Exam Thursday

If you did not do as well as you hoped on Exam #1:

1. Make sure to work through the practice problems, lecture problems, problems from the first exam, and lab problems

2. Make an appointment to meet with me and come prepared with specific questions

What determines a specie's geographic range?

Geographic range of the
Crenulated grasshopper
***Cordillacris crenulata* (Bruner)**

Geographic range of the coastal redwood
(Sequoia sempervirens)

What determines a species geographic range?

<u>Hypotheses Acting Over Ecological Time Scales</u>

1. Dispersal limitation

2. Tolerance to environmental variables

<u>Hypotheses Acting Over Evolutionary Time Scales</u>

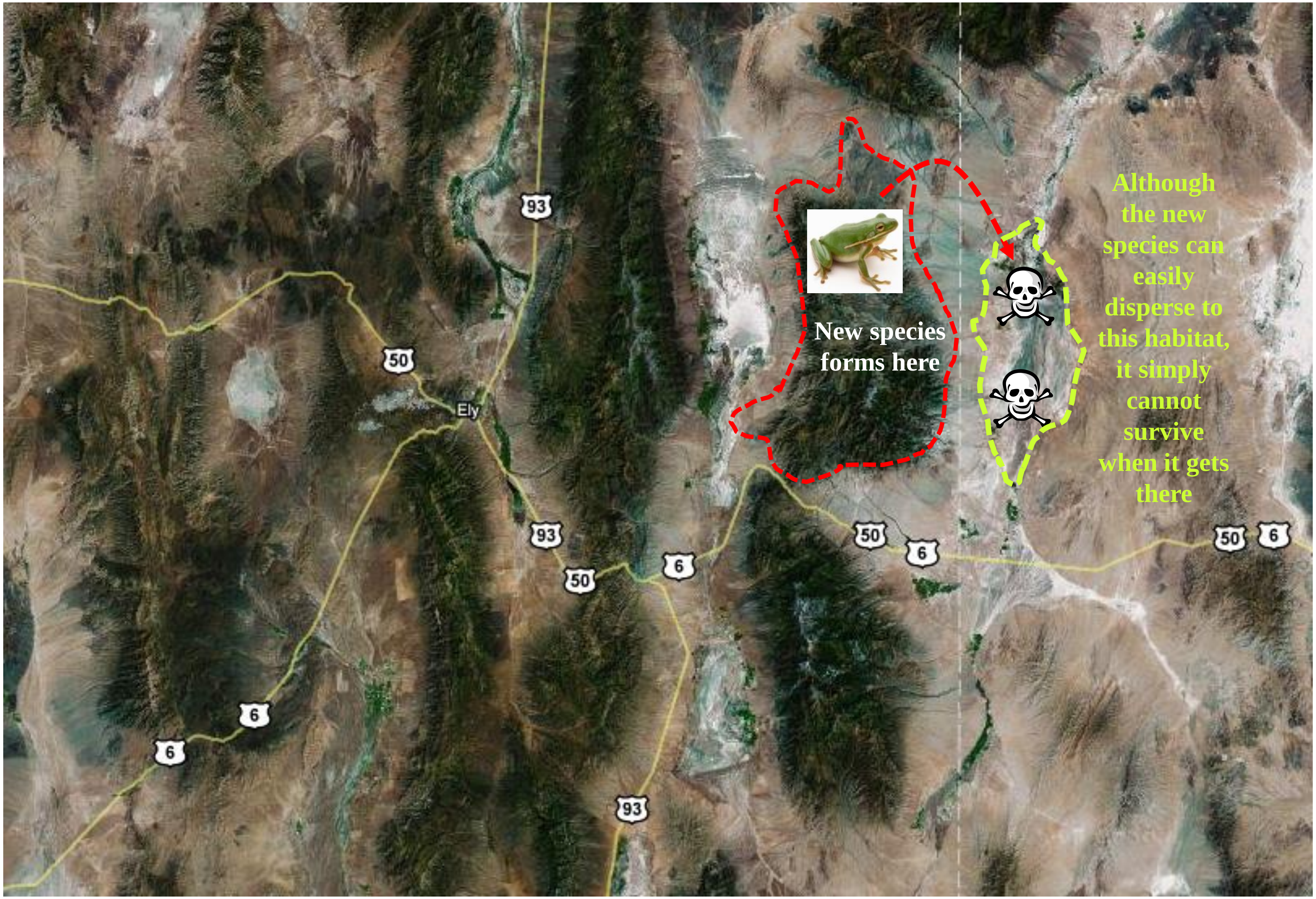
1. Availability of genetic variation

2. Degree to which gene flow swamps adaptation

3. Speciation

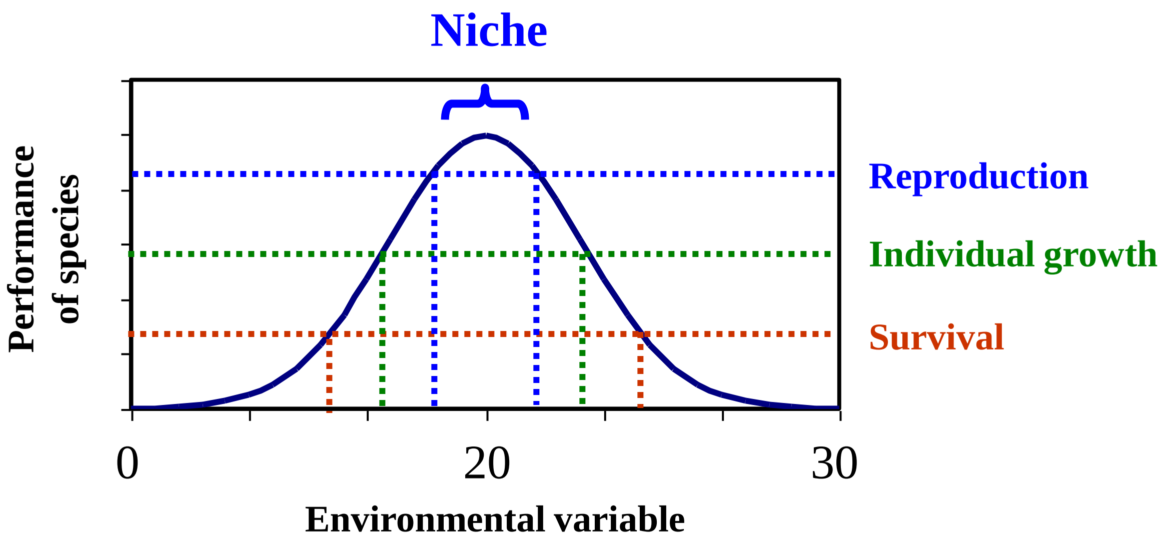
Hypothesis 1: Dispersal limitation

Hypothesis 2: Tolerance to environmental variables

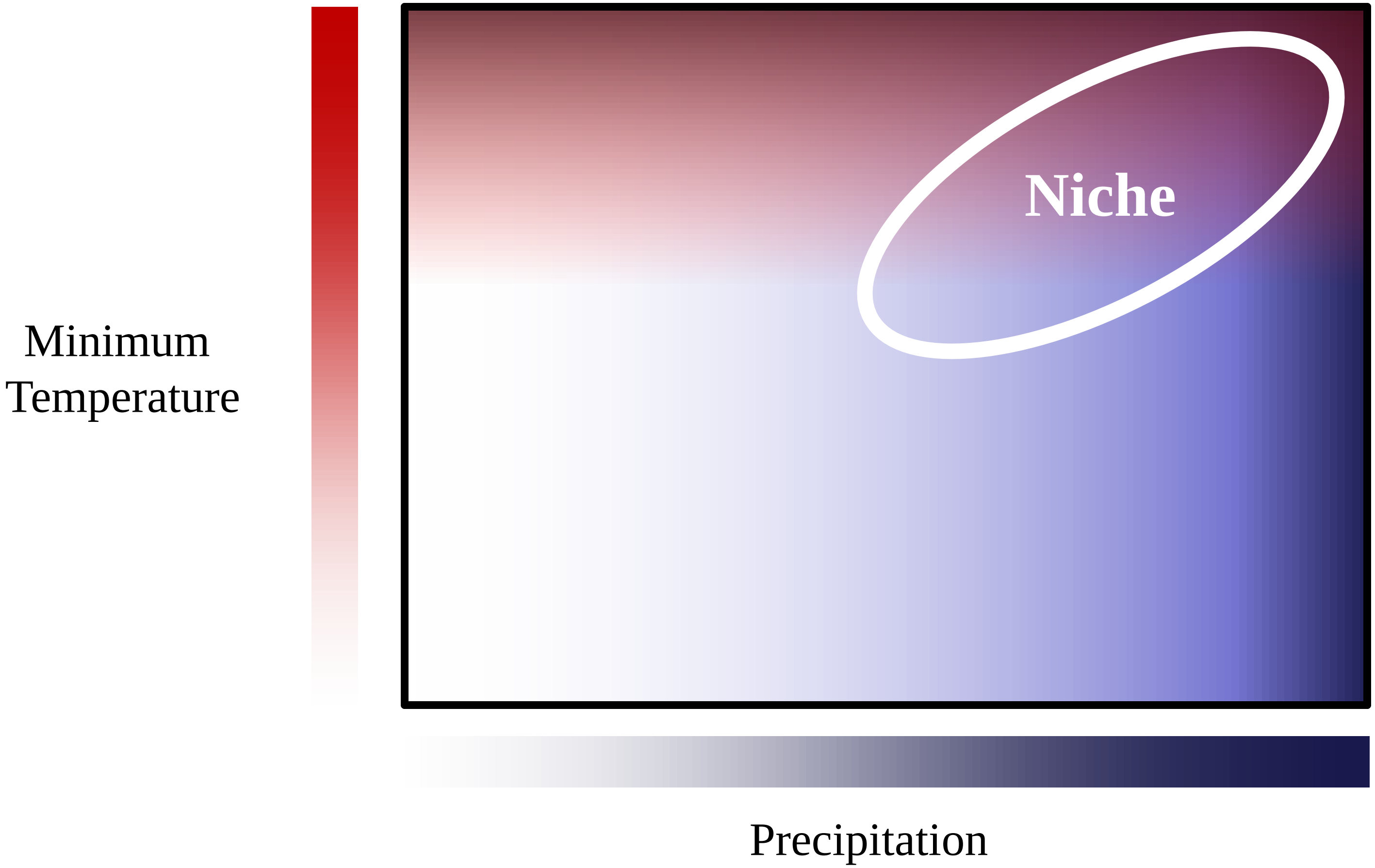


The second hypothesis has been formalized by the concept of the ‘Ecological Niche’

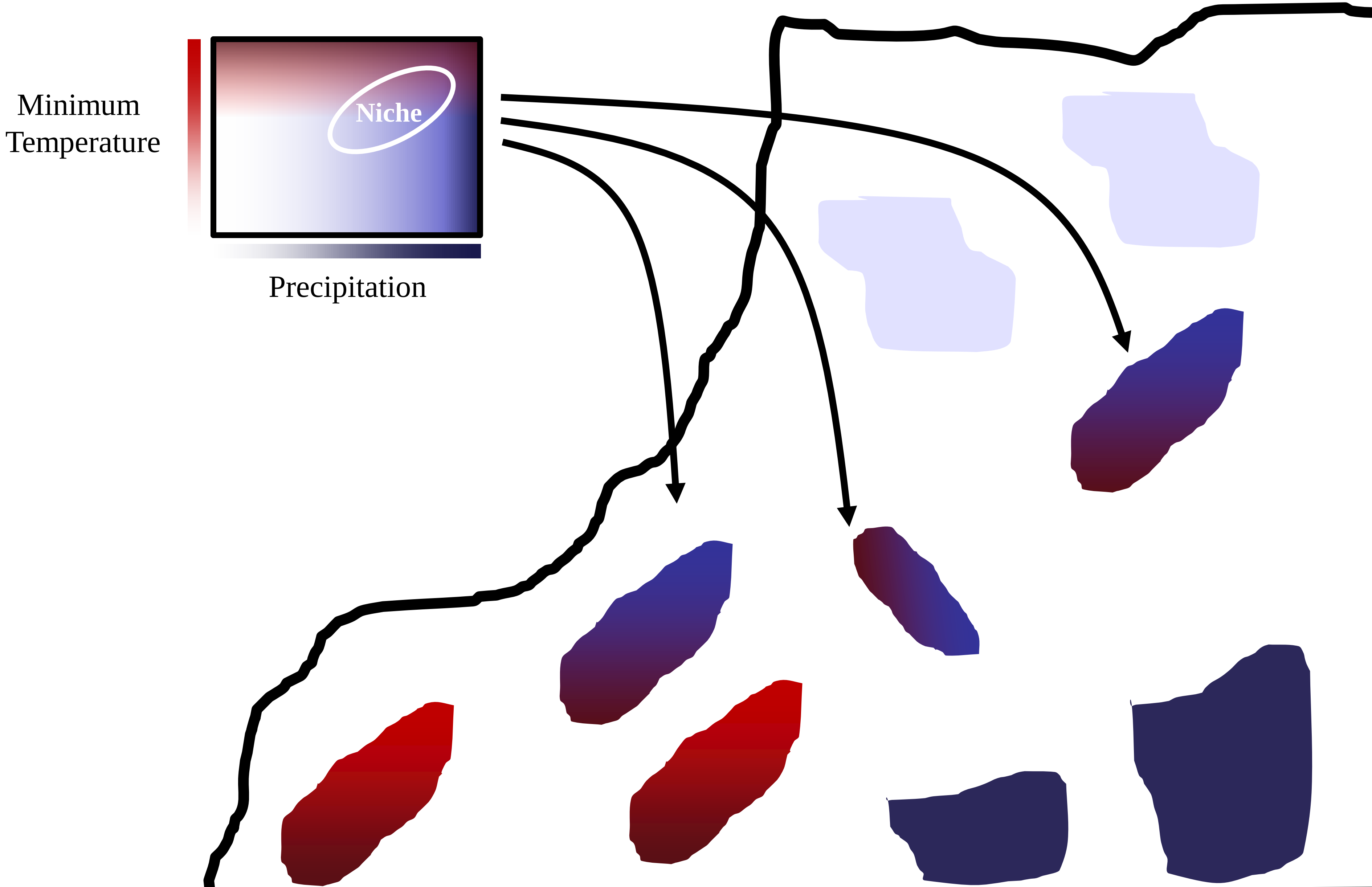
Niche – The total range of conditions and resources under which the individual or population lives and replaces itself. (Hutchinson, 1957)



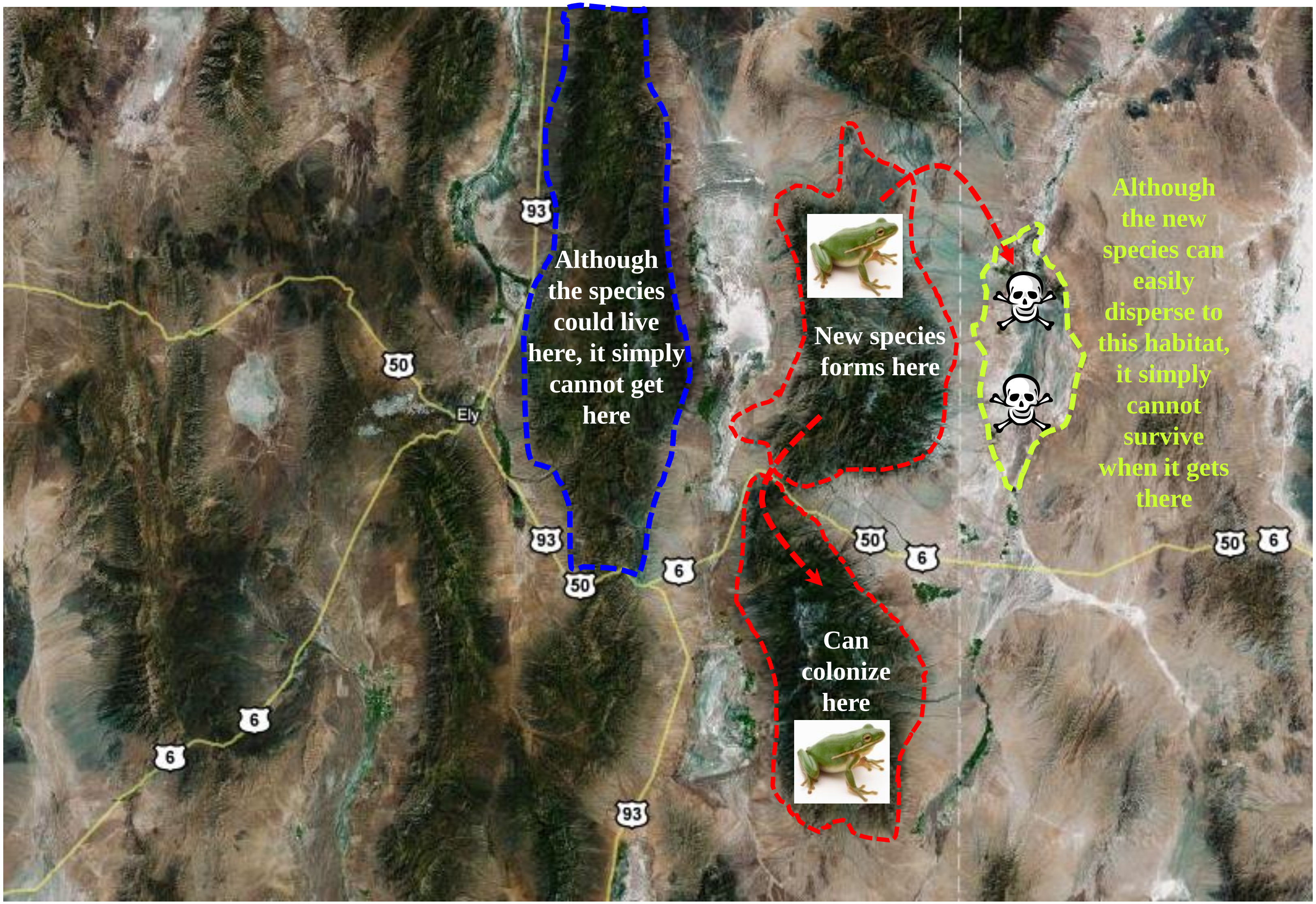
Real niches are multi-dimensional



The species' niche defines a set of suitable habitats



Summarizing the two ecological hypotheses

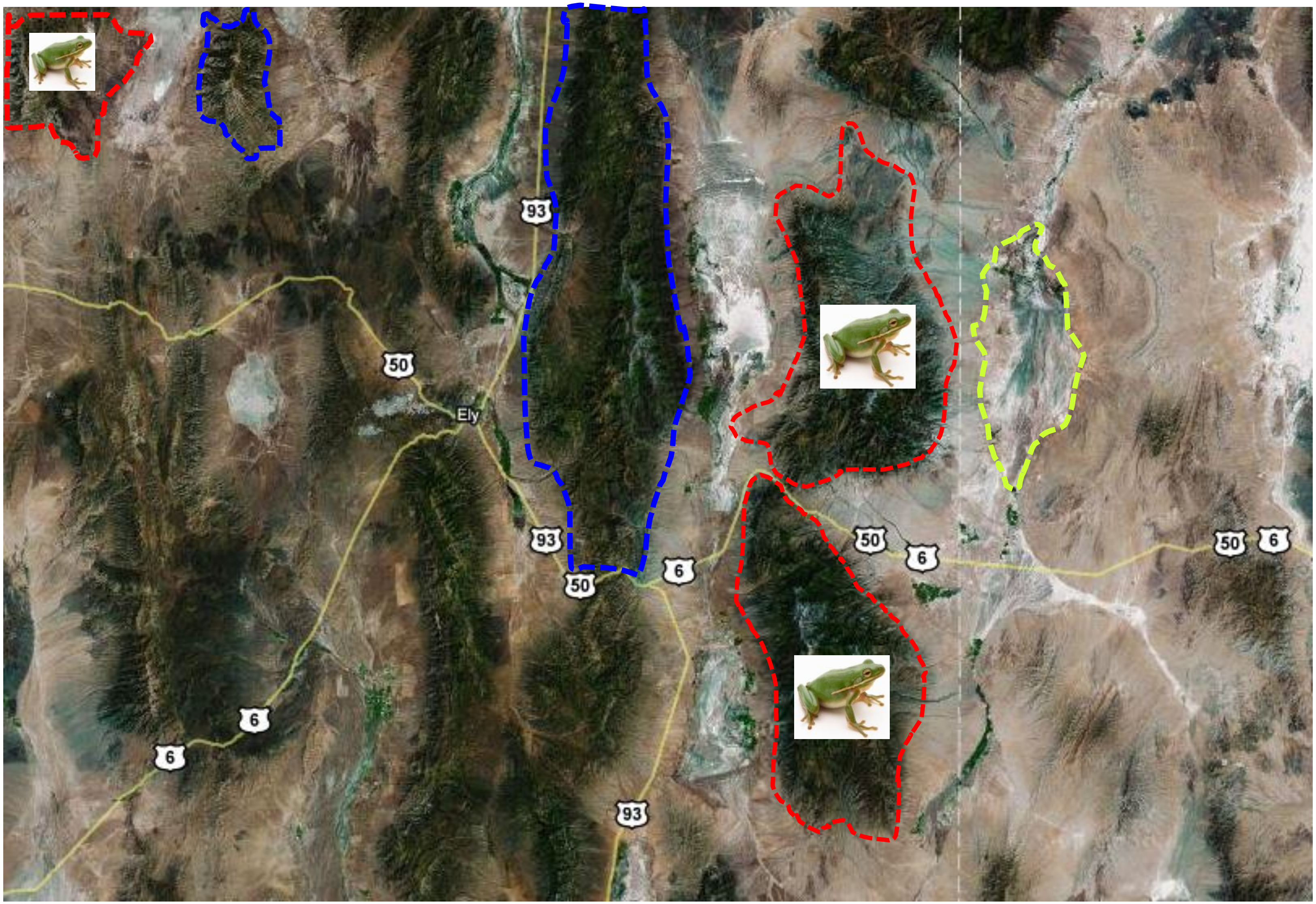


How can we distinguish between them?

Possibility 1: Experimental manipulation

Possibility 2: Statistical estimation

Experimental manipulation

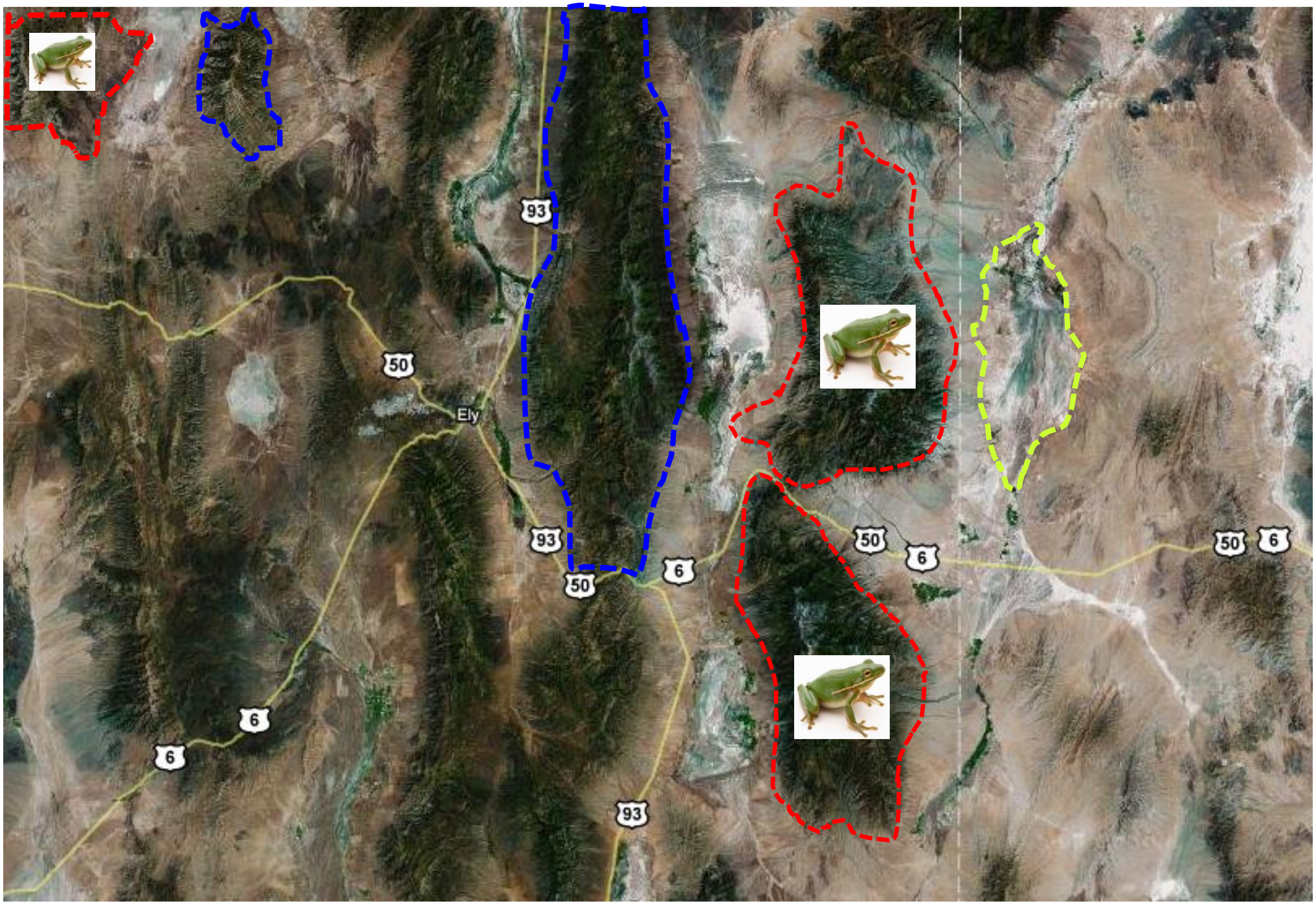


Experimental manipulation

- What experiments would you conduct?

- How would you interpret the possible outcomes?

Statistical estimation



Statistical estimation

Frog Present?	Precipitation	Minimum Temp.
0	5mm	2C
0	6mm	3C
0	4mm	1C
0	5mm	2C
0	4mm	3C
0	7mm	4C
1	11mm	10C
1	12mm	8C
1	11mm	7C
1	13mm	9C
1	12mm	8C
1	10mm	8C

How could you use this data to gain insight into the frog's niche?

Using the t-test to identify the niche

Frog Present?	Precipitation	Minimum Temp.
0	5mm	2C
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0	4mm	1C
0	5mm	2C
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1	12mm	8C
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1	12mm	8C
1	10mm	8C

Let's first focus on precipitation

$\bar{Y}_0 = 5.17mm$

$\bar{Y}_1 = 11.50\ mm$

$s_0^2 = 1.37\ mm^2$

$s_1^2 = 1.10\ mm^2$

$$t = \frac{\bar{Y}_0 - \bar{Y}_1}{\sqrt{\left(\frac{(n_0-1)s_0^2 + (n_1-1)s_1^2}{n_0+n_1-2}\right)\left(\frac{n_0+n_1}{n_0 n_1}\right)}}$$

$$t = \frac{5.17 - 11.50}{\sqrt{\left(\frac{(6-1)*1.37+(6-1)*1.10}{6+6-2}\right)\left(\frac{6+6}{6*6}\right)}} = -9.88$$

Because the value of our test statistic, t, is greater in magnitude than the critical value, $t_{0.025,10}$ =2.228, areas where the frog lives are significantly wetter than areas where the frog does not live. Thus, we tentatively conclude that precipitation is an important part of the frog's niche

Limitations of this simple statistical approach

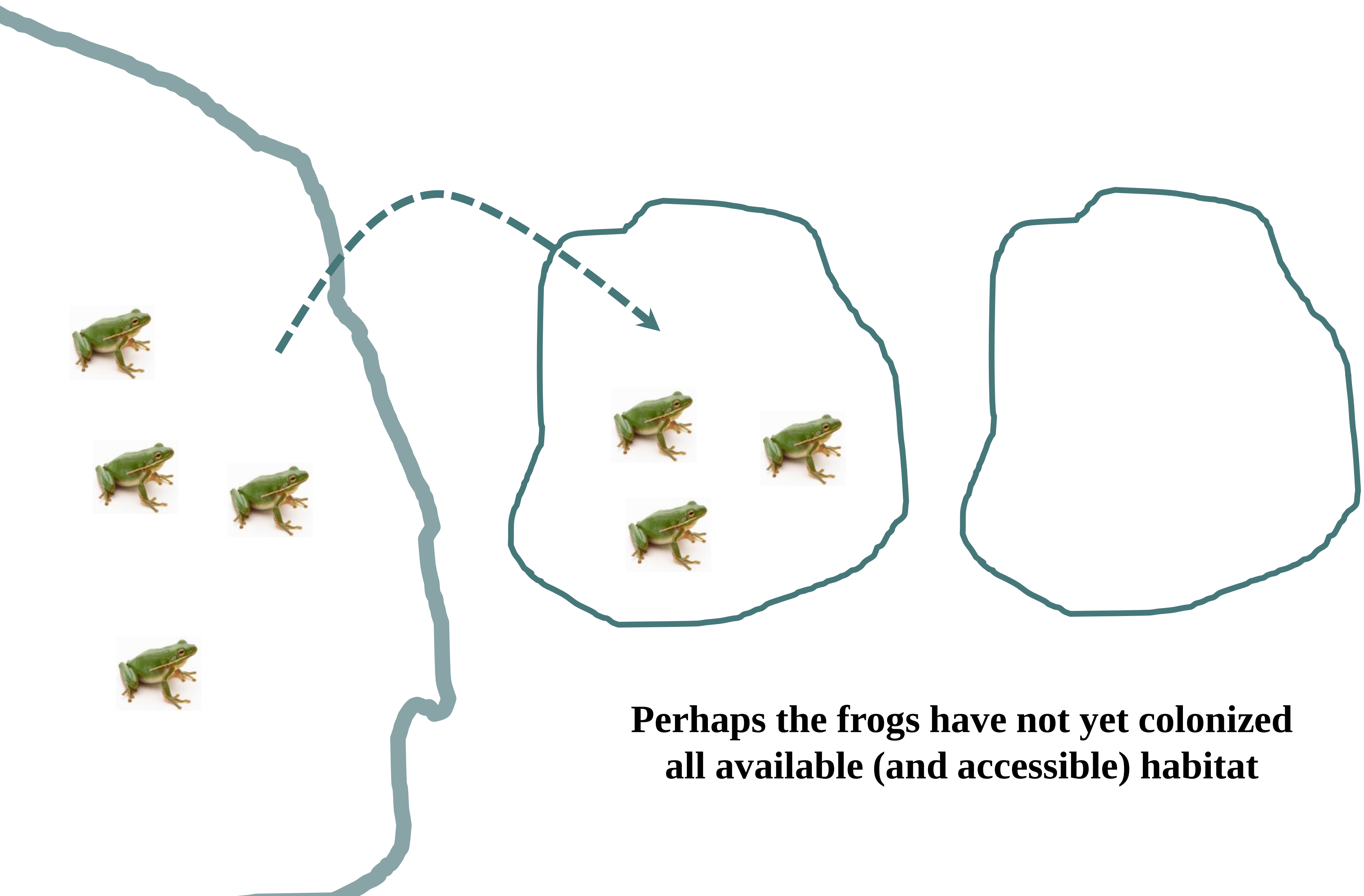
- **Does not produce a predictive model**

- **Sensitive to correlations among environmental variables**

➔ We can improve our ability to predict and understand the niche by using more sophisticated statistical approaches

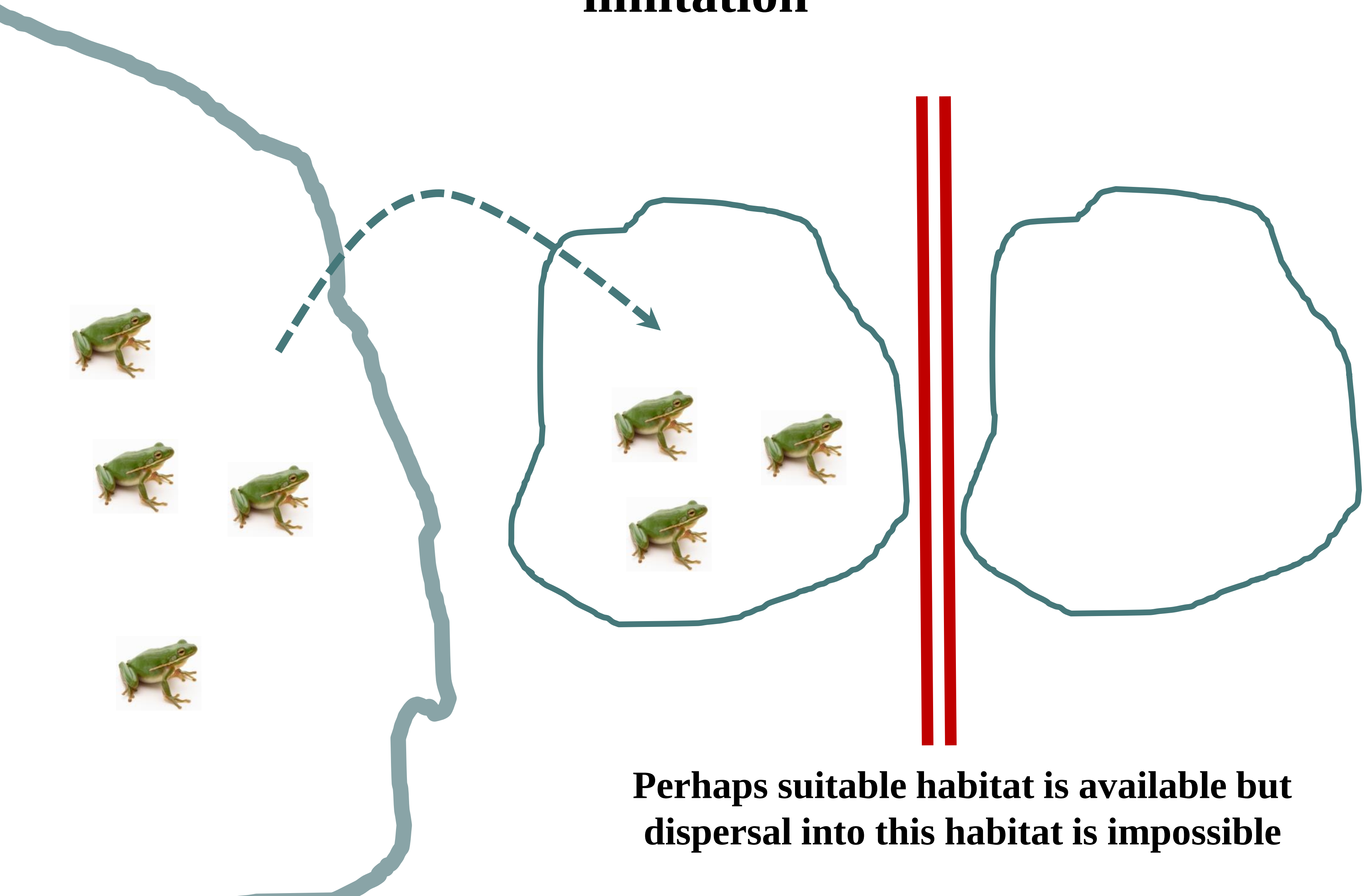
Even more sophisticated statistical approaches can be misled in three ways

Problem #1 for the statistical approach: Non-equilibrium



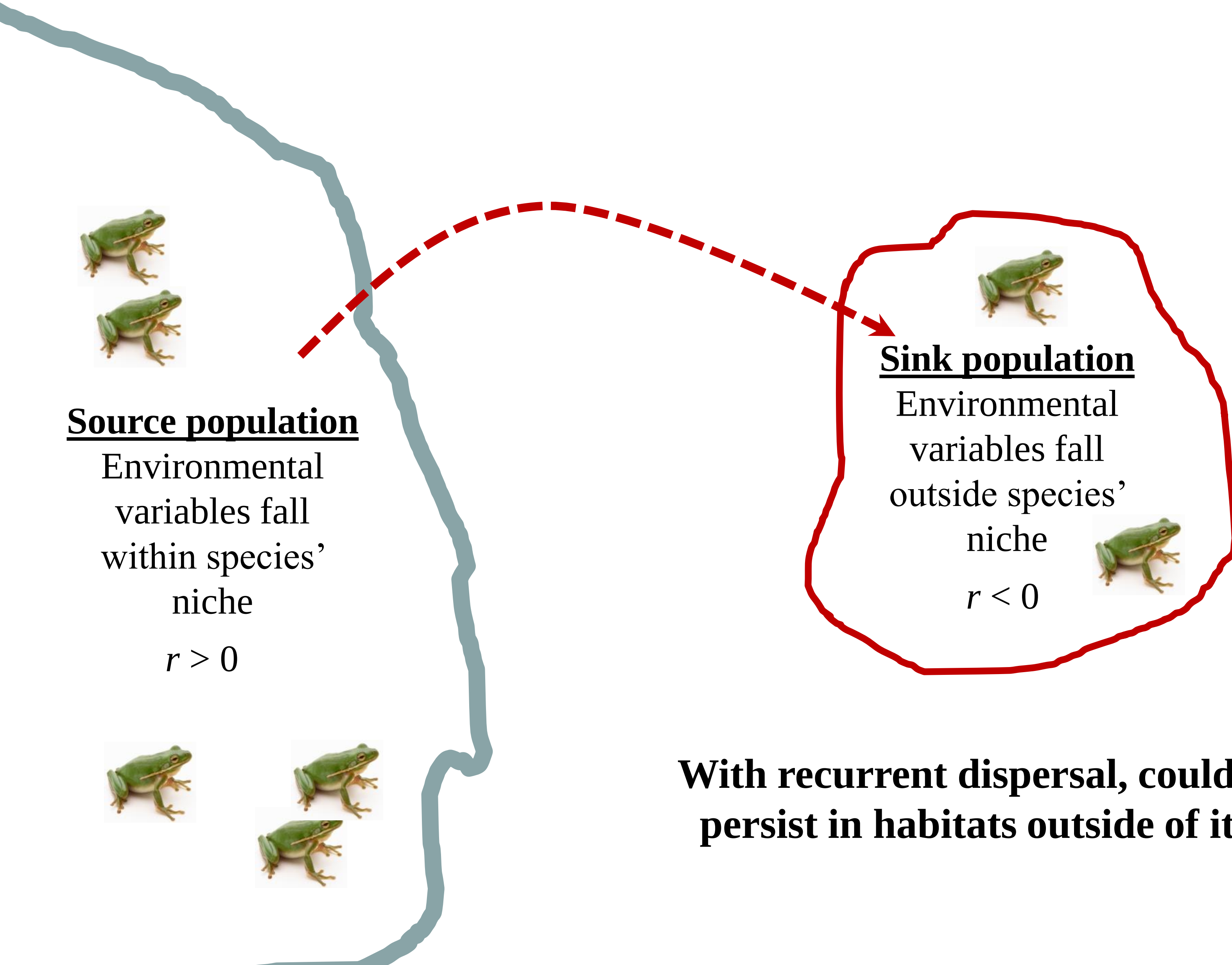
Perhaps the frogs have not yet colonized all available (and accessible) habitat

Problem #2 for the statistical approach: Dispersal limitation



Perhaps suitable habitat is available but dispersal into this habitat is impossible

Problem #3 for the statistical approach: Population sinks



With recurrent dispersal, could a species persist in habitats outside of its niche?

A model of sources and sinks

The question: Could a population persist outside of its niche?

Source (r > 0)

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K}\right) - mN_1$$

Sink (r < 0)

$$\frac{dN_2}{dt} = r_2 N_2 + mN_1$$

We can ignore density dependence in the sink, because population size should remain small

What is the population size in the sink at equilibrium?

What determines how abundant a species is in a sink?

A model of sources and sinks

The question: Could a population persist outside of its niche?

The equilibrium is: $\hat{N}_1 = \frac{(r_1 - m)}{r_1} K \qquad \hat{N}_2 = \frac{mK(m - r_1)}{r_1 r_2}$

$\hat{N}_2$ Will be positive, and thus a sink population maintained, any time:

$m < r_1$

This makes sense, because only when this condition holds does the source population grow rapidly enough to replace the individuals emigrating to the sink.

Summary of species ranges over ecological time scales

<u>A species may be present in a particular geographic region because:</u>

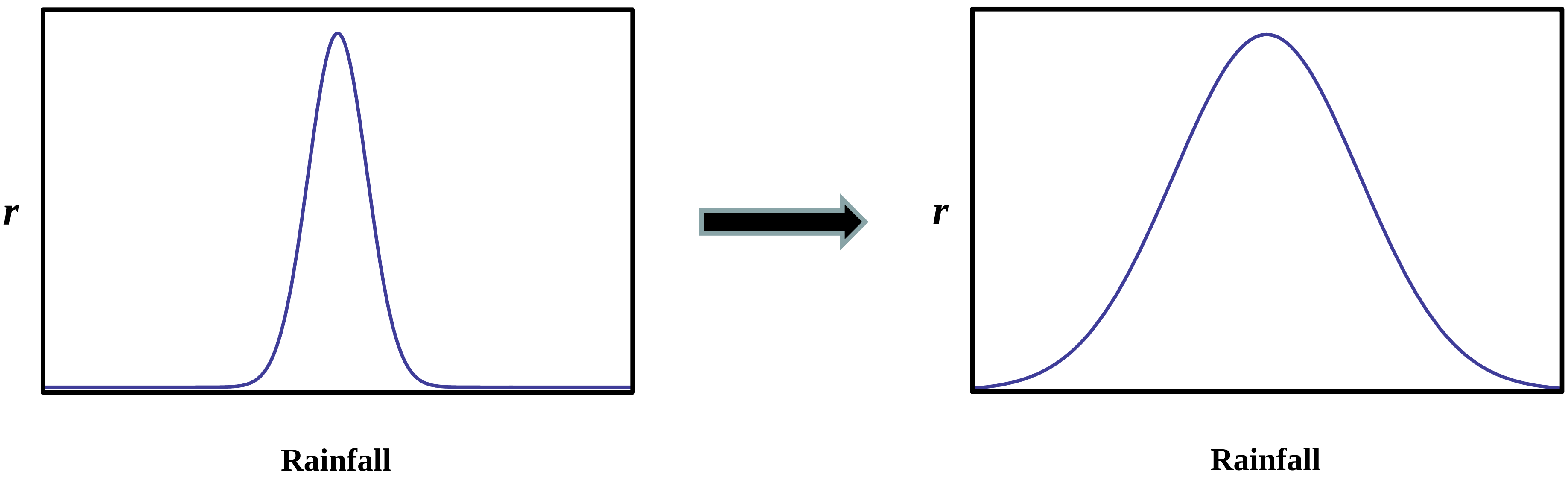
1. The geographic region is part of the species niche
2. The geographic region is outside of the species niche but recurrent immigration occurs from a region within the species niche
3. Non-equilibrium. The population is going extinct but has not yet done so

<u>A species may be absent from a particular geographic region because:</u>

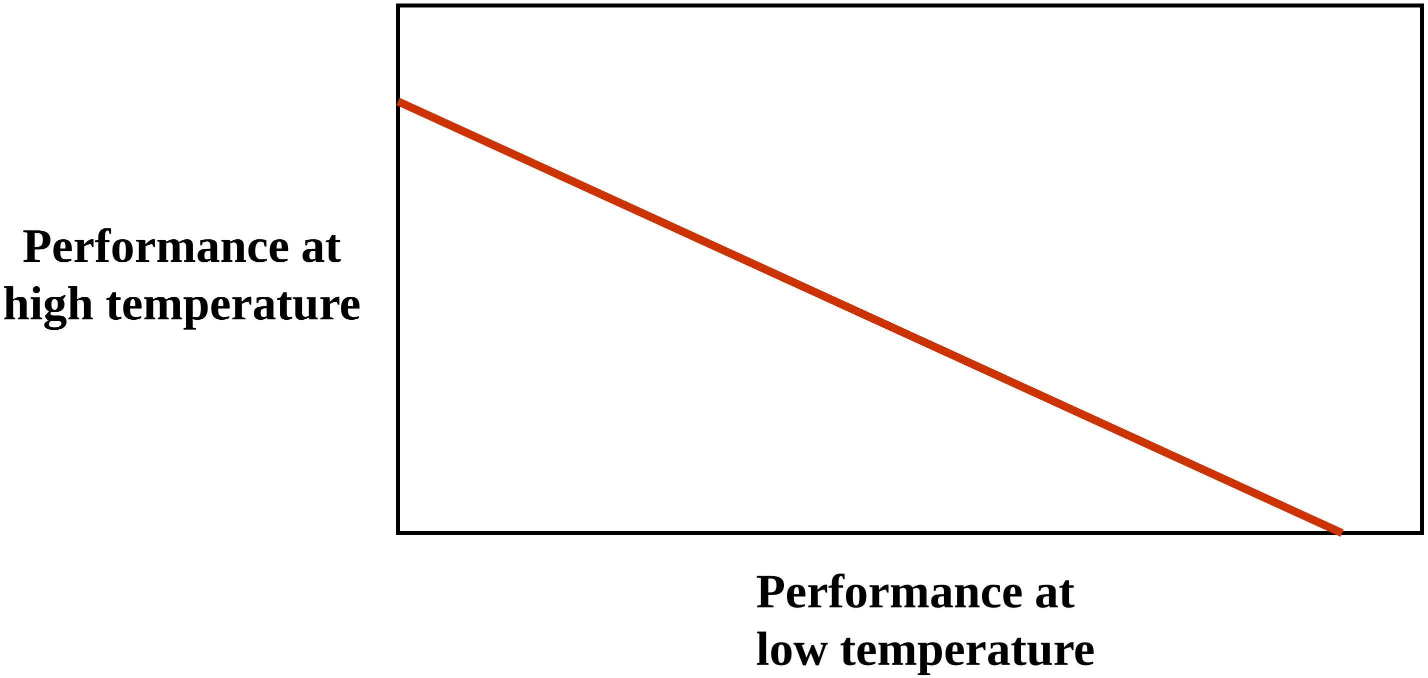
1. The geographic region is outside of the species niche
2. The geographic region is inside of the species niche but is beyond the dispersal distance of the species
3. Non-equilibrium. Some suitable habitat has not yet been colonized, but it will be given sufficient time.

The evolution of species' geographic ranges

Why don't species evolve to live everywhere? Or, put differently, why don't species evolve an infinitely wide niche?



Trade-offs are ubiquitous



Trade-offs: an extreme example

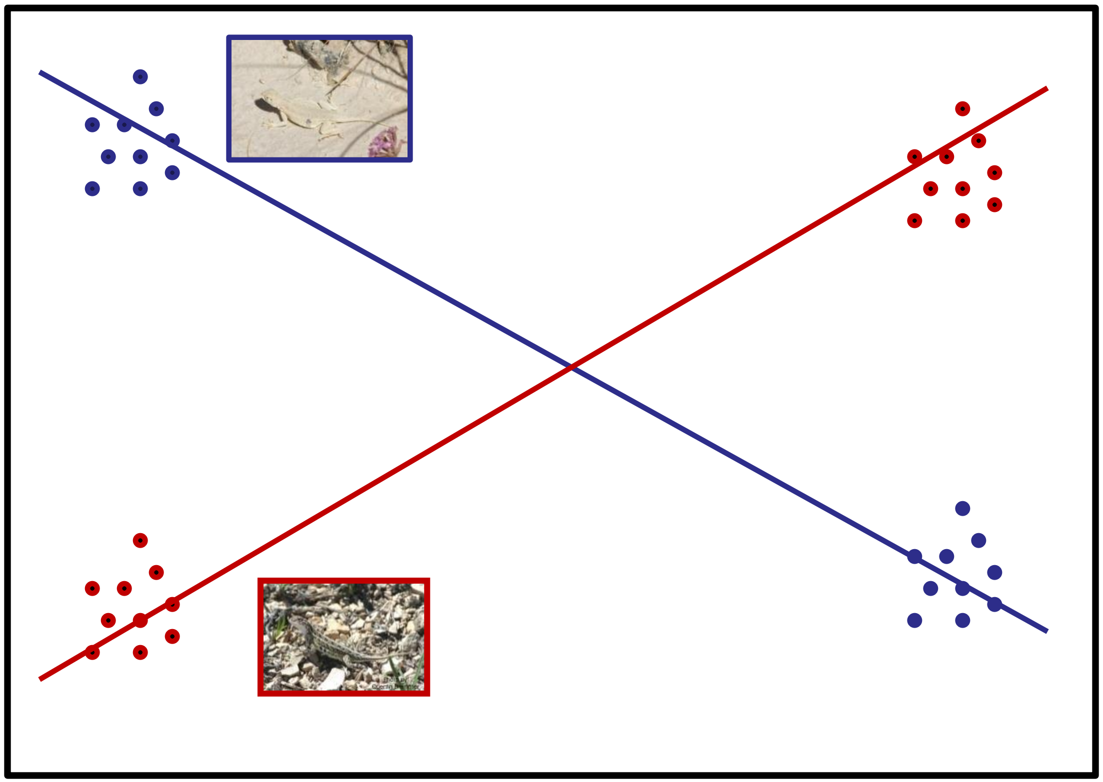
White Sands National Monument

Pinyon juniper woodlands

Holbrookia maculata ruthveni
Bleached Earless Lizard

Holbrookia maculata
Common Lesser Earless Lizard

Trade-offs: an extreme example



Lizard Performance

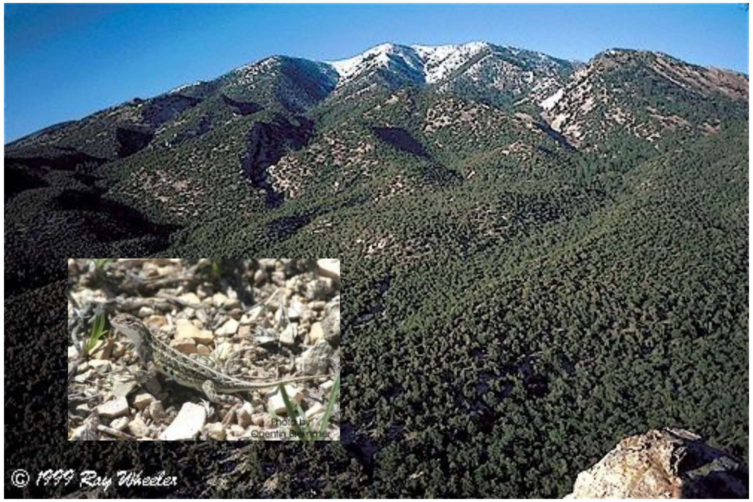
White Sands National Monument

Pinyon-Juniper woodland

It is simply not possible to perform well in both habitats

The evolution of species' geographic ranges

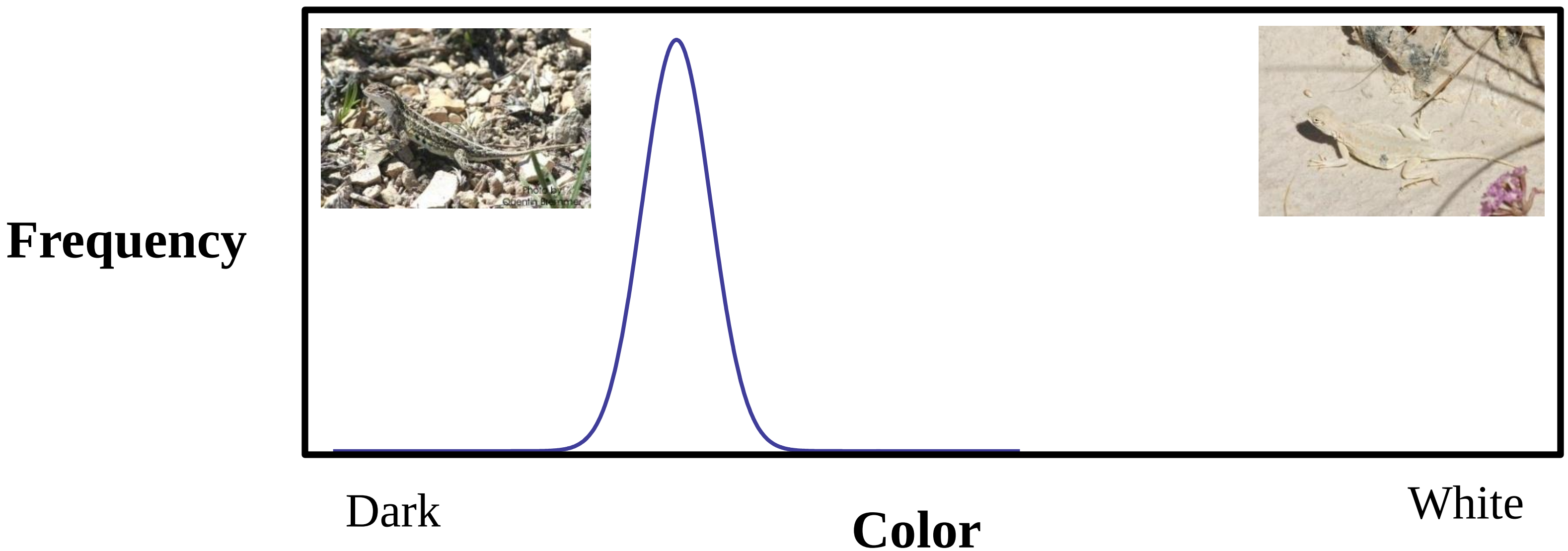
Even if trade-offs exist, why don't species simply adapt to local environmental conditions and thus increase their geographic range?



Dark populations on dark habitats

White populations on white habitats

Why can range not always expand through adaptation?
Reason 1: Lack of genetic variation



Why can range not always expand through adaptation?
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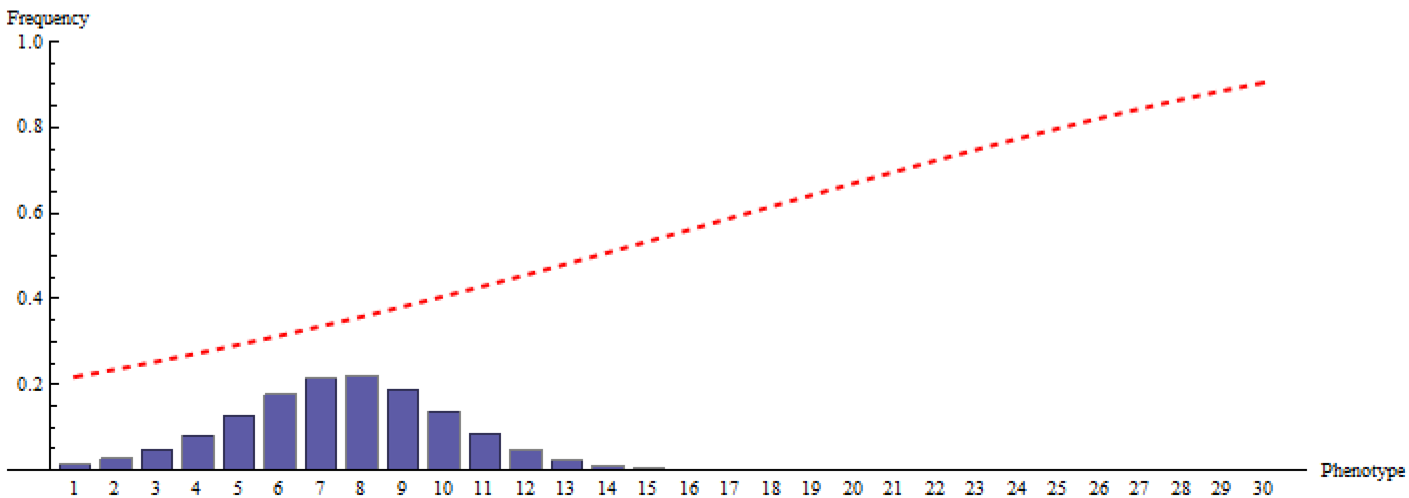


Why can range not always expand through adaptation?
Reason 1: Lack of genetic variation

Increasing thermal stress

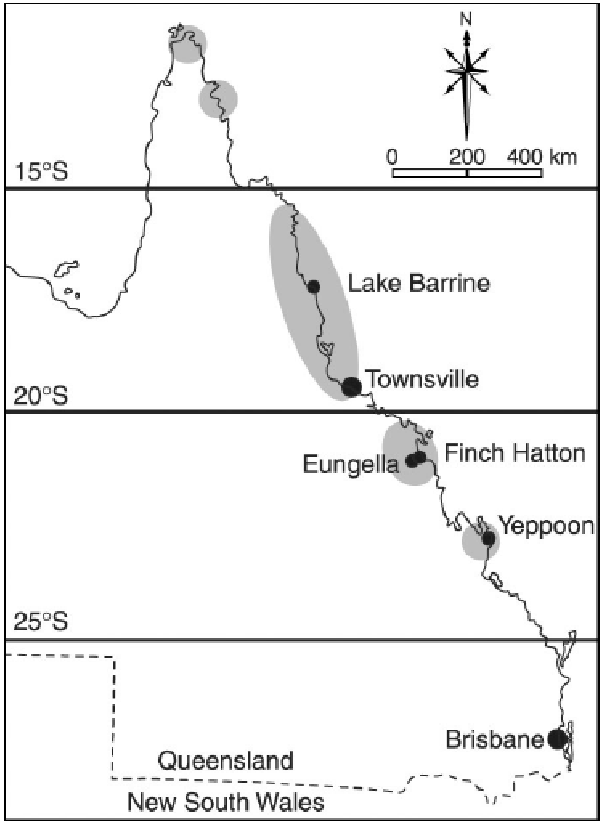


Fig. 1. Regions of northeastern Australia where *D. birchii* are found (shaded areas). The locations of the four sites sampled repeatedly to test for laboratory adaptation (small circles) and two major cities (medium circles) are also indicated.

Drosophila birchii

Hoffman et al 2003. Science.

• Can *Drosophila birchii* expand its geographic range into regions of greater thermal stress?

• To this end, studied whether increased desiccation resistance could evolve in *Drosophila birchii*

Why can range not always expand through adaptation?
Reason 1: Lack of genetic variation

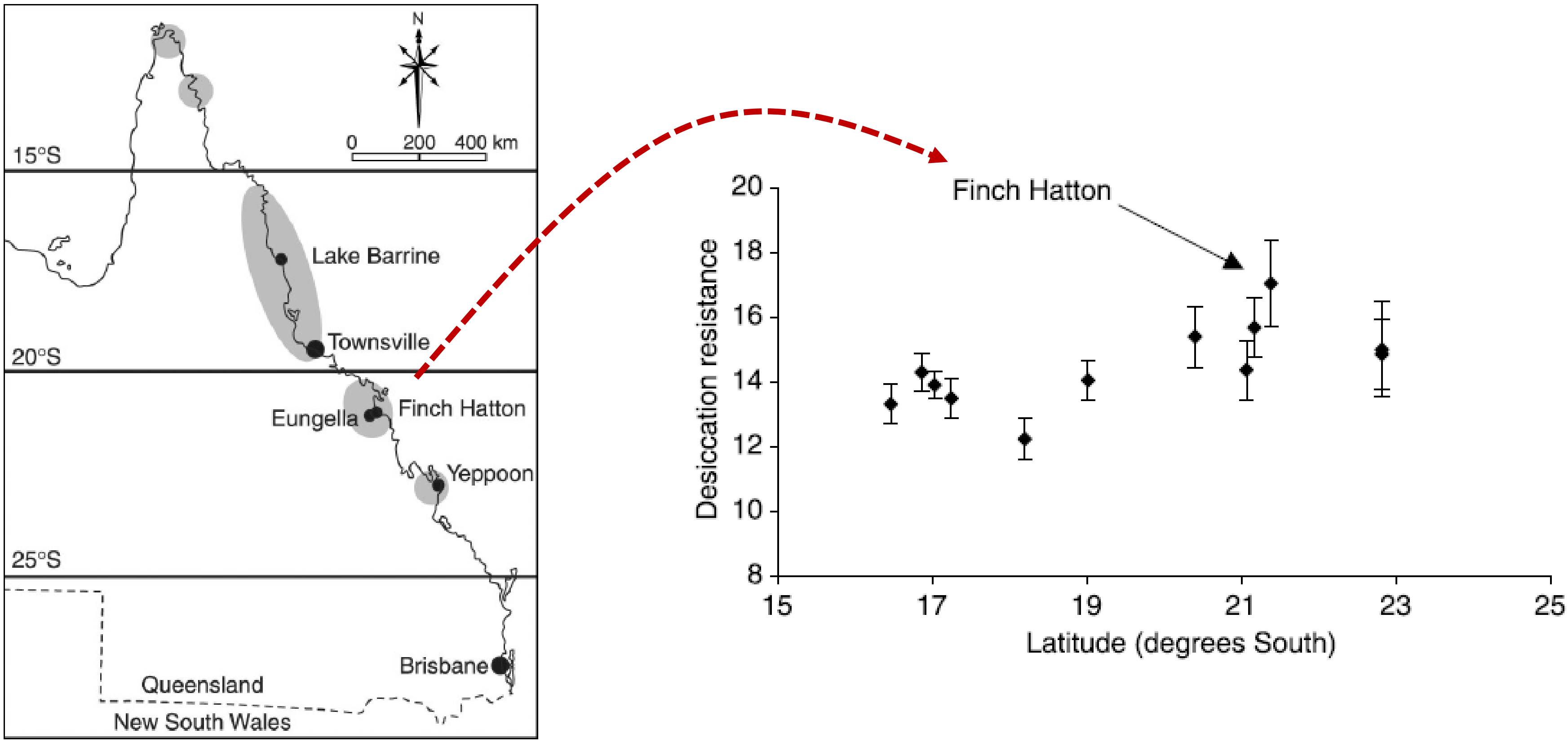
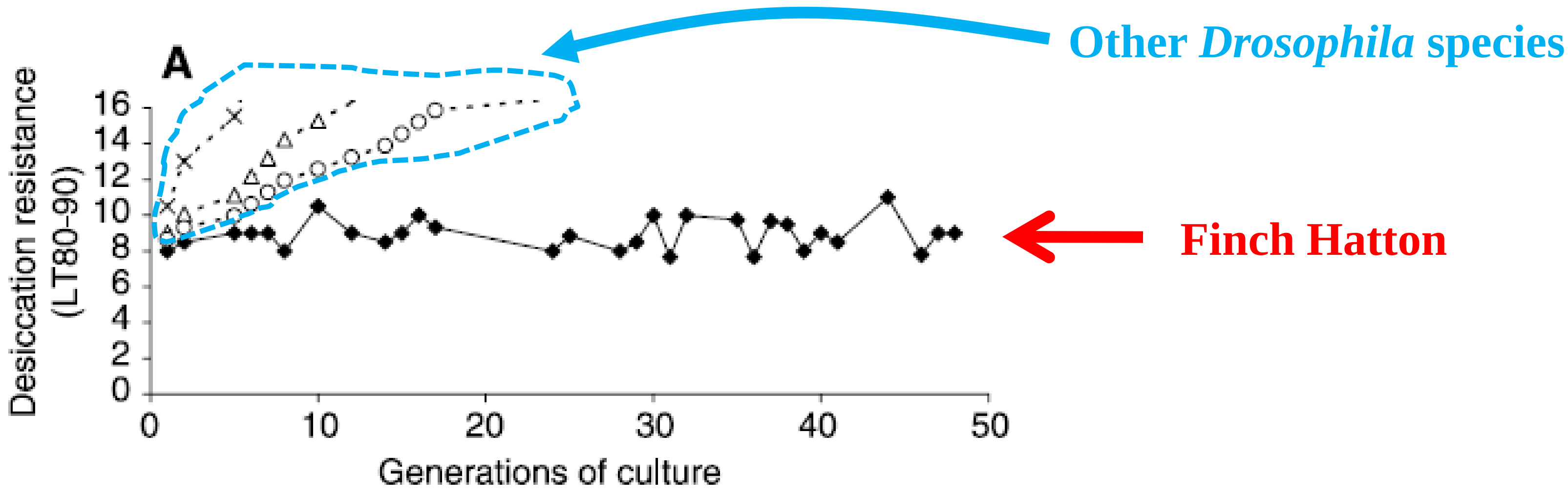


Fig. 1. Regions of northeastern Australia where *D. birchii* are found (shaded areas). The locations of the four sites sampled repeatedly to test for laboratory adaptation (small circles) and two major cities (medium circles) are also indicated.

Why can range not always expand through adaptation? Reason 1: Lack of genetic variation



• Selected for increased desiccation resistance in laboratory cultures derived from the most resistant population

• Found no response to selection over 50 generations!!!

Why can range not always expand through adaptation? Reason 1: Lack of genetic variation

Table 1. Parent-offspring comparisons for desiccation resistance and wing traits in *D. birchii* from the Finch Hatton population.

Parental comparison	Number of families	Regression coefficient	Probability	Narrow-sense heritability	Standard error of heritability
		Desiccation resistance			
Female	122	<0.001	0.992	0	0.090
Male	121	−0.058	0.453	0	0.154
Midparent	113	−0.037	0.64	0	0.095
		Wing size (centroid)			
Female	66	0.353	0.003	0.706	0.230
Male	66	0.193	0.054	0.386	0.108
		Wing aspect			
Female	66	0.411	<0.001	0.821	0.198
Male	66	0.340	<0.001	0.680	0.158

- Estimated heritability of desiccation resistance in most resistant (Finch Hatton) population
- Found NO additive genetic variance for desiccation resistance
- Together, these results suggest that the geographic range of *D. birchii* is limited by a lack of genetic variation

Why can range not always expand through adaptation?
Reason 2: Gene flow swamps adaptation

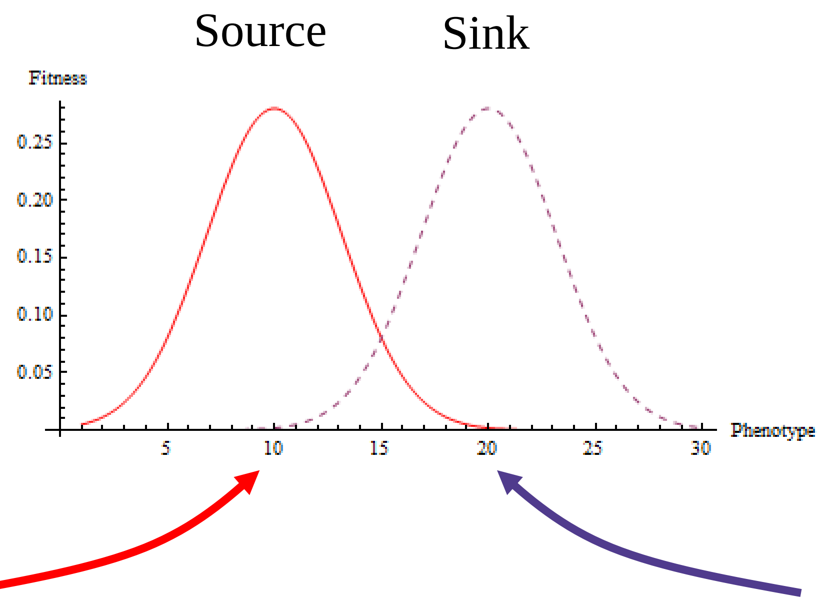
Source population

Sink population

Why can range not always expand through adaptation? Reason 2: Gene flow swamps adaptation

• Because the ancestral source population has a vastly greater population density, genes flow primarily from source to sink

• The consequence of this is that adaptation to the sink is swamped

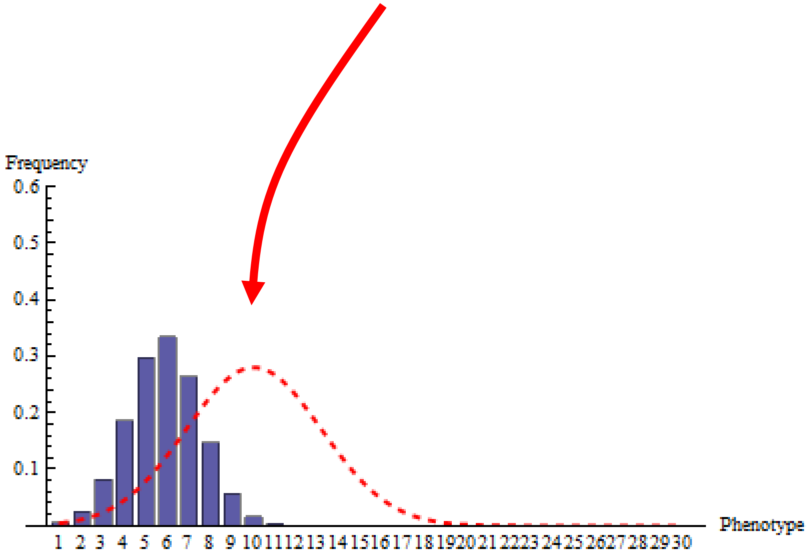


Optimum phenotype in source population

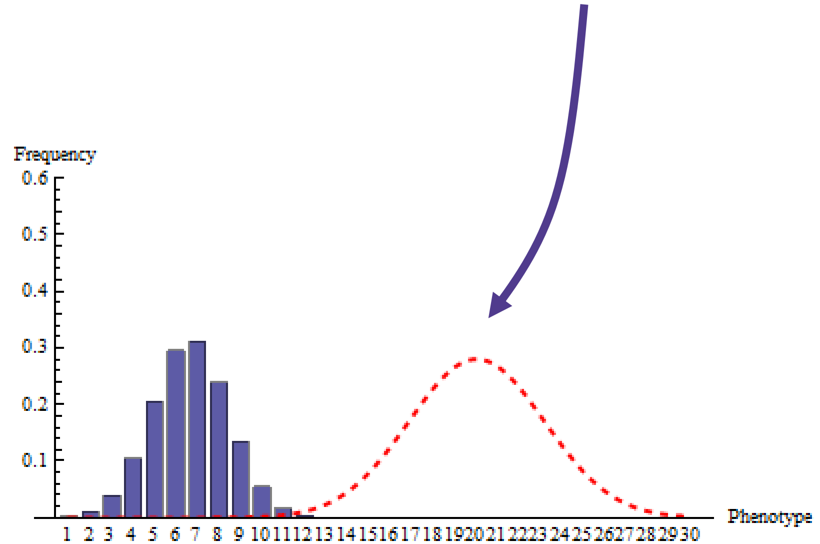
Optimum phenotype in sink population

Why can range not always expand through adaptation?
Reason 2: Gene flow swamps adaptation

Optimum phenotype in source population



Optimum phenotype in sink population



Why can range not always expand through adaptation? Reason 3: Speciation

Even if a species has sufficient genetic variation and local adaptation is not swamped by gene flow, adapting to new habitats/niches may lead to the formation of a new species rather than a broader niche!

Current Habitat

- Hot climate
- Favors early flowering

Novel Habitat

- Cool climate
- Favors late flowering

Why can range not always expand through adaptation?
Reason 3: Speciation

Sweet Vernal Grass
Anthoxanthum odoratum

J. Antanovics

Studied populations of *A. odoratum* growing on tailings of the Trelogan Mine, UK and adjacent populations not on tailings

Why can range not always expand through adaptation? Reason 3: Speciation

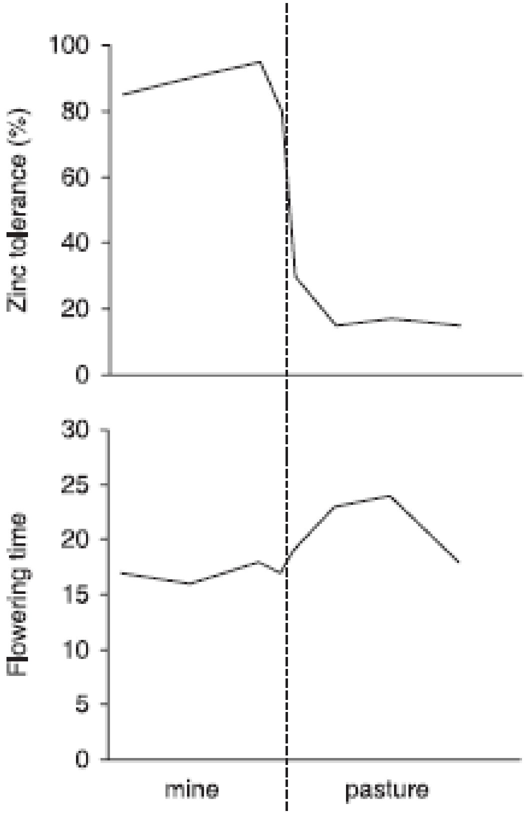


Fig. 1. *Anthoxanthum odoratum* shows higher zinc tolerance (top panel) and earlier flowering (bottom panel) on the tailings of a zinc mine than on the adjacent pasture (adapted from fig. 1 in Antonovics & Bradshaw 1970). These data are based on eight samples along a 100 m transect (x-axis) perpendicular to the transition between the mine and pasture. Flowering time represents stigma emergence in days after 9 June 1966.

- Plants on mine tailings flower significantly earlier
- This difference in flowering time results in a 43% reduction inter-population mating
- Suggests that adaptation and range expansion is causing speciation

Summary of geographic ranges

- Over ecological time scales, species ranges are determined by dispersal and the niche

- Over evolutionary time scales, species ranges evolve in response to trade-offs, genetic variation, gene flow, and speciation