The Abdus Salam International Centre for Theoretical Physics

United Nations Educational, Scientific and Cultural Organization

IAEA International Atomic Energy Agency

2022-1

Workshop on Theoretical Ecology and Global Change

2 - 18 March 2009

Range Models

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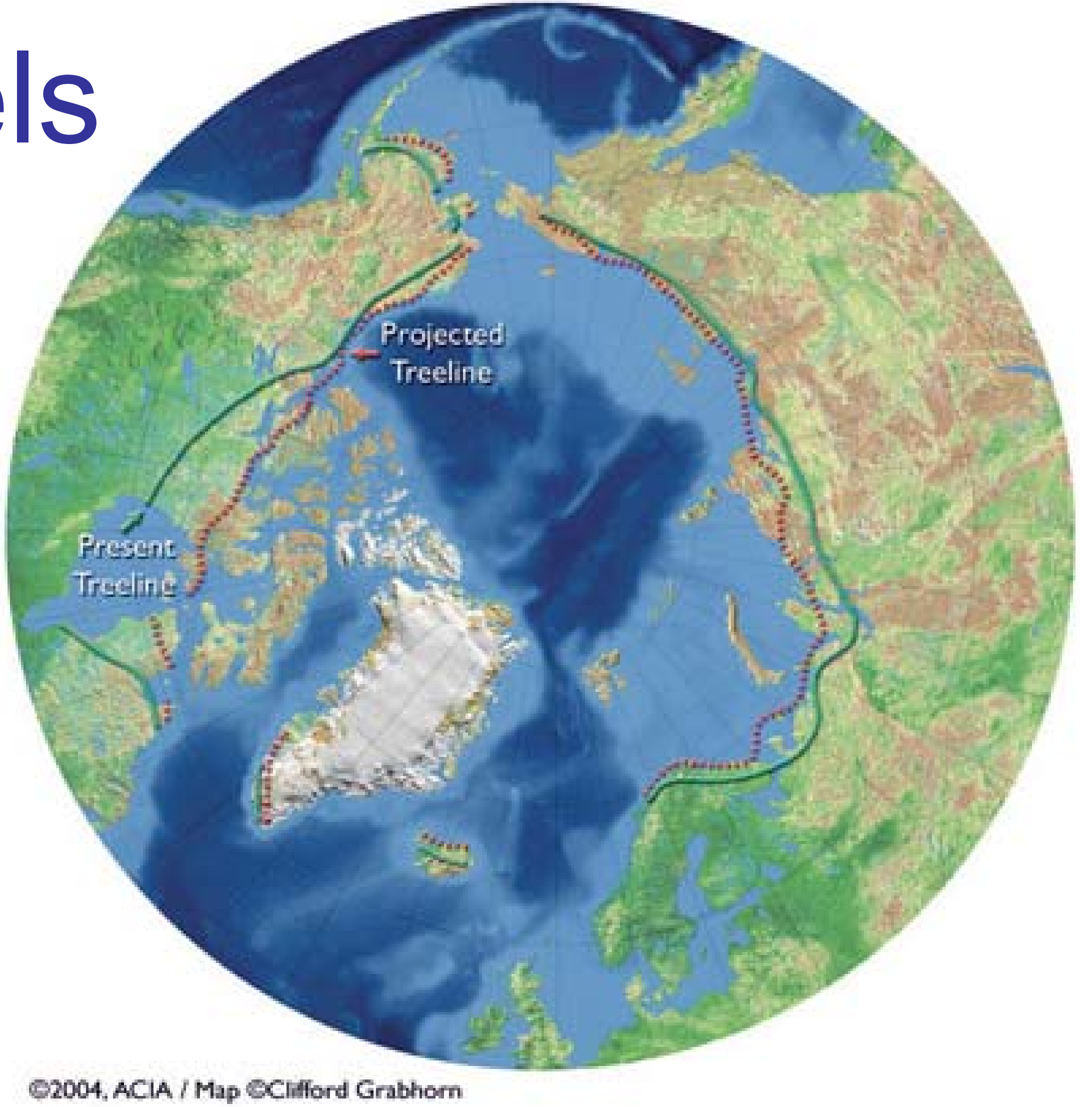
Range models
1. Theory



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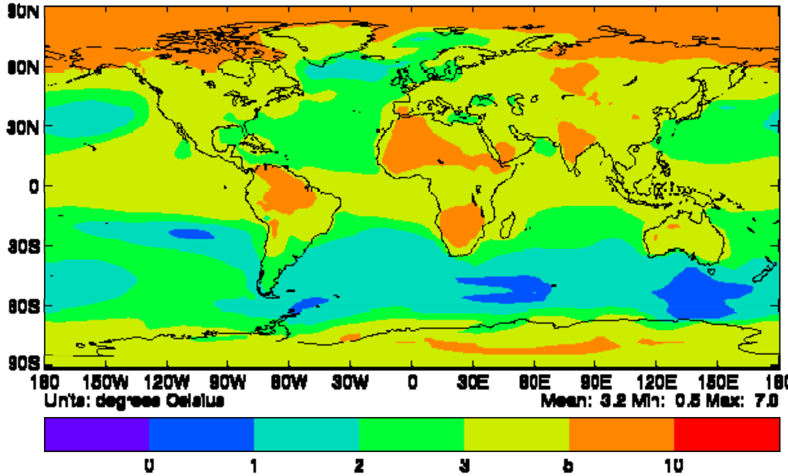
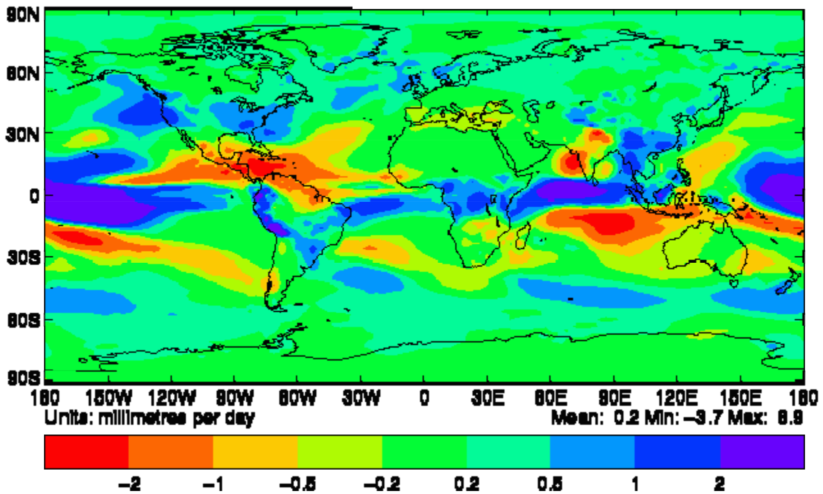
THE UNIVERSITY
of NORTH CAROLINA
at CHAPEL HILL

Climate-induced range shifts and extinctions?

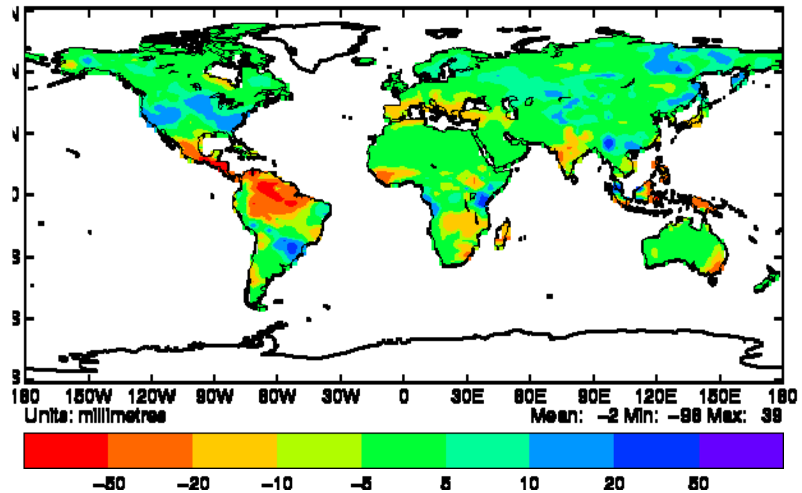
Temperature (°C)



Precipitation (mm day^{-1})



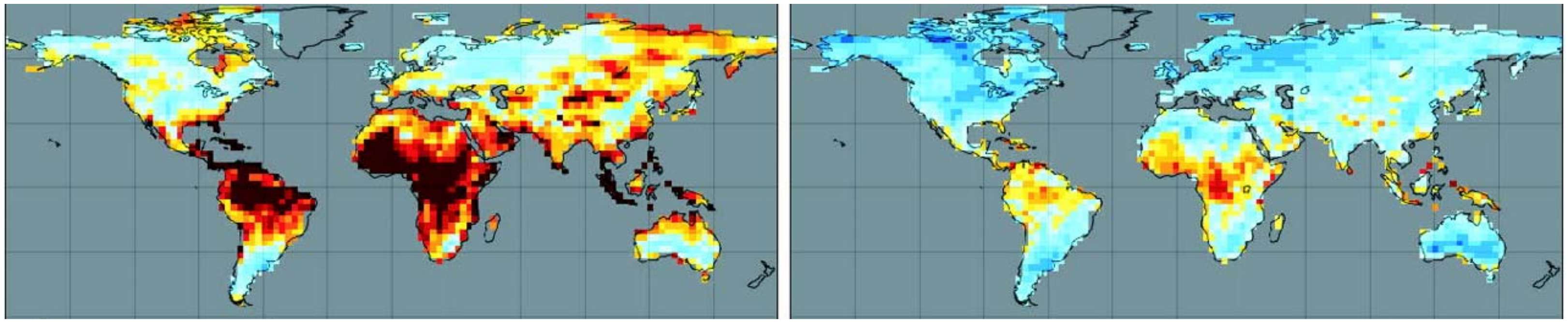
Soil moisture (mm)



1960-1990 to 2070-2100
(Hadley Center)

Climate-induced range shifts and extinctions?

Novel Climates by 2100



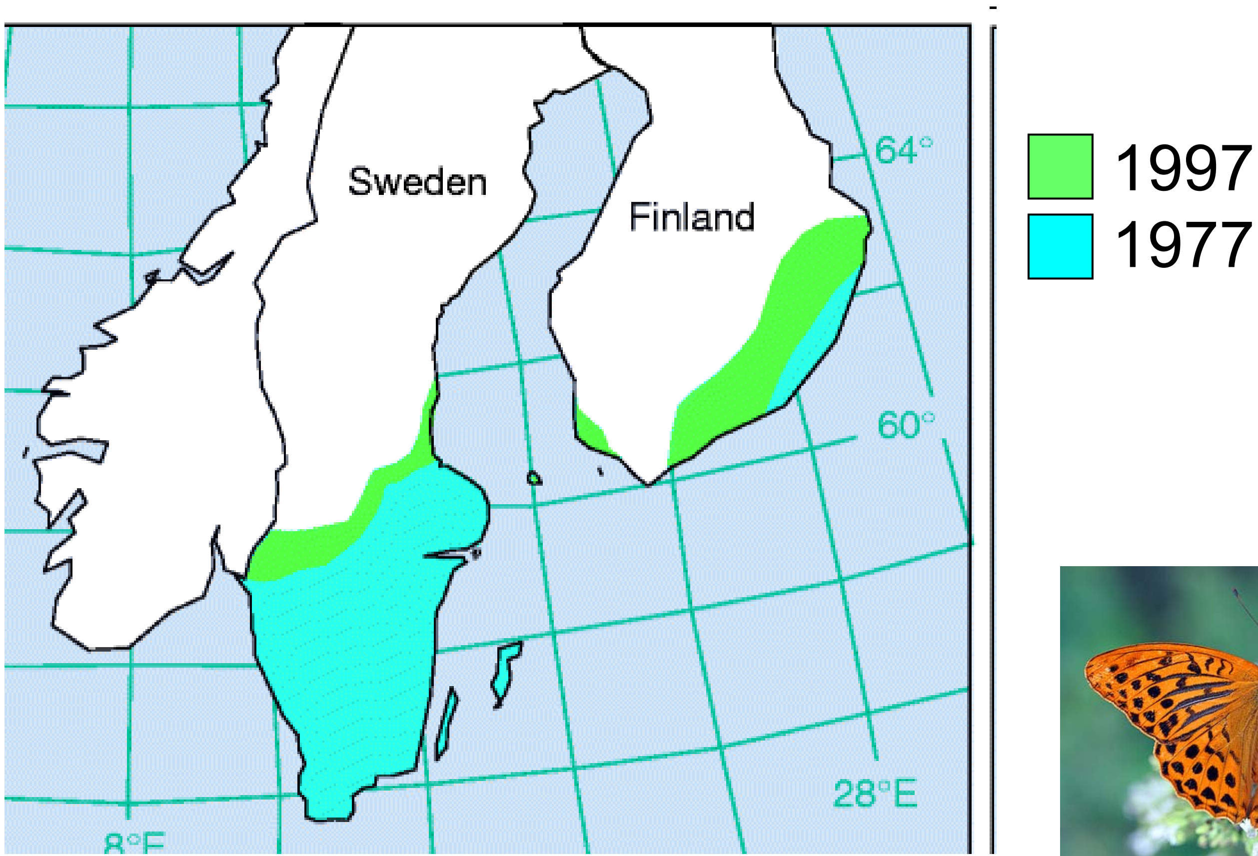
High emissions scenario — Low emissions scenario

Increasing climate novelty

(Williams *et al*. 2007)

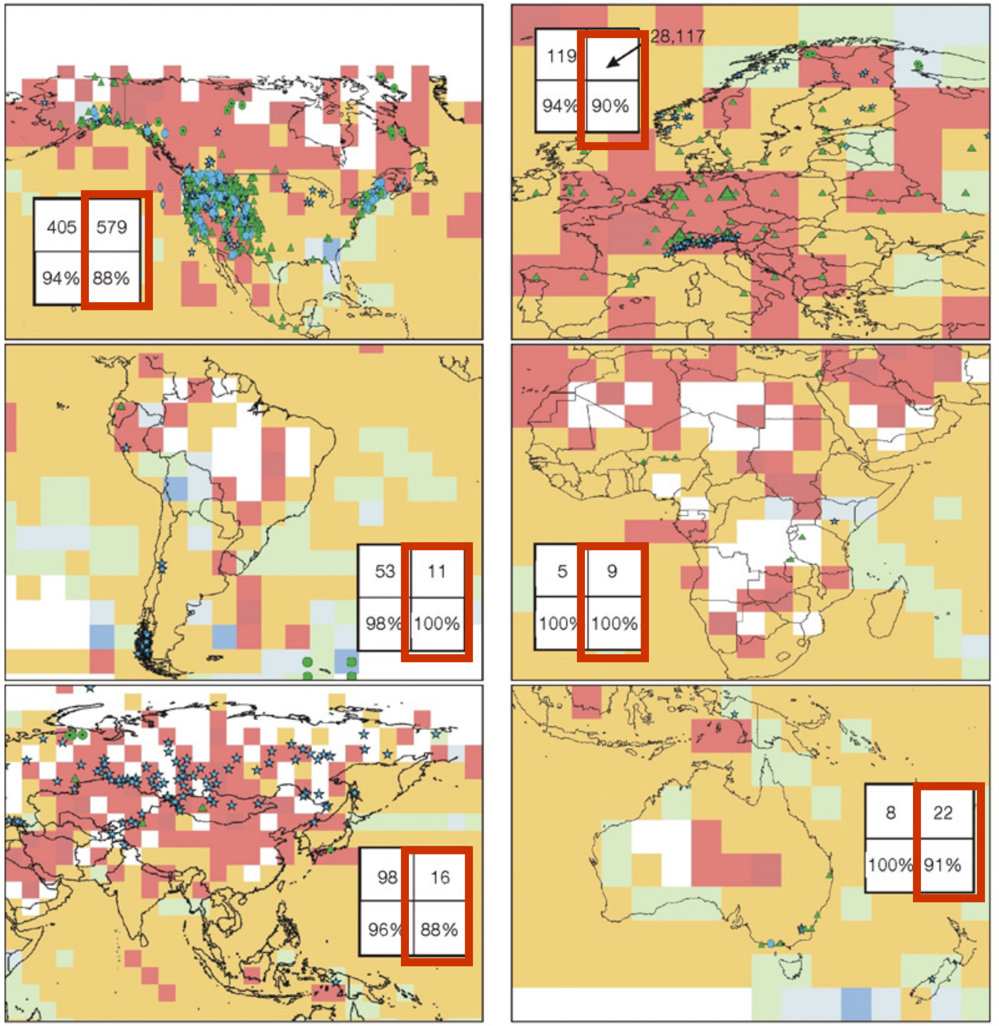
Recent range shifts

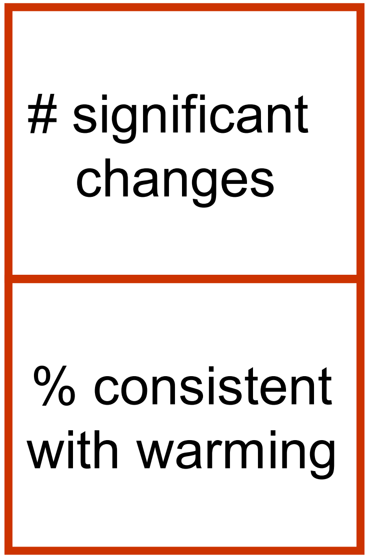
35 European non-migratory butterflies:
63% N range shift of 30-240 km during last century



Argynnis paphia
(Parmesan et al 1999)

Recent biological responses to warming



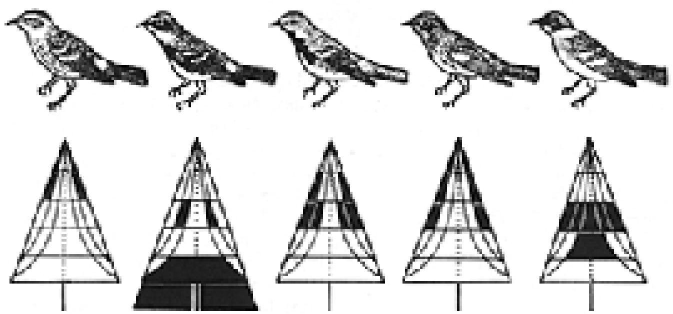


(Rosenzweig et al. 2008)

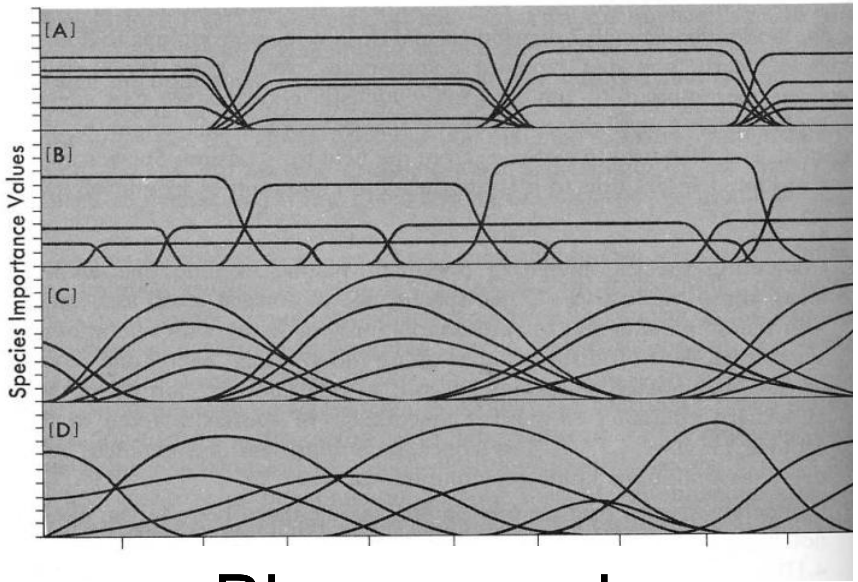
Climate-induced range shifts and extinctions?

(SEED on Thomas et al. 2004)

What sets a species' range boundary?

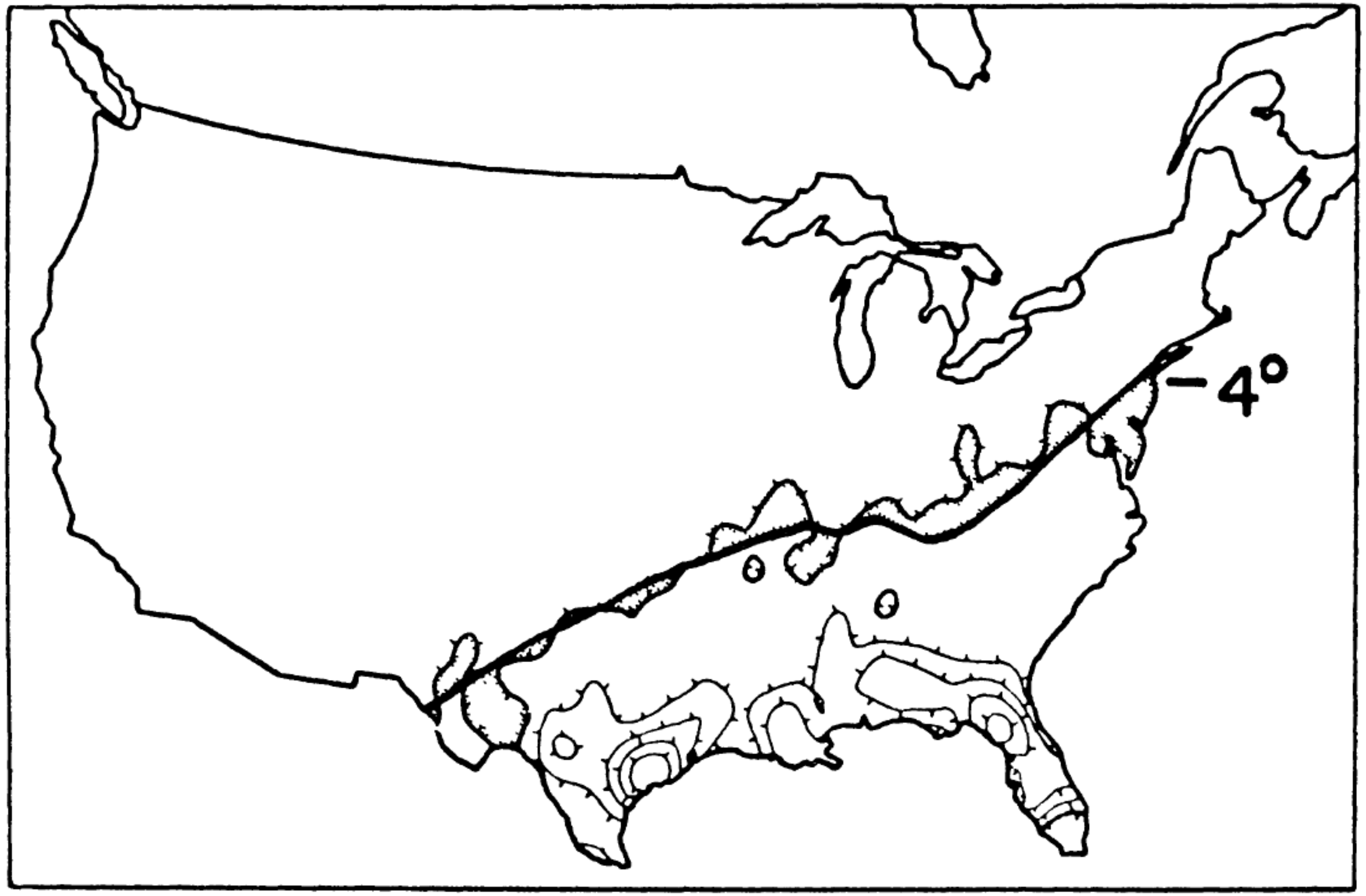


Community ecology

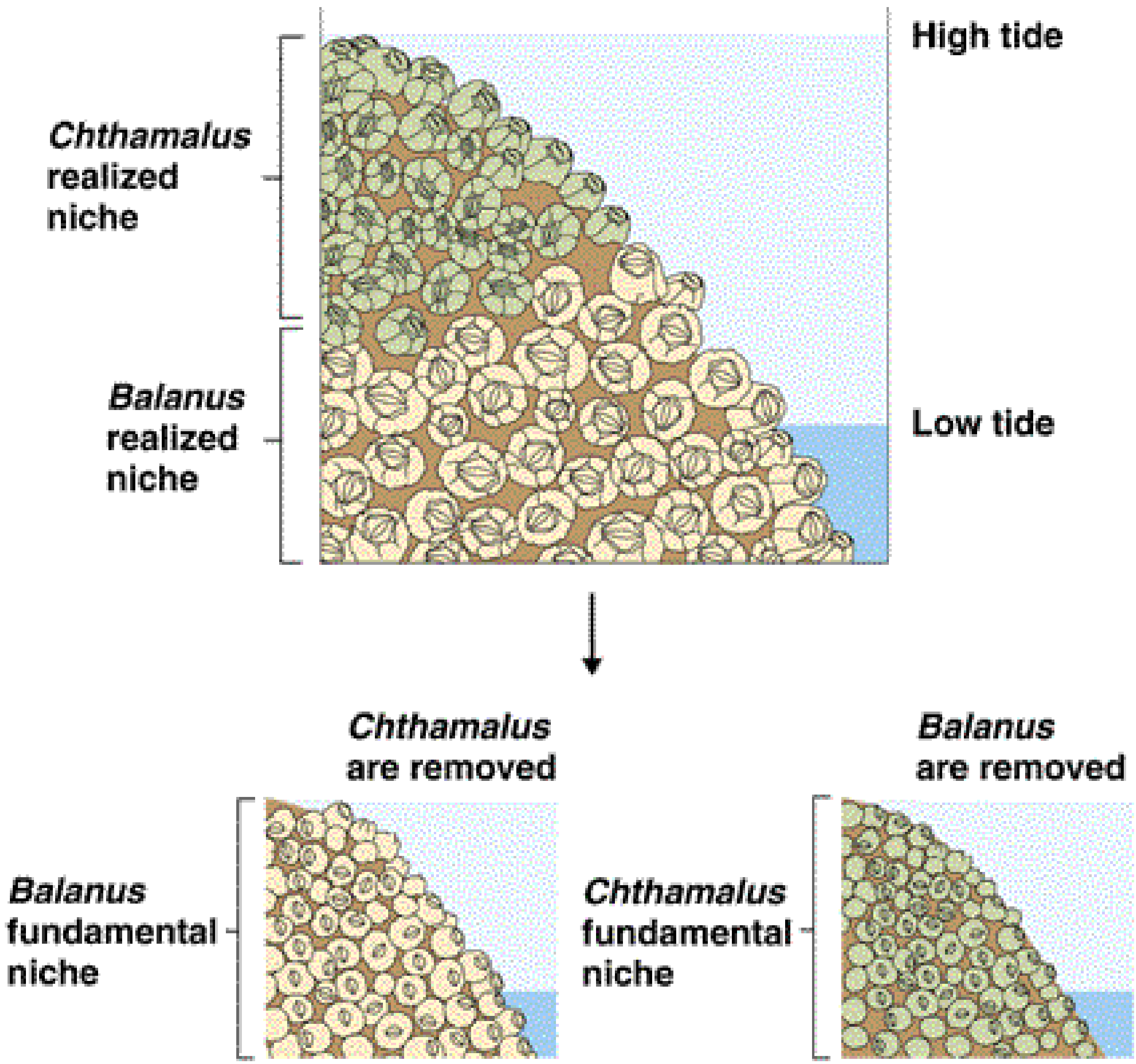


Biogeography

SCALE



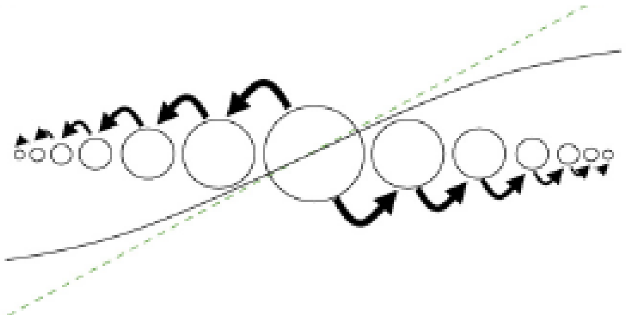
Eastern Phoebe
metabolic constraint
(Root 1988)



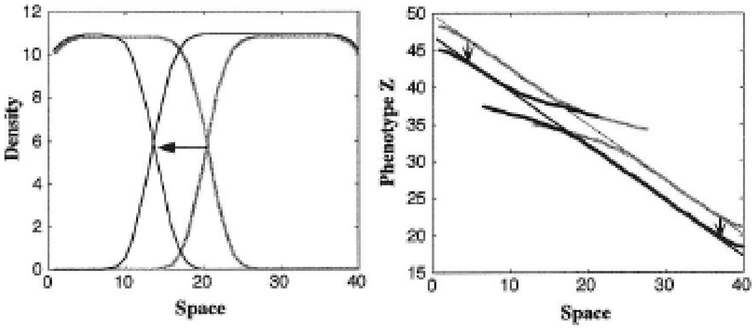
(Connell 1961)

Theory

Gene flow along selection gradient
(Kirkpatrick & Barton 1997)

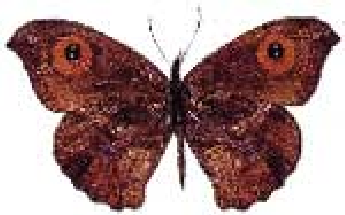


Incorporate species interactions
(Case & Taper 2000)



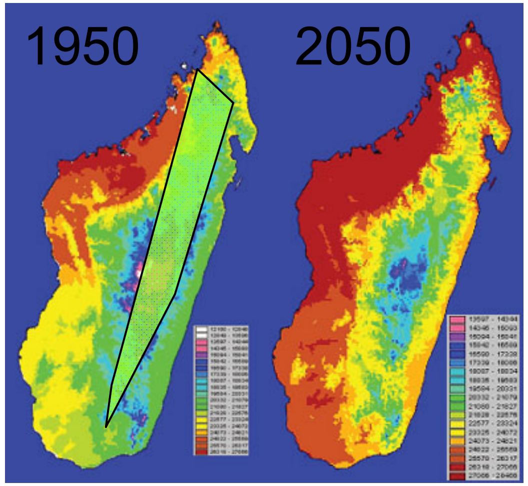
Practice: Correlative models

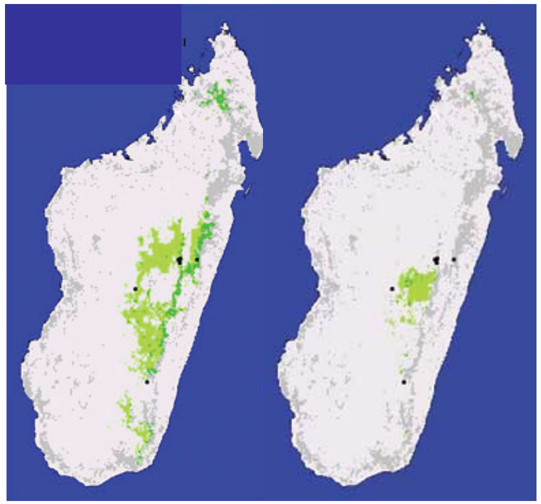
specimen localities



Climatic
envelope

Temperature





(Lees 2002)

Range models – Theory

Single populations

Multiple populations

Patch models

Genetic models

SPACE

TIME (no genotypic variation)

Trait evolution in response to climate change

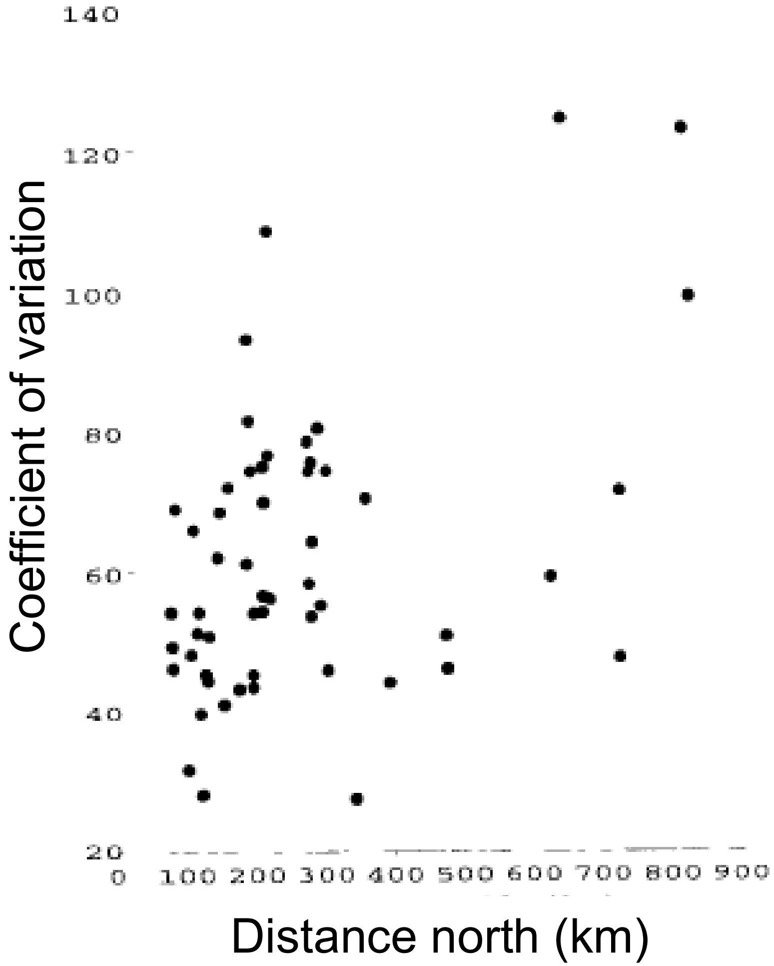
Single populations

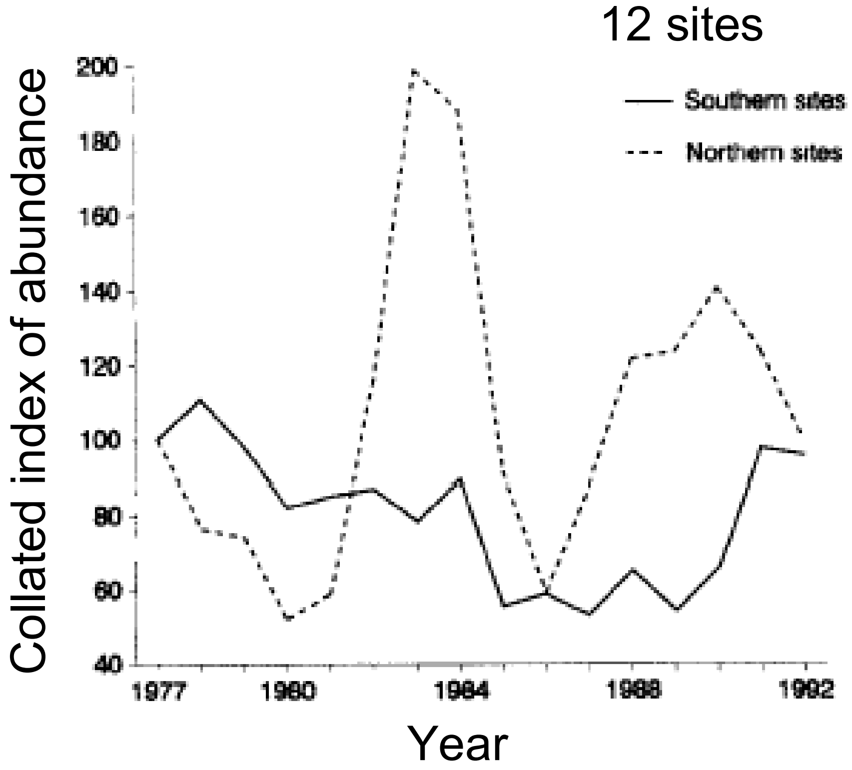
$$N_{t+1}=N_t + b - d + i - e$$

b- births
d- deaths
i- immigrants
e- emigrants

Species occur when b-d+i-e>0
Hard to detect how parameters changes causes range edge

Population fluctuations at northern range





Less density regulation?
Abiotic factors?

24 species of British butterflies
1976-1992
(Thomas et al. 1994)

Multiple populations

Environmental heterogeneity, no evolution

colonization - extinction

$$\frac{dn(x)}{dt} = n(x)[k(x)-n(x)]c(x) - e(x)n(x)$$

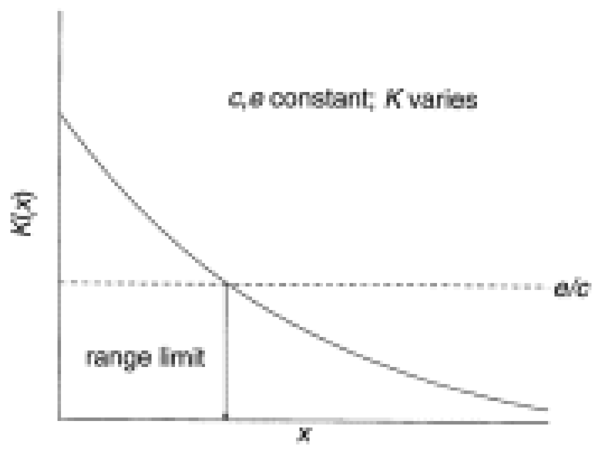
$n^*(x)=k(x)-e(x)/c(x)$

absent where

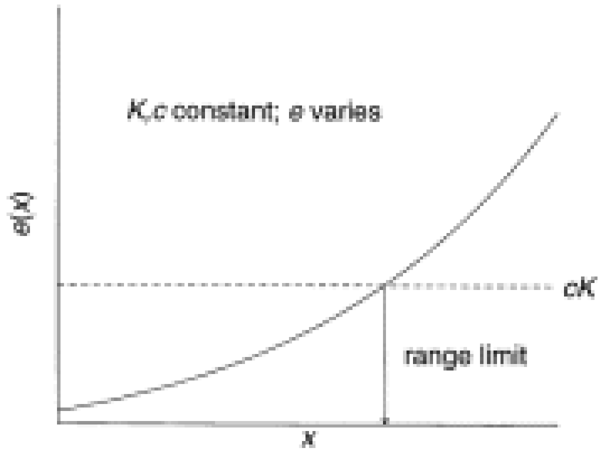
$k(x)<e(x)/c(x)$

$k(x)$- fraction of suitable patches
$e(x)$- extinction rate (per occupied patch)
$e(x)$- colonization rate of suitable, empty patches (per occupied patch)

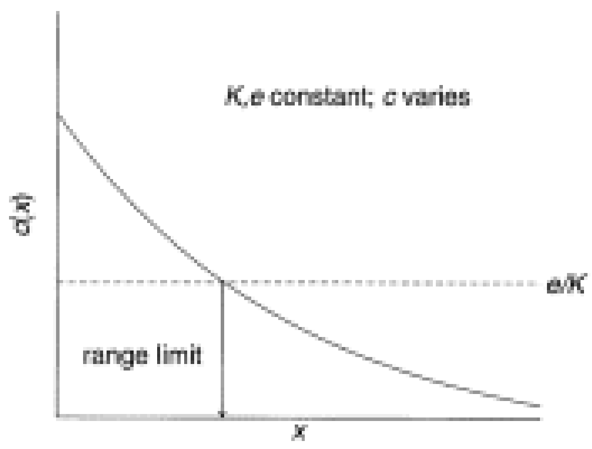
Gradient in habitat availability



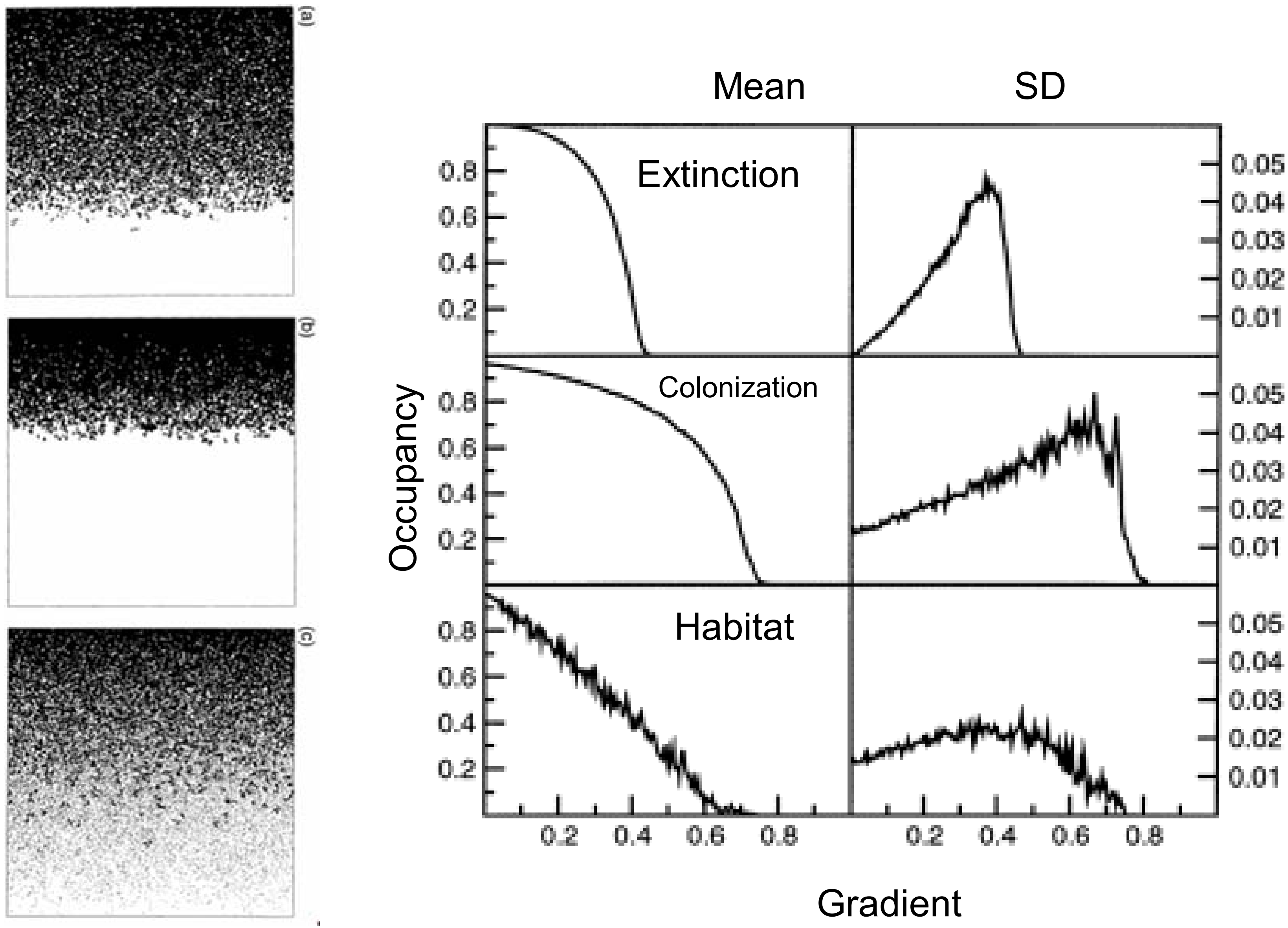
extinction rate



colonization success



Levins metapopulation models
(Holt and Keitt 2000)

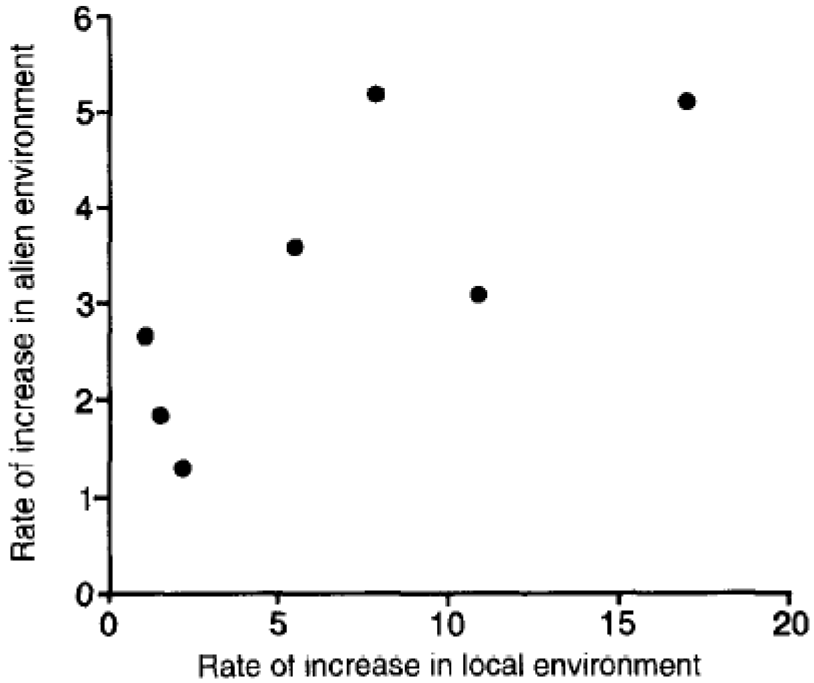


(a)
(b)
(c)
Mean
SD
Extinction
Colonization
Habitat
Occupancy
Gradient
0.2
0.4
0.6
0.8
0.01
0.02
0.03
0.04
0.05

Multiple populations

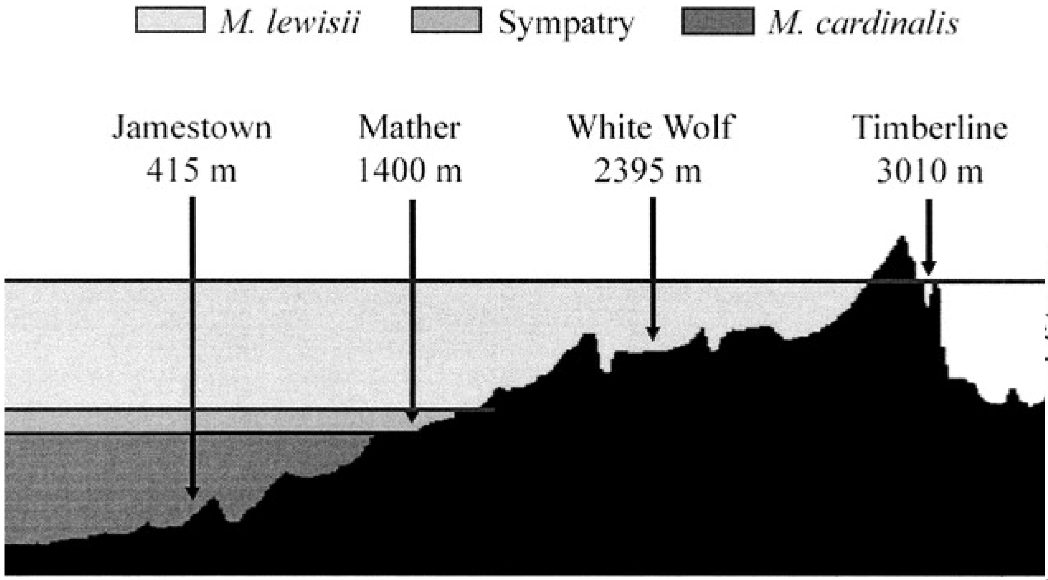
Environmental heterogeneity with evolution

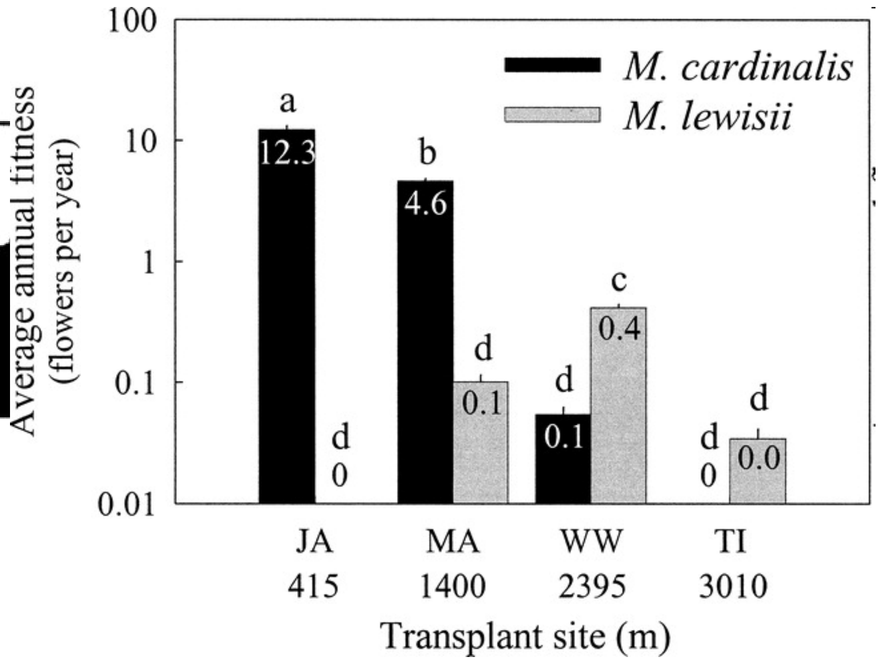
What prevents traits evolving to enable an organism to expand its range boundaries? (Mayr 1962)



Species from poor environments-
Weak performance in other environments

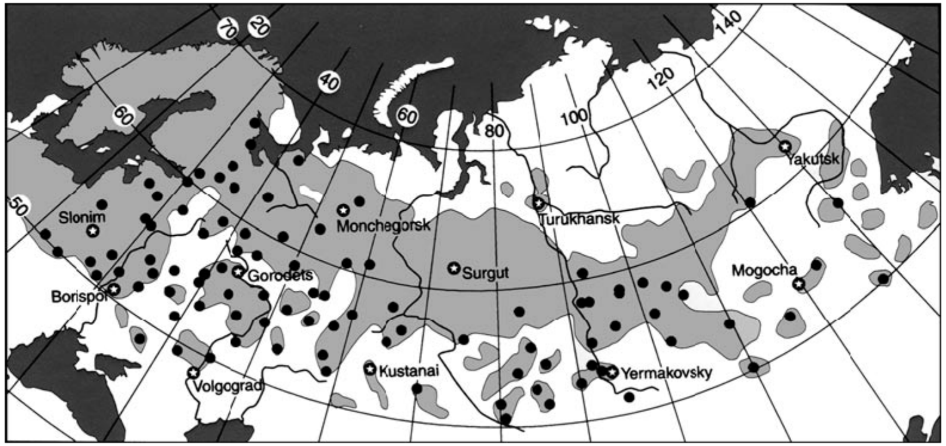
Phlox drummondi
(Schmidt and Levin 1985)

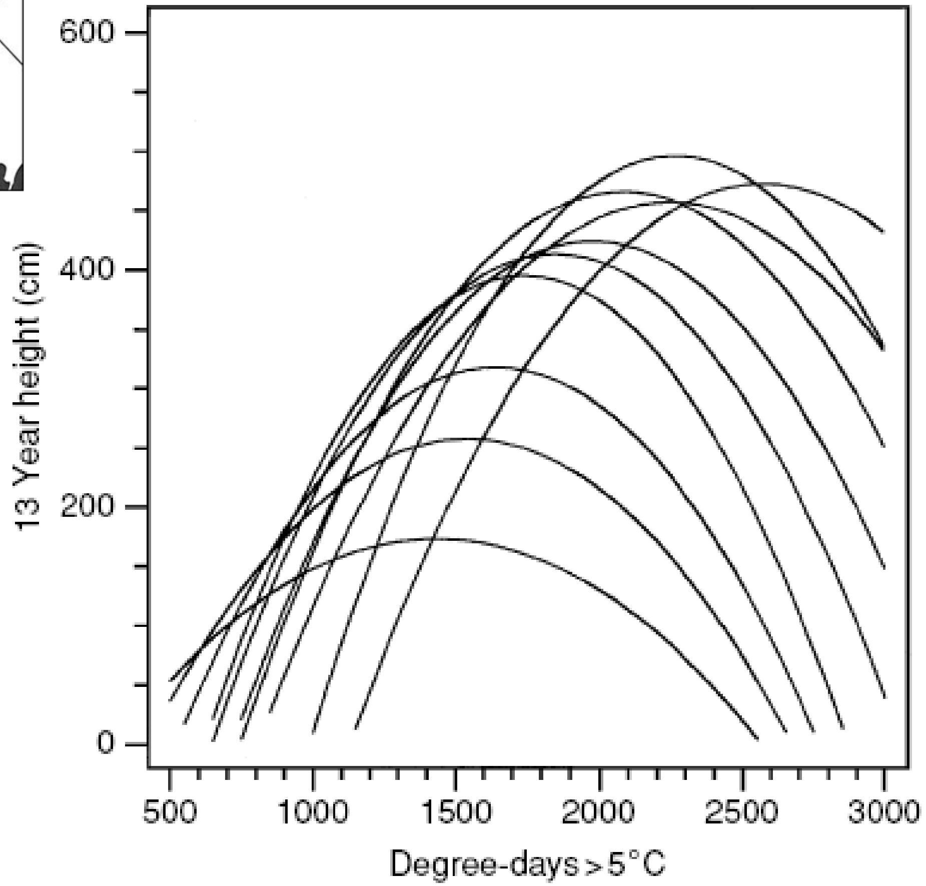




greatest average fitness at elevations
central within the range

(Angert and Schemske 2005)





Pinus sylvestris
(Rehfeldt et al. 2002)

What prevents traits evolving to enable an organism to expand its range boundaries? (Mayr 1962)

LOW HERITABILITIES (proportion phenotypic var due to genetic var)

1. Low *n*: low genetic variation
2. Directional selection in marginal environments
3. Environmental variability in marginal environments

$$\mathrm{Var}(\mathit{Phenotype}) = \mathrm{Var}(\mathit{Genotype}) + \mathrm{Var}(\mathit{Environment}) + 2\ \mathrm{Cov}(G,E)$$

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GENETIC INTERACTIONS

4. Require evolution of multiple traits
5. Genetic trade-offs between fitness in favorable and stressful envi

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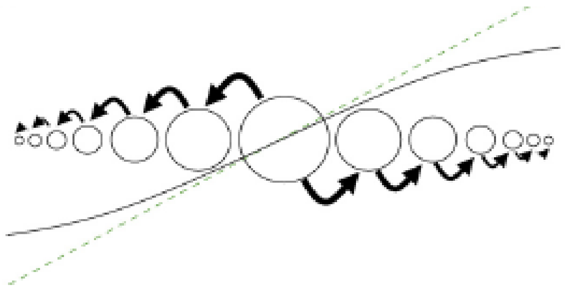
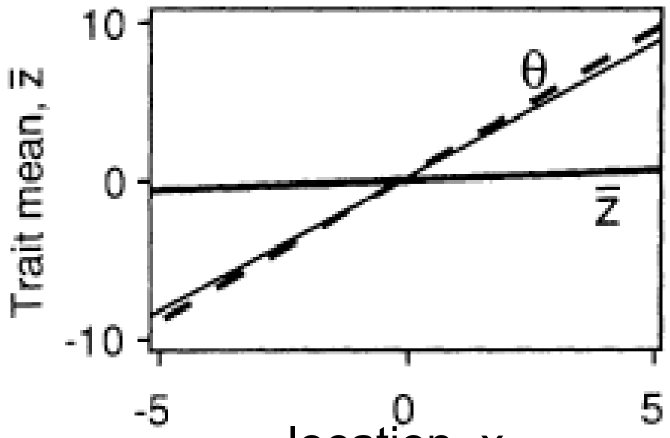
GENETIC INTERACTIONS

4. Require evolution of multiple traits
5. Genetic trade-offs between fitness in favorable and stressful envi

6. Deleterious mutations under stressful conditions
7. Genotypes favored in marginal populations swamped by gene flow from center





location, x

Z- trait mean
θ- trait optimum
b- rate of environmental change in space

θ=bx

Gene flow Directional selection

$$\frac{\partial \bar{z}}{\partial t} = \frac{\sigma^2}{2}\frac{\partial^2 \bar{z}}{\partial x^2} + \sigma^2 \frac{\partial \ln(n)}{\partial x}\frac{\partial \bar{z}}{\partial x} + G\frac{\partial \bar{r}}{\partial \bar{z}},$$

diffusion asymmetrical

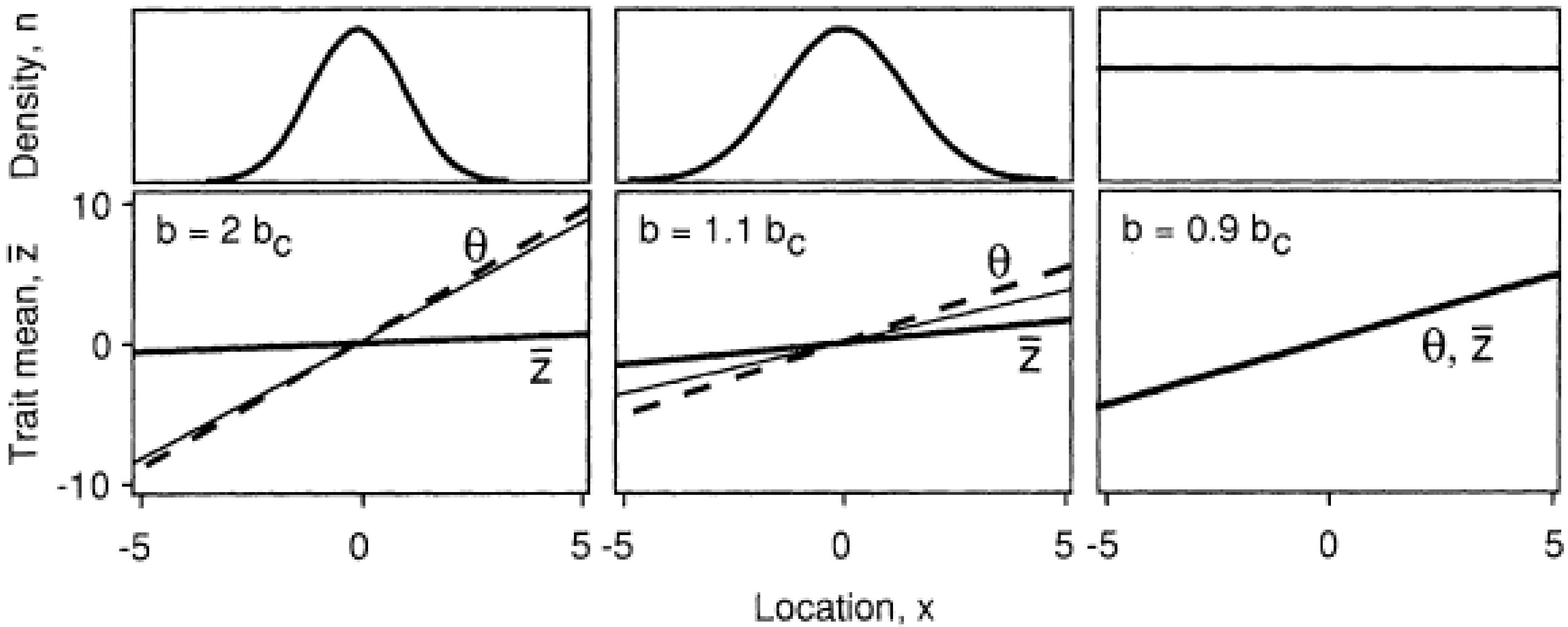
Fitness decreases with distance from optimum

$$r(z) = r_{\max} - \frac{(\theta(x) - z)^2}{2V_s}$$

σ^2- variance in offspring dispersal
n- population size
G- additive genetic variance
V_s- strength of stabilizing selection
(Kirkpatrick & Barton 1997)

Equilibrium population density increasing function of local fitness

$$n(x) = ke^{\bar{r}\gamma}$$

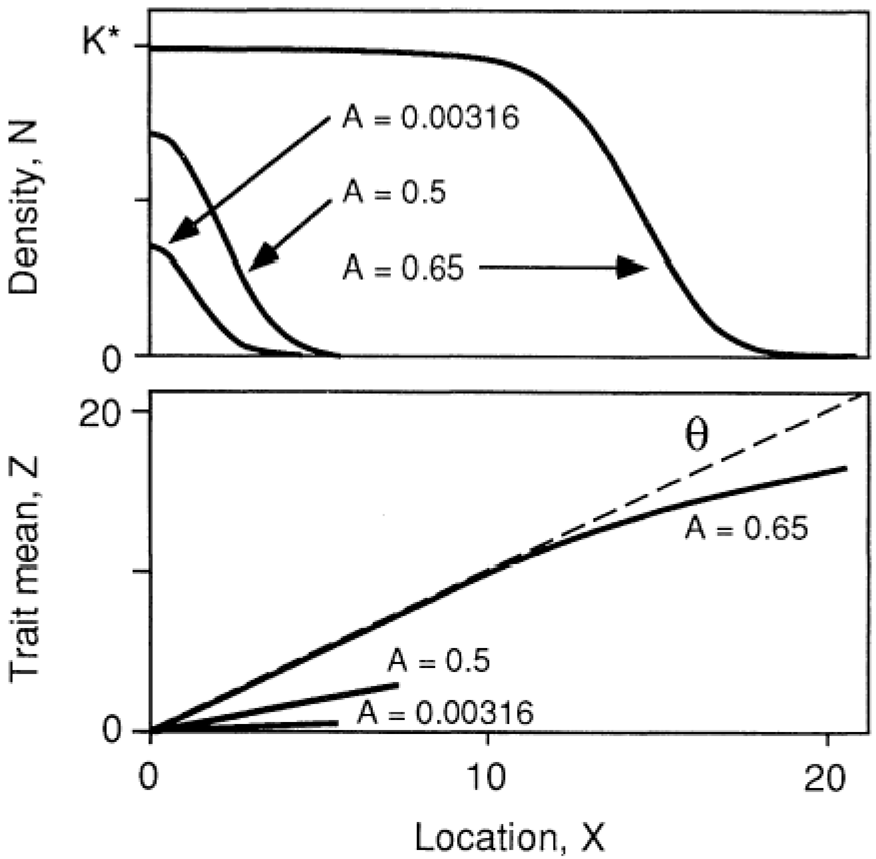


σ²- variance in offspring dispersal
n- population size, k- carrying cap
G- additive genetic variance
V_s- strength of stabilizing selection
γ- strength of density regulation

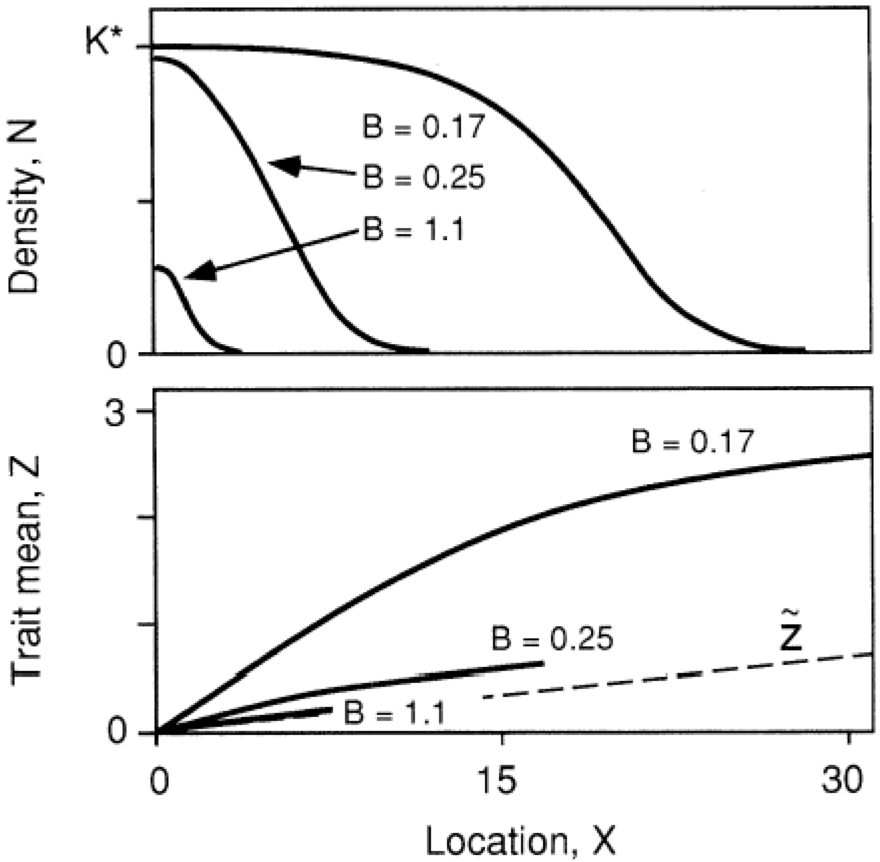
$$\frac{\partial \bar{z}}{\partial t} = \frac{\sigma^2}{2}\frac{\partial^2 \bar{z}}{\partial x^2} + \frac{(bx - \bar{z})}{V_s}\left[G - \sigma^2\gamma\frac{\partial \bar{z}}{\partial x}\left(b - \frac{\partial \bar{z}}{\partial x}\right)\right]$$

(Kirkpatrick & Barton 1997)

A- potential for local adaptation

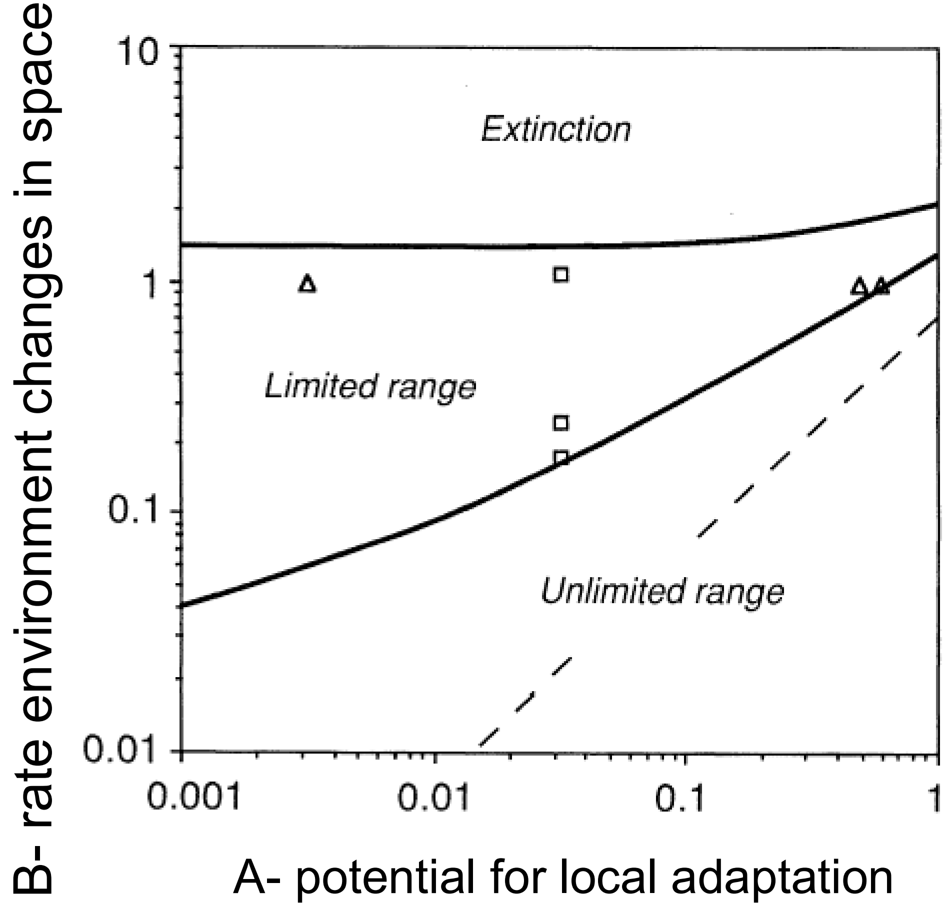


B- rate environment changes in space

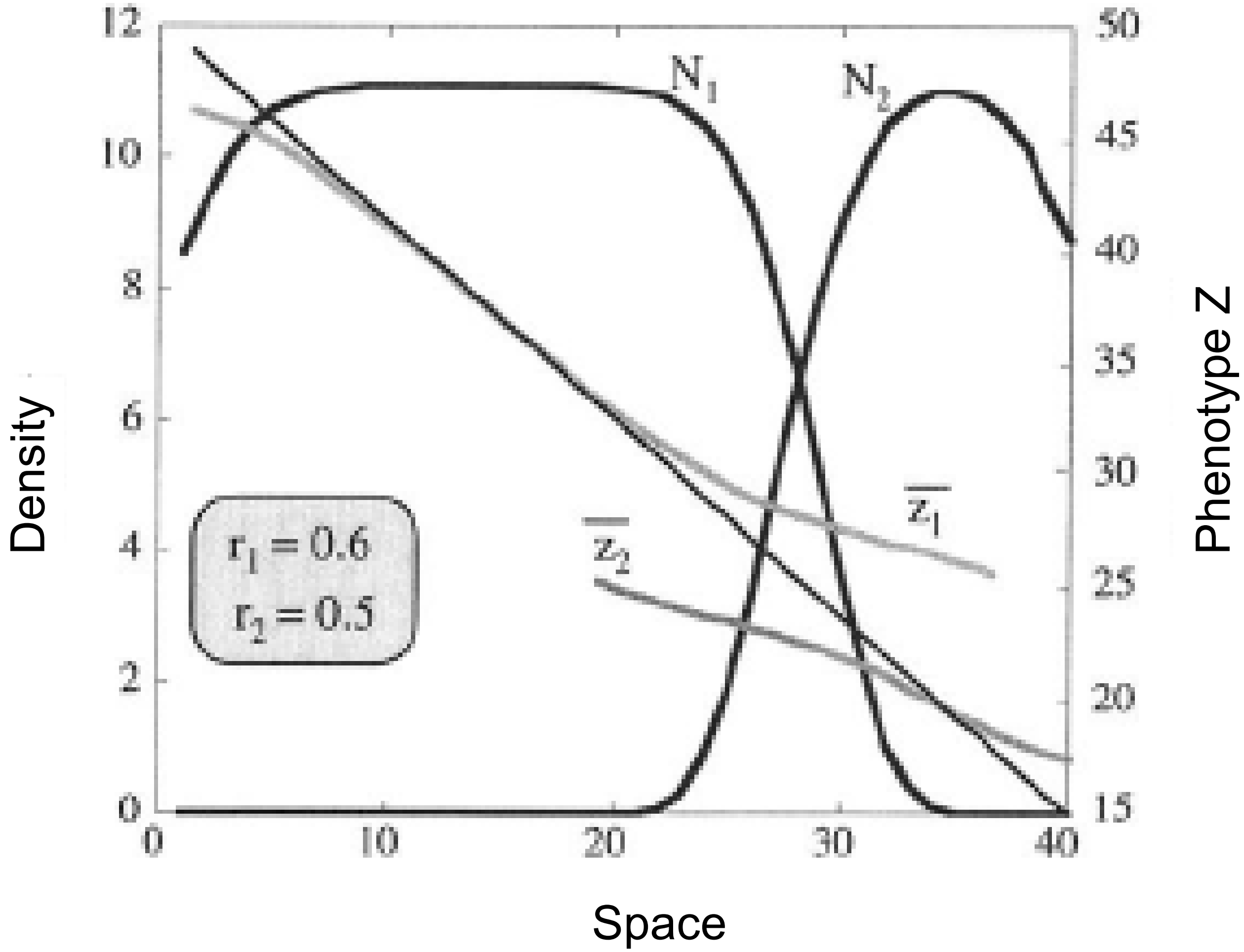


$$A = \frac{G}{2V_s r^*} = \frac{h^2 I_s}{2r^*},$$

$$B = \frac{b\sigma}{r^* \sqrt{2V_s}},$$

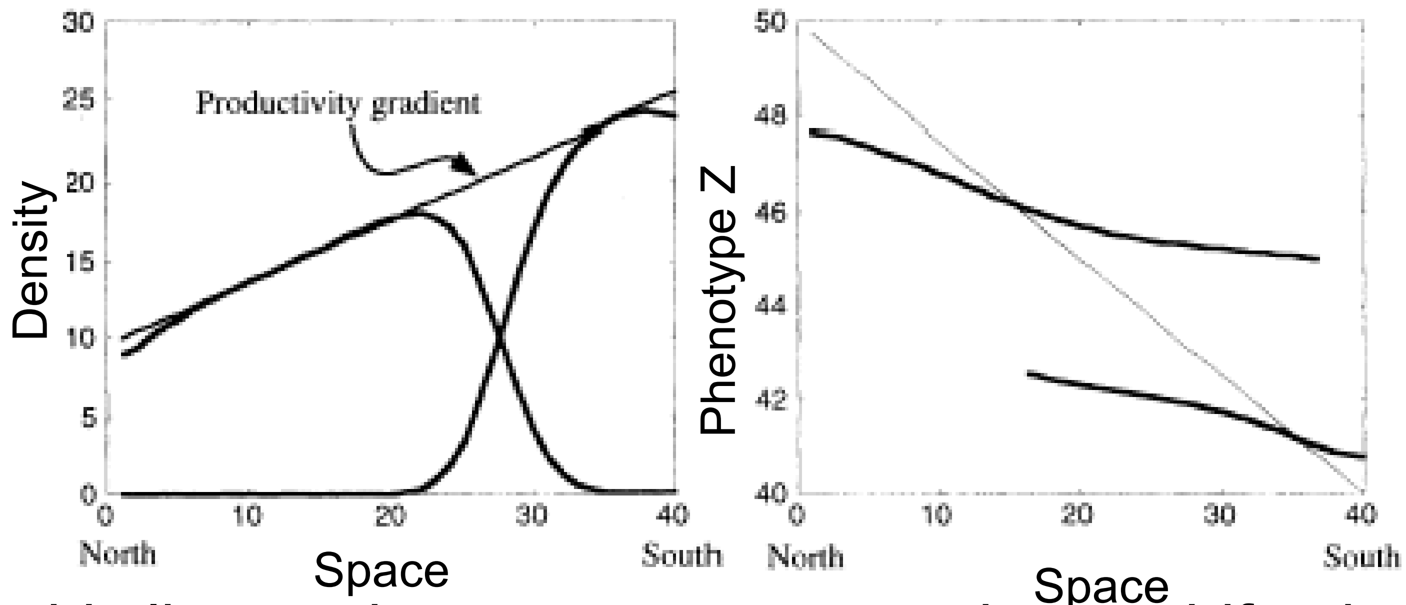

B- rate environment changes in space
10
1
0.1
0.01
0.001
0.01
0.1
1
Extinction
Limited range
Unlimited range
A- potential for local adaptation

Species interactions



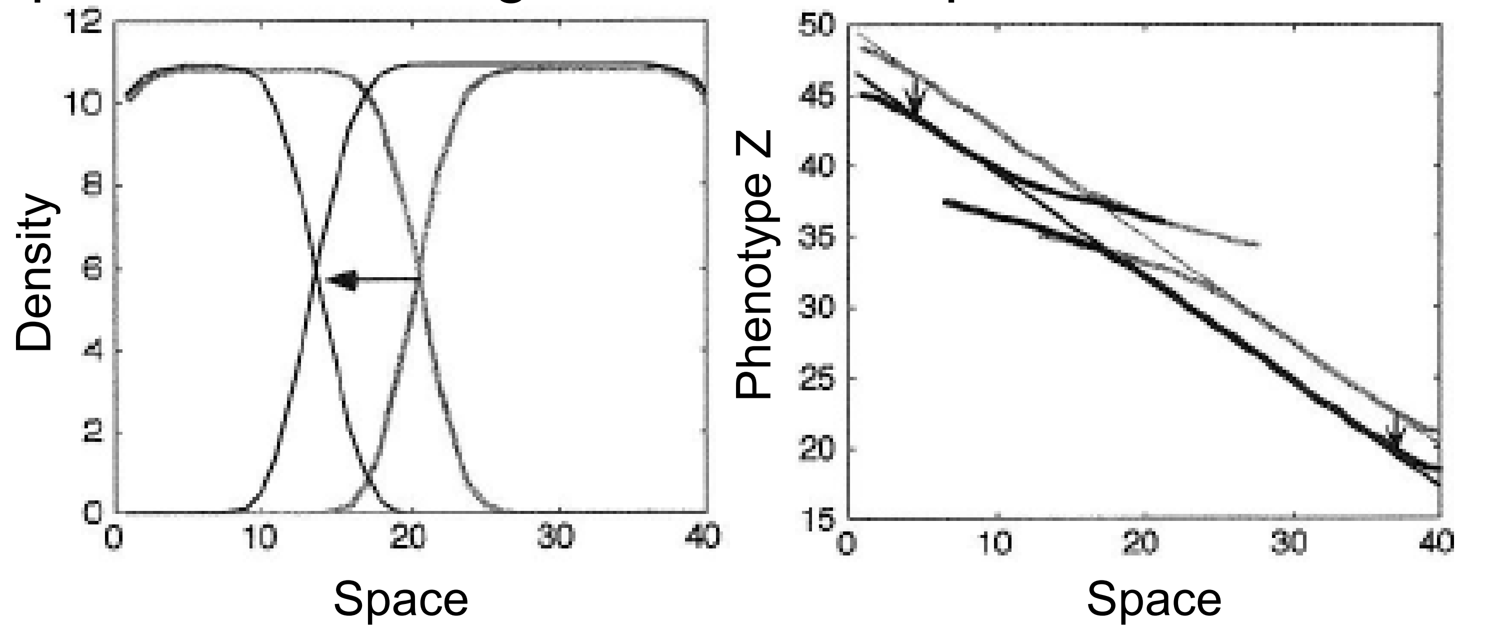
(Case & Taper 2000)

Productivity gradient



Rapid climate change

optimum shifts down



Range models – Theory

Single populations

Multiple populations

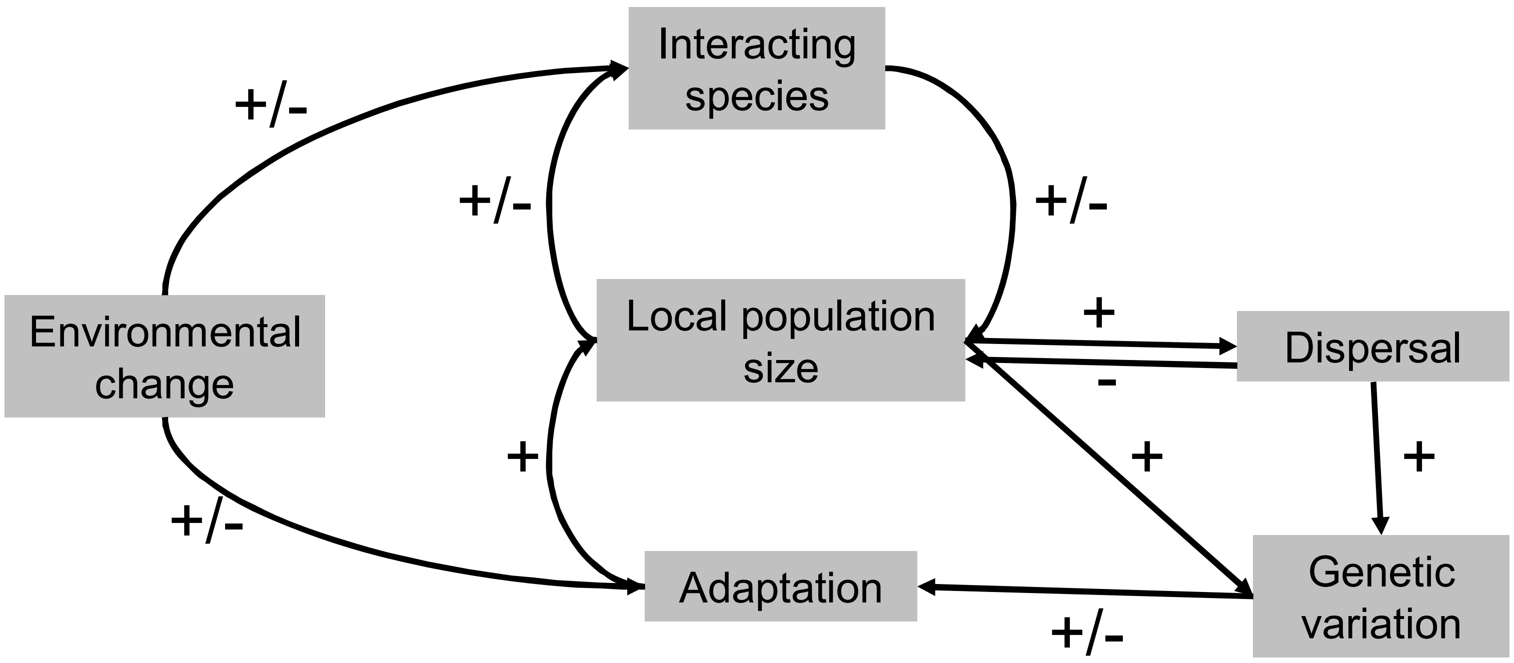
Patch models

Genetic models

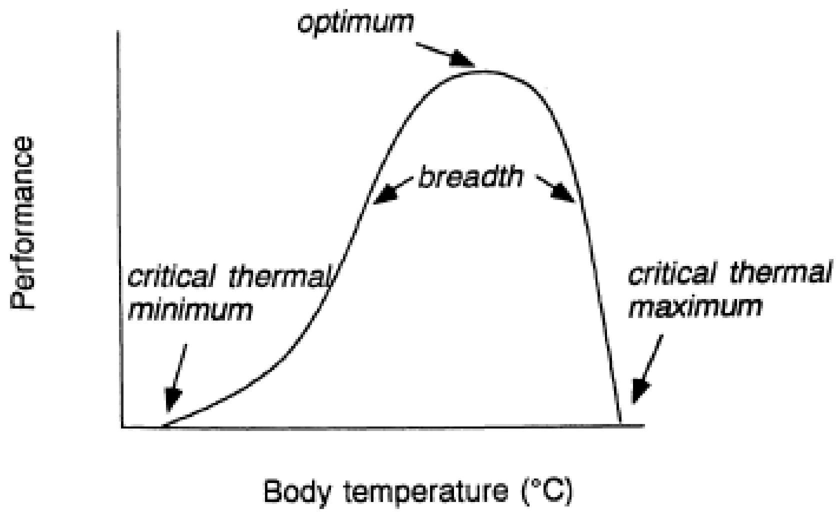
SPACE

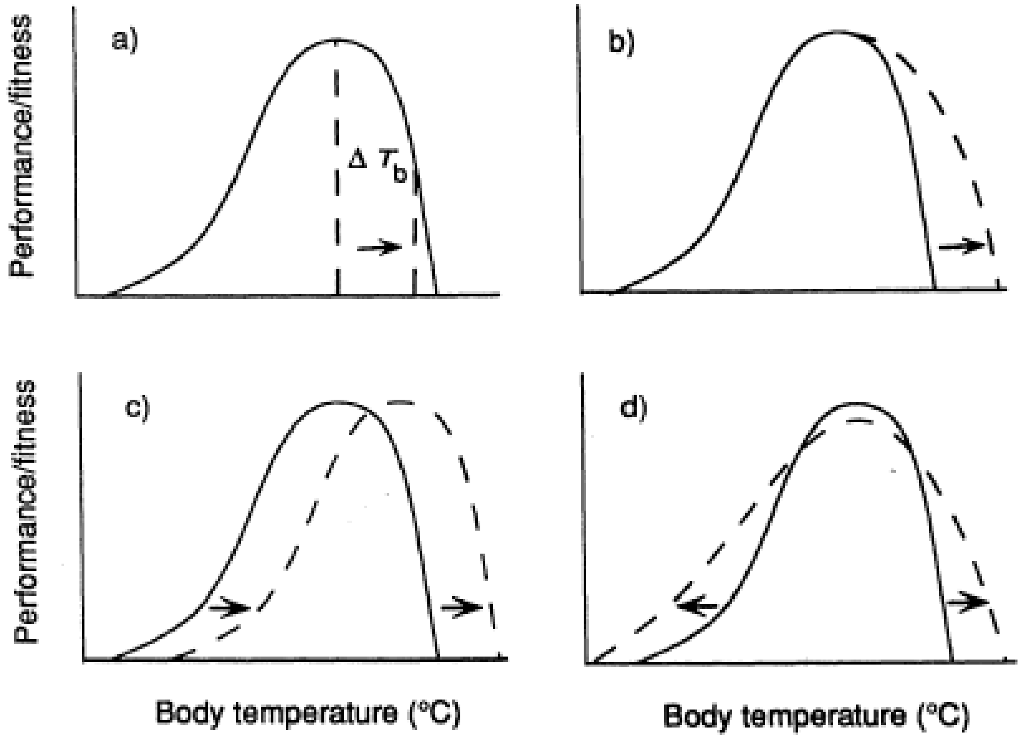
TIME (no genotypic variation)

Trait evolution in response to climate change

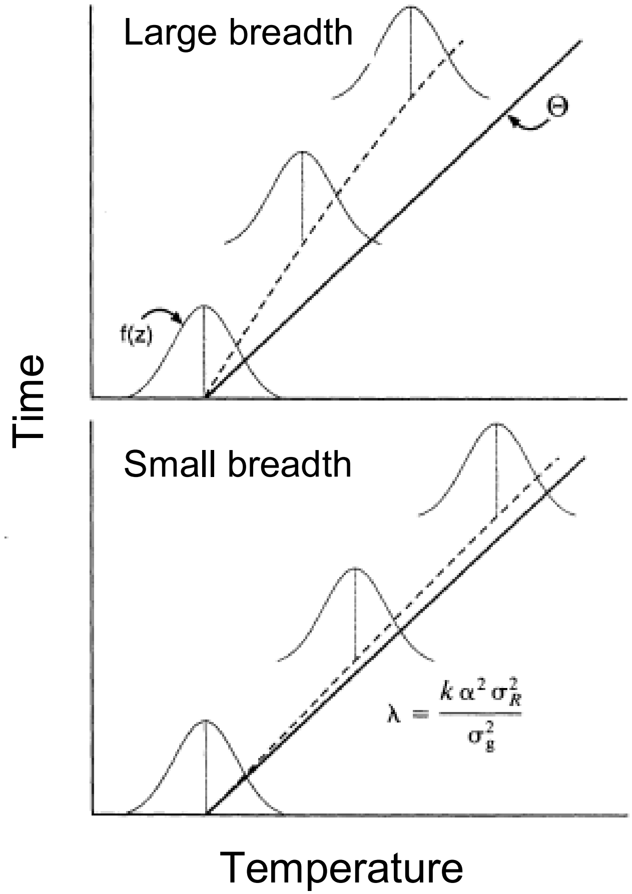


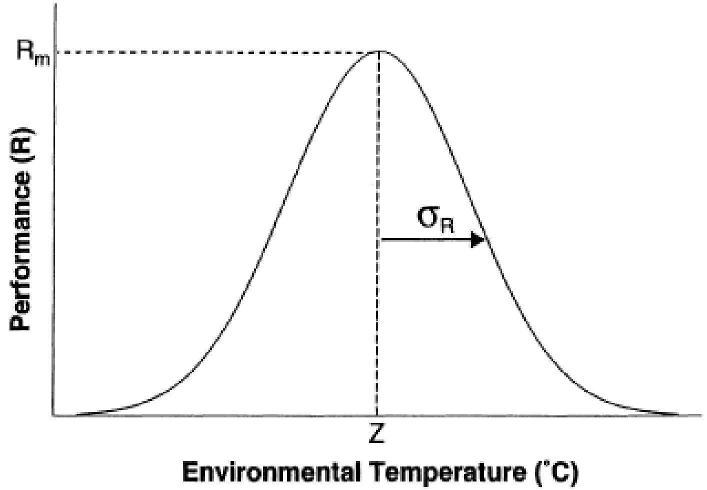
(Lynch and Lande 1993)





(Huey and Kingsolver 1993)





$$\lambda = \frac{k\,\alpha^2\,\sigma_R^2}{\sigma_g^2}$$

Fitness directly proportional to performance

$r = \alpha R$

k- rate of change of environmental temperature

σ_g^2- genetic variance

- - Mean phenotype

— Environmental optimum

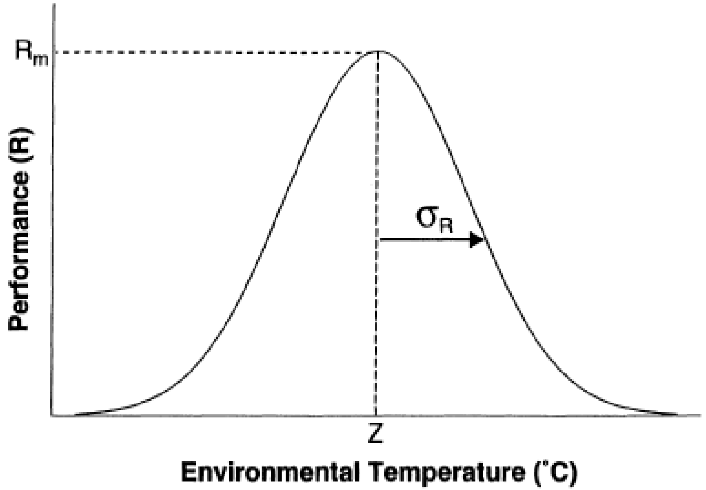
Large performance breadth

→ Increase evolutionary lag

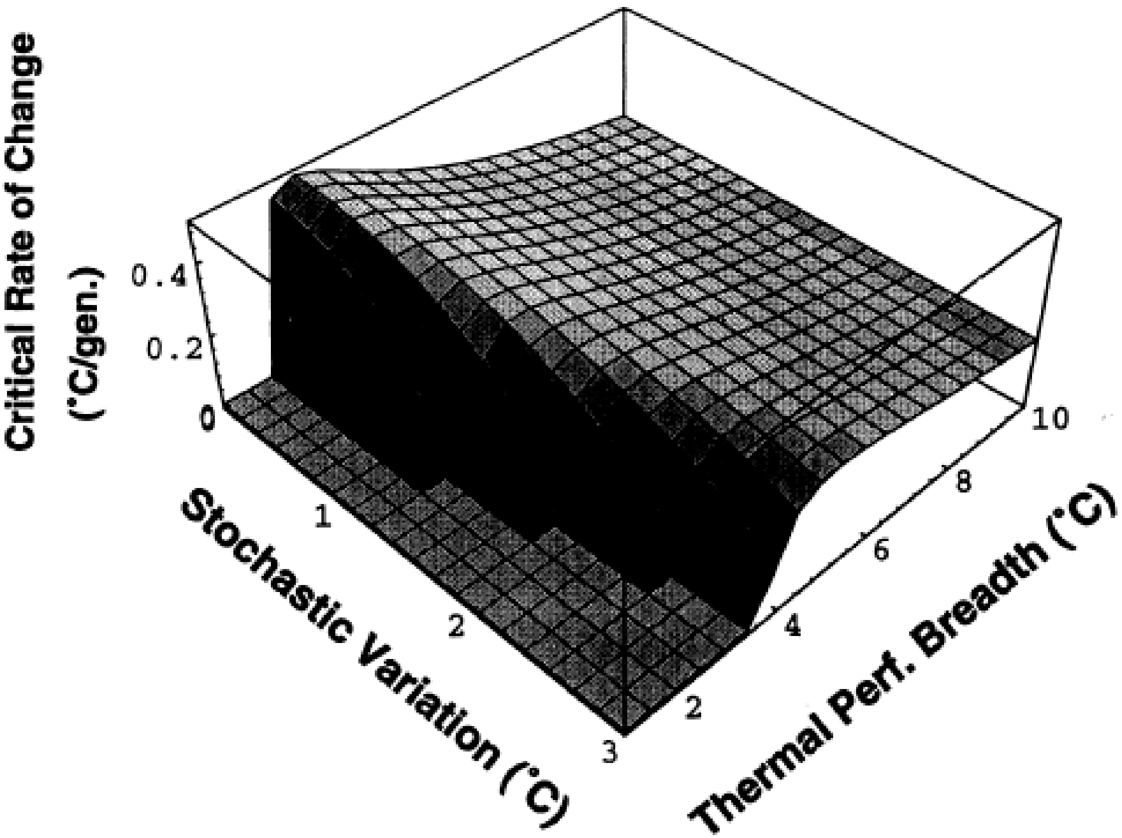
(Huey and Kingsolver 1993)

Critical rate of environmental change, k_c

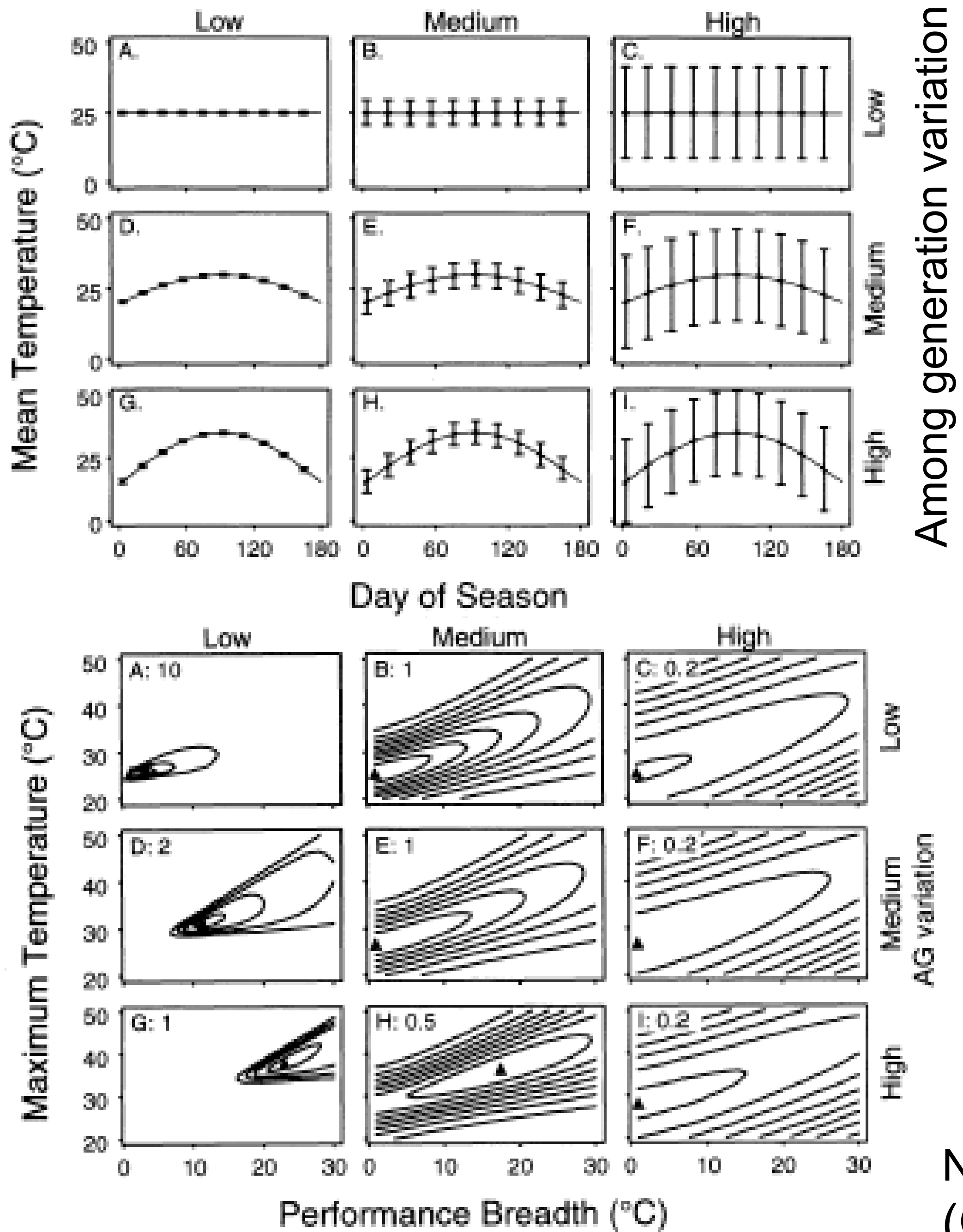
$$k_c = \frac{h^2\sigma_Z^2}{\alpha\sigma_R}\left(2\alpha R_m - \frac{\sigma_Z^2}{\alpha^2\sigma_R^2}\right)^{0.5}$$



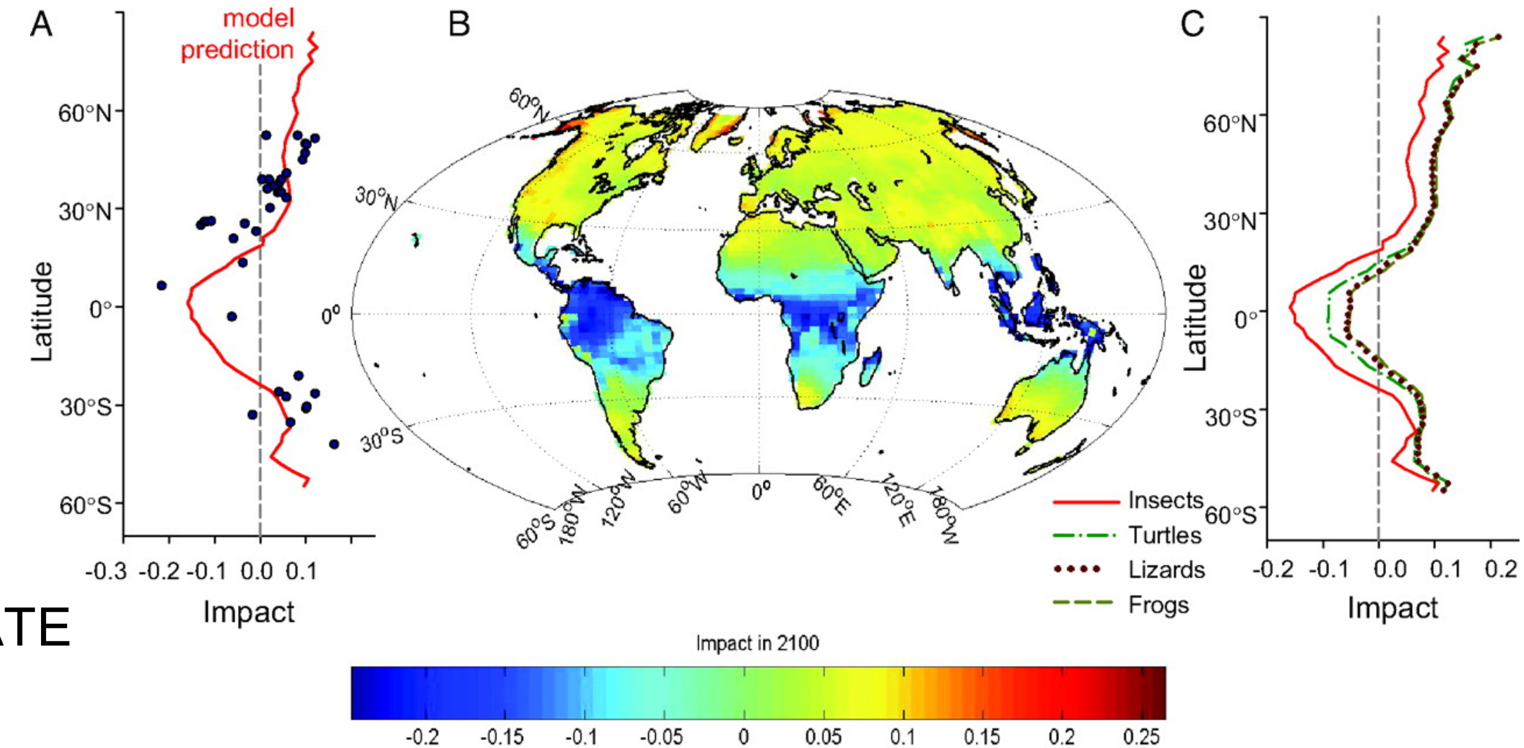
σ_g^2- genetic variance
Heritability $h^2 = \sigma_g^2 / \sigma_z^2$



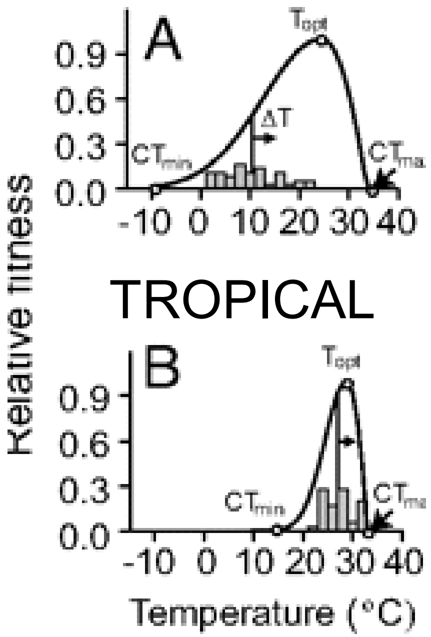
Within generation variation



Numbers: contour interval
(Gilchrist 1995)



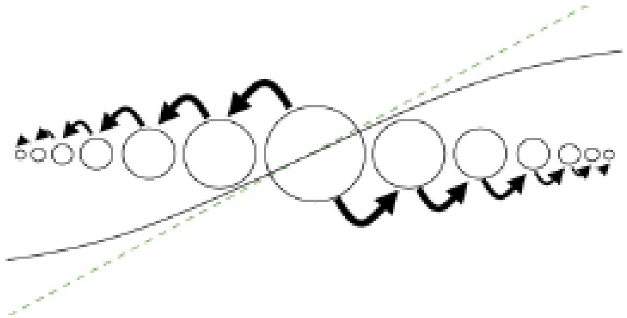
TEMPERATE



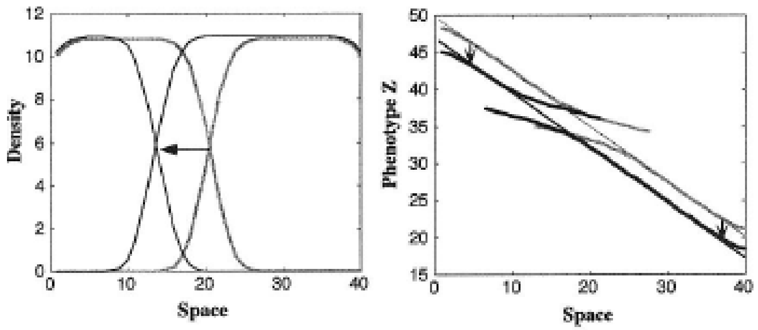
(Deutsch *et al*. 2008)

Theory

Gene flow along selection gradient
(Kirkpatrick & Barton 1997)



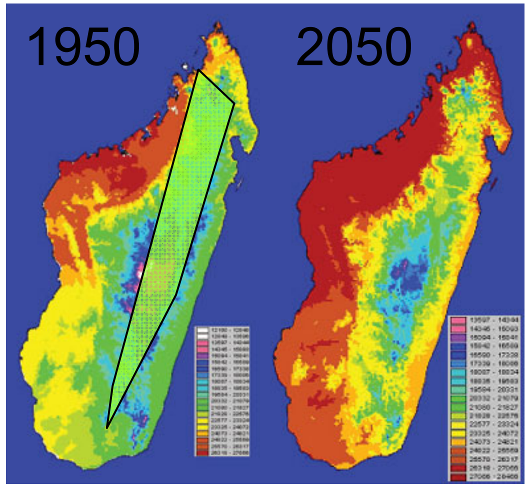
Incorporate species interactions
(Case & Taper 2000)

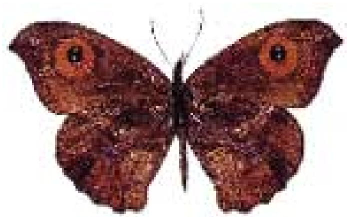


Practice: Correlative models

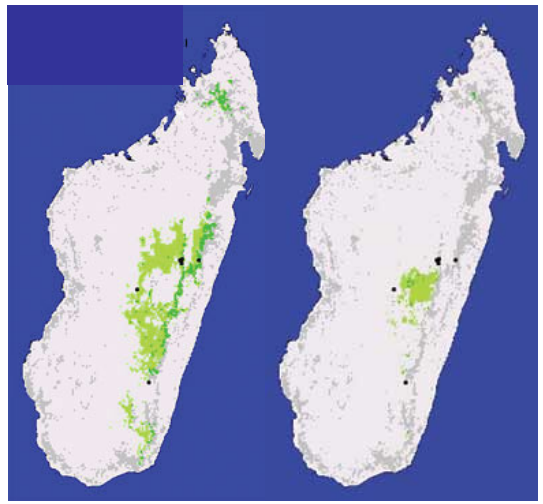
specimen localities

Temperature



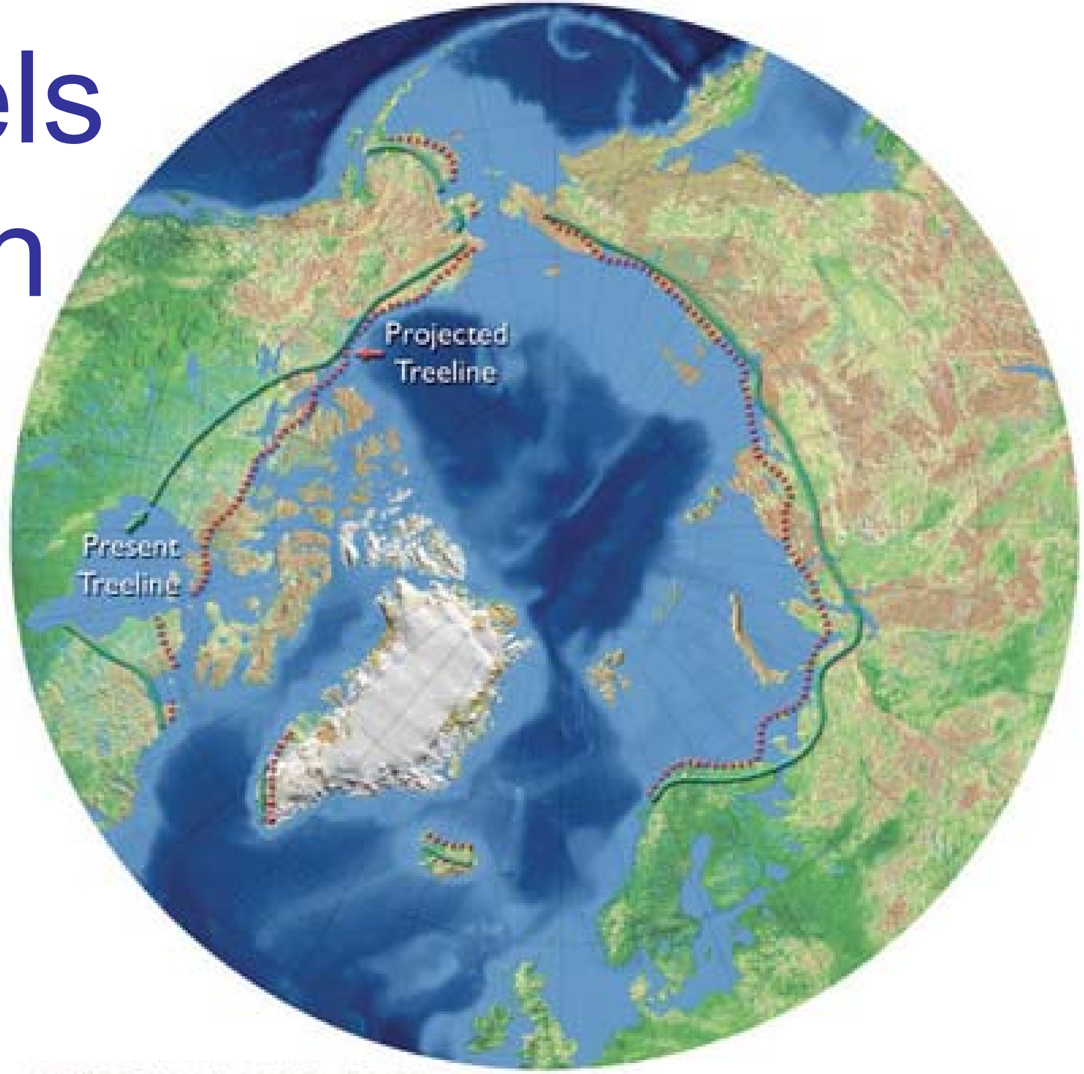


Climatic envelope



(Lees 2002)

Range models
2. Application



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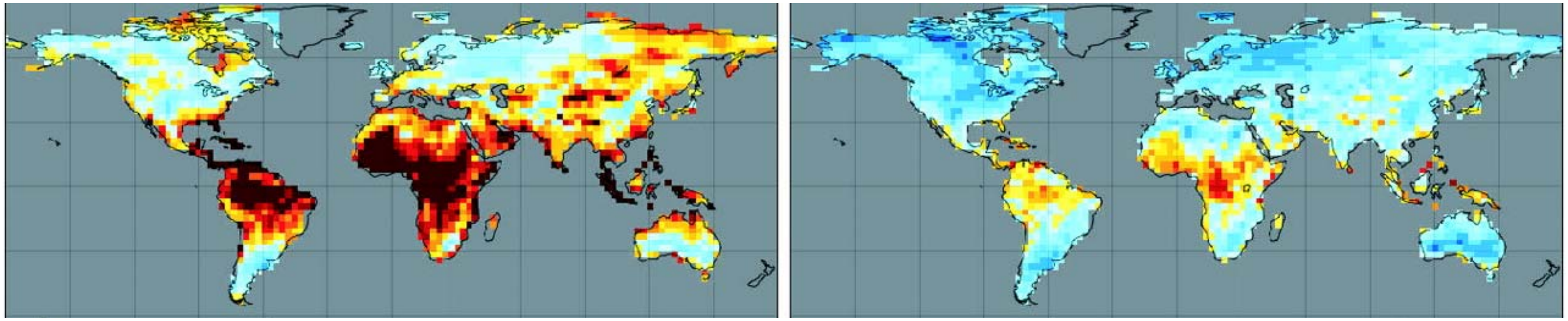
http://www.bio.unc.edu/Faculty/Buckley/Lab/

THE UNIVERSITY of NORTH CAROLINA at CHAPEL HILL

Climate-induced range shifts and extinctions?

Novel Climates by 2100

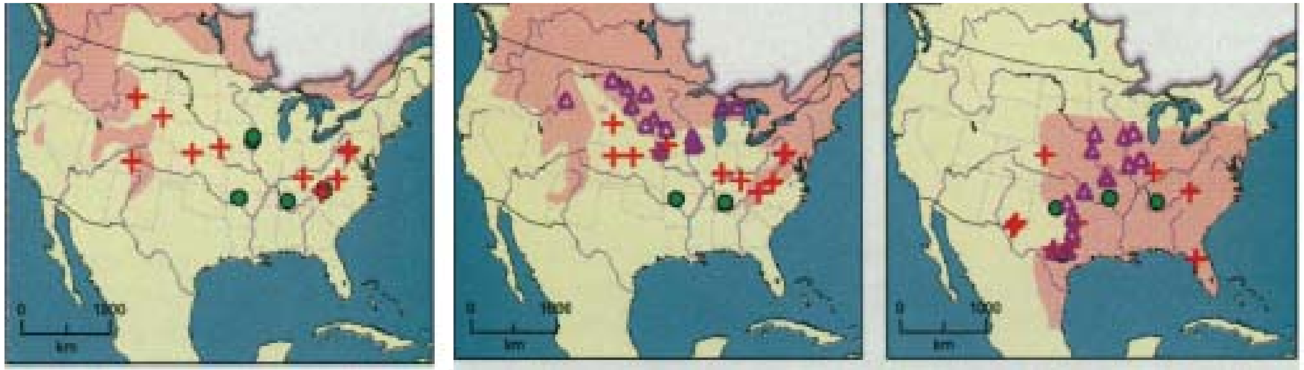


High emissions scenario

Low emissions scenario

Increasing climate novelty

(Williams *et al*. 2007)

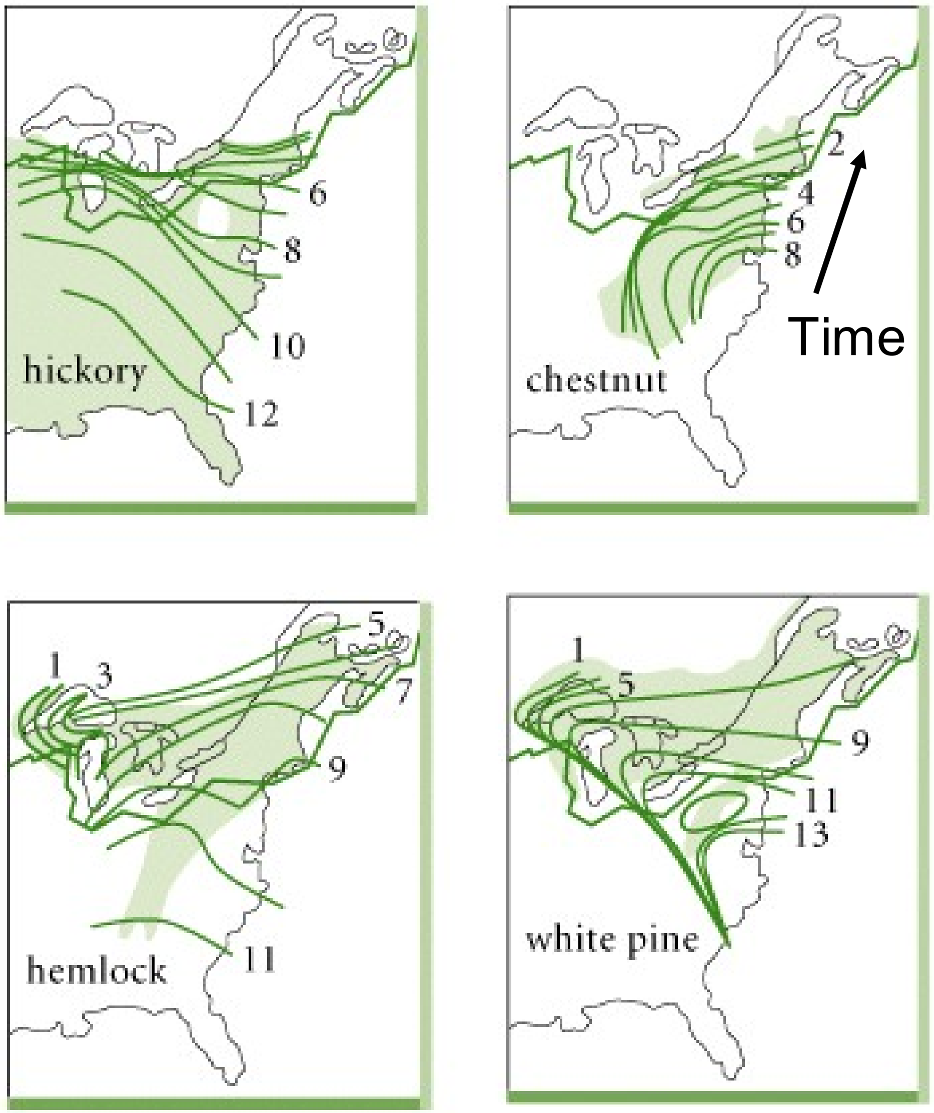


US mammals

Modern

Quarternary fossil

(Graham *et al*. 1996)

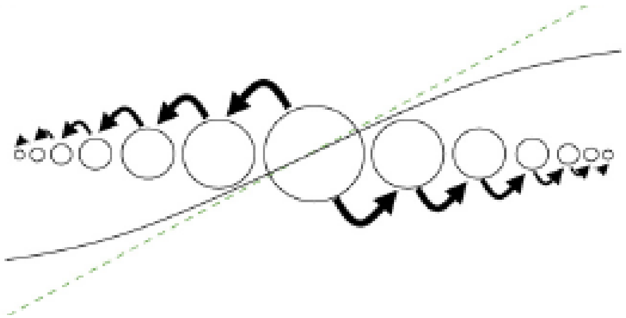


Trees
(Davis 1976)

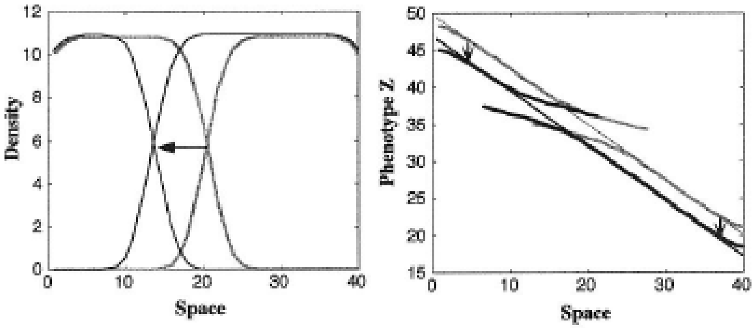
(Channell & Lomolino 2000)

Theory

Gene flow along selection gradient
(Kirkpatrick & Barton 1997)



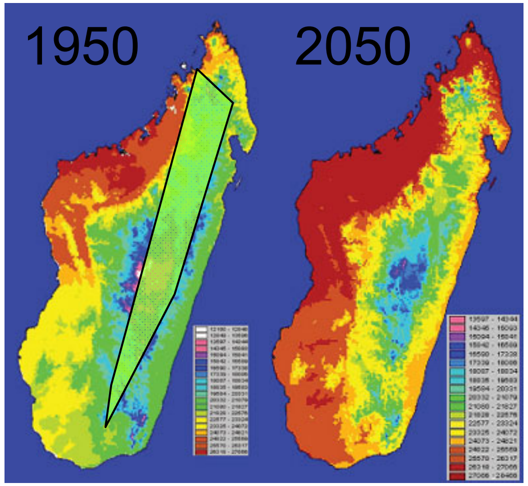
Incorporate species interactions
(Case & Taper 2000)

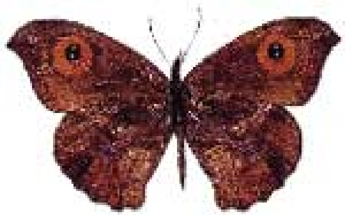


Practice: Correlative models

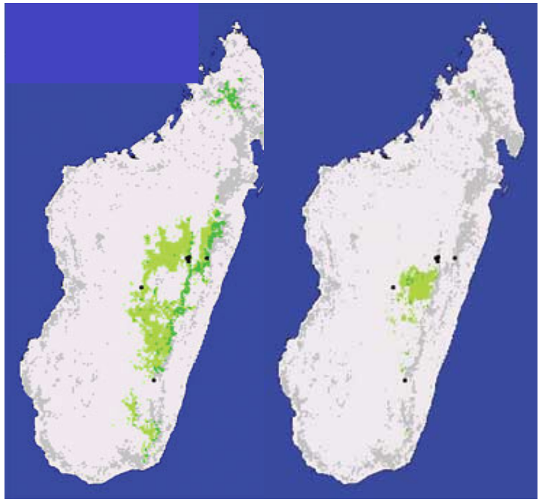
specimen localities

Temperature





Climatic envelope



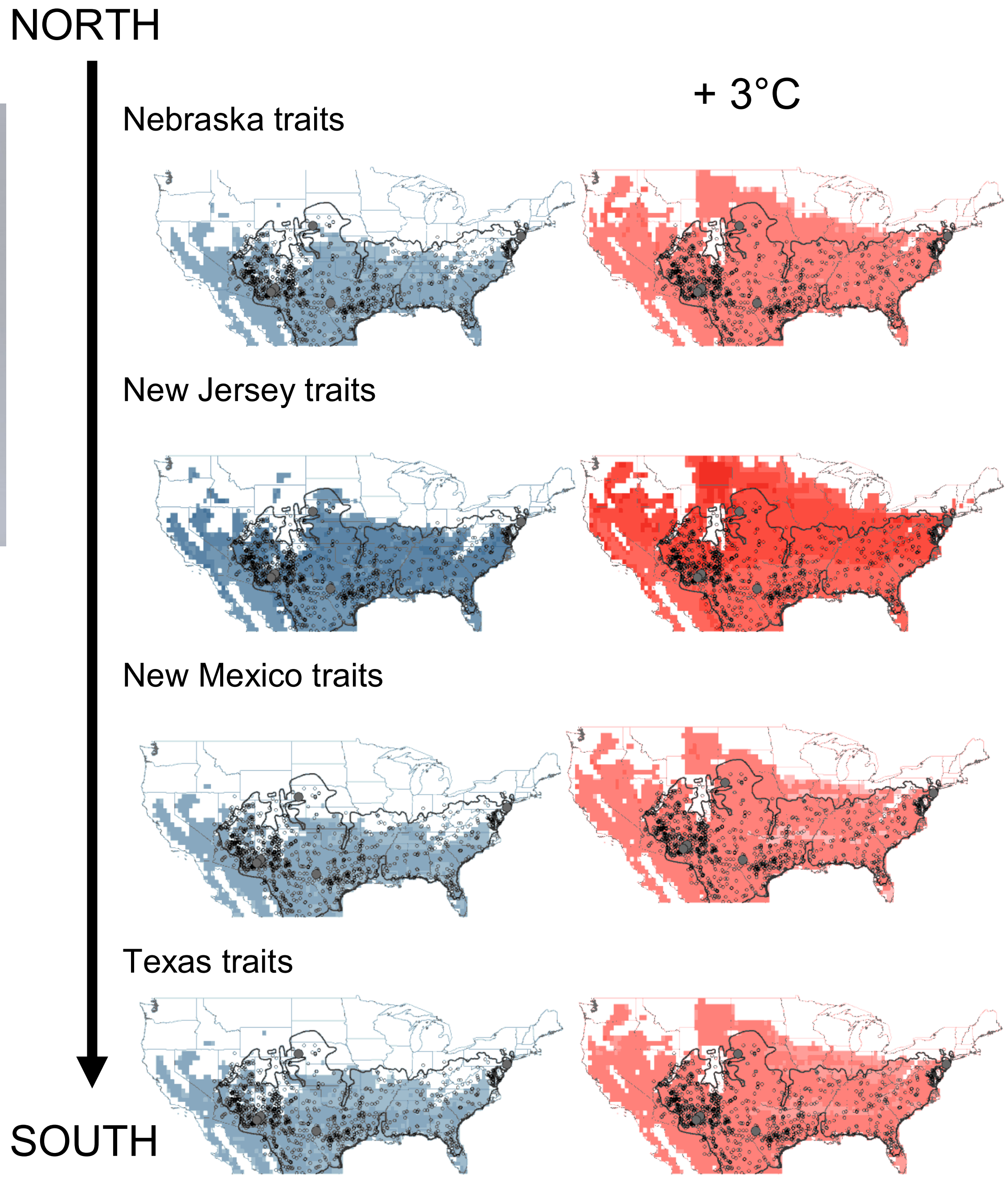
(Lees 2002)

Limitations of correlative models

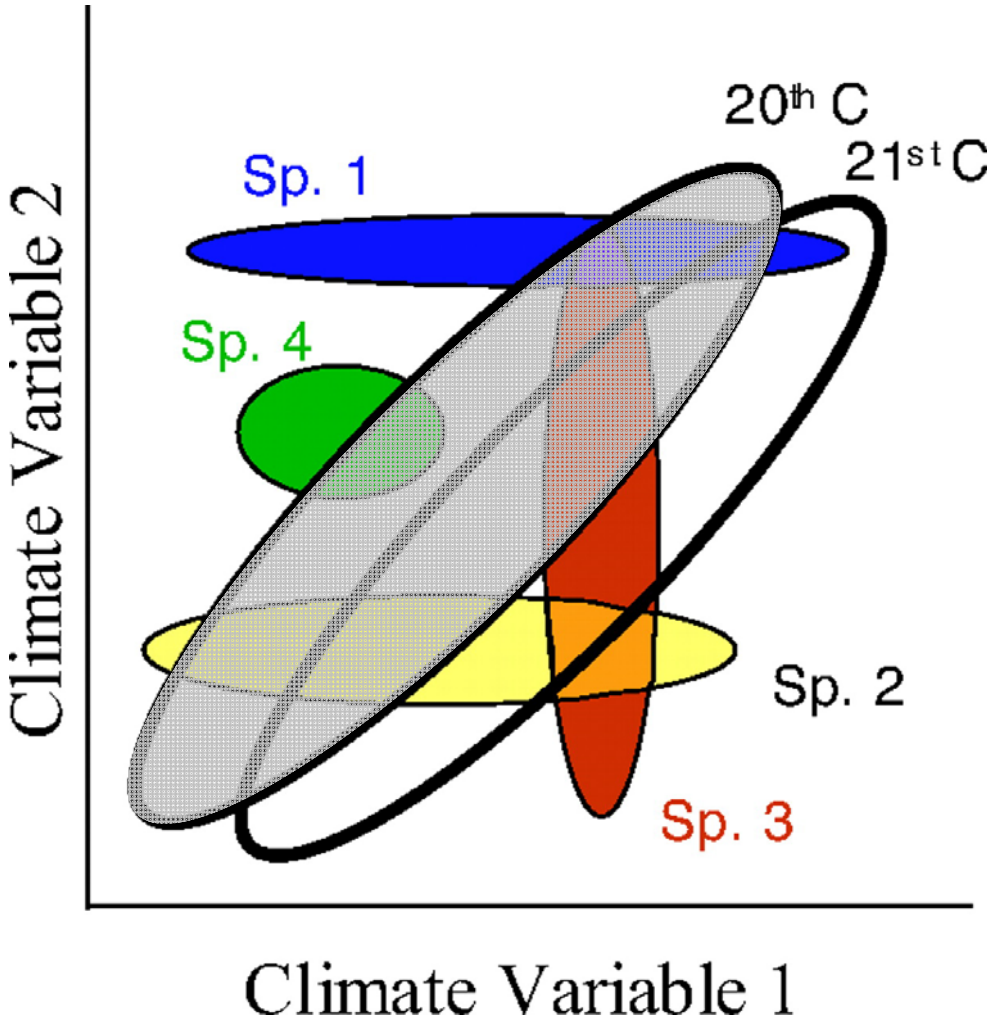
- Other determinants of current range?
- Extinctions?
- Nonlinear response to climate change?

Trait variation and evolution

Sceloporus undulatus
(Buckley 2008)

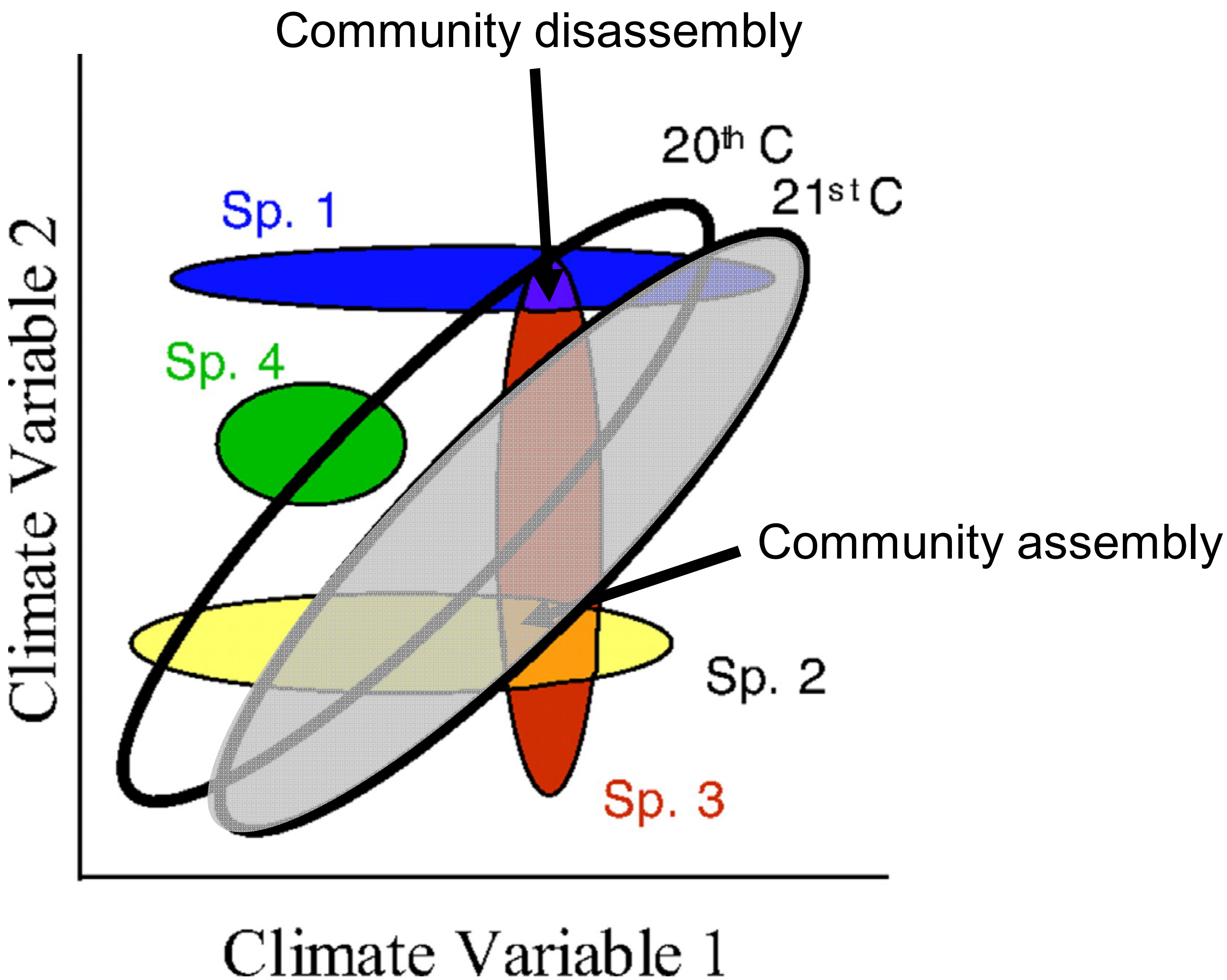


Species interactions



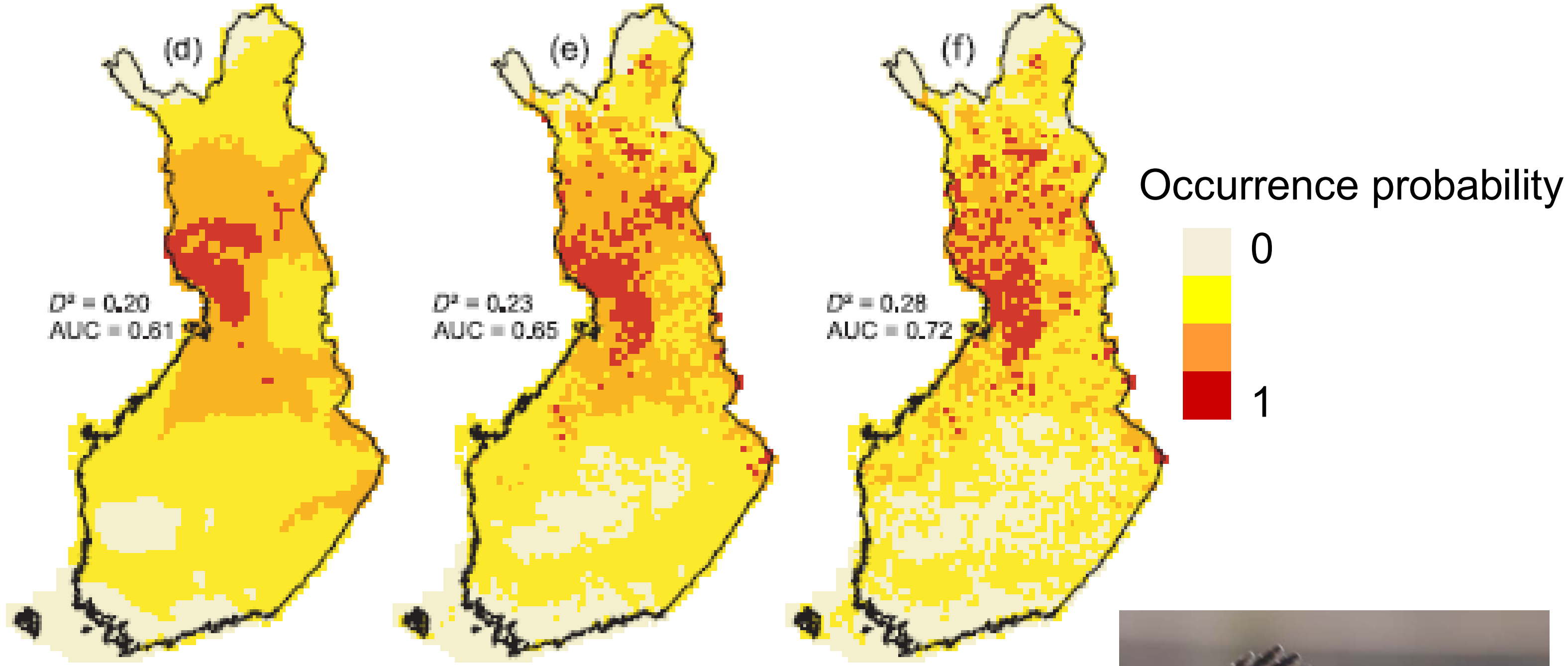
(Williams *et al*. 2007)

Species interactions



(Williams *et al*. 2007)

Climate +habitat +woodpeckers



Hawk owl
(Heikkinen *et al*. 2007)

Species Range Dynamics Working Group

NCEAS

NESCent, USA

MOVEMENT

* Cost of movement
* Dispersal barriers
* Habitat quality
* Spatial configuration of habitat

ENVIRONMENT → PHYSIOLOGY → DEMOGRAPHY

ENVIRONMENT

* Downscaling climate models
* Spatial and temporal variation in current and future environment
* Translating environmental change into body temperature change

PHYSIOLOGY

* Acclimation and plasticity in physiology and behavior
* Interactions of multiple changing environmental variables
* Variation in environmental tolerance within and among populations
* Hard climatic constraints verses cumulative effects

DEMOGRAPHY

* Growth, phenology, survival and recruitment
* Metapopulation structure
* Life stages
* Mating
* Time scales

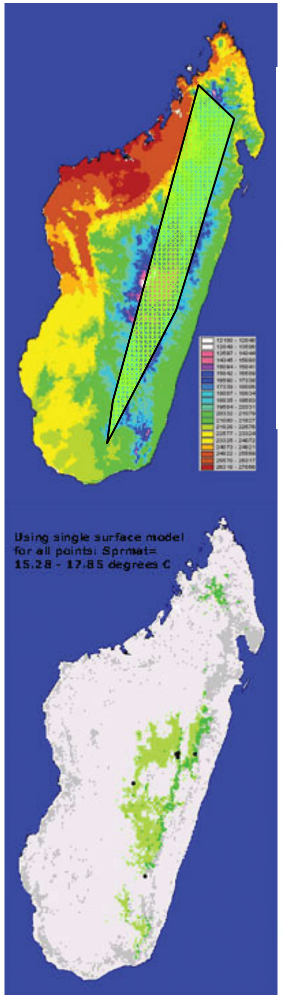
BIOTIC INTERACTIONS

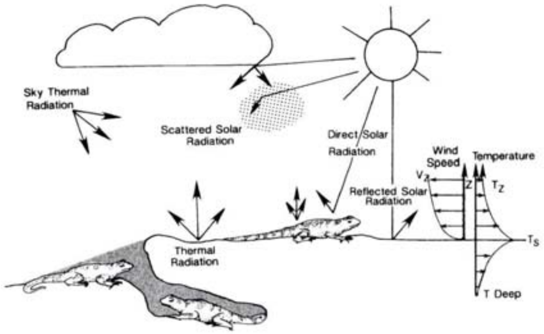
* Loss and gain of competitors and predators
* Interaction cascades
* Phenological asynchrony
* Disease
* Hosts, mutualists, pollinators
* Differential importance of biotic processes across range

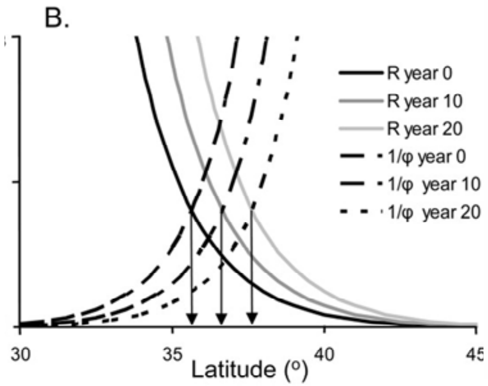
(assumes no evolution)

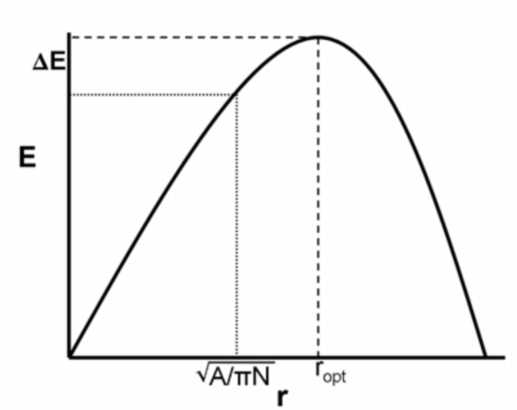
Range models

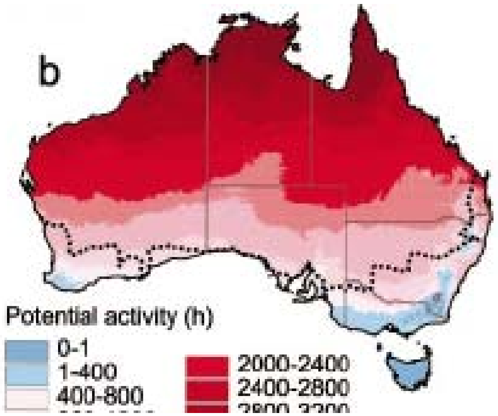
correlative models | biophysical models | performance curves | foraging energetic models

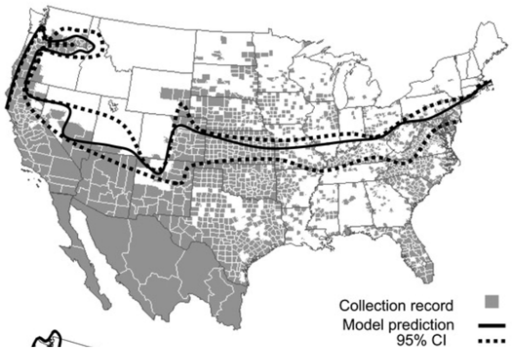


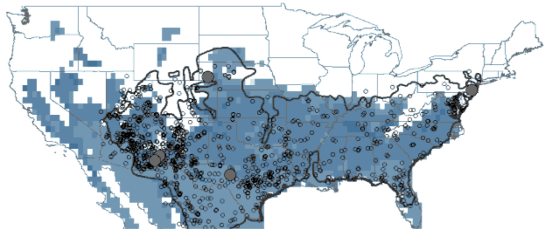






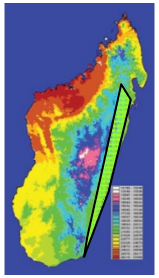


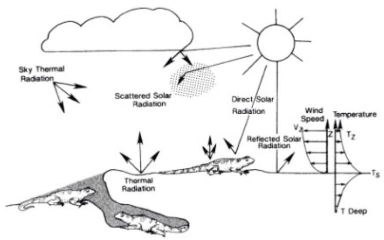


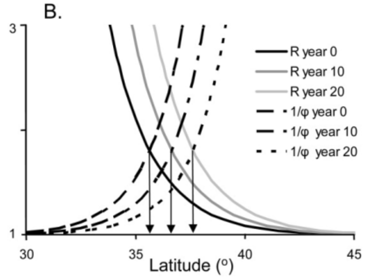


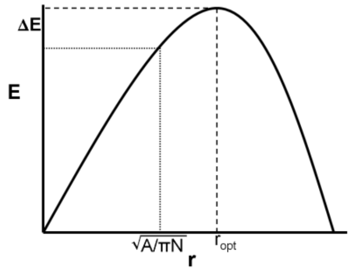
(Kearney & Porter 2004) (Crozier & Dwyer 2006) (Buckley 2008)

Range models

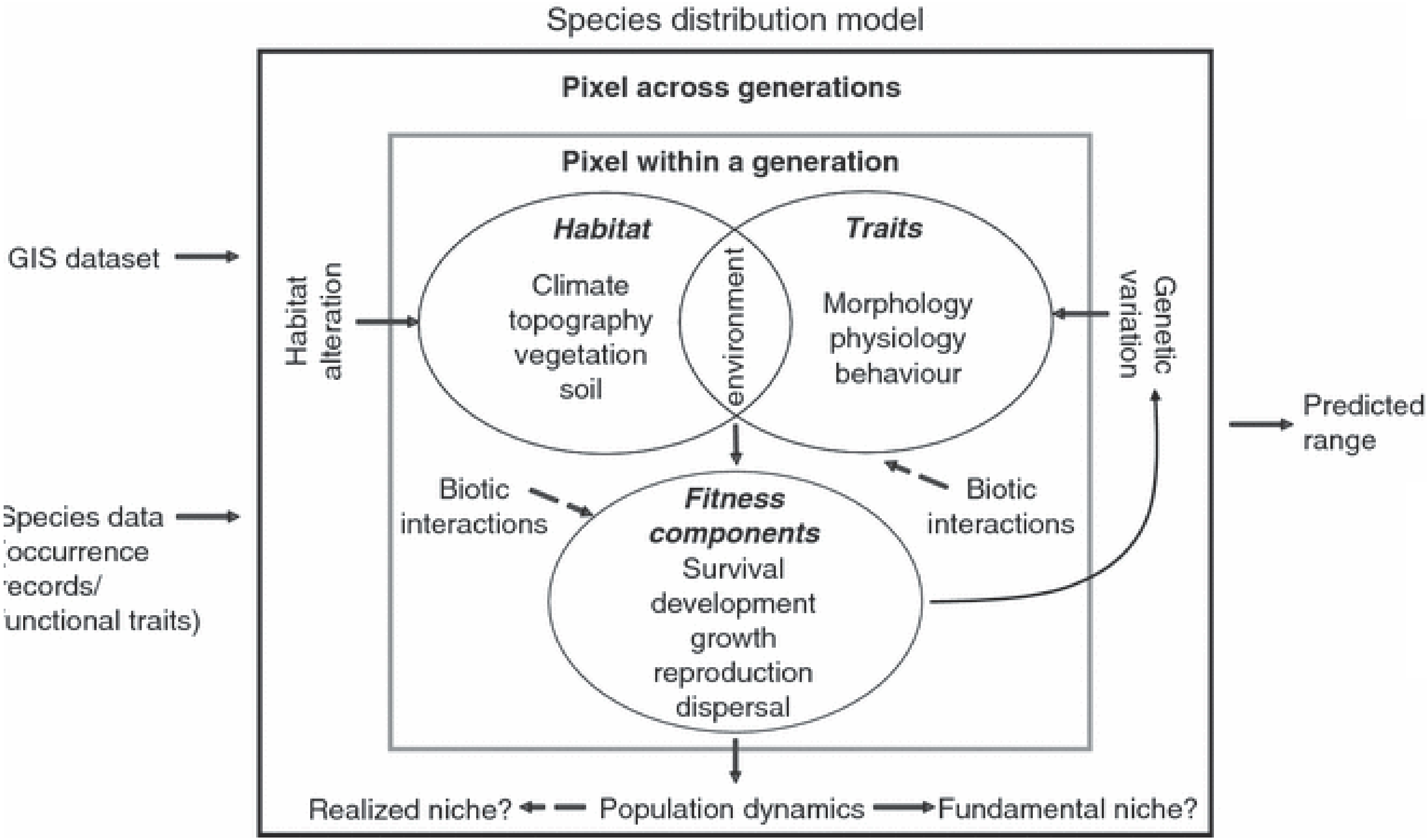




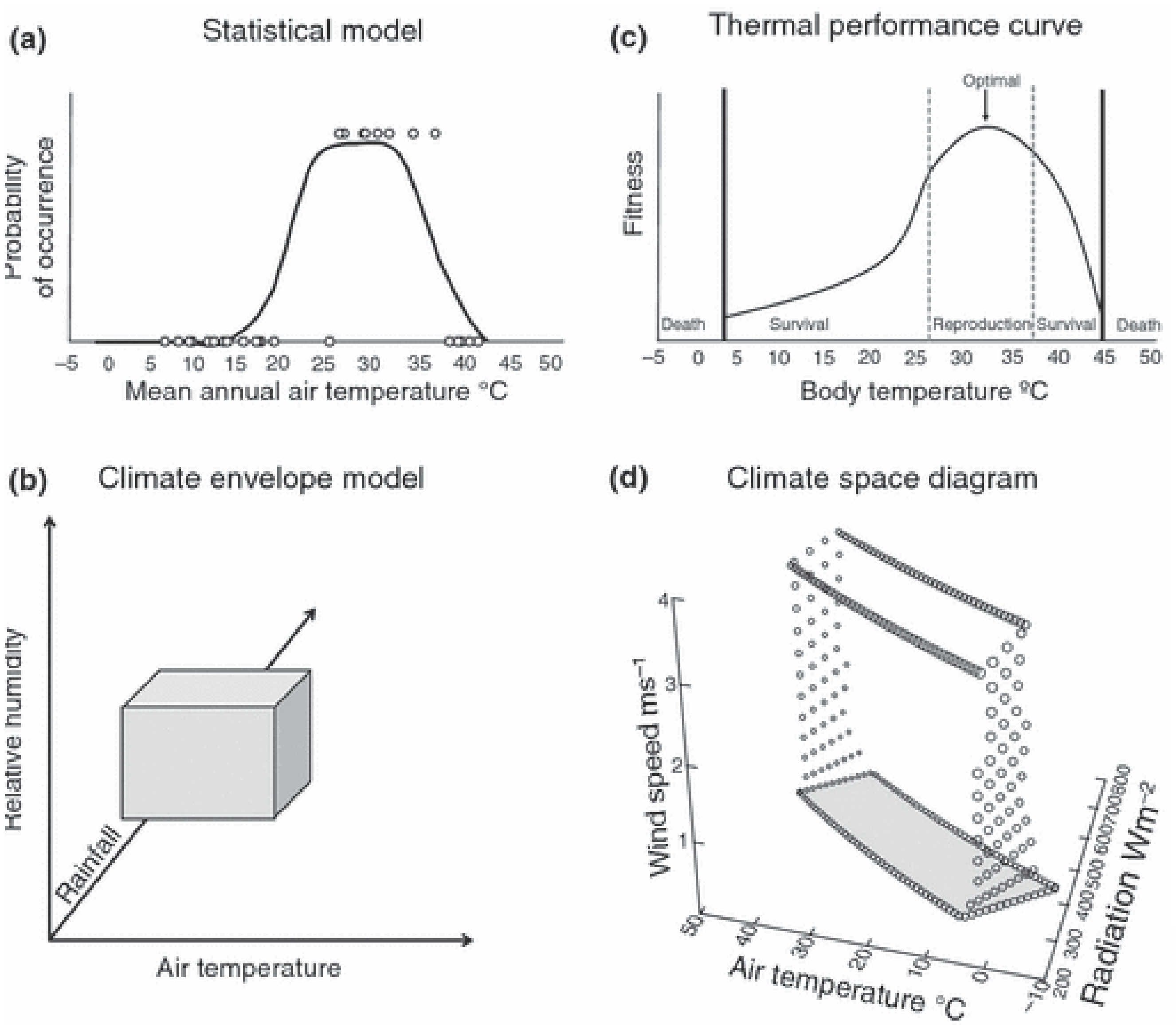




	correlative models	biophysical models	performance curves	foraging energetic models
Data	localities	traits, thresholds	demography	traits
Demography			X	X
Geographic Variation		X		X
Biotic Constraints	implicit	difficult	possible	possible



(Kearney and Porter 2009)



(Kearney and Porter 2009)

Model Comparison

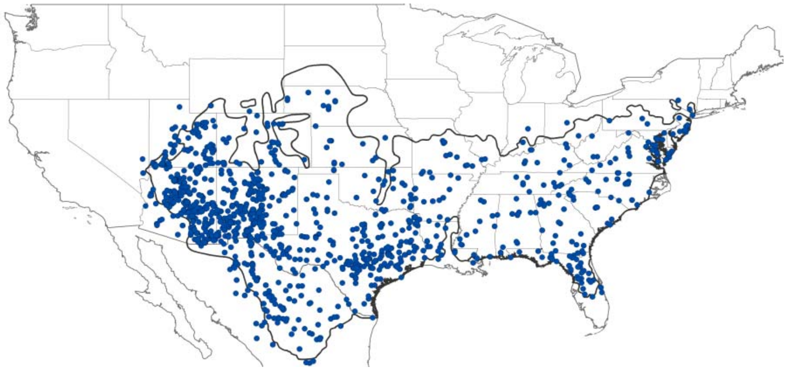
correlative — biophysical models — performance curves — foraging energetic models

Model species

Distribution data

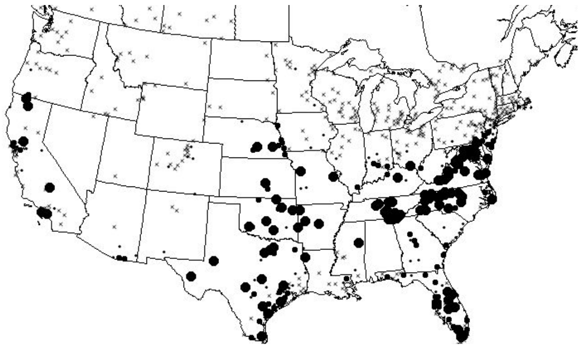
Fence lizard
Sceloporus undulatus

HerpNET

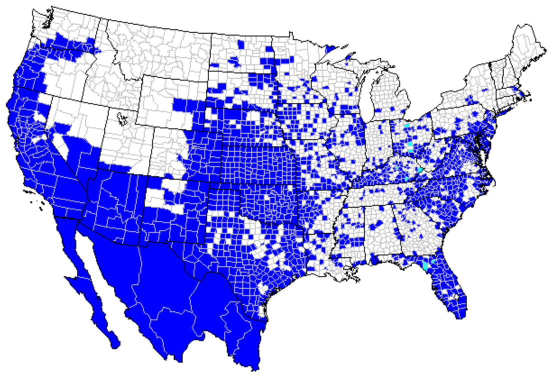


Sachem skipper butterfly
Atalopedes campestris

4th of July Butterfly counts



Butterflies and Moths of NA



Environmental data

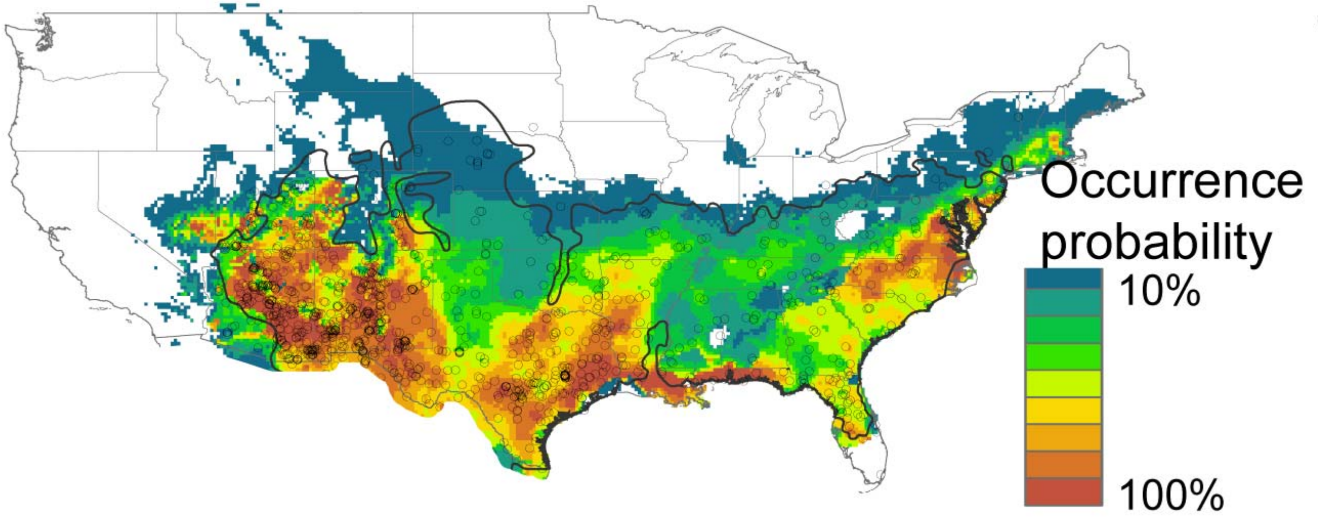
10' resolution, New *et al*. 2002

Fence lizard range models

correlative models | biophysical models | performance curves | foraging energetic models

Max ent

10% threshold



Locality

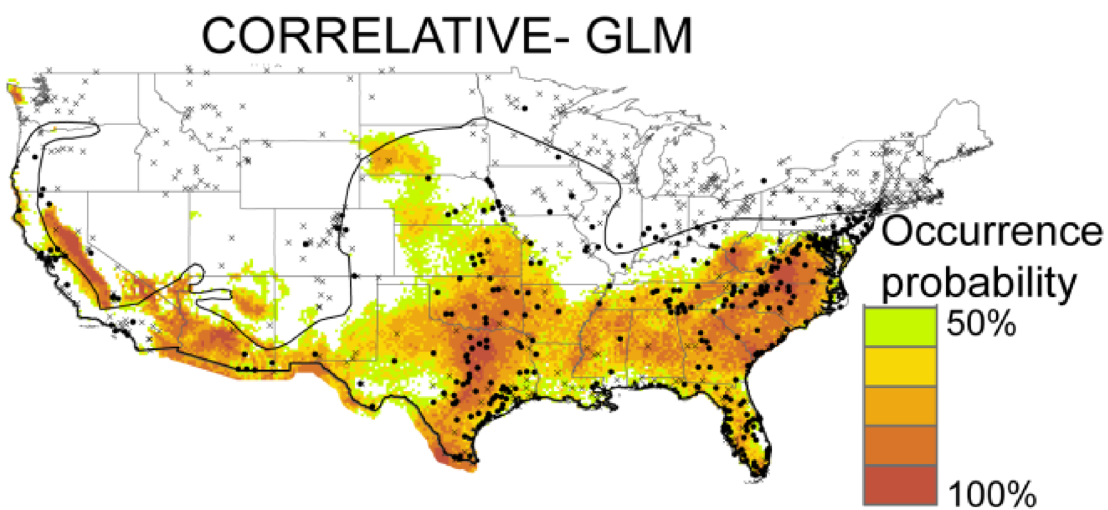
Atlas range

(NESCent/ NCEAS WG)

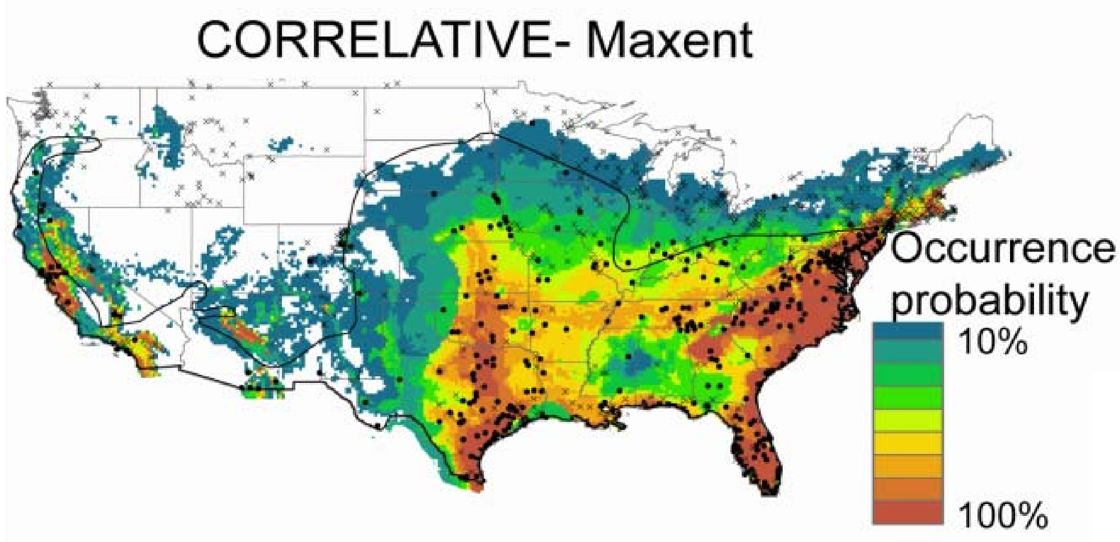
Sachem skipper range models

correlative models — biophysical models — performance curves — foraging energetic models

GLM
50% Threshold

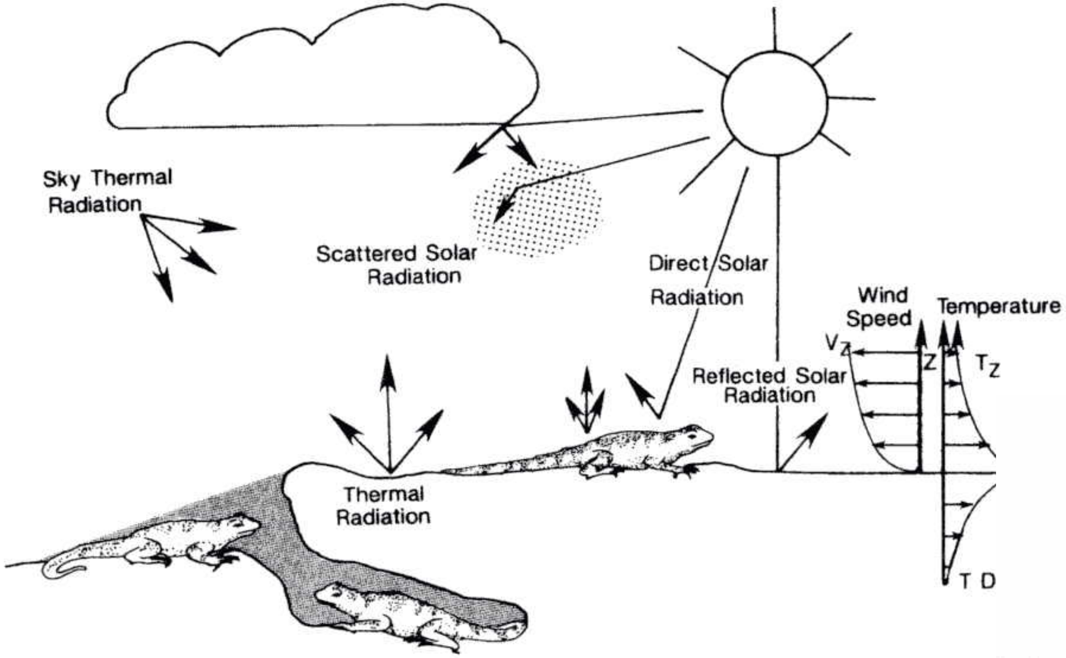


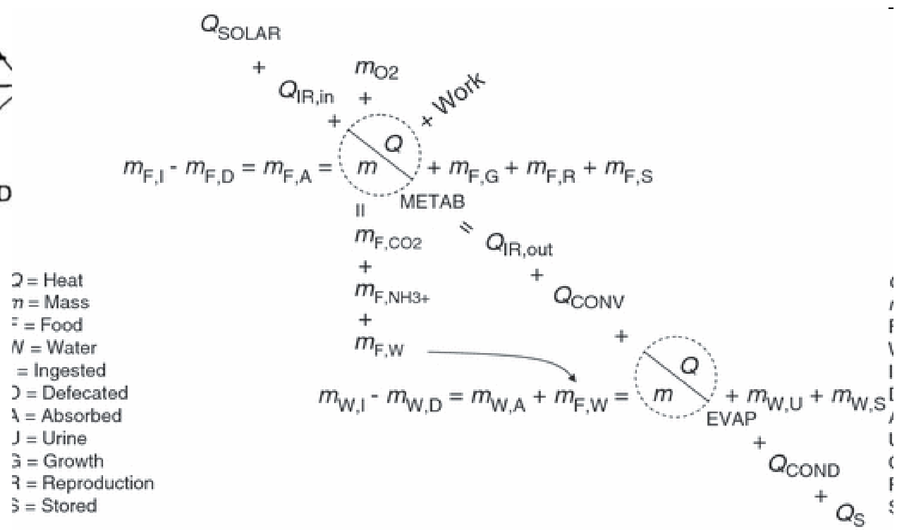
MaxEnt
10% Threshold



Fence lizard range models

correlative models | **biophysical models** | performance curves | foraging energetic models

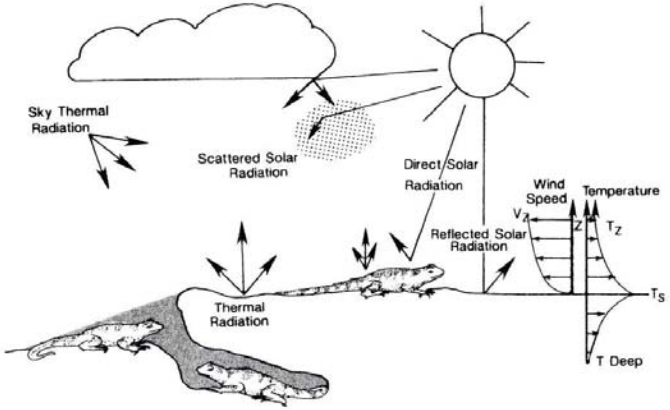




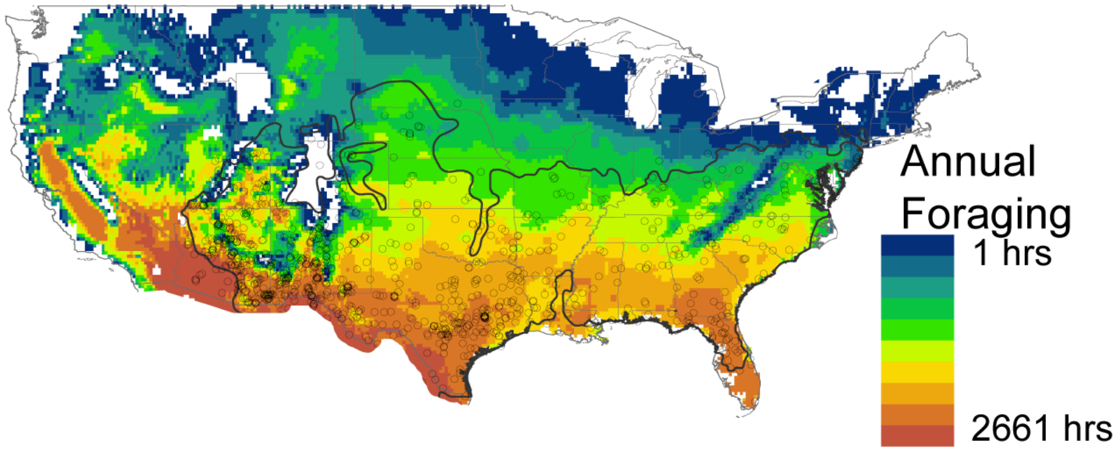
(Grant & Porter 1992)

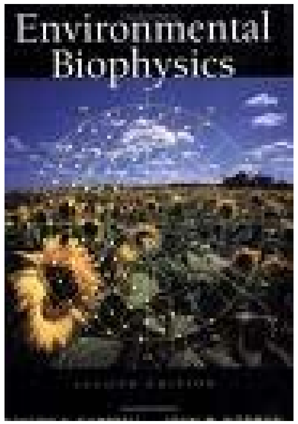
Fence lizard range models

correlative models | **biophysical models** | performance curves | foraging energetic models

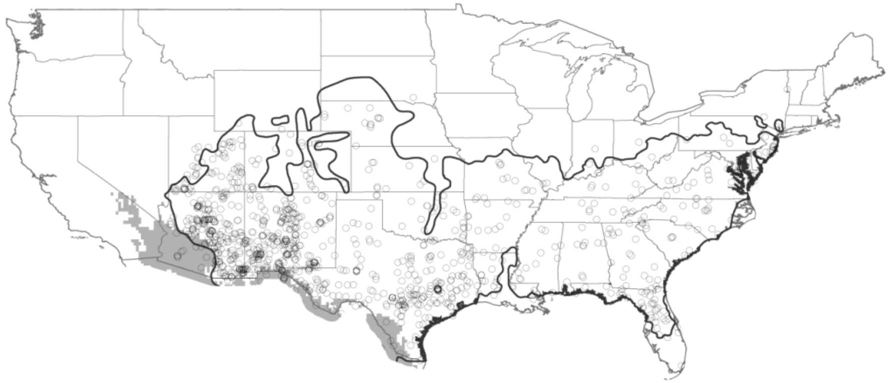


(Grant & Porter 1992)





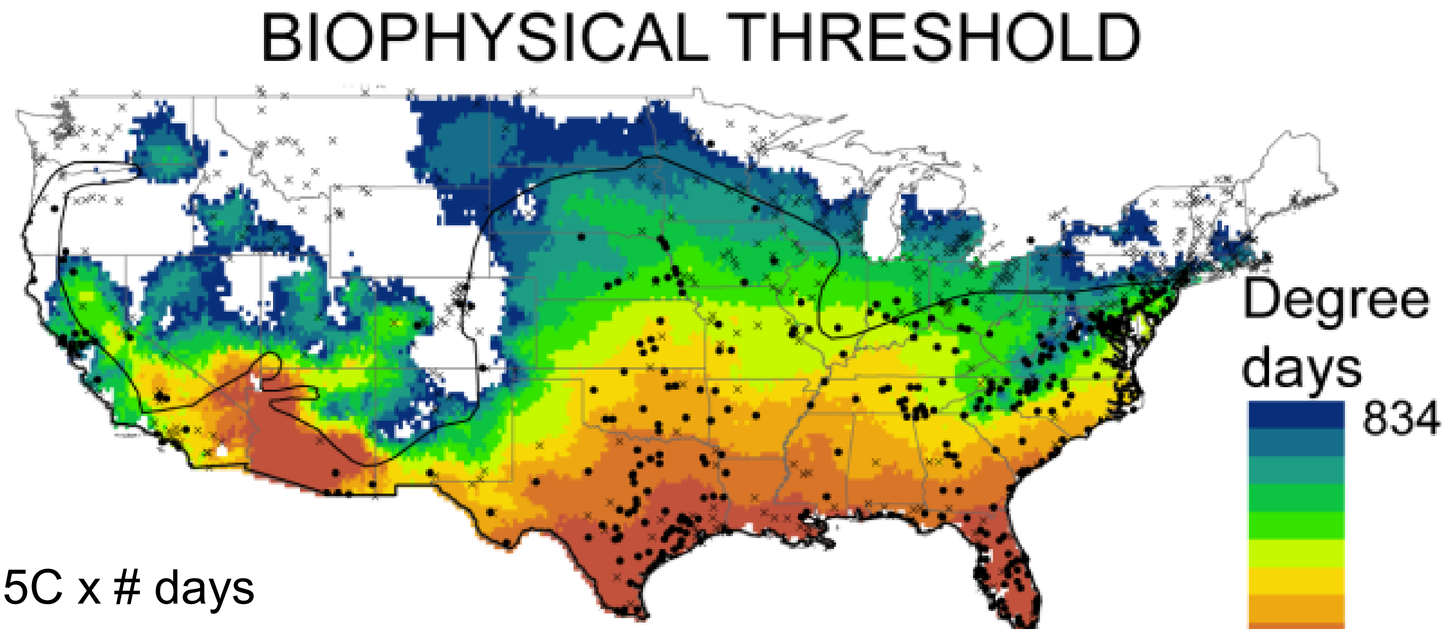
(Campbell and Norman 1988
Implemented by Buckley 2008)



1315 hr/yr threshold

Sachem skipper range models

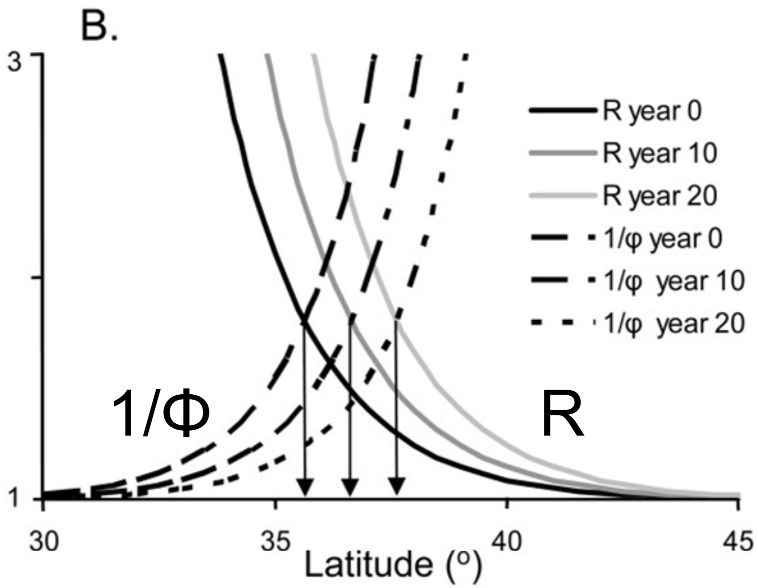
correlative models | biophysical models | performance curves | foraging energetic models

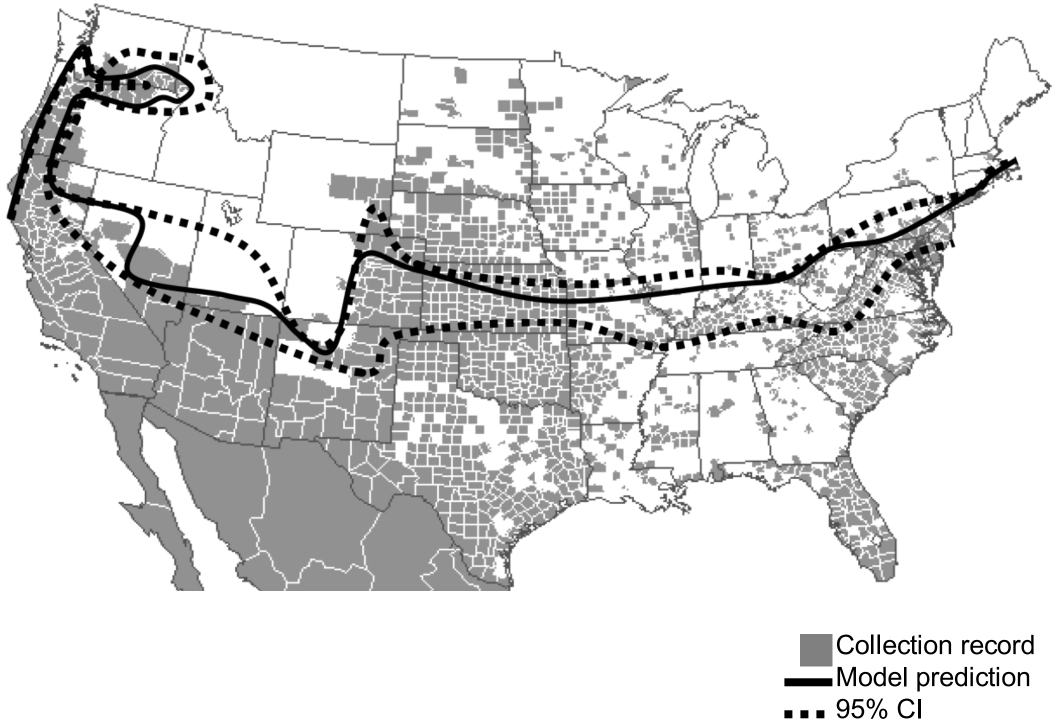


degrees over 15.5C x # days

Sachem skipper range models

correlative models | biophysical models | **performance curves** | foraging energetic models





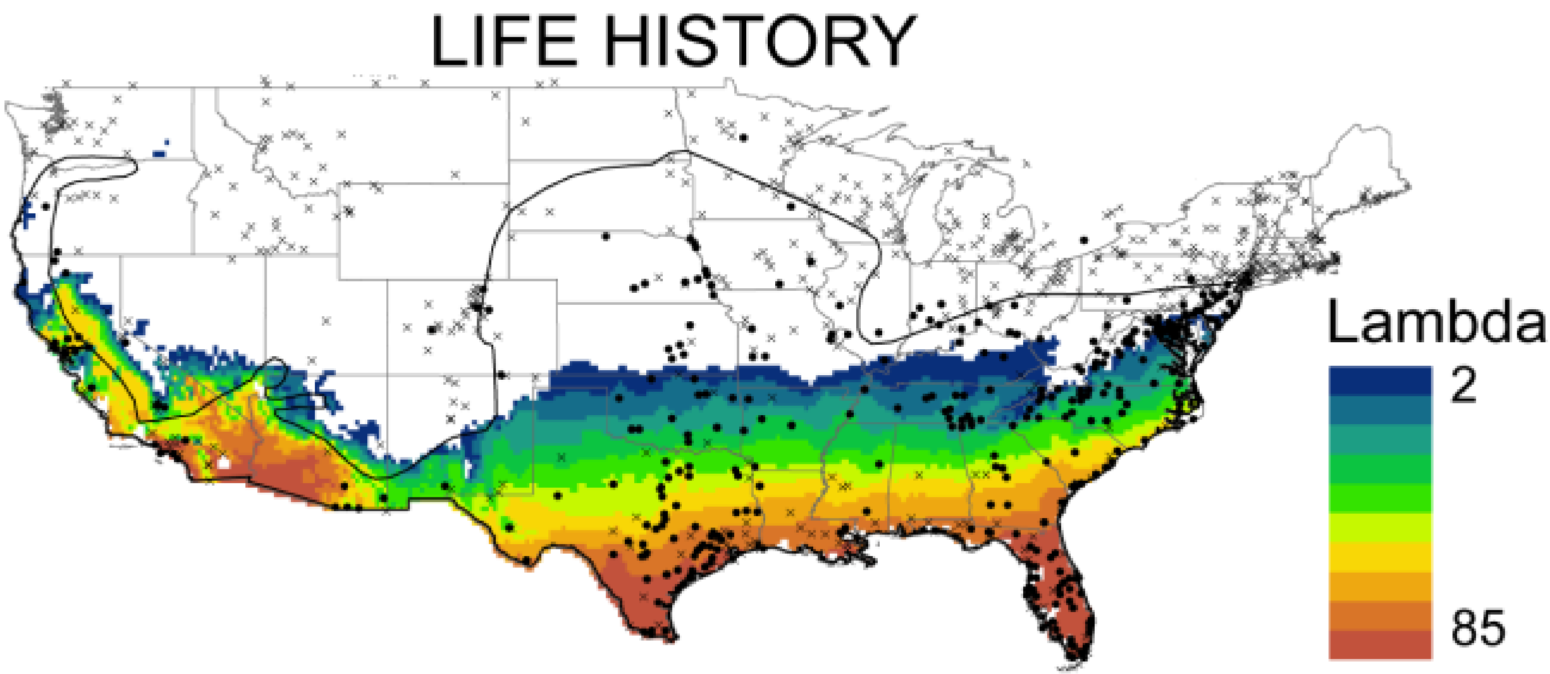
R- net summer recruitment

Φ- winter survival

(Crozier & Dwyer 2006)

Sachem skipper range models

correlative models | biophysical models | **performance curves** | foraging energetic models



Fence lizard range models

correlative models — biophysical models — **performance curves** — foraging energetic models

net reproductive rate

sum annually maturity to death

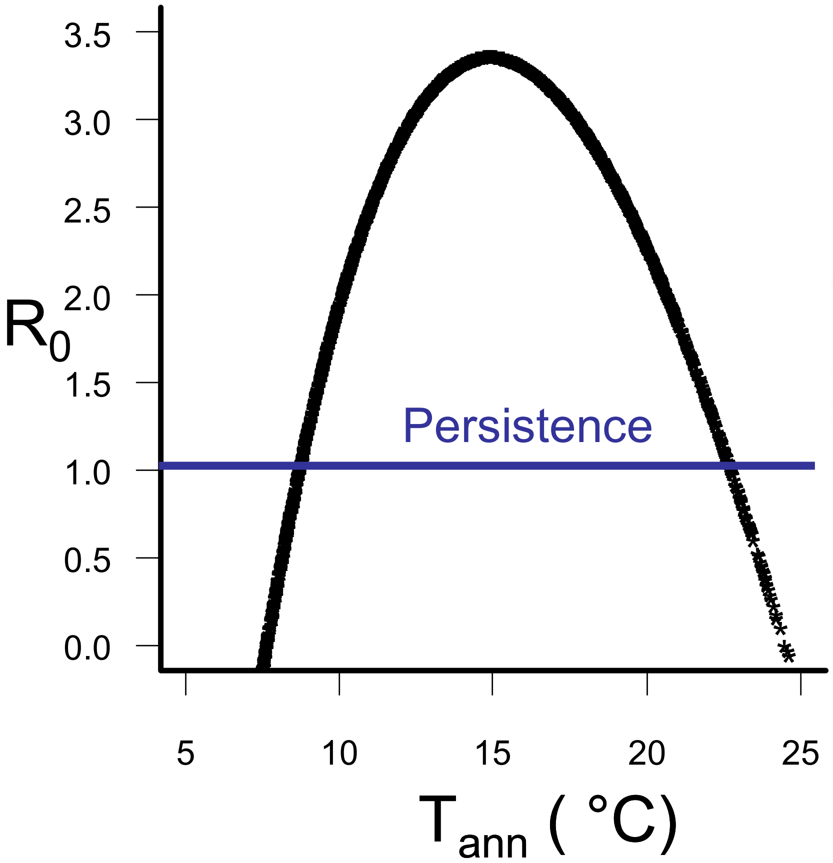
$$R_0 = \sum_{x=\alpha}^{L} S_j S_a(T)^{(x-\alpha)} m(T)$$

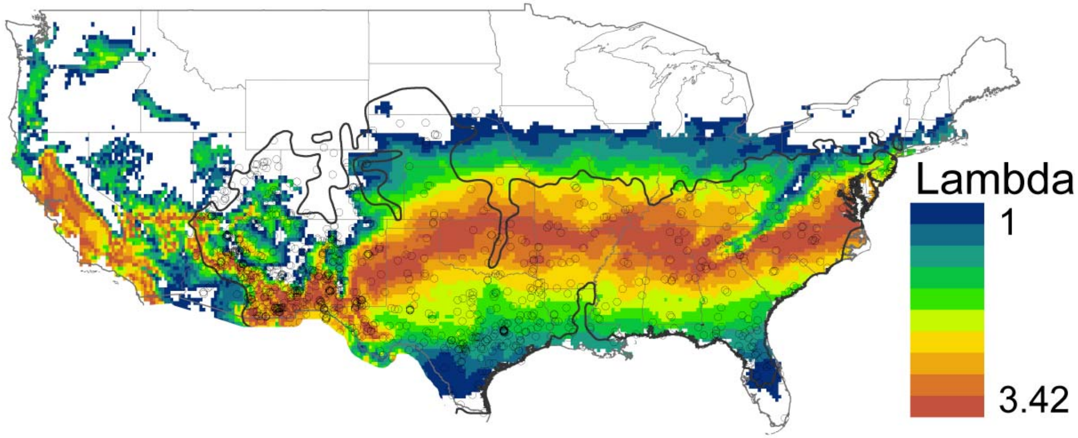
juvenile and adult (T) survival

annual fecundity (T)

Fence lizard range models

correlative models | biophysical models | **performance curves** | foraging energetic models





Fence lizard range models

correlative models | biophysical models | performance curves | foraging energetic models

environmental conditions

individual energetics

population dynamics

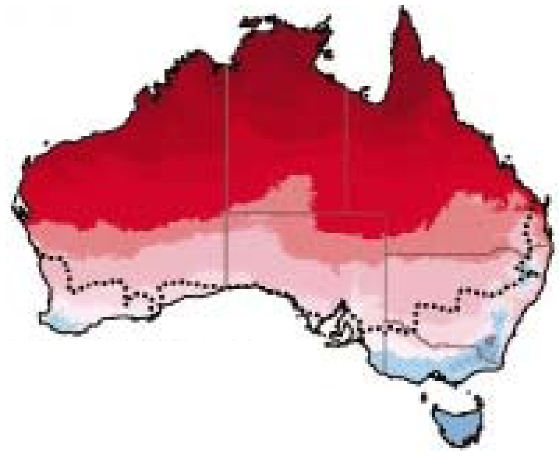
can extend to include biotic factors
(adaptation, movement, species' interactions, …)

Mechanistic range models

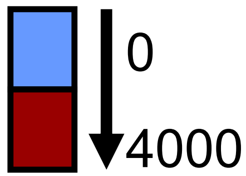
environmental conditions

individual energetics

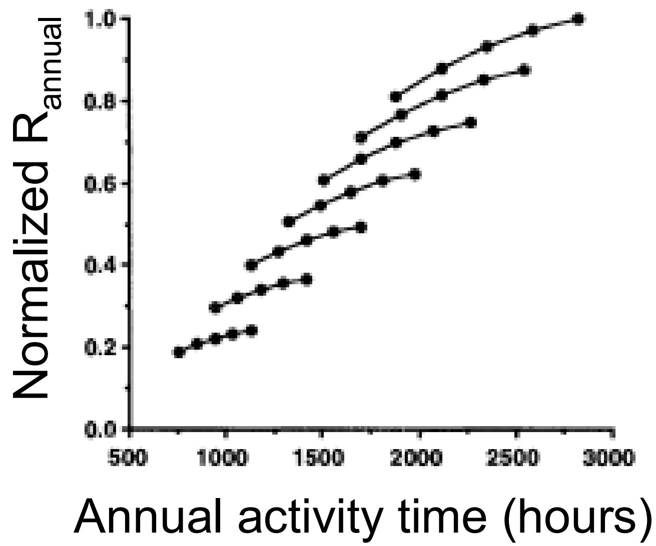
population dynamics



Potential activity (h)



Gecko
(Kearney & Porter 2004)



Fence lizard
(Adolph & Porter 1993)

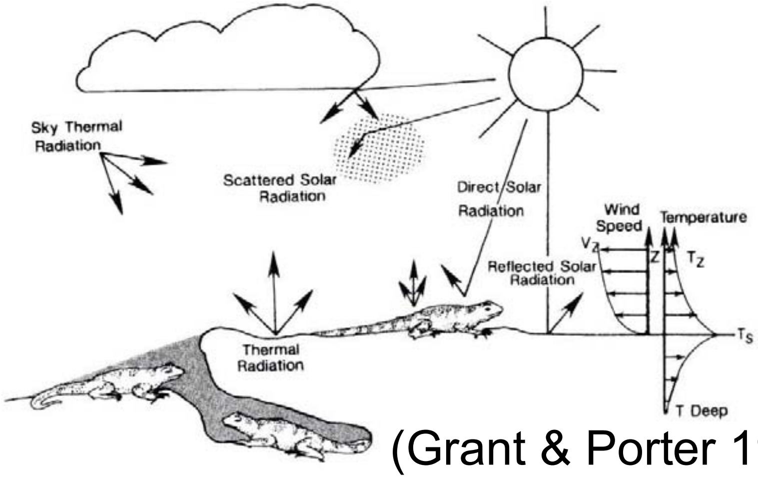
Dynamic foraging energetic model

environmental conditions

individual energetics

population dynamics

Foraging duration & performance



(Grant & Porter 1992)

PARAMETERS

Body temperature range, T_b
Body size → Metabolic rate
Sprint speed
Prey size
Gut capacity

Environmental temperature, T_e (Campbell & Norman 2000)
Assume forage when T_e within 20-80% quantiles of T_b

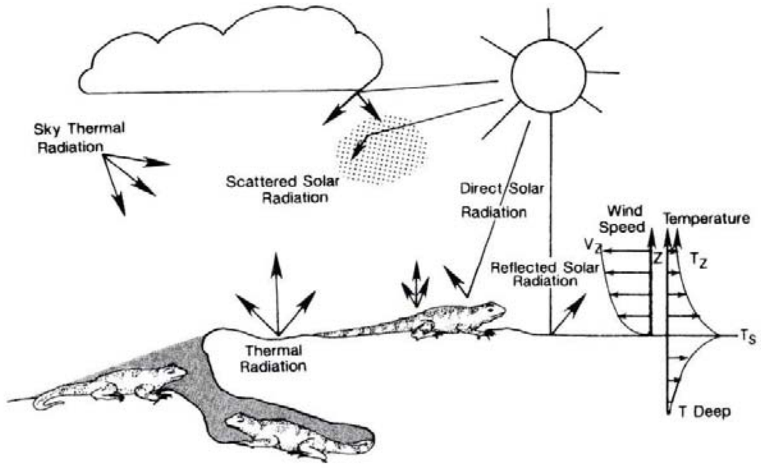
Dynamic foraging energetic model

environmental conditions

individual energetics

population dynamics

Foraging duration & performance



PARAMETERS

Body temperature range, T_b
Body size → Metabolic rate
Sprint speed
Prey size
Gut capacity

Optimal foraging model

Optimize energetic yield / time

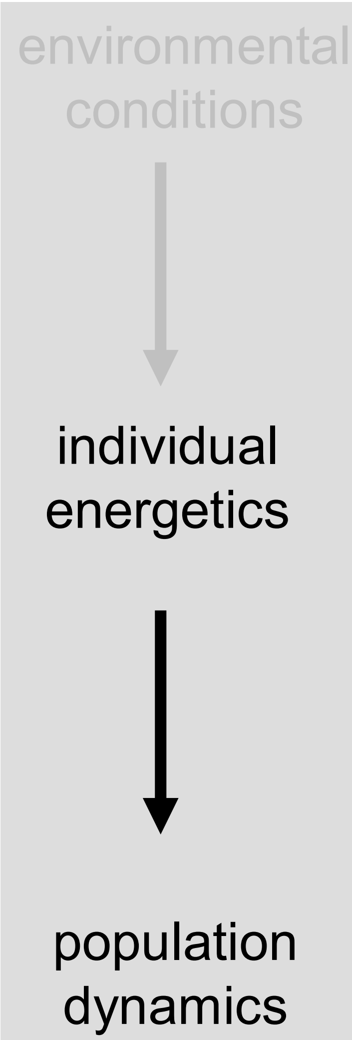
$$E(r) = \frac{\text{energy intake} - \text{pursuit costs}(r) - \text{waiting costs}(r)}{\text{pursuit time}(r) + \text{waiting time}(r)}$$

$r \rightarrow$ foraging radius

PARAMETERS

Insect abundance

Dynamic foraging energetic model



Population dynamic model

$$\Delta N = [\underbrace{bE(r)}_{\text{Birth}}\; t_f - \underbrace{c(t-t_f) - m}_{\text{Death}}]N$$

t_f → foraging duration
t → total time
c → costs (offspring) for maintenance while not foraging

PARAMETERS

b → converts energy into offspring (eggs/J x $S_{maturity}$)
m → mortality

(Buckley & Roughgarden JAE 2005)

Dynamic foraging energetic model

environmental conditions

↓

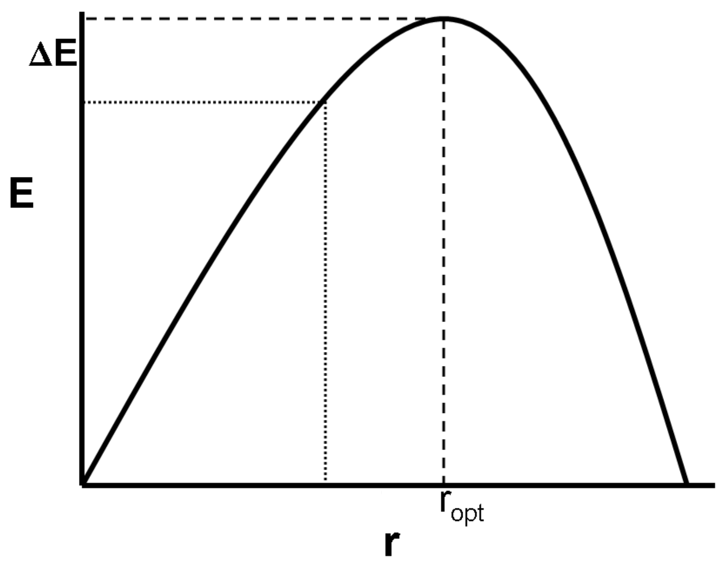
individual energetics

↓

population dynamics

Population dynamic model

$$\Delta N = [bE(r)\, t_f - c(t - t_f) - m]N$$



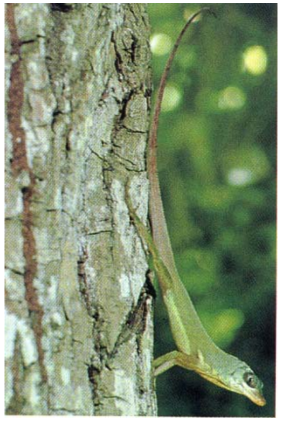
t_f → foraging duration
t → total time
c → costs (offspring) for maintenance while not foraging

PARAMETERS

b → converts energy into offspring (eggs/J x $S_{maturity}$)
m → mortality

Density-dependence in $E(r)$
Can solve for equilibrium population size

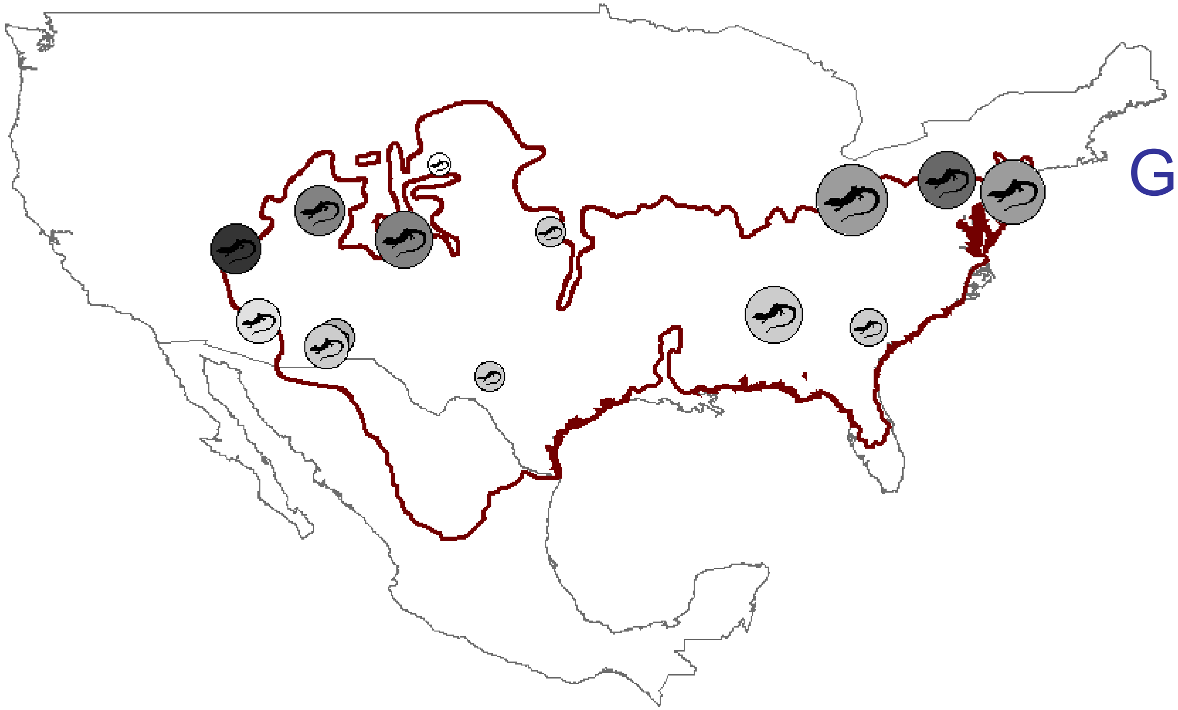
Abundance patterns of solitary and sympatric anoles along elevation gradients?



Does biology matter when predicting climate change responses?

Sceloporus undulatus
(Leaché and Reeder 2002)

Does biology matter when predicting climate change responses?

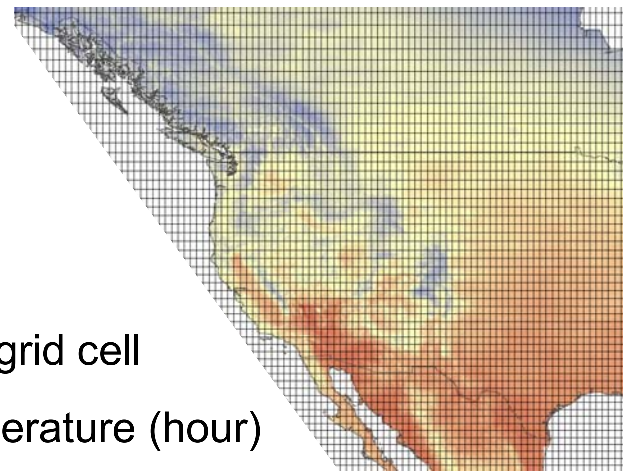


Geographic variation in

- Size (SVL)
- Survival
- Development rate

Insect abundance

Assumes no trait plasticity



0.5° grid cell

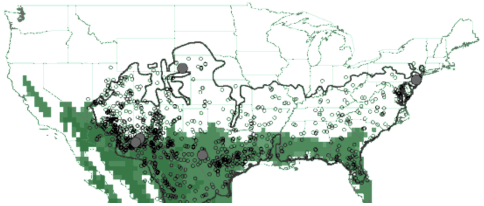
temperature (hour)

(Buckley AmNat 2008)

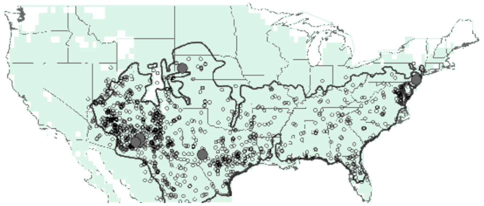
Dynamic foraging energetic model

Population SVL

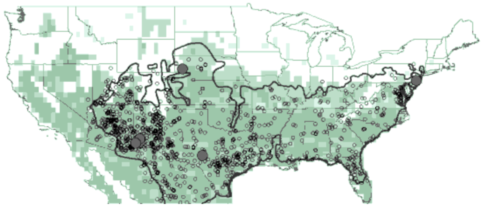
Nebraska traits



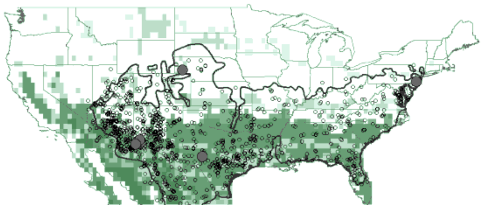
New Jersey traits



New Mexico traits



Texas traits

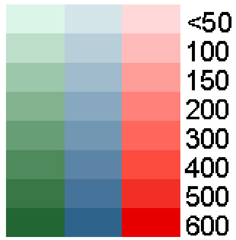


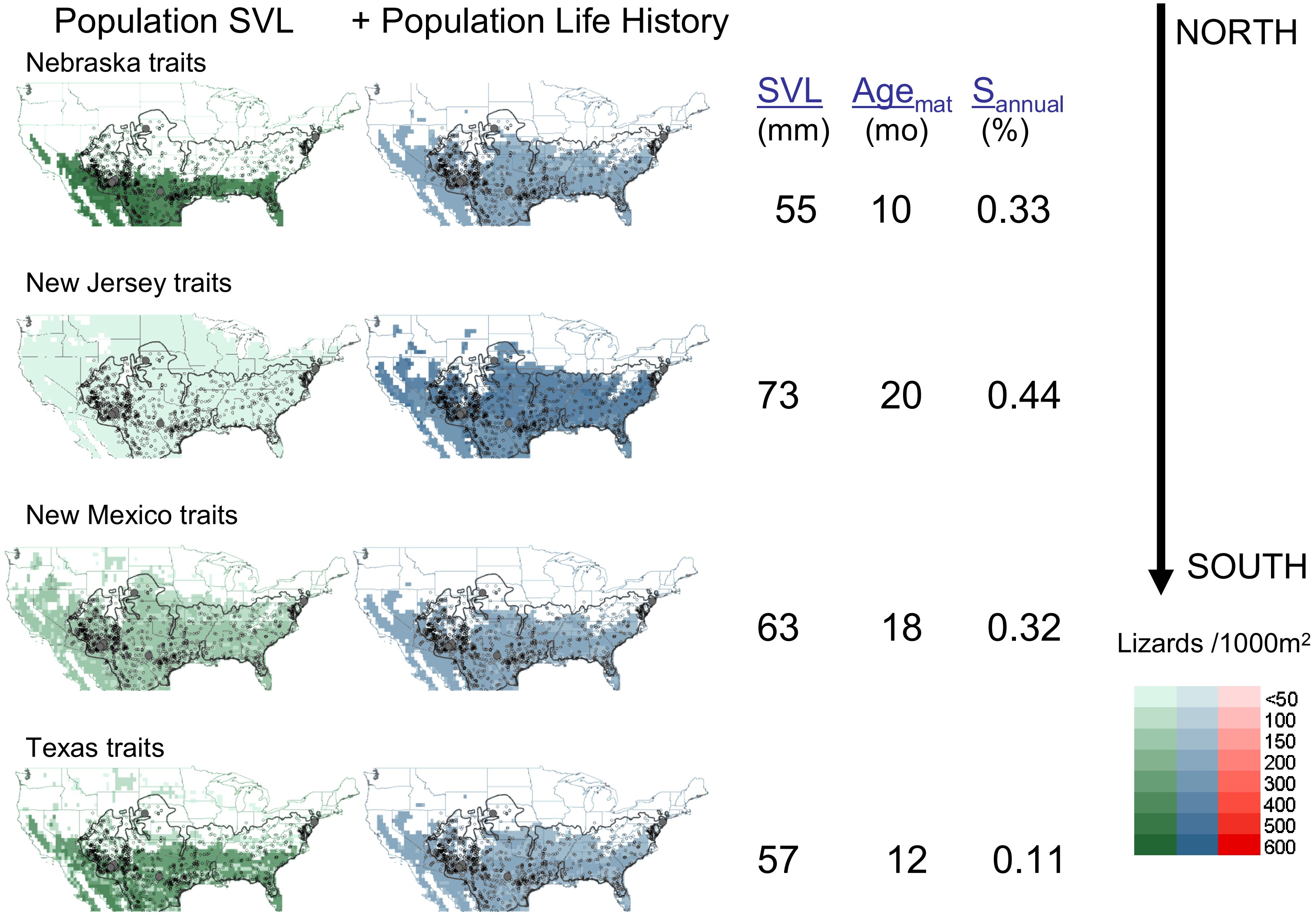
	SVL (mm)	Age_{mat} (mo)	S_{annual} (%)
Nebraska traits	55		
New Jersey traits	73		
New Mexico traits	63		
Texas traits	57		

NORTH

SOUTH

Lizards /1000m²





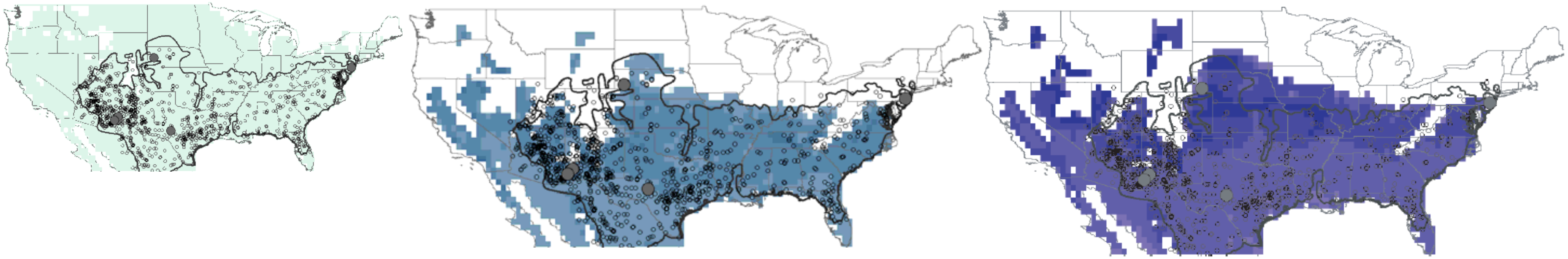
Population SVL
+ Population Life History
Nebraska traits
New Jersey traits
New Mexico traits
Texas traits
SVL (mm)
Age_mat (mo)
S_annual (%)
55 10 0.33
73 20 0.44
63 18 0.32
57 12 0.11
NORTH
SOUTH
Lizards /1000m²
<50
100
150
200
300
400
500
600

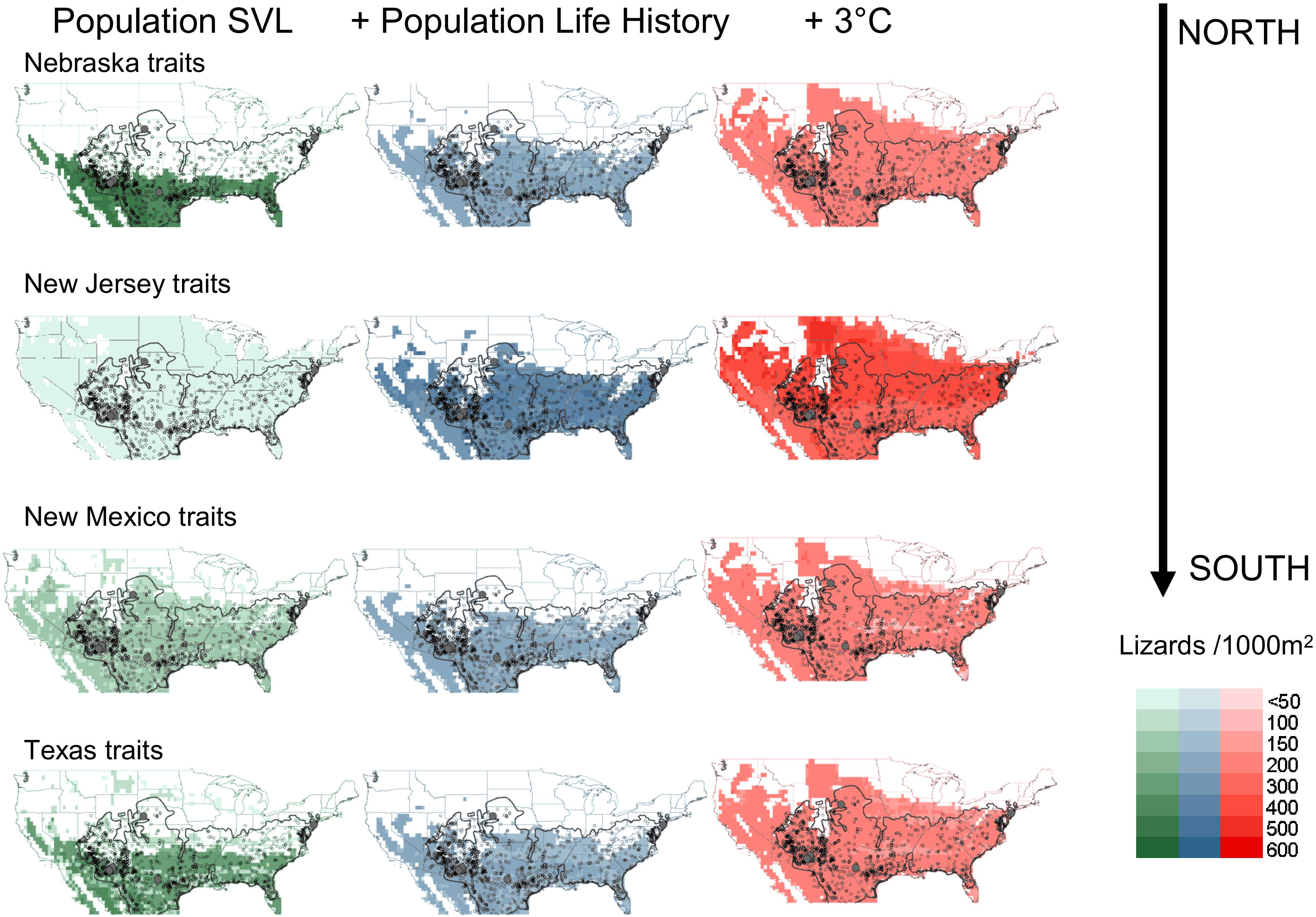
Population SVL

+ Population Life History

+ Population Insect Abundance

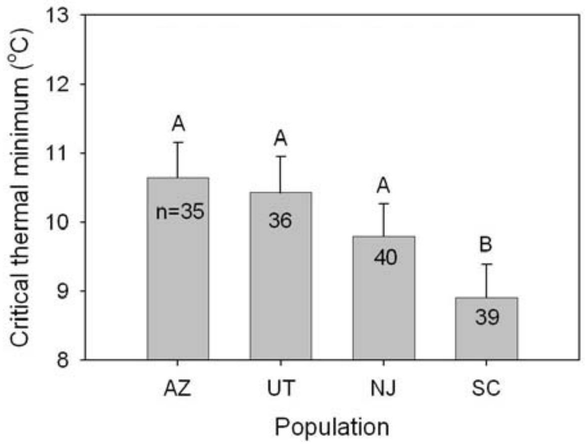
New Jersey traits

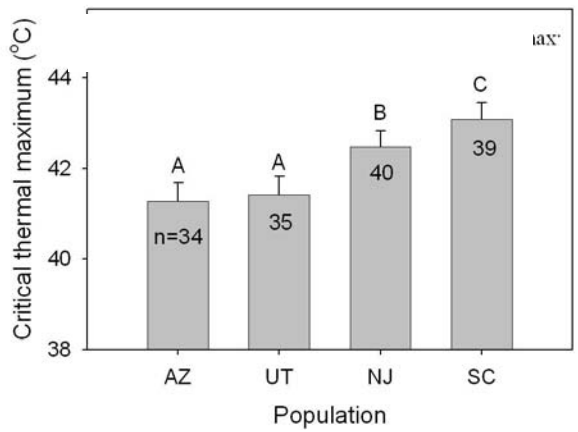




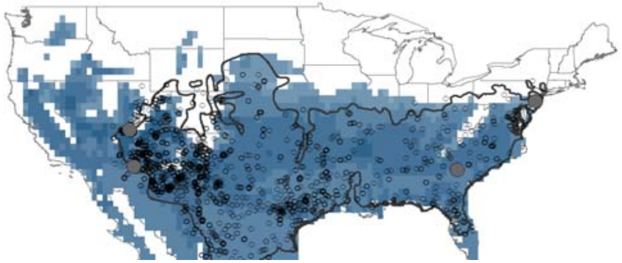
Population SVL
+ Population Life History
+ 3°C
NORTH
SOUTH
Nebraska traits
New Jersey traits
New Mexico traits
Texas traits
Lizards /1000m²
<50
100
150
200
300
400
500
600

Range implications of physiological variation?

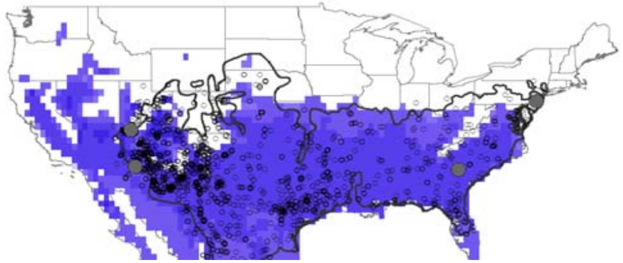




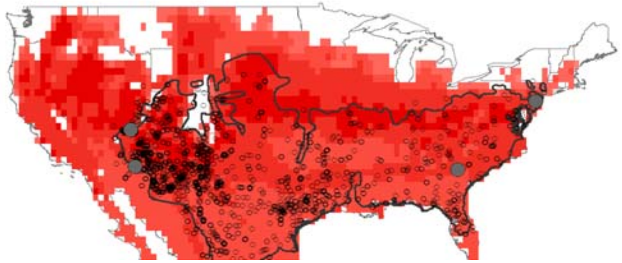
New Jersey SVL + Thermal Limits



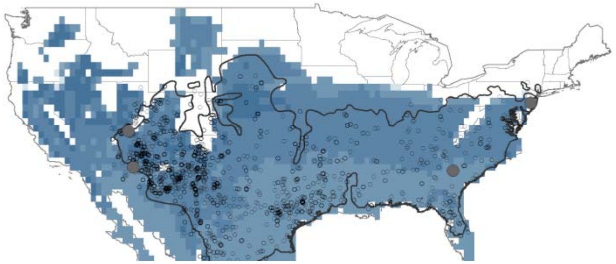
+ NJ Metabolic Rates



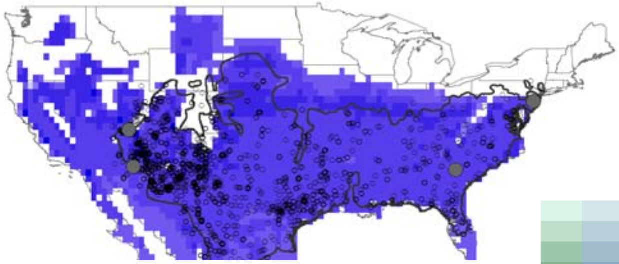
+ 3°C



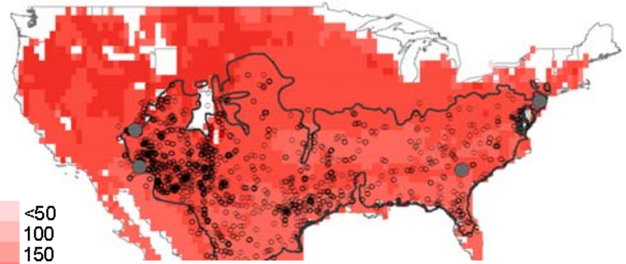
South Carolina SVL +Thermal Limits

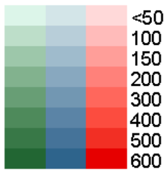


+ SC Metabolic Rates



+ 3°C

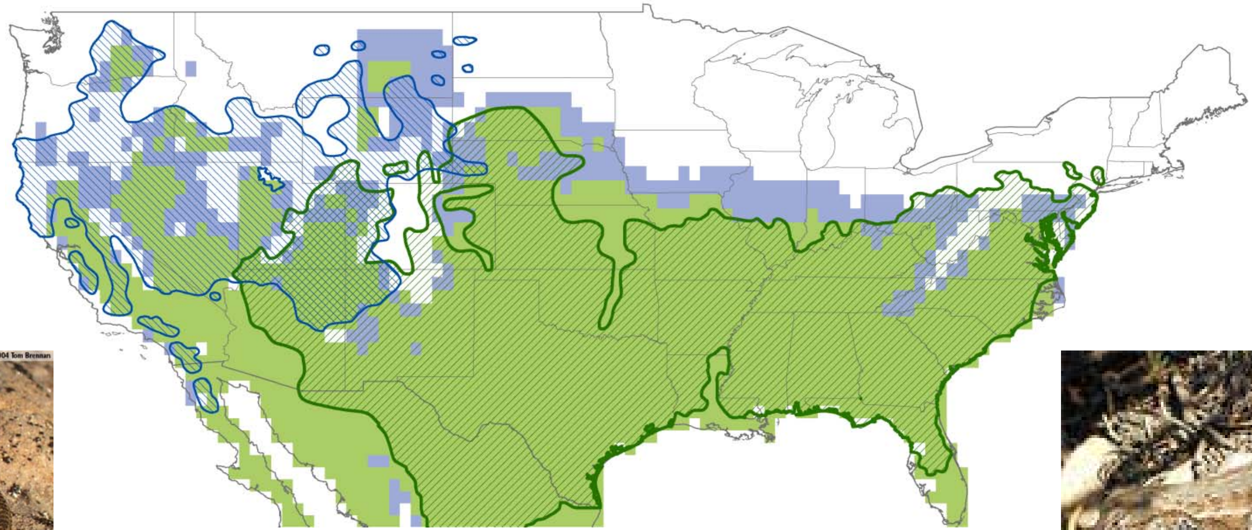




Lizards /1000m²

(Ehrenberger, Buckley, and Angilletta)

Species interactions?



Sceloporus graciosus

predicted

observed

Sceloporus undulatus

predicted

observed

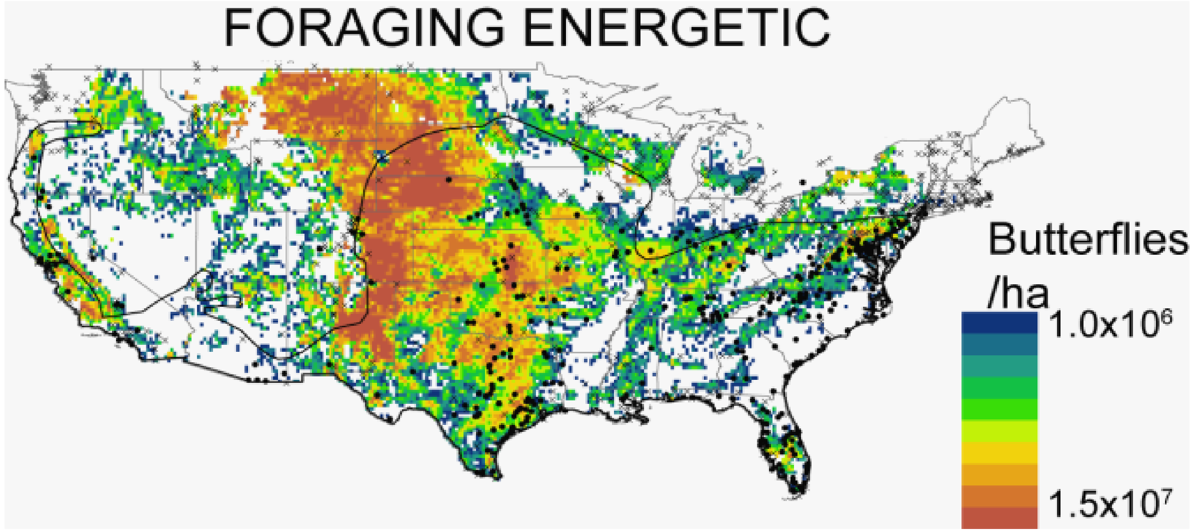
(Buckley 2008)

Sachem skipper range models

correlative models | biophysical models | performance curves | **foraging energetic models**

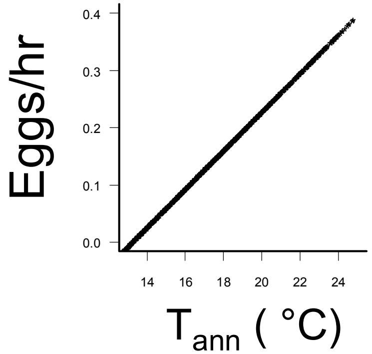
$R_0 = bE - Y$

eggs/J J -J

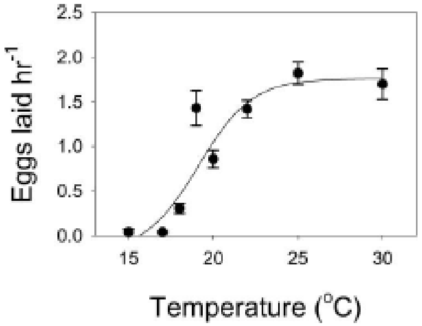


Thermal constraints

Egg maturation (Berger 2008)



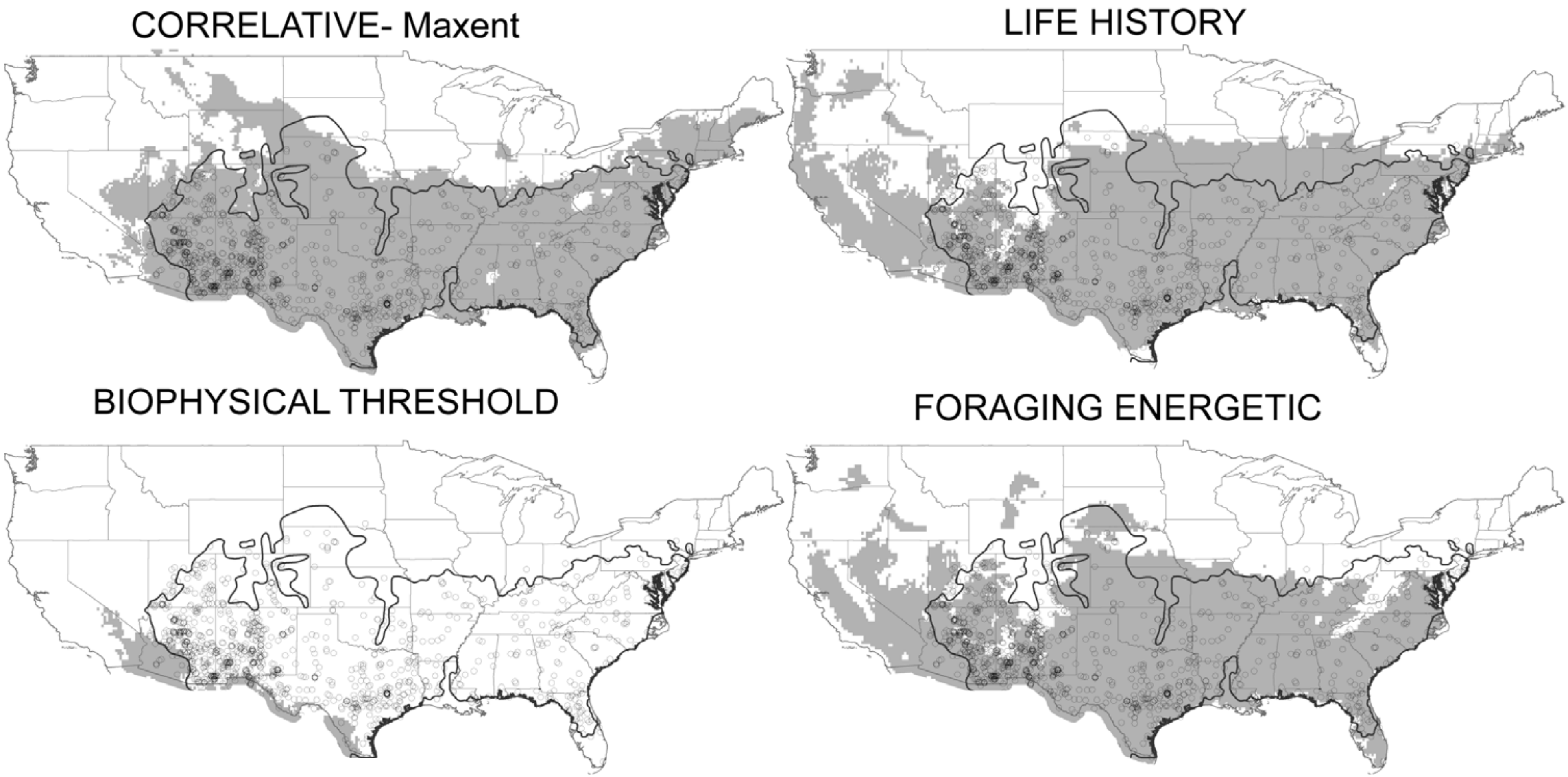
Ovipositing (Gotthard 2007)



Density dependence in nectar resources

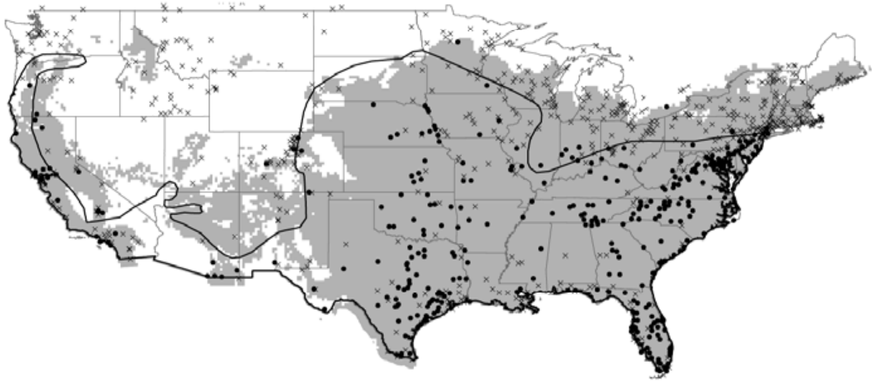
$$\left(1 - \frac{N for_{rate} ren_{rate}}{P}\right)$$

Fence lizard range models

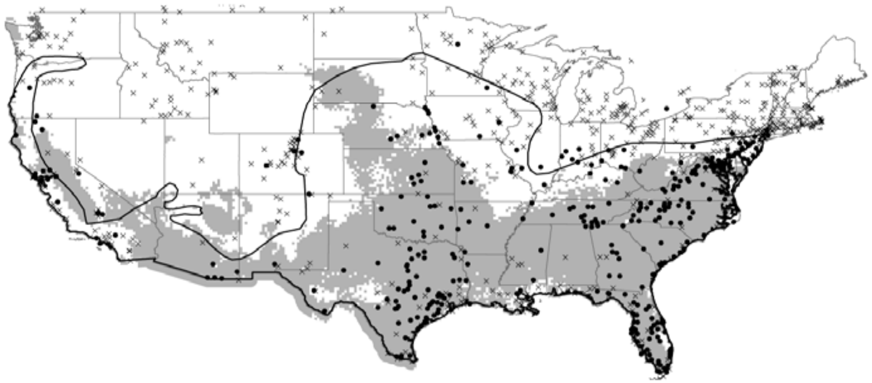


Sachem skipper range models

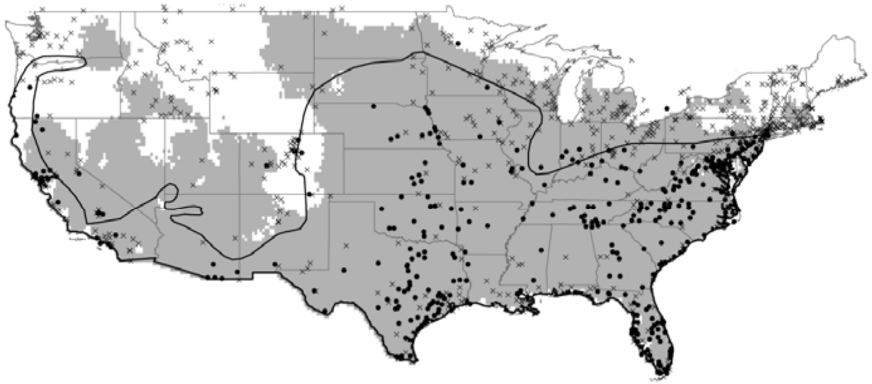
CORRELATIVE- Maxent



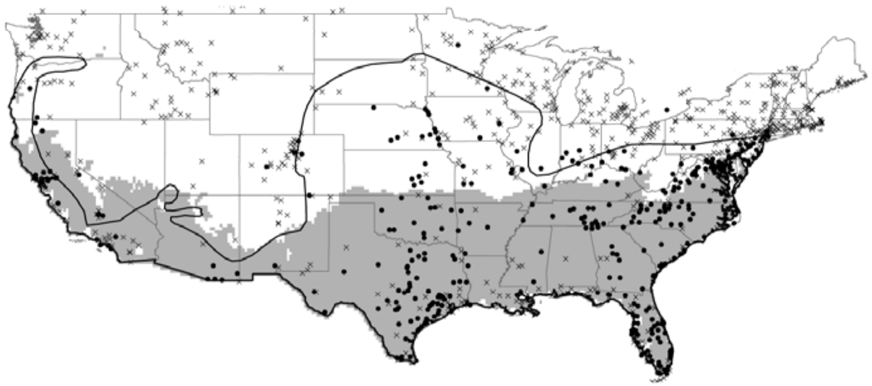
CORRELATIVE- GLM



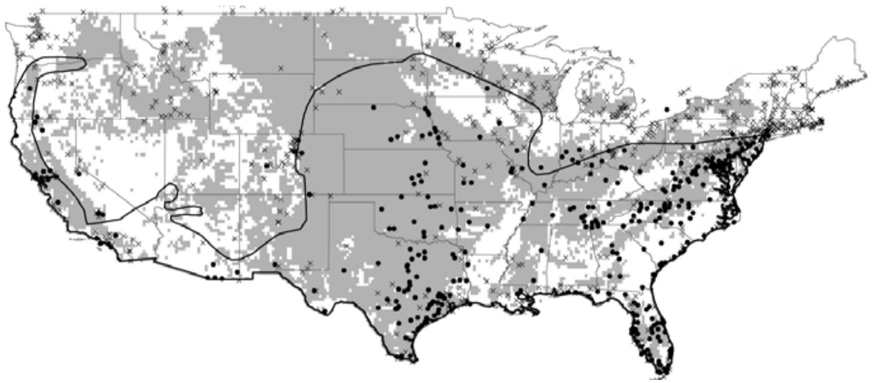
BIOPHYSICAL THRESHOLD

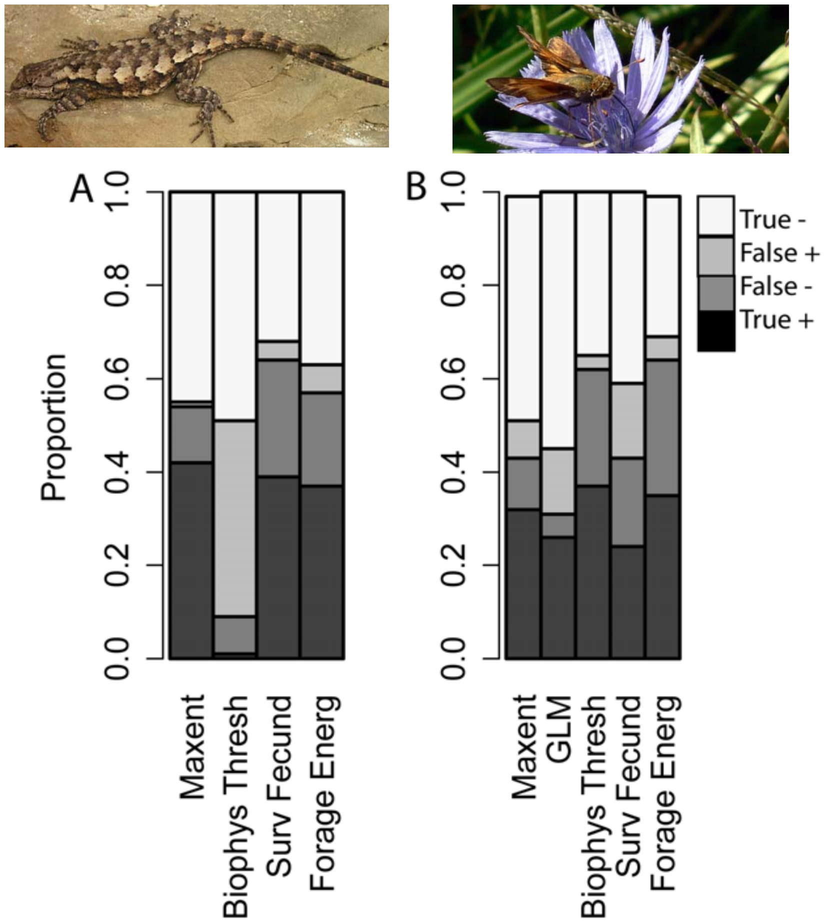


LIFE HISTORY



FORAGING ENERGETIC

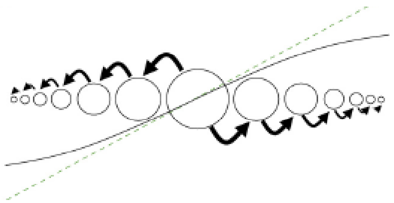


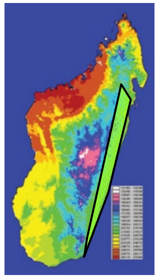


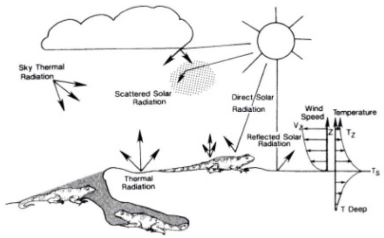
Model	*S. undulatus*				*A. campestris*				
	% +	% -	% true	% localities	% +	% -	% true	% survey +	% survey -
Correlative- Maxent	0.98	0.78	0.87	0.99	0.80	0.81	0.81	0.97	0.44
Correlative- GLM					0.64	0.92	0.81	0.73	0.81
Biophysical threshold	0.02	0.86	0.50	0.04	0.92	0.58	0.72	0.94	0.43
Life history	0.90	0.56	0.71	0.88	0.61	0.68	0.65	0.77	0.69
Foraging energetic	0.85	0.65	0.74	0.84	0.88	0.51	0.66	0.90	0.31

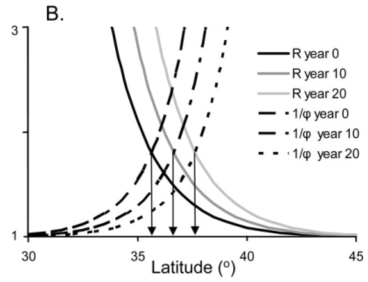
Range models

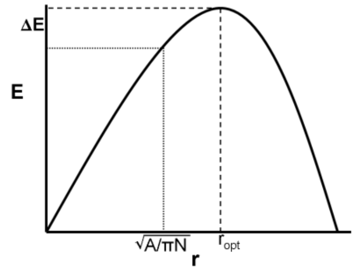
theoretical models | correlative models | biophysical models | performance curves | foraging energetic models











• Large but narrowing divide between theory and application

• Correlative models readily provide abundant range information
Mechanistic models emerging as viable alternative

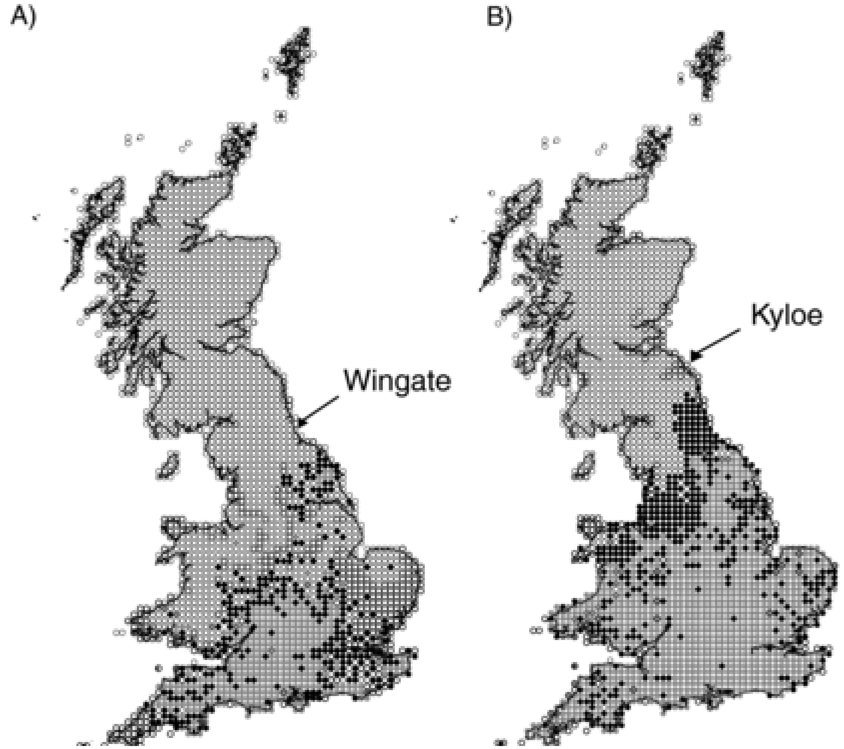
• Mechanistic models enable incorporating physiology, & demography, biotic constraints & evolution, individualistic responses

Assisted migration ?

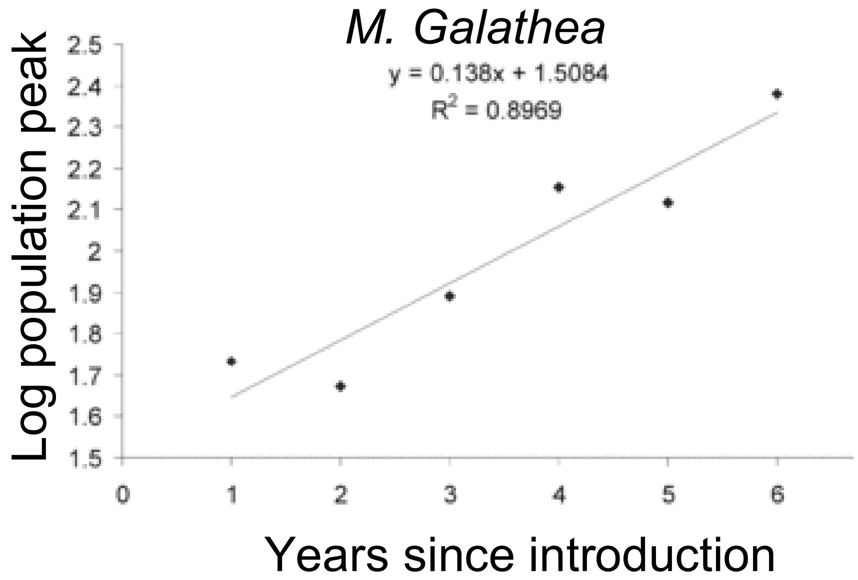
(Nature 2008)

Melanargia galathea
(marbled white)

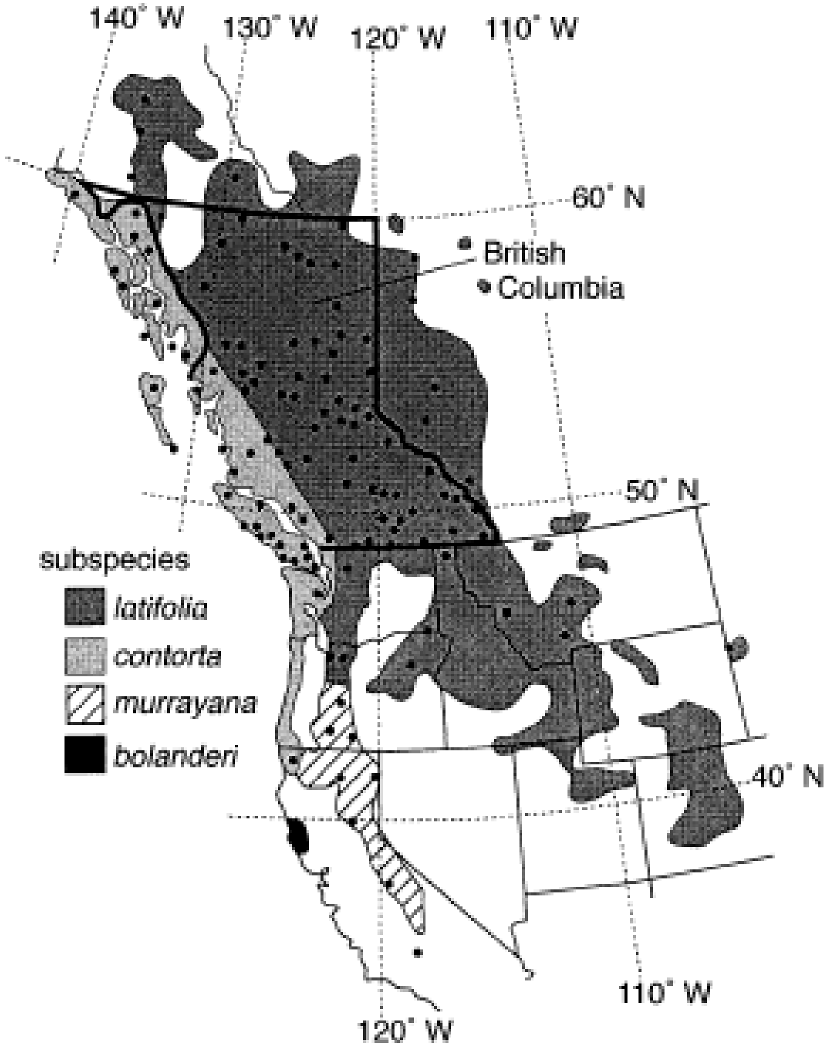
Thymelicus sylvestris
(small skipper)

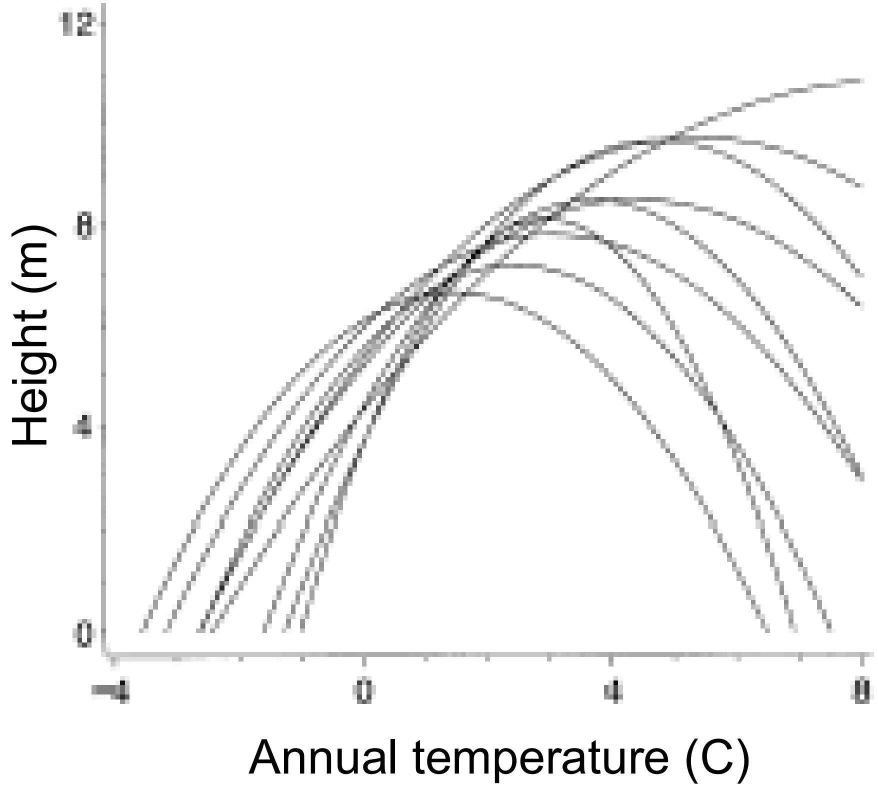


■ Newly occupied 1995-1999

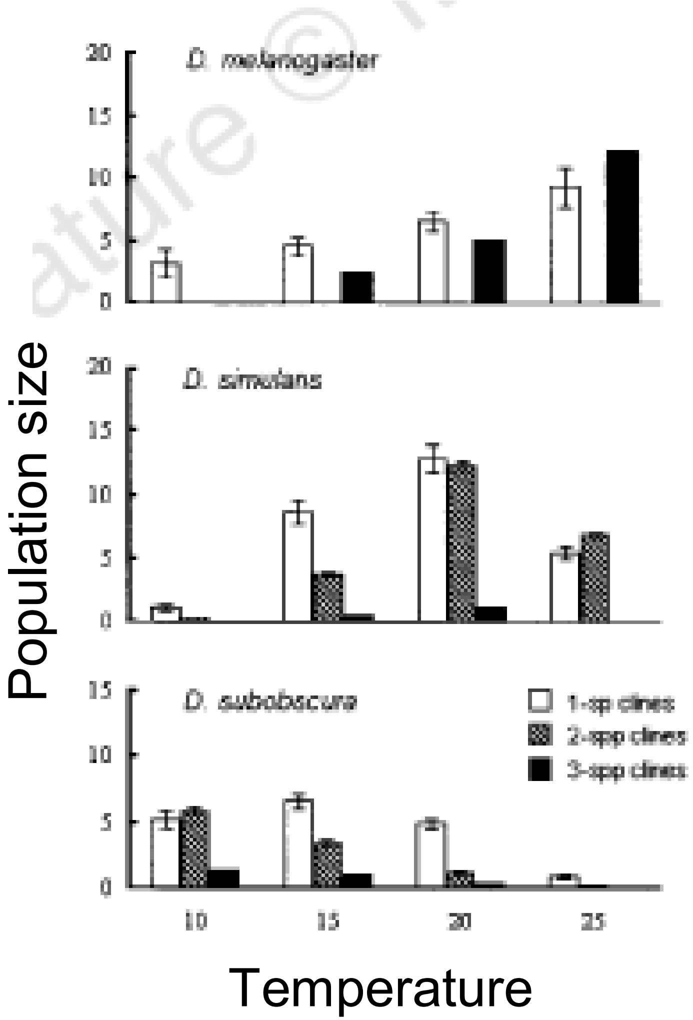


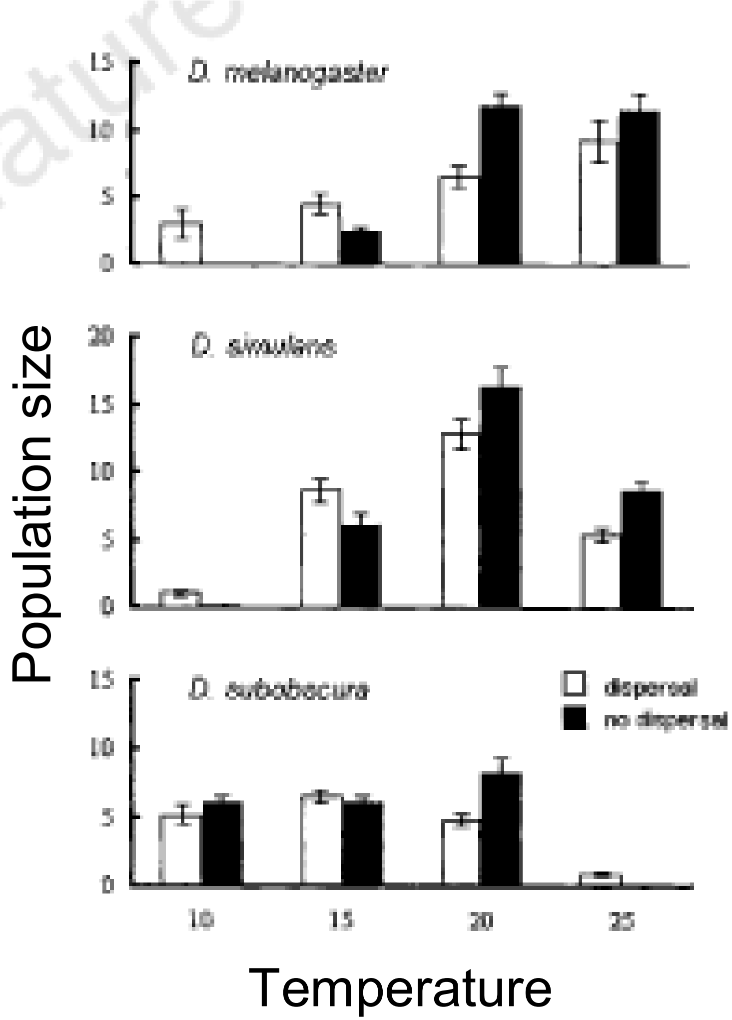
(Willis et al. 2009)





Pinus contorta
(Rehfeldt et al. 1999)





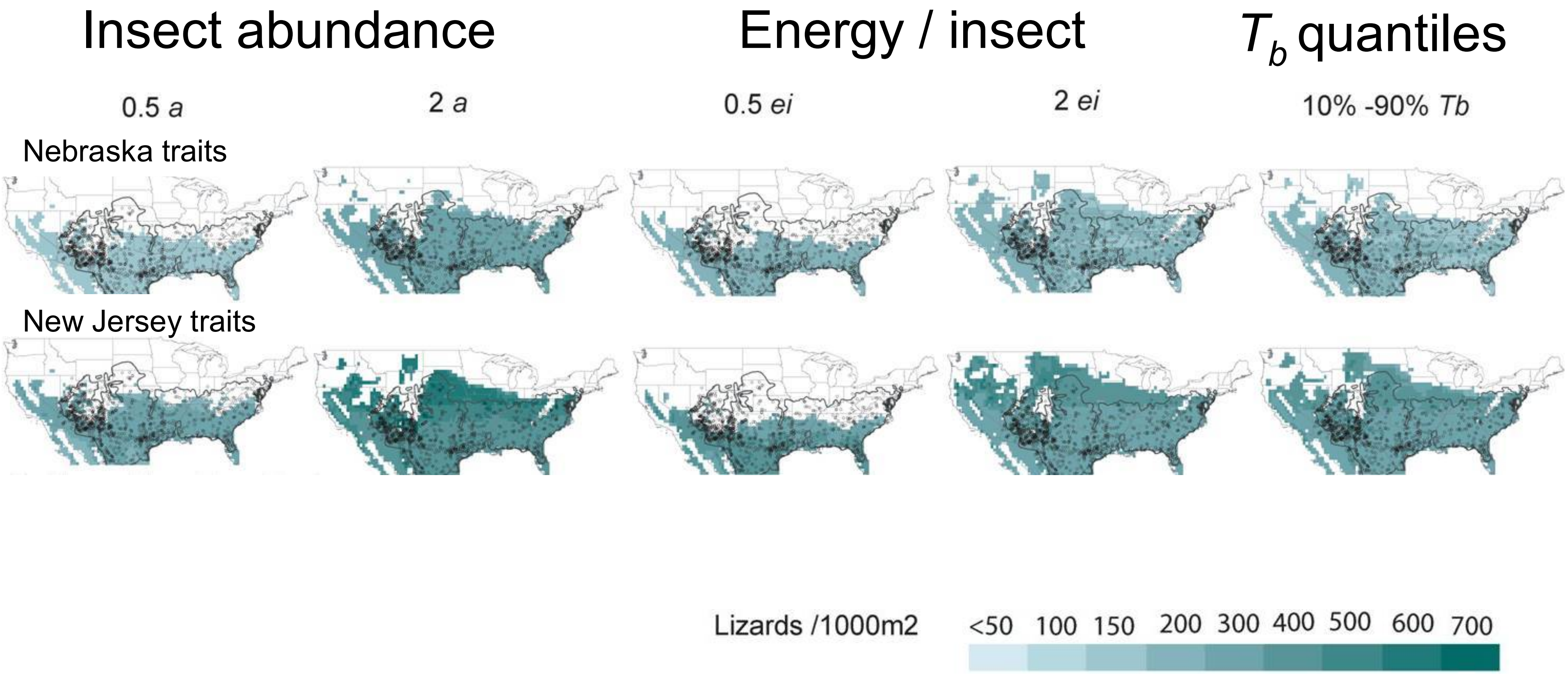
Species interactions

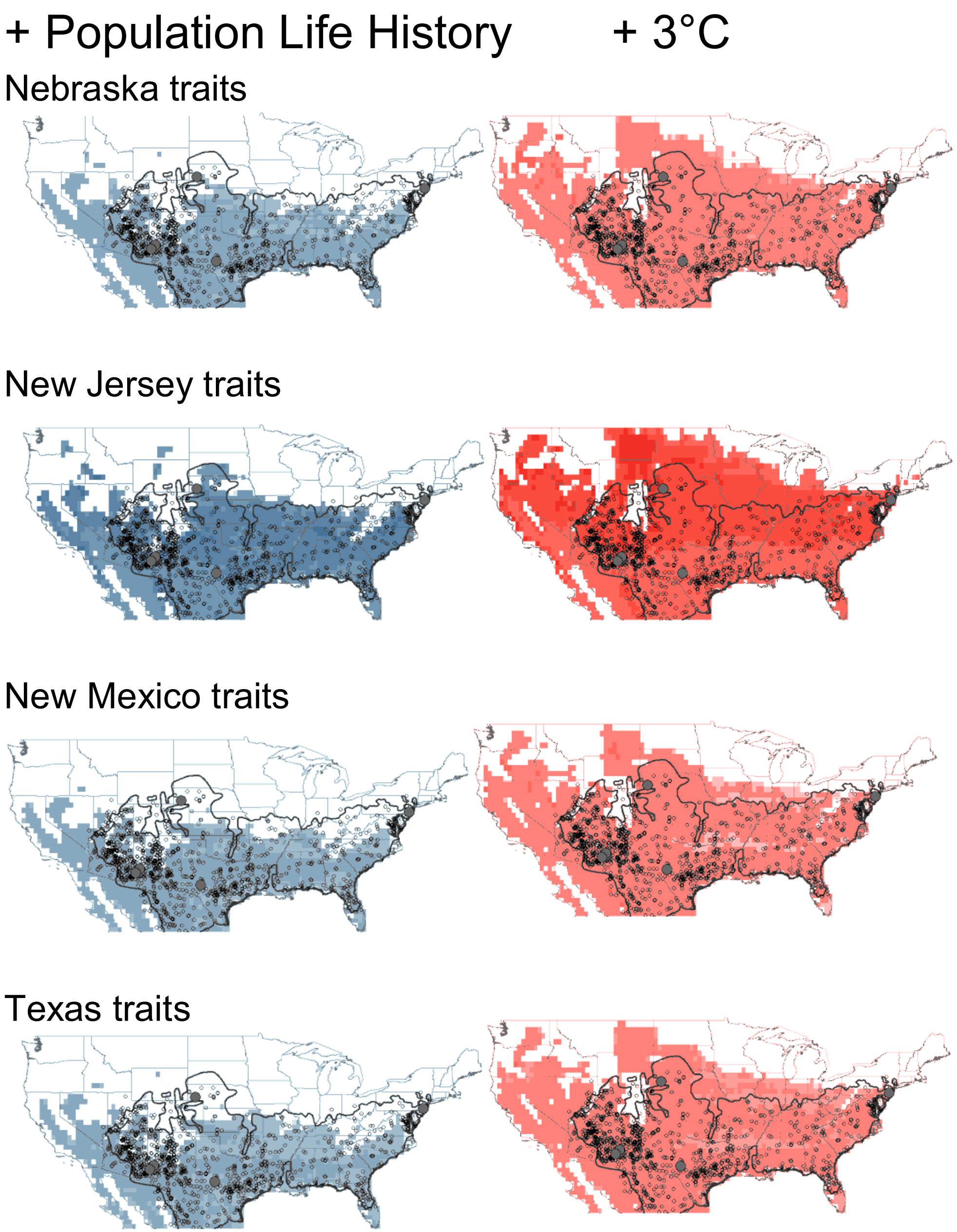
- 1-sp
- 2-sp
- 3-sp

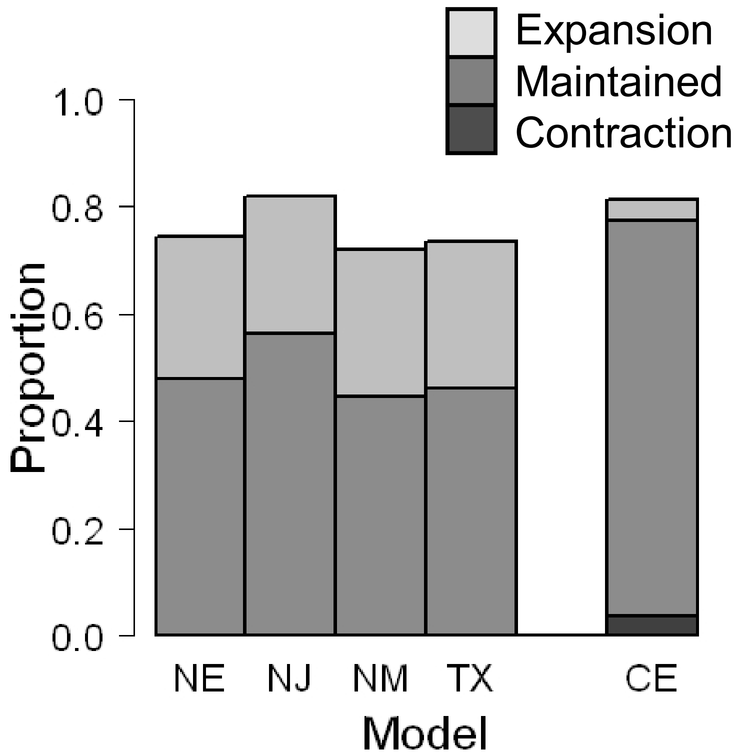
- Dispersal
- No dispersal

Drosophila
(Davis 1998)

Model sensitivity







Dynamic model better omission / commission performance

Species interactions?
Adaptive potential?