RITA CASTILHO

MARINE BIOGEOGRAPHY AND EVOLUTION

PHYLOGEOGRAPHY

History of Biogeography

outline

WHAT IS PHYLOGEOGRAPHY

MARKERS

MODELS

AVISE'S HYPOTHESIS and COROLLARIES

POPULATION GENETICS, PHYLOGEOGRAPHY

Questions

- How is genetic variation distributed in time and space?
- What factors account for the spatial and temporal distribution of genetic lineages?

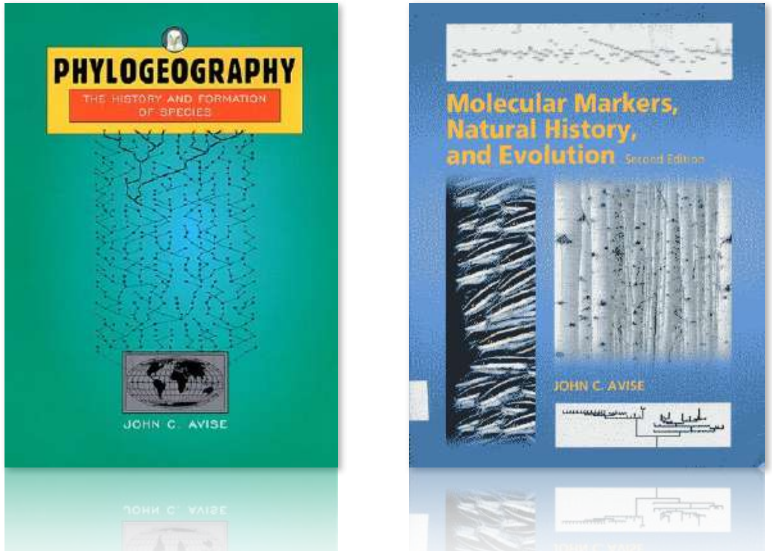
Phylogeography: introduction

What is phylogeography?

The are the benefits of phylogeography?understanding genetic structure

How do we do it?

historical and present-day genetic data



Phylogeography: introduction

What is phylogeography?

A field of study concerned with the principles and processes governing the ***geographic distribution of genealogical lineages***, especially those within and among closely related species.

Avise 2000

Understanding genetic structure

Phylogeography

provide a means of examining the *history of genetic exchange* among populations, with the potential to distinguish *biogeographic patterns of genetic variation* caused by *gene flow* from those caused by *common ancestry*.

Schaal 1998

Phylogeography: introduction

Population genetics

Within populations
Shallow timescale

Phylogeography: introduction

Population genetics

Within populations
Shallow timescale

Phylogenetics

Between species
Deep timescale

Phylogeography: introduction

Population genetics

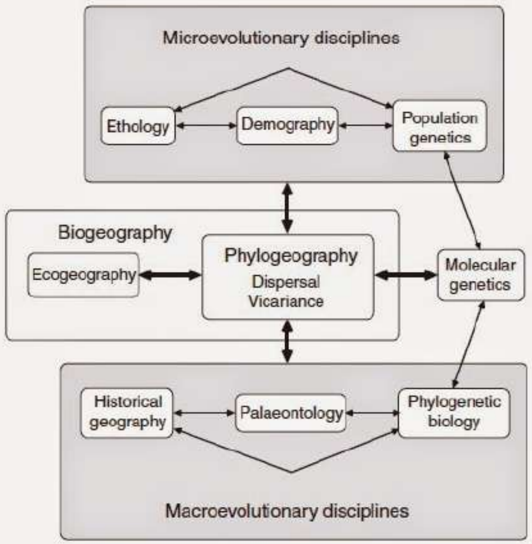
Within populations
Shallow timescale

Phylogenetics

Between species
Deep timescale

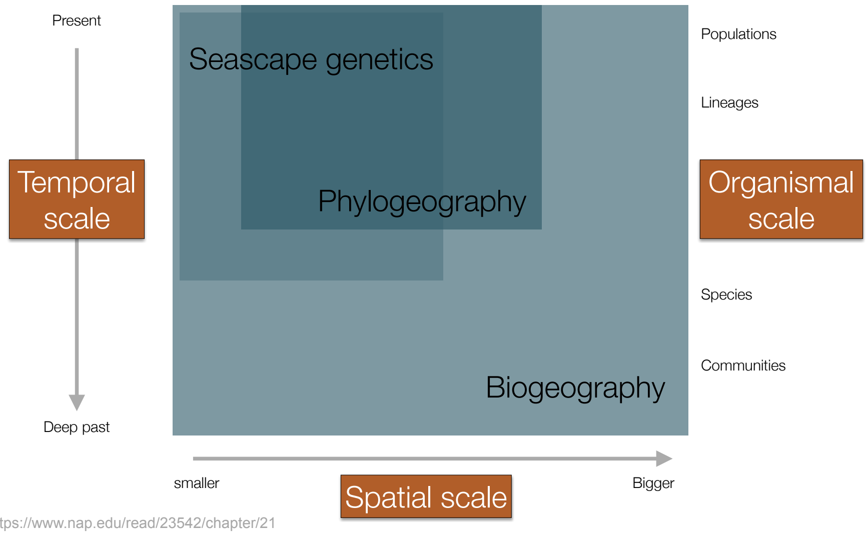
Phylogeography

Between populations and species
Medium timescale
Plus geography



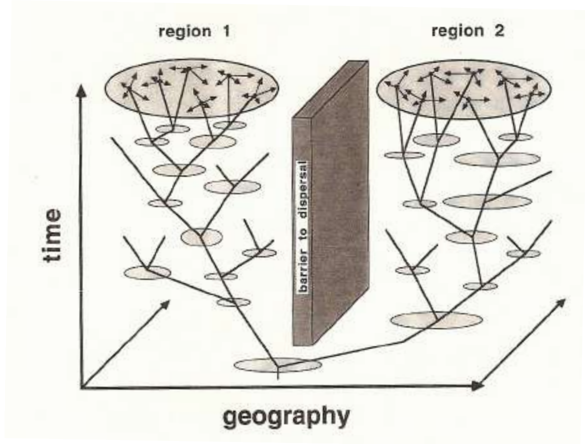
Avise 2000

Phylogeography



https://www.nap.edu/read/23542/chapter/21

Phylogeography: introduction



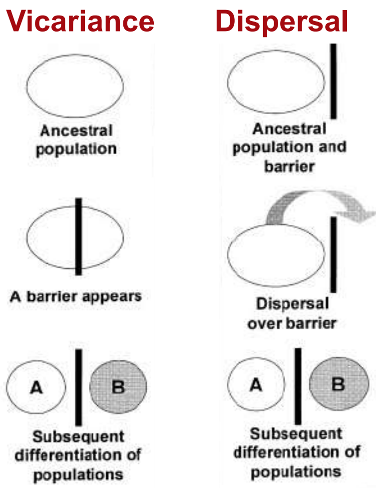
Gene genealogies of interest are mapped in space and time.

Avise 2000

Phylogeography: introduction

Goal: To understand the factors contributing to the formation of population (or species-level) genetic structure.

Can evaluate alternative historical scenarios that account for current spatial patterns.



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PHYLOGEOGRAPHY

Phylogeography: early years

Phylogeography was essentially *descriptive*:

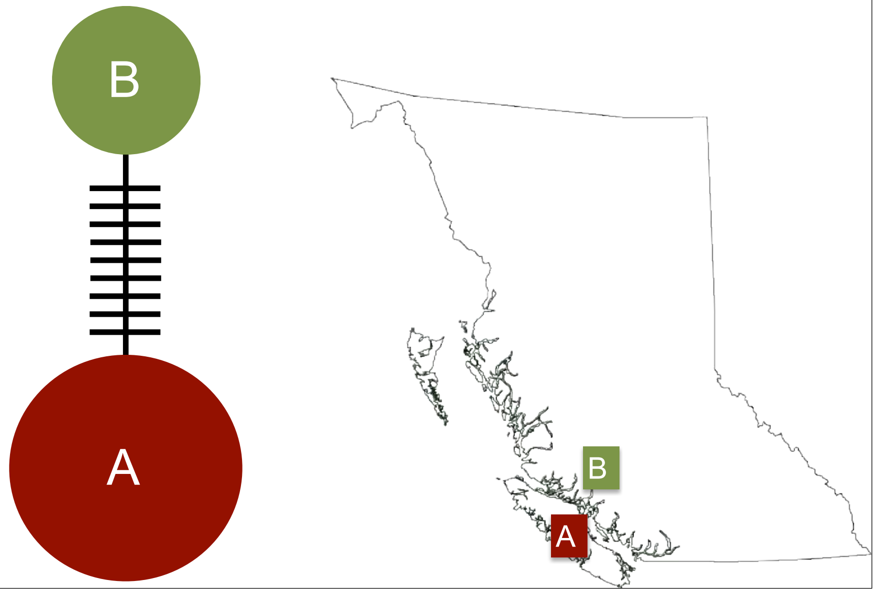
Plot haplotypes on map

Classify pattern of phylogeographic structure

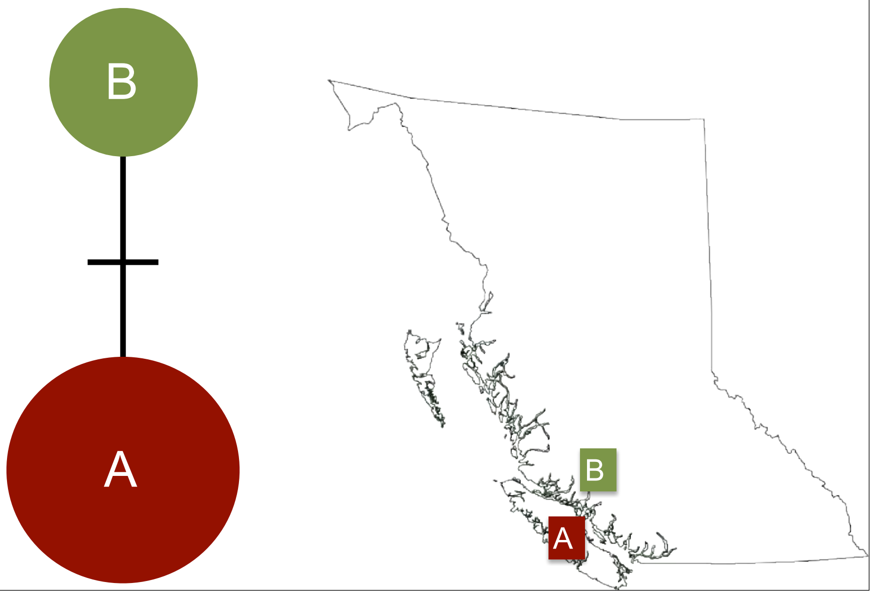
Consider historical explanations

Look for concordance among different species (comparative phylogeography)

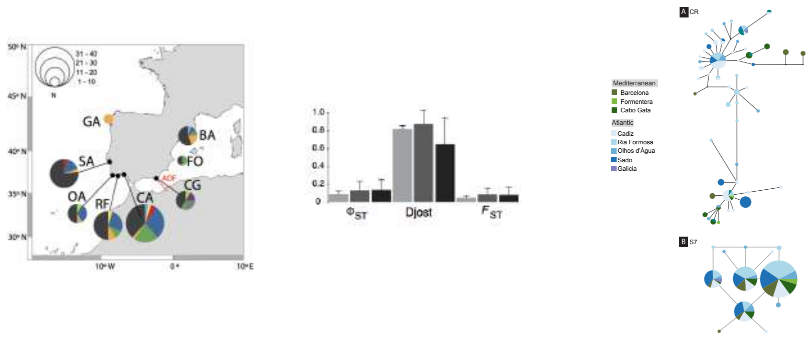
Deep divergence



Shallow divergence - gene flow



Phylogeography: early years

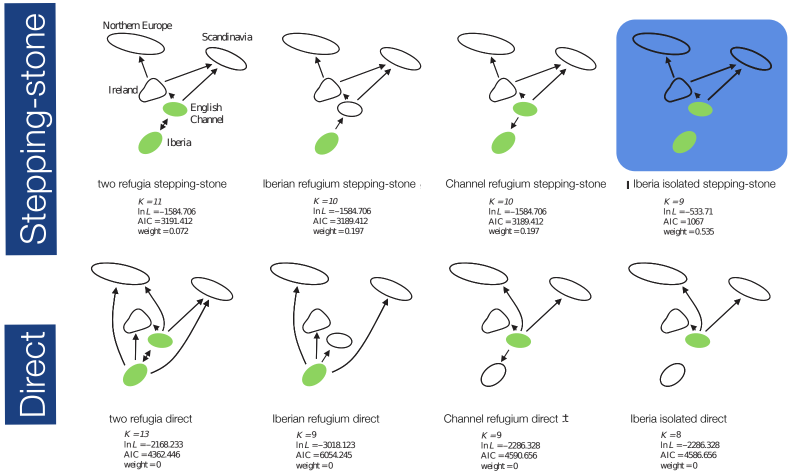


Region	Locations	Code	Mitochondrial D-loop: N	NH	NP	Haplotype diversity ± s.d.	Nucleotide diversity ± s.d	PS	First intron of S7 gene: N	NH	Gene diversity ± s.d.	Nucleotide diversity ± s.d	Observed Heterozygosity
	Barcelona	BA	16	9	3	0.92 ± 0.04	0.0520 ± 0.0274	38	15	5	0.65 ± 0.07	0.0017 ± 0. 0013	0.53
M	Formentera	FO	2	2	1				3	1			
	Cabo de Gata	CG	12	6	2	0.88 ± 0.06	0.0167 ± 0.0098	10	13	4	0.64 ± 0.07	0.0015 ± 0.0013	0.46
	Cadiz	CA	39	19	13	0.88 ± 0.04	0.0151 ± 0.0084	25	22	6	0.72 ± 0.05	0.0019 ± 0.0015	0.41
	Ria Formosa	RF	23	13	8	0.94 ± 0.03	0.0111 ± 0.0066	17	40	6	0.62 ± 0.04	0.0016 ± 0.0013	0.45
A	Olhos de Água	OA	12	7	6	0.91 ± 0.08	0.0170 ± 0.0100	18	12	5	0.78 ± 0.07	0.0023 ± 0.0017	0.42
	Sado	SA	26	7	4	0.72 ± 0.08	0.0145 ± 0.0083	12	30	4	0.73 ± 0.03	0.0019 ± 0.0014	0.40
	Galicia	GA	1	1	1				1	1			

Notes.
N, number of individuals per location; NH, haplotype richness; NP, number of private haplotypes; PS, number of polymorphic sites.

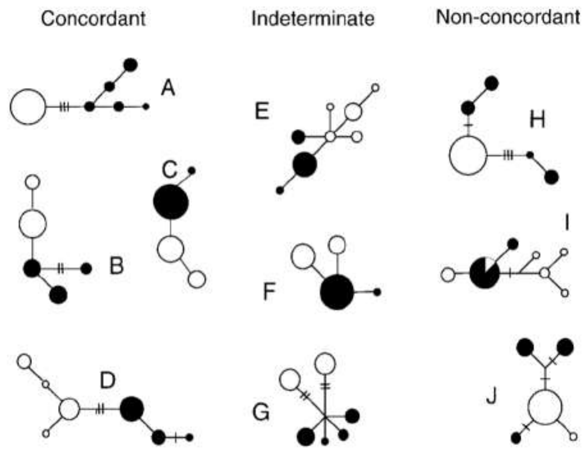
Phylogeography: recent years

Hypoteses testing



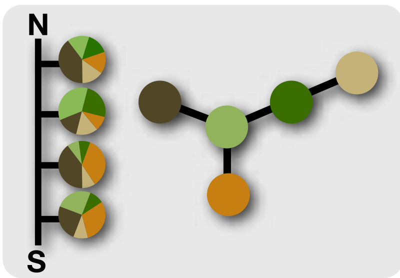
Provan & Maggs 2011. PRSL

Phylogeographic data



Maggs et al. (2008). *Ecology.*

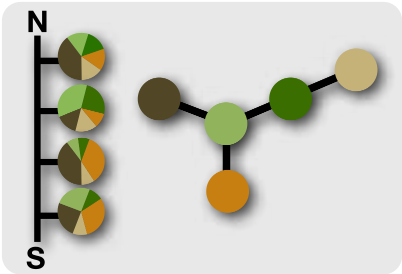
Phylogeographic data



Maggs et al. (2008). *Ecology.*

Phylogeographic data

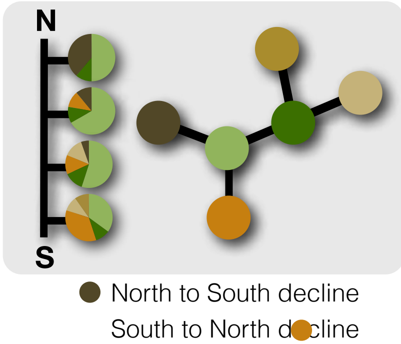
Null model = panmixia



Maggs et al. (2008). *Ecology*.

Phylogeographic data

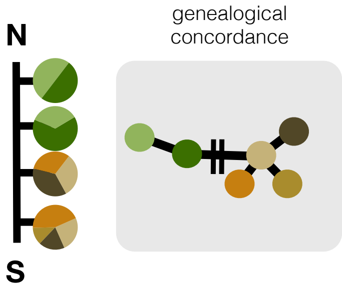
Latitudinal cline



Maggs et al. (2008). *Ecology*.

Phylogeographic data: expectations

no geographic contact



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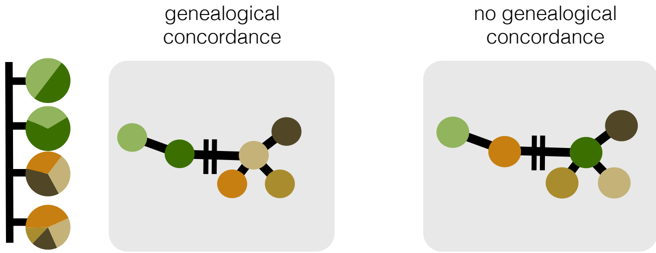
Phylogeographic data: expectations

no geographic contact



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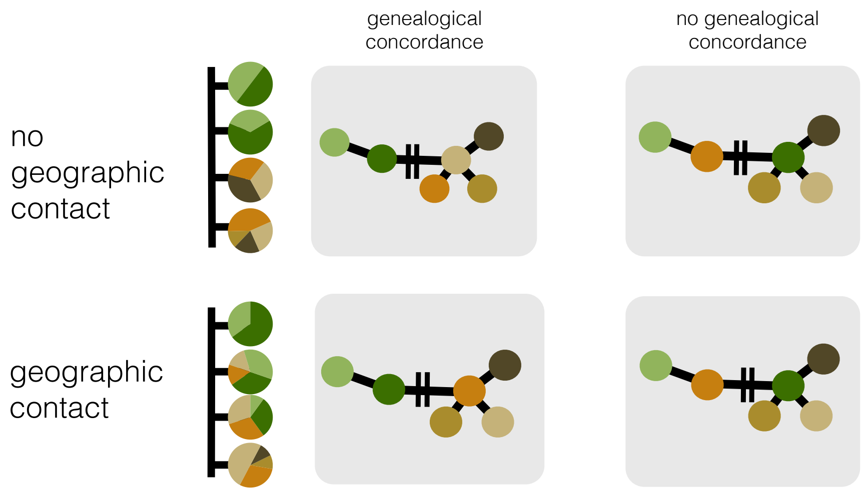
Phylogeographic data: expectations



Maggs et al. (2008). *Ecology.*

Avise phylogeography

Phylogeographic hypotheses and corollaries

(Corollary:
1.something that naturally follows;
2.proposition that follows with little or no proof required from one already proven;
3. A deduction or an inference;
4. A natural consequence or effect; a result)

Avise phylogeography

H1 Most species are composed of **geographic populations** whose members occupy recognisable matrilineal branches.
Populations of most species display **significant phylogeographic structure** supported by mtDNA data.

H2 Species with **limited or shallow phylogeographic population structure** have life histories conducive to **dispersal** and have occupied ranges free of firm, long-standing impediments to gene flow.
Non-subdivided, high-dispersal species have **limited or no phylogeographic structure**.

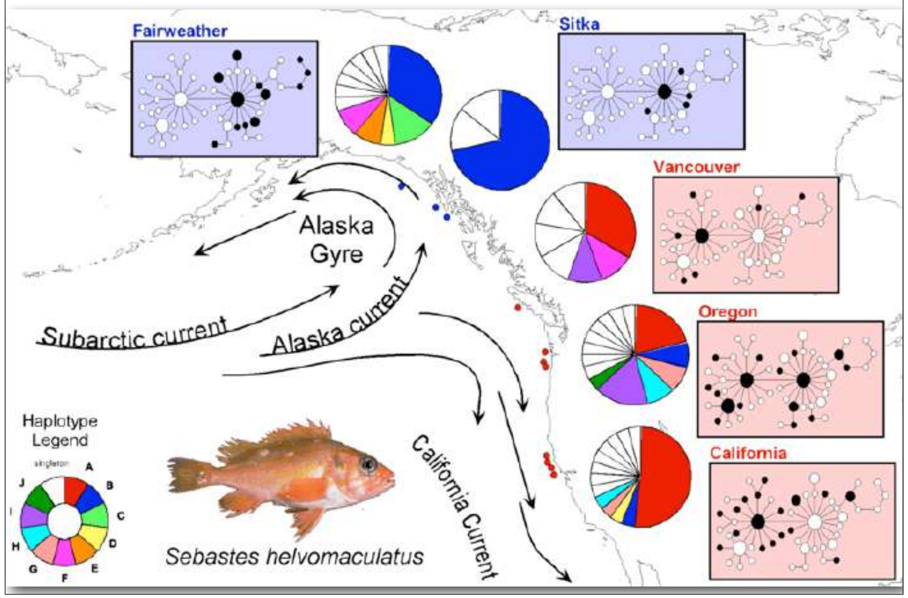
H3 **Major phylogeographic units within a species reflect** long-term historical barriers **to gene flow**

Hypothesis 1

Most species are composed of
geographic populations
whose members occupy recognisable matrilineal branches.

Populations of most species display
significant phylogeographic structure
supported by mtDNA data.

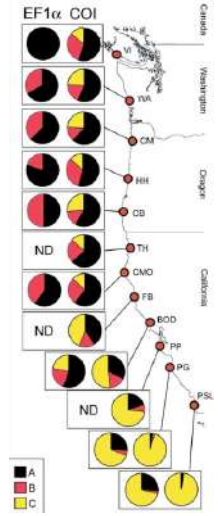
Hypothesis 1 - example 1



Hypothesis 1 - example 2

Sotka et al. 2004. ME

Balanus glandula frequencies of haplotypes of COI and EF1

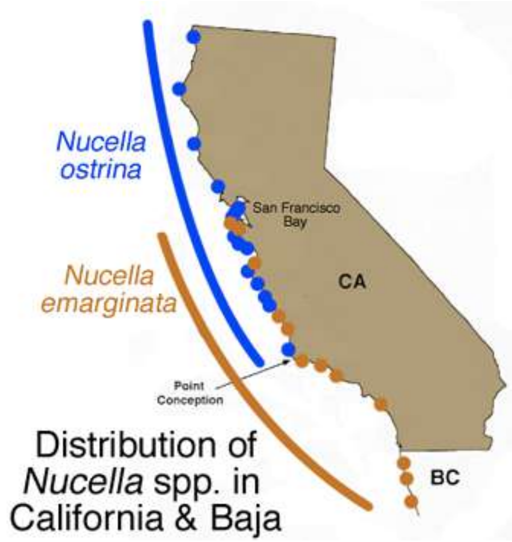


Hypothesis 2

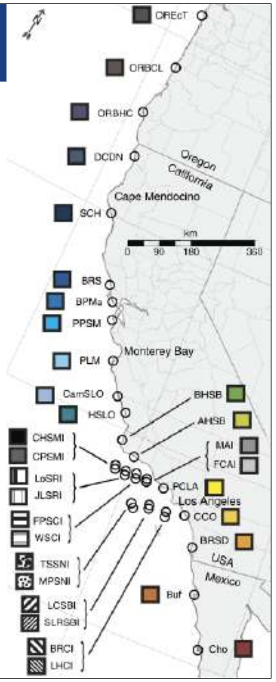
Species with
limited or shallow phylogeographic population structure
have life histories conducive to **dispersal** and have occupied ranges free of firm, long-standing impediments to gene flow.

Non-subdivided, high-dispersal species have **limited or no phylogeographic structure**.

Hypothesis 2

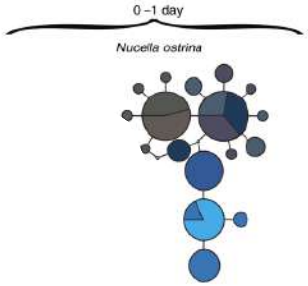


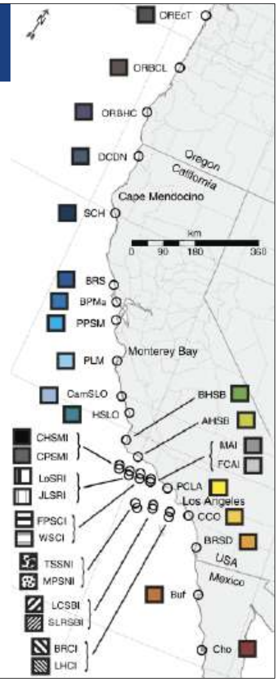
Hypothesis 2



Dawson et al. 2014. Ecological Monographs

Hypothesis 2





Dawson et al. 2014. Ecological Monographs

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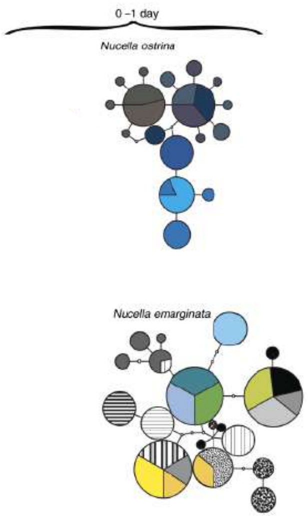

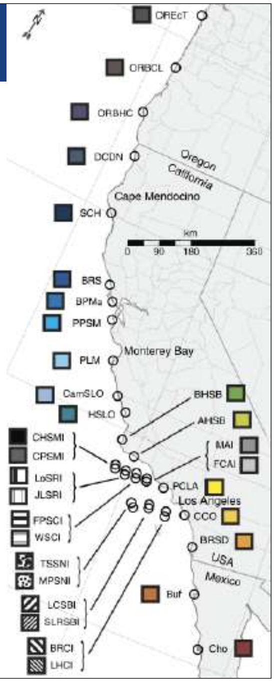

Dawson et al. 2014. Ecological Monographs

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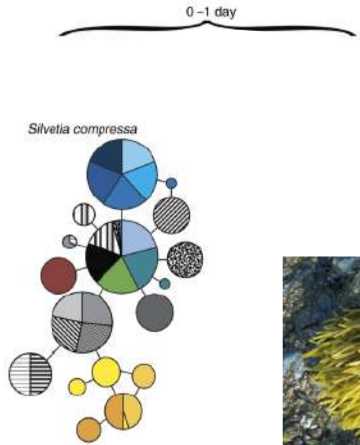

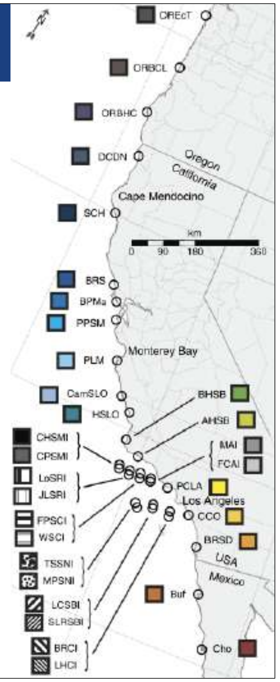

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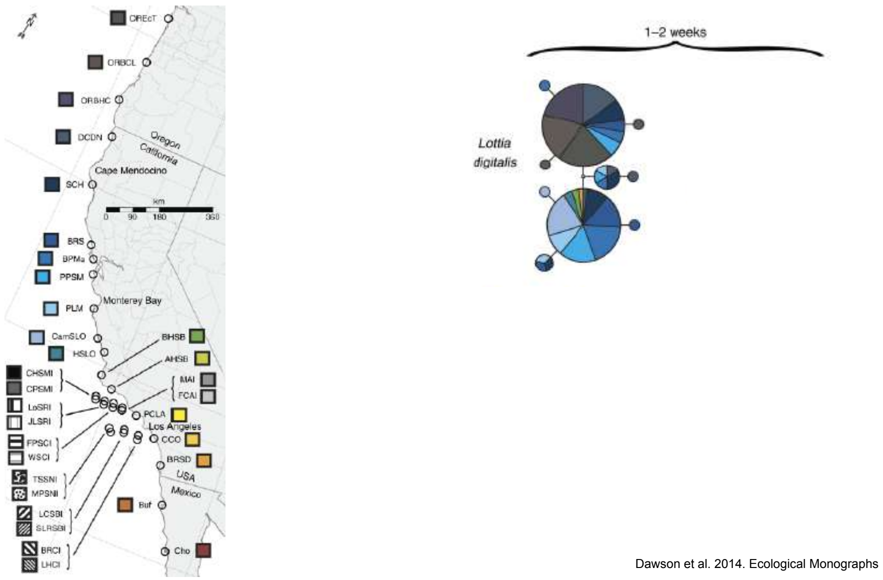

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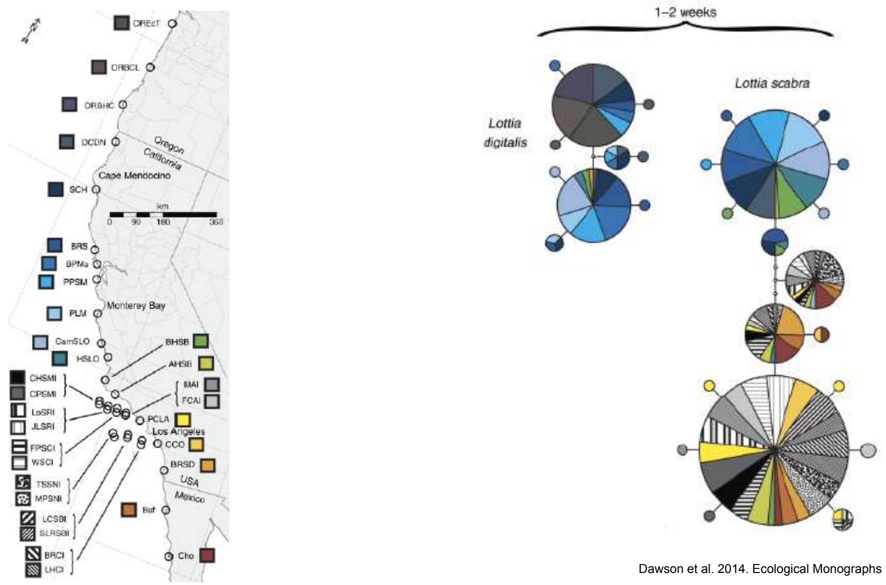

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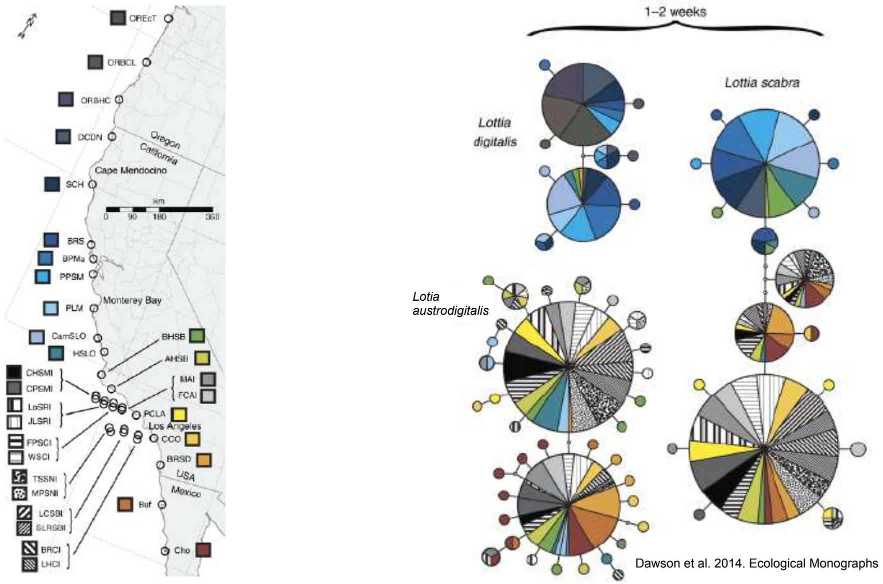


Dawson et al. 2014. Ecological Monographs

Hypothesis 3

Major phylogeographic units within a species reflect
long-term historical barriers
to gene flow

Hypothesis 1 - example 1

Marine Ecology. ISSN 0173-9565

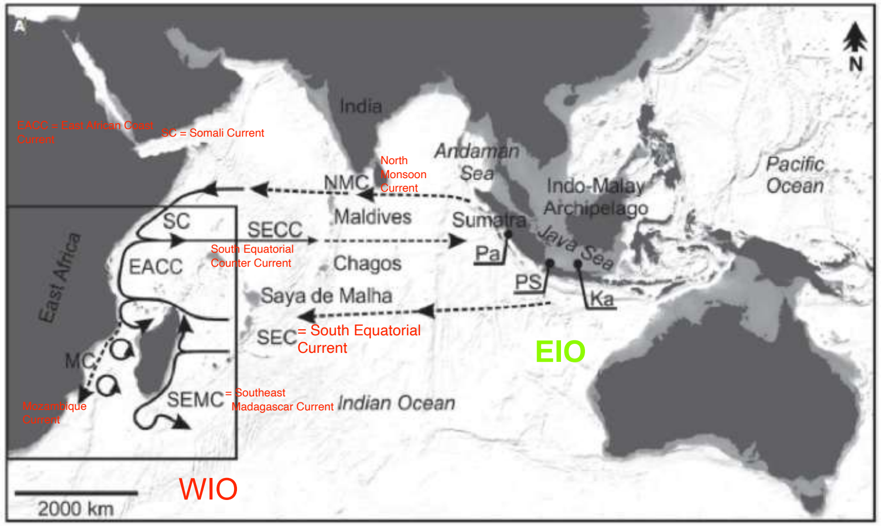
ORIGINAL ARTICLE

Highly restricted gene flow between disjunct populations of the skunk clownfish (*Amphiprion akallopisos*) in the Indian Ocean

Filip Huyghe & Marc Kochzius

Marine Biology, Vrije Universiteit Brussel (VUB), Brussels, Belgium

Hypothesis 1 - example 1



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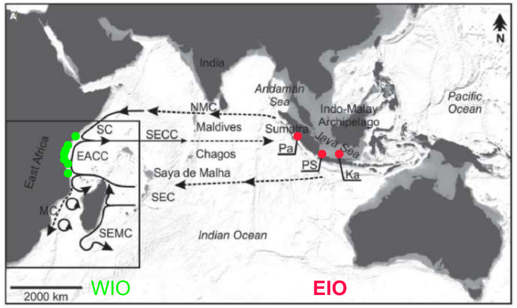

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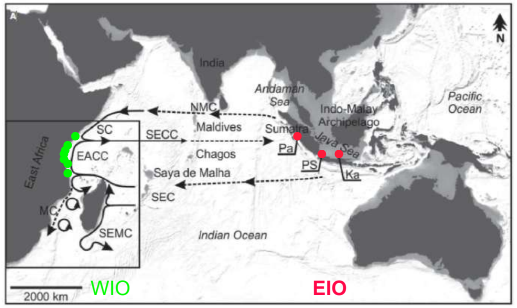

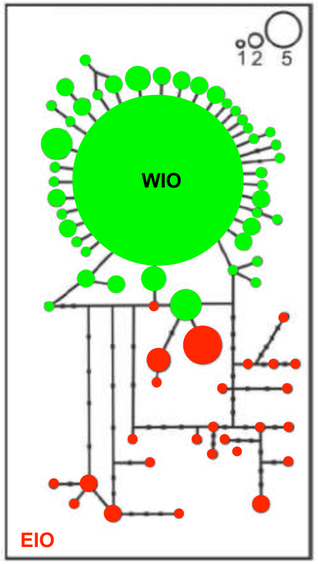

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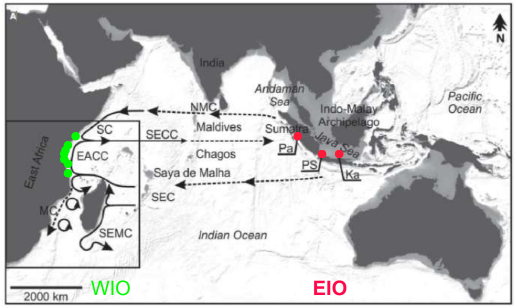
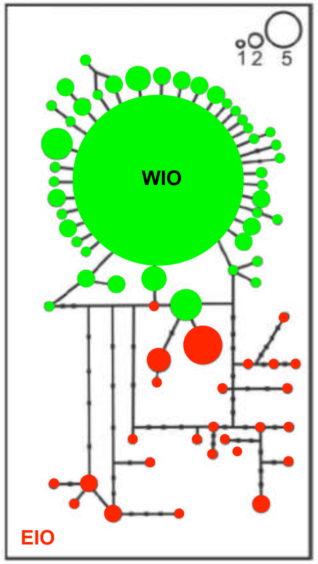
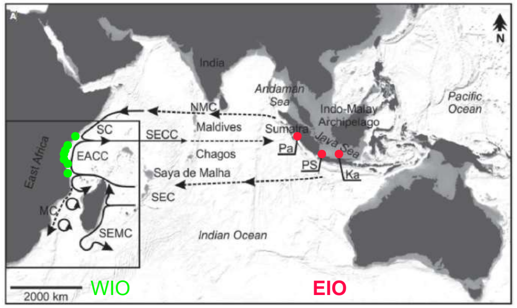
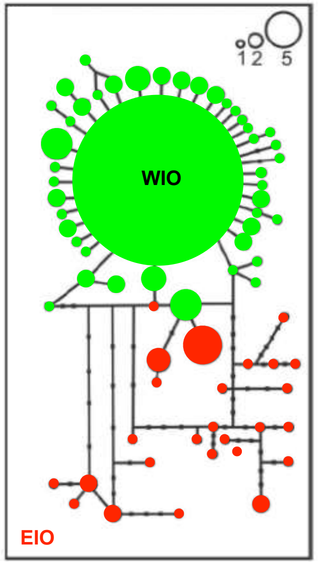




None of the identified 69 haplotypes was shared between the WIO and EIO.

Hypothesis 1 - example 1

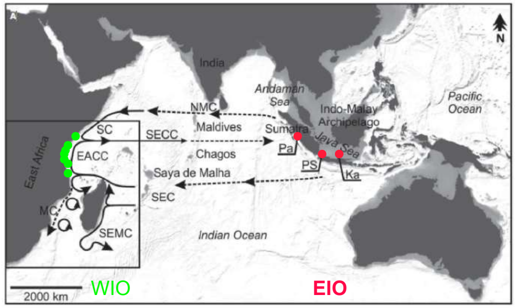


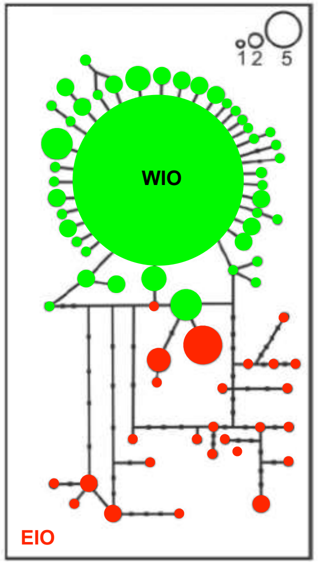


None of the identified 69 haplotypes was shared between the WIO and EIO.

Haplotype as well as nucleotide diversity was considerably higher in the EIO than in the WIO.

Hypothesis 1 - example 1





None of the identified 69 haplotypes was shared between the WIO and EIO.

Haplotype as well as nucleotide diversity was considerably higher in the EIO than in the WIO.

Support for EIO as the geographical origin of the species

Hypothesis 1 - example 1

Given
the **large distance** between the disjunct populations
the **short pelagic larval** duration, long-distance dispersal is rather unlikely.

Hypothesis 1 - example 1

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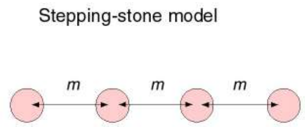
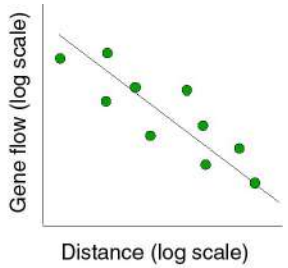
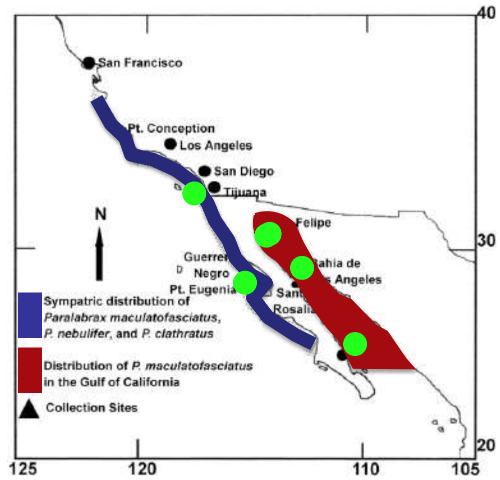


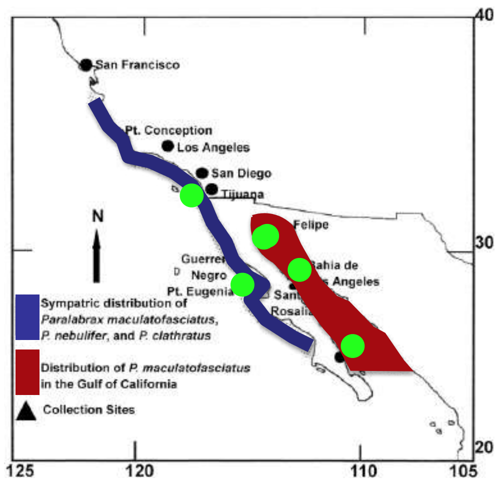


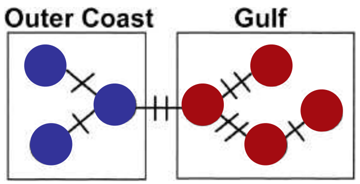
Alternatively a **stepping-stone model** involving islands in the Central Indian Ocean is a more likely scenario for colonization of the WIO.

Hypothesis 3



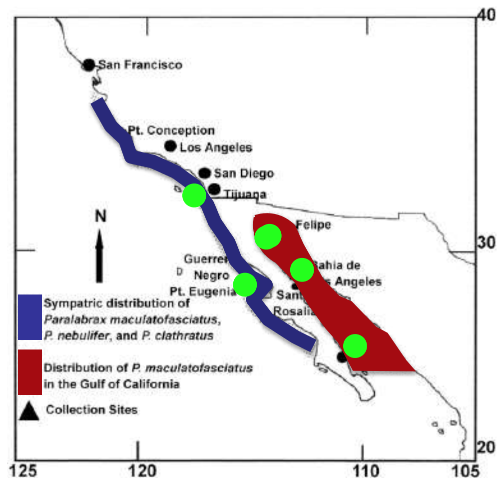
Hypothesis 3

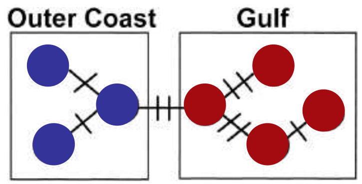




Hypothesis 3

Major phylogeographic units within a species reflect long-term historical barriers to gene flow.





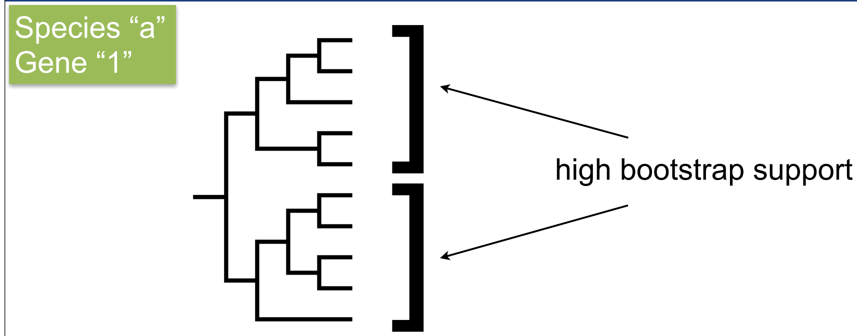
Hypothesis 3

This hypothesis includes **four corollaries** that represent different aspects of genealogical concordance.

Intraspecific monophyletic groups distinguished by large genealogical gaps usually arise from long-term extrinsic (biogeographic) barriers to gene flow.

Major phylogeographic units within a species reflect long-term historical barriers to gene flow.

Hypothesis 3: C1



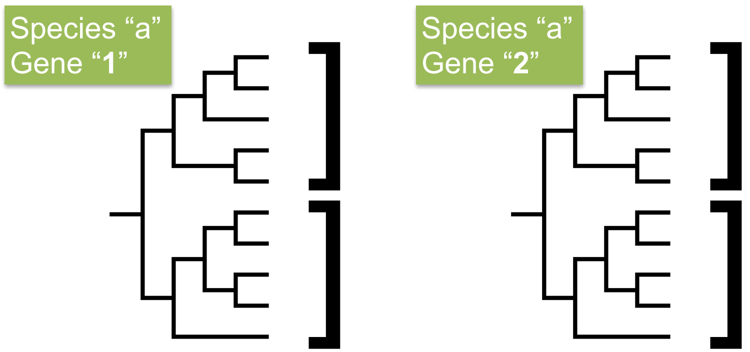
Concordance across sequence characters within a gene. (Agreement across characters within a gene)

A

Every deep phylogenetic split in the intraspecific gene tree is supported by multiple diagnostic characters within mtDNA. If this is not the case, such matrilineal separations would not be evident in data analysis (not supported by bootstrap).

Avise, J.C. (2000) Phylogeography: the history and formation of species. Harvard University Press, Cambridge, MA.

Hypothesis 3: C2

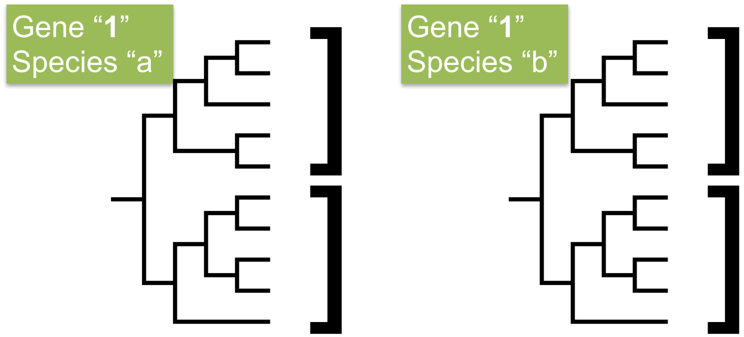


B

Concordance in significant genealogical partitions across *multiple genes* within a species. (Agreement across genes)
Empirical examples show general agreement between deep phylogeographic topologies in multiple gene trees within the species. These deep branch separations characterize the same sets of geographic populations.

Avise, J.C. (2000) Phylogeography: the history and formation of species. Harvard University Press, Cambridge, MA.

Hypothesis 3: C3

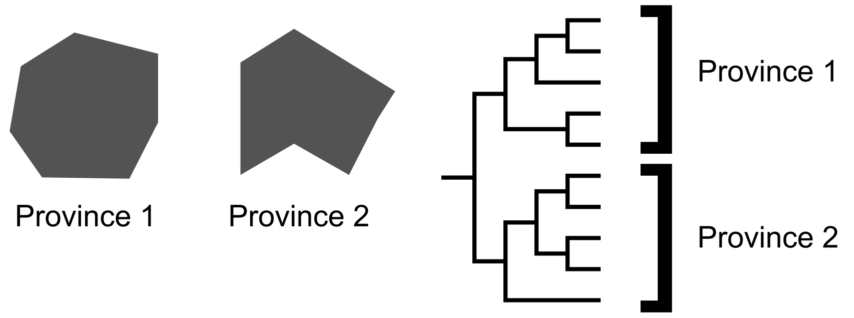


C

Concordance in the geography of gene-tree partitions across multiple co-distributed species. (Agreement across co-distributed species)
Several co-distributed species with comparable natural histories or habitat requirements proved to be phylogeographicaly structured in similar fashion. In particular, divergent branches in the intraspecific gene trees might map consistently to the same geographic regions.

Avise, J.C. (2000) Phylogeography: the history and formation of species. Harvard University Press, Cambridge, MA.

Hypothesis 3: C4



D

Concordance of gene-tree partitions with spatial boundaries between traditionally recognized biogeographic provinces. (Agreement with other biogeographic data)

An emerging generality from molecular phylogeography studies is that deeply separated phylogroups at the intraspecific level often are confined to biogeographic provinces or subprovinces as identified from traditional faunal lists.

Avise, J.C. (2000) Phylogeography: the history and formation of species. Harvard University Press, Cambridge, MA.

RITA CASTILHO

MARINE BIOGEOGRAPHY AND EVOLUTION

ISLAND BIOGEOGRAPHY

outline

- Basic concepts and history
- Equilibrium Theory of Island Biogeography
- Violations to the assumptions
- Research
- Additional patterns of insular biota

Island Biogeography

Islands are important natural laboratories for the study of biogeography, ecology, population genetics and evolutionary biology

Island Biogeography

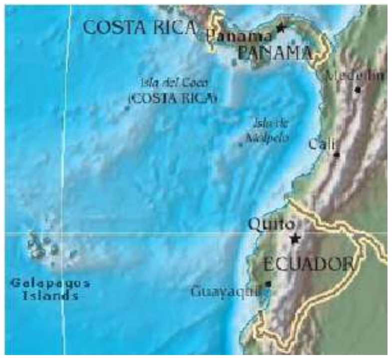
Why?

Defined boundaries

Island Biogeography

Why?

Isolated



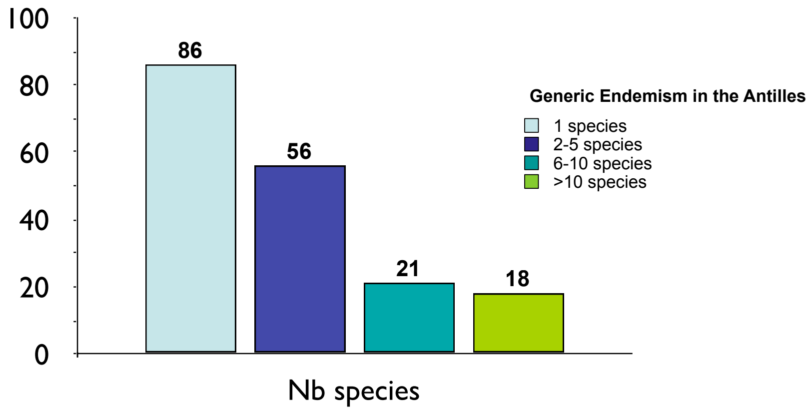
Island Biogeography

Islands as laboratories for the study of **evolution and co-evolution (HIGH ENDEMISM).**

More than 20 (!!) percent of Hawaiian reef fishes are found nowhere else in the world.

Island Biogeography

Islands as laboratories for the study of **evolution and co-evolution (HIGH ENDEMISM).**



Island Biogeography

Historical Background

*"There are only **two** possible hypotheses to account for the stocking of an oceanic island with plants from a continent:*

– Dispersal or vicariance?
– Historical, evolutionary, static theory of islands

Island Biogeography

Historical Background

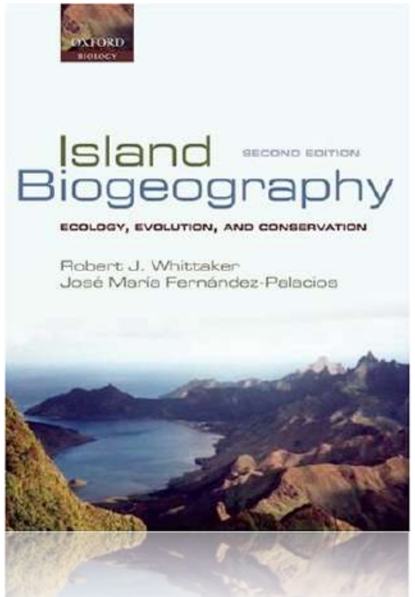
- Past several centuries - uniqueness of islands
- Pre mid-1900s
  – Dispersal or vicariance?
  – Static theory of islands
- 1967 - MacArthur and Wilson's ETIB
  – Radical shift in thought
  – Dynamic, process-based theory based

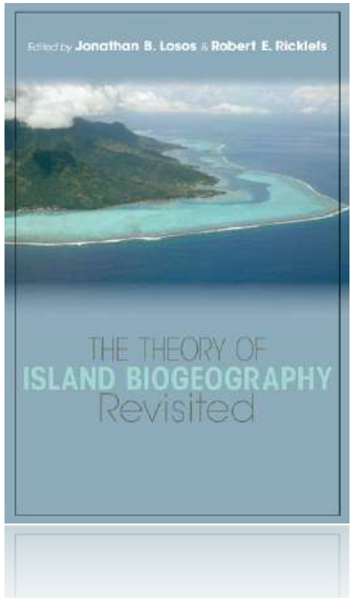
Equilibrium Theory of Island Biogeography

Equilibrium theory of island biogeography
(MacArthur and Wilson, 1967)

MacArthur RH and Wilson EO. The theory of island biogeography. Princeton University Press, 1967.

Island Biogeography





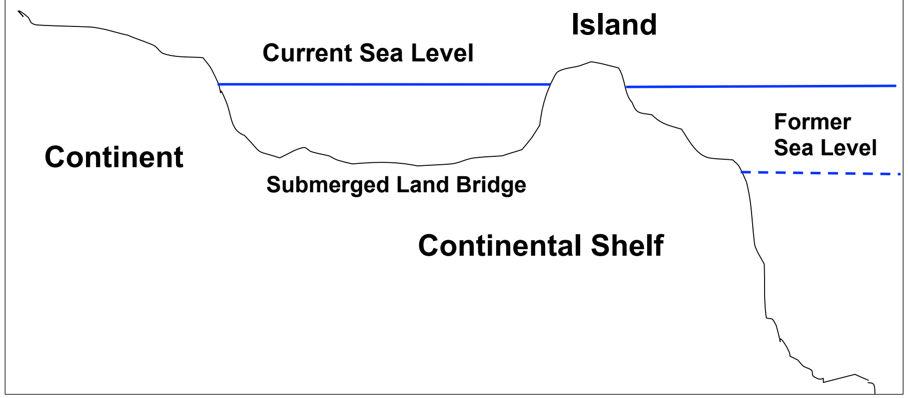
Island Types

Types of islands

Island Types

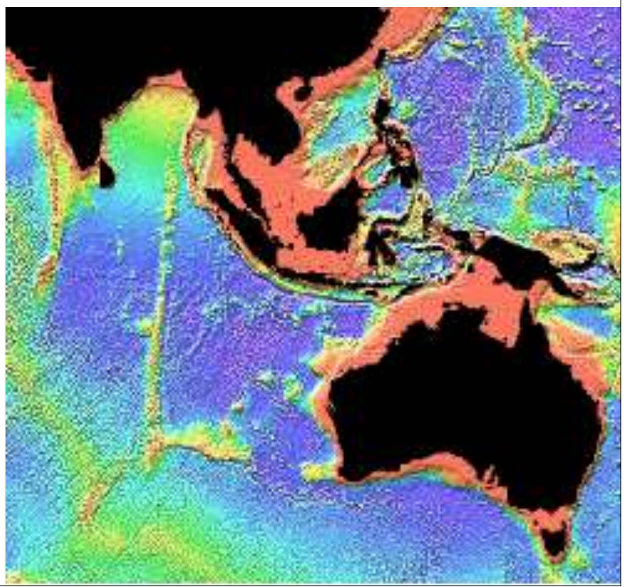
Continental Islands

Formed on continent; may have formerly been connected to mainland by **land bridge**.



Island Types

Areas in orange: land exposed during the LGM



Equilibrium Theory of Island Biogeography

Why does this matter?

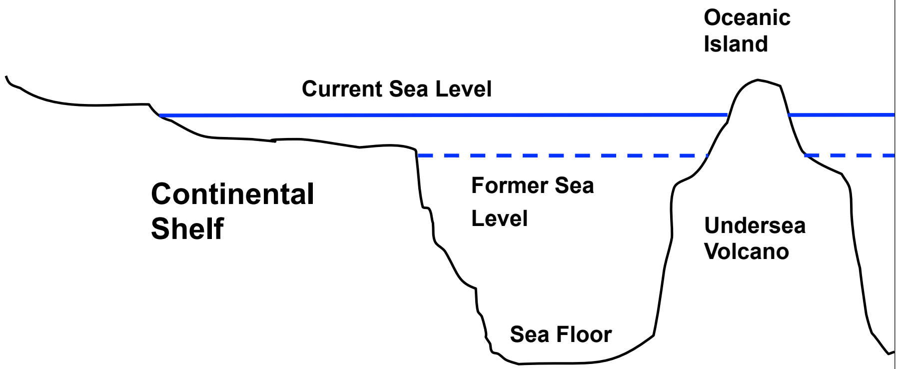
Continental islands are formed as part of a continent, subsequently separated from mainland, so main processes will be:

1. Vicariance (inherit their initial biota from the mainland)
2. Speciation
3. Extinction
4. Dispersal

Island Types

Oceanic Islands

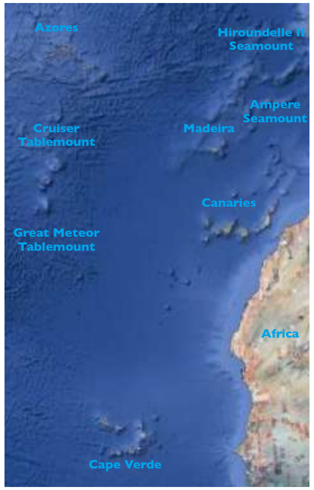
Never connected to continent; usually formed by volcanic activity and isolated from continent by deep ocean.



Island Types

Examples of Oceanic Islands

- Iceland
- Japan
- Aleutians
- Bermuda
- Caribbean Islands
- Hawaiian Islands
- South Pacific Atolls
- **Azores**
- **Madeira**
- Canaries



Island Types

San Salvador's offshore cays: Rising sea level caused erosion of San Salvador, leaving many small, erosion-resistant islands, or cays ("keys").

Island Types

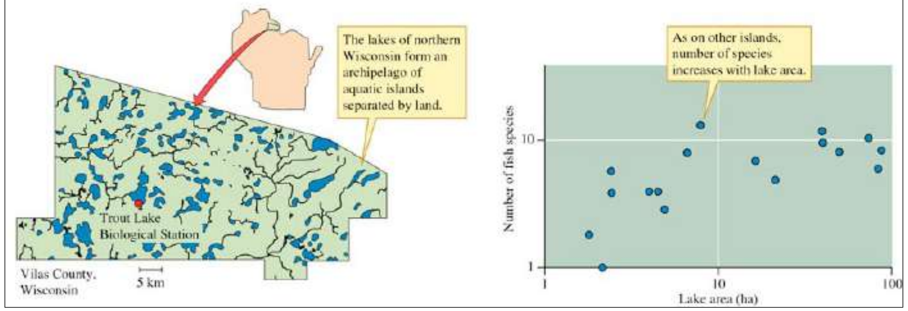
Terrestrial habitat islands: Isolated region on larger land mass, such as:

- mountain top;
- forest remnant surrounded cleared land;
- forest remnant on island in river or lake;
- water-filled tree hole in forest

Island Types

Lakes as Islands

Lakes can be considered as habitat islands.
Differ widely by degree of isolation.
The number of species increases with the area of an insular environment.
Positive relationship between area and fish species richness.



Equilibrium Theory of Island Biogeography

Why does this matter?

Oceanic islands are volcanic islands, recent origin, never connected to any continent, so main processes will be:

1. Dispersal
2. Speciation
3. Extinction

Initially no species present; entire biota acquired either through dispersal or speciation

Equilibrium Theory of Island Biogeography

Purpose of model:

- Develop unifying theory to predict species diversity for all "island" systems

MacArthur RH and Wilson EO. The theory of island biogeography. Princeton University Press, 1967.

Equilibrium Theory of Island Biogeography

Purpose of model:

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Equilibrium Theory of Island Biogeography

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- Predict species diversity (not abundance)
- Include only the most important factors explaining species diversity on islands

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Equilibrium Theory of Island Biogeography

Purpose of model:

- Develop unifying theory to predict species diversity for all “island” systems
- Predict species diversity (not abundance)
- Include only the most important factors explaining species diversity on islands
- Assume all other factors have small influence
- Replace previous research unable to predict patterns

MacArthur RH and Wilson EO. The theory of island biogeography. Princeton University Press, 1967.

Equilibrium Theory of Island Biogeography

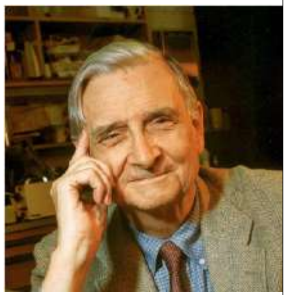
Central concepts:

- **Dynamic Equilibrium**: opposing forces (immigration and extinction) maintain some constancy or equilibrium of species number despite species turnover

- **Informed by basic characteristics of insular biota:**
  - **Species area-relationship**
  - **Species isolation-relationship**
  - **Species turnover**

Equilibrium Theory of Island Biogeography

MacArthur



Wilson

Species richness on an island represents a dynamic equilibrium controlled by the rate of immigration of new species and the rate of extinction of previously established species.

Equilibrium Theory of Island Biogeography

Model Assumptions

1. **Diversity is driven by two factors**
   - Distance from mainland
   - Island size
2. **Species are equal**
   - Dispersal abilities
   - Survival abilities
3. **Evolutionary history is not important**
4. **Characteristics of island habitats do not matter**

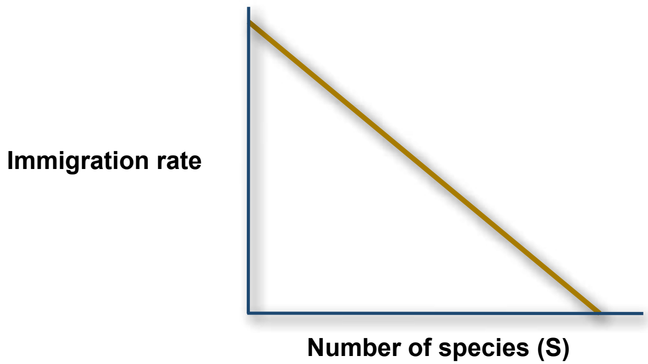
MacArthur RH and Wilson EO. The theory of island biogeography. Princeton University Press, 1967.

Equilibrium Theory of Island Biogeography

WHAT IS THE ETIB?

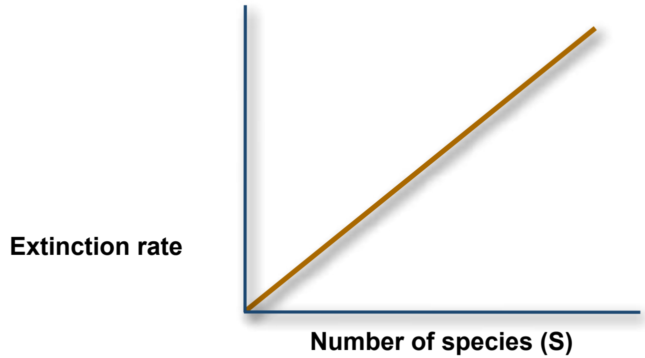
Equilibrium Theory of Island Biogeography

Equilibrium Theory of Island Biogeography

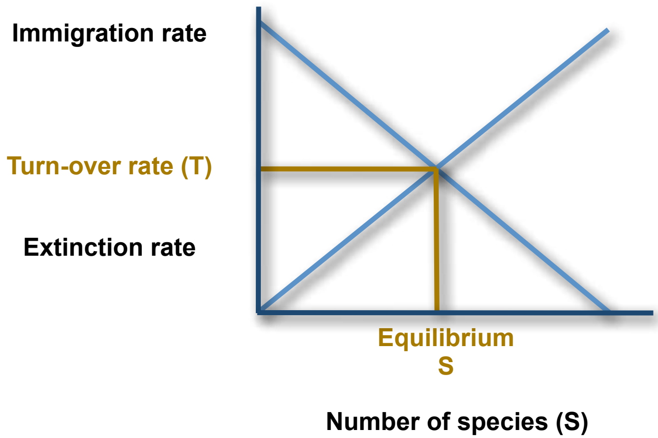


How is the immigration rate measured?
Why does the immigration rate decline as a function of S?

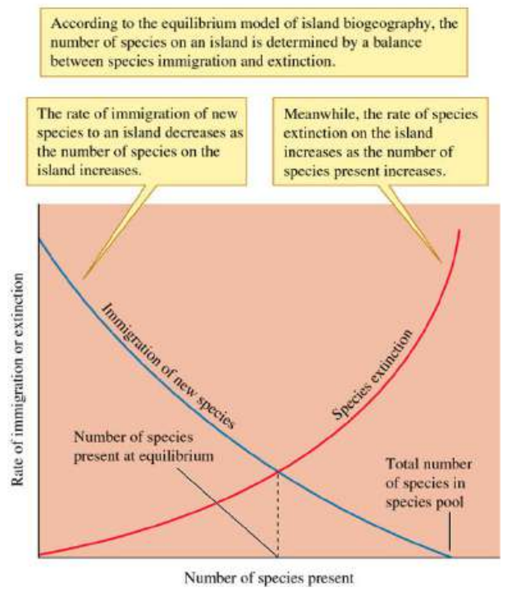
Equilibrium Theory of Island Biogeography



Equilibrium Theory of Island Biogeography



Equilibrium Theory of Island Biogeography



Island Patterns: species-area relations

Model Assumptions

1. **Diversity is driven by two factors**
   - Island size

MacArthur RH and Wilson EO. The theory of island biogeography. Princeton University Press, 1967.

Island Patterns: species-area relations

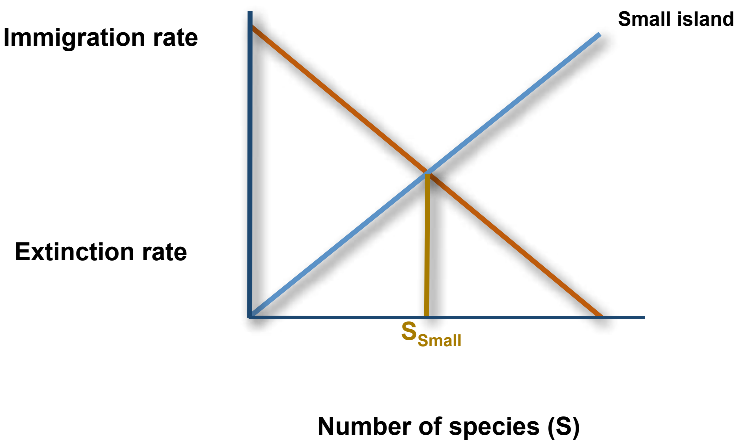
Hawaii

A somewhat smaller island

Much of the variation is explained solely by the size of the island…

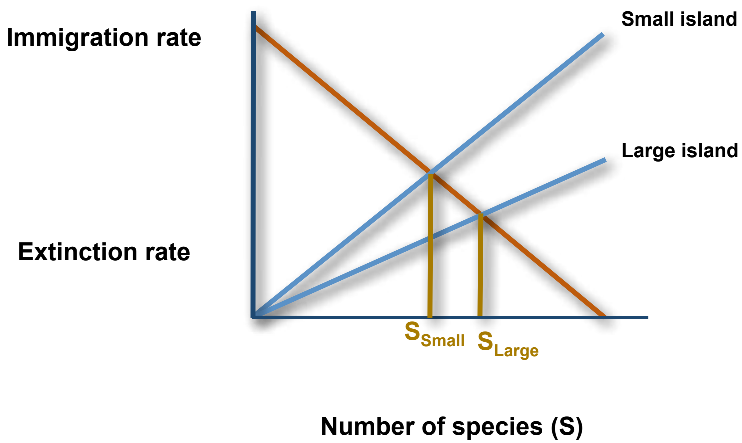
Island Patterns: species-area relations

For the same distance to continent, how does the probability of extinction for each species vary with island size?



Island Patterns: species-area relations

For the same distance to continent, how does the probability of extinction for each species vary with island size?



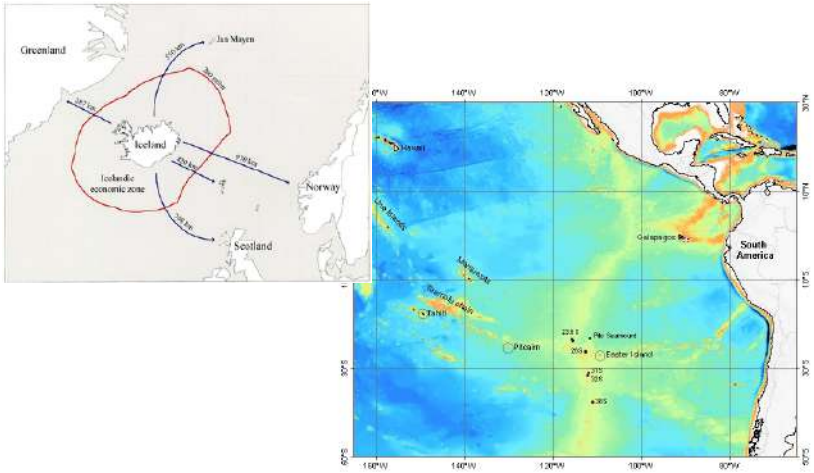
Island Patterns: species-isolation

Model Assumptions

1. **Diversity is driven by two factors**
   - Island size
   - Distance from mainland

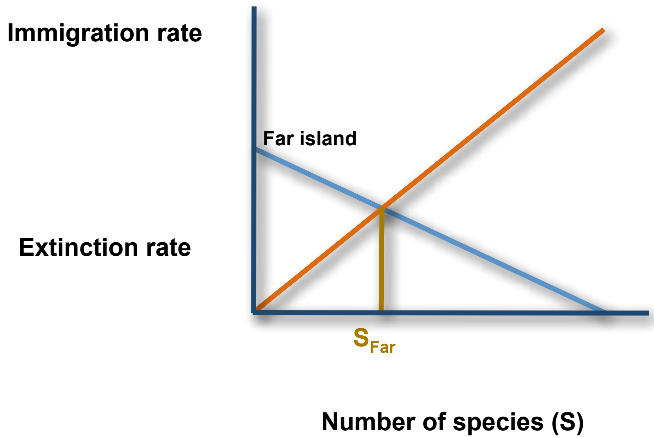
MacArthur RH and Wilson EO. The theory of island biogeography. Princeton University Press, 1967.

Island Patterns: species-isolation

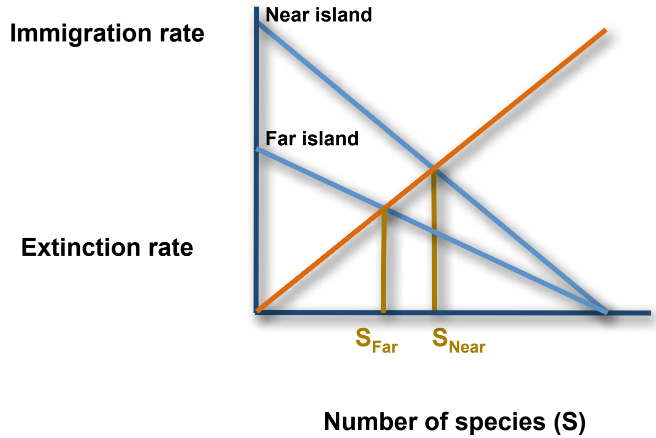


Much of the variation is explained solely by the distance of island to continent….

Island Patterns: species-isolation



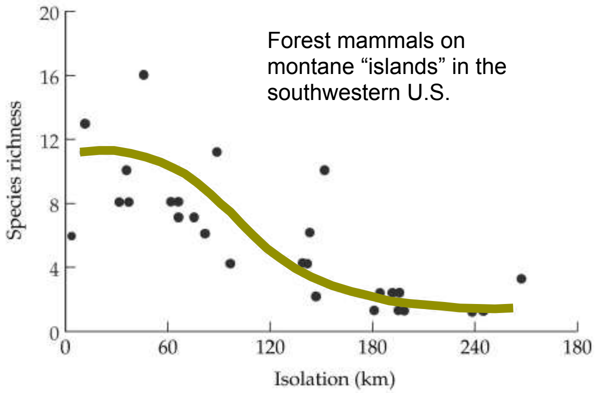
Island Patterns: species-isolation



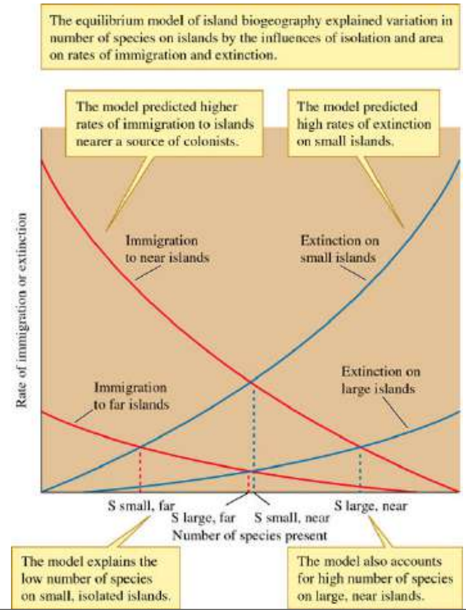
Island Patterns: species-isolation

Species-isolation relationship

Species richness declines as isolation increases, as a negative exponential or sigmoidal function



Equilibrium Theory of Island Biogeography



Equilibrium Theory of Island Biogeography

HOW TO TEST THIS THEORY?

MacArthur RH and Wilson EO. The theory of island biogeography. Princeton University Press, 1967.

FIG. 3. *Upper*: Control mangrove island IN1. *Lower*: Experimental mangrove island SQ1 (arrow), near Squirrel Key. Tiny fumigated island E1 is in foreground.

Equilibrium Theory of Island Biogeography

Everglades National Park Photo

An empirical test: Insects on mangrove islands

(Wilson and Simberloff 1969; Simberloff and Wilson 1969)

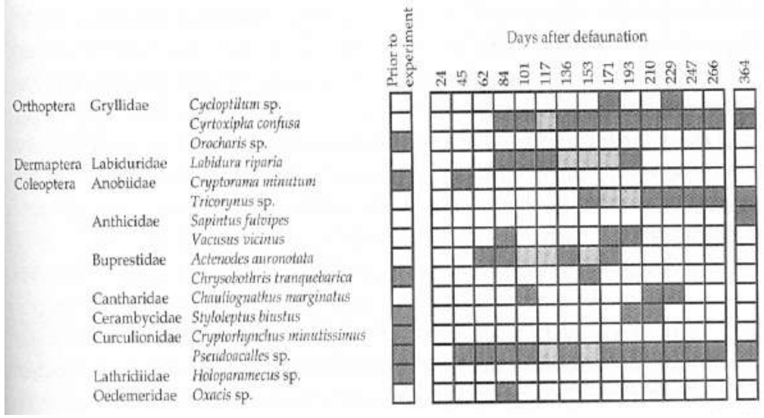
- Identified 6 mangrove islands of varying size and distance from the mainland
- Carefully censused the arthropod community of each island
- Covered each island with canvas and fumigated to kill all arthropods
- Tracked recolonization of the islands over several years

Equilibrium Theory of Island Biogeography

Equilibrium Theory of Island Biogeography

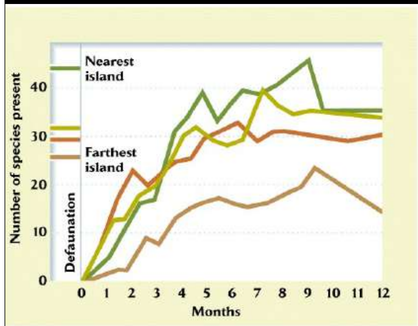
An empirical test: Insects on mangrove islands

(Wilson and Simberloff 1969; Simberloff and Wilson 1969)



Black squares = species present
Grey squares = species inferred to be present

Equilibrium Theory of Island Biogeography



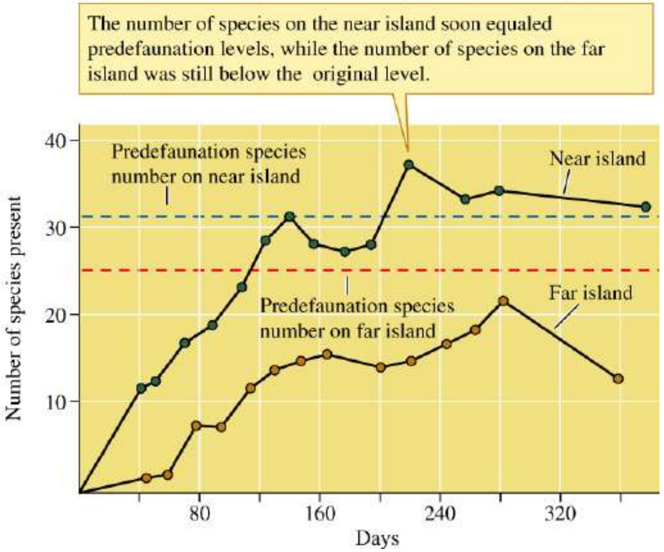
An empirical test: Insects on mangrove islands

(Wilson and Simberloff 1969; Simberloff and Wilson 1969)

- Substantial species turnover occurred over the course of the experiment
- Estimated the turnover rate to be .67 species per day!
- Provides essential support to the equilibrium theory

Taken together, these results support the equilibrium model

Equilibrium Theory of Island Biogeography



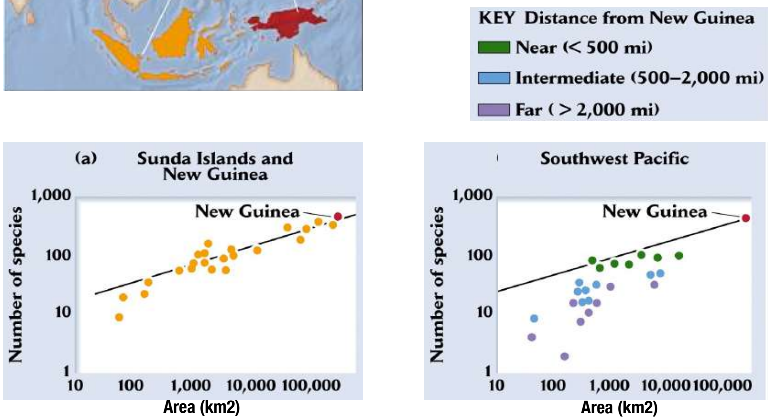
Empirical evidence

EMPIRICAL EVIDENCE

MacArthur RH and Wilson EO. The theory of island biogeography. Princeton University Press, 1967.

Empirical evidence

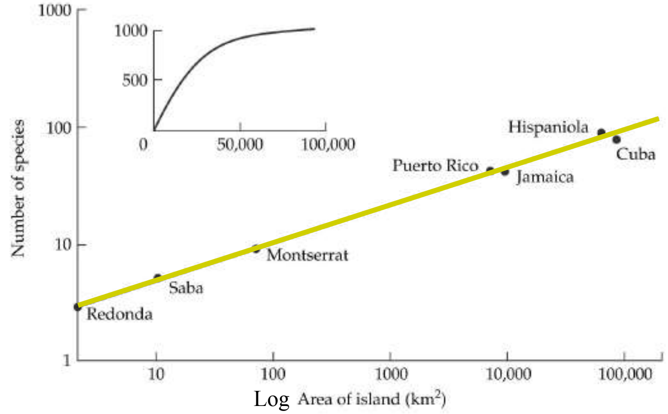
Bird biodiversity



Both area and distance affect bird diversity

Empirical evidence

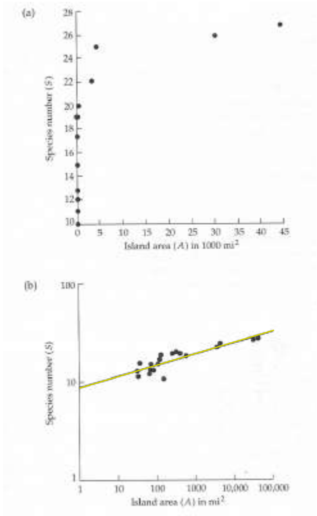
(Breeding land birds of the West Indies; Gotelli and Abele, 1982)

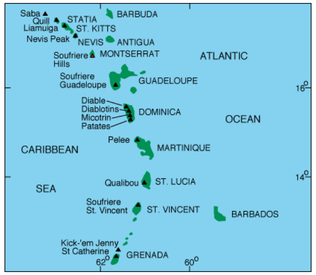


Empirical evidence

A test of the species area relationship

(Breeding land birds of the West Indies; Gotelli and Abele, 1982)





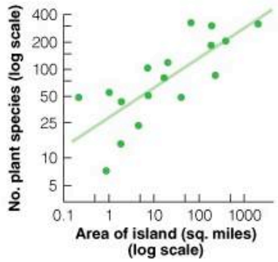
Trend has also been shown to hold for:

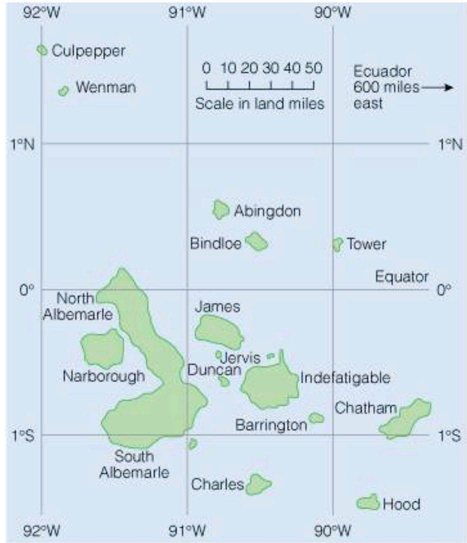
Fish in lakes of different areas
Mammals that occupy isolated mountain tops
Insects that live in thistle heads

Empirical evidence

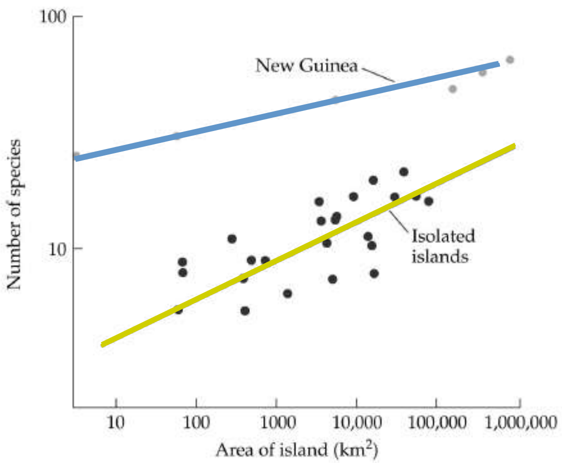
A test of the species area relationship

(Breeding land birds of the West Indies; Gotelli and Abele, 1982)





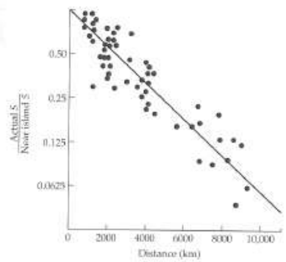
Empirical evidence



Empirical evidence

The equilibrium model may also explain the common observation that species richness decreases with distance from the mainland

Birds of the Bismarck islands (Diamond, 1972)



Species richness decreases with distance from New Guinea (mainland)

Equilibrium Theory of Island Biogeography

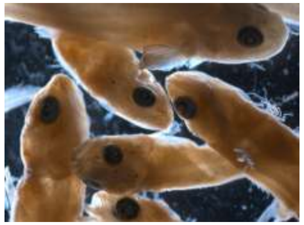
Model Assumptions

1. **Diversity is driven by two factors**
   - Distance from mainland
   - Island size
2. **Species are equal**
   - Dispersal abilities

MacArthur RH and Wilson EO. The theory of island biogeography. Princeton University Press, 1967.

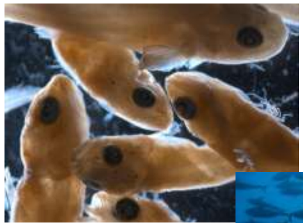
Island Biogeography

Passive transport
CURRENTS



Island Biogeography

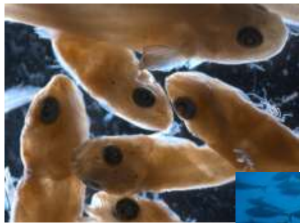
Passive transport
CURRENTS



Active transport
SWIMING

Island Biogeography

Passive transport
CURRENTS

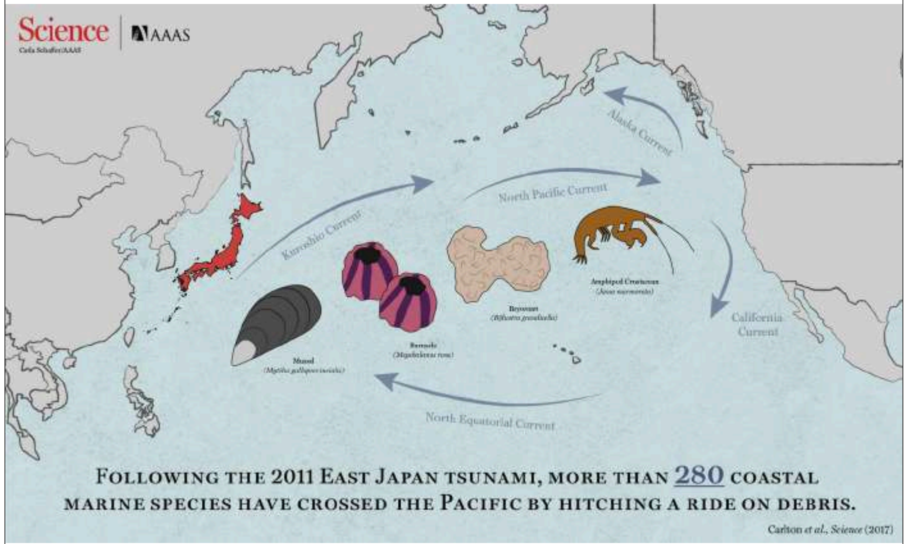


Active transport
SWIMING

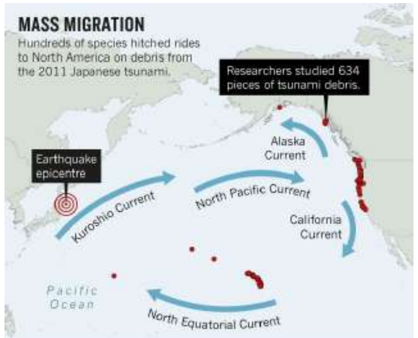
Passive floating
RAFTING

Island Biogeography

Island Biogeography



Island Biogeography



Equilibrium Theory of Island Biogeography

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MacArthur RH and Wilson EO. The theory of island biogeography. Princeton University Press, 1967.

Krakatoa

Krakatoa

In **1883** there was a volcanic eruption on the island of Krakatoa that eliminated **all life** there.

Scientists have visited since collecting data on the colonization and species richness of the island.

Equilibrium Theory of Island Biogeography

Krakatoa

Photo of the Krakatoa eruptive activity a few hours before the major explosions (taken on August 26, 1883 from a ship crossing the Sunda Strait.

Equilibrium Theory of Island Biogeography

MacArthur RH and Wilson EO. The theory of island biogeography. Princeton University Press, 1967.

Equilibrium Theory of Island Biogeography

Krakatoa

MacArthur and Wilson's Theory of Island Biogeography predicted that the equilibrium value for birds species would be 30, that the time to reach equilibrium would be 40 years, and the turnover rate would be 1 species a year.

Equilibrium Theory of Island Biogeography

Krakatoa

Birds Species:
1908 – 13 species
1921 – 27 species
1934 – 27 species
5 species had been replaced between the 1921 and 1934 surveys

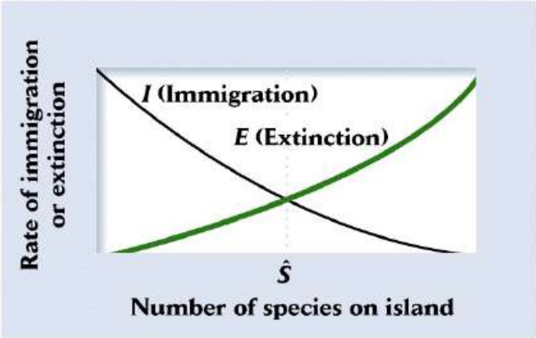
Equilibrium Theory of Island Biogeography

WHAT HAVE WE LEARNED?

MacArthur RH and Wilson EO. The theory of island biogeography. Princeton University Press, 1967.

Equilibrium Theory of Island Biogeography

What have we learned?



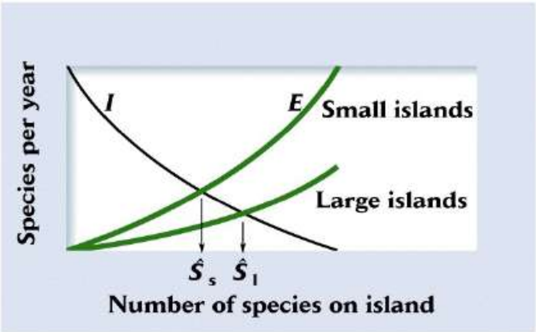
Immigration rate decreases as island diversity increases

Species equilibrium on islands is a balance of immigration and local extinction

Extinction increases as island diversity increases

Equilibrium Theory of Island Biogeography

What have we learned?

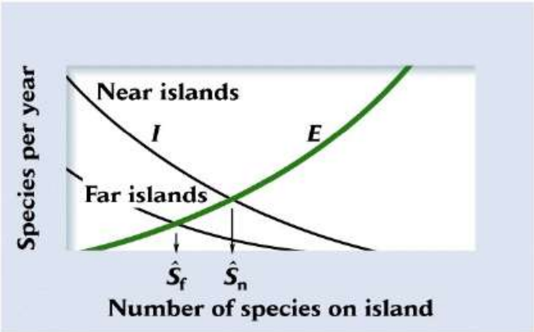


Smaller islands have lower species diversity

Probability of extinction increases with more species

Equilibrium Theory of Island Biogeography

What have we learned?

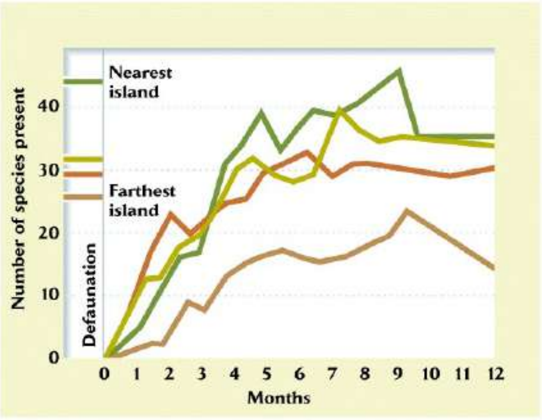


Islands further from mainland have lower immigration rates

More distant islands have lower species diversity

Equilibrium Theory of Island Biogeography

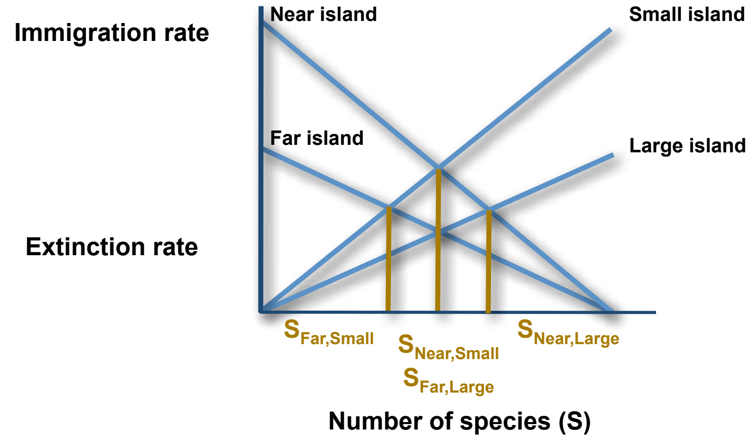
What have we learned?



More distant islands had lower species diversity

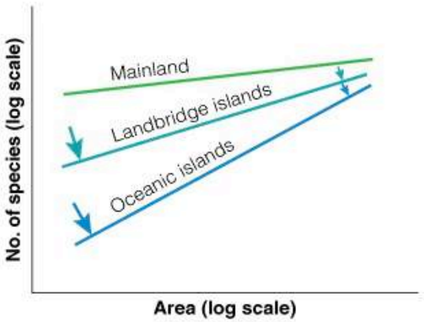
Closer islands had greater rates of immigration and recovered more species faster

Equilibrium Theory of Island Biogeography



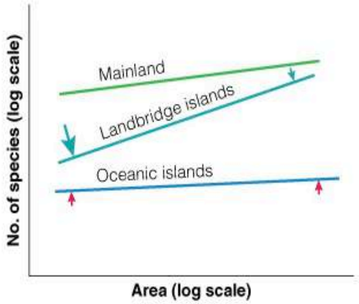
Island Biogeography

Equilibrium



(a) Equilibrium model

Non-equilibrium



(b) Nonequilibrium model

History of Biogeography

outline

WHAT IS PHYLOGEOGRAPHY

MARKERS

MODELS

AVISE’S HYPOTHESIS and COROLLARIES