



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?

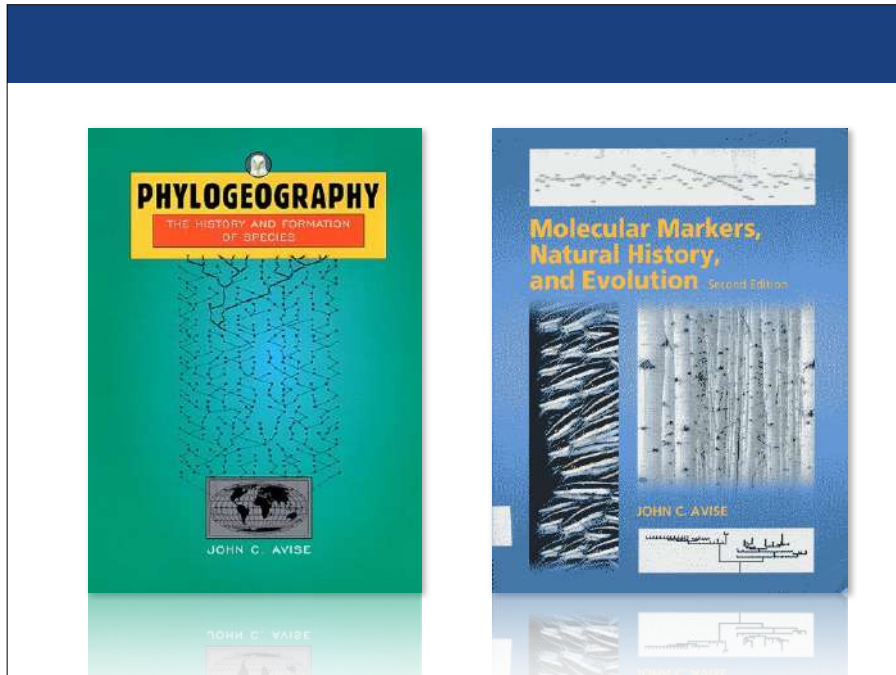
Phylogeography: introduction

What is phylogeography?

What 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

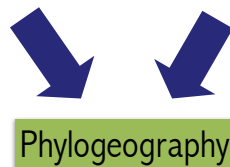
Phylogeography: introduction

Population genetics

Within populations
Shallow timescale

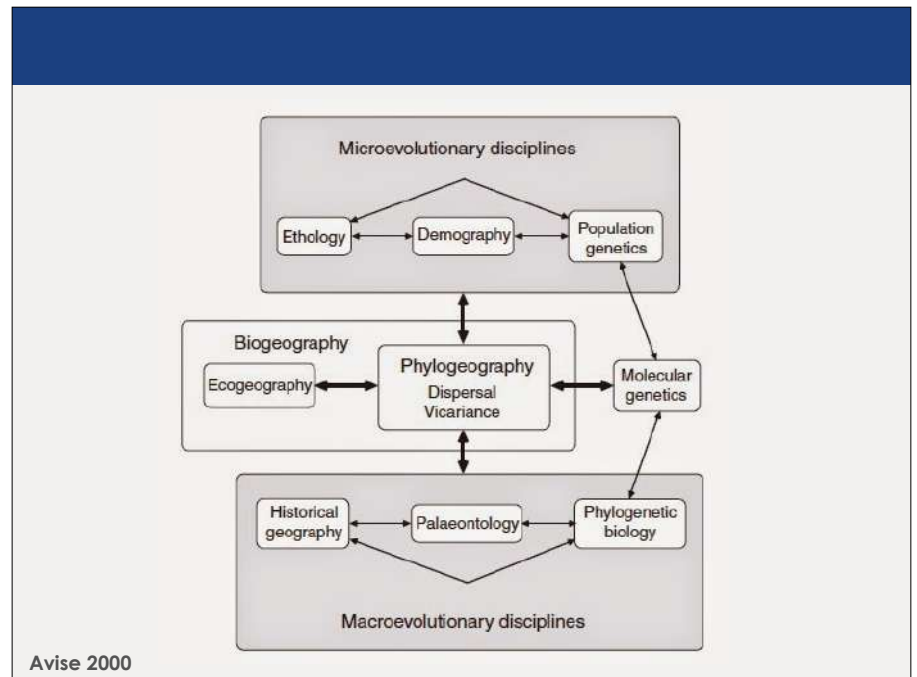
Phylogenetics

Between species
Deep timescale

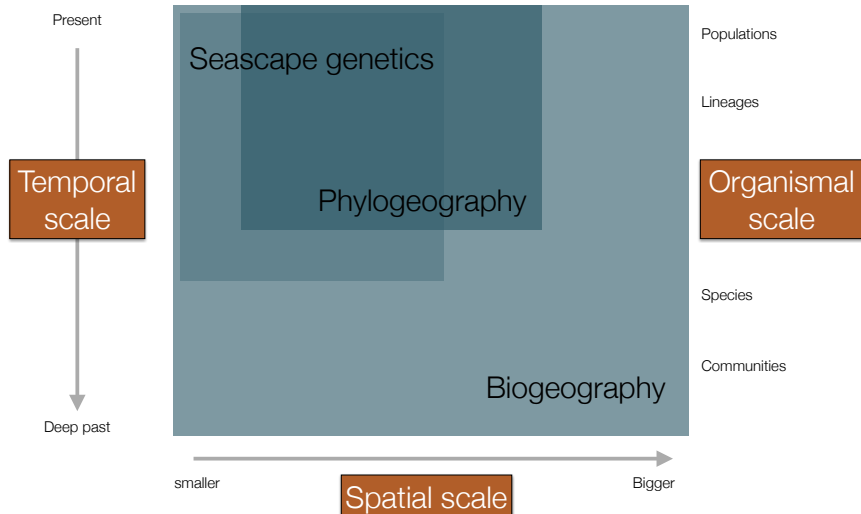


Phylogeography

Between populations and species
Medium timescale
Plus geography

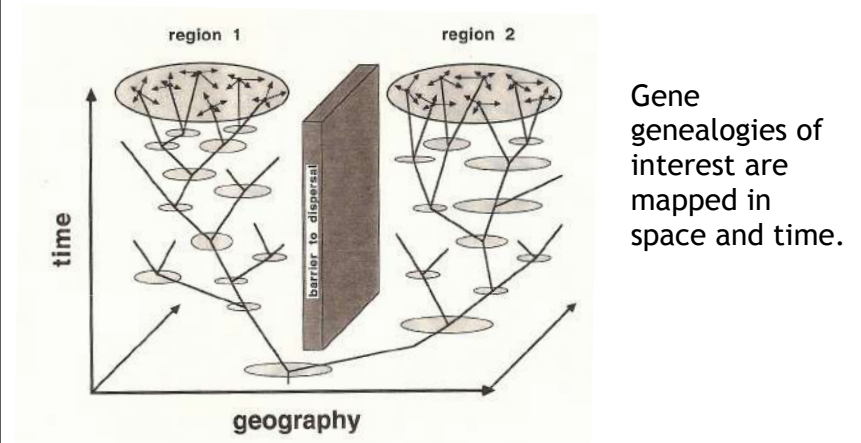


Phylogeography



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

Phylogeography: introduction

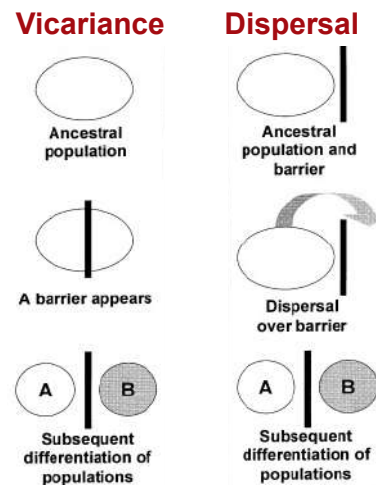


Avise 2000

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.



Determinants of genetic structure

Historical relationships and contemporary gene flow influence spatial patterns of genetic variation.

Similarity due to gene flow



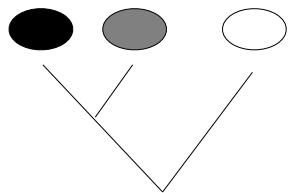
Determinants of genetic structure

Historical relationships and contemporary gene flow influence spatial patterns of genetic variation.

Similarity due to gene flow



Similarity due to historical relationships



Understanding genetic structure

Within species, *genetic exchange* has been emphasized as the cause of similarity.

Understanding genetic structure

Traditionally:

Within species, *genetic exchange* has been emphasized as the cause of similarity.

Among species, *historical relationship* has been emphasized as the cause of similarity.

Understanding genetic structure

We can tease apart
contemporary forces of genetic exchange
from
historical relationships

Understanding genetic structure

Phylogeography uses principles from

population genetics

and

phylogenetics

Understanding genetic structure

Phylogeography uses principles from **population genetics** and **phylogenetics**.

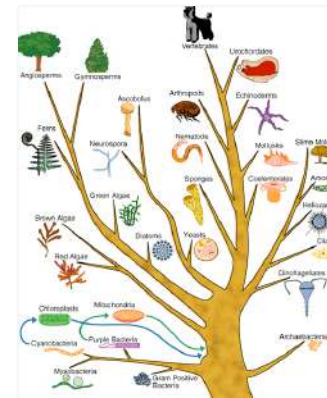
However...

Understanding genetic structure

Does not assume an equilibrium between genetic drift and gene flow

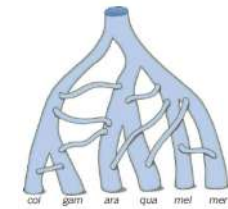
Assumes reticulation

Understanding genetic structure



Evolution can be displayed in a bifurcating pattern

There are exceptions.... Lateral gene transfer



More web than tree. The pattern of evolution seen in the *An. gambiae* species complex resembles a network more than a tree. This type of evolutionary network is referred to as reticulate evolution (RE).

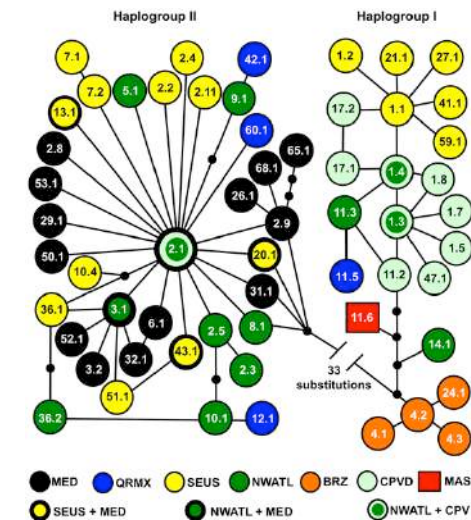
Understanding genetic structure

Does not assume an equilibrium between genetic drift and gene flow

Assumes reticulation

Relies on the use of **gene genealogies**
[phylogeographic methods provide historical information that individuals or populations cannot]

Genetic variation



<http://journals.plos.org/plosone/article?id=10.1371/journal.pone.0068956>

Genetic variation

We need significant genetic variation at the appropriate level
(i.e. among the populations or taxonomic units under investigation)

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Chloroplast DNA
faster rates of molecular evolution but still low (and variable among species)
no recombination
chloroplast capture can occur (e.g. in oaks, sunflowers, poplar)

Organelle genomes are essentially a single locus - inferences based on multiple loci give more accurate estimations of the population history of a species

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Nuclear DNA
problems of intra-allelic recombination, heterozygosity and gene families

Phylogeography: early years

Phylogeography was essentially *descriptive*:

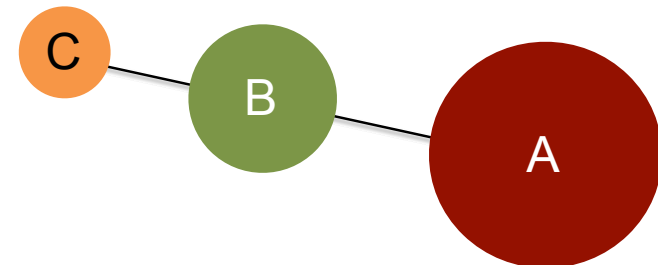
Plot haplotypes on map

Classify pattern of phylogeographic structure

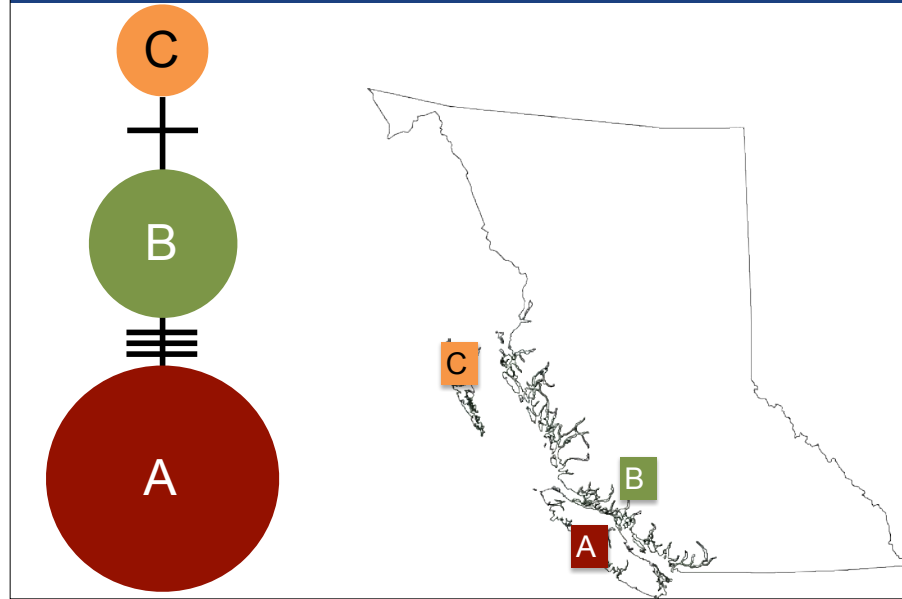
Consider historical explanations

Look for concordance among different species (comparative phylogeography)

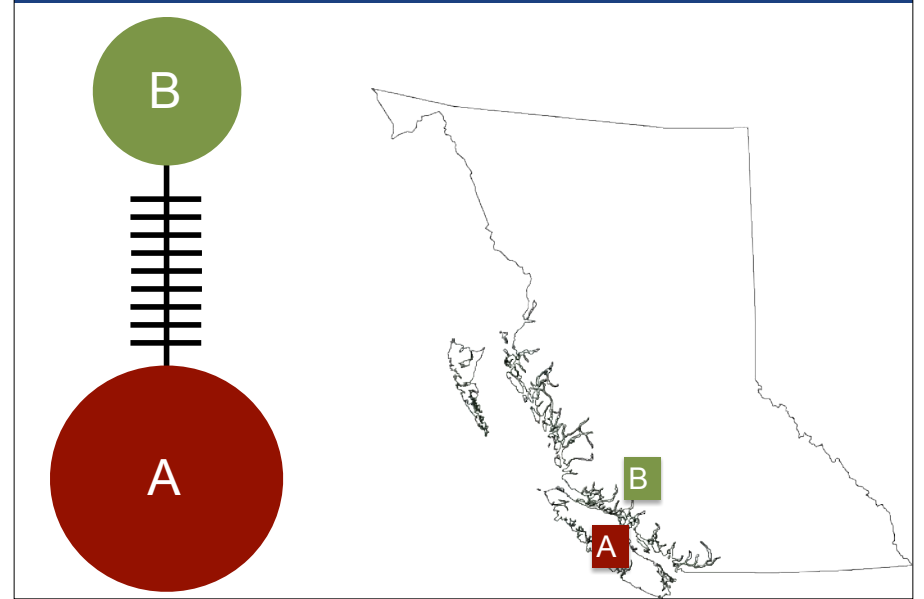
Haplotype network



Where did C originate from?



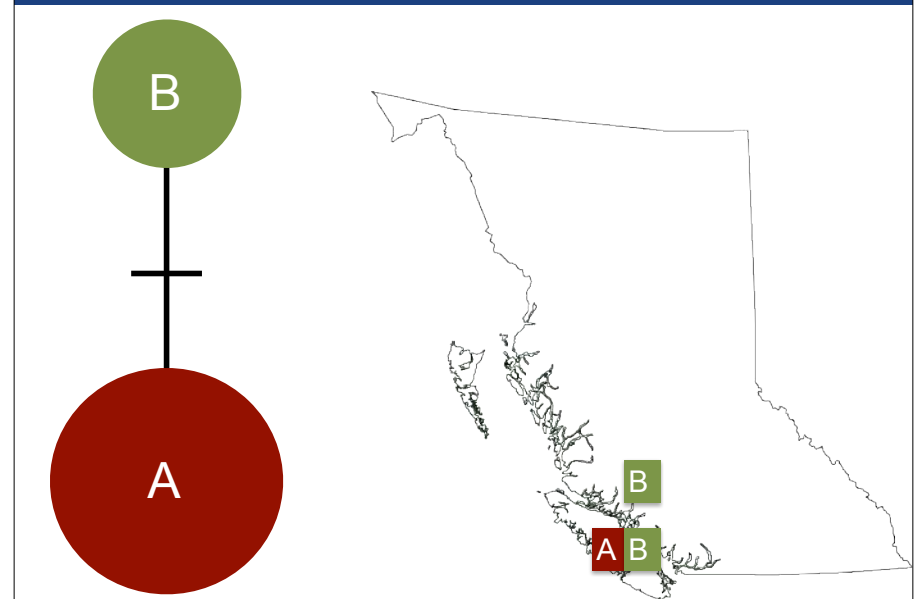
Deep divergence



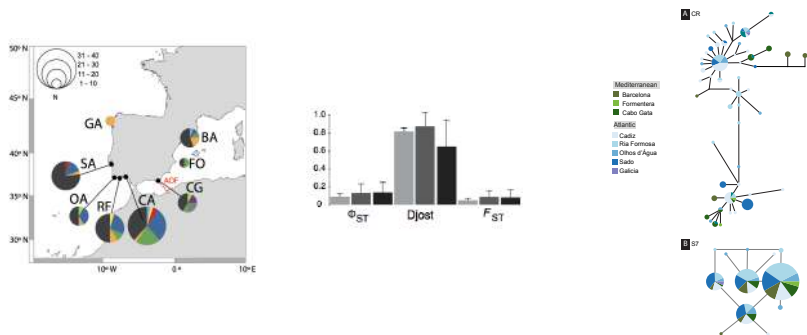
Shallow divergence



Gene flow



Phylogeography: early years

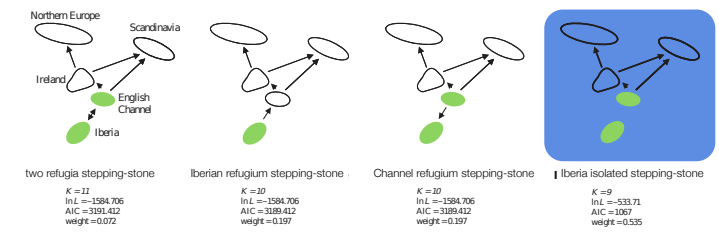


Region	Locations	Code	Mitochondrial D-loop				First intron of S7 gene				Observed Heterozygosity		
			N	NH	NP	Haplotype diversity \pm s.d.	Nucleotide diversity \pm s.d.	PS	N	NH		Gene diversity \pm s.d.	Nucleotide diversity \pm s.d.
M	Barcelona	BA	16	9	3	0.92 \pm 0.04	0.0520 \pm 0.0274	38	15	5	0.65 \pm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

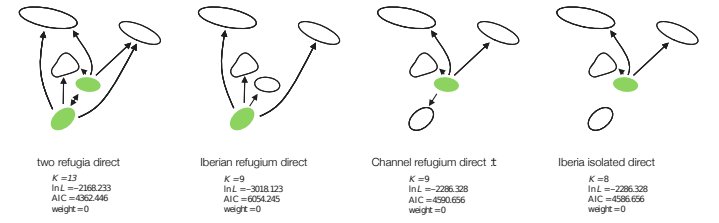
Notes: N, number of individuals per location; NH, haplotype richness; NP, number of private haplotypes; PS, number of polymorphic sites.

Hypotheses testing

Stepping-stone

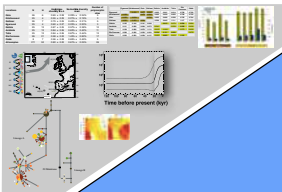


Direct



Provan & Maggs 2011. PRSL

The idea



Hypothesis: Oceanic fronts may act as a barrier to dispersal for littoral fish irrespective of the life-history traits.

Questions Hypotheses

Predictions:
 (1) populations separated by oceanic fronts belong to genetically differentiated subunits;
 (2) the degree of connectivity between populations is related to early-life-history traits and dispersal capabilities.

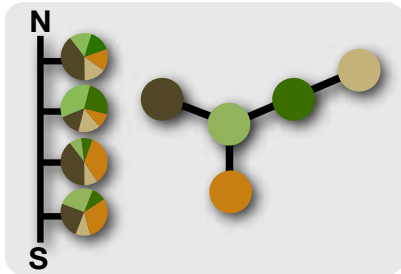
Testing by:
 (1) plotting standardized species F_{st}
 (2) estimating pairwise F_{st} ;
 (3) mapping posterior probabilities of population membership and
 (4) mapping spatial location of genetic discontinuities for different species.

Expectations in phylogeographic data

How do we reconstruct the **origin, dispersal, and extinction** of taxa?

Phylogeographic data

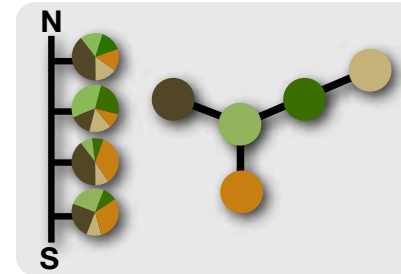
Null model



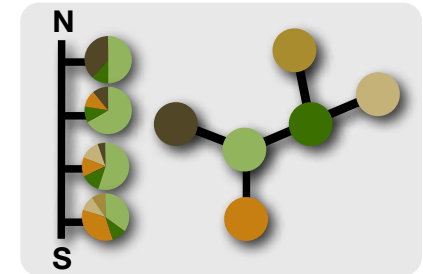
Maggs et al. (2008). *Ecology*.

Phylogeographic data

Null model



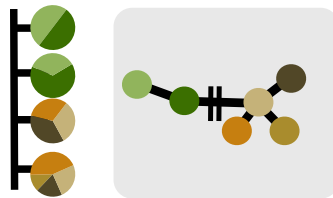
Latitudinal cline



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

Phylogeographic data: expectations

no geographic contact

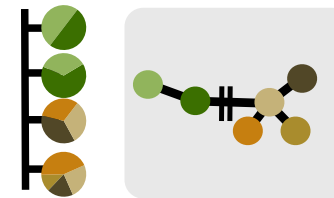


genealogical concordance

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

Phylogeographic data: expectations

no geographic contact



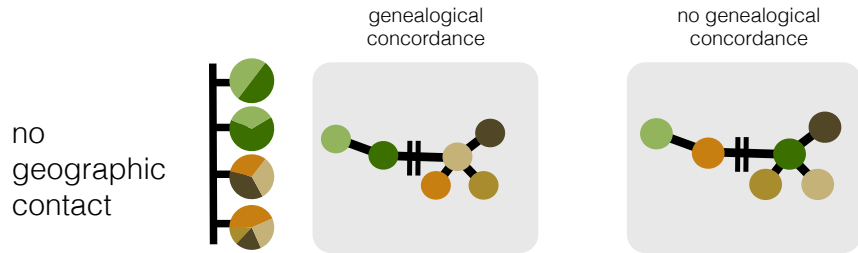
genealogical concordance

no genealogical concordance

?

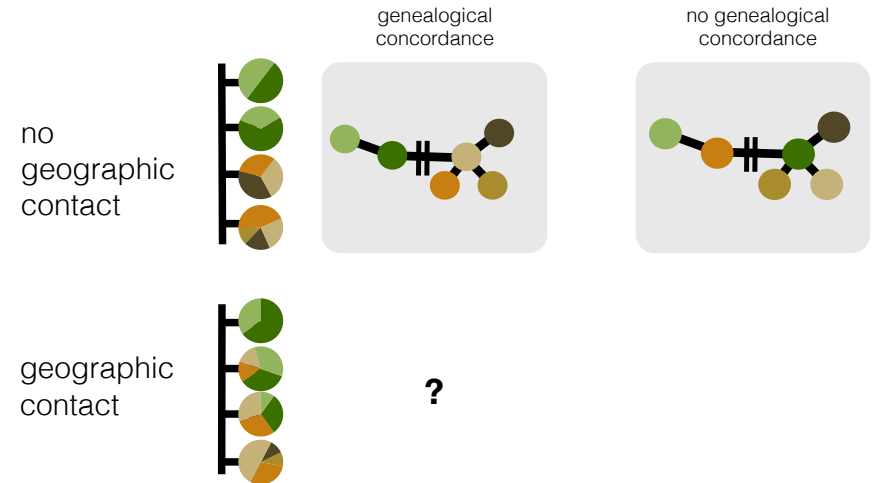
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Phylogeographic data: expectations



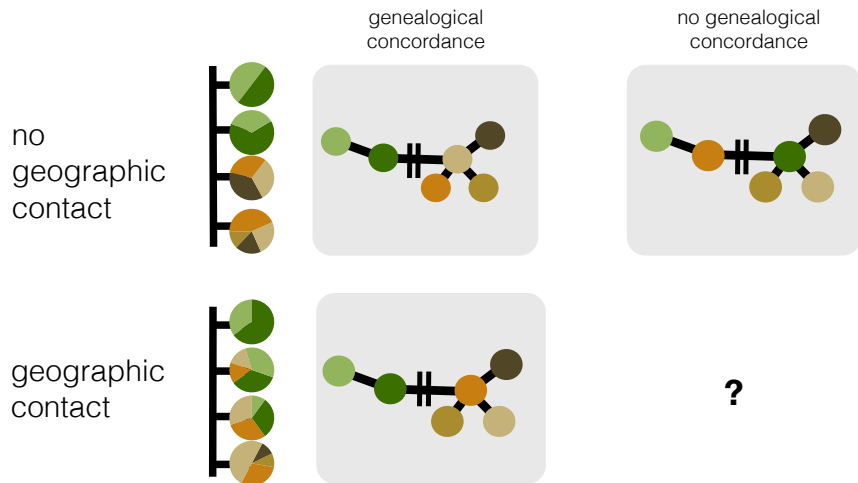
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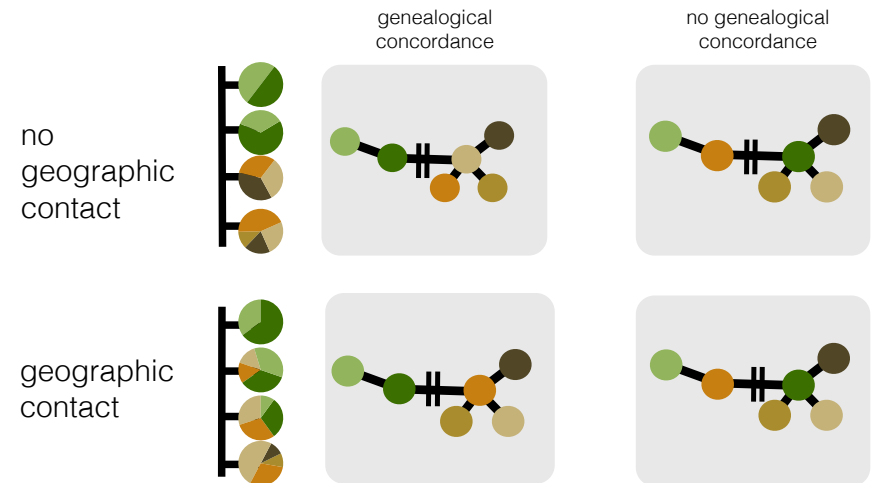
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Awise phylogeography

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)

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.

ORIGINAL ARTICLE

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

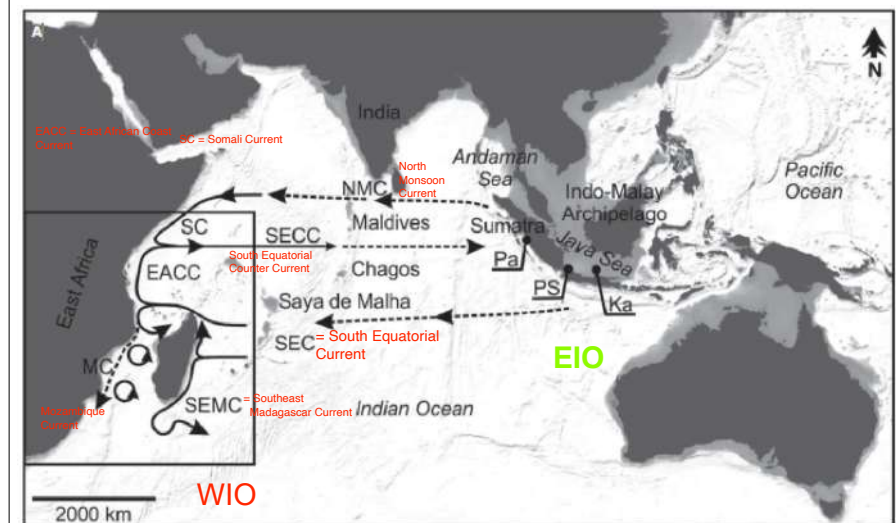
Filip Huyghe & Marc Kochzius

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

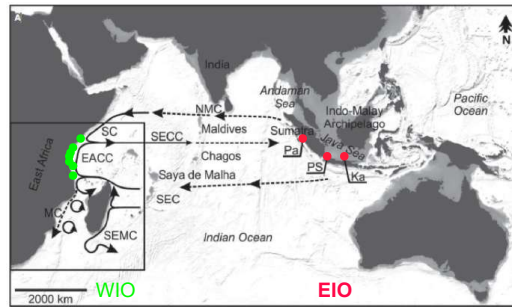


Marine Ecology. ISSN 0173-9565

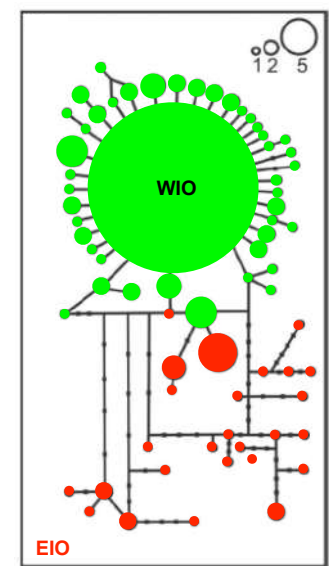
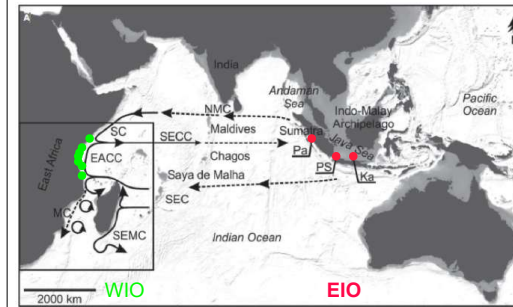
Hypothesis 1



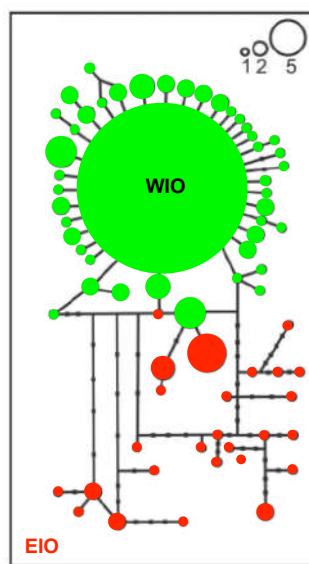
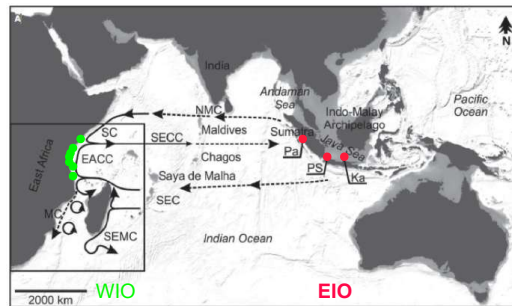
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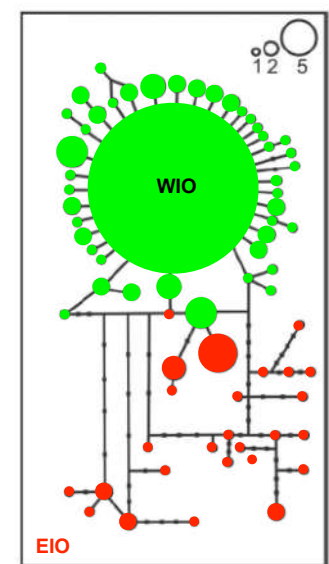
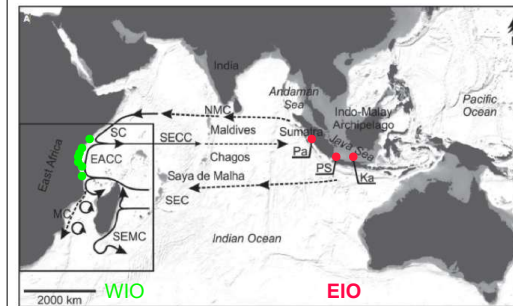


Hypothesis 1



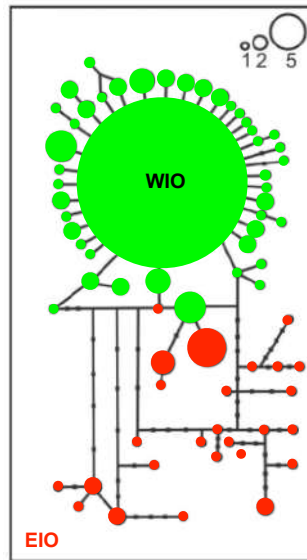
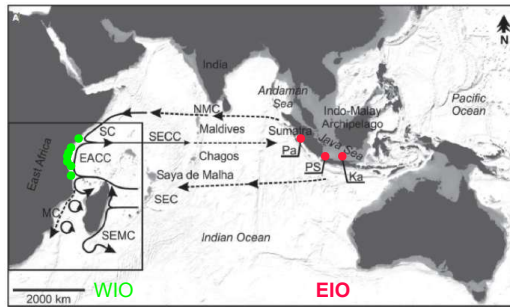
None of the identified 69 haplotypes was shared between the WIO and EIO.

Hypothesis 1



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

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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

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

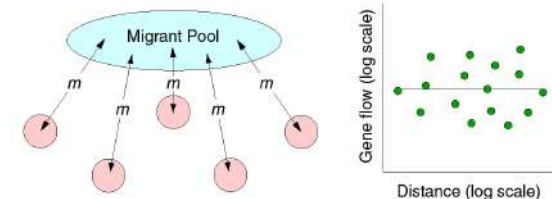
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Given
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Alternatively a **stepping-stone model** involving islands in the Central Indian Ocean is a more likely scenario for colonization of the WIO.

Hypothesis 1

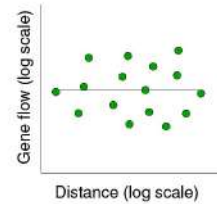
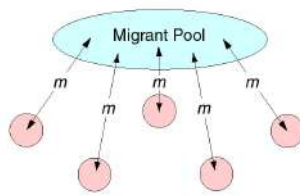
Island Model



Wright, S. 1931. Evolution in Mendelian populations. *Genetics* 16:97-159.

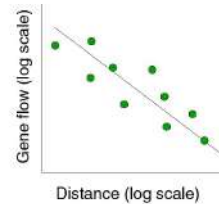
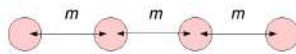
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Island Model



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Stepping-stone model

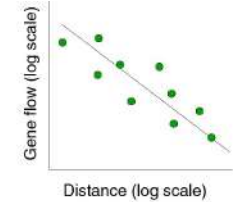
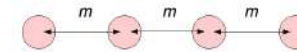


Kimura, M., and W. H. Weiss. 1964. The stepping stone model of genetic structure and the decrease of genetic correlation with distance. *Genetics* 49:561-576.

Hypothesis 1

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

Stepping-stone model



Kimura, M., and W. H. Weiss. 1964. The stepping stone model of genetic structure and the decrease of genetic correlation with distance. *Genetics* 49:561-576.

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



PHYLOGEOGRAPHY

Hypothesis 3

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

Hypothesis 3

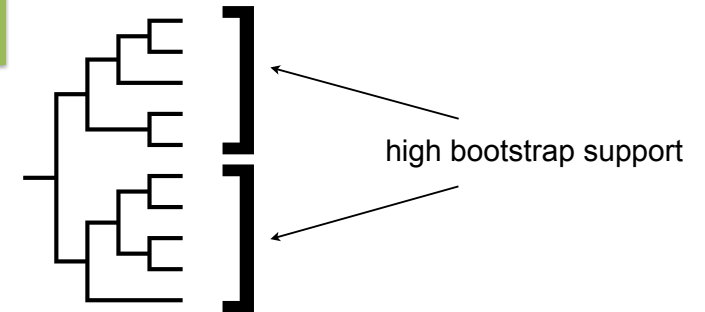
This hypothesis includes **four corollaries** that represent different aspects of genealogical concordance.

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

Species "a"
Gene "1"



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

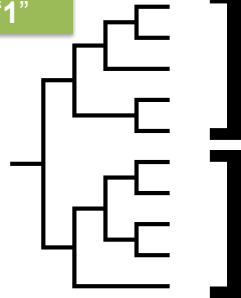
A

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).

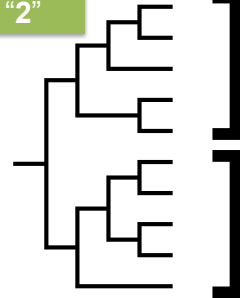
Awise, J.C. (2000) Phylogeography: the history and formation of species. Harvard University Press, Cambridge, MA.

Hypothesis 3: C2

Species "a"
Gene "1"



Species "a"
Gene "2"



B

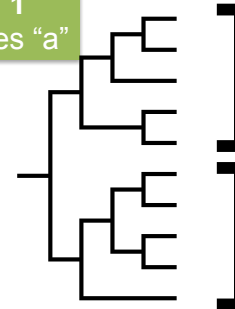
Concordance in significant genealogical partitions across multiple genes within a species. (Agreement across genes)

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.

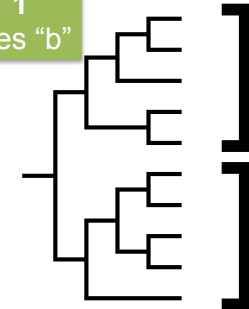
Awise, J.C. (2000) Phylogeography: the history and formation of species. Harvard University Press, Cambridge, MA.

Hypothesis 3: C3

Gene "1"
Species "a"



Gene "1"
Species "b"



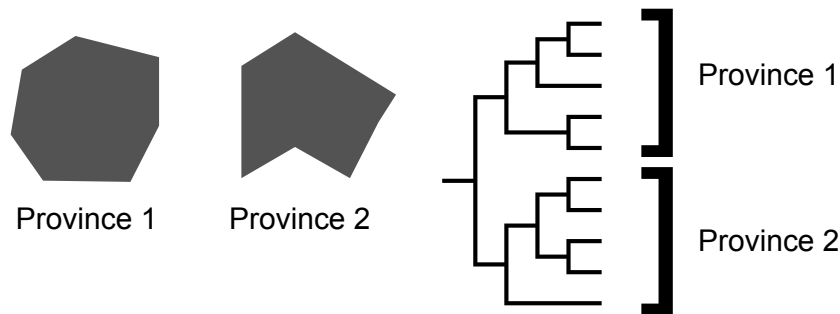
C

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 phylogeographically structured in similar fashion. In particular, divergent branches in the intraspecific gene trees might map consistently to the same geographic regions.

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

Hypothesis 3: C4



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

D 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.

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

Conceptual approaches

Classical population genetics

based on allele frequencies

alleles are either the same or different, no degrees of similarity

Conceptual approaches

Classical population genetics

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alleles are either the same or different, no degrees of similarity

SUMMARY STATISTICS (descriptive, exploratory statistics)

- How many alleles are there per locus per population?
- What are allelic frequencies?
- What is the proportion of heterozygous individuals?
- What would be the proportion of heterozygous individuals in HW equilibrium?
- What are the distances between populations?
- Are distinct loci in linkage equilibrium?
- How many positions vary in a nucleotide alignment?
- How many different haplotypes are there?
- How different are haplotypes?
- What is the average difference between two sequences in a population?
- Is most of the variation within or between populations?

Conceptual approaches

Classical population genetics

based on allele frequencies

alleles are either the same or different, no degrees of similarity

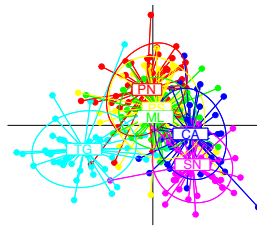
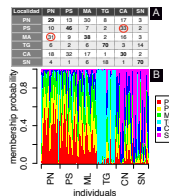
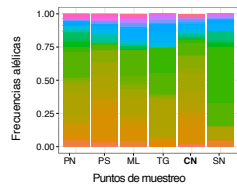
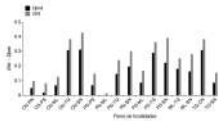
Conceptual approaches

Classical population genetics

based on allele frequencies

alleles are either the same or different, no degrees of similarity

Localidad	Código	Longitud	Latitud	N	AT	Map	Ar (SD)	H _s	H _e	G _{st}
Portugal - Norte	PN	-8.8	40.7	45	136	15	15.4	0.77	0.86	0.10
Portugal - Sur	PS	-6.4	37.1	43	133	11	15.6	0.83	0.88	0.06
Málaga	ML	-4.3	36.6	40	131	14	15.1	0.76	0.88	0.14
Tanger	TG	-5.9	35.9	40	112	11	12.6	0.69	0.80	0.14
Islas Canarias	CA	-15.9	29.3	42	142	22	16.9	0.79	0.89	0.11
Senegal	SN	-17.6	14.8	37	135	19	16.7	0.77	0.88	0.12

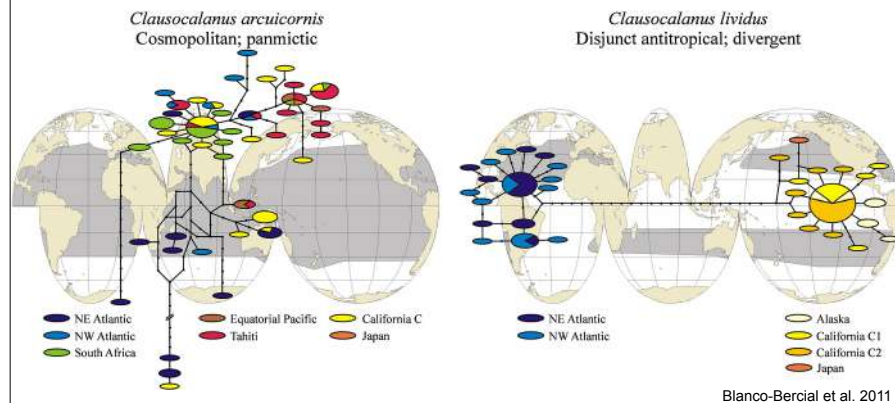


Conceptual approaches

Phylogeography

based on gene genealogies

both the frequencies of sequence haplotypes and their relationship is considered



Conceptual approaches

Phylogeography

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History of Biogeography

outline

WHAT IS PHYLOGEOGRAPHY

MARKERS

MODELS

AVISE'S HYPOTHESIS and COROLLARIES