Determinants of Distribution

1) The Niche

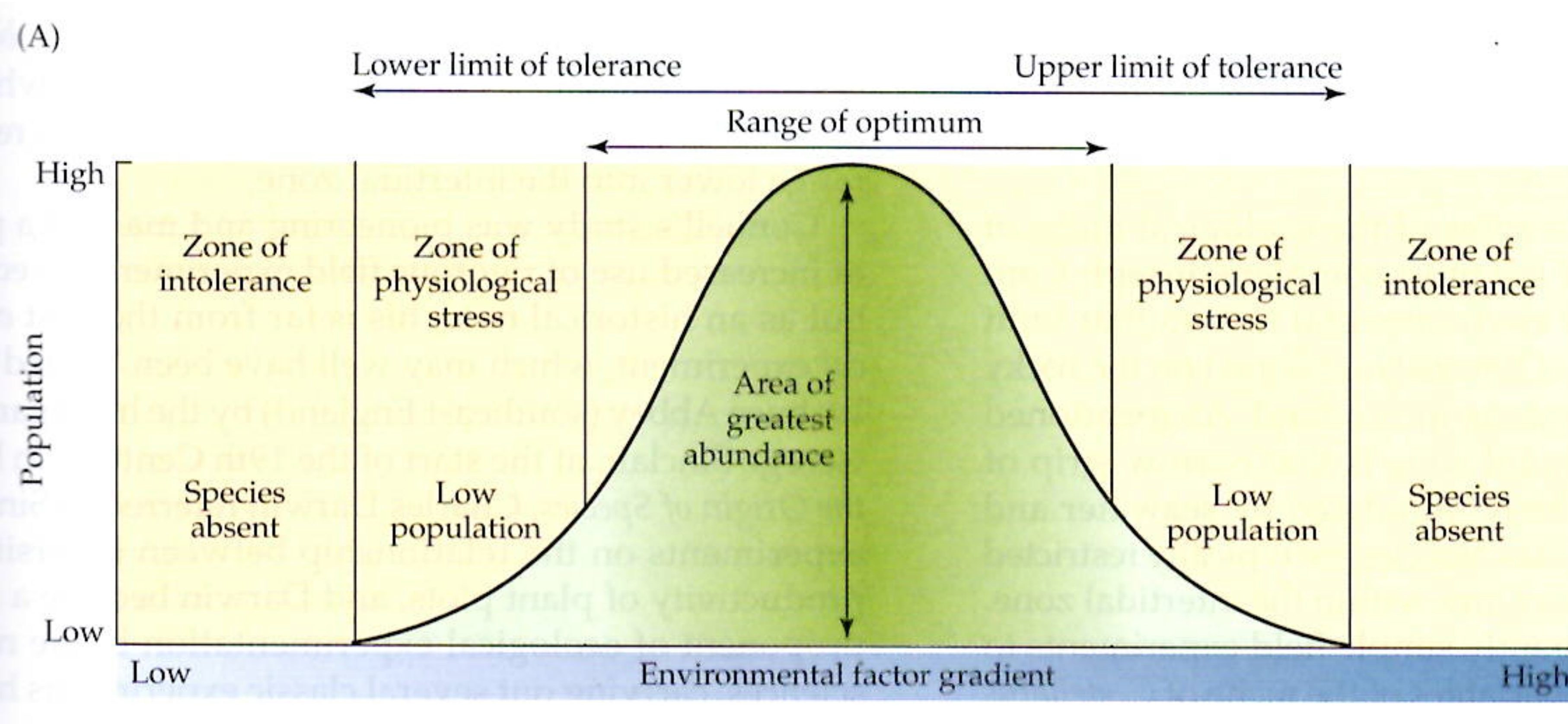
The geographic range of a species can be viewed as a spatial reflection of its niche

Fundamental Niche: total range of abiotic environmental conditions in which a taxon can survive and reproduce

From Hutchinson (1957) the n-dimensional hypervolume (or multidimensional space) that describes the range of abiotic environmental conditions in which a taxon can survive and reproduce (each abiotic factor is a single dimension)

Determinants of Distribution

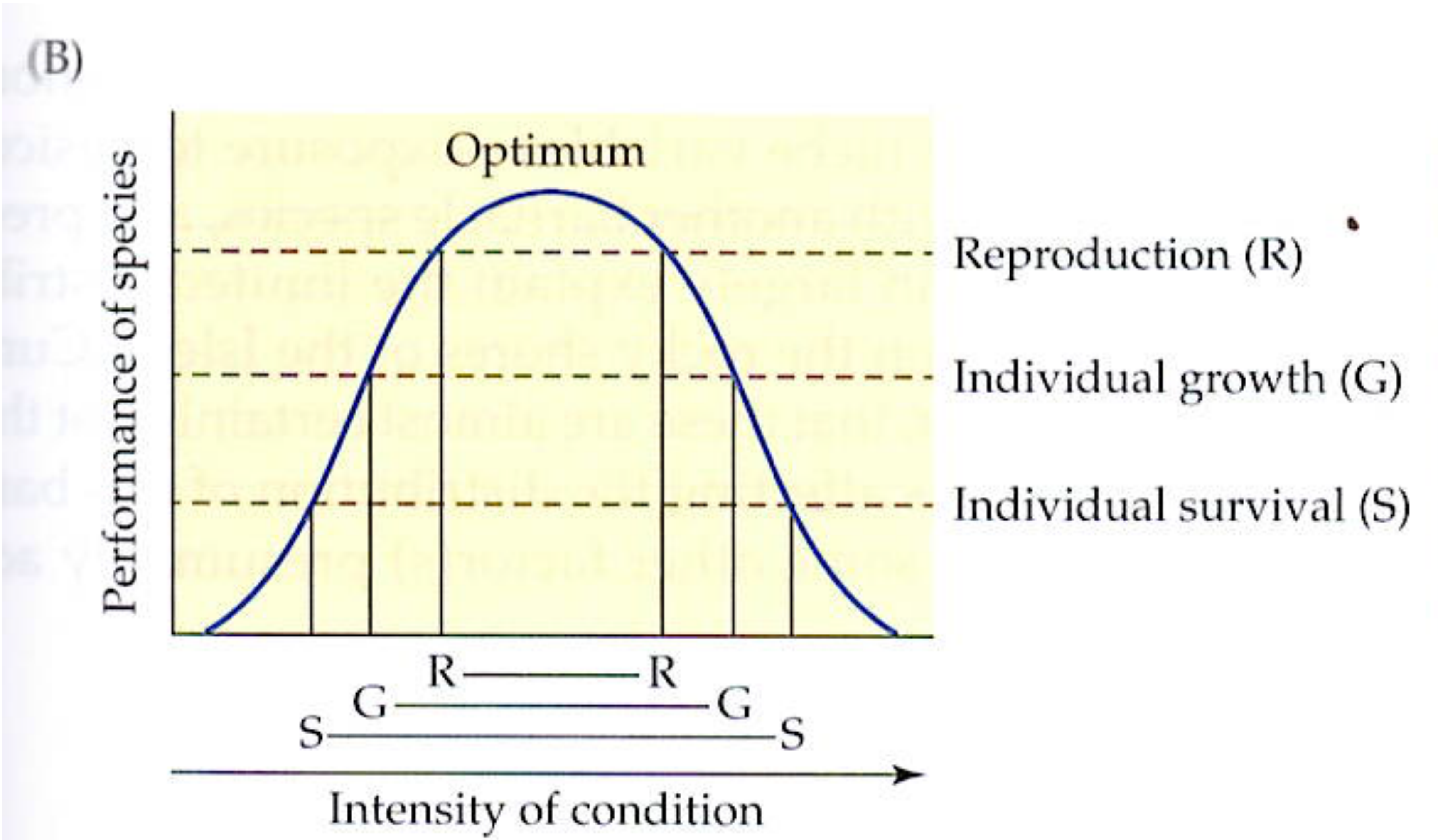
We often expect species to show a Gaussian distribution along a given environmental gradient: the "abundance-center hypothesis"



Multiple environmental factors or gradients can affect a species' distribution – this is what Hutchinson meant by the n-dimensional hypervolume

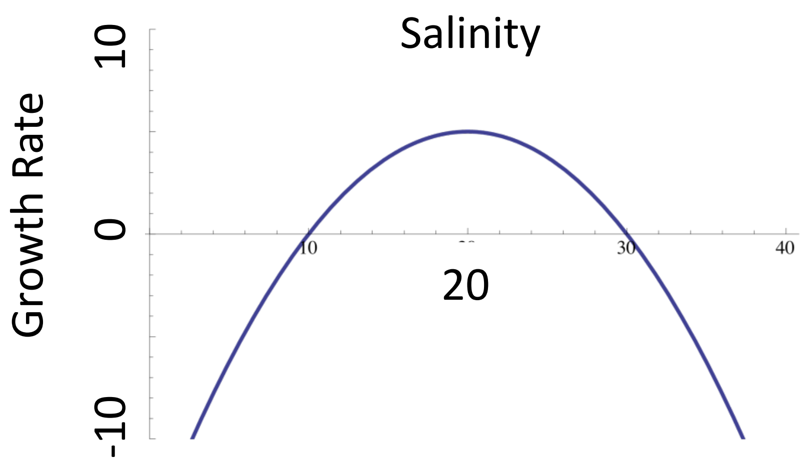
Determinants of Distribution

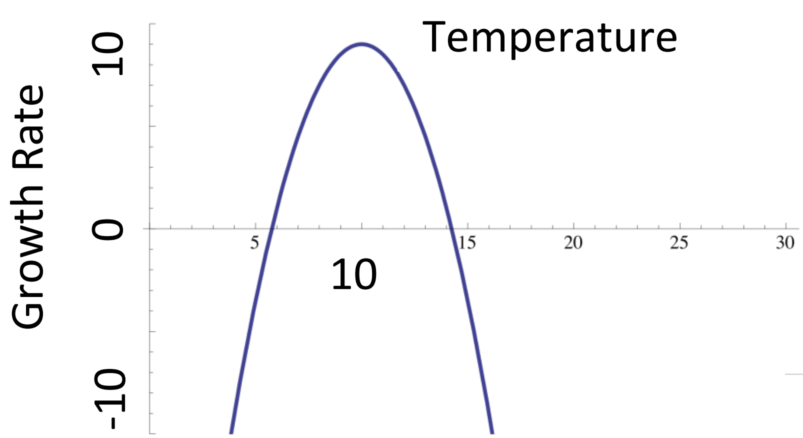
The capacity of individuals of a species to survive, grow and reproduce may reach limits at different distances from the optimal condition.

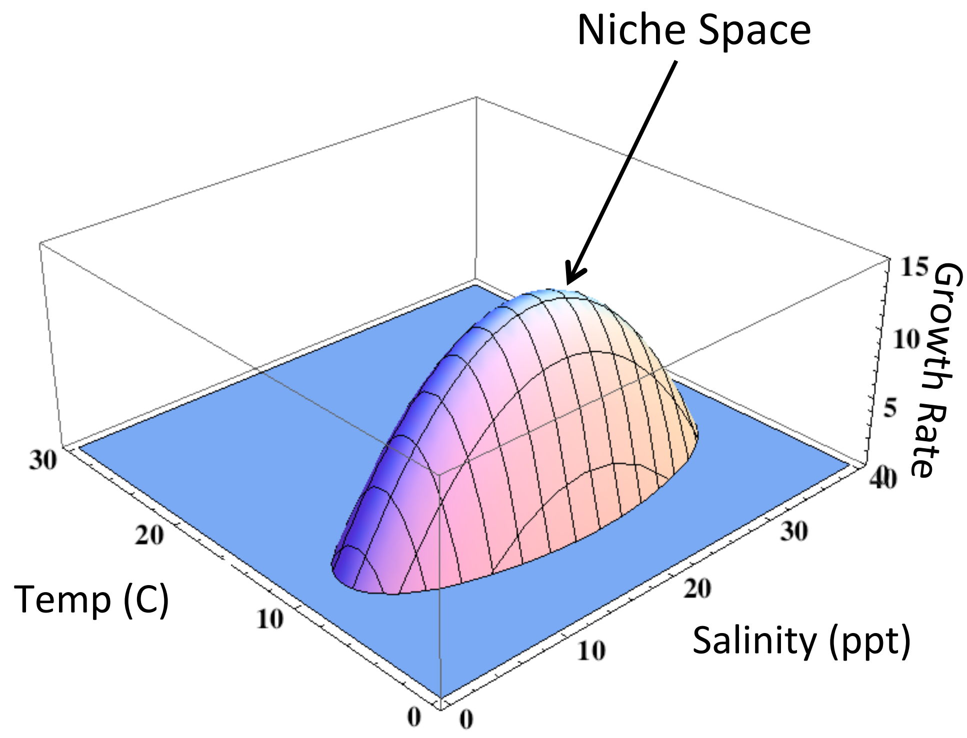


Determinants of Distribution

1) The Niche







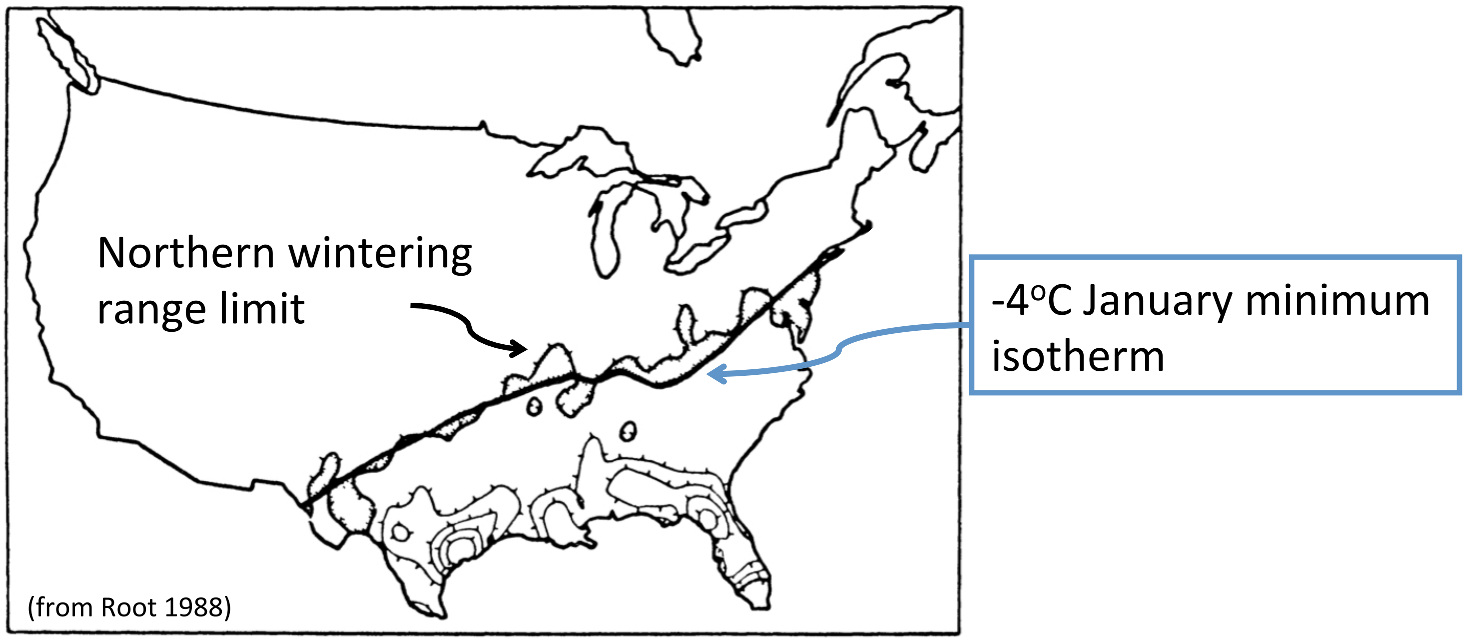
Determinants of Distribution

1) The Niche

When do range boundaries coincide with the fundamental niche?

Eastern Phoebe

http://upload.wikimedia.org/wikipedia/commons/c/c7/Eastern_Phoebe1.jpg



(from Root 1988)

Northern range limit is correlated with metabolic costs of thermoregulation for at least 14 species (in multiples of basal metabolic rate: MR = ~2.5 x BMR)

Determinants of Distribution

1) The Niche

When do range boundaries coincide with the fundamental niche?

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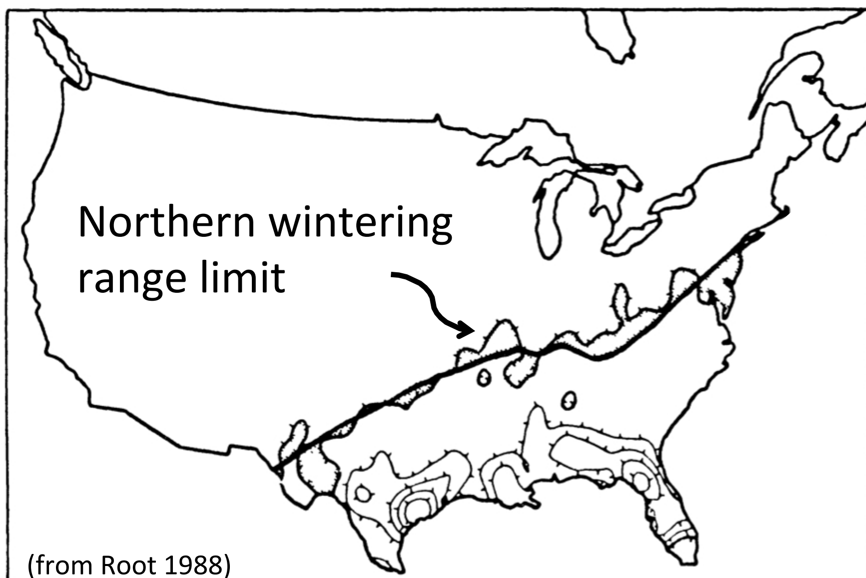
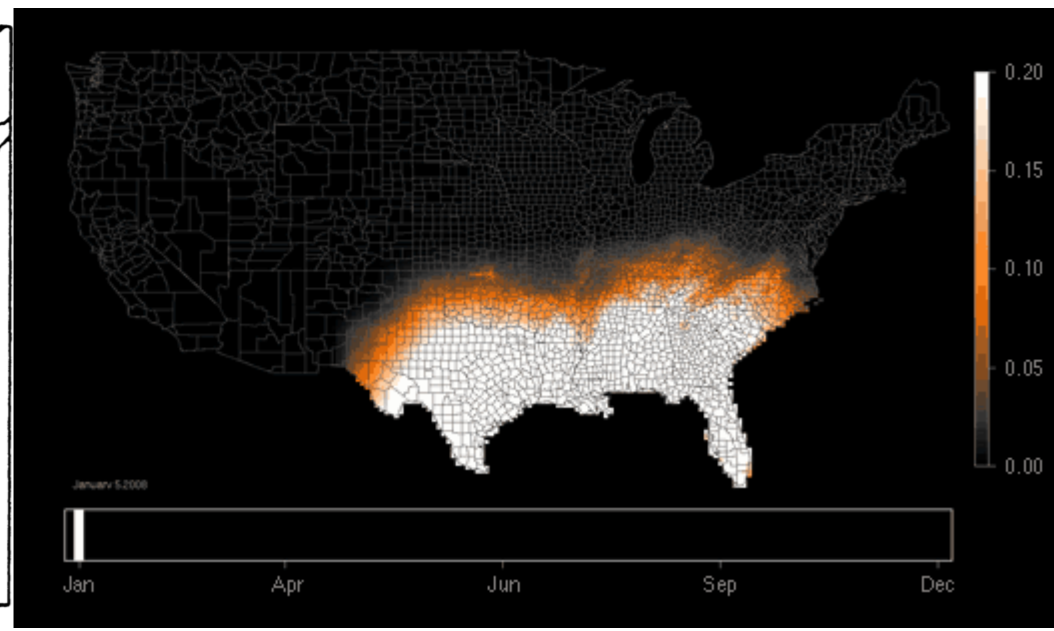
Eastern Phoebe





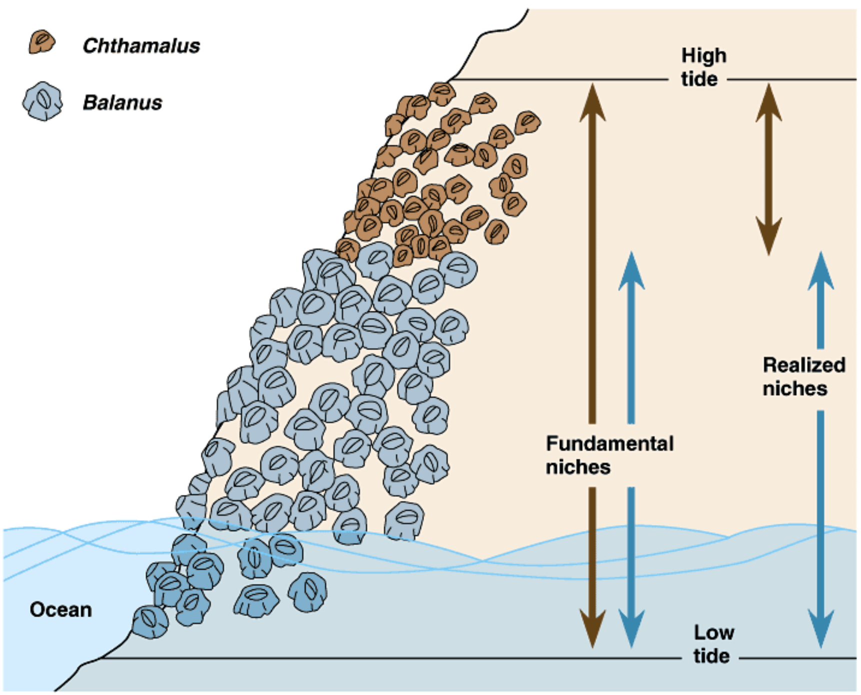
http://upload.wikimedia.org/wikipedia/commons/c/c7/Eastern_Phoebe1.jpg

http://ebird.org/plone/ebird/news/patterns-from-ebird-eastern-phoebe

Determinants of Distribution

1) The Niche

Realized Niche: A subset of the fundamental niche comprising the actual environmental conditions in which a taxon survives and reproduces in nature, including biotic factors (competition, predation, mutualism, etc).



Balanus: realized niche ~ fundamental niche

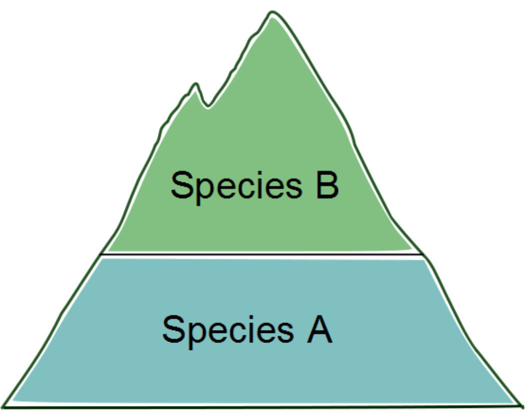
Chthamalus: constrained by competitive interactions to narrower realized niche

How could we test this experimentally?

Determinants of Distribution

1) The Niche

Realized Niche: A subset of the fundamental niche comprising the actual environmental conditions in which a taxon survives and reproduces in nature, including biotic factors (competition, predation, mutualism, etc).



Cordillera Vilcabamba
Main Andes

A natural experiment...with birds

Species A and B are closely related ~ similar niche

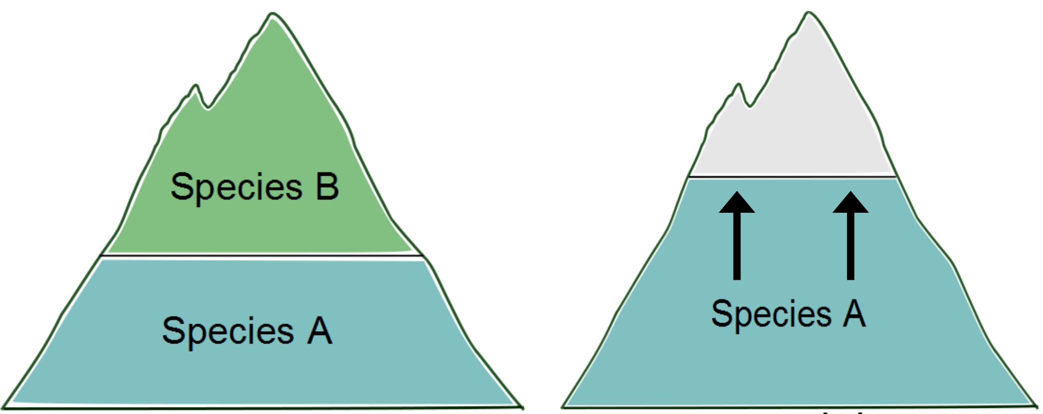
In the main Andes:
- both species present
- ranges do not overlap

Terborgh & Weske 1975, Ecology

Determinants of Distribution

1) The Niche

Realized Niche: A subset of the fundamental niche comprising the actual environmental conditions in which a taxon survives and reproduces in nature, including biotic factors (competition, predation, mutualism, etc).



Cordillera Vilcabamba
Main Andes

Cerros del Sira
100 km from Andes

In a range isolated from the Andes:

- high elevation species absent
- low elevation species expands range upward

Ecological release: expansion of the realized niche of a species where few competitors exist but an undiminished range of resources and habitats is present

Terborgh & Weske 1975, *Ecology*

Determinants of Distribution

1) The Niche

<u>Important caveats to the niche as the main determinant of a species' range:</u>

a) Species may occupy unfavourable areas

b) Species may be absent in favourable areas

Determinants of Distribution

1) The Niche

<u>Important caveats to the niche as the main determinant of a species' range:</u>

a) Species may occupy unfavourable areas

- $r = b + i - d - e$
- populations can be a *source* (birth rate exceeds death rate; $b > d$) or *sink* (death rate exceeds birth rate; $d > b$)
- sink populations depend on immigration (i) from source populations
- peripheral populations of a species range are often sink populations

b) Species may be absent in favourable areas

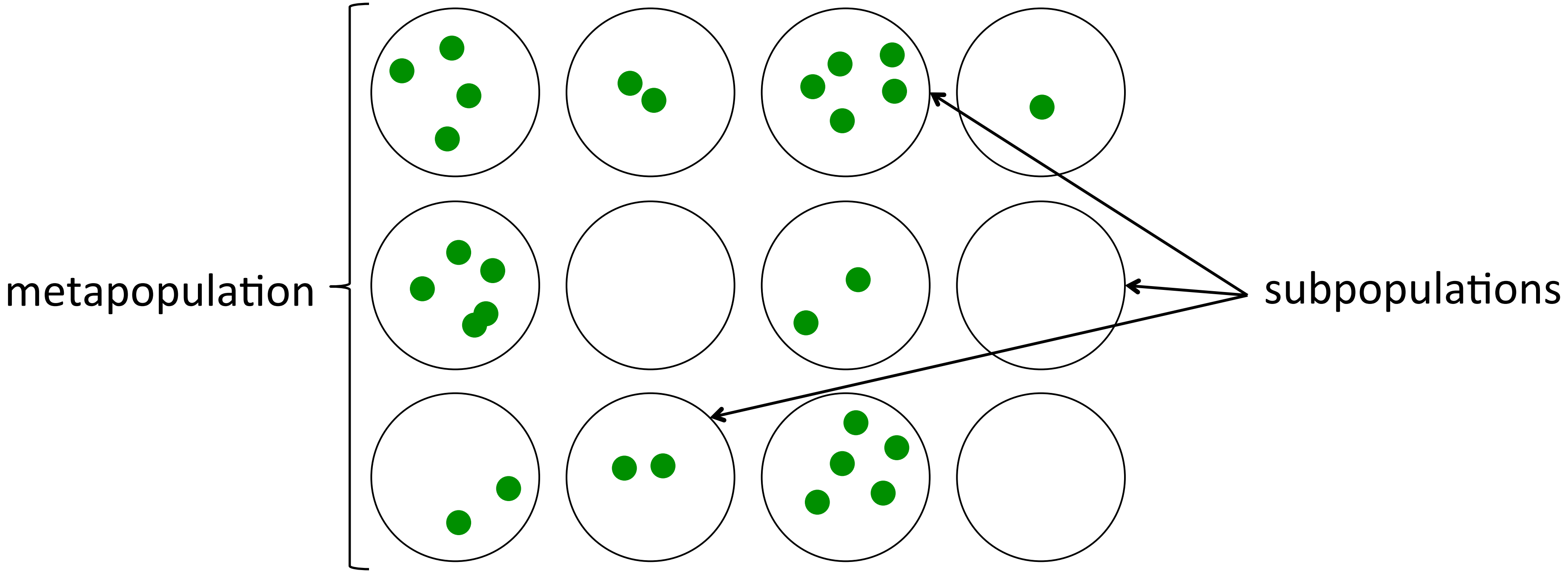
- due to geographic barriers or isolation

c) Metapopulation structure when suitable niche space is patchy, some patches may be occupied intermittently

Determinants of Distribution

2) Metapopulation structure

Metapopulation: a population consisting of a set of subpopulations linked by a cycle of alternating colonization and extinction (Levins 1970)



Determinants of Distribution

2) Metapopulation structure

Representation of source and sink habitats and relative magnitude of the four processes that determine growth and persistence of populations

"Excess" individuals in Habitat 1 disperse, resulting in higher emigration than immigration

Habitat 2 is able to persist due to higher immigration than emigration, despite lower births than deaths

Metapopulation source/sink dynamics more likely to occur toward the periphery of a species' range (based on the abundance-center hypothesis)

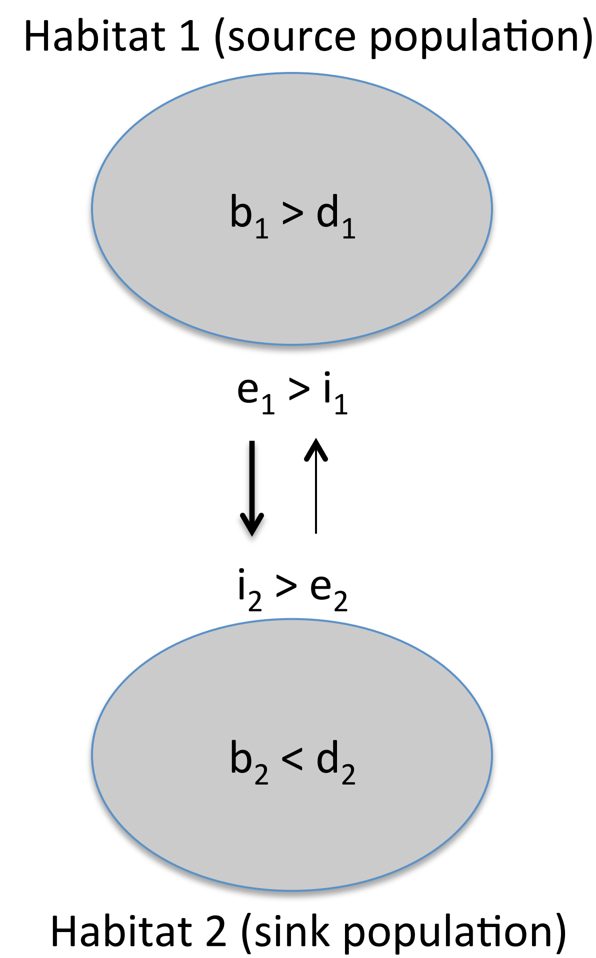
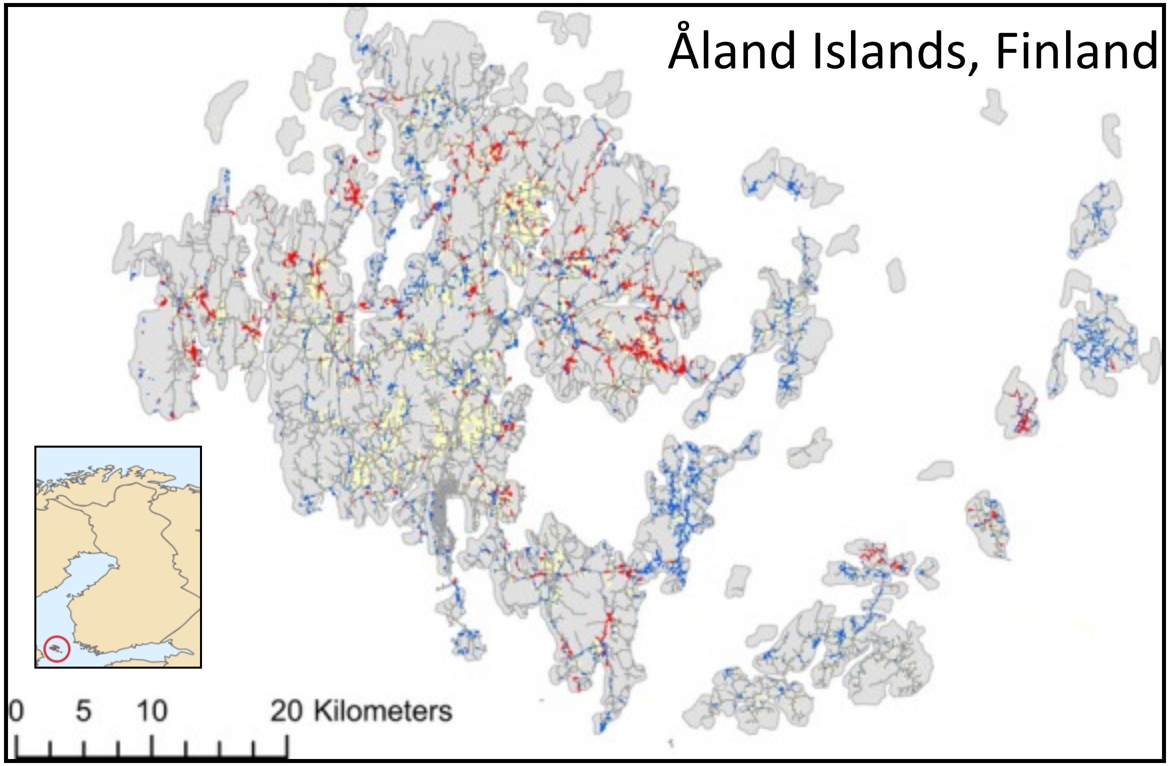


Fig from ch. 4, Lomolino et al. 2006

Determinants of Distribution

2) Metapopulation structure

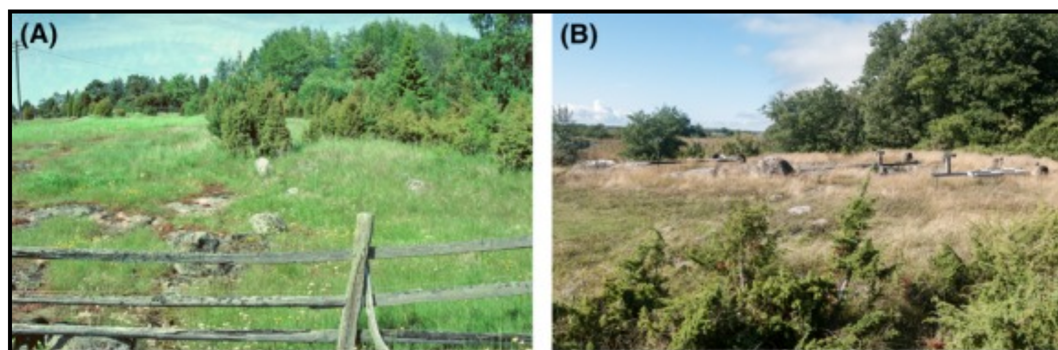


Glanville fritillary butterfly
(*Melitaea cinxia*)

Photograph courtesy of Hannu Aarnio.

~ 4000 dry meadows in 2012

Red = occupied
Blue = unoccupied

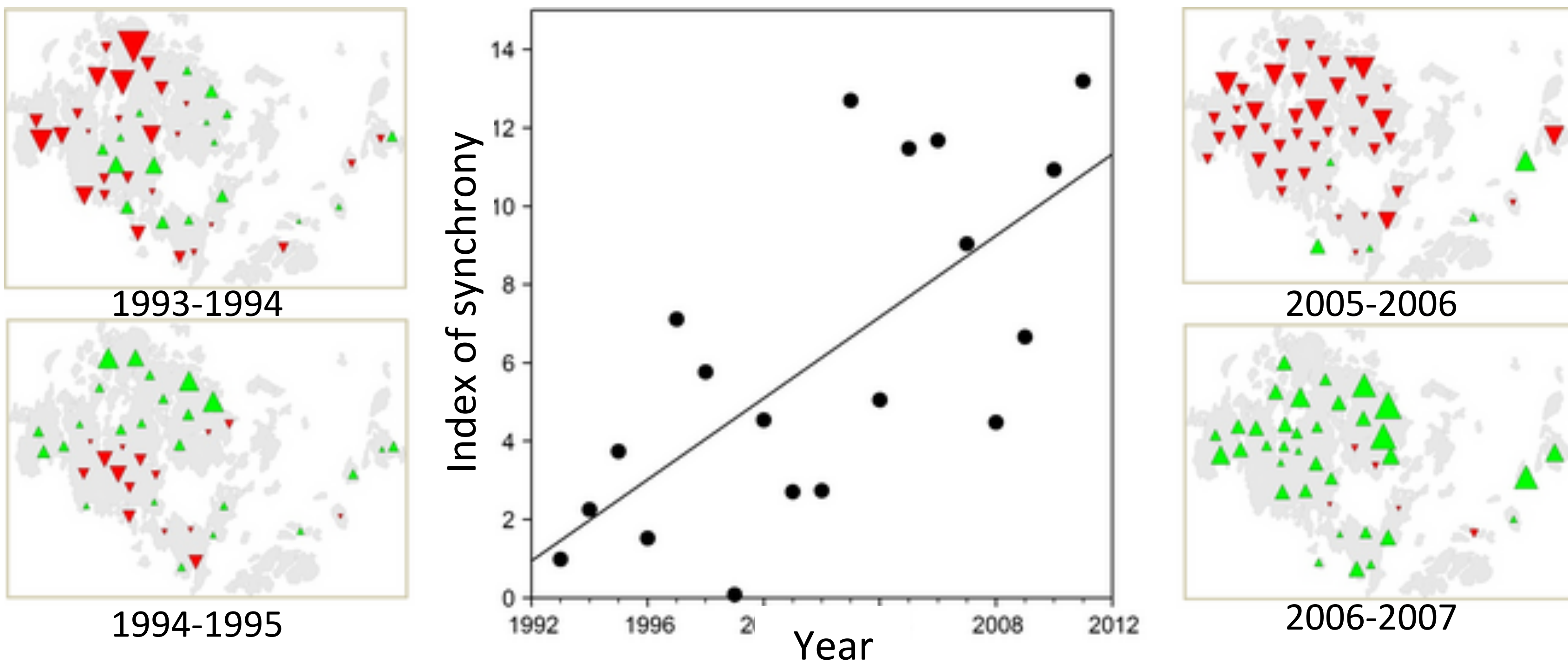


Ojanen, S.P et al. 2013 *Ecology and Evolution*

Determinants of Distribution

2) Metapopulation structure

Glanville fritillary on the Åland Islands became more synchronous over time, possibly due to increasing frequency of extreme weather events:



Red down-pointing triangles = decline; Green up-pointing triangles = increase
Size of the triangle ~ magnitude of per capita change

Ojanen, S.P et al. 2013 *Ecology and Evolution*

Determinants of Distribution

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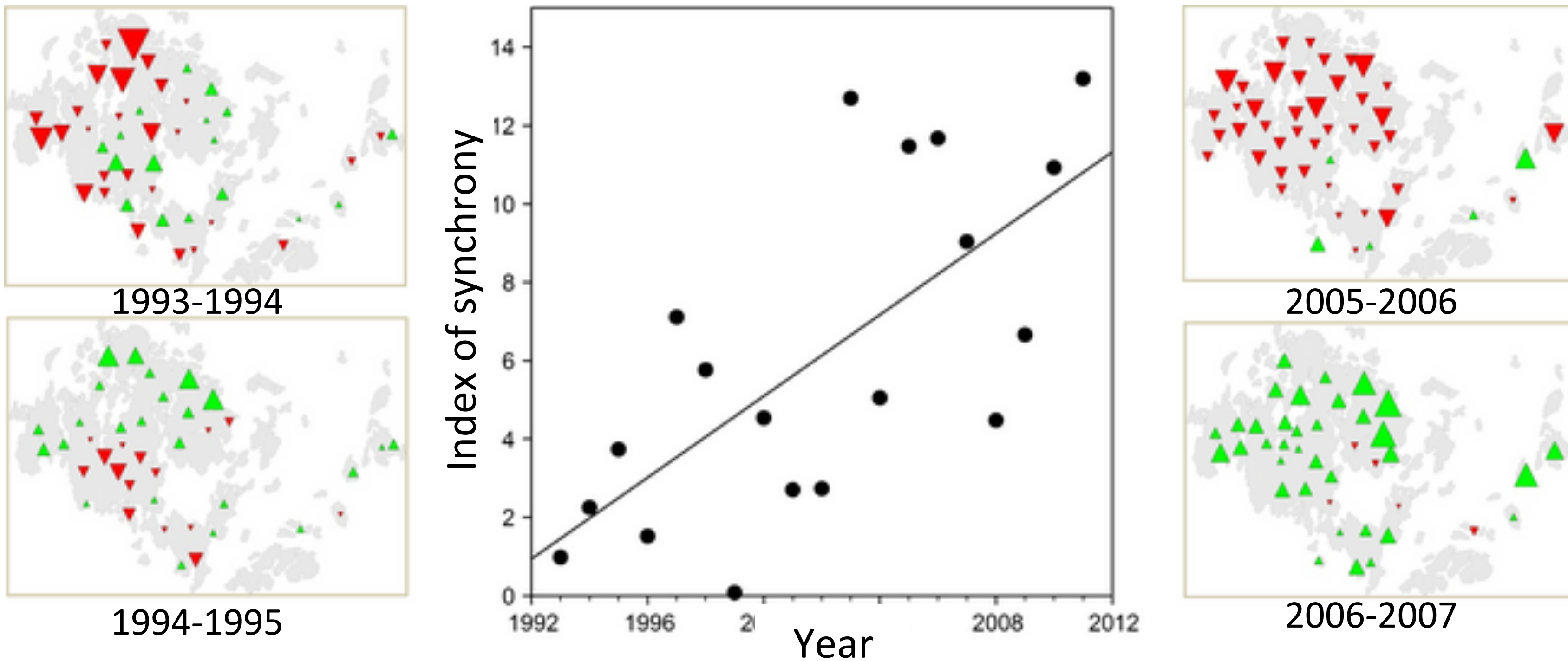


An example of why it is important to consider the dynamics of populations, and how they may shift with changing environmental conditions

Ojanen, S.P et al. 2013 *Ecology and Evolution*

Determinants of Distribution

3) Disturbance

Habitat disturbance can cause abrupt range limits.
Countless examples, but one in our research is the high Andean treeline:

Manu National Park, Peru (photos M. Chappell, Z. Peterson)

Peruvian farmers in highland communities set fires to maintain fresh grass sprouts for cattle

Anthropogenic treeline at ~ 3400 m, upper limits of forest species

High-elevation species that move upslope with climate change hit "grass ceiling"

Determinants of Distribution

3) Disturbance

Disturbance-adapted animals? Urban adapters?

American Crow
(*Corvus brachyrhynchos*)

Common Starling
(*Sturnus vulgaris*)

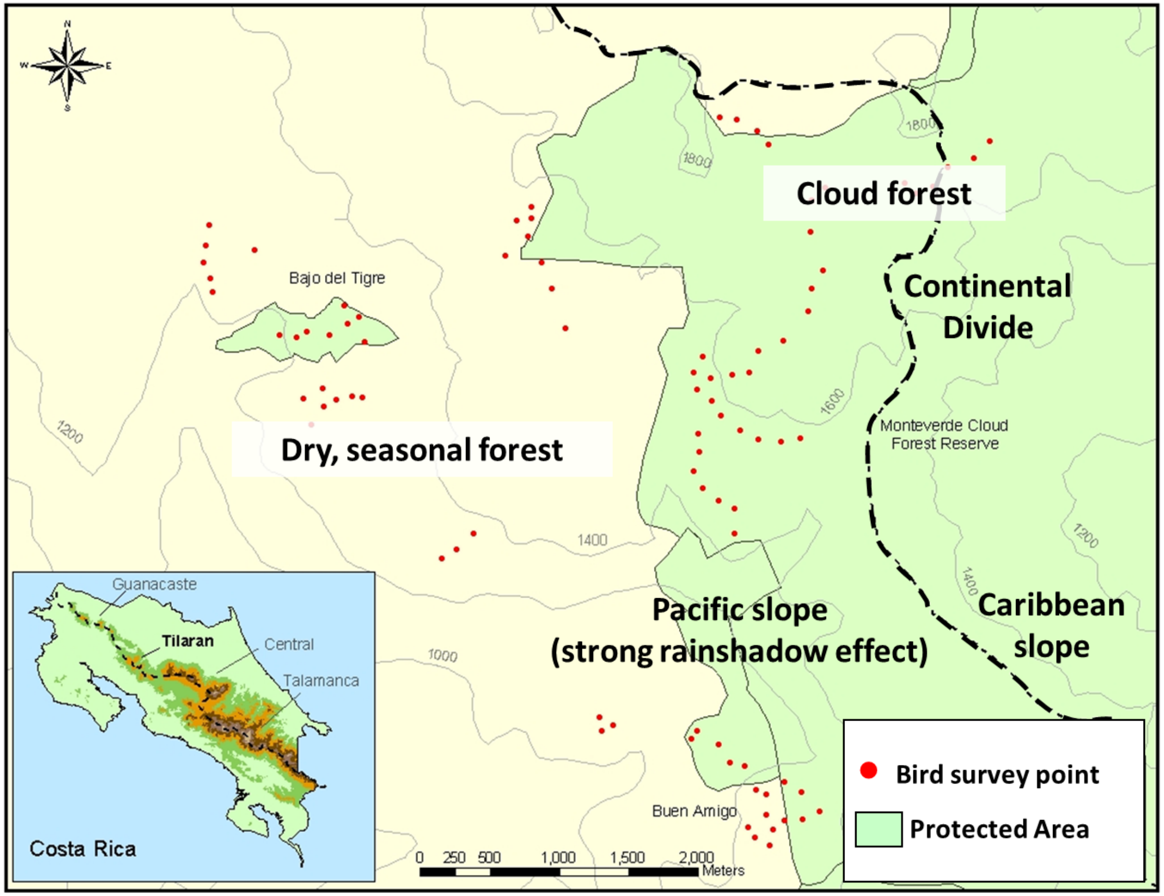
We typically think of disturbance as a factor limiting where species can occur, or disrupting the continuity of species distributions

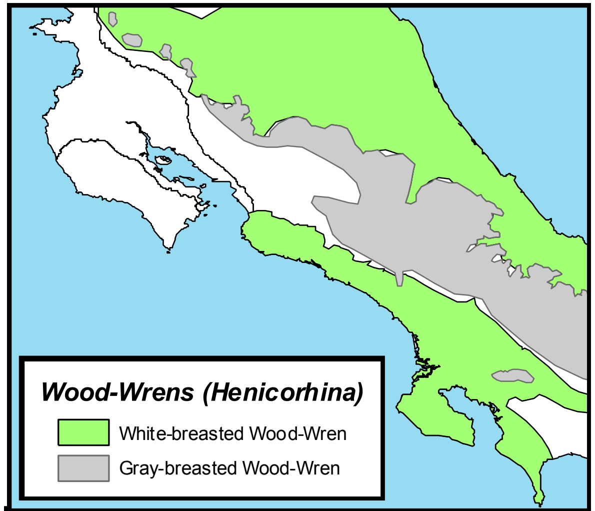
But for some species, disturbance can facilitate expansion of ranges into previously uninhabited areas.

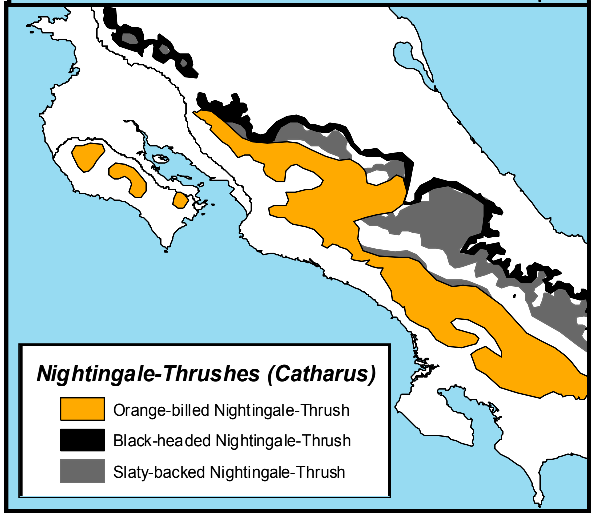
Determinants of Distribution

4) Biotic Interactions: Direct Competition

Direct competition – testing species replacements
Monteverde, Tilarán Mountains, Costa Rica 1100-1800m



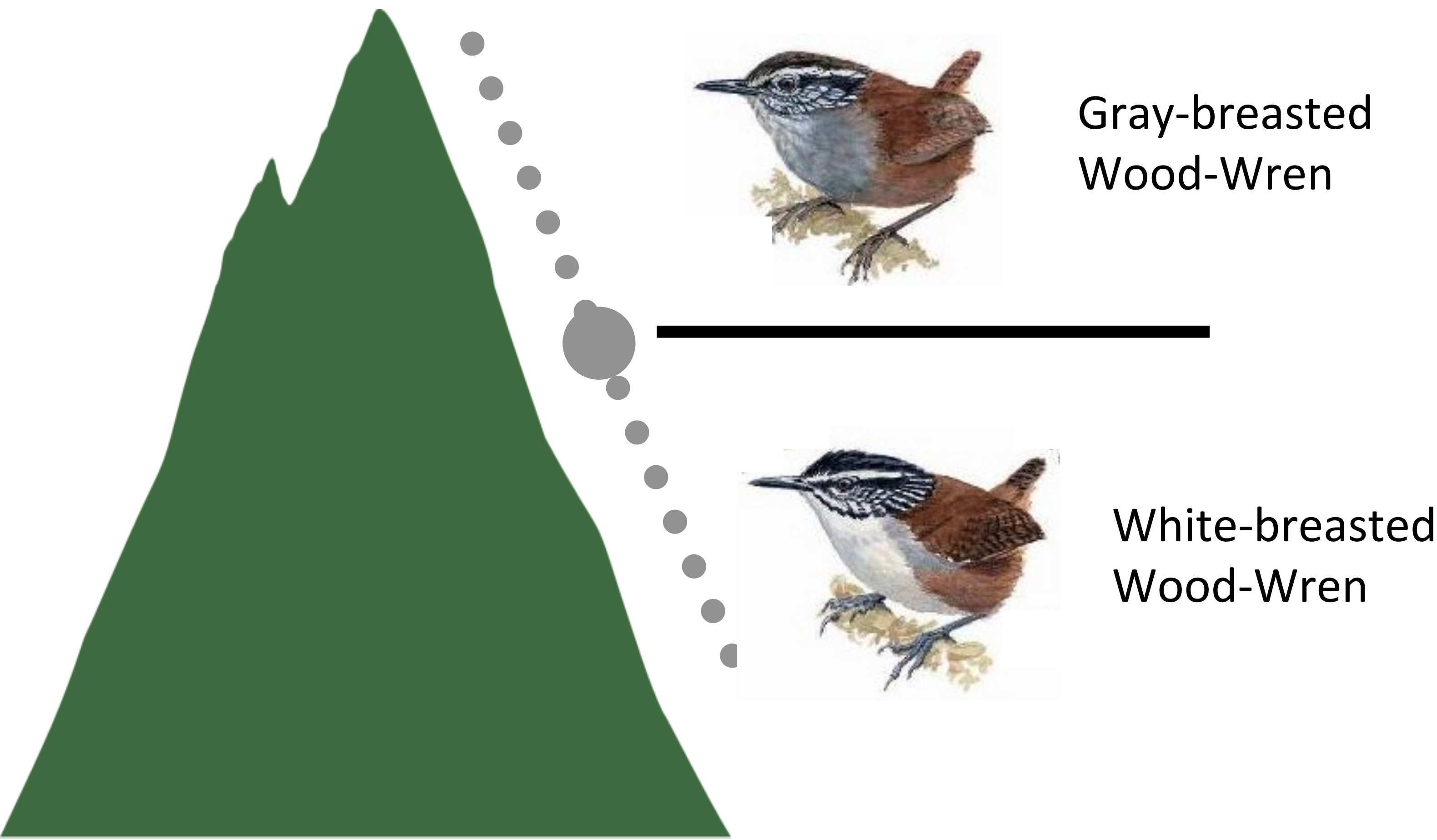




Determinants of Distribution

4) Biotic Interactions: Direct Competition

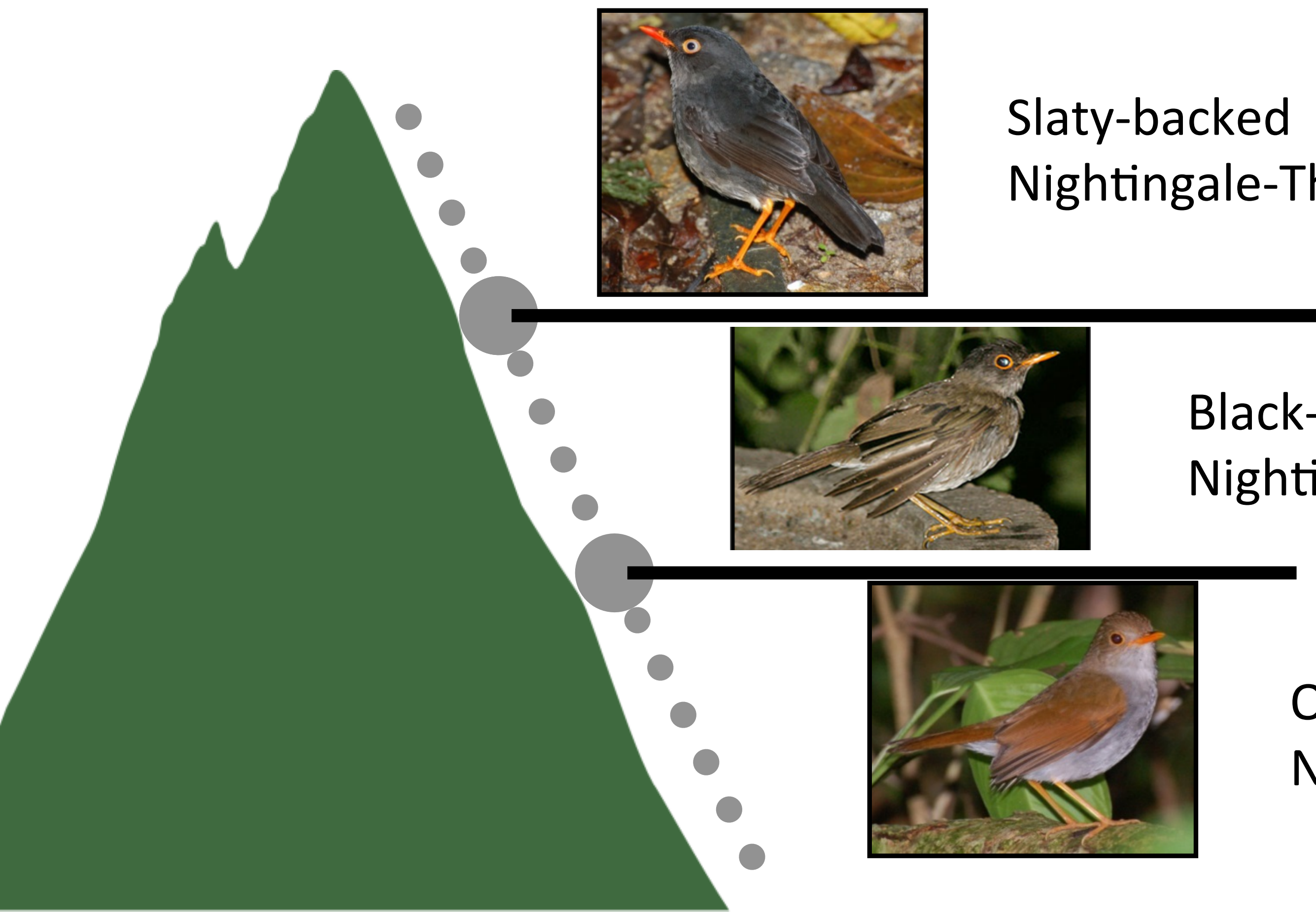
Target species: Wood-Wrens



Determinants of Distribution

4) Biotic Interactions: Direct Competition

Target species: Nightingale-Thrushes



Slaty-backed Nightingale-Thrush

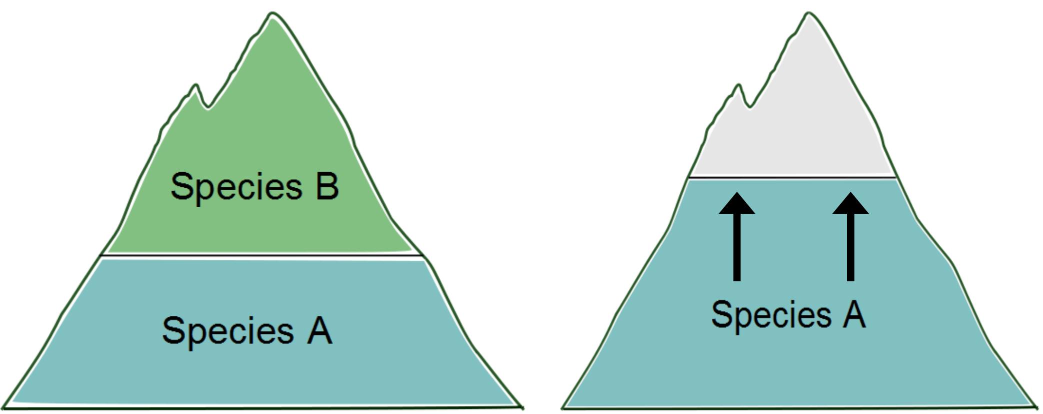
Black-headed Nightingale-Thrush

Orange-billed Nightingale-Thrush

Determinants of Distribution

4) Biotic Interactions: Direct Competition

Our previous example of species replacements and competition was a "natural experiment" with observational evidence of ecological release.



For birds that defend territories using song...

we can use territory defense as a behavioural metric of competitive interactions

...and design an experiment

Does interspecific competition reinforce range boundaries of species along elevational gradients?

Terborgh & Weske 1975, Ecology

Jankowski et al. 2010, Ecology

Determinants of Distribution

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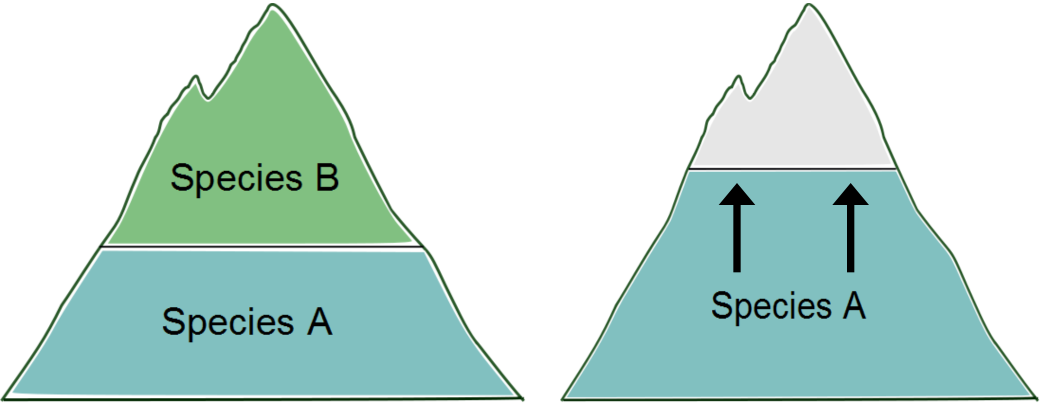

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Behavioral responses recorded:

- Closest approach to speaker (meters)
- Latency to approach speaker (seconds)
- Average length of inter-song intervals


Behavioral responses recorded:
• Closest approach to speaker (meters)
• Latency to approach speaker (seconds)
• Average length of inter-song intervals
#@*!?

Determinants of Distribution

4) Biotic Interactions: Direct Competition

If species are interspecifically aggressive at contact zones, this supports the hypothesis of direct competition

Playback protocol to test species aggressive responses:

Trial 1		Trial 2	
Observation (Control)	Playback (Congener/ Conspecific)	Observation (Control)	Playback (Congener/ Conspecific)
8 min. obs	3 min. song, 5 min. obs	8 min. obs	3 min. song, 5 min. obs

Determinants of Distribution

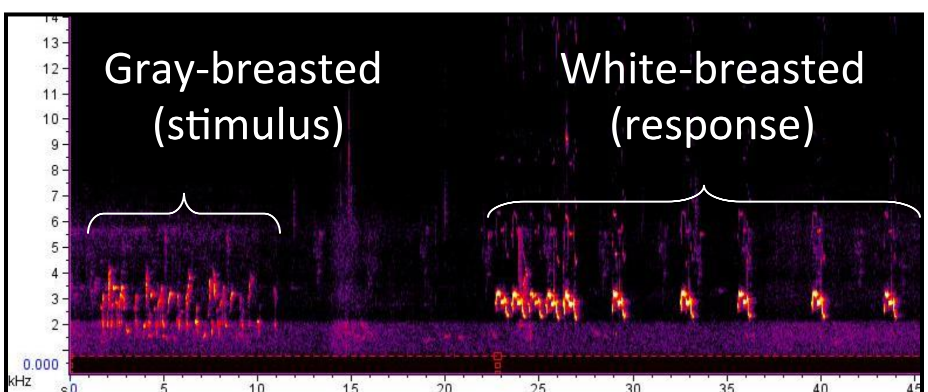
4) Biotic Interactions: Direct Competition

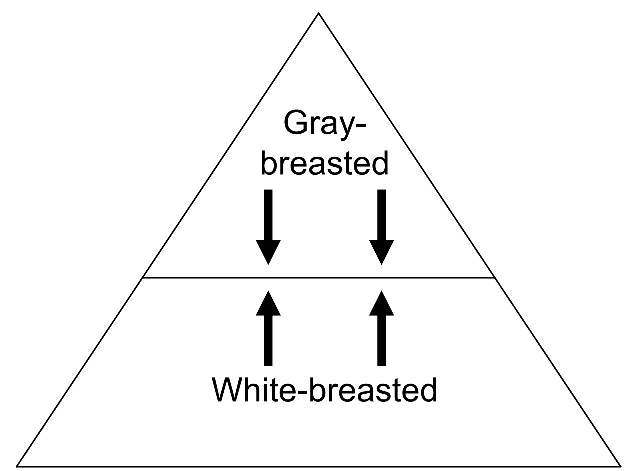
Song played to bird:

Control

Congener (other species)

Conspecific (same species)





Jankowski et al. 2010, *Ecology*

Determinants of Distribution

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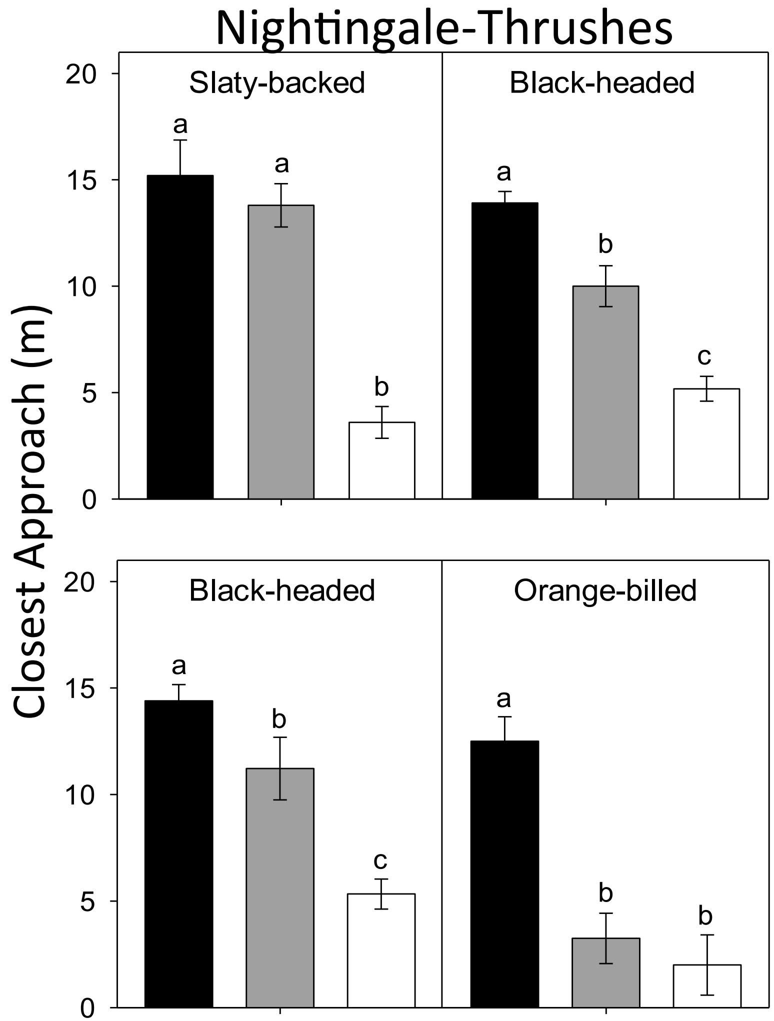

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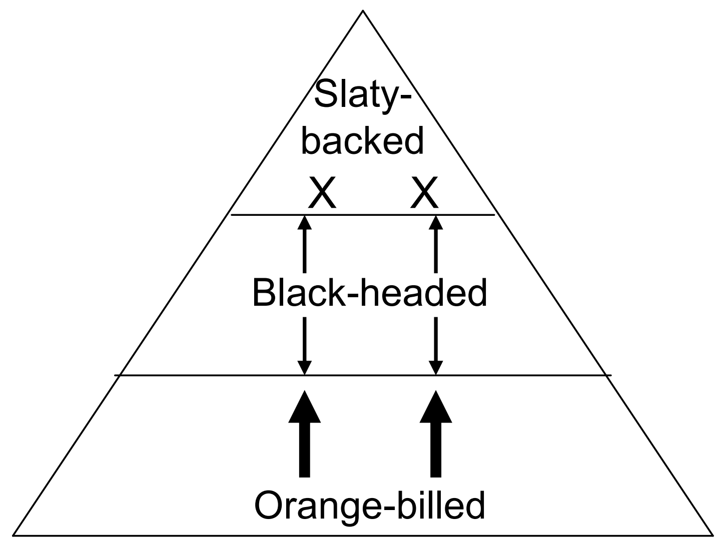


Determinants of Distribution

4) Biotic Interactions: Diffuse Competition

Diffuse competition: the combined effect of competition with many other species – one species is negatively affected by numerous other species that collectively cause significant depletion of shared resources (MacArthur 1972).

Add more nest boxes (i.e., cavities) ⟶ more cavity nesters ⟶ less open cup nesters

Western bluebird (*Sialia mexicana*)

American robin (*Turdus migratorius*)

(Bock *et al.* 1992)

Determinants of Distribution

5) Biotic Interactions: Predation

For tropical birds, nest predation is a major source of mortality

In Manu, Peru, we are gathering data to understand:

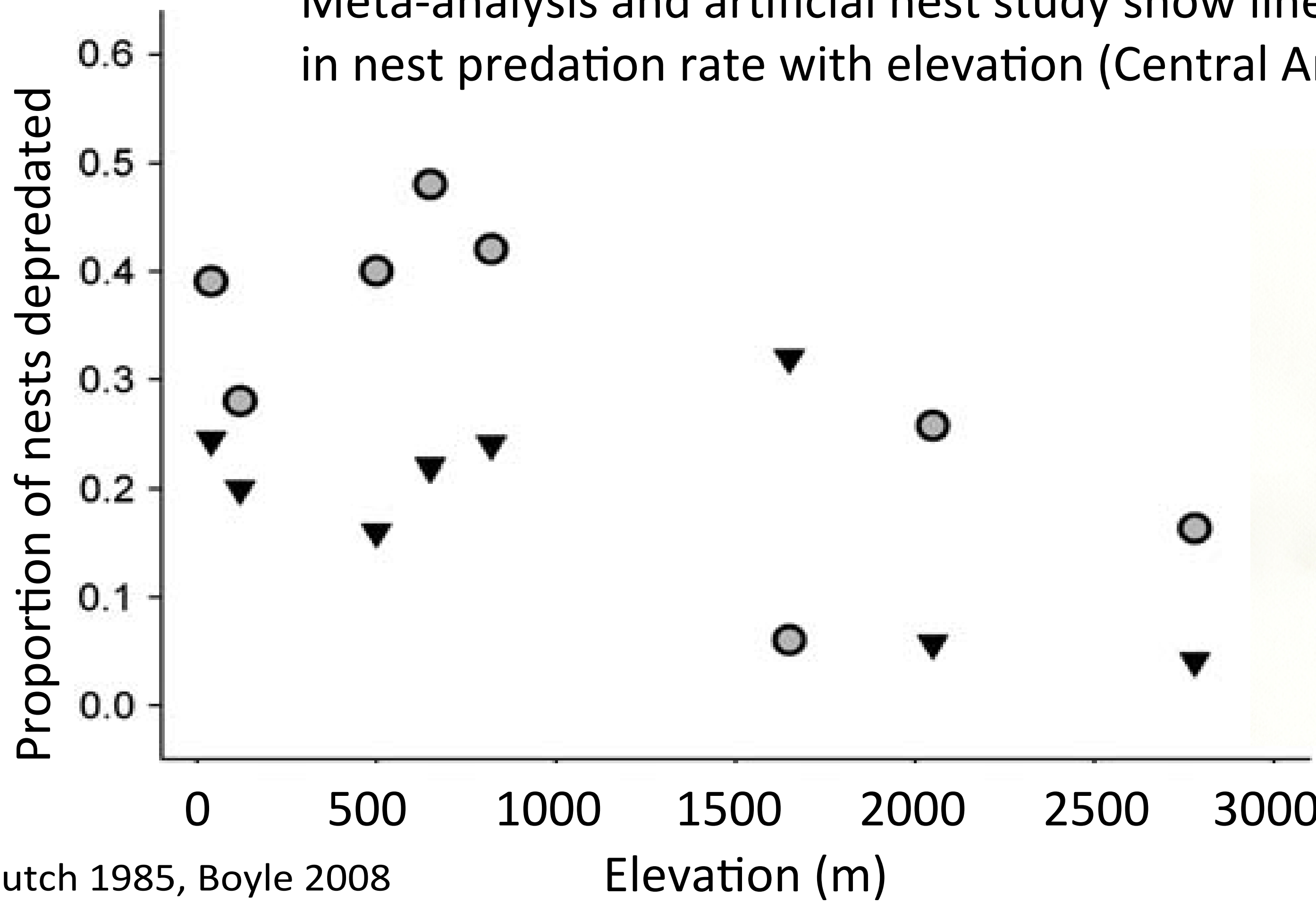
1) how nest predation changes with elevation?

2) how does the nest predator community change with elevation?

Determinants of Distribution

5) Biotic Interactions: Predation

Meta-analysis and artificial nest study show linear decrease in nest predation rate with elevation (Central America)

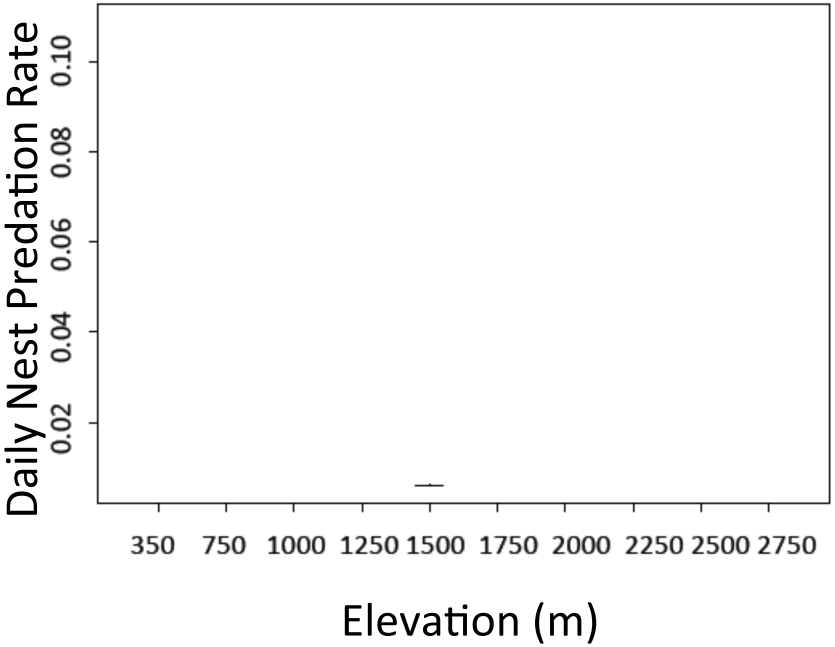


Skutch 1985, Boyle 2008

Determinants of Distribution

5) Biotic Interactions: Predation

How do rates of nest predation change with elevation in Manu National Park, Peru?



Determinants of Distribution

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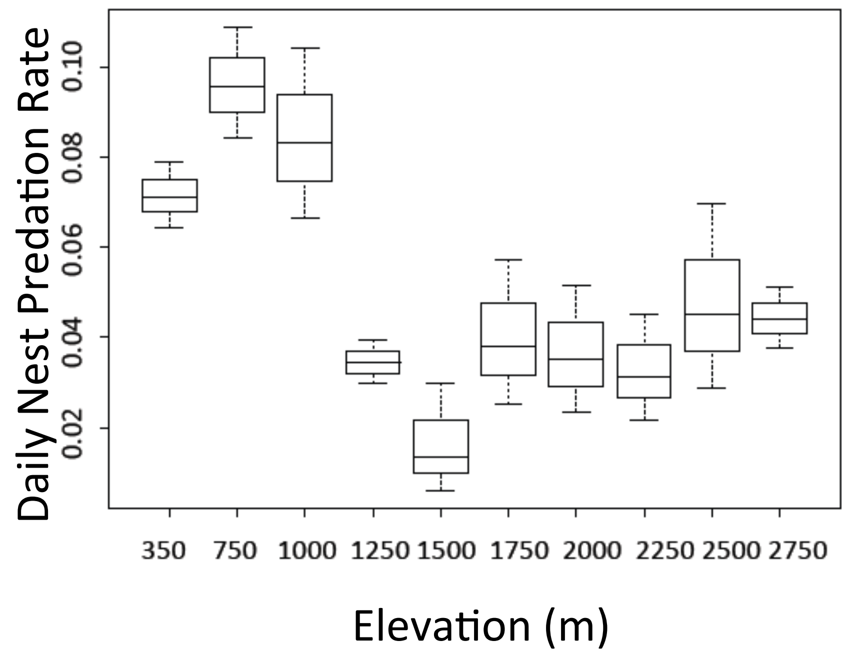

Determinants of Distribution

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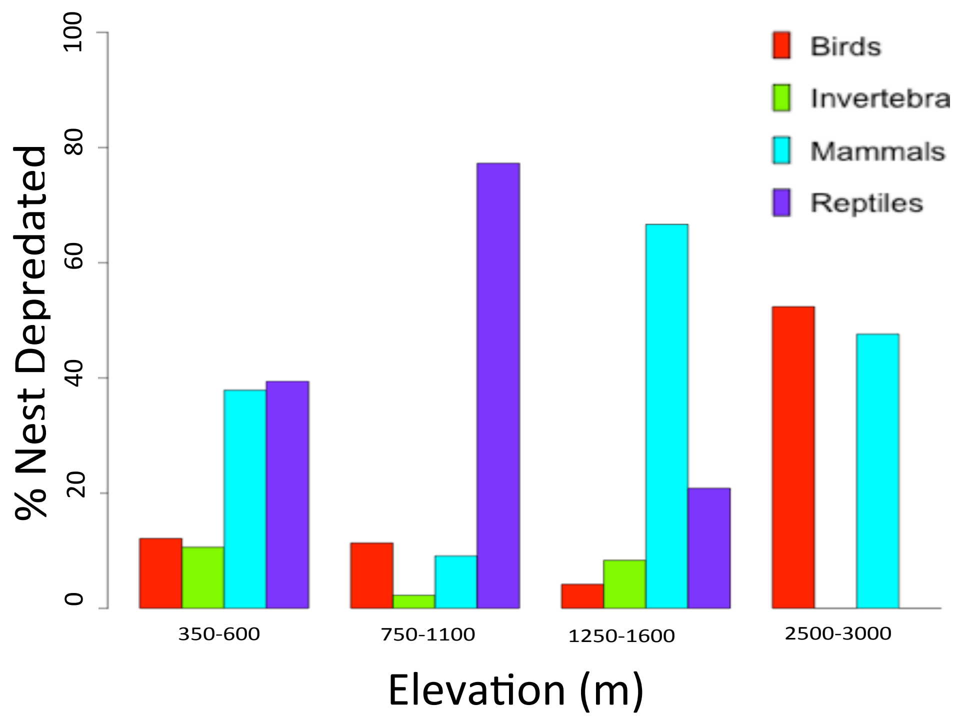


Determinants of Distribution

5) Biotic Interactions: Predation

Catching the culprits...

...using motion triggered camera traps aimed at nests...

Predation by saddleback tamarin on quail-dove nest

Predation by aracaris on white-tipped dove nest

Predation by *Pseustes* snake on antbird nestlings

Determinants of Distribution

5) Biotic Interactions: Predation

Learning lots about the natural history of tropical birds...including who eats whom

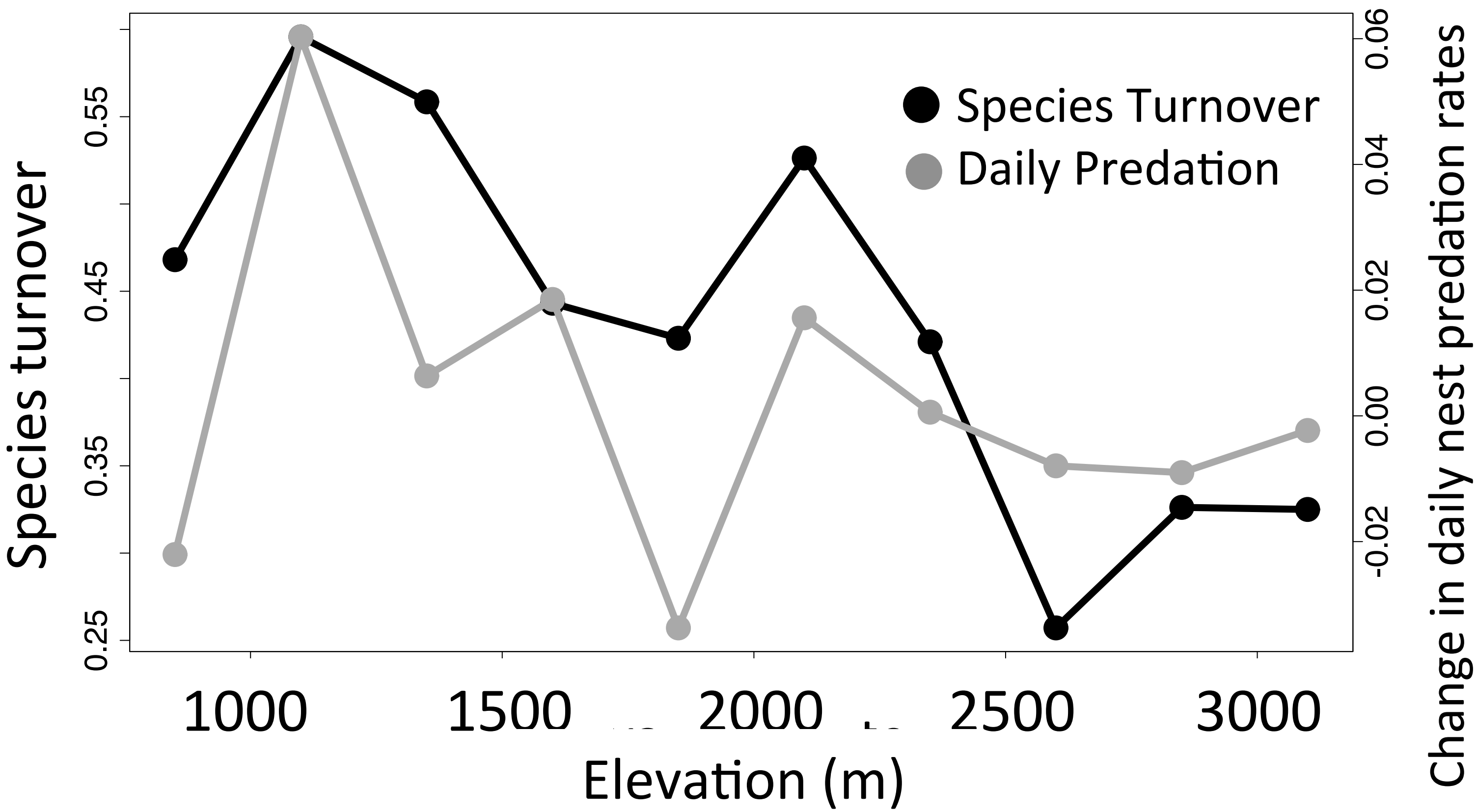
Cock-of-the-Rock nestling and adult (*Rupicola peruviana*)

http://cdn-7.itsnature.org/wp-content/uploads/2010/04/Cock-of-the-Rock-antbird.jpg

Determinants of Distribution

5) Biotic Interactions: Predation

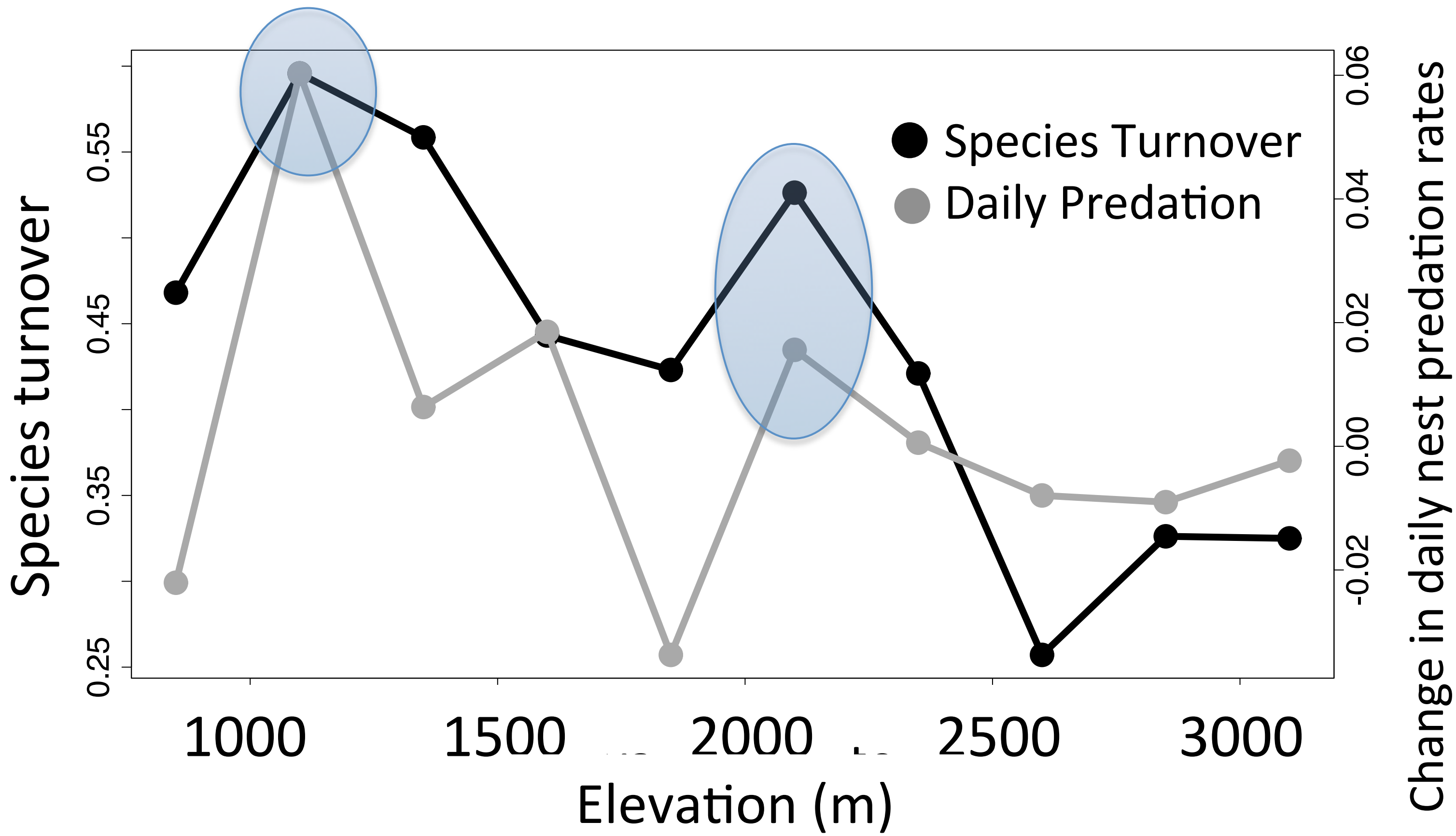
Species turnover is high = many species in the community have range boundaries in the same place



Determinants of Distribution

5) Biotic Interactions: Predation

Highest change in species composition (species turnover) corresponds with the highest rates of daily nest predation



Determinants of Distribution

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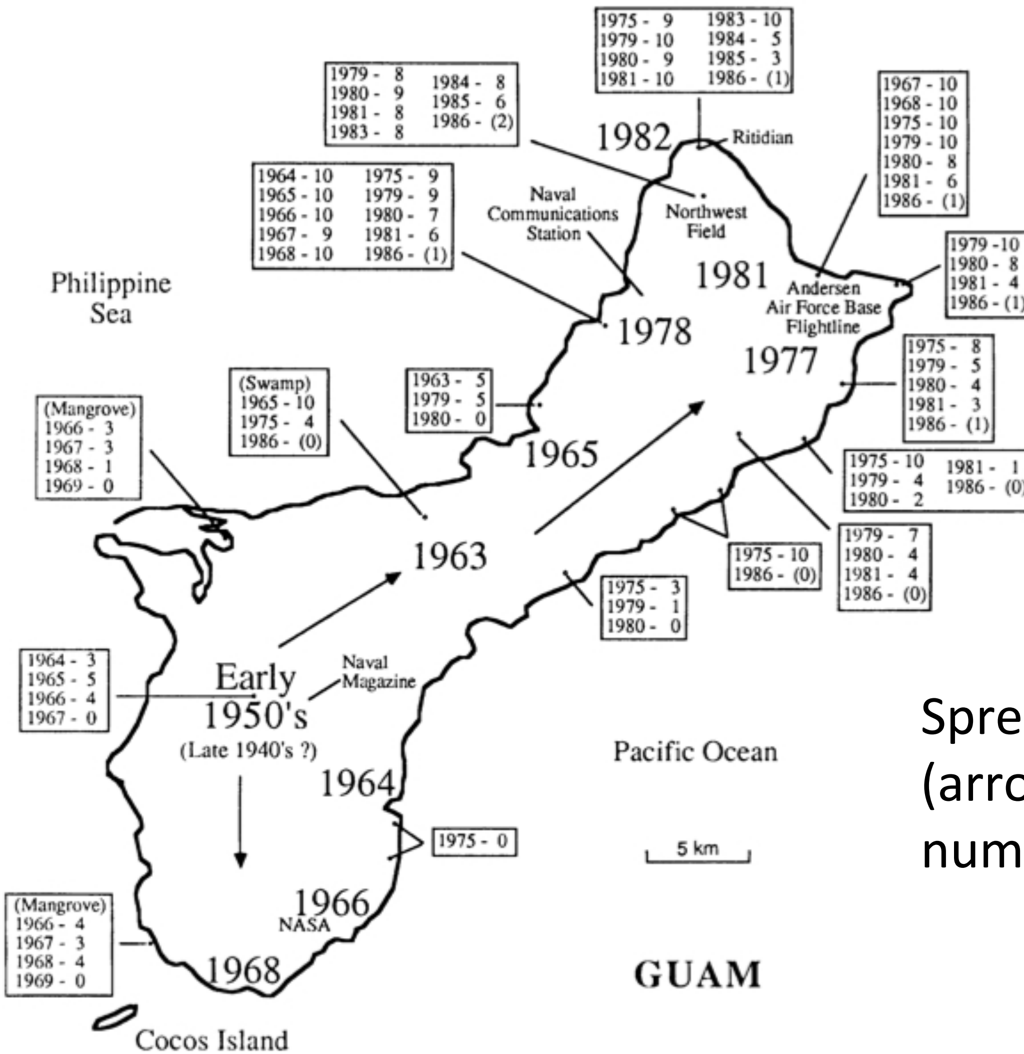


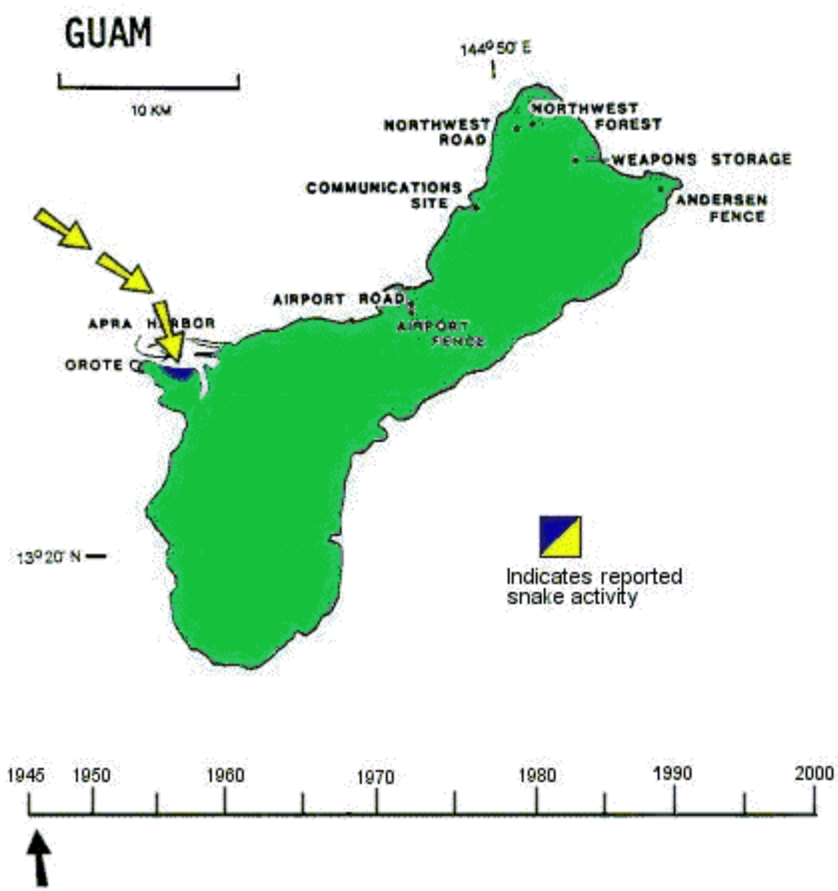
Brown tree snake (*Boiga irregularis*)

Spread of brown tree snake on Guam (arrows) and subsequent declines in numbers of native birds across years

Savidge 1987 *Ecology*

Determinants of Distribution

5) Biotic Interactions: Predation



Brown tree snake (*Boiga irregularis*)

USGS Timeline of the Brown tree snake travel across Guam

One of many examples where a predator introduced to a naïve native community results in drastic cascading changes

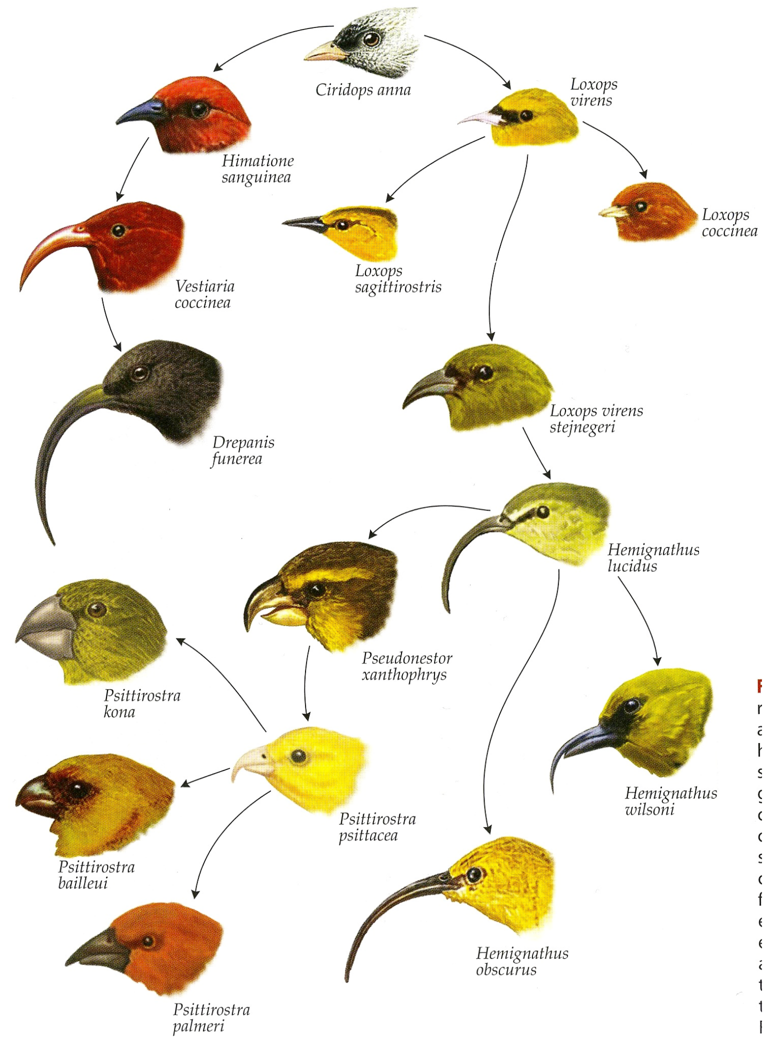
http://www.fort.usgs.gov/resources/education/bts/invasion/colonize.asp#dispersal

Determinants of Distribution

5) Biotic Interactions: Parasitism

One of the best examples of parasites affecting species distributions comes from Hawaii

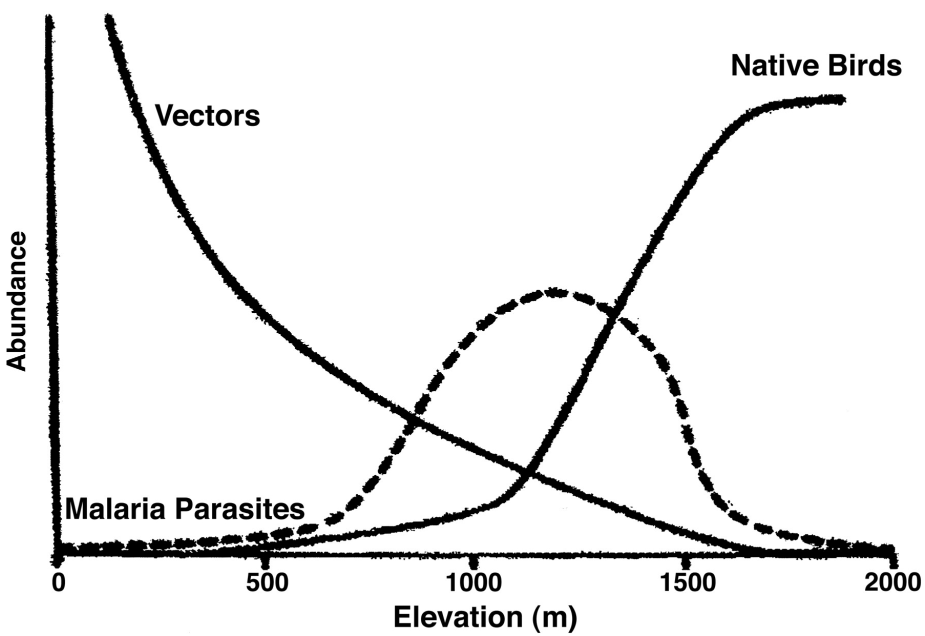
Human introductions of mosquitoes and avian malaria has eliminated all species from low and middle elevations on the islands.

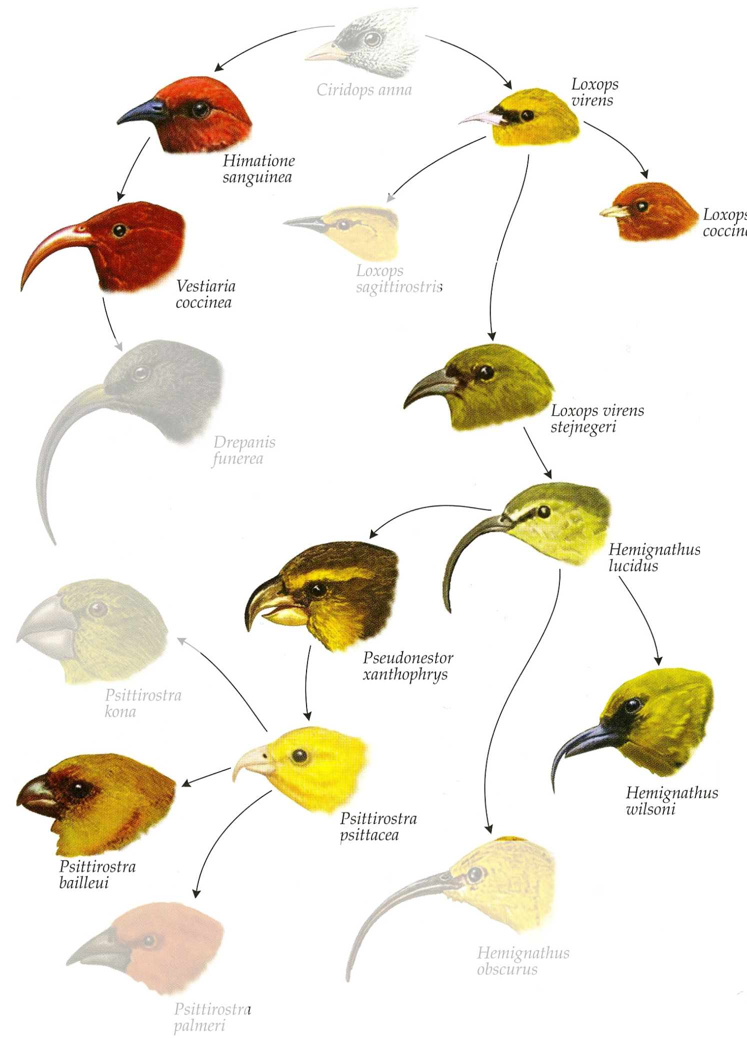


Determinants of Distribution

5) Biotic Interactions: Parasitism

Persisting populations are buffered by thermal limits to development and transmission of *Plasmodium* parasites



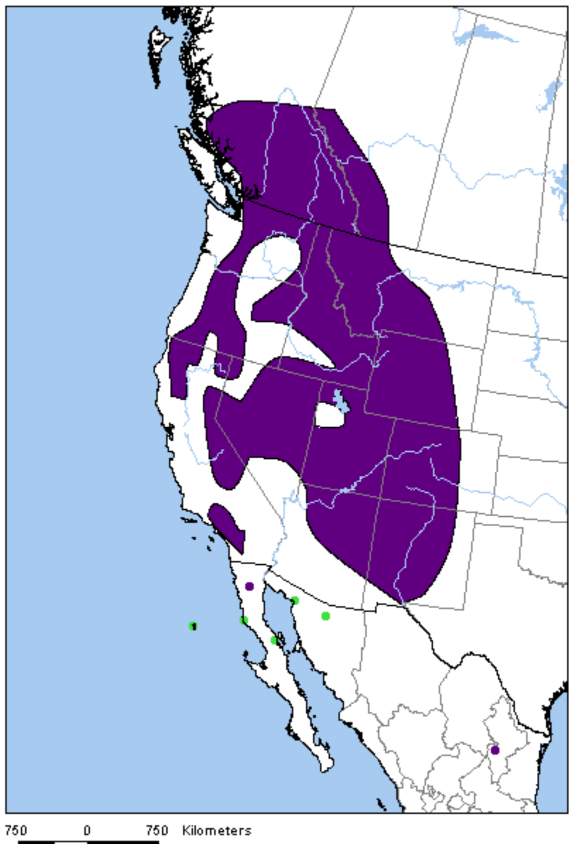


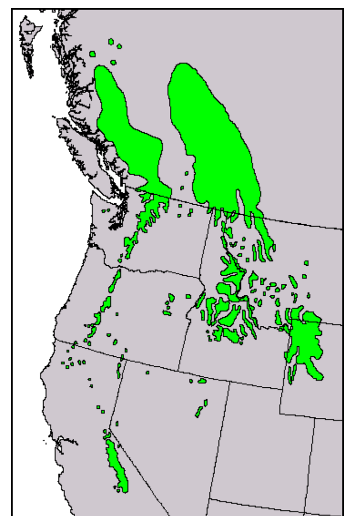
Benning *et al*. 2002 *PNAS*

Determinants of Distribution

6) Biotic Interactions: Mutualism

Clark's nutcracker (*Nucifraga columbiana*) and whitebark pine (*Pinus albicaulis*)





Whitebark, limber, Colorado pinyon, single-leaf pinyon and southwestern white pines depend on nutcrackers for seed dispersal

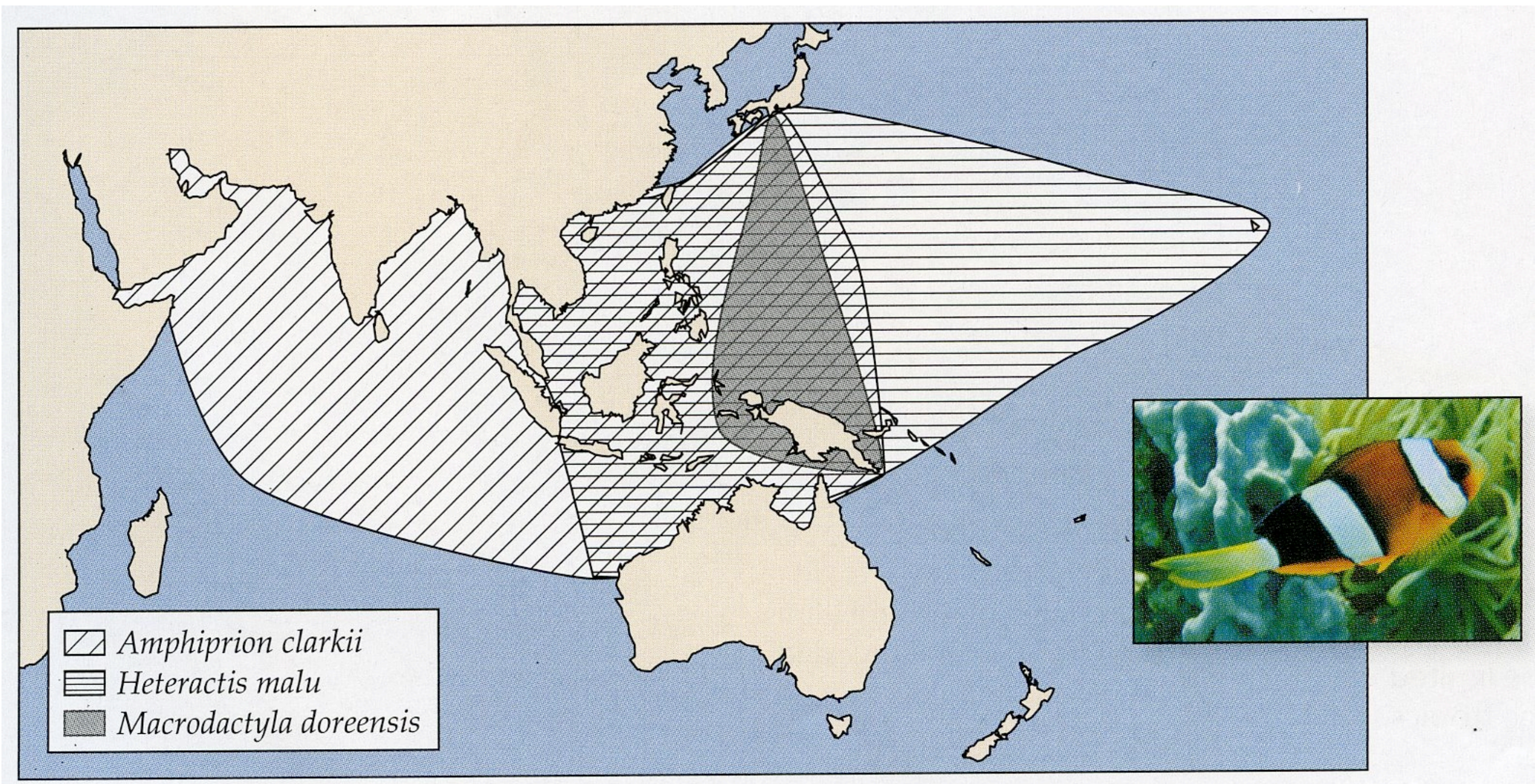
This interaction has changed the trees' seeds, cones, and even overall shape in comparison with other wind-dispersed pine species

http://www.allaboutbirds.org/guide/clarks_nutcracker/lifehistory

Determinants of Distribution

6) Biotic Interactions: Mutualism

Indo-Pacific clownfish (*Amphiprion clarkii*) and two sea anemones (*Heteractis malu* and *Macrodactyla doreensis*)



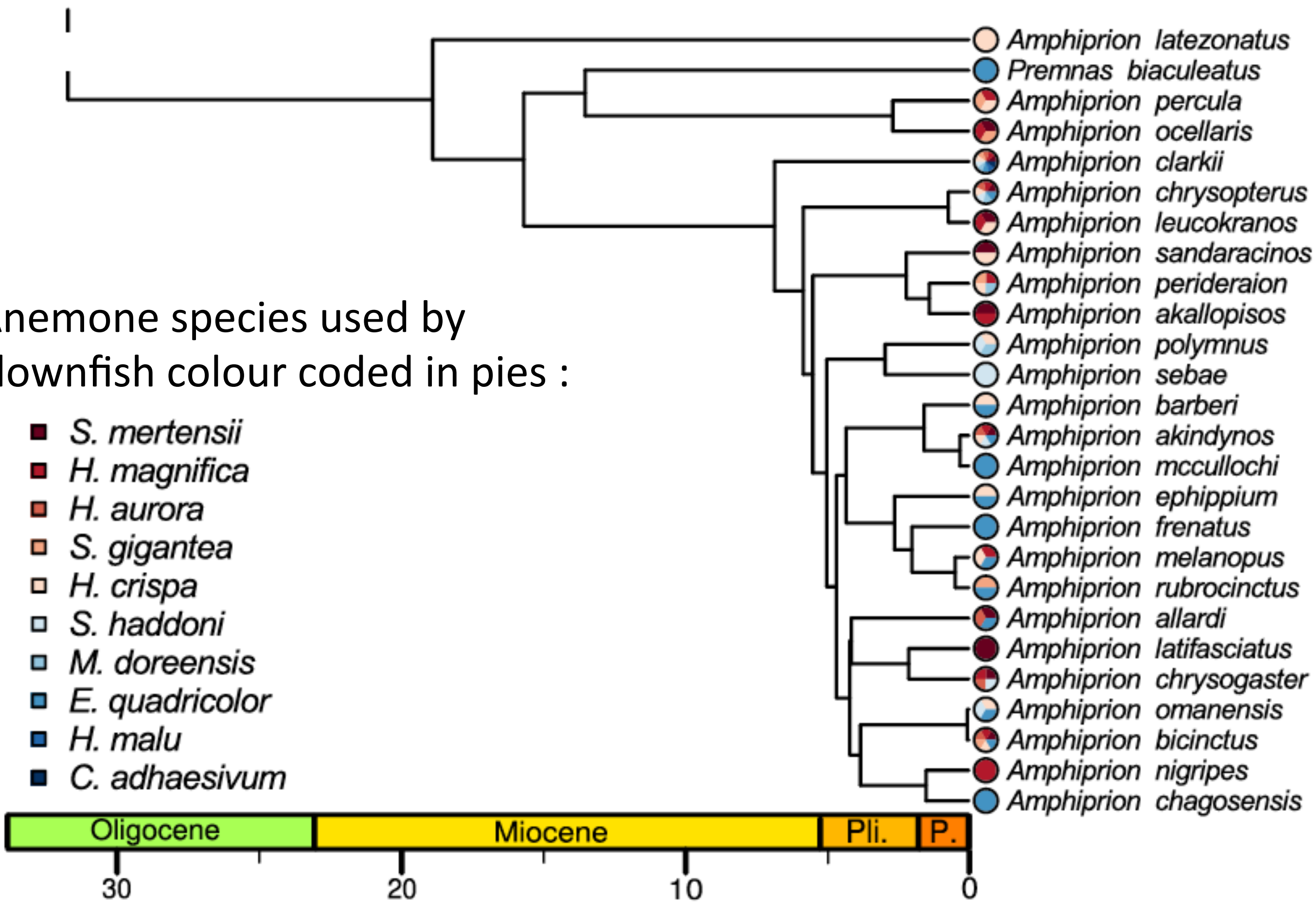
Mutualisms are seldom perfect predictors of distribution.

Determinants of Distribution

6) Biotic Interactions: Mutualism

Timing of clownfish radiation with interacting sea anemone species shown for each clownfish (*Amphiprion*) species

Anemone species used by clownfish colour coded in pies :



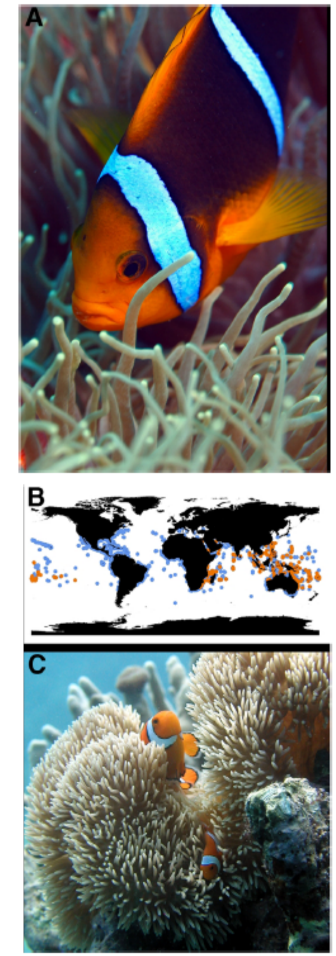
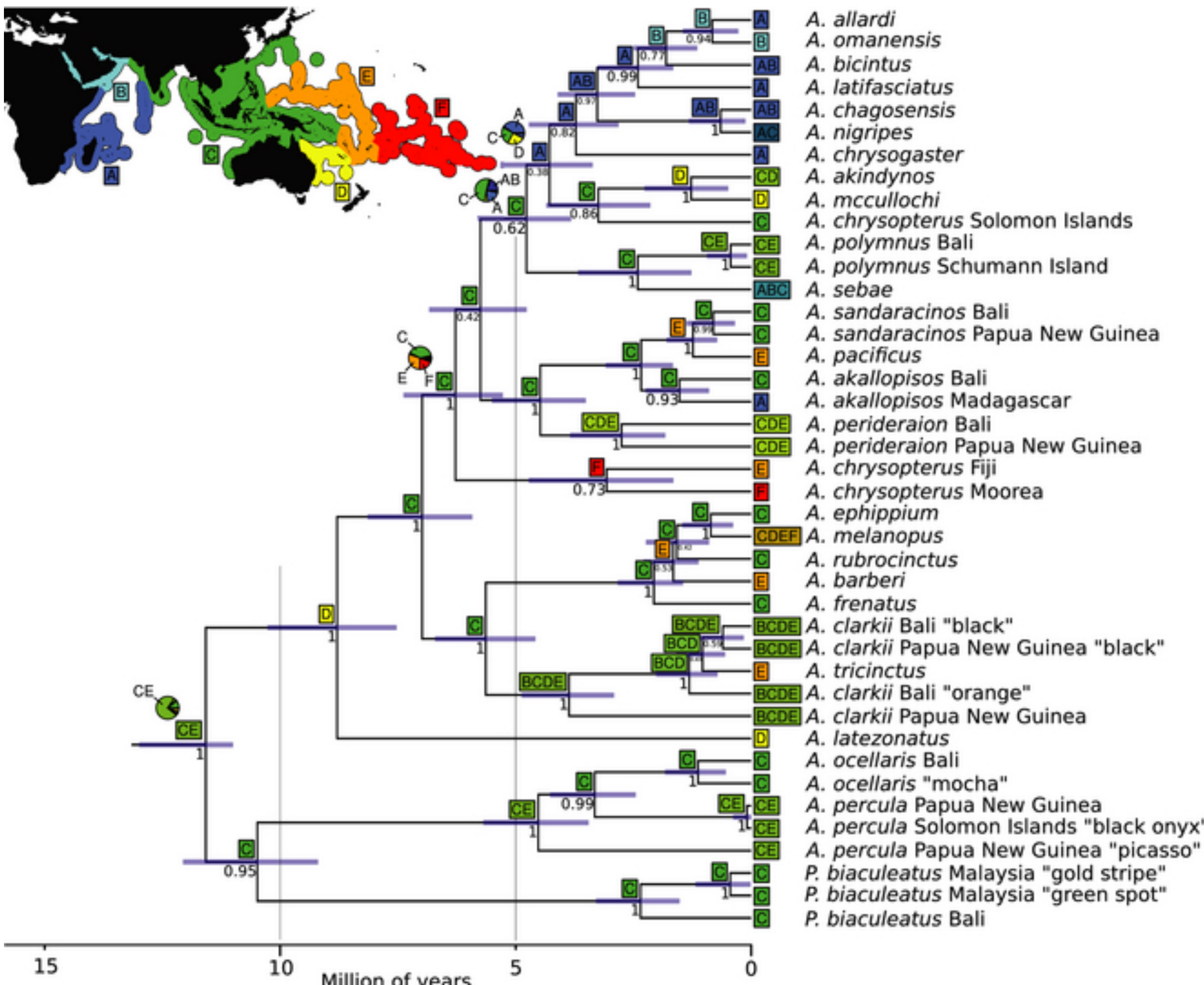


Figure 7 ***Chronogram of the clownfishes radiation.*** Branch lengths are given in MY. The interacting sea anemone species are shown for each clownfish species. Sea anemone names abbreviations as in Figure 5.

Determinants of Distribution

6) Biotic Interactions: Mutualism



Letters A-F represent Indo-Pacific provinces

26 species of tropical clownfish occupy ~ 10 species of sea anemones

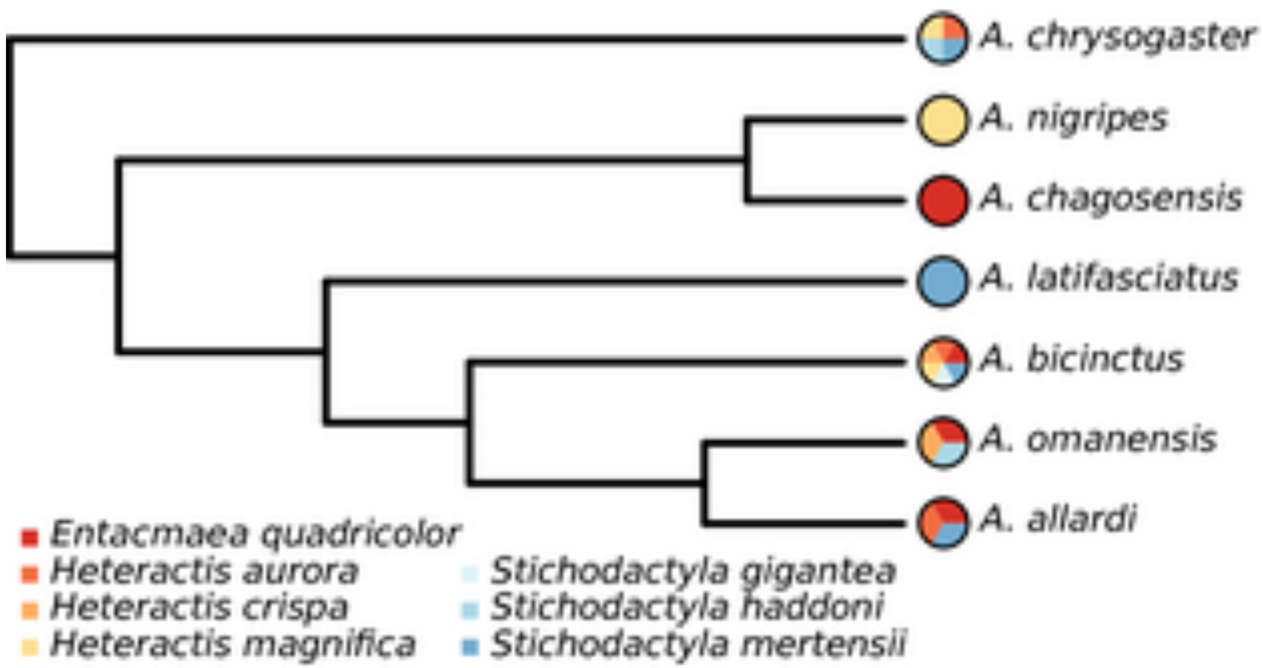
Clownfish have a mucus layer to avoid stings from anemones

Anemones provide shelter and protection from predators to clownfish

Determinants of Distribution

6) Biotic Interactions: Mutualism

Radiation of clownfish has two geographical replicates. Phylogeny of the east African clade (Genus *Amphiprion*) and pie charts coloured according to mutualistic sea anemone species (sea anemone species shown below)

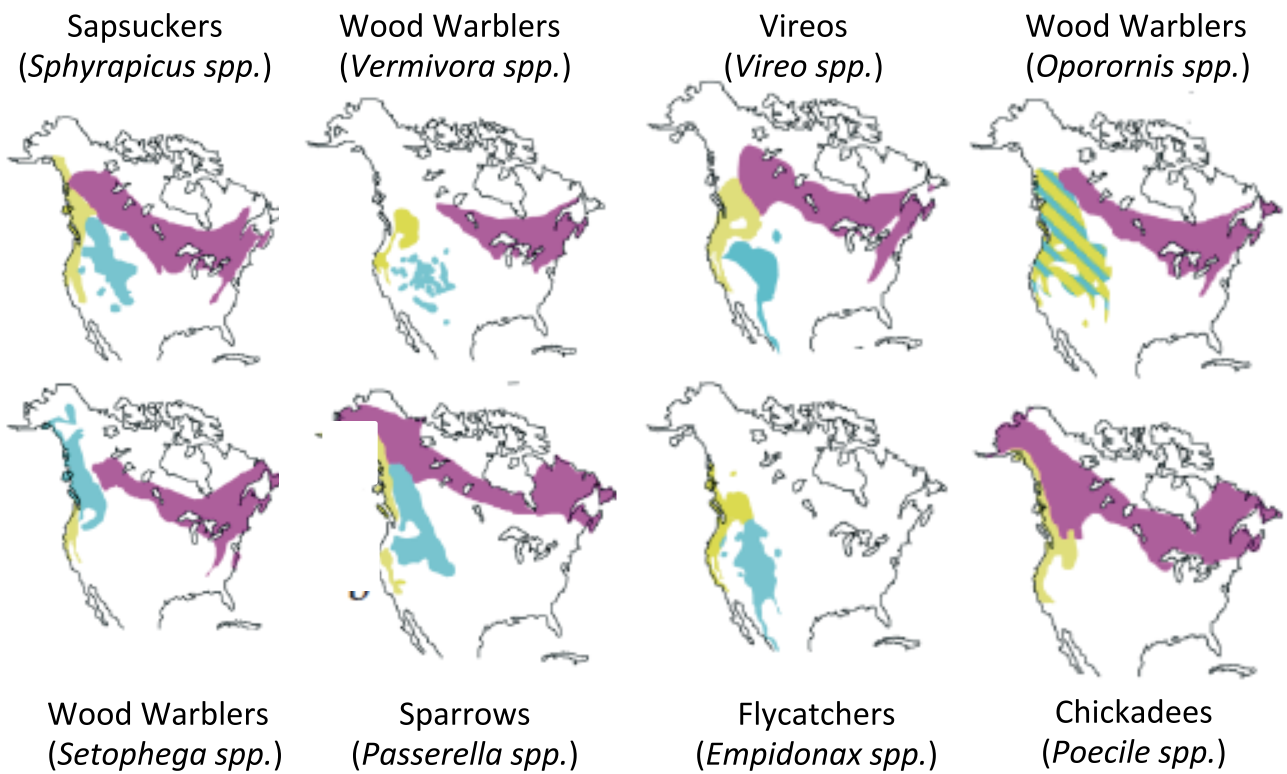


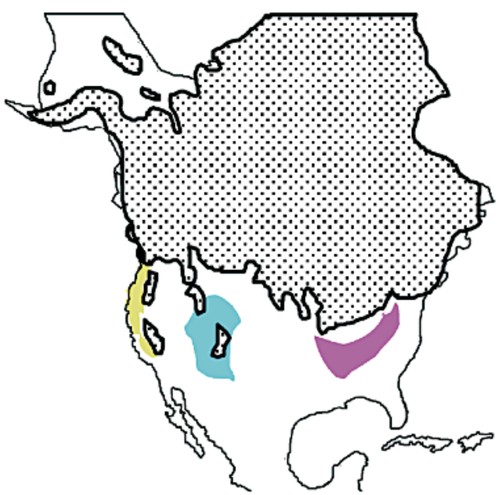
The strength and specificity of the interaction between species will ultimately determine the extent to which the distributions or range limits are affected.

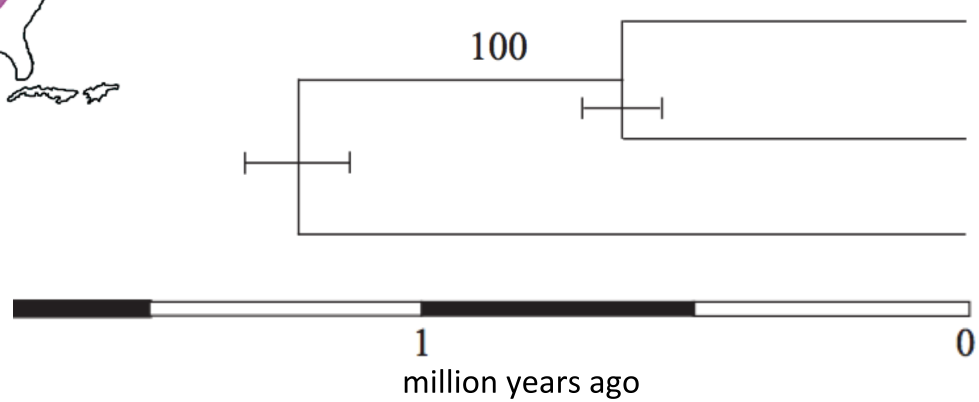
Determinants of Distribution

7) Historical Factors

Several species of NA birds have geographical divides in the rockies







Pacific

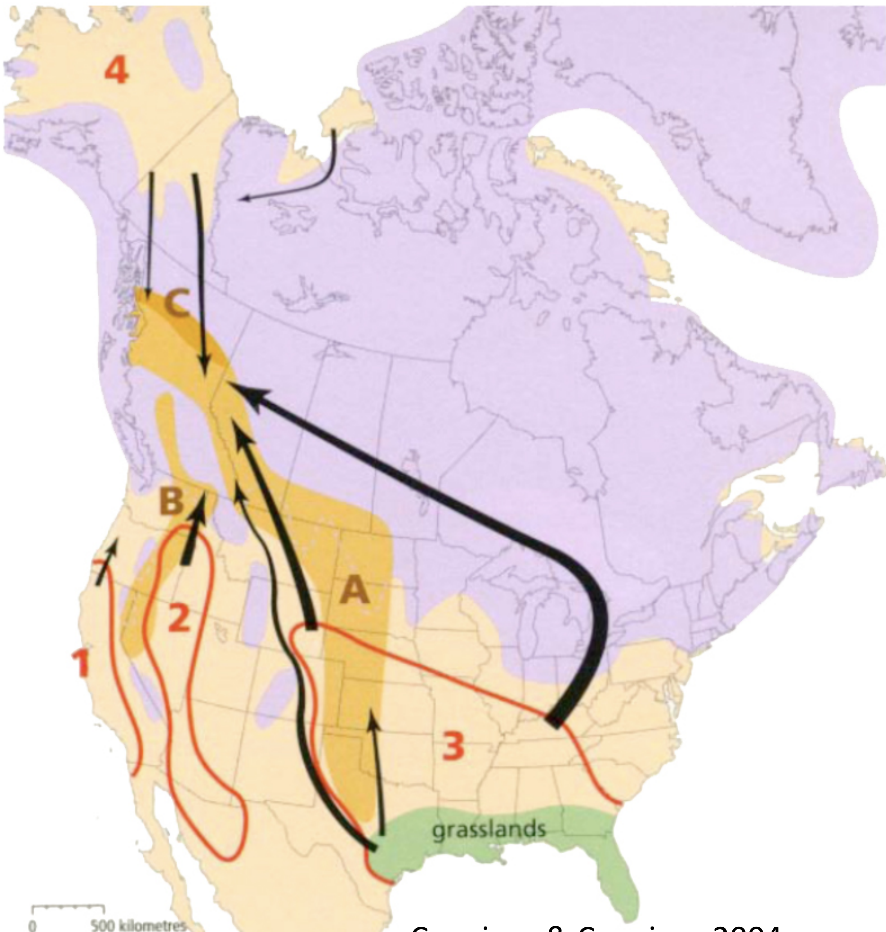
Interior

Boreal

Weir & Schluter 2004

Determinants of Distribution

7) Historical Factors



Cannings & Cannings 2004

Several areas with high concentration of species with secondary contact as ranges tracked glacial retreat

Many of these "suture zones" cluster around the Rocky Mountains of BC

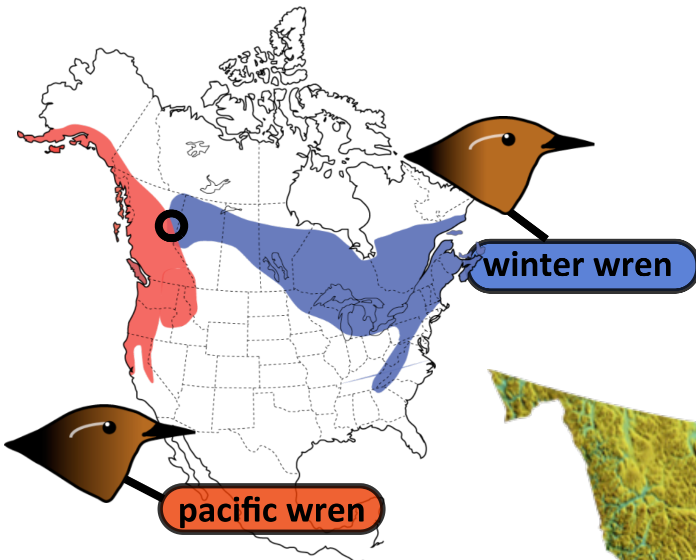
ice cover

I - 4 refguia

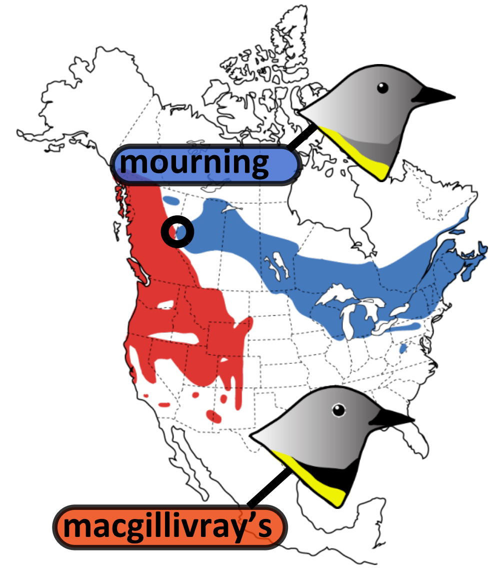
A - C secondary contact

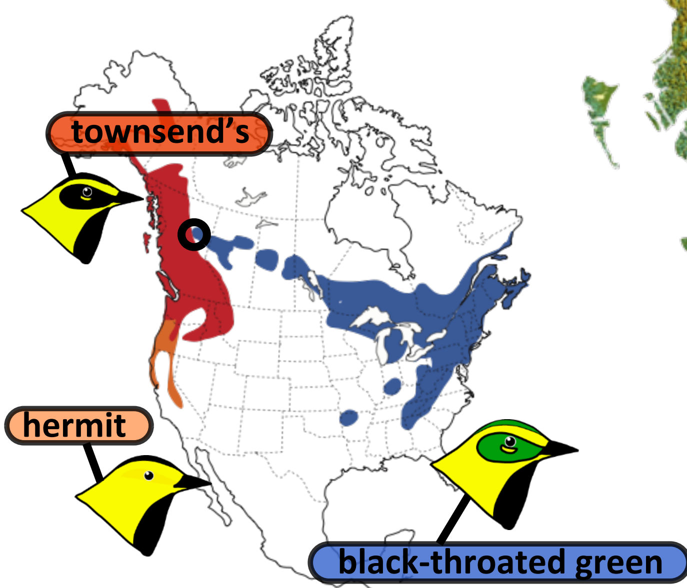
Determinants of Distribution

7) Historical Factors



Bird species with contact zones in the BC Rockies





Toews et al. 2011