Community Structure
Temporal Patterns

Temporal Patterns – Seasonality

- Phenology – study of repeated patterns in time and their relationship to physical aspects of the environment
  - ➢Seasonal changes that are repeated each year
  - ➢These can affect community function, e.g., plant phenology may determine number of generations of insect herbivores per year and annual impact of herbivory; newt emergence from ponds freeing tadpoles from predation (M:240-247)
  - ➢Often modeled as a simple sine wave with annual periodicity, but may be too simple (note cascading community effects that complicate patterns in a web of interacting species)

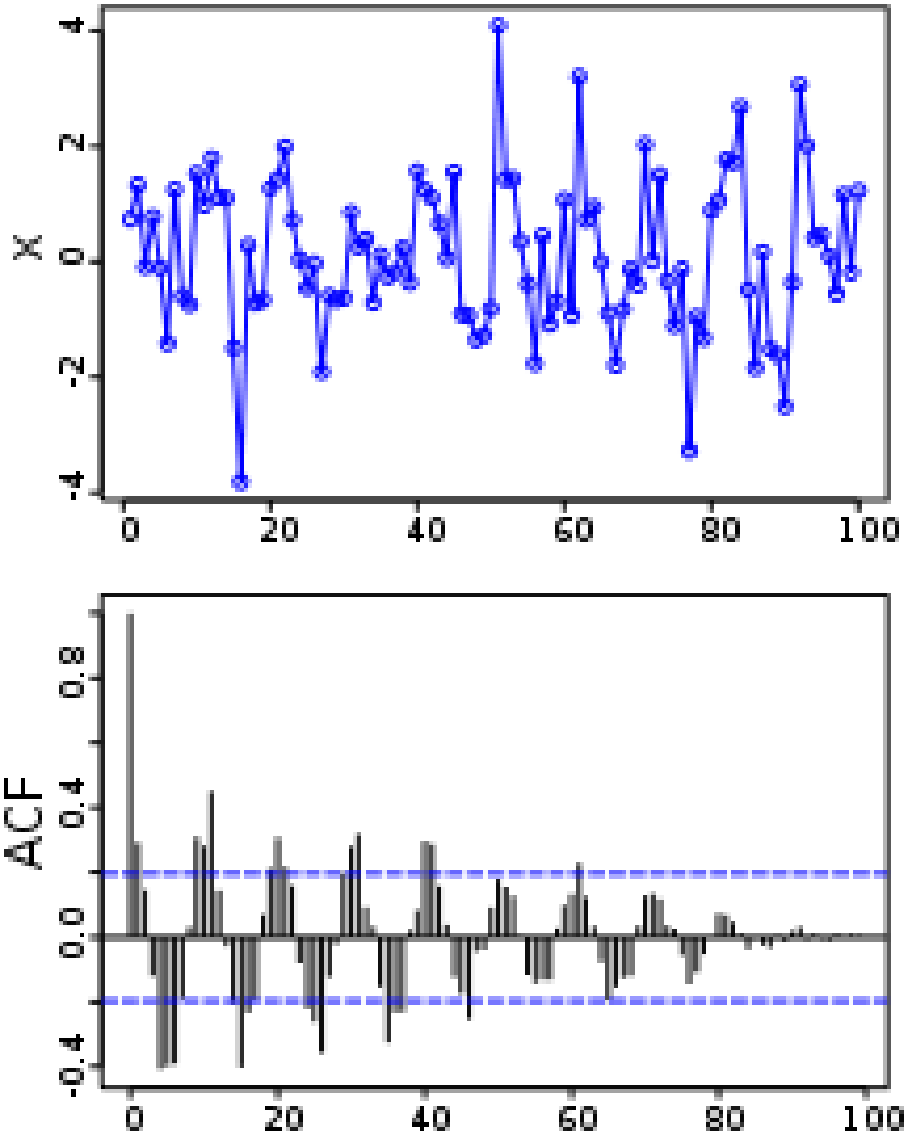
Autocorrelation

Modified from Wikipedia entry

Autocorrelation is the cross-correlation of a signal with itself.

It is the similarity between pairs of observations as a function of the temporal or spatial separation between them.

It is a mathematical tool for finding repeating patterns, such as the presence of a periodic signal that is buried under noise



Community Structure
Temporal Patterns

Temporal Patterns –

time scales other than seasonal

- Cycles – non-directional, predictable changes (like seasonality, but in this case on time scales other than one year)

  ➢Famous examples are microtine rodent cycles

- compare to succession – directional change in species composition to a new endpoint (not cyclical in absence of perturbation)

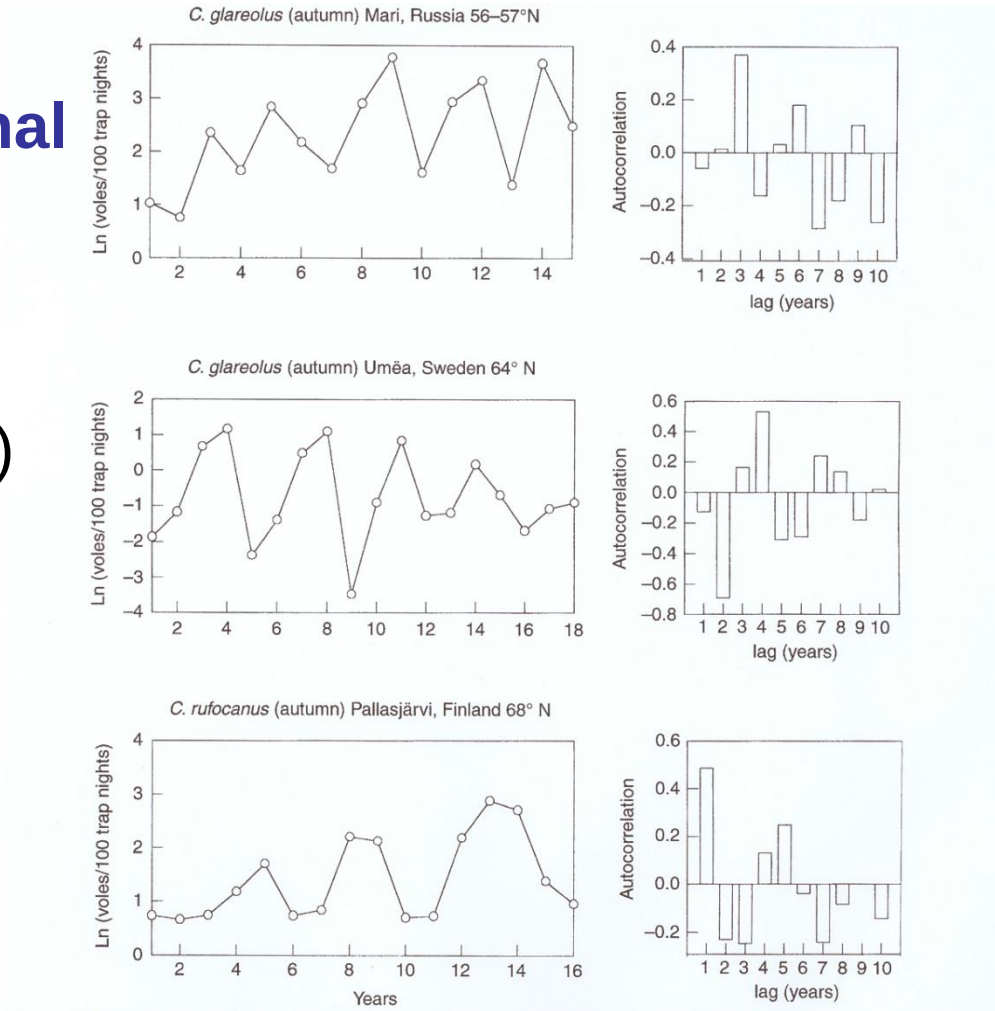


Fig. 6. Selected time series plots and correlograms of Ln-transformed autumn population abundance (voles/100 trap nights) for northern European voles to illustrate the increase in cycle periods with latitude and the asymmetric nature of high-amplitude cycles. Mari data from Zhigalski (1992), Uměa data from Hörnfeldt (1994), and Pallasjärvi data from Henttonen *et al.* (1987).

Inchasusti and Ginzburg. 1998. JAE 67:180-194

Community Structure
Temporal Patterns - Succession

- Succession – directional change in species composition to a new endpoint (not cyclical in absence of perturbation)
- Primary succession – succession starting in an empty (new) habitat
- Secondary succession – recovery of a formerly established community following a disturbance that “re-sets the clock”

Community Structure
Temporal Patterns - Succession

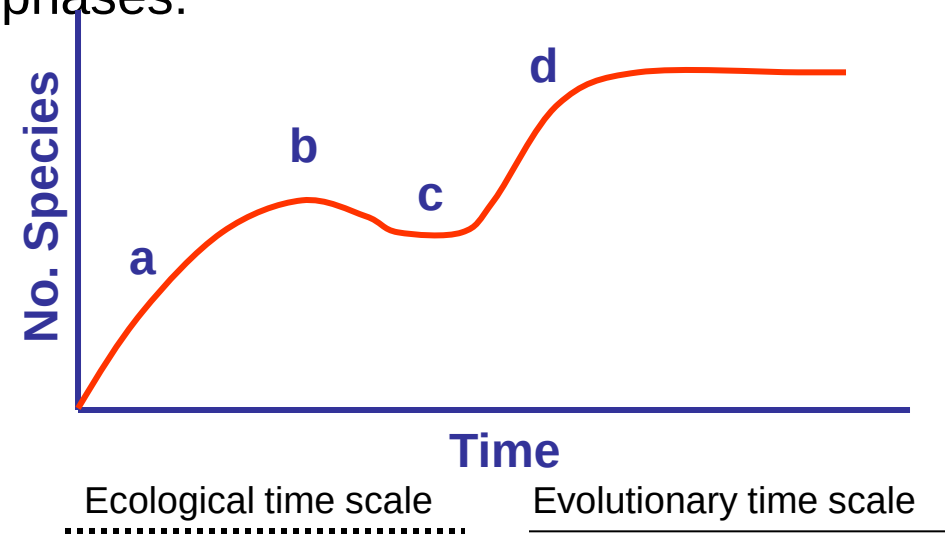
Steps for secondary succession:

1. Disturbance
2. Colonization - Pioneered by “fugitive” or “opportuntistic” species. Characterized by high dispersal and rapid growth (weeds; ruderal spp; opportunistic spp., etc)
3. Replacement – 3 models
   a) Facilitation – pioneers modify environment to encourage later arrivals (classical model)
   b) Inhibition – 1st come 1st served and once established, further invasion is resisted (compare to lottery model)
   c) Tolerance – later colonists are species able to tolerate relatively low resource availability
4. Climax
   a) One predictable endpoint (monoclimax)
   b) Different endpoints depend on conditions (ex., fire, soil, moisture,etc)
   c) Priority effects – identity of first arrivals directs subsequent pattern

Community Structure

Primary succession and beyond

Community formation (colonization of empty space… such as an island) may have four phases:



Note: a – c are typical successional phenomena

a) Non-interactive phase - number of spp and density of individuals is low, therefore little competition

b) Interactive phase – No. spp increases, competition becomes more prevalent; predators arrive; some extinctions.

c) Assortative phase – Spp that can co-exist begin to predominate, unstable species ‘combinations’ disappear. Community becomes more efficient and specialized.

d) Evolutionary phase – New spp arise on the island (endemics = spp found only in this location)

Community Structure
Temporal Patterns - Succession

- In general, reasons for community change are poorly understood.

- Has practical implications for predicting success of introduced species (still not possible to do this well) and managing dynamic ecosystems.

Community Structure
Species diversity

- Recall Simberloff and Wilson paper:
  - Regained approximate number of species on islands, but not same list of spp
  - Spp richness may be more predictable than specific spp identity (supports idea of functional redundancy, etc, previous slide)

Community Structure
Species richness

An example: Latitudinal gradient in species richness

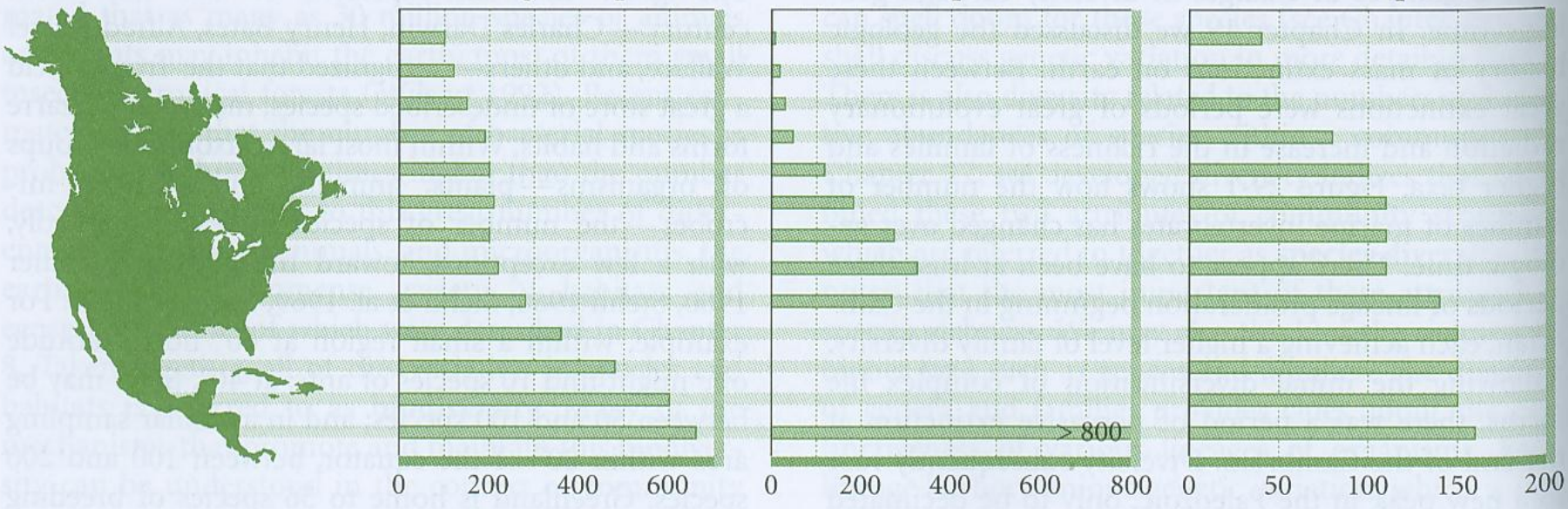


FIGURE 29-2 Numbers of species of breeding birds, trees, and mammals by latitude. The bars correspond to positions on the map to the left. (*From Meffe and Carroll 1997; after Briggs 1995.*)

Community Structure
Species richness

1. Historical explanations
   a. Time – temperate and polar regions not had enough time to refill since glaciation
      Criticism: Many warm temperate regions unglaciated in Eocene, but still depauparate relative to tropics and latitudinal gradient present in early fossils (Mesozoic and Cenozoic)
   b. Time-Stability – need long periods of benign and predictable climate for spp diversity to increase

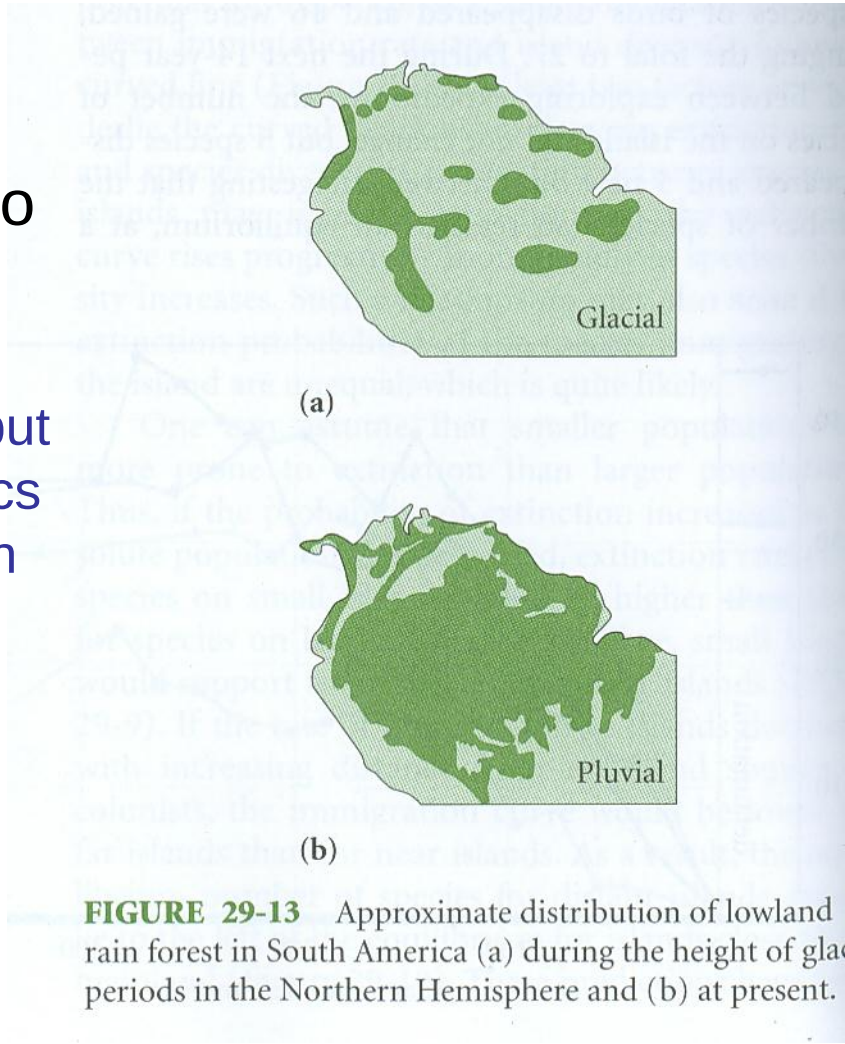


FIGURE 29-13 Approximate distribution of lowland rain forest in South America (a) during the height of glac periods in the Northern Hemisphere and (b) at present.

Community Structure
Species richness

2. Ecological (equilibrium) hypotheses – assumes gradients reflect current conditions
   a. Climatic stability – stable env permits evolution of increasingly finely divided niches, and more spp on same resource base

      Criticism: Polar regions are stable and stability of tropics is debatable; assumes resources limit speciation

   b. Life-is-hard theory – few spp at poles because LIH.
      Criticism: Some lineages have solved freezing problem (Notothenoid fishes)

   c. Productivity – less energy is needed to sustain self in tropics than at poles, less E for maintenance means easier to maintain minimum pop size
      - Stability of productivity – longer growing season in tropics provides for more time to increase pop size above min

Community Structure
Species richness

d. Competition – Physical environment is selective force in temperate and polar regions, competition more important in tropics… spp more commonly at K in tropics than in temperate and polar zones (greater subdivision of food resources in tropics, greater role for catastrophic mortality at poles) Th. Dobzhansky

e. Predation – Proportionately more predators and parasites in tropics than in temp and polar; These restrict prey pops and reduce competition so more spp can fit in tropics (Dan Janzen)

f. Intermediate Disturbance – Lack of stability on local scale in rainforest and coral reefs promotes spp diversity. These habitats have a high rate of non-catastrophic disturbance. Continual local disturbance permits multiple successional stages to be present simultaneously at intermediate spatial scale…. Keeps one or few spp from dominating. (J. Connell; M: fig. 12.8)

g. Habitat heterogeneity – General increase in habitat complexity from poles to tropics (Darwin and Wallace)

Community Structure
Species richness

3. Note: Longitudinal gradients also exist.

Ex: tropical marine organisms of many taxa

spp in Indo West Pacific > West Atlantic > East Pacific > East Atlantic

Shelf areas are:

6,570,000 – 1,280,000 – 380,000 – 400,000 km^2

Also, more archipelagos in Indo W. Pacific, suggesting a species-area relationship

Community Structure
Species richness

Historical Effects – non-equilibrium communities

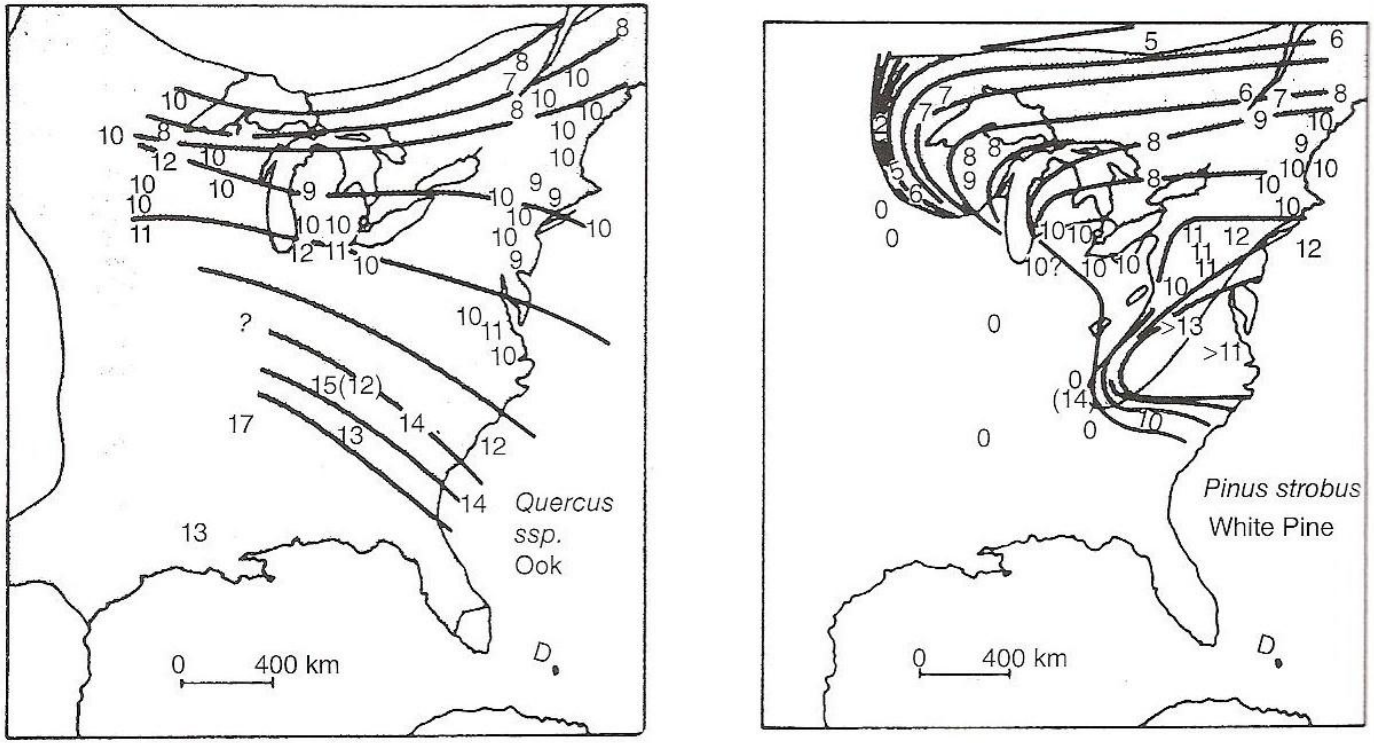


Fig. 12.3 Reconstructions of the northward progression of common forest trees after the last Pleistocene glaciation, showing different rates of movement by different species. Numbered lines indicate approximate northern limits of species ranges in thousands of years before present. (Reprinted with kind permission from Springer Science+Business Media: Forest Succession: Concepts and application, Quaternary history and the stability of forest communities, 1981, pages 144–145, Davis, M. B., figures 10.8 and 10.9. © 1981 Springer-Verlag.)

Analysis of minnows in streams in mid-western US reveals patterns of community structure

Rivers in Ozark drainages: Wisconsin Driftless (isolated from upland drainages in Pleistocene, probably represents relict upland community that was once widespread and spp that have dispersed in from other Pleistocene refuges);

Gasconade River (in Missouri drainage) and White River have separate connections to Mississippi R, unaffected by Pleistocene glaciation episodes.

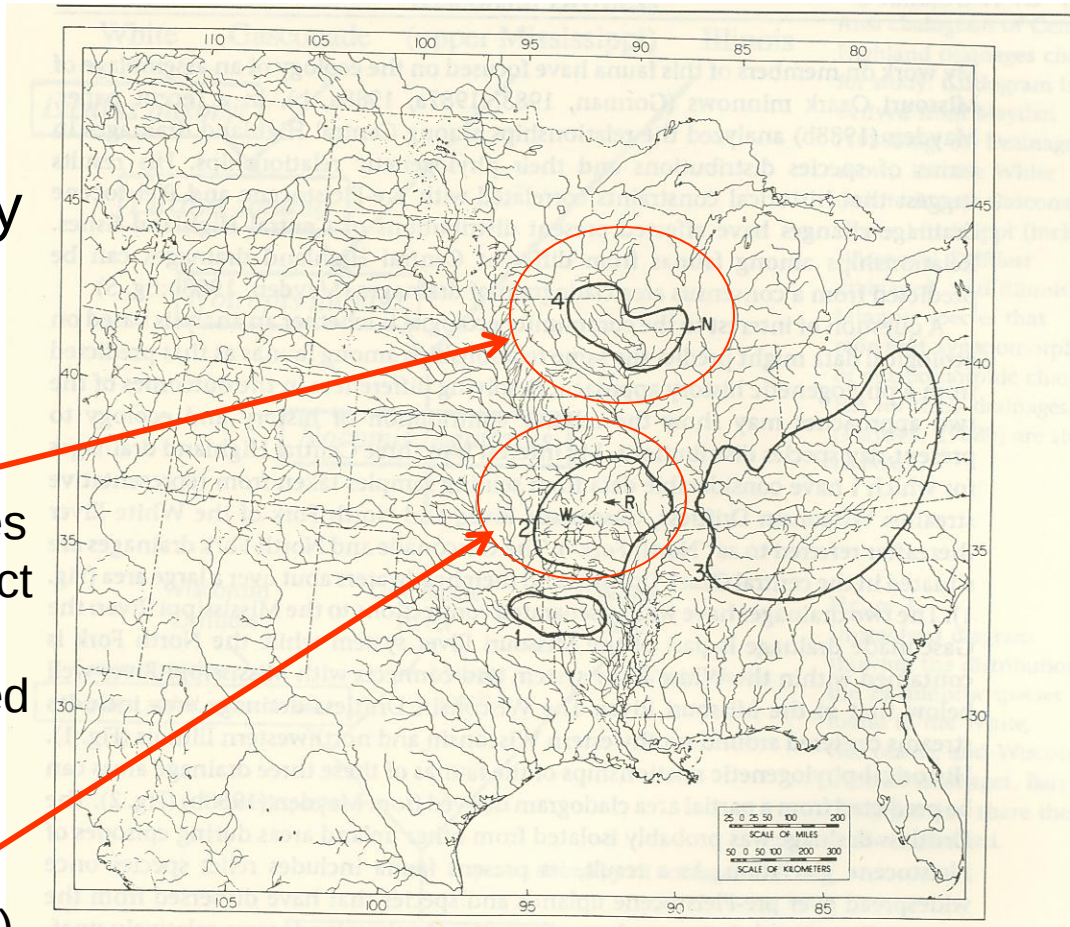
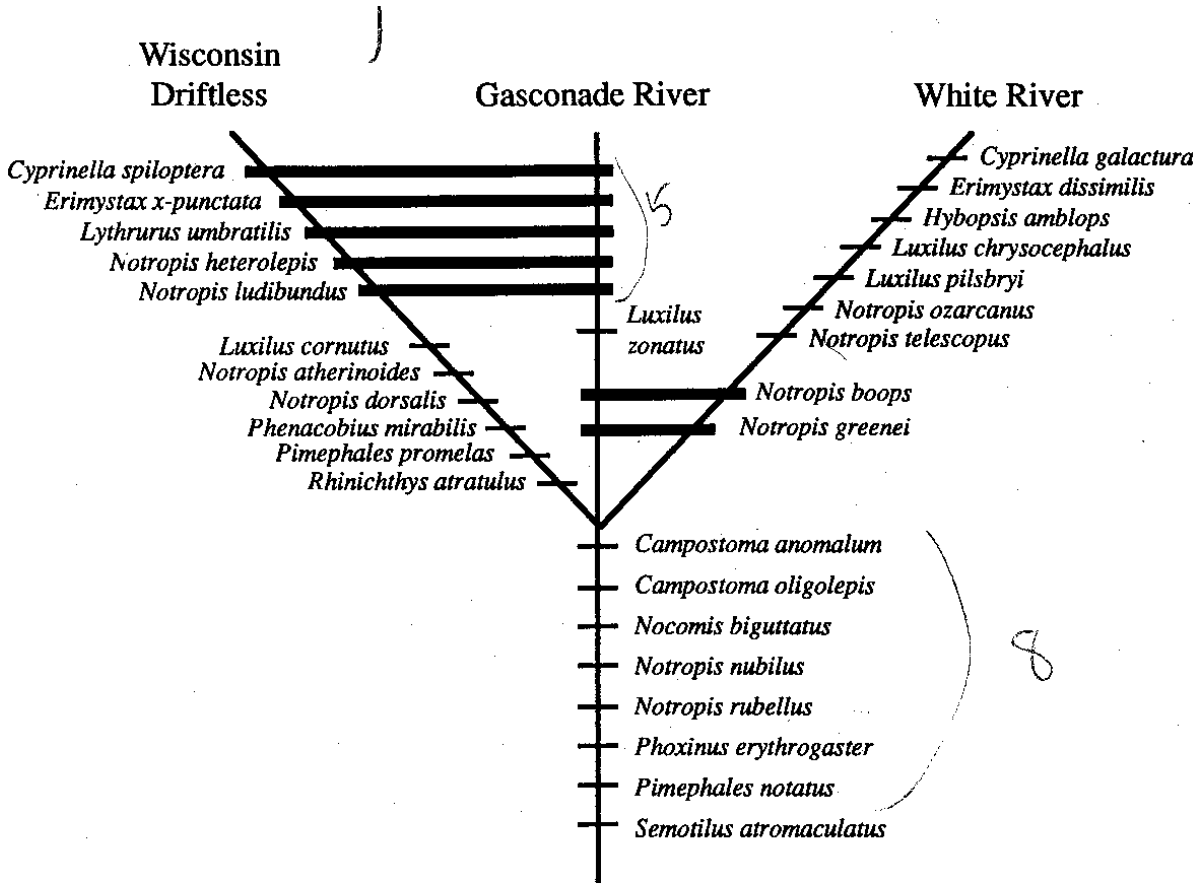


Figure 1.
Major Central Highland regions in North America (Mayden, 1987b) and locations of selected drainages and streams. Regions shown: 1, Ouachita Highlands; 2, Ozark Highlands; 3, Eastern Highlands; 4, present distribution of Central Highland fishes about the Wisconsin Driftless region. Boundaries of Highland regions and distribution of fishes of the Driftless region were redrawn from Mayden (1987b). Selected streams: N, Nippersink Creek, upper Fox River drainage; R, Roubidoux Creek, Gasconade River drainage; W, headwaters of the North Fork of the White River drainage.

Gorman, O. T. 1992. Evolutionary ecology and historical ecology: Assembly, structure, and organization of stream fish communities, pp 659-688. In, Mayden, R. L. (ed) Systematics, Historical Ecology, and North American Freshwater Fishes. Stanford Univ Press

Community Structure

Figure 4.
Phenograms showing relationships among drainages based on a phenetic analysis of shared species. Two possible relationships are shown: (a) *Notropis boops* and *N. greenei* were primitively present in all drainages and became extinct in the Wisconsin Driftless, or (b) these species originated in one Ozark drainage and dispersed to the other.



29 spp of minnows

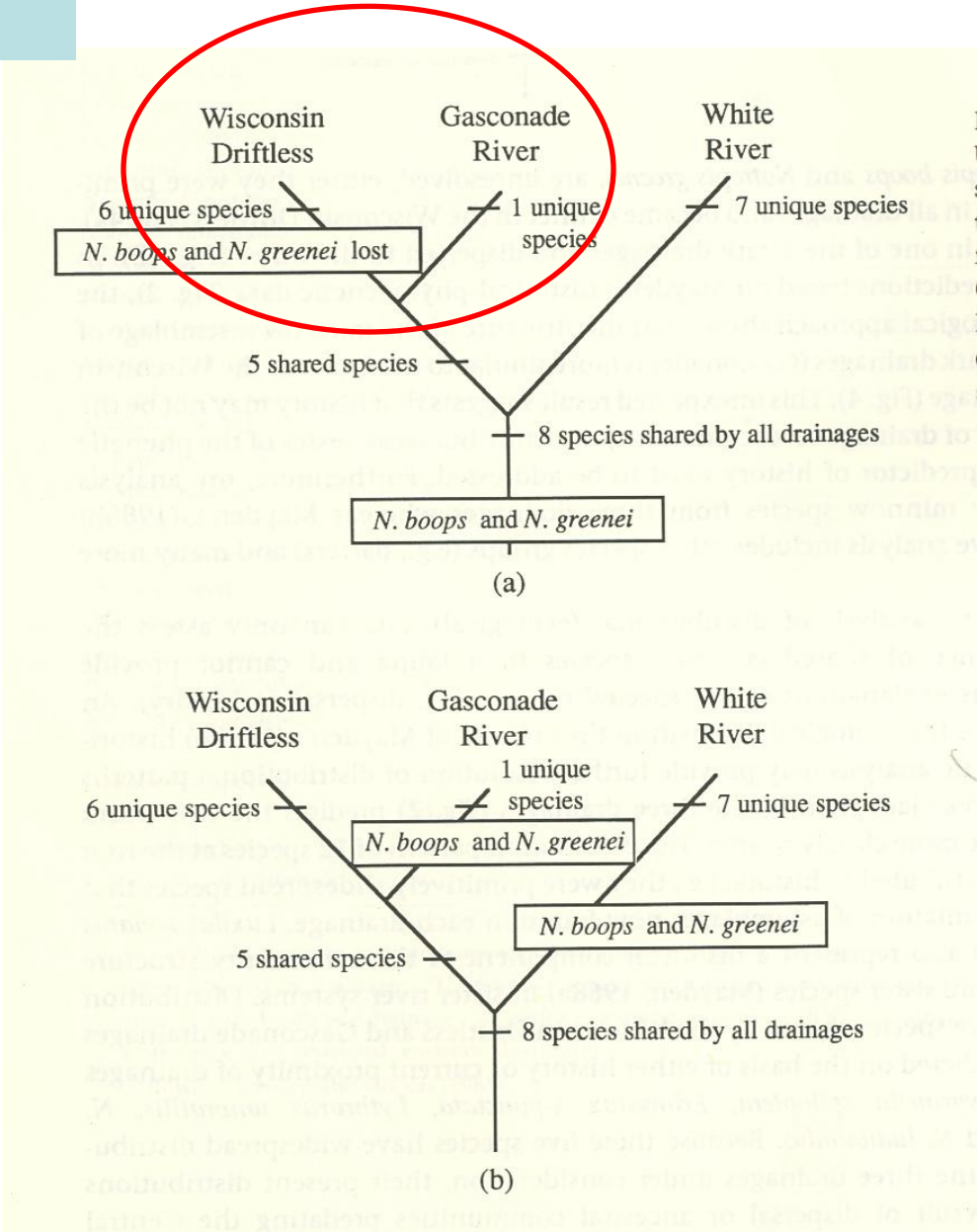
Community Structure

Note: these two systems share more species

Note: simple area cladograms yield predictions that don't require phylogenies.

Alternative hypotheses about history of community change in these drainages. A. *Notropis boops* and *N. greenei* originally present in all drainages, then extinct in Wisconsin. B. Species originate in one Ozark basin and dispersed to the other

General discussion in Lossos. 1996.



Example of analysis of range distributions with null model: Means and Simberloff. 1987. J of Biogeography 14:551-568

Three hypotheses to explain range boundaries

1. Immigration rates increase and extinction rates decrease from base to tip of peninsula (peninsula effect – an equilibrium hypothesis)
2. Peninsula is geologically young (time hypothesis)
3. Peninsula has low diversity of habitats (habitat diversity hypothesis)

Using null model, found boundaries are more common than expected by chance in the middle of peninsula, in counties with high elevation that drops off to the south… most consistent with hypothesis 3.

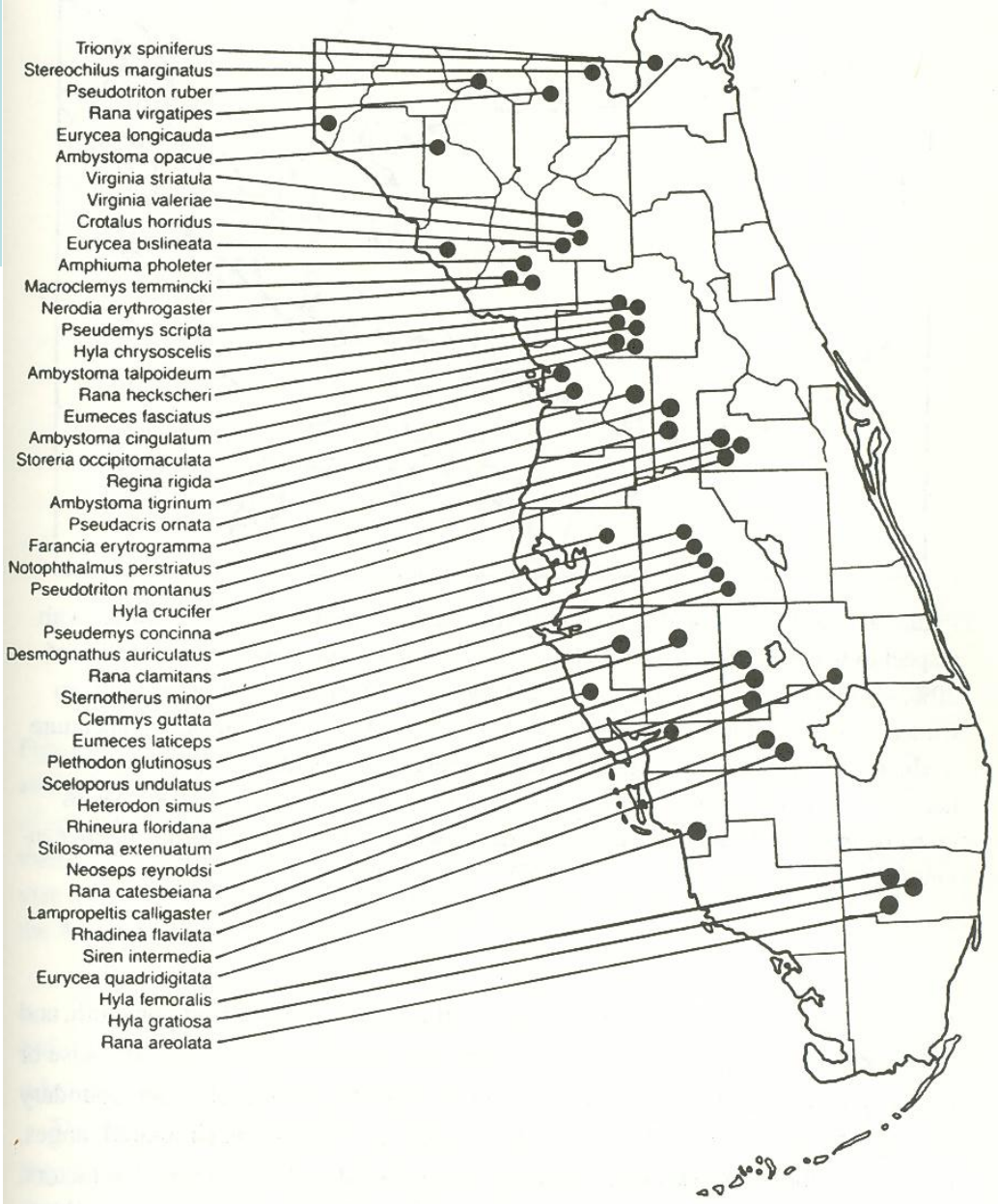
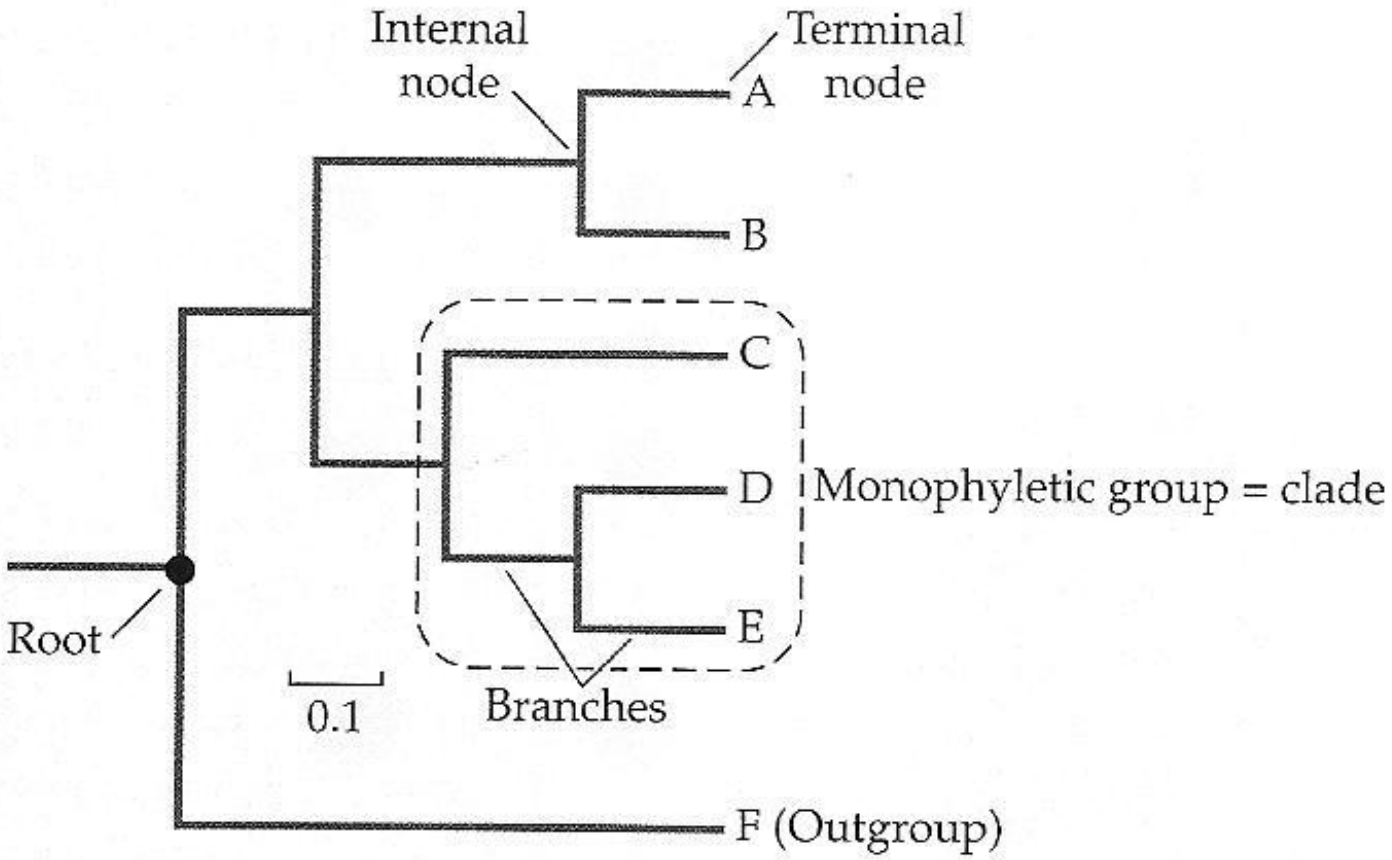


Figure 9.5. Distribution of tipward range termini of amphibians and reptiles in the Florida peninsula. Compared to null model simulations, these range boundaries are clustered in counties with the highest elevations and greatest habitat diversity in the state. From Means and Simberloff (1987), with permission.

Phylogeny 101

Phylogeny describes the evolutionary relationships of a set of organisms



Community Phylogenetics

Incorporating phylogenetic information into community analyses can make historical hypotheses testable. Recall Connell's complaint of the Ghost of Competition Past.

- **Competitive-relatedness or phylogenetic limiting similarity hypothesis**: Species with similar functional traits use resources and habitats similarly… predicts fewer closely related species co-existing than expected by chance.
- **Habitat Filtering hypothesis**: Closely related species have similar environmental requirements… predicts communities will contain more closely related species than expected by chance.
- Test by evaluating phylogenetic overdispersion

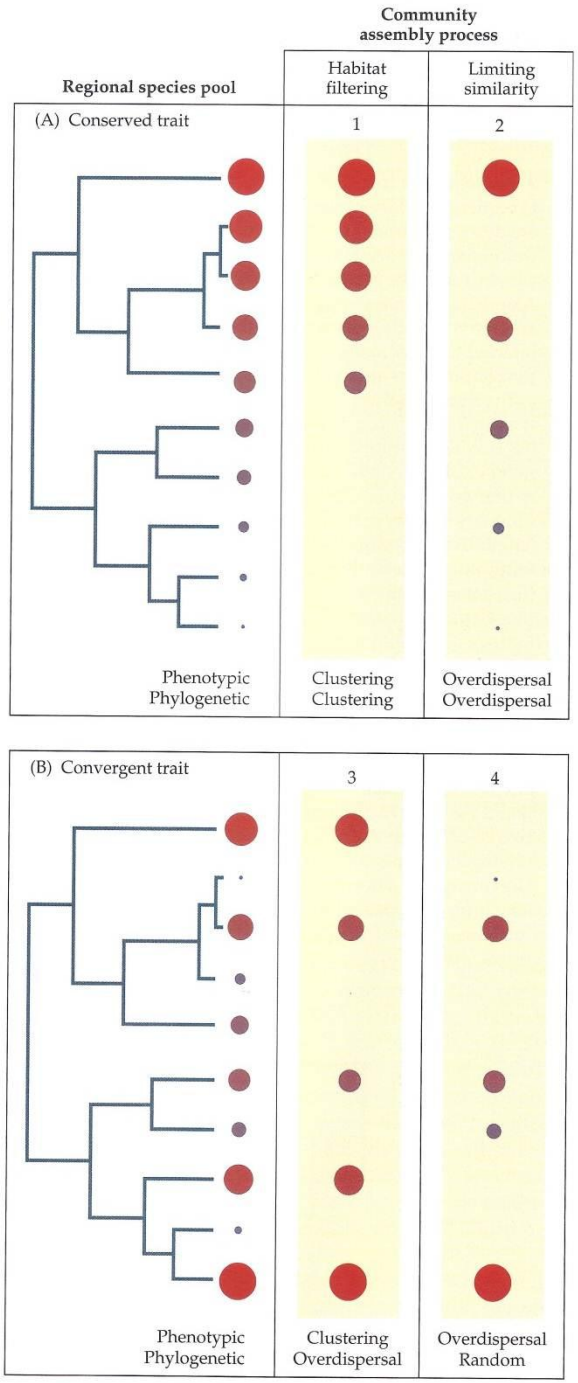


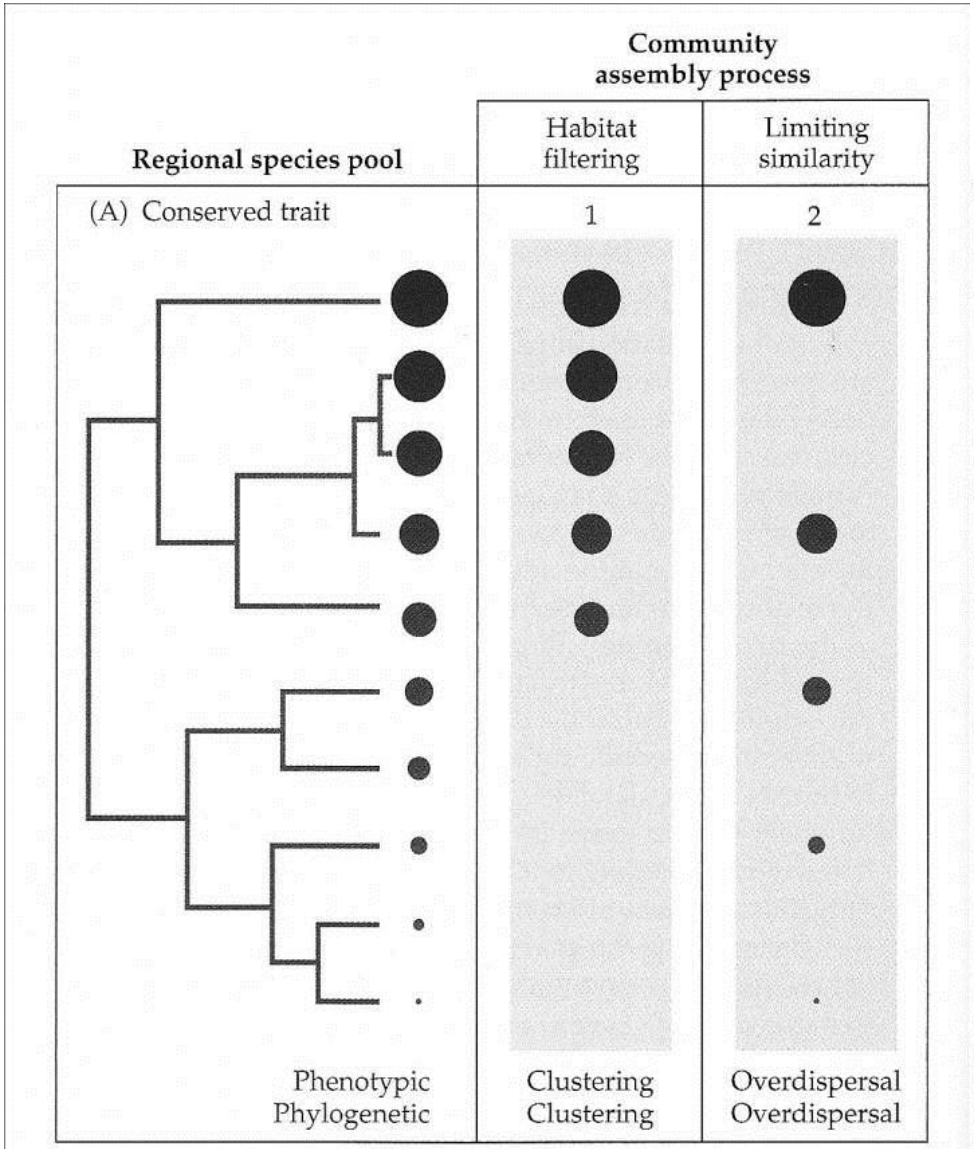
Figure 15.3 An illustration of how processes at the regional and local levels may interact to determine the phylogenetic structure of a community. The red dots represent a quantitative trait (e.g., seed size, specific leaf area, mouth size) and the size of the dot represents the value of that trait (e.g., species with similar-sized dots have similar trait values). In the regional species pool (left panels), the trait may be (A) conserved or (B) convergent across a phylogeny. The results of two different community assembly processes, habitat filtering and limiting similarity (interspecific competition) are illustrated in the right-hand portion of the figure. The shaded boxes represent four hypothetical communities (numbered 1–4), each containing five species selected from the regional pool of ten species. Habitat filtering favors species with similar trait values (communities 1 and 3), thus generating phenotypic clustering within communities; the phylogenetic structure within a community depends on whether traits are conserved or convergent. Limiting similarity prevents species with similar trait values from co-occurring, producing phenotypic overdispersion in communities 2 and 4. The phylogenetic structure is overdispersed in community 2, but can be clustered, random, or overdispersed when traits are convergent (community 4). (After Pausas and Verdú 2010.)

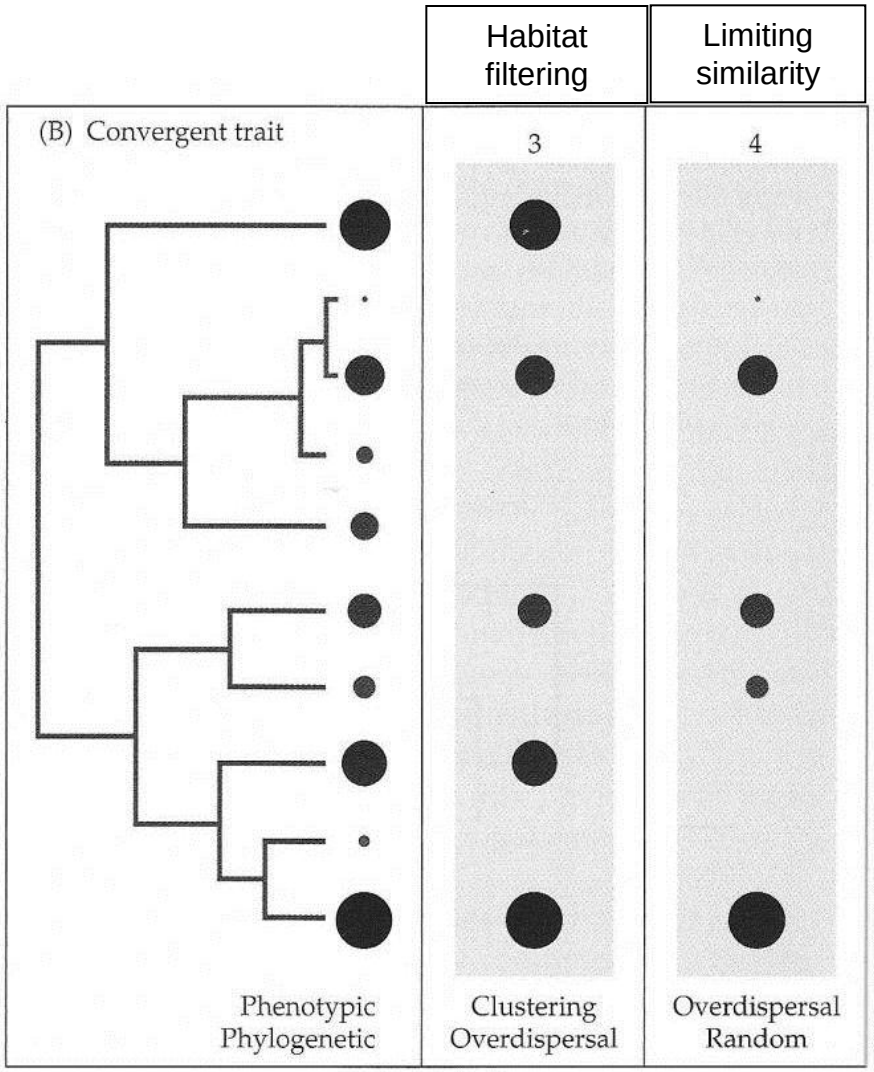
Original textbook figure with legend

Mittlebach, GG. 2012. Community Ecology. Sinauer Press, Sunderland, MA

Community Phylogenetics

Alternative hypotheses are testable because they predict different patterns of species-trait composition





Community Phylogenetics
Tropical Hummingbird Communities

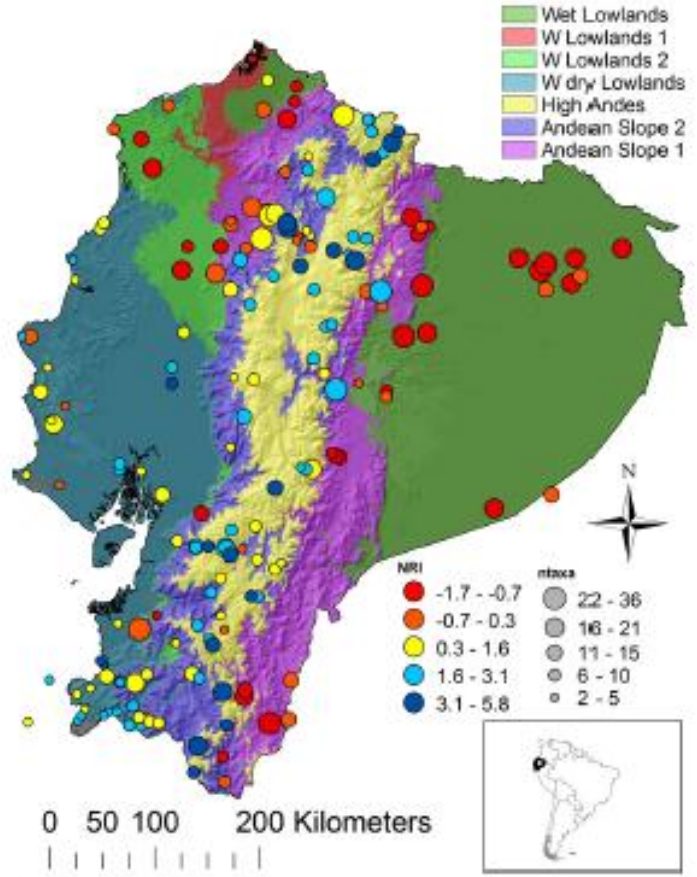


Fig. 1. Map of Ecuador with communities and corresponding NRI values. Size of the circles is proportional to the number of species in each community (ntaxa). Background colors represent the result of an environmental classification (see *Materials and Methods*).

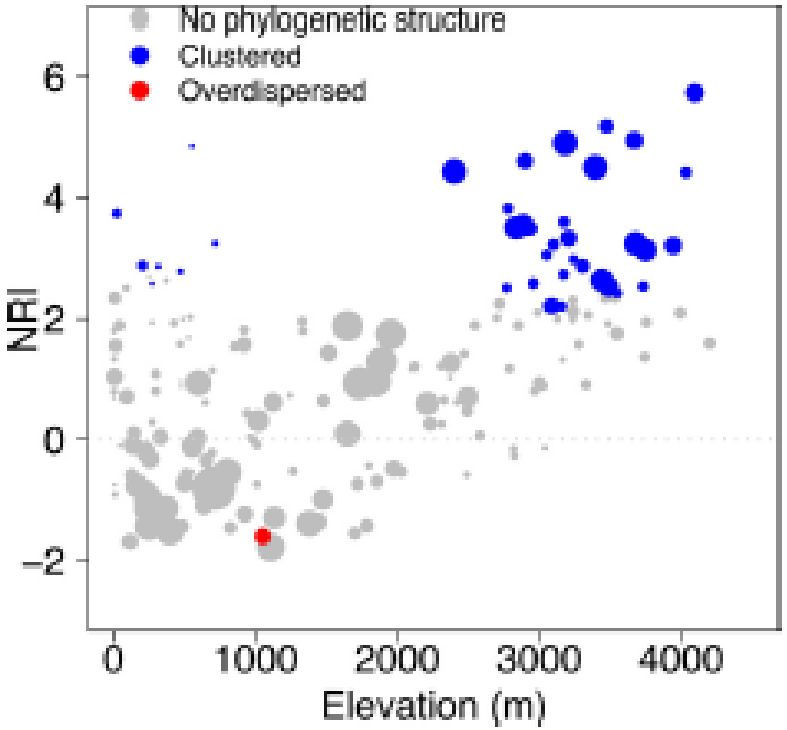


Fig. 2. Plot of NRI versus elevation. The size of the circle is proportional to the number of species in the community.

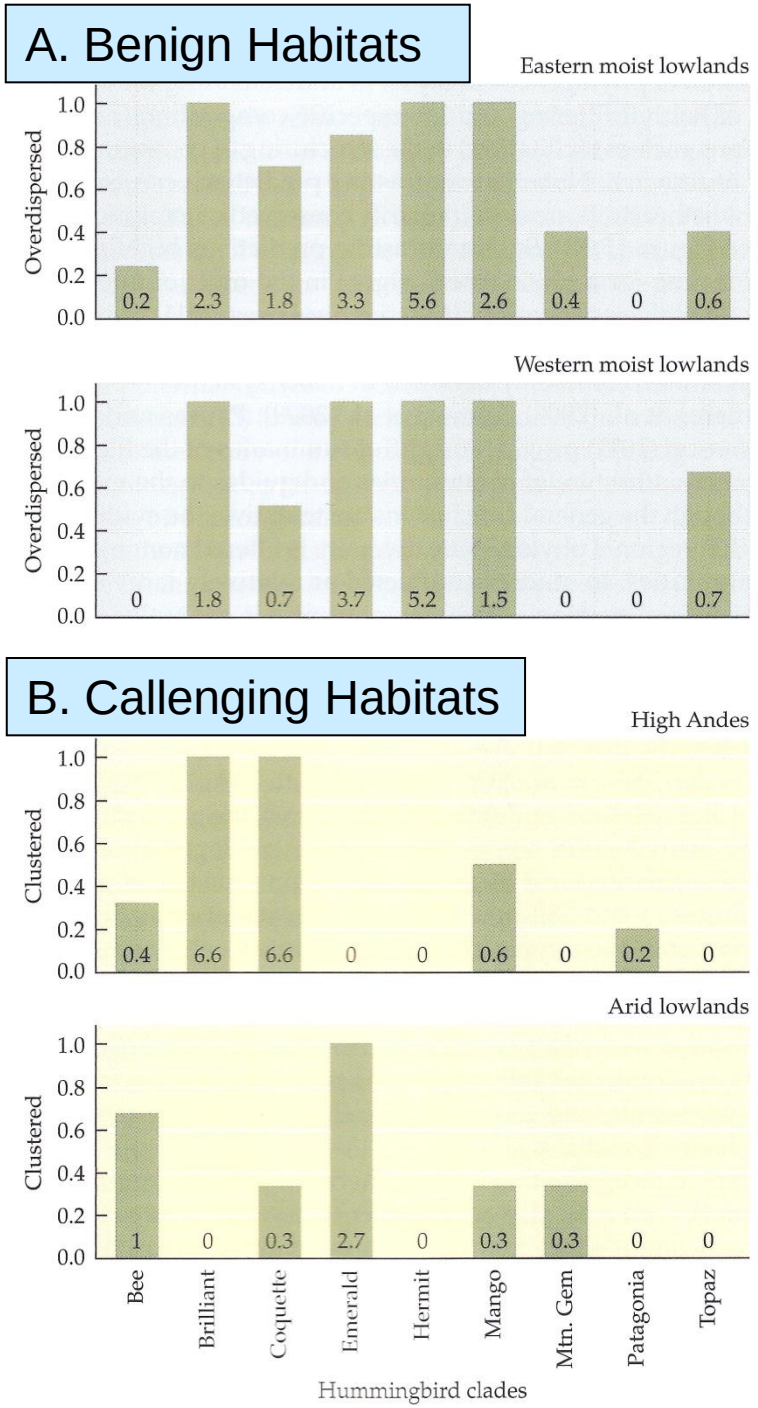
Graham CH, et al. 2009. PNAS 106:19673-19678

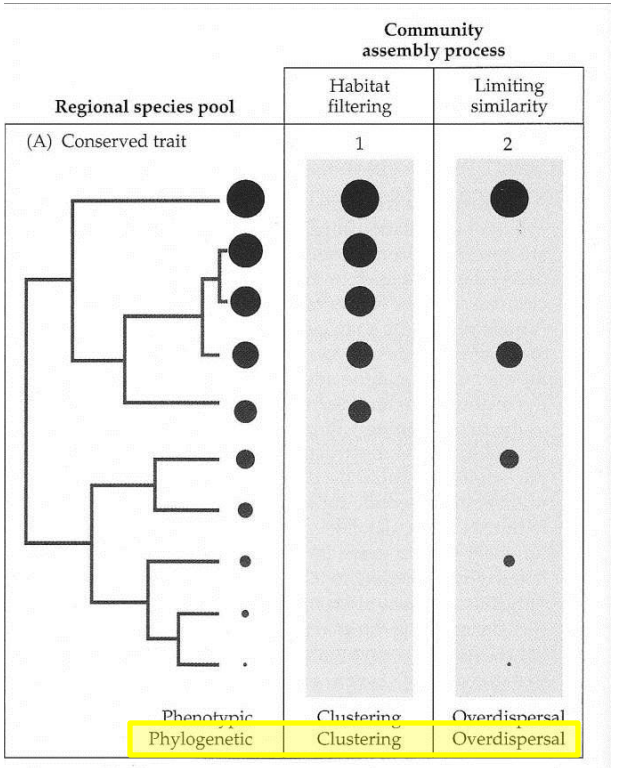
- Compared 189 hummingbird communities.
- Hummingbirds phenotypically clustered (traits phylogenetically conserved)
- 28% of communities phylogenetic clustering;
- 2% phylogenetic overdispersion
- NRI = net relatedness index

A. Clades in top 10th percentile of phylogenetically overdispersed communities (limiting similarity = competition hyp)

B. Clades in top 10th percentile of phylogenetically clustered communities (habitat filtering)

Numbers in bars are mean number of species per community





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B. Clades in top 10th percentile of phylogenetically clustered communities (habitat filtering)

Numbers in bars are mean number of species per community

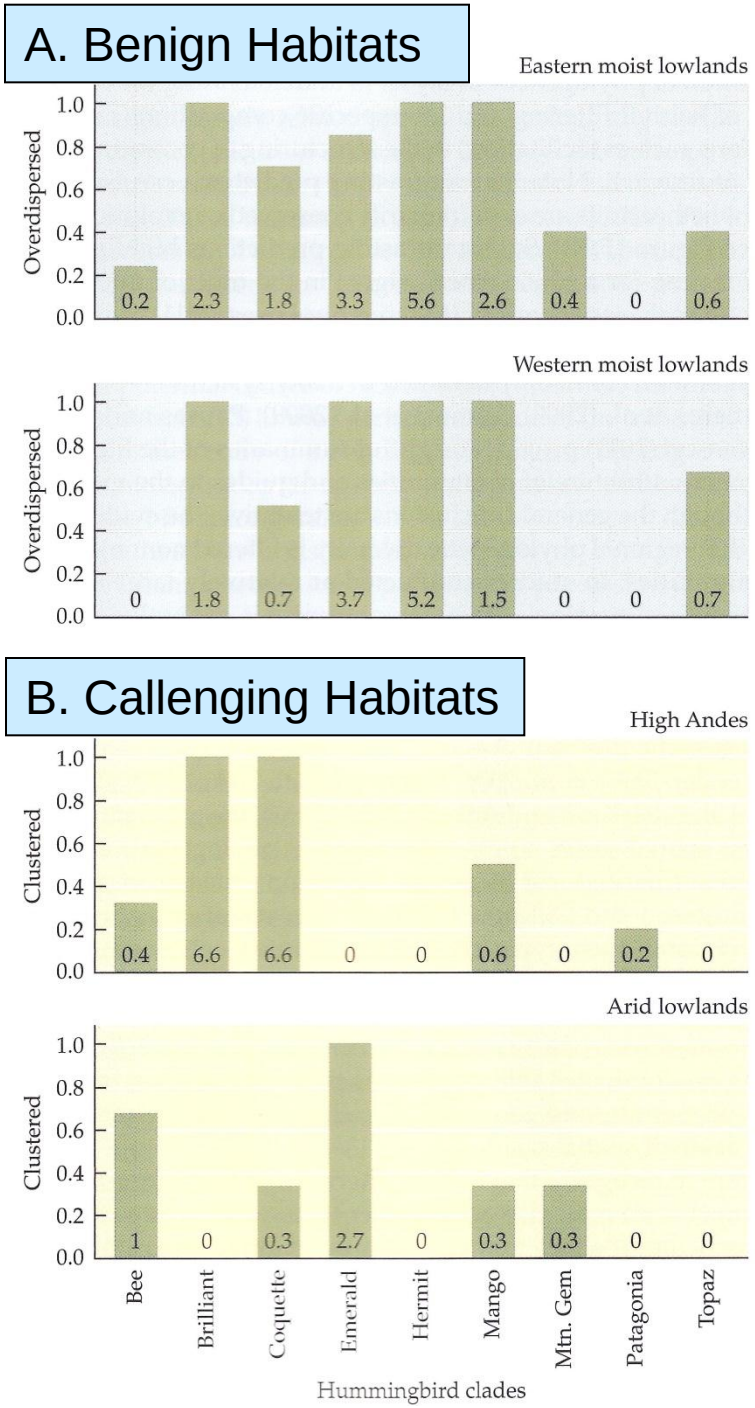


Figure 15.5 Hummingbird communities in Ecuador show the greatest phylogenetic dispersion in the environmentally benign moist lowlands; they show the greatest phylogenetic clustering in the challenging environments of the high Andes and the dry western lowlands. (A) Histograms show hummingbird clades represented in the top tenth percentile of phylogenetically overdispersed communities that exist in the eastern and western moist lowlands. (B) Histograms show the clades in the top tenth percentile of phylogenetically clustered communities existing in the high Andes and the dry regions west of the Andes. Hummingbird clades are listed along the *x* axis. The *y* axis shows the proportion of communities where a given clade is represented; the numbers in the bars are the mean numbers of species per community. Overdispersed and clustered communities tend to be represented by different clades in a manner consistent with their ecologies. (After Graham et al. 2009.)

Graham CH, et al. 2009. PNAS 106:19673-19678

Adaptive Radiation and Community Assembly

- Two alternative patterns of speciation and community assembly
- One has species differences due to allopatric (independent) evolution, the other due to sympatric evolution and niche partitioning
- Phylogenetic analysis may be able to separate these

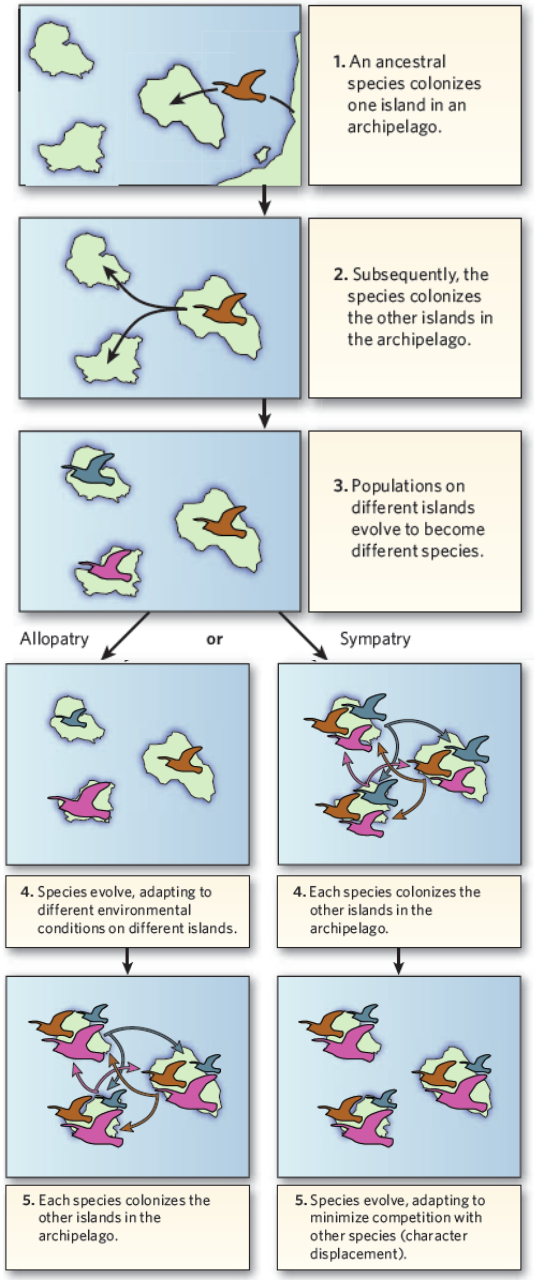
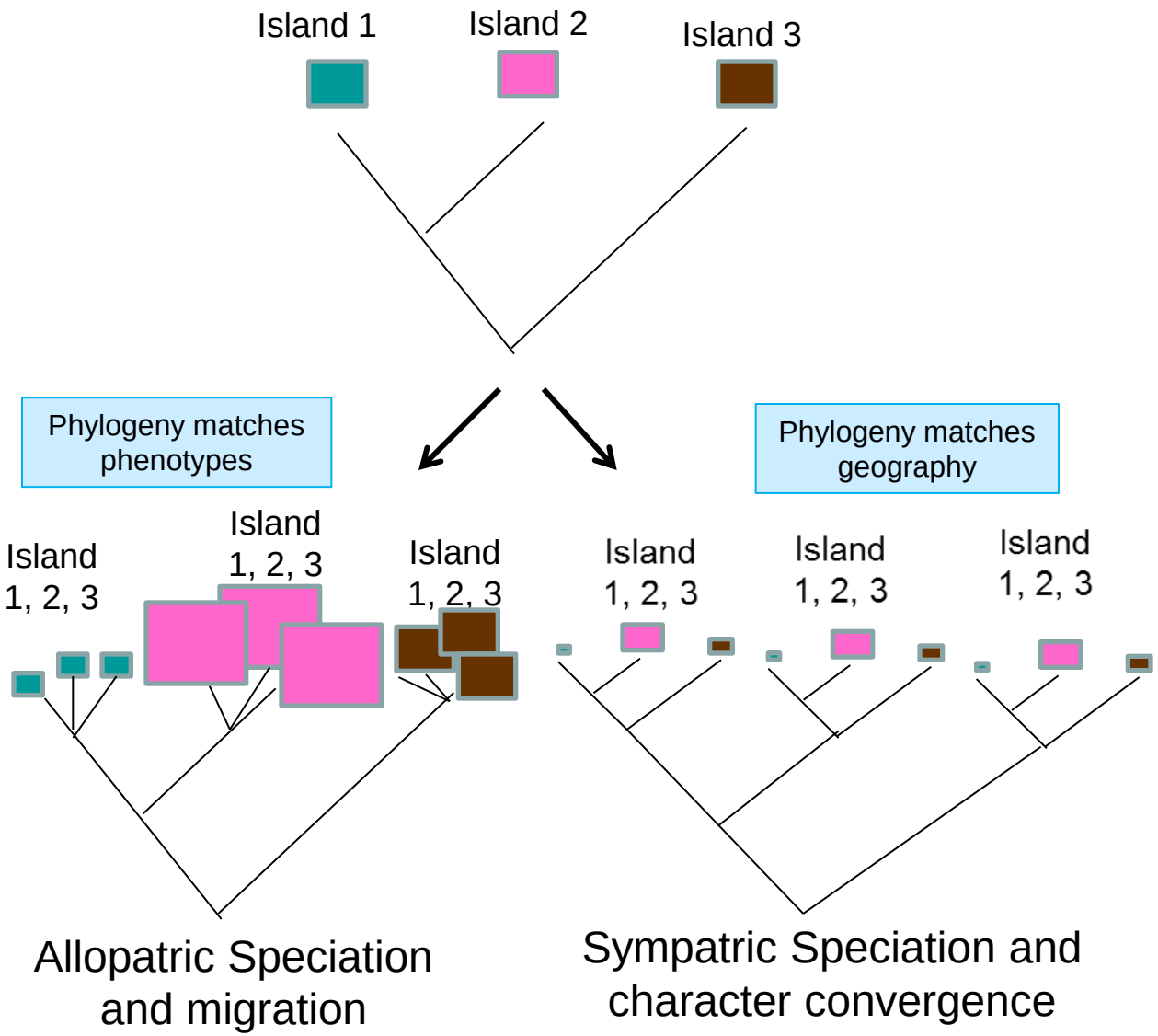
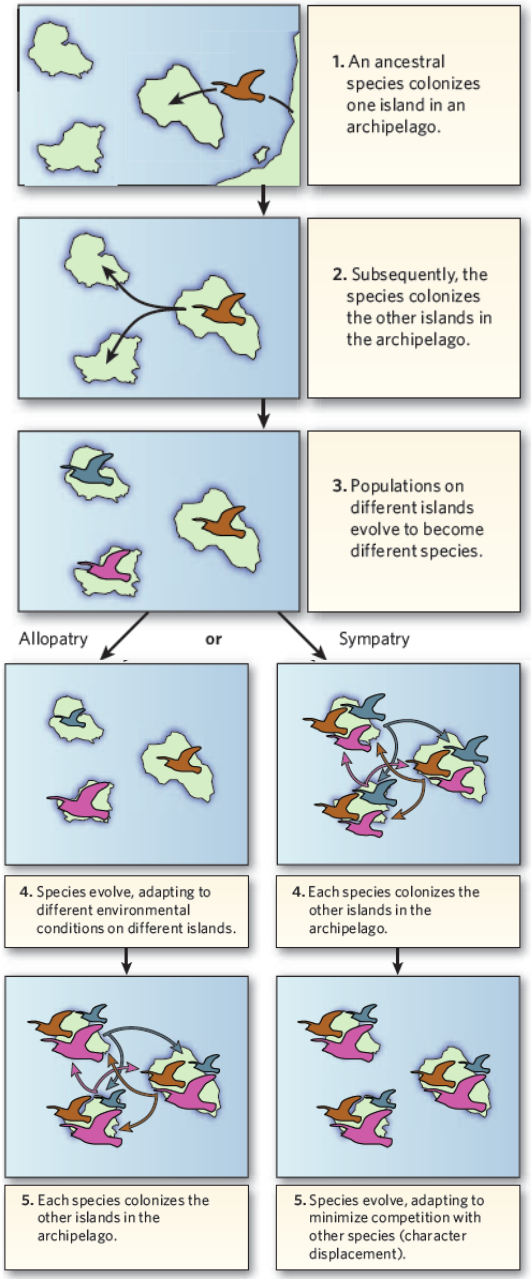


Figure 3 | Two variants of a model of allopatric speciation and subsequent sympatry in an archipelago. The top three panels apply to both models. The lower panels illustrate the possible roles of ecological divergence in allopatry (left) and character displacement in sympatry (right). (Conceptual framework from refs 8 and 16.)

Adaptive Radiation and Community Assembly





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Adaptive Radiation and Community Assembly

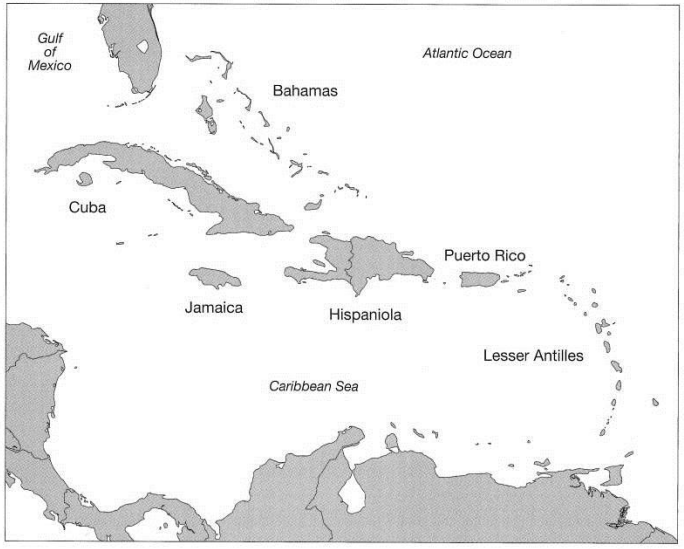
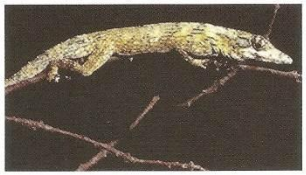


FIGURE 3.1
The West Indies. The Greater Antilles are the islands of Cuba, Hispaniola, Jamaica, and Puerto Rico and nearby smaller islands.

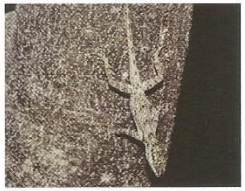
Crown giant
Large body, large toe pads
Cuba: *Anolis equestris*
Hispaniola: *A. ricordii*
Jamaica: *A. garmani*
Puerto Rico: *A. cuvieri*

Trunk–crown
Medium body, large toe pads
Cuba: *Anolis allisoni*
Hispaniola: *A. chlorocyanus*
Jamaica: *A. grahami*
Puerto Rico: *A. evermanni*

Twig
Short body, slender legs and tail
Cuba: *Anolis angusticeps*
Hispaniola: *A. insolitus*
Jamaica: *A. valencienni*
Puerto Rico: *A. occultus*



Trunk
Vertically flattened body, long forelimbs
Cuba: *Anolis loysianus*
Hispaniola: *A. distichus*
Jamaica: none found
Puerto Rico: none found



Trunk–ground
Stocky body, long hindlimbs
Cuba: *Anolis sagrei*
Hispaniola: *A. cybotes*
Jamaica: *A. lineatopus*
Puerto Rico: *A. gundlachi*

Grass–bush
Slender body, very long tail
Cuba: *Anolis alutaceus*
Hispaniola: *A. olssoni*
Jamaica: none found
Puerto Rico: *A. pulchellus*

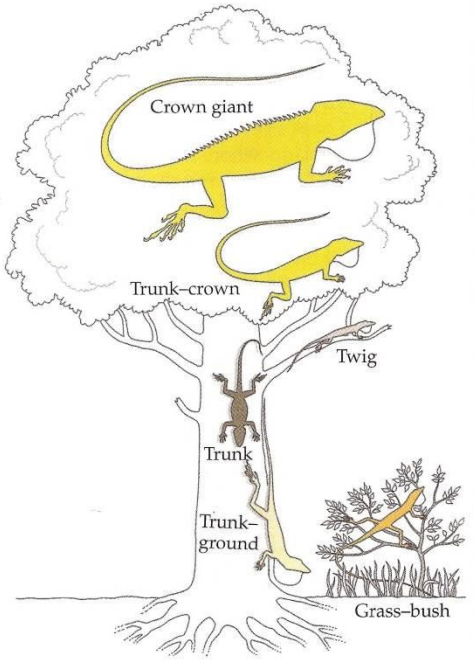
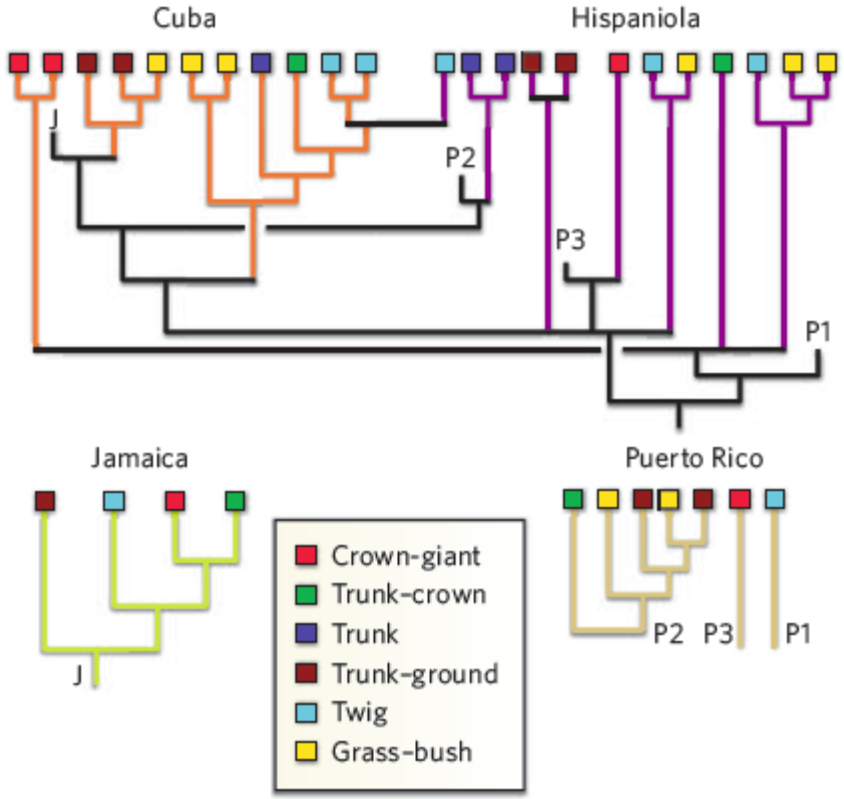


Figure 8.6 Adaptive radiation among *Anolis* lizards in the islands of the Greater Antilles. Interspecific competition has led to a variety of niche specialists (inset drawing; lizard body outlines are drawn to approximate scale relative to one another). Lizards adapted to corresponding niches on the different islands look substantially similar, although radiation has been independent on each island and thus the species listed are not closely related. Photos illustrate one species (named in color type) exemplifying each niche. (From Losos 2009, 2010; photographs courtesy of Jonathan Losos.)

Adaptive Radiation

- Phylogeny matches geography more than it matches phenotypes
- Convergent evolution of functional types



Losos and Ricklefs. 2009. Nature 457:830-836

TABLE 1. The ecological geneticist's creed.

Creed	Explanation
Explaining the abundance and distribution of organisms is a genetic problem.	The ecological amplitude of a species both within and among communities has a genetic component.
The forces maintaining species diversity and genetic diversity are similar.	An understanding of community structure will come from considering how these kinds of diversity interact.
Adaptation is a dynamic process, operationally definable, and not just an emotional matching of the character to the environment.	Fitness and the contribution of phenotypes to fitness can be measured in terms of the mortality and fecundity of individuals within populations.
Environmental change will be accompanied by changes in both genetic composition and changes in numerical dynamics.	Genetic response is likely to result in compensatory changes in fitness and life-history components.
The distinction between "ecological time" and "evolutionary time" is artificial and misleading.	Changes of both kinds may be on any time scale: in principle, evolutionary and ecological changes are simultaneous.
The genetic quality of offspring is as important as the quantity.	Sexual systems are concerned with regulating the genetic quality of offspring.
The view that there is always an "evolutionary play" within an "ecological theater" is artificial and misleading.	The "ecological play" often happens in the "evolutionary theater." Selection at the genic or cellular levels may have phenotypic effects with enormous ecological consequences. Genetic events may drive ecology, rather than vice versa.
Speciation is an ongoing and commonplace process, occurring constantly and persistently around us.	It is only deemed to be rare by taxonomists, and the use of Latin binomials by ecologists is at best a crude approximation.
Environments are most appropriately defined by the ecology and genetics of the organisms themselves, and only indirectly by environmental measurements.	We can recognize three types of environments: external, ecological, and selective. Their measurement and interpretation have important consequences for population and evolutionary dynamics.
A population to an ecologist is not the same as it is to a geneticist.	Understanding the contrasting way in which the term is used is essential for unifying ecology and genetics.

Antonvic, J. 2003. Towards a community genomics? Ecology 84:598-601