

6. The Assembly of Diversity

Regional Processes

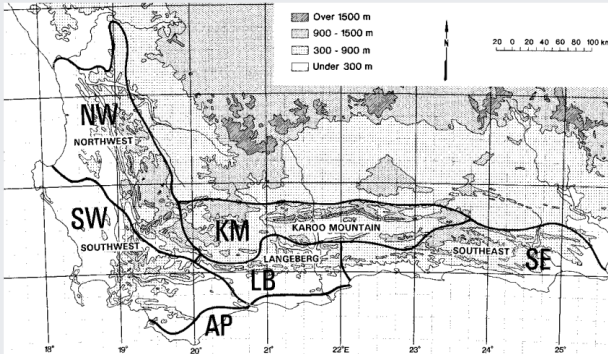
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Local vs Regional scale processes

The diversity of local biological communities is a balance of regional and local processes - Ricklefs 1987

Regional scale



- speciation
- extinction
- dispersal

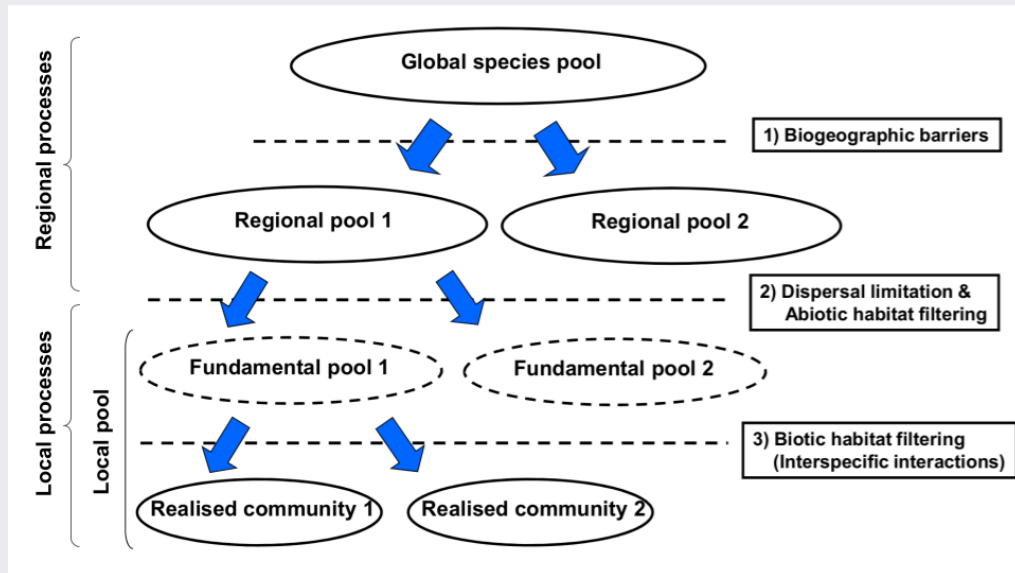
Local scale



- environmental filtering
- interspecific interactions (competition, predation, pathogens, mutualisms)
- adaptation
- stochastic variation

Assembly of species pools across scales

Community assembly can be thought of as the successive filtering of species pools descending in spatial (and temporal) scale from global to local



We often split it into **regional** versus **local** processes

Global species pool = all species on the planet (or in the defined study domain, e.g. Cape Floral Region)

Regional species pools = the species that are present in each region (e.g. a biogeographic region or mountain), limited by barriers to dispersal

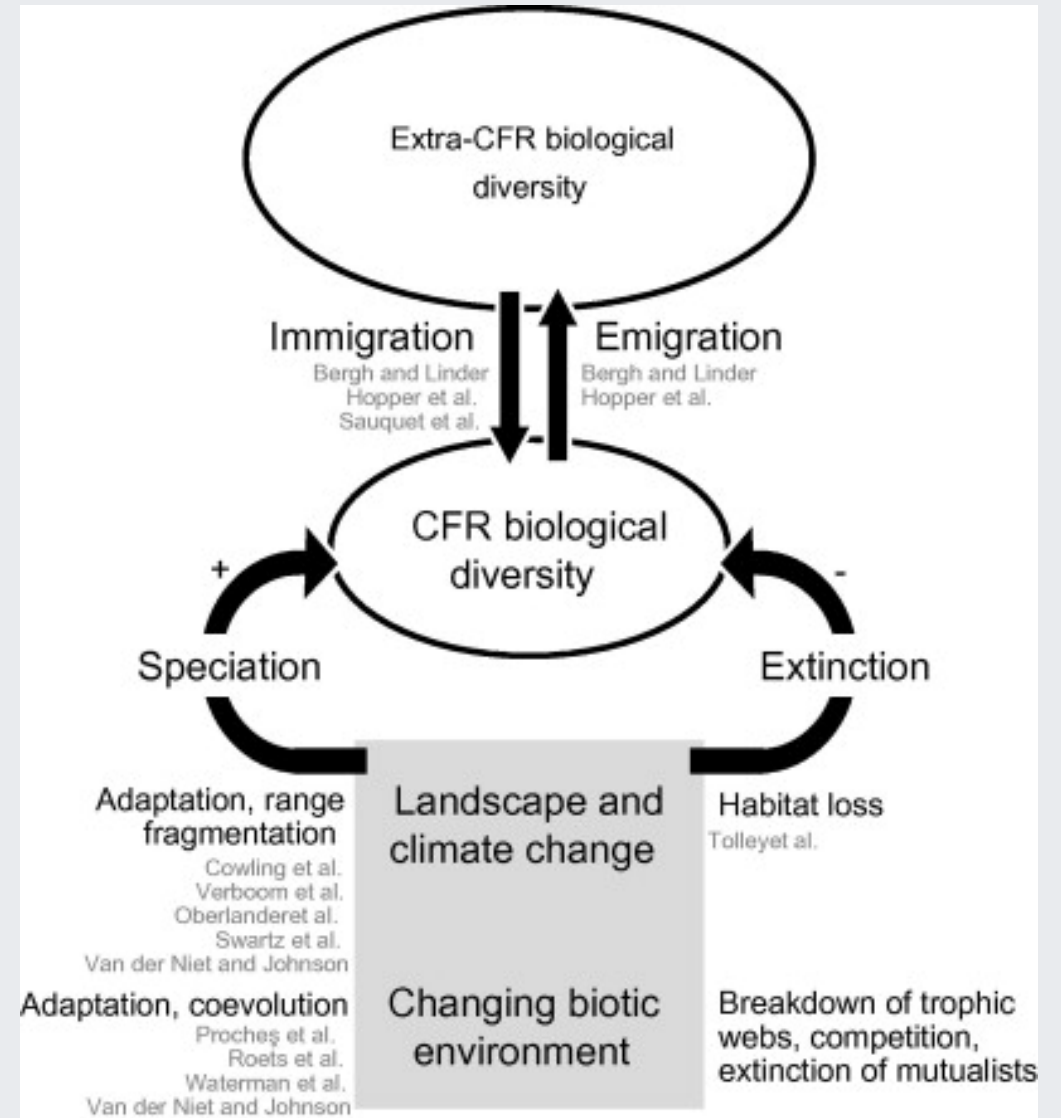
Fundamental species pool = species with the potential to occur in a particular location (i.e. can disperse there and find the appropriate abiotic conditions)

Realised community = the actual observed local community (i.e. a subset of the fundamental species pool with the ability to coexist, either stably or unstably)

Functional or phylogenetic structure can be created or altered at any step...

Regional processes

- speciation
- extinction
- dispersal



Verboom et al. 2009

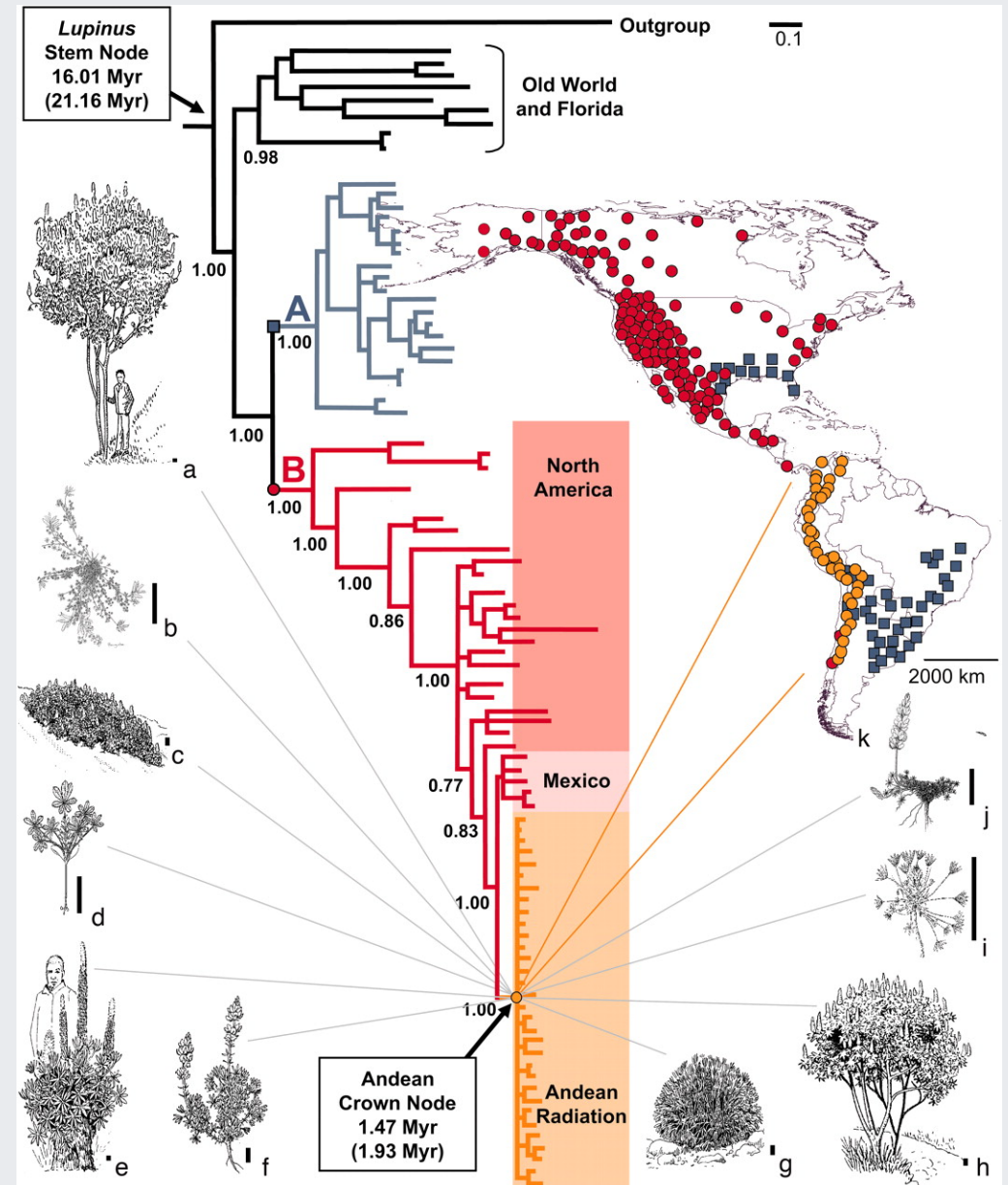
Speciation

Driven by many processes, but dramatic radiations often triggered by major events/changes that create **new habitats and opportunities** for adaptive divergence, or cause **isolation**, or both.

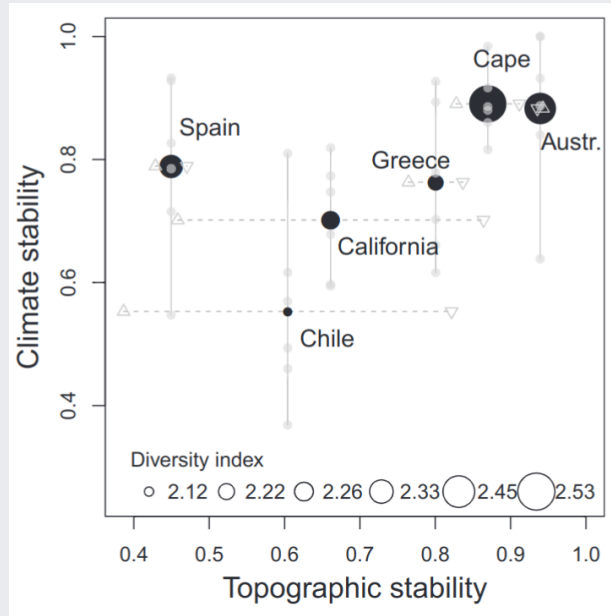
E.g. The radiation of the genus *Lupinus* was driven by the uplift of the Andes

The uplift created diverse new habitats, because it created steep climatic gradients and exposed new geology/soils. It also split populations by creating new barriers to dispersal (e.g. high mountains between lowland populations, or deep valleys between high elevation populations).

Hughes and Eastwood 2006

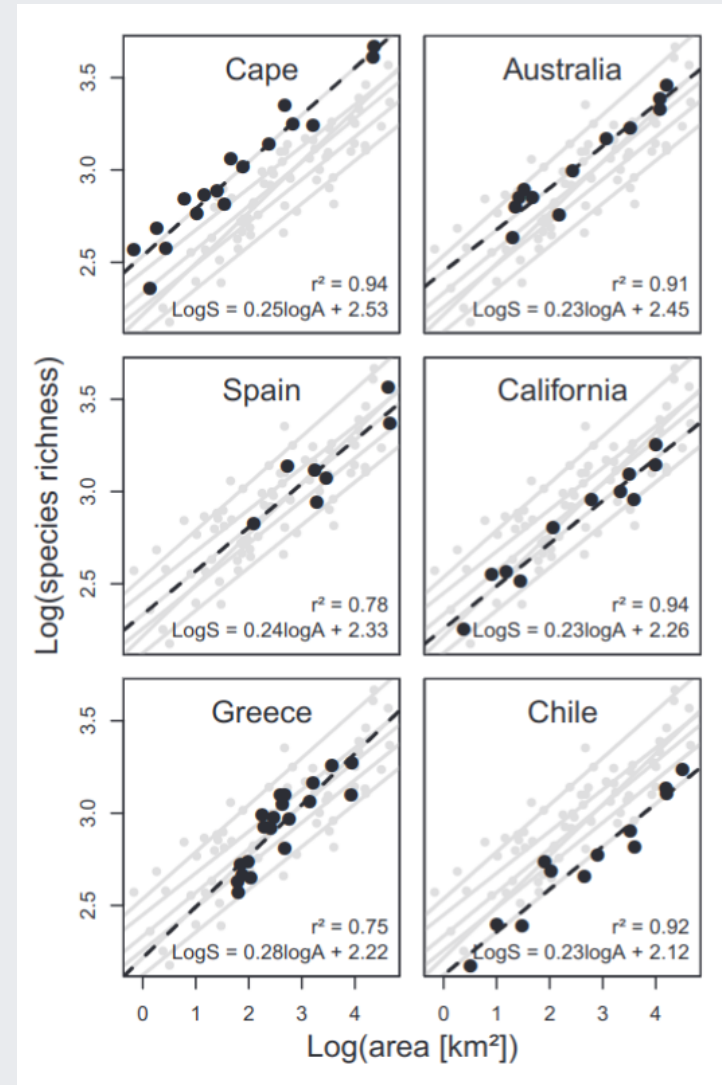


Extinction and stability



Major change can be bad for diversity though... Too much, and things go extinct!

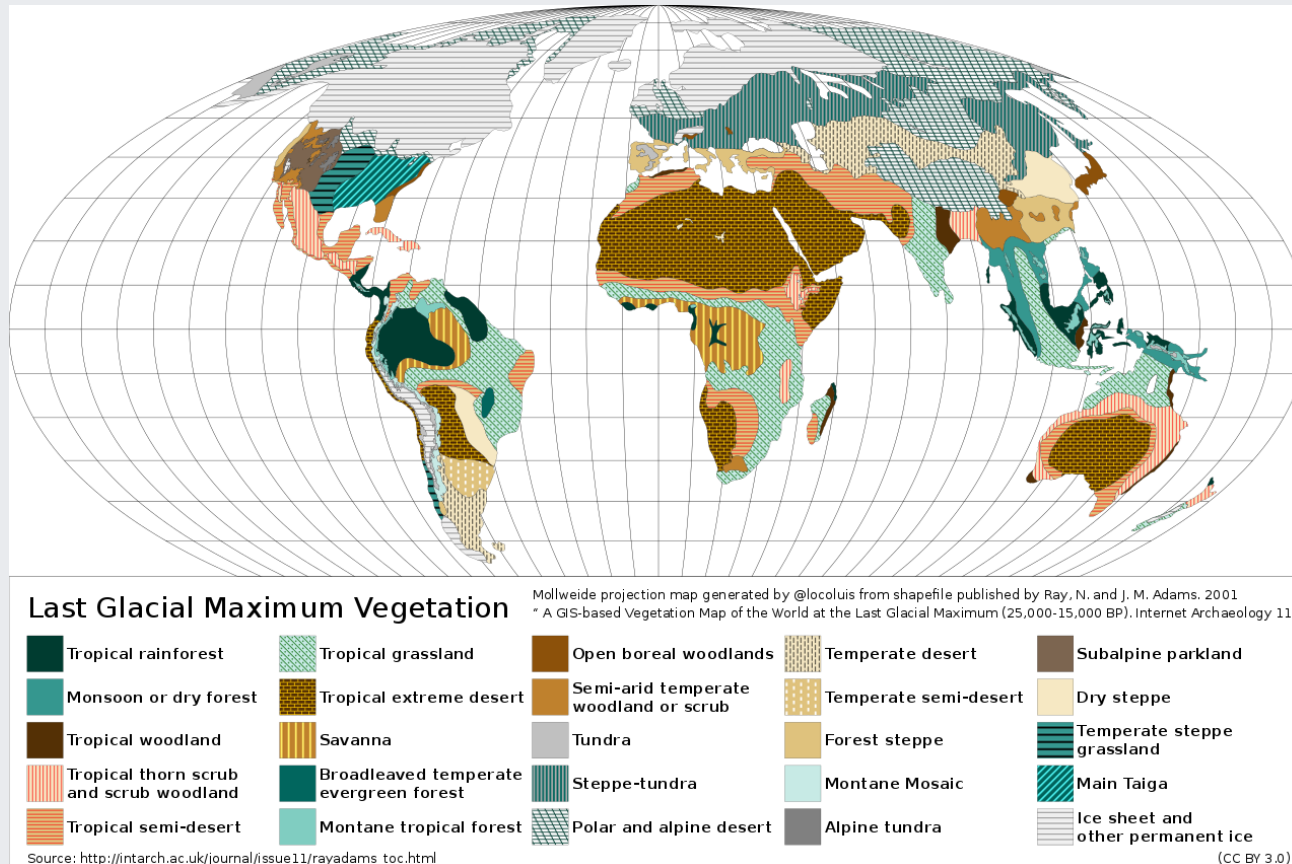
Environmental stability is key for maintaining high diversity.



Cowling et al. 2015

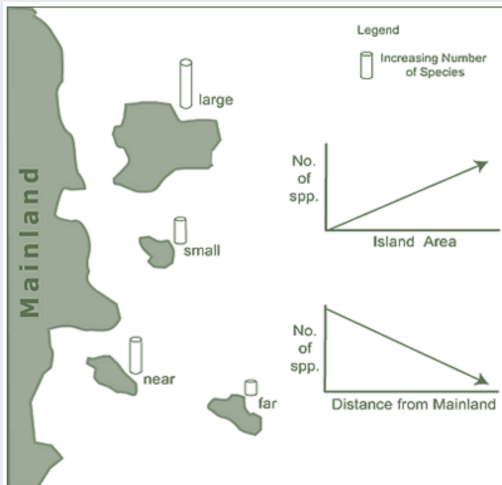
Extinction and stability

Much of the northern latitudes was buried in ice at the Last Glacial Maximum 15-25 k years ago!!!



Dispersal (and extinction)

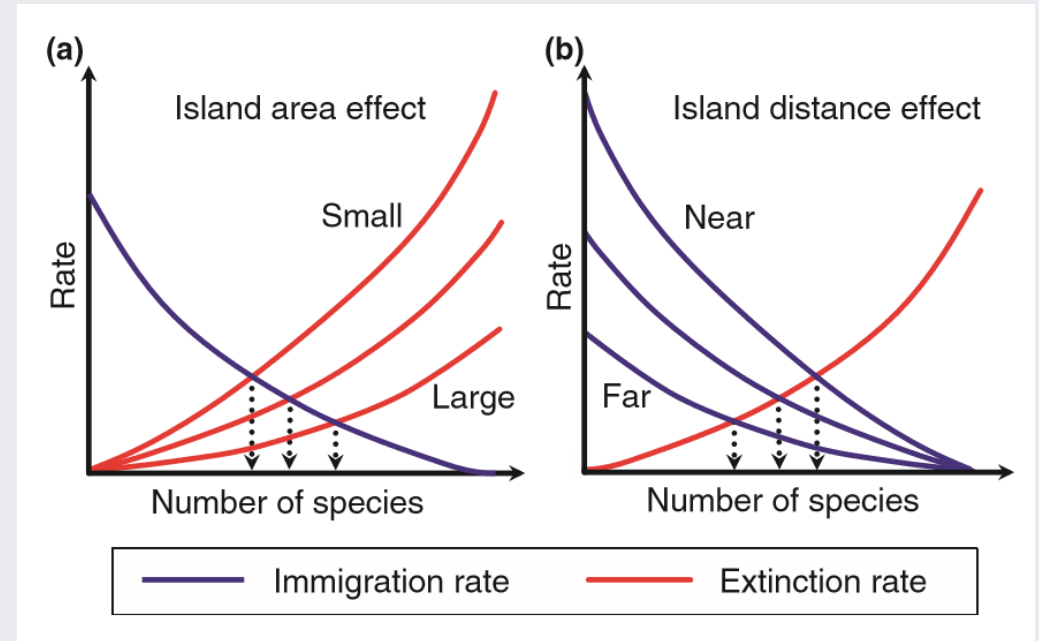
The Equilibrium Theory of Island Biogeography



Larger islands, closer to the mainland have more species.

- Larger = lower extinction (larger populations)
- Closer = higher immigration

MacArthur and Wilson 1967



An extension of IBT is to consider specific habitats as islands in a sea of unfavourable habitat (e.g. forest fragments in Fynbos).

Figure from Warren et al. 2015

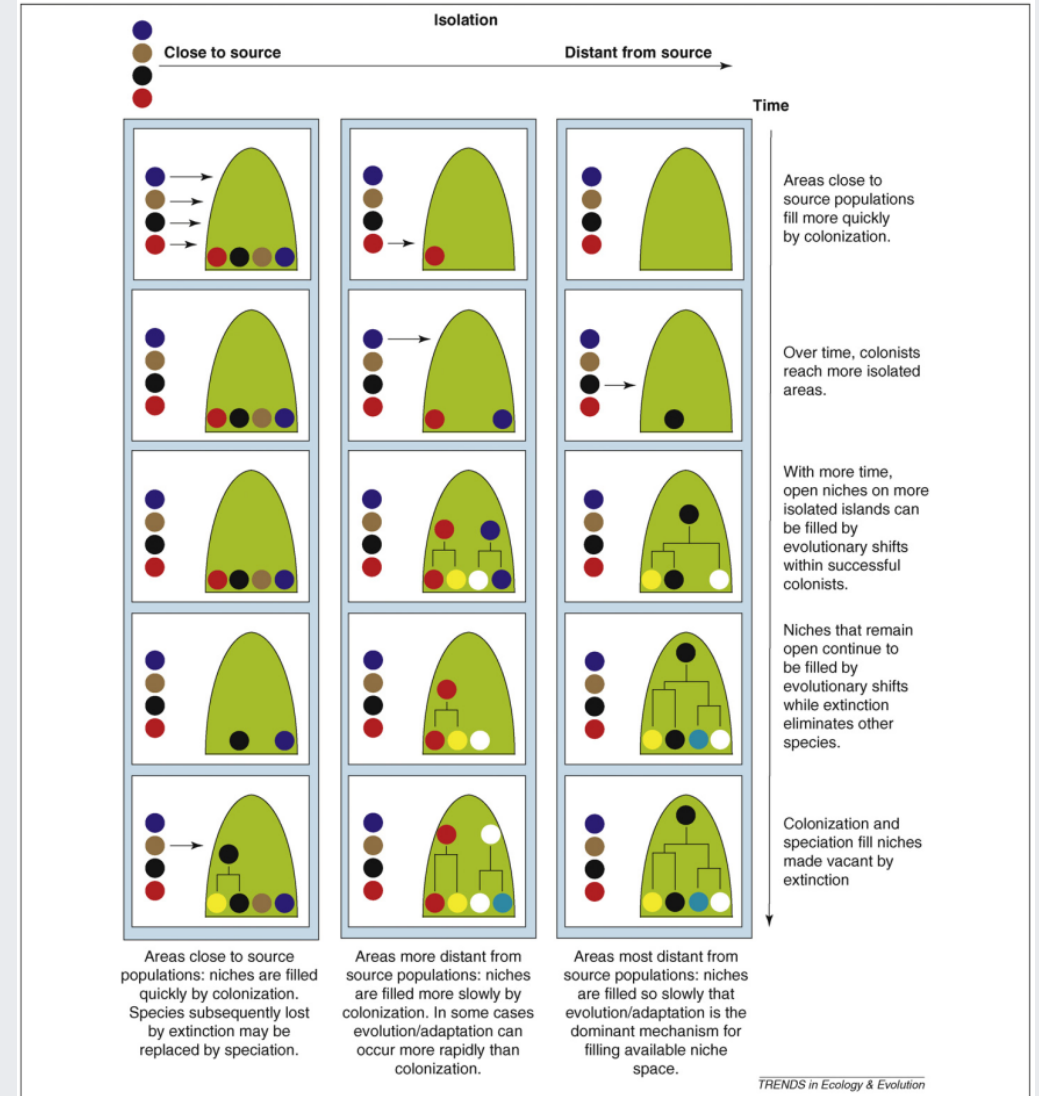
Dispersal and *speciation*

Island Biogeography Extended

Better connected islands/habitats are likely to be dominated by colonization, leaving little opportunity (niche space) for *in situ* speciation

Isolated islands/habitats where immigration is rare are likely to see local adaptation and *in situ* speciation over time, resulting in a community of close relatives

Emerson and Gillespie 2008



Environmental heterogeneity

A driver of diversity across scales?

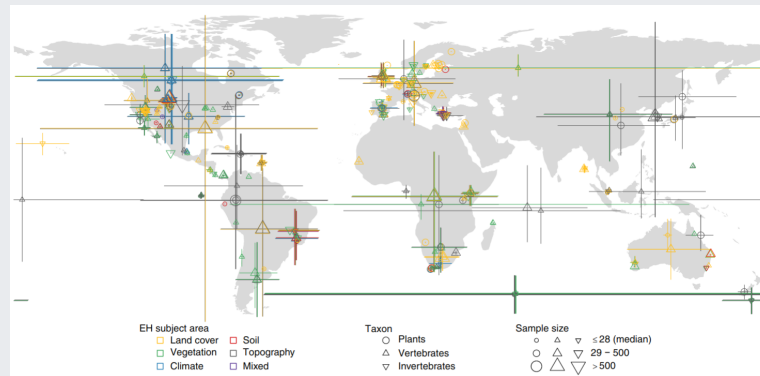
The Environmental Heterogeneity (EH) hypothesis (Ricklefs 1977 and others)

Ecological (~local):

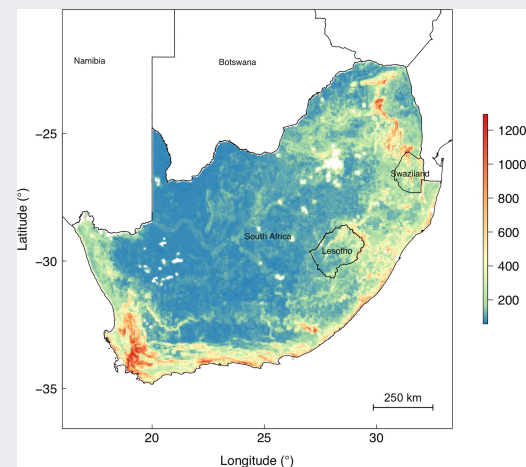
- Provides greater available niche space (and/or refuges), enhancing coexistence

Evolutionary (~regional):

- Provides more opportunities for isolation and divergent adaptation, promoting diversification (speciation) and persistence (less extinction)



A meta-analysis of different taxa across the globe found strong support for EH (Stein et al. 2014).



Cramer and Verboom 2017 found good support for EH explaining plant diversity across South Africa.

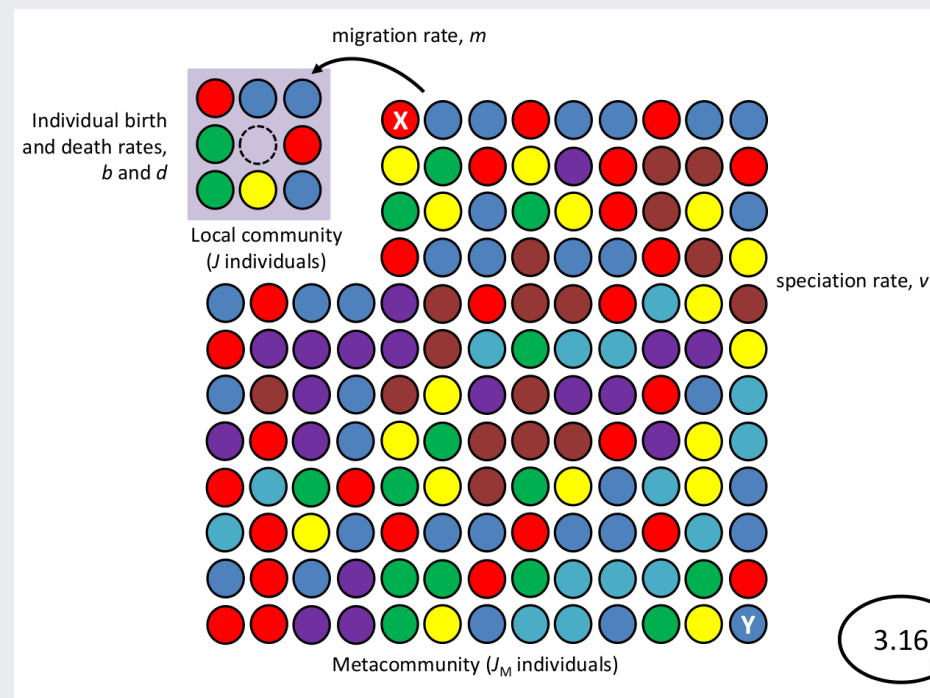
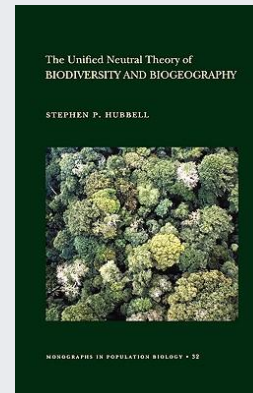
"Neutral" models

The Unified Neutral Theory of Biodiversity and Biogeography - Hubbell 2001

All individuals of all species are functionally equivalent and local processes (competition etc) are mostly irrelevant...

Local communities are determined by birth, death and migration, which depend only on species abundances...

Local patterns of functional and phylogenetic diversity are determined by the regional species pool (the "Metacommunity" in this case) and dispersal constraints...

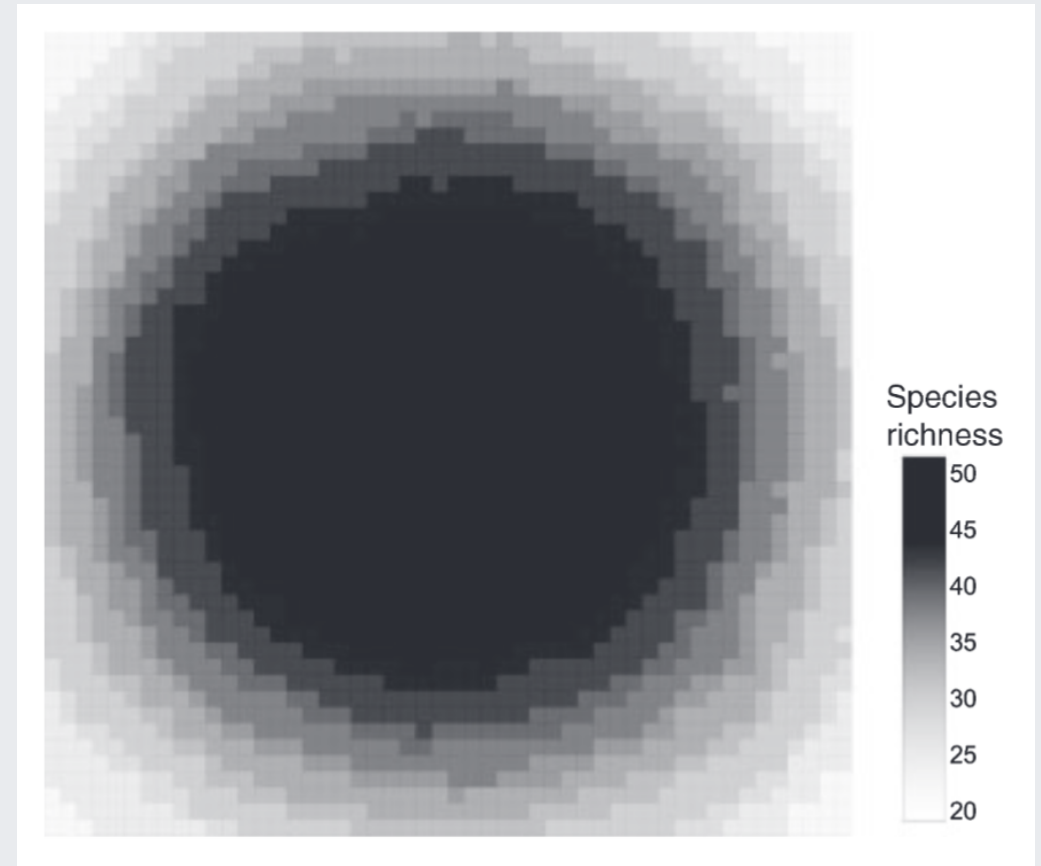


"Neutral" models

The Mid-Domain Effect (MDE), Colwell & Lees 2000

- aims to explain spatial patterns in species richness invoking only stochasticity and geometrical constraints
- predicts a hump-shaped pattern in species richness in the mid-domain, because that's where most species ranges will overlap (if all else is equal, i.e. no ecological effects)
- it's essentially a spatially bounded neutral model where communities are linked by short-distance migration

Neutral models generally predict that local diversity is determined by regional processes...



Rangel and Diniz-Filho 2005

To what extent is variation in diversity the result of local determinism (i.e. ecology) vs regional processes (i.e. evolution and biogeography)?

Local determinism makes 3 predictions (Ricklefs 2004)

1. diversity should be strongly correlated with physical aspects of the environment
 - see EH hypothesis
2. local diversity in comparable habitats should not vary between regions
 - see Stability slides, comparing MTEs
3. local diversity, above some saturation level, should be independent of regional diversity
 - Type I = local diversity \propto regional diversity
 - Type II = local diversity saturates

There is evidence for and against each, suggesting that the patterns we see are a mix of the two...

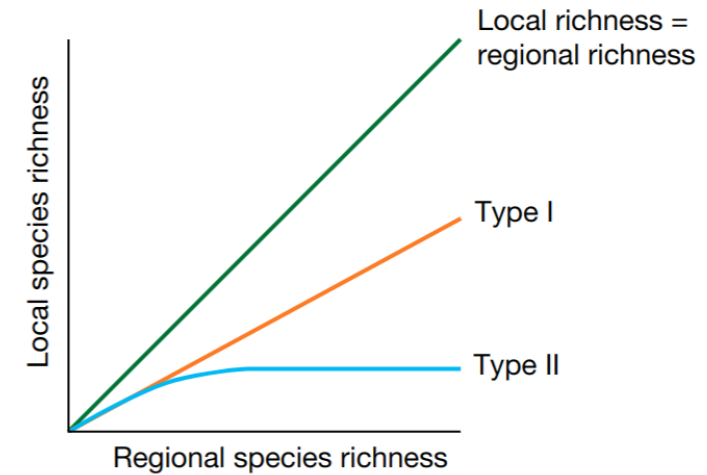


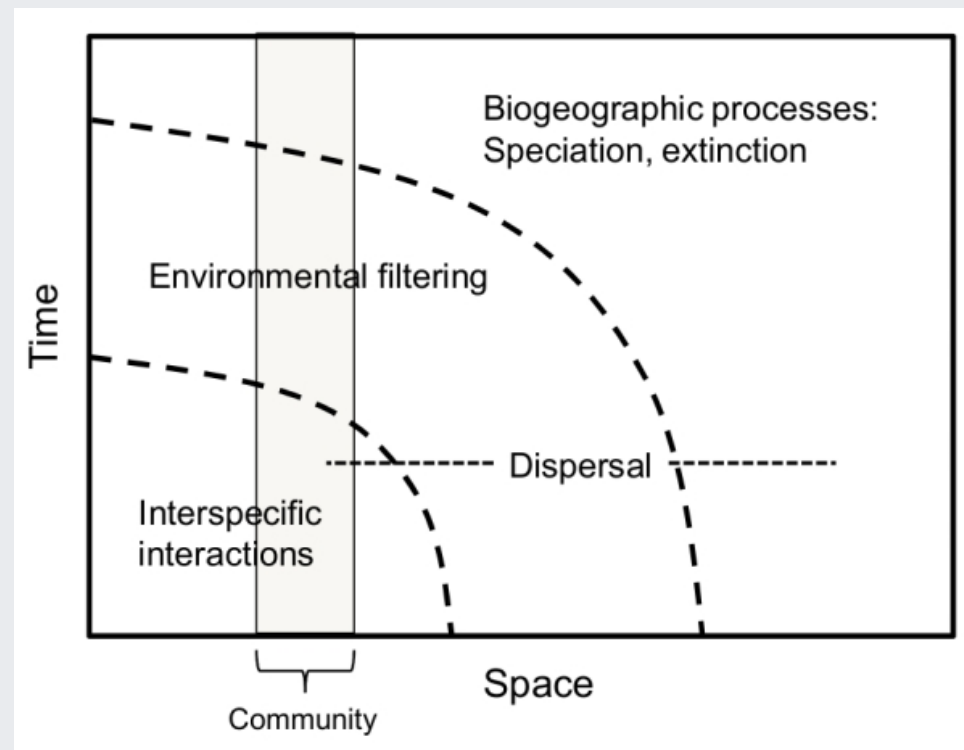
Figure 3 Relations between local and regional species richness, illustrating the form of type I and type II relationships and the limiting condition where local richness equals regional richness.

Gaston 2000

Community assembly processes

While processes vary with spatial or temporal scale, the distinction is somewhat arbitrary

- local patterns are affected by regional processes
- regional patterns are affected by local processes
- ecology and evolution are intricately intertwined



Take-home

Diversity patterns are influenced by a range of processes, which operate at various temporal and spatial scales.

Some are more local, operating in ecological time. Others are more regional, operating over evolutionary time.

There is a continuum, so it's not straightforward to distinguish the ecological from the evolutionary.

Ecology and evolution are intricately intertwined. It's not advisable to study either without cognisance of the other.

References

Gotelli, N. J. and R. K. Colwell (2001). "Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness". In: *Ecology letters* 4.4, pp. 379-391. ISSN: 1461-023X, 1461-0248. DOI: 10.1046/j.1461-0248.2001.00230.x.

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Whittaker, R. H. (1972). "Evolution and measurement of species diversity". En. In: *Taxon* 21.2-3, pp. 213-251. ISSN: 0040-0262, 1996-8175. DOI: 10.2307/1218190.

Thanks!

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