Phylogenetic Niche/Trait Conservatism

Ty Taylor for trait-based ecology course

What's a niche?

- Grinellian niche: "The niche-relationships of the California thrasher" The Auk 1917.
 - Defined based on observed habitat characteristics within species distribution (coarse scale).
- Eltonian niche: Animal Ecology 1927
 - Emphasizing local-scale biotic interactions.
- Reviewed by Soberon (2007)

What's a niche?

- Hutchinsonian niche (1957): The set of biotic and abiotic conditions within which a species can persist. Fundamental vs. realized niche.
 - Where intrinsic growth rate $(r_0 = per-capita birth rate minus death rate) ≥ 0.$
- Reviewed and applied to current understanding by Holt (2009)

Holt 2009

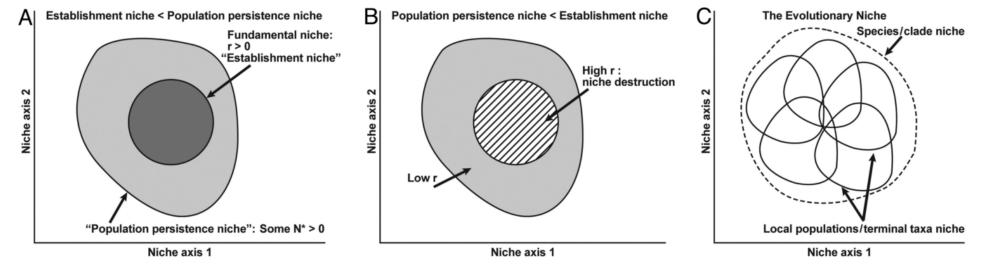


Fig. 2. Alternative niche concepts. (A) With Allee effects, the population persistence niche > the establishment niche. (B) With niche destruction, sites with a high initial growth rate are vulnerable to extinction, so lie outside of the population persistence niche, along these axes. In plant ecology, the term persistence niche is sometimes used to denote the role of individual adult survival through disturbances in permitting population persistence, for populations that have already established (90). I am using the term population persistence niche more broadly, to emphasize distinct aspects of the niche at the population rather than individual level. (C) The evolutionary niche. This figure (adapted from ref. 64) can describe many scenarios: (i) a species with geographic variation among niches of local populations; (ii) frames of a species over time, with niches wandering over its history within broad limits (bounded niche evolution); (iii) aggregate niche of a clade, with specialists descended from an ancestral generalist; and (iv) an adaptive radiation, where from an ancestral specialist (not shown) a clade collectively wanders through much more niche space than represented in any species.

- Sometimes niche-related traits evolve rapidly, sometimes very slowly
- "Niche conservatism (NC) is the retention of niche-related ecological traits over time."
 - Note interchangeable use of 'niche' and 'trait'.
- Phylogenetic niche conservatism (PNC) = retention of traits within clades (among related species)

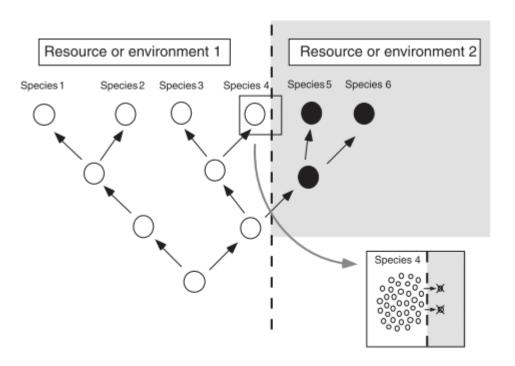
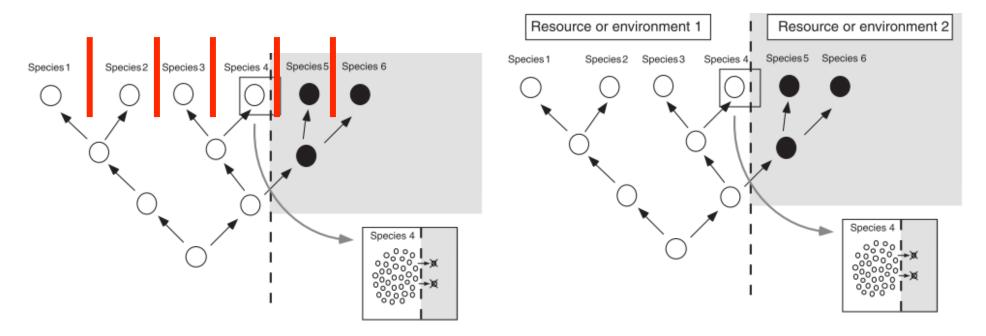


Figure 1 Niche conservatism creates phylogenetic patterns in ecological data. For a given ecological variable, the clade originates as a single ancestral species that utilizes a given environment or resource (e.g. diet, host, habitat, climatic regime). Early in the history of the group, there is a niche shift to utilize an alternate resource or environment. At the present time, there are four

- Contrasting fine vs. coarse-scale niches
 - What are some examples at each scale?
 - What gives rise to the barriers (depicted in the inset) in each example?
 - Crisp et al., 2009: Biome stasis at speciation outweighs biome shifts 25:1

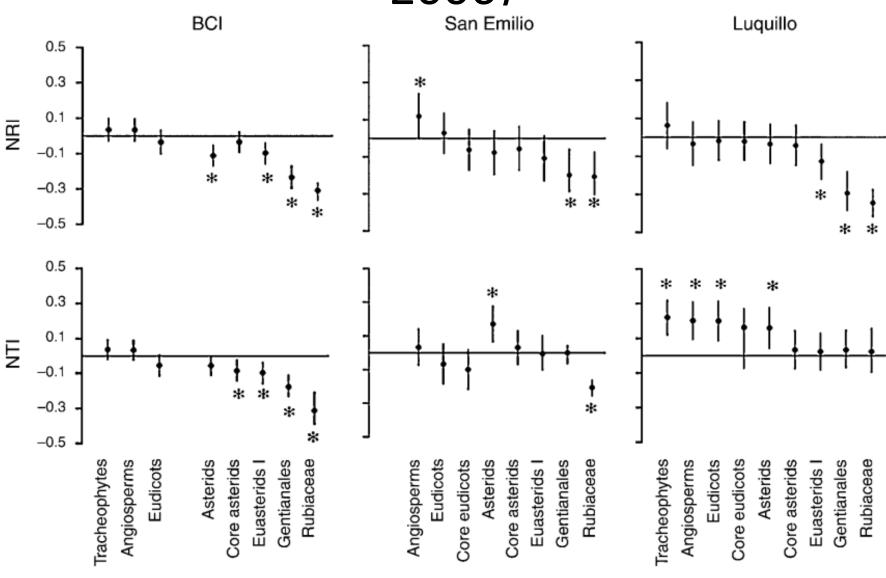


- "A test of NC without a related question or application is somewhat meaningless."
- NC is scale-dependent

Community assembly

Competition **Environmental** filtering

Community assembly (Swenson et al., 2006)



Community assembly (Swenson et al., 2006)

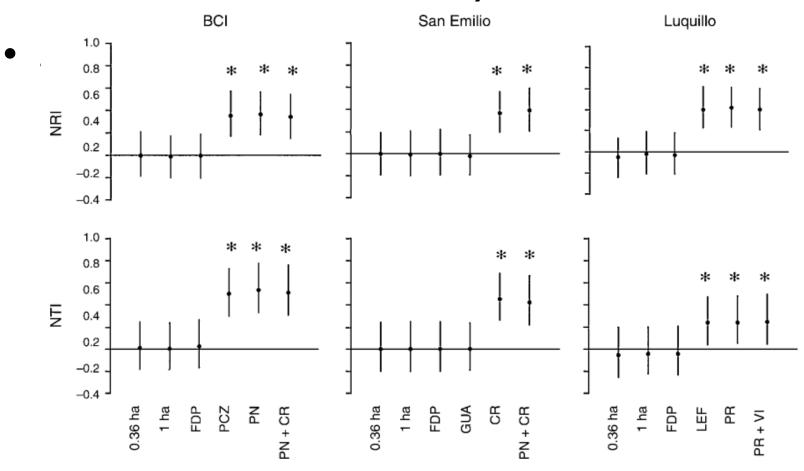


Fig. 2. The median NRI and NTI scores for BCI, San Emilio, and Luquillo FDPs using six different species pool sizes. Positive values indicate phylogenetic clustering, and negative values indicate phylogenetic overdispersion. The bars represent 95% confidence intervals. Key to abbreviations: FDP, forest dynamics plot; PCZ, Panama Canal Zone; PN, Panama; PN+CR, Panama and Costa Rica; LEF, Luquillo Experimental Forest; PR, Puerto Rico; PR+VI, Puerto Rico and the Virgin Islands; GUA, Santa Rosa and Palo Verde National Parks; CR, Costa Rica.

^{*} P < 0.05 (Wilcoxon test).

- Species distribution models (SDM)
 - Mapping the climatic distribution of a species provides a predictor for climatic factors that set range limits.
 - NC can be tested by asking whether the SDM for one species predicts the geographic range of its sister species (Peterson et al., 1999)

- Species distribution models (SDM)
 - Is that good enough? Does the current realized niche of a species tend to reflect its fundamental niche?
 - Take care with 'forbidden combinations!'
 - Jared Diamond (1975) catalogued all bird species occurring on each of many small islands, all nearby to each other.
 - Dubbed all combinations of species that never occurred together as "forbidden combinations".
 - Received much flack and sparked much debate over dynamics of realized vs. fundamental niches.

- Climatic change
 - Paleontology suggests the climate change induced movement of species more than changes in traits or extinction (p. 1314).
 - Review of 53 bird species showed 48 tracked their previous climatic niches as climate changed (p. 1316; Tingley et al., 2009)



Figure 1.7. Distribution of closed canopy megathermal rainforests during the Late Paleocene/Early Eocene thermal maximum (Morley, 2000a). Paleogeography and paleocoastlines from Smith et al. (1994). Occurrences of evaporites and bauxites from Boucot et al. (in press). Dotted lines are floristic province boundaries.

Figure from chapter 1 of Bush et al., 2011

• Collett 2011: Lowland tropical rainforest particularly susceptible to climate change because they will have to move up to 1000km to find thermal refuge.

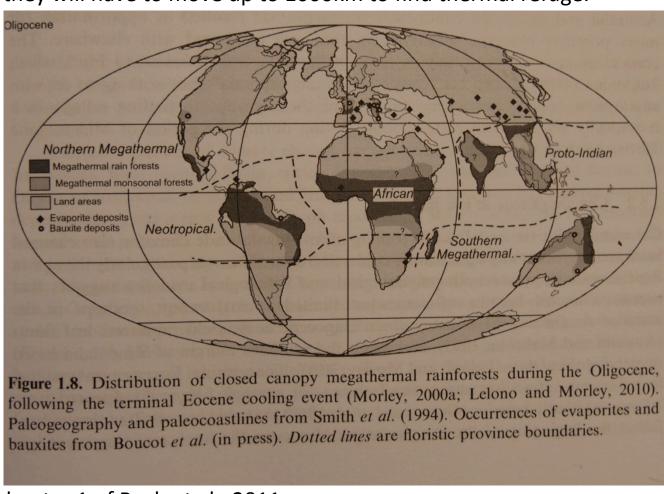


Figure from chapter 1 of Bush et al., 2011

- Invasive species
 - Wiens and Graham (2005) found a strong relationship between native and introduced range limits.
- Species interactions
 - Figs and fig wasps
 - Fungus-farming ants and their fungi (Chapela et al., 1994)
 - Herbivores and plants (Wieblen et al., 2006)

Chapela et al., 1994: fungus-farming ants and their fungi

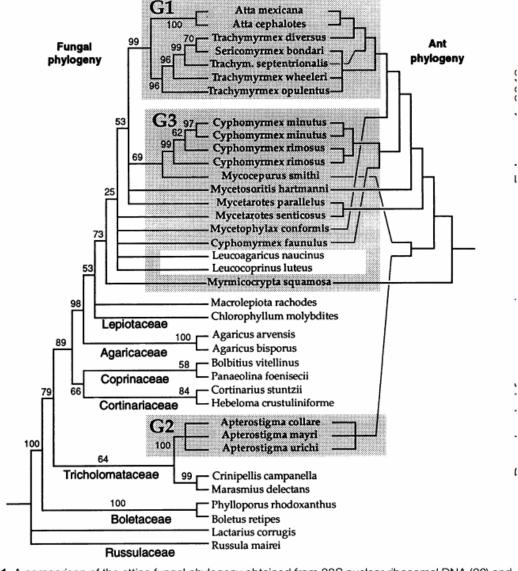


Fig. 1. A comparison of the attine fungal phylogeny obtained from 28S nuclear ribosomal DNA (20) and

Wieblen et al., 2006

- Assessed host-plant phylogenetic conservatism of insect-herbivores in
- Found that 25-44% of herbivores feeding on more than one plant species were clustered on the plant phylogenetic tree; 0-6% were overdispersed.

Phylogenetic and functional diversity and ecosystem (aggregate) function

- Cadotte et al., 2009: Phylogenetic diversity explains grassland productivity better than traits.
- So where do traits come into the picture?
- Why is PNC typically about the environment or phylogeny and not the traits?

Proportion NC:not NC

- Using realized niches as a baseline, how can we assess what proportion of species or clades show NC in response to climate change or invasions?
 - Extinction and non-invasion typically make no data points!

Hof et al., 2010

- Phylogenetic signals in the climatic niches of the world's amphibians.
- First analysis for PNC in entire clade worldwide.

Hof et al., 2010 - methods

- Ordination technique
 - Climatic niche estimated based on species locations
 - Defines the mean and variance (breadth) of environmental conditions used by the species
 - What you see is what you get: No population dynamics or ecophysiological estimates involved

Hof et al., 2010 - methods

- Blomberg's randomization
 - Take phylogenetic tree and randomly distribute data (traits, etc.) across tips.
 - Ask whether that data fits the phylogeny better than when randomly distributed
- Vicariance component analysis (VCA)
 - How much of species-level niche variance is explained at different taxonomic levels

Hof et al., 2010 - methods

ANOSIM

- Niche dissimilarity calculated as Euclidean distance (in ordination space) between sp pairs.
- Then ask: Is average dissimilarity between species within a group (e.g., genus) less than dissimilarity between species of different groups?
 - Yes = PNC!

Wilcoxon rank sums

- Calculated pairwise niche overlap (on OMI axes 1 and 2)
- Asked: is niche overlap higher within groups than between them?
 - Yes = PNC!

Hof et al., 2010 - results

- PNC observed in majority of cases using all analyses.
- However, phylogenetic signal was variable among different regions within each clade.
 - E.g., using ANOSIM, 3 of 13 analyses showed larger within-family niche differences than between family niche differences.

Hof et al., 2010 - Discussion

- Their analyses were based on realized climatic niches
 - How would you expect the results to differ if based on fundamental niches?
- Can their results be used to infer amphibian clade responses to climate change?

Ackerly 2009

- Introducing the 'felsen;
- 1 felsen = 1 unit of variance between sister taxa in ln-tranformed traits per million years.
- Measured rate of accrual of variance in trait values within clades for:
 - Traits: mature height, seed size, leaf size
 - Clades: Aesculus, Acer (north temperate);
 Caenothus, Arbutoideae, (California); lobeliads and silverswords (Hawaii)

Ackerly 2009

- Accrual of variance in height through time.
- 0.14 (Acer) to 0.79 felsens (silversword)
- Average rates: seed size < height < leaf size

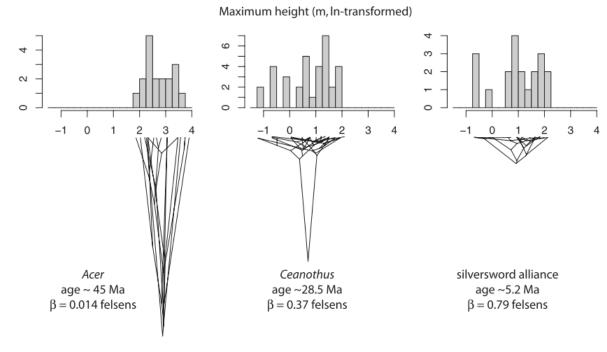


Fig. 2. Traitgrams for height evolution in *Acer* (*Left*), *Ceanothus* (*Center*), and the Hawaiian silversword alliance (*Right*). Horizontal breadth of each phylogeny corresponds to range of In-transformed height values among terminal taxa, and vertical height is scaled to crown age of clade. Evolutionary rates (in felsens) are shown for each tree, analyzing the data with an UBM model.

Questions for John Wiens

- Where are the traits in PNC?
- Why does phylogenetic diversity explain ecosystem function better than functional diversity?
- Is climatic niche modeling enough to predict species/clade responses?
- How can we improve our ability to predict those responses?

Discussion with John Weins

- Previous suggestions that narrower niche width is correlated with niche diversification
 - He tried to find this in newts but didn't, it seemed the other way around.
- Where is niche conservatism now?
 - Some still think "it's stupid" -> answer is whether
 you find it a useful way of thinking or not.

Discussion with John Wiens

- What's the way forward with PNC?
 - Mechanisms behind it are largely unknown.
- So is it dangerous to use it if we don't understand why it works (e.g., to predict species/clade/ ecosystem responses)?
 - PNC helps to see patterns. We can use those patterns to generate hypotheses, and test those at the species scale. We can then use that more mechanistic knowledge to inform further investigation at the phylogenetic scale.
- (Ty) The feedback of research between scales is important and a way forward for PNC and species/ecosystem predictions.

Citations

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Other resources

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- Olalla-Tarraga et al., 2011. Climatic niche conservatism and the evolutionary dynamics in species range boundaries: global congruence across mammals and amphibians. Journal of Biogeography 38:2237-2247.
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