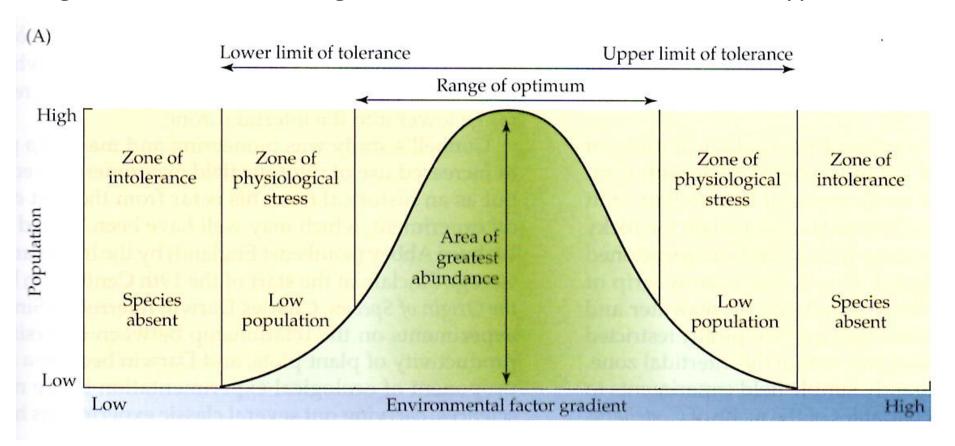
### 1) The Niche

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

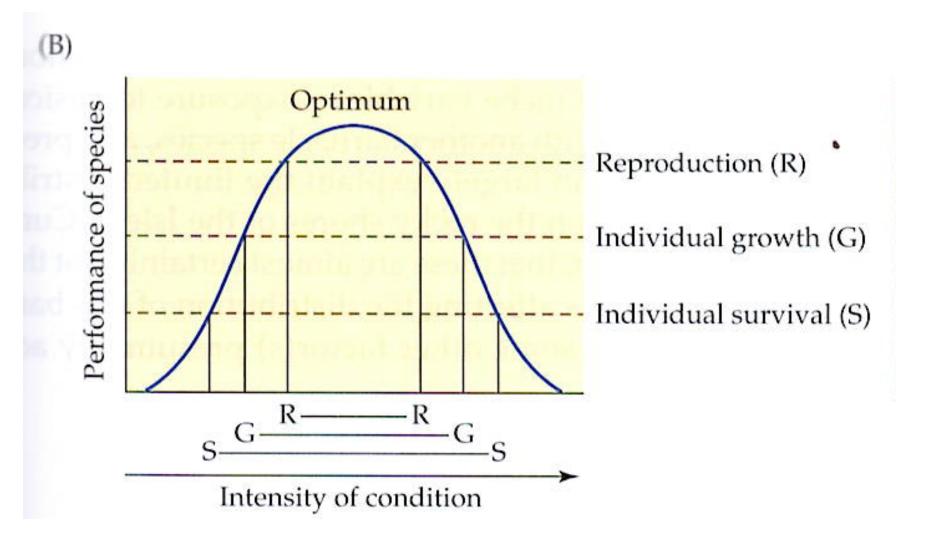
From Hutchinson (1957) the n-dimensional hypervolume (or multidimensional space) that describes the range of abiotic environmental conditions in which a taxon can survive and reproduce (each abiotic factor is a single dimension)

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

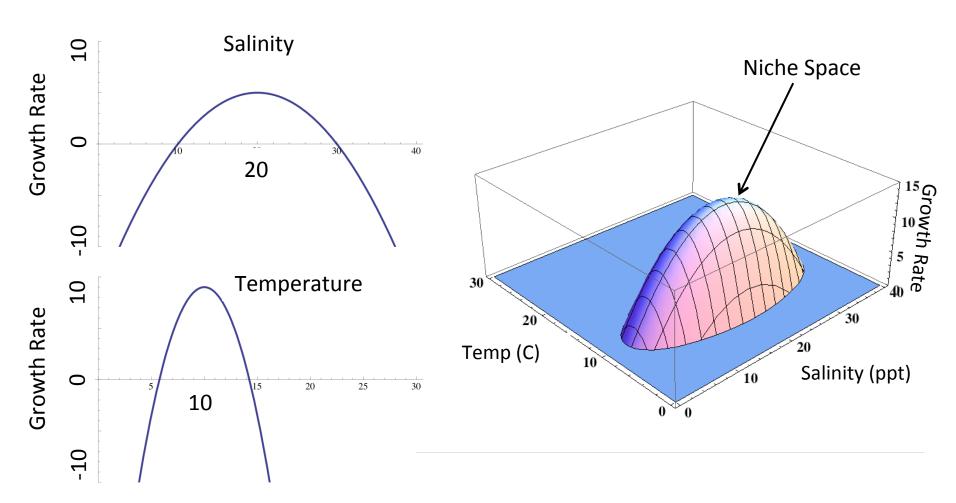


Multiple environmental factors or gradients can affect a species' distribution – this is what Hutchinson meant by the n-dimensional hypervolume

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



### 1) The Niche



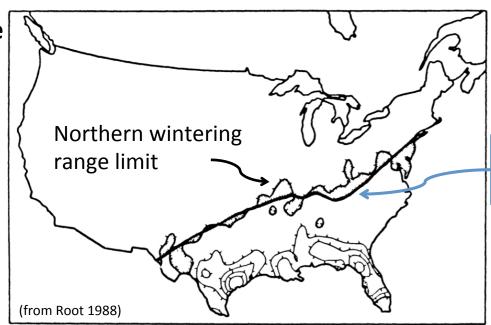
### 1) The Niche

When do range boundaries coincide with the fundamental niche?

#### **Eastern Phoebe**



http://upload.wikimedia.org/ wikipedia/commons/c/c7/ Eastern Phoebe1.jpg



-4°C January minimum isotherm

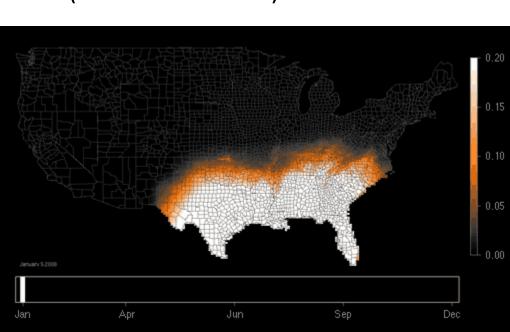
Northern range limit is correlated with metabolic costs of thermoregulation for at least 14 species (in multiples of basal metabolic rate: MR =  $^{2}$ .5 x BMR)

### 1) The Niche

Northern wintering

When do range boundaries coincide with the fundamental niche?

Northern range limit is correlated with metabolic costs of thermoregulation for at least 14 species (MR =  $^2$ 2.5 x BMR)





(from Root 1988)

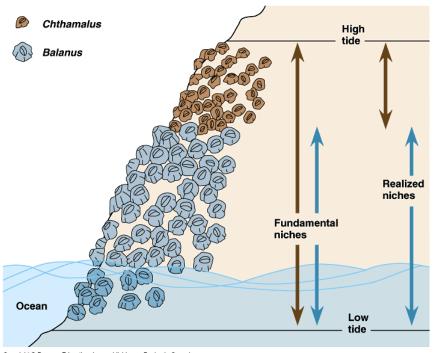
range limit

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

**Eastern Phoebe** 

### 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

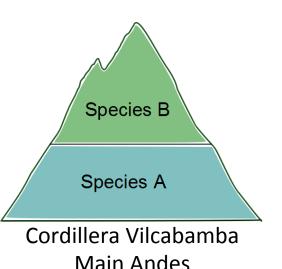
Chthamalus: constrained by competitive interactions to narrower realized niche

How could we test this experimentally?

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#### 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).



A natural experiment...with birds

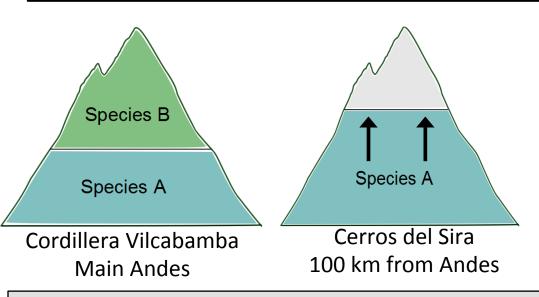
Species A and B are closely related ~ similar niche

In the main Andes:

- both species present
- ranges do not overlap

### 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).



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

### 1) The Niche

Important caveats to the niche as the main determinant of a species' range:

a) Species may occupy unfavourable areas

b) Species may be absent in favourable areas

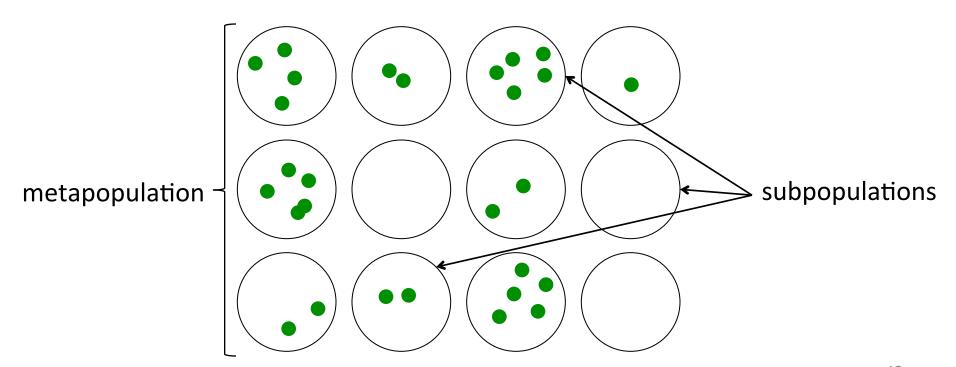
### 1) The Niche

Important caveats to the niche as the main determinant of a species' range:

- 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

### 2) Metapopulation structure

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



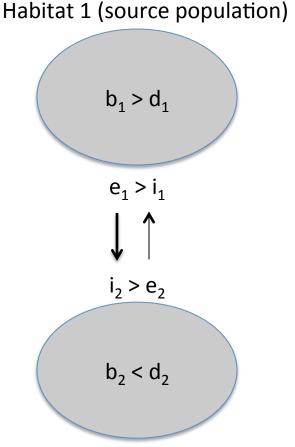
#### 2) Metapopulation structure

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

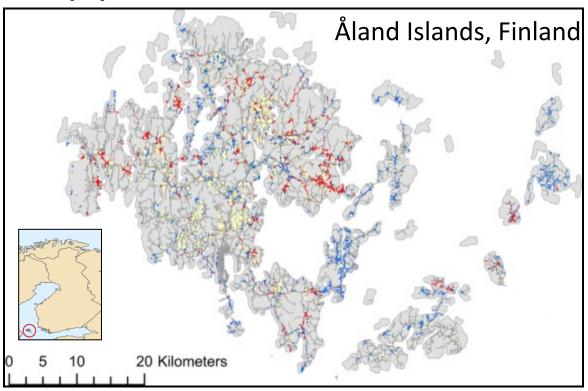
Metapopulation source/sink dynamics more likely to occur toward the periphery of a species' range (based on the abundance-center hypothesis)



Habitat 2 (sink population)

Fig from ch. 4, Lomolino et al. 2006

#### 2) Metapopulation structure



Glanville fritillary butterfly (Melitaea cinxia)



Photograph courtesy of Hannu Aarnio.

~ 4000 dry meadows in 2012

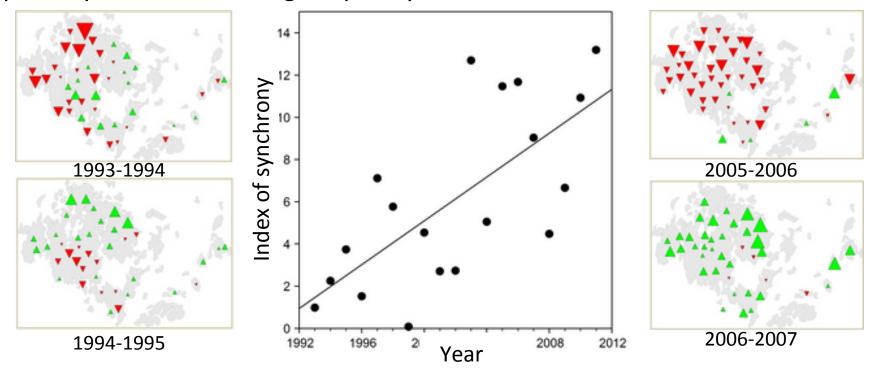
Red = occupied Blue = unoccupied





### 2) Metapopulation structure

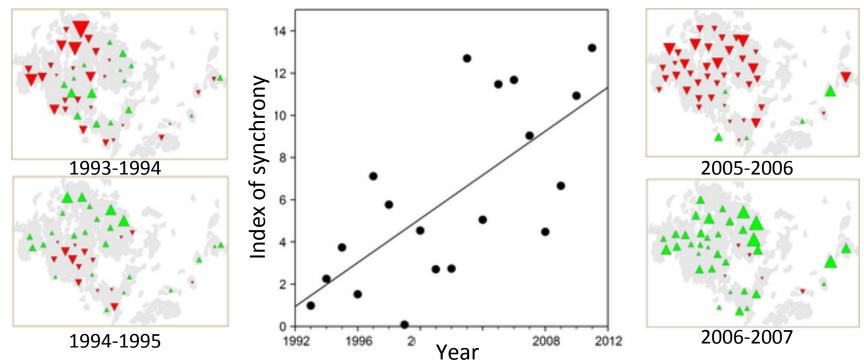
Glanville fritillary on the Åland Islands became more synchronous over time, possibly due to increasing frequency of extreme weather events:



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

### 2) Metapopulation structure

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



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

#### 3) Disturbance

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



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"





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

### 3) Disturbance

Disturbance-adapted animals? Urban adapters?



American Crow (Corvus brachyrhynchos)



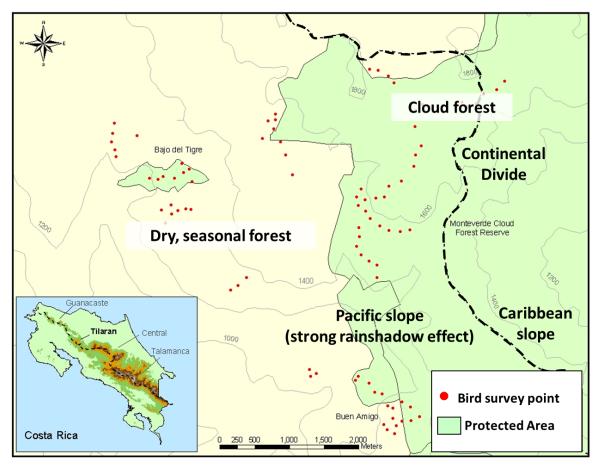
Common Starling (Sturnus vulgaris)

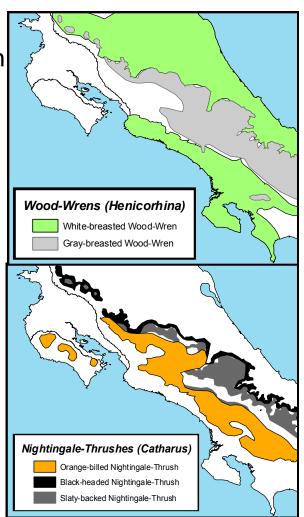
We typically think of disturbance as a factor limiting where species can occur, or disrupting the continuity of species distributions

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

#### 4) Biotic Interactions: Direct Competition

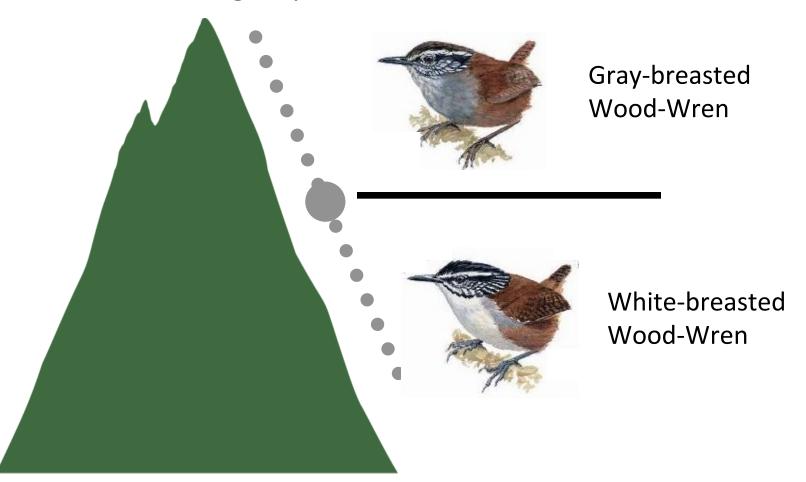
Direct competition – testing species replacements Monteverde, Tilarán Mountains, Costa Rica 1100-1800m





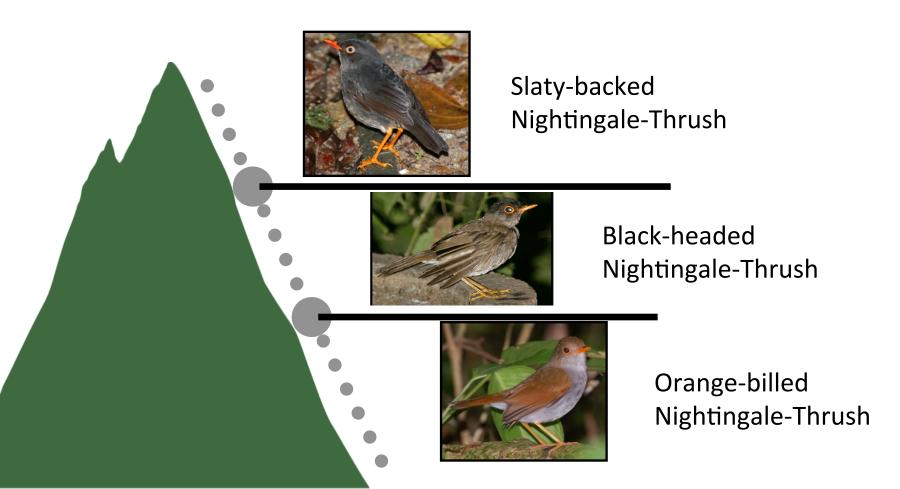
4) Biotic Interactions: Direct Competition

Target species: Wood-Wrens



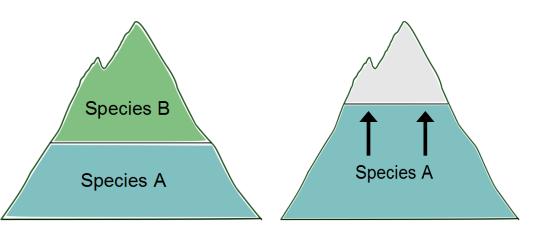
4) Biotic Interactions: Direct Competition

Target species: Nightingale-Thrushes



### 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...

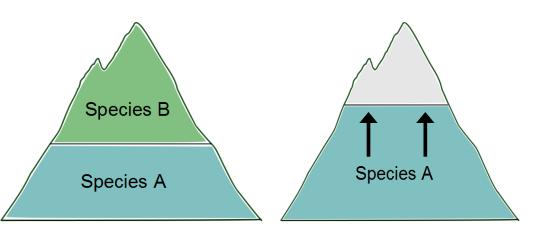
we can use territory defense as a behavioural metric of competitive interactions

...and design an experiment

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

### 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

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





#### 4) Biotic Interactions: Direct Competition

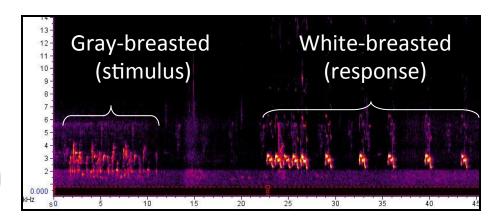
If species are interspecifically aggressive at contact zones, this supports the hypothesis of direct competition

Playback protocol to test species aggressive responses:

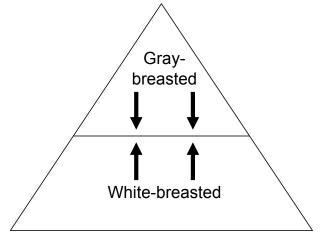
Trial 1		Trial 2	
Observation (Control)	Playback (Congener/ Conspecific)	Observation (Control)	Playback (Congener/ Conspecific)
8 min. obs	3 min. song, 5 min. obs	8 min. obs	3 min. song, 5 min. obs

### 4) Biotic Interactions: Direct Competition





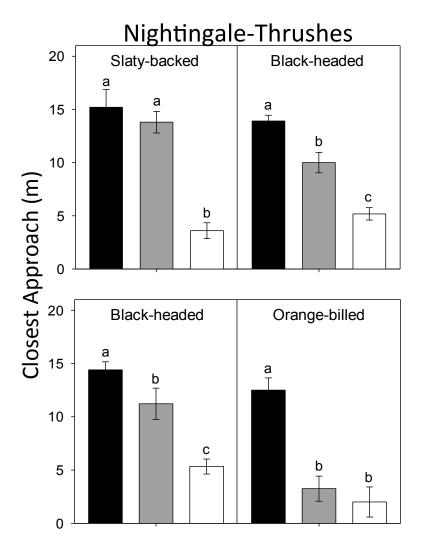


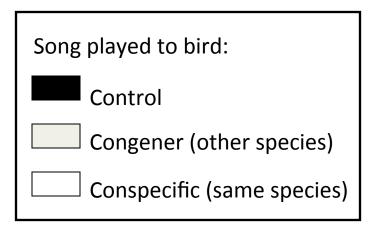


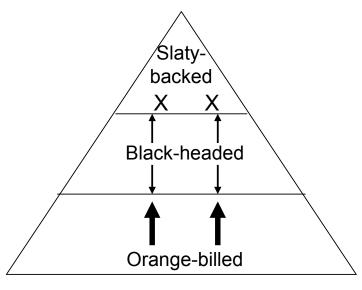
Jankowski et al. 2010, Ecology



### 4) Biotic Interactions: Direct Competition







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)  $\rightarrow$  more cavity nesters  $\rightarrow$  less open cup nesters



Western bluebird (*Sialia mexicana*)



American robin (*Turdus migratorius*)

### 5) Biotic Interactions: Predation



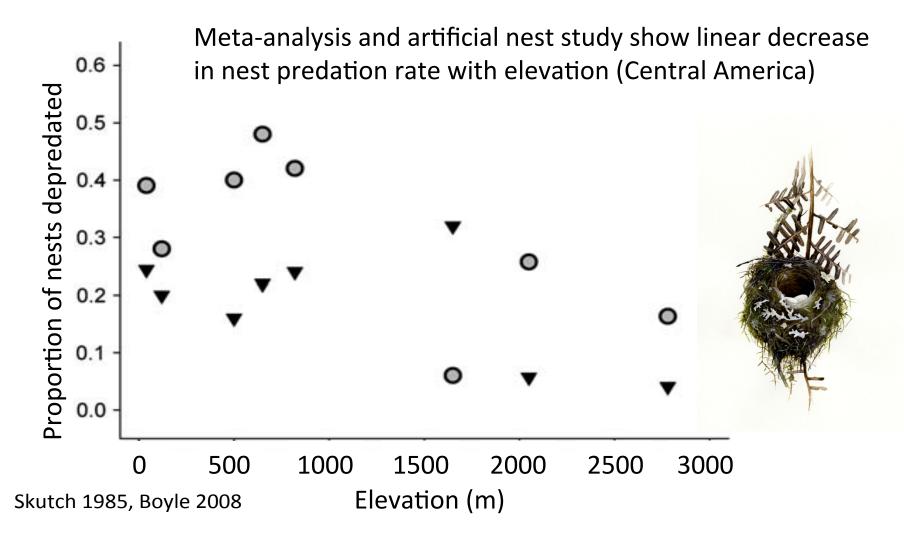


For tropical birds, nest predation is a major source of mortality

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?

### 5) Biotic Interactions: Predation

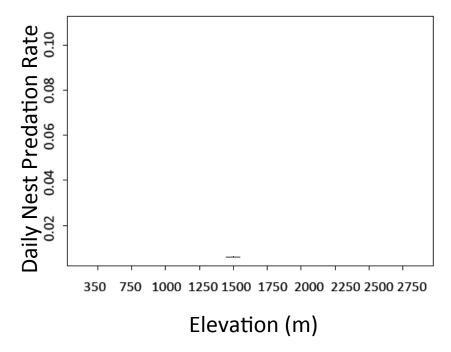


### 5) Biotic Interactions: Predation





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

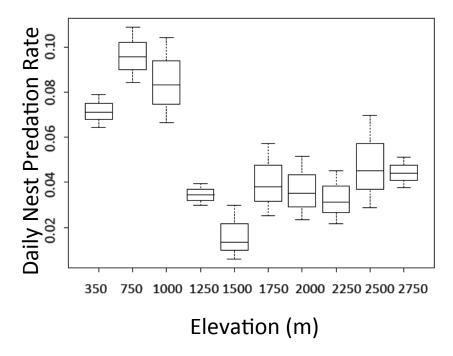


### 5) Biotic Interactions: Predation





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

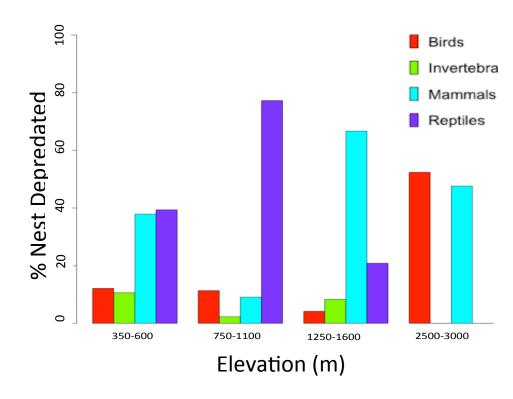


### 5) Biotic Interactions: Predation





How does the nest predator community change with elevation in Manu National Park, Peru?



### 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



### 5) Biotic Interactions: Predation





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

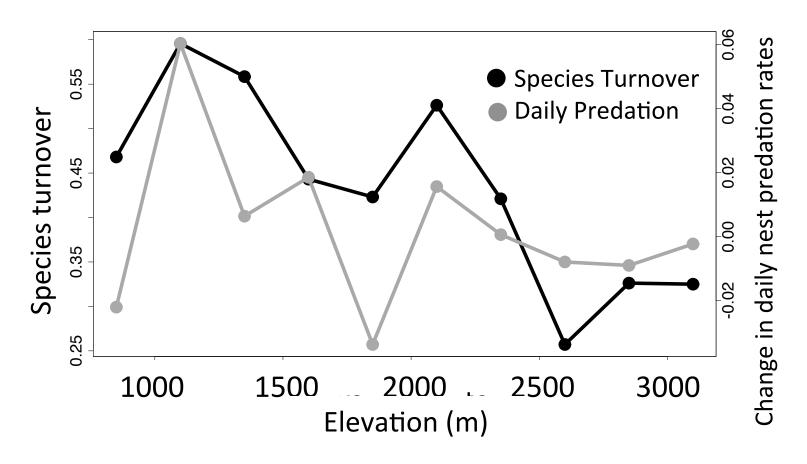
Cock-of-the-Rock nestling and adult (Rupicola peruviana)



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

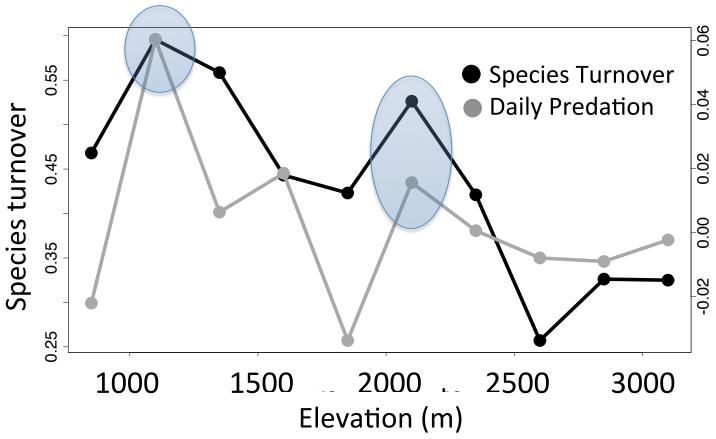
#### 5) Biotic Interactions: Predation

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



#### 5) Biotic Interactions: Predation

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



Change in daily nest predation rates

1979 -10

1980 - 8

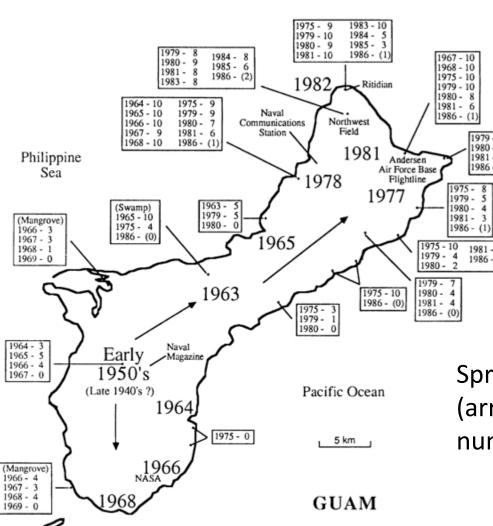
1981 - 4

1986 - (1)

1981 - 1

1986 - (0)

#### 5) Biotic Interactions: Predation



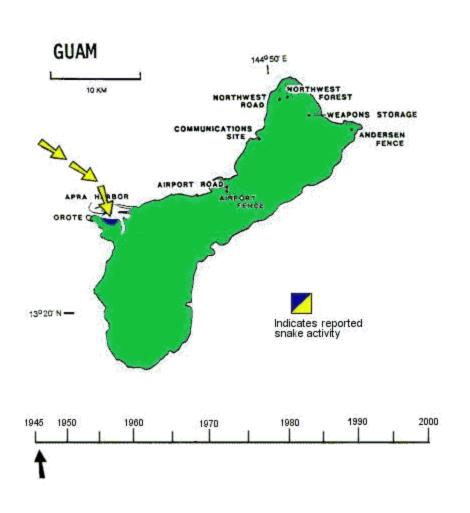
Cocos Island



Brown tree snake (Boiga irregularis)

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

#### 5) Biotic Interactions: Predation





Brown tree snake (Boiga irregularis)

USGS Timeline of the Brown tree snake travel across Guam

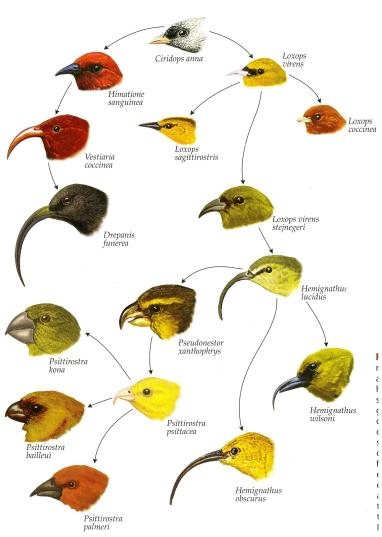
One of many examples where a predator introduced to a naïve native community results in drastic cascading changes

#### 5) Biotic Interactions: Parasitism

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

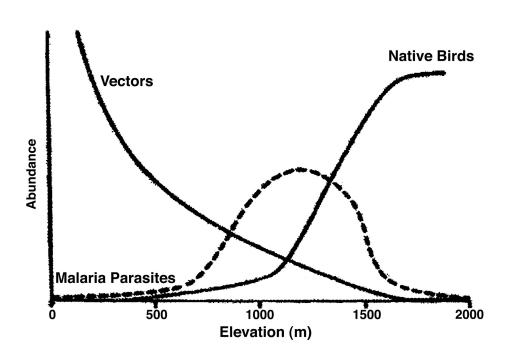
Human introductions of mosquitoes and avian malaria has eliminated all species from low and middle elevations on the islands.

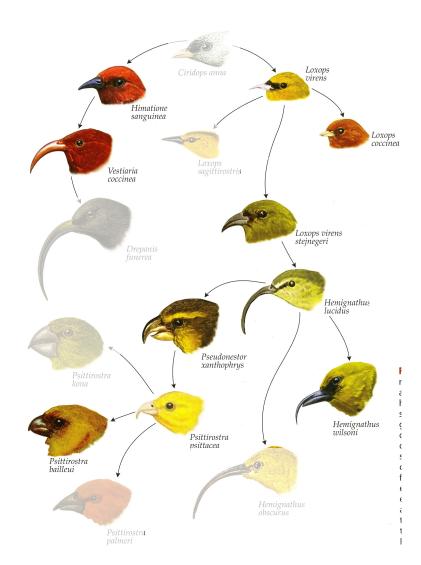




#### 5) Biotic Interactions: Parasitism

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





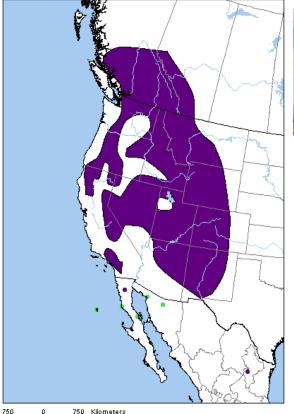
Benning et al. 2002 PNAS

#### 6) Biotic Interactions: Mutualism

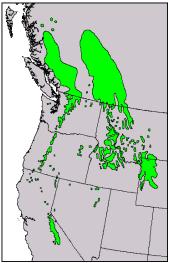
Clark's nutcracker (Nucifraga columbiana) and whitebark pine (Pinus albicaulis)









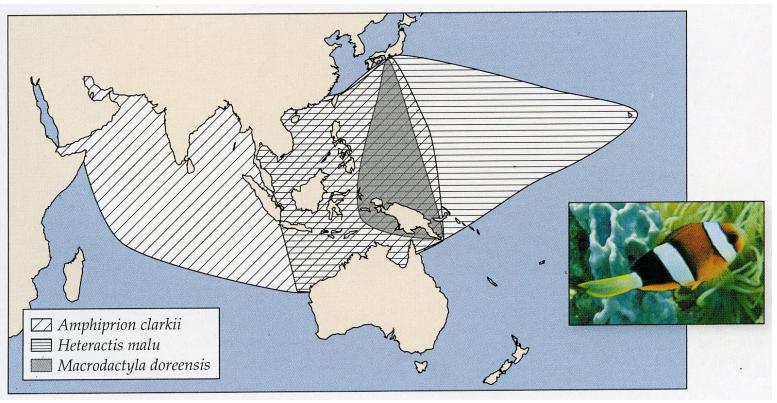


Whitebark, limber, Colorado pinyon, single-leaf pinyon and southwestern white pines depend on nutcrackers for seed dispersal

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

#### 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.

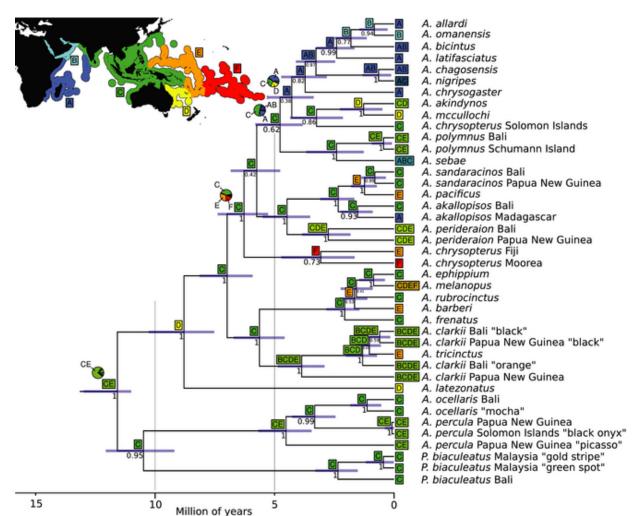
#### 6) Biotic Interactions: Mutualism

Timing of clownfish radiation with interacting sea anemone species shown for

each clownfish (Amphiprion) species Amphiprion latezonatus Premnas biaculeatus Amphiprion percula Amphiprion ocellaris Amphiprion clarkii Amphiprion chrysopterus Amphiprion leucokranos Amphiprion sandaracinos Amphiprion perideraion Anemone species used by Amphiprion akallopisos Amphiprion polymnus clownfish colour coded in pies: Amphiprion sebae Amphiprion barberi S. mertensii Amphiprion akindynos Amphiprion mccullochi H. magnifica Amphiprion ephippium H. aurora Amphiprion frenatus S. gigantea Amphiprion melanopus H. crispa Amphiprion rubrocinctus Amphiprion allardi S. haddoni Amphiprion latifasciatus M. doreensis 🖱 Amphiprion chrysogaster E. quadricolor Amphiprion omanensis H. malu Amphiprion bicinctus Amphiprion nigripes C. adhaesivum Amphiprion chagosensis Oligocene Miocene

**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.

#### 6) Biotic Interactions: Mutualism



Letters A-F represent Indo-Pacific provinces

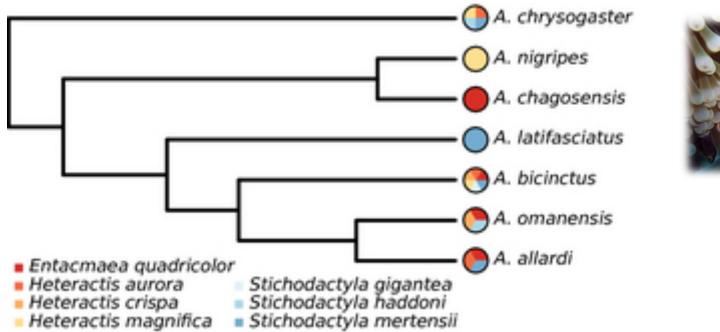
26 species of tropical clownfish occupy ~ 10 species of sea anemones

Clownfish have a mucus layer to avoid stings from anemones

Anemones provide shelter and protection from predators to clownfish

#### 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.

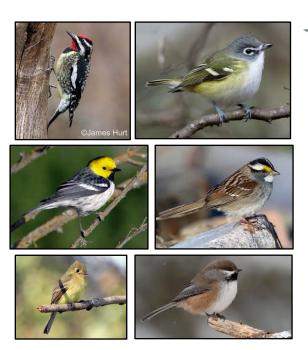
#### Sapsuckers **Wood Warblers** Vireos **Wood Warblers** (Sphyrapicus spp.) (Vermivora spp.) (Vireo spp.) (Oporornis spp.) 7) Historical Factors Several species of NA birds have geographical divides in the rockies Chickadees **Wood Warblers Sparrows Flycatchers** (Empidonax spp.) (Poecile spp.) (Setophega spp.) (Passerella spp.) Pacific 100 Interior **Boreal**

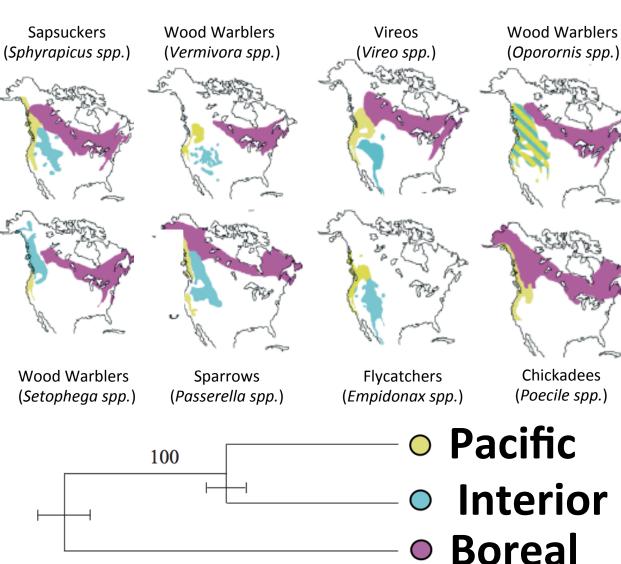
million years ago

Weir & Schluter 2004

#### 7) Historical Factors

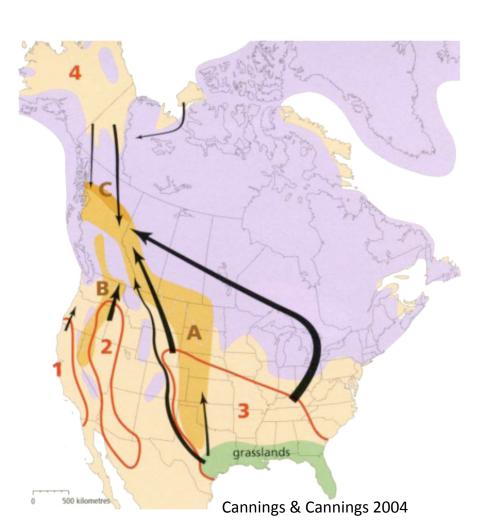
Several species of NA birds have geographical divides in the rockies





Weir & Schluter 2004 million years ago

#### 7) Historical Factors



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

- 4 refguia

secondary contact

### **7) Historical Factors**

