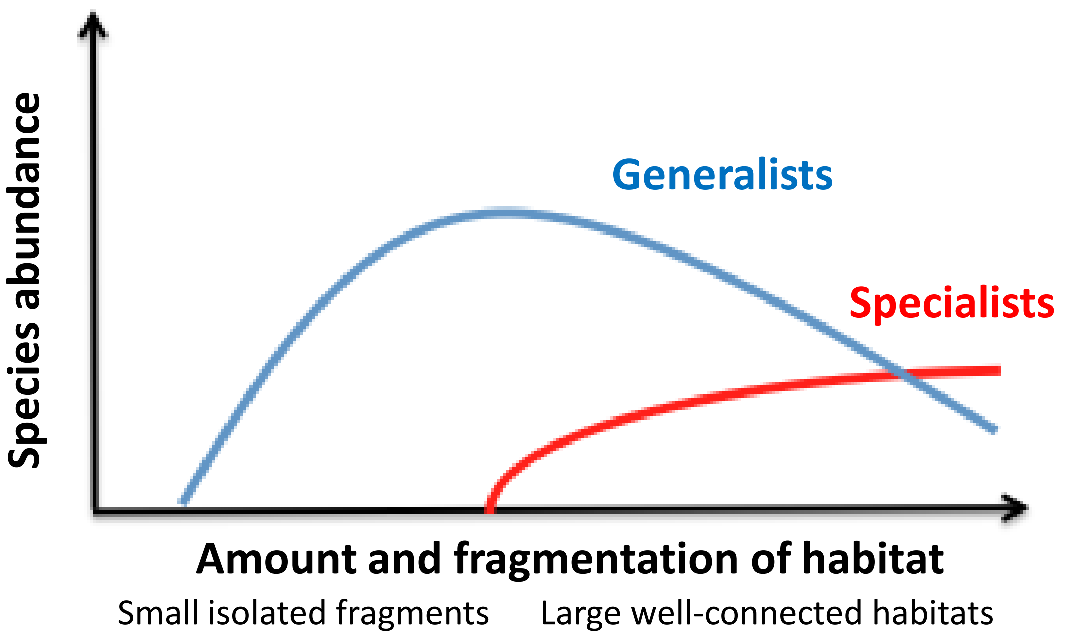
Understanding assembly processes: effects of traits on the responses of species to abiotic factors and inter-specific interactions

Example: specialist/generalist tradeoff

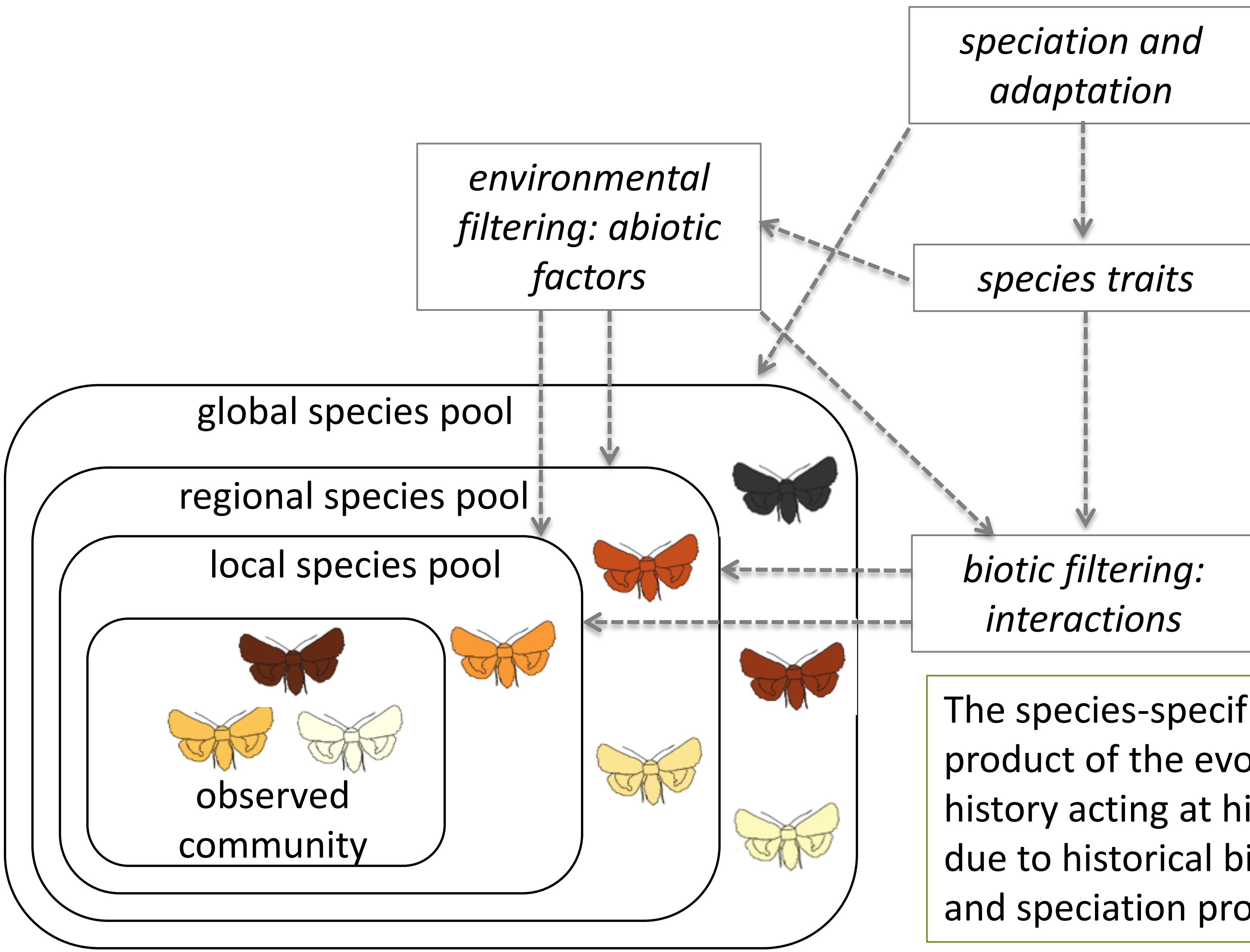
Specialist-generalist coexistence in disturbed environments (e.g. Nee & May 1992; Seifan et al. 2013):

Resource specialist species are superior competitors but worse dispersers and colonizers.

Resource generalists are inferior competitors but better dispersers and colonizers.



Understanding assembly processes: speciation and adaptation



The species-specific traits are the product of the evolutionary history acting at highest scales, due to historical biogeography and speciation processes.

Understanding assembly processes: historical biogeography

Example: Plant communities in Australia (Kooyman et al 2011, Rosetto et al 2015)

The distribution and assembly of species reflect interactions and competition between different floristic elements at different stages of continental occupation. Rather than the environmental filtering at regional scales, the evolutionary and biogeographic history acting at continental scale explains the Australian tropical plant communities.

Community Ecology from an applied perspective

How does what we have learnt today link to what we want to study as applied ecologists?

- As applied community ecologists dealing with topics related to the management of ecological communities, it is essential to mechanistically understand how our subject community is assembled:

  1. For instance, one central question in applied community ecology is what are the processes behind the responses of the community to a particular temporal or spatial change such as forest management, pollution, temperature change, habitat loss... Which can be viewed as environmental filters

  2. And for the conservation of ecological communities, it is essential to know at which scales such environmental changes are acting, as we should e.g. focus the management actions at the most critical scale

Community Ecology from an applied perspective

How does what we have learnt today link to what we want to study as applied ecologists?

3. By understanding the processes we will also be able to classify the species/communities in relation to their vulnerability to environmental change

4. Especially in the field of conservation biology, surrogate species such as indicator, umbrella and keystone species are very much used to indicate other species of conservation interest. For this purpose, understanding how biotic interactions structure the communities is essential.

Community Ecology from an applied perspective

How does what we have learnt today link to what we want to study as applied ecologists?

5. By understanding the processes assembling our subject community, we will also be able to make predictions on how the community would change by changing some biotic or abiotic parameters. This is especially useful for making predictions on how e.g. climate change will influence our community, or to e.g. test how our community will respond to different forest management/restoration scenarios.

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