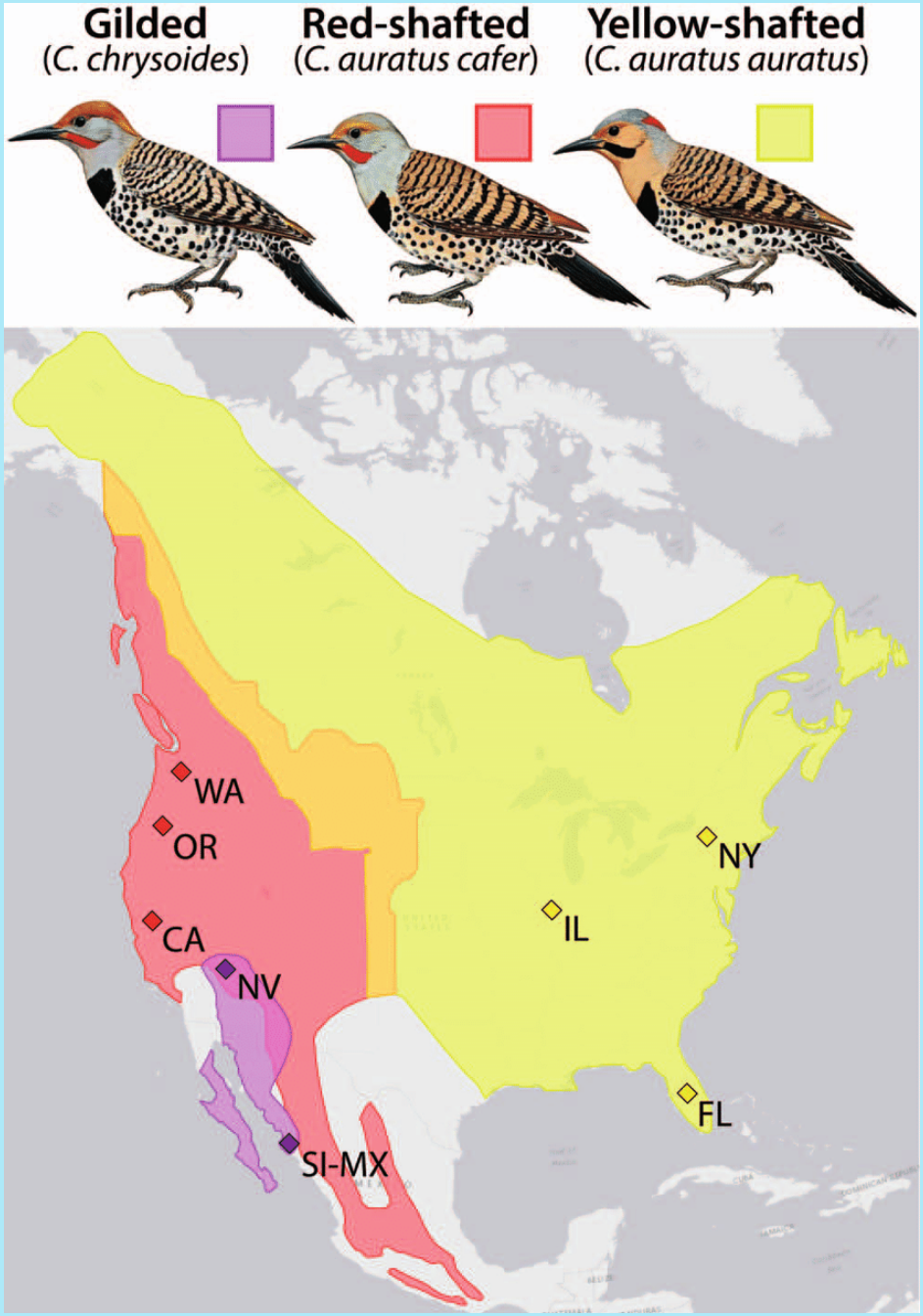
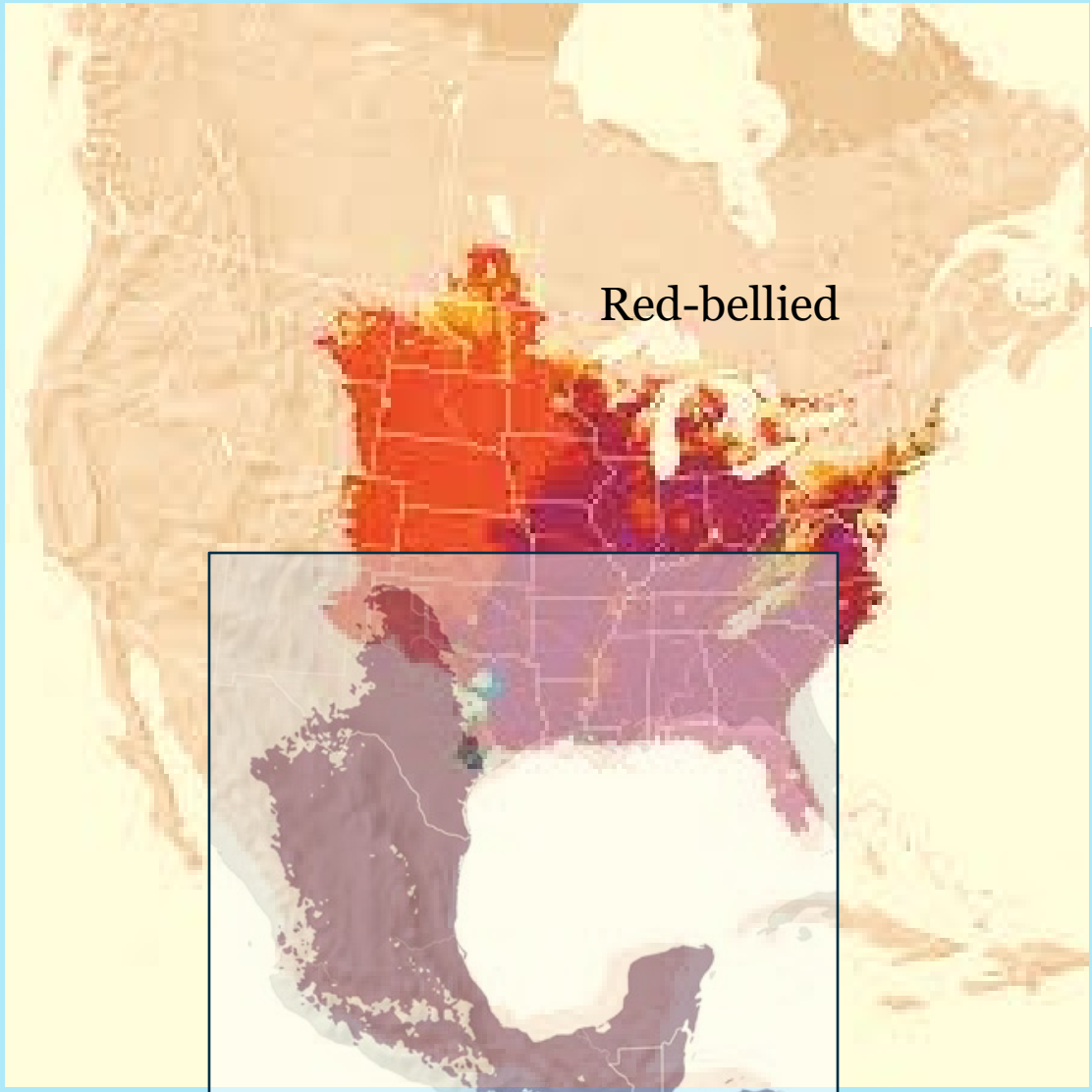
HYBRID ZONES

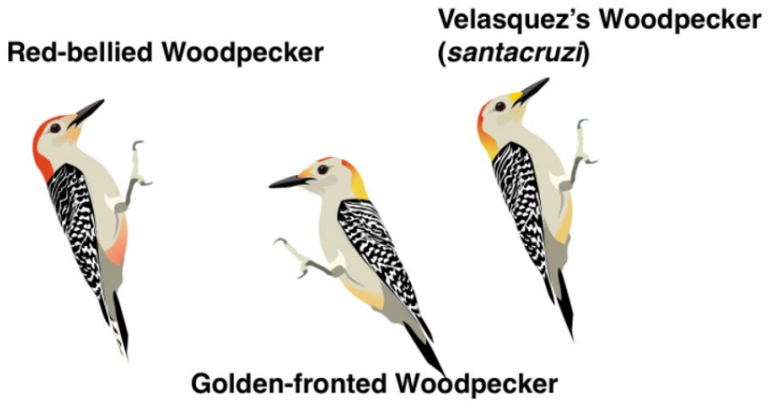
FREQUENCY OF HYBRIDS

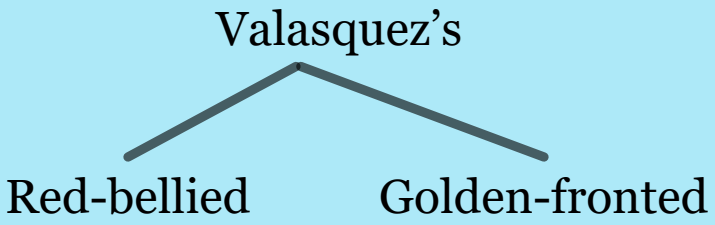
- Once thought extremely rare
- Hybrid speciation fairly common – DNA analysis



Great Plains Hybrid Zones


Red-bellied
Golden-fronted


Red-bellied Woodpecker
Velasquez's Woodpecker
(santacruzi)
Golden-fronted Woodpecker


Valasquez's
Red-bellied
Golden-fronted

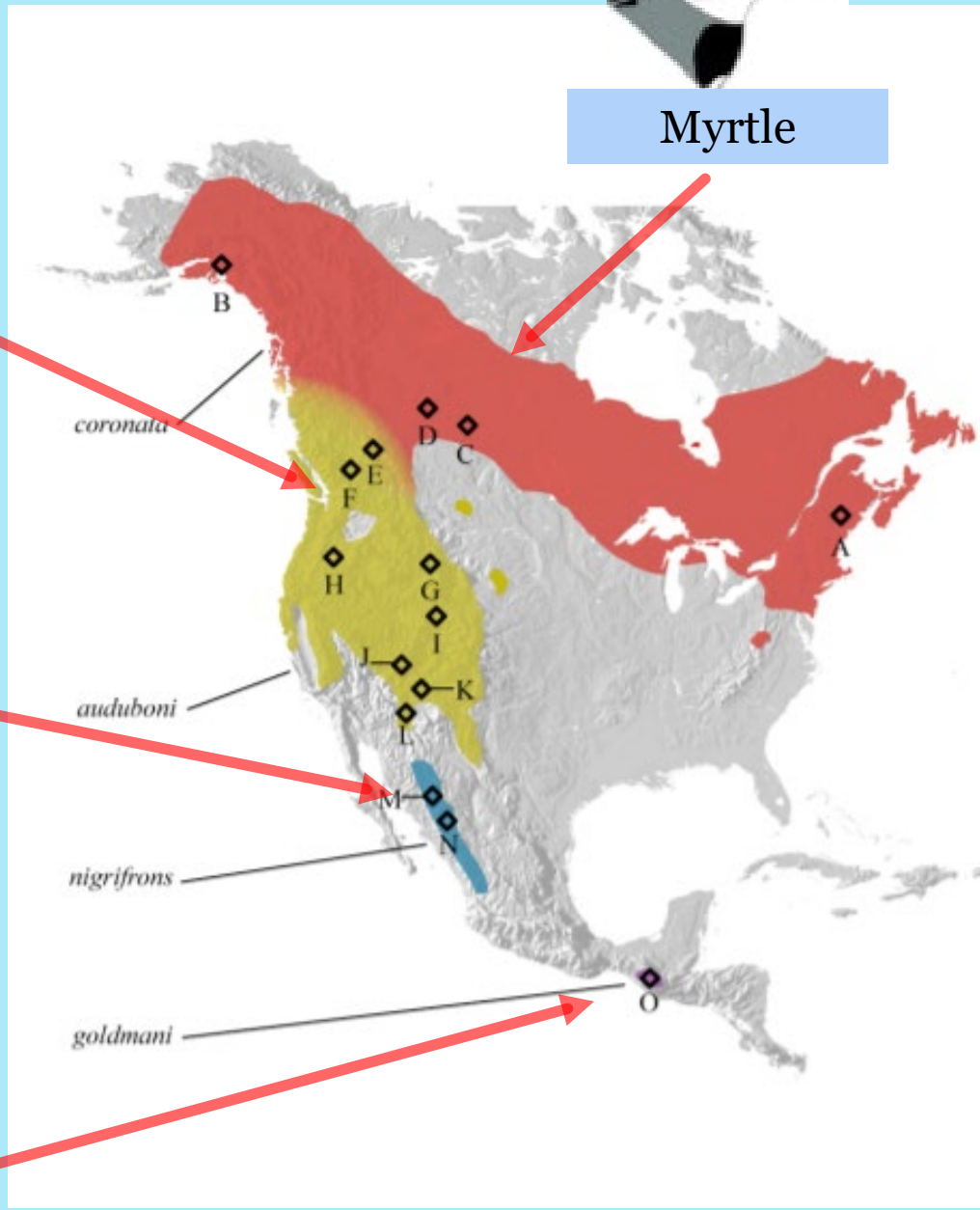
YELLOW-RUMPED WARBLER

Myrtle

Audubon's

Black-fronted

Goldman's



HYBRID ZONES

- Examples of incomplete **speciation**

- Also sources of **speciation**
  - Genetic differences have evolved
  - But don’t prevent interbreeding

QUESTIONS
I'LL TRY TO ANSWER

- How do hybrid zones form ?
- What makes the Titmouse hybrid zone stable since the Pleistocene?
- Why don't these two interbreeding species become a new species?
- Why doesn't one species push the other out?

HYBRID ZONES: NATURAL LABORATORIES

- May form when divergent populations re-contact:
  - **Secondary contact**

- Unique opportunities to study
  - **Speciation**
  - **Adaptation**
  - Ecology
  - Behavior
  - Morphology
  - Climate change

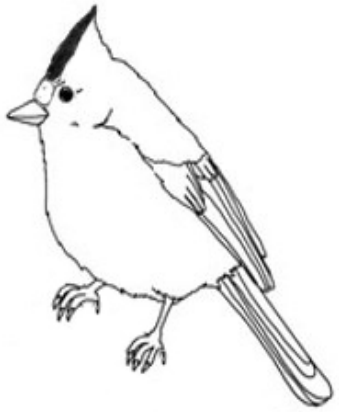
HYBRID ZONES: NATURAL LABORATORIES

- Relative strength of **selection** vs **dispersal**
- Extent & cause of divergence
- Relative influences of **natural** and **sexual selection**
  - Which traits diverged ?
  - Which traits contribute to reproductive isolation ?
  - Which traits contribute to adaptative success ?

- Titmice surveys
  - 1955,
  - early 2000s
  - 2014 (Tx & Ok)
  - Examination over time

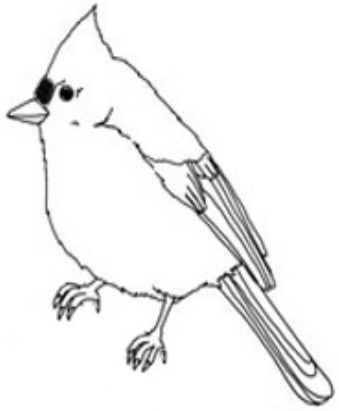
SECONDARY CONTACT

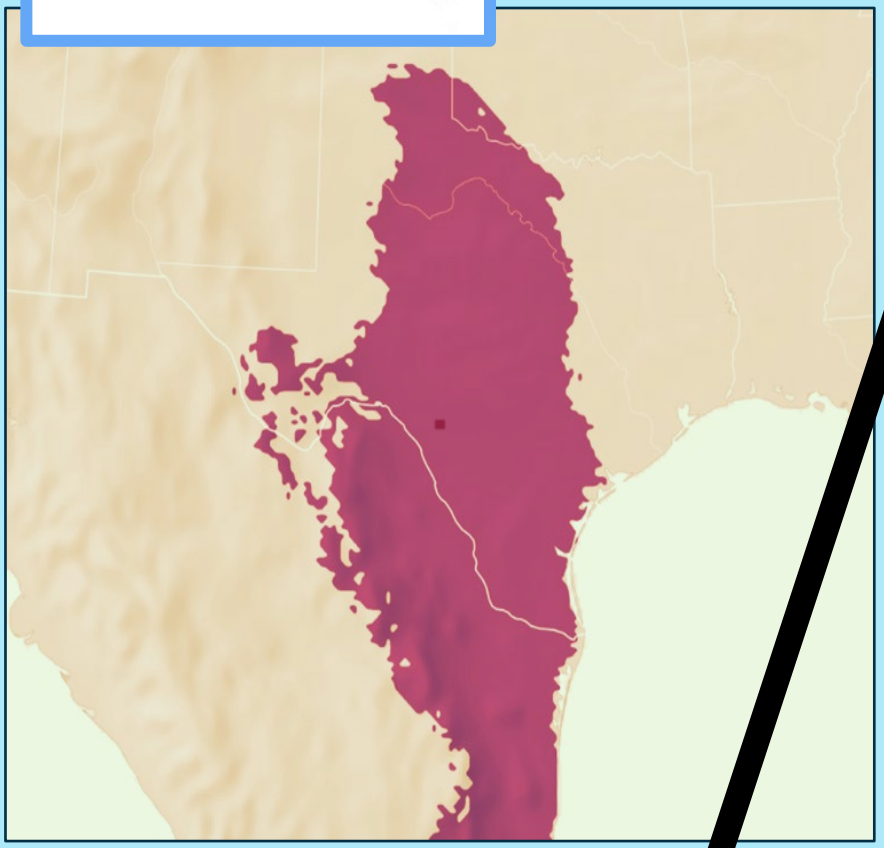
Black-crested

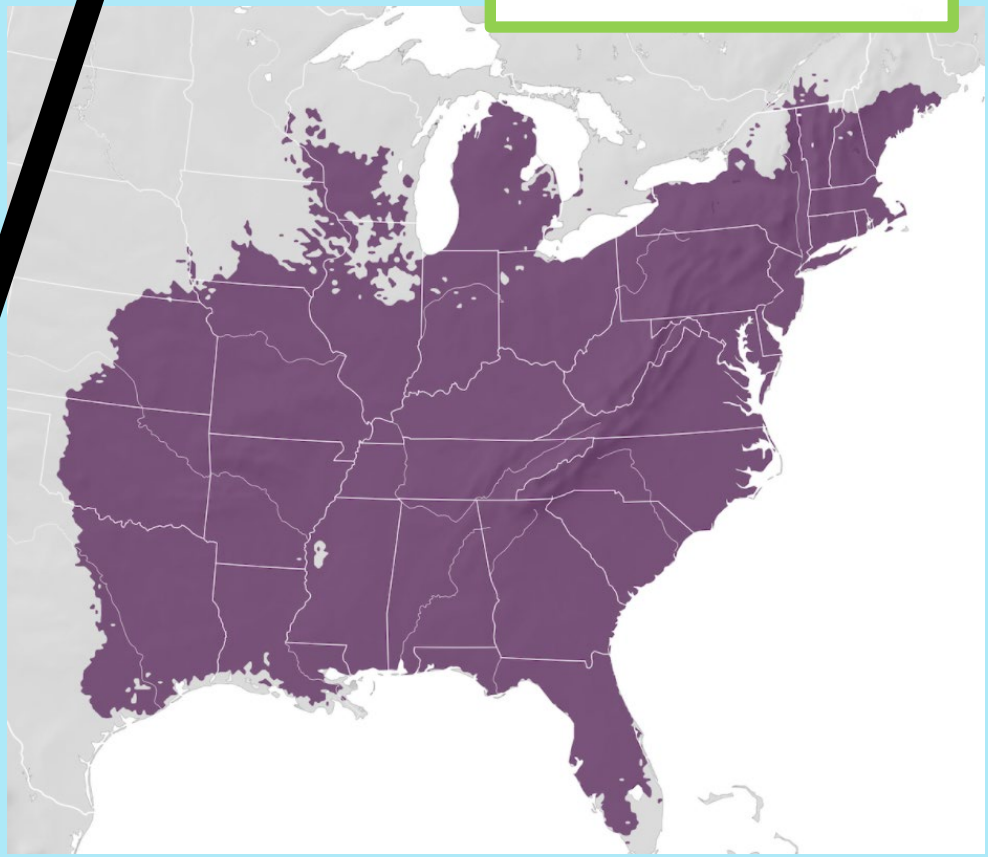


DIVERGENCE

Tufted

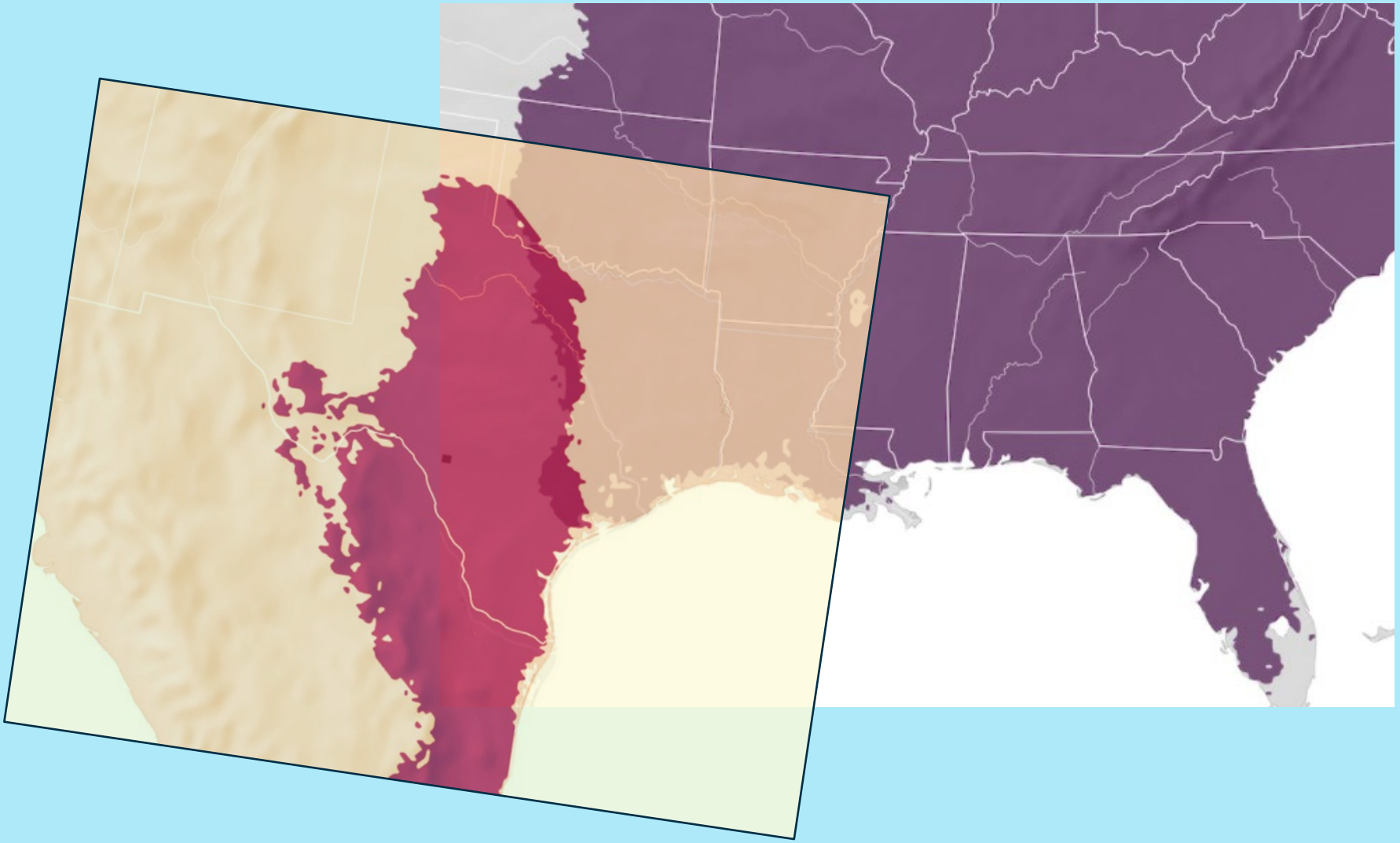






SECONDARY CONTACT

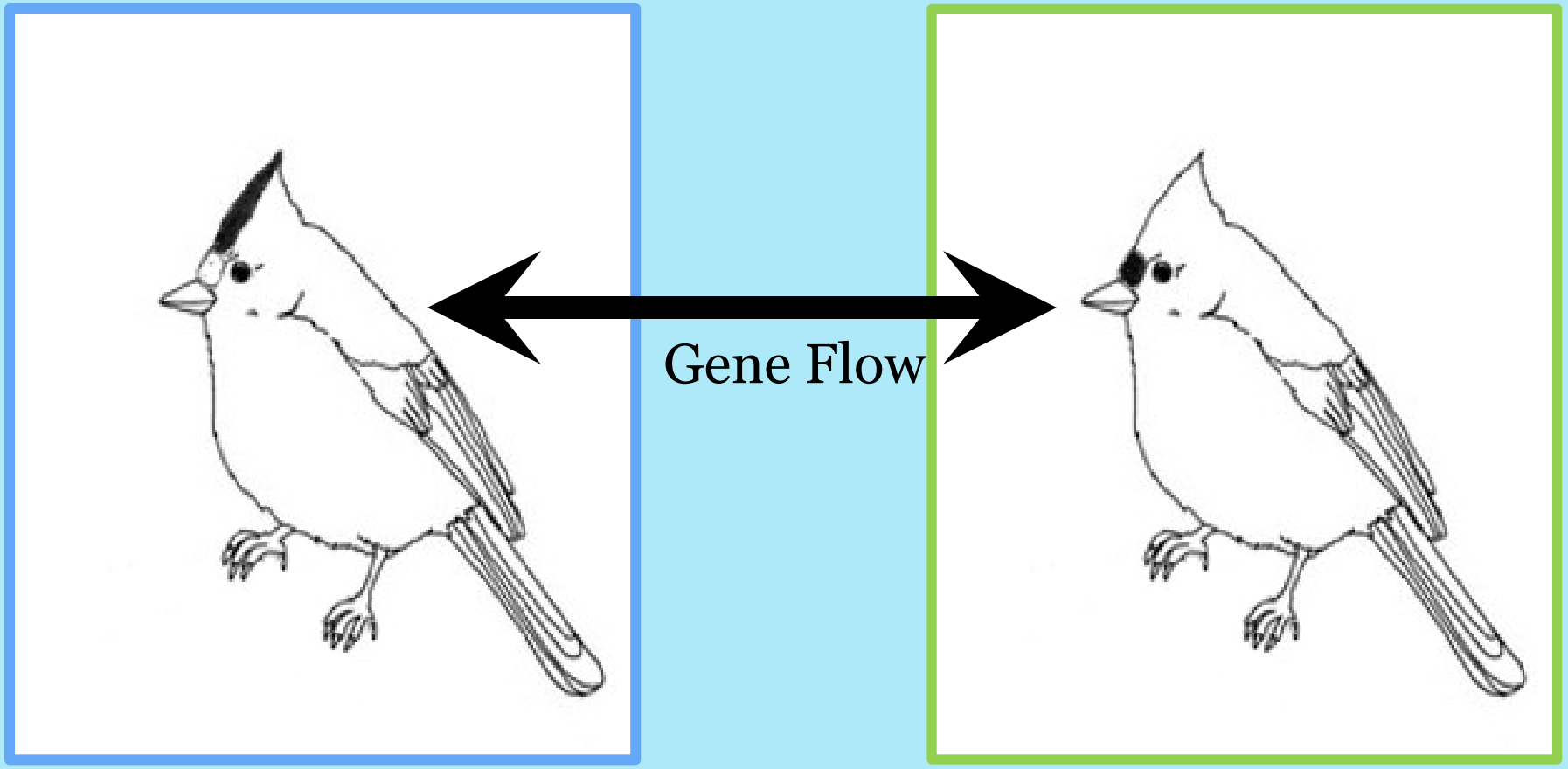
Populations eventually meet



WHAT HAPPENS NEXT?

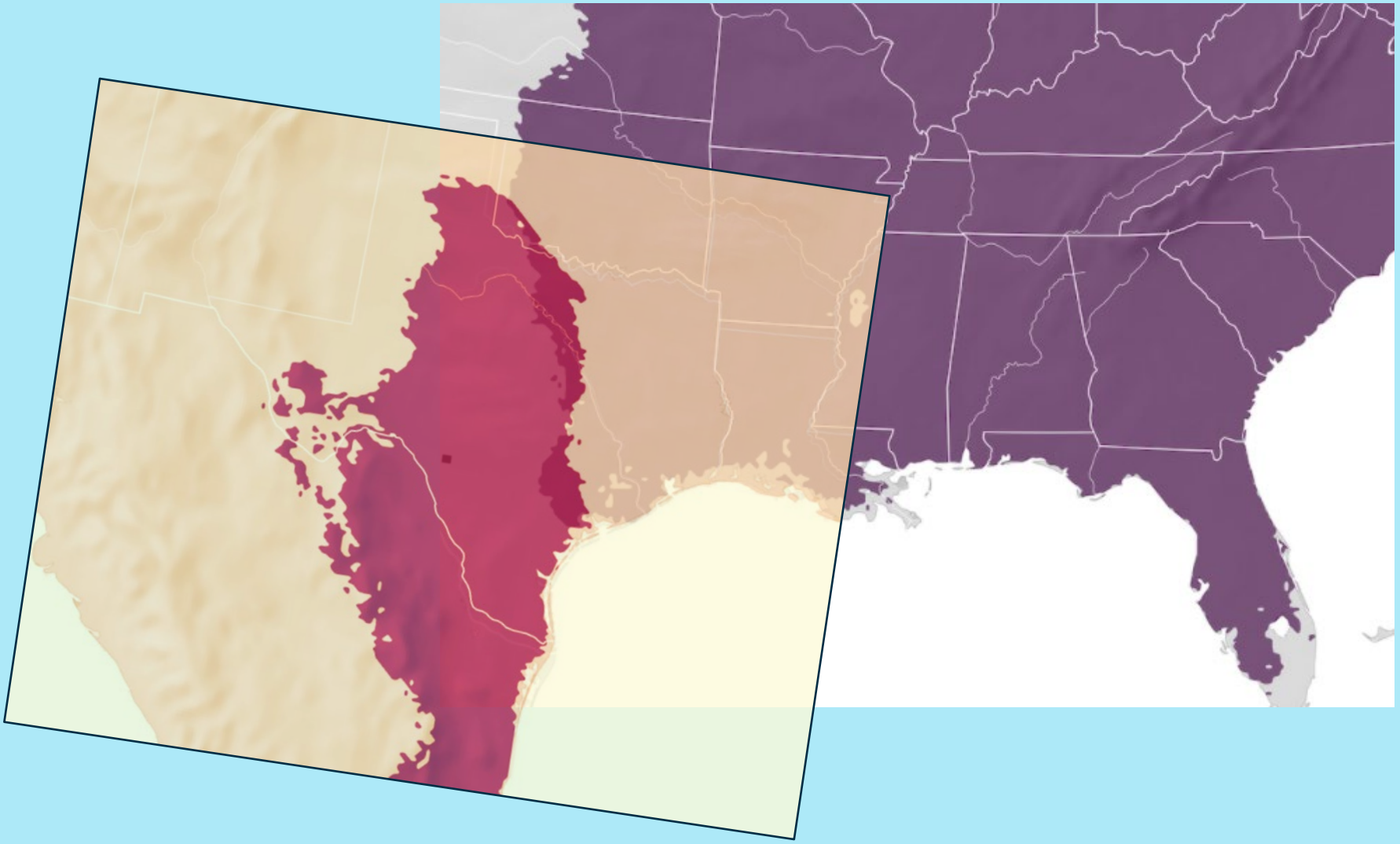
Whoopie !!!

Populations start to interbreed



Haven’t changed so much that they can’t interbreed.

HYBRID ZONE IS CREATED



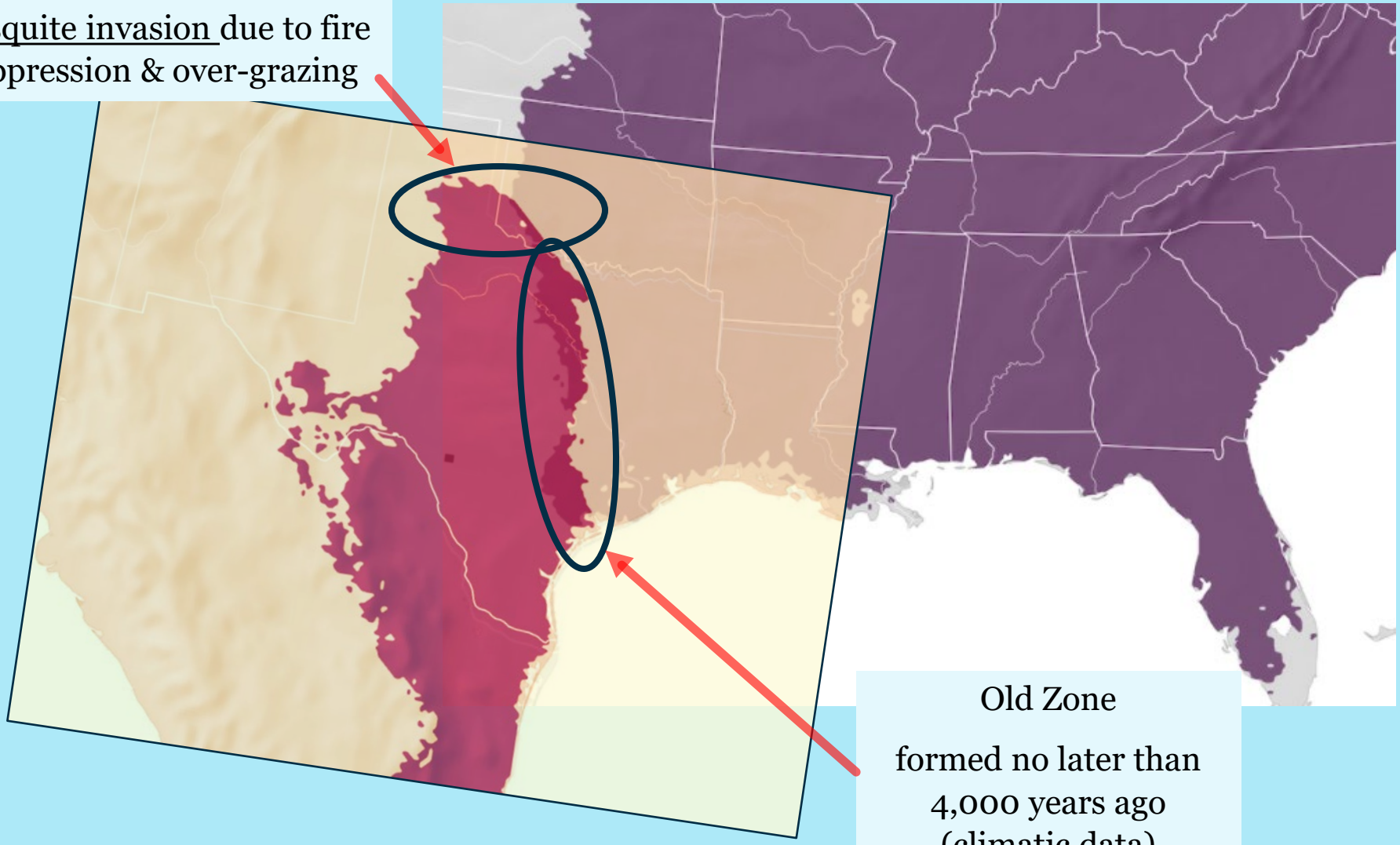
2 HYBRID ZONES

Young Zone

Formed in last 100 years

change in habitat & subsequent range expansion

mesquite invasion due to fire suppression & over-grazing



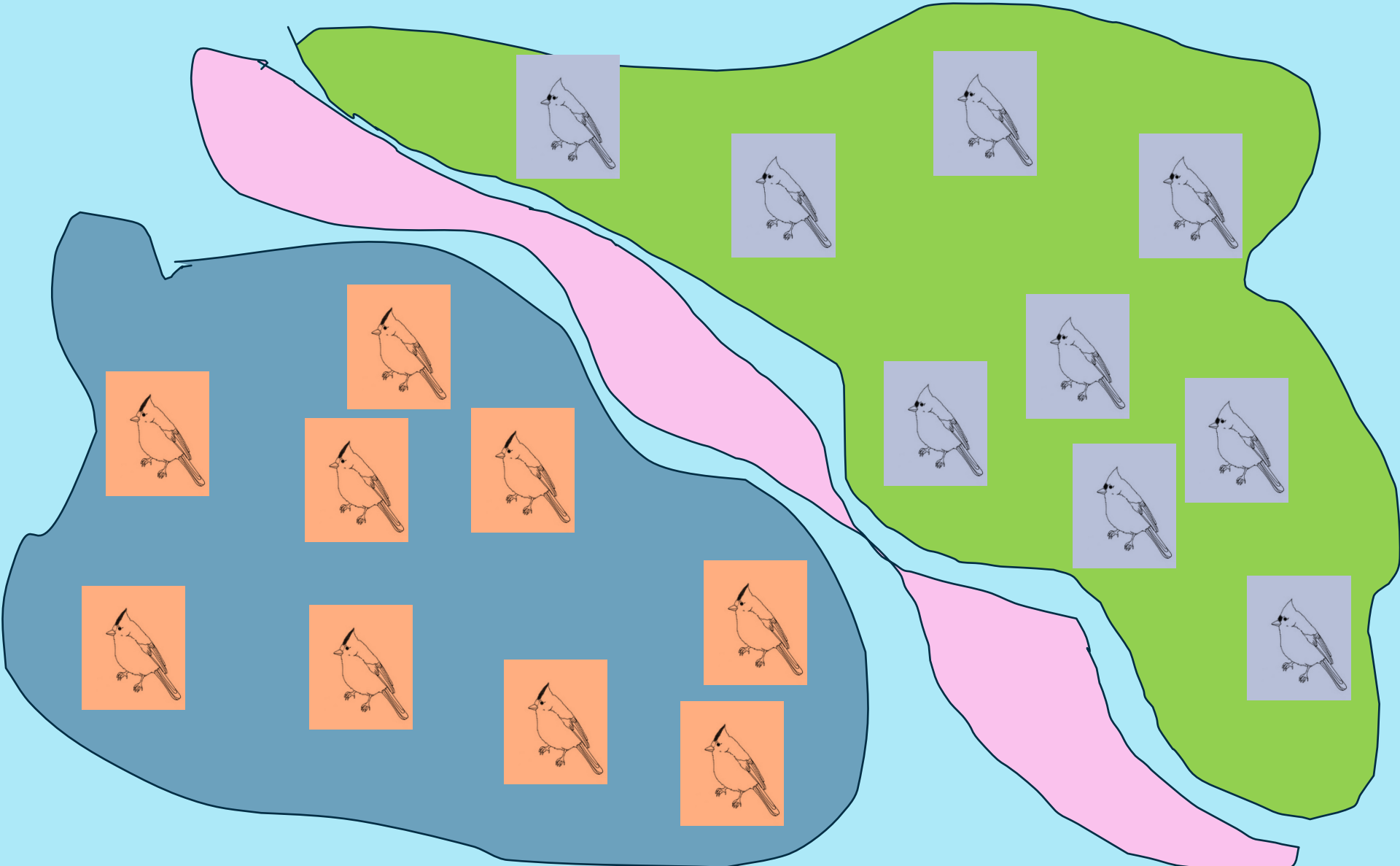
Old Zone

formed no later than 4,000 years ago (climatic data)

SECONDARY CONTACT

Something brings the populations back together

Habitats change.....



SECONDARY CONTACT

- 2 main possibilities

1. No interbreeding
2. With interbreeding

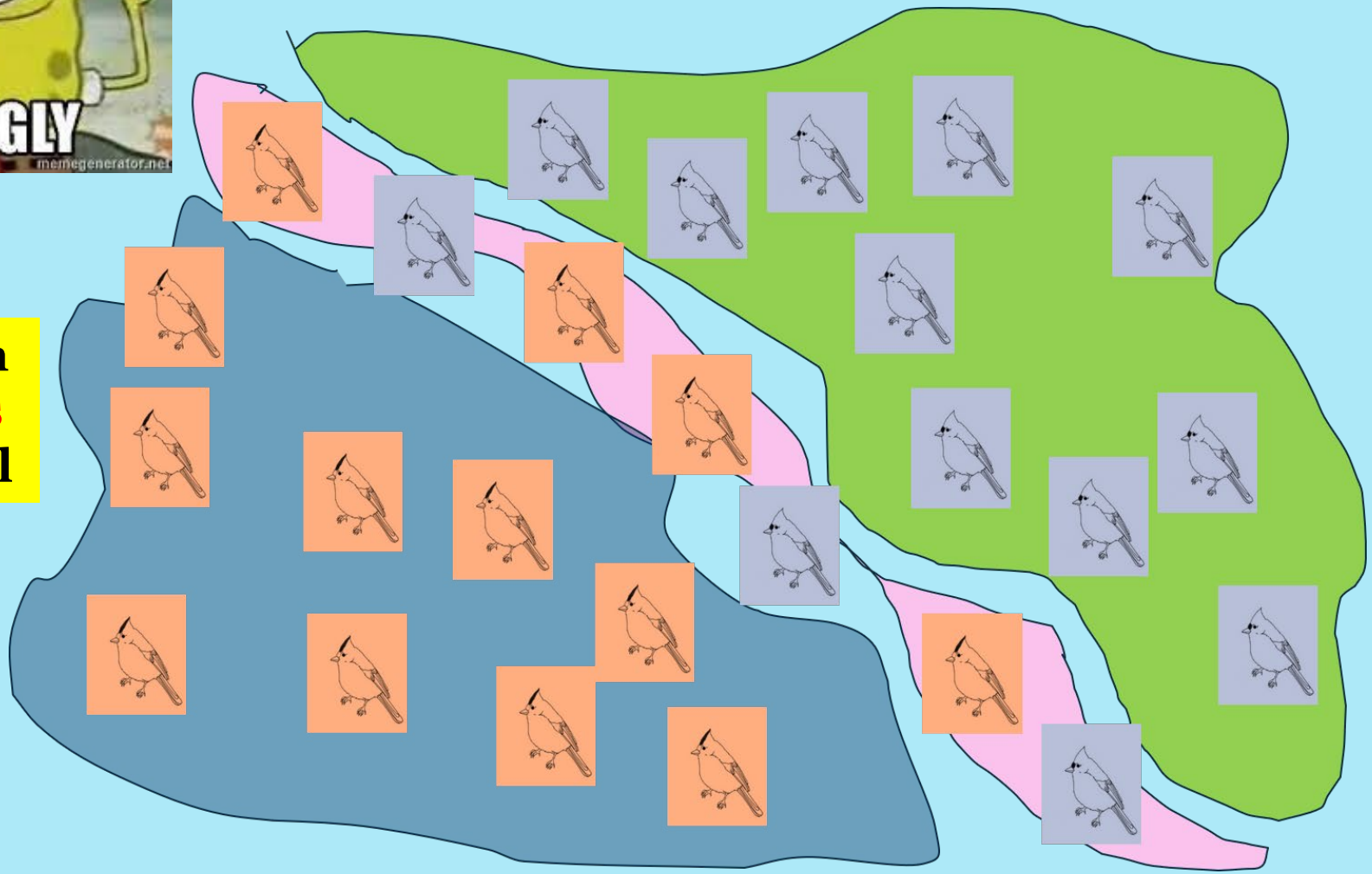
NO
INTERBREEDING

SECONDARY CONTACT

NO INTERBREEDING

Male ornamentation/display
Unattractive
FEMALE CHOICE !!!

Selection
balances
Dispersal



SECONDARY CONTACT

Unsuccessful in new habitat

Selection overwhelms Dispersal

NO INTERBREEDING

SECONDARY CONTACT

NO INTERBREEDING

Dispersal overwhelms Selection

1 species out-competes (ecologically)

SECONDARY CONTACT

NO INTERBREEDING

Dispersal overwhelms Selection

1 species out-competes (ecologically)

WITH
INTERBREEDING

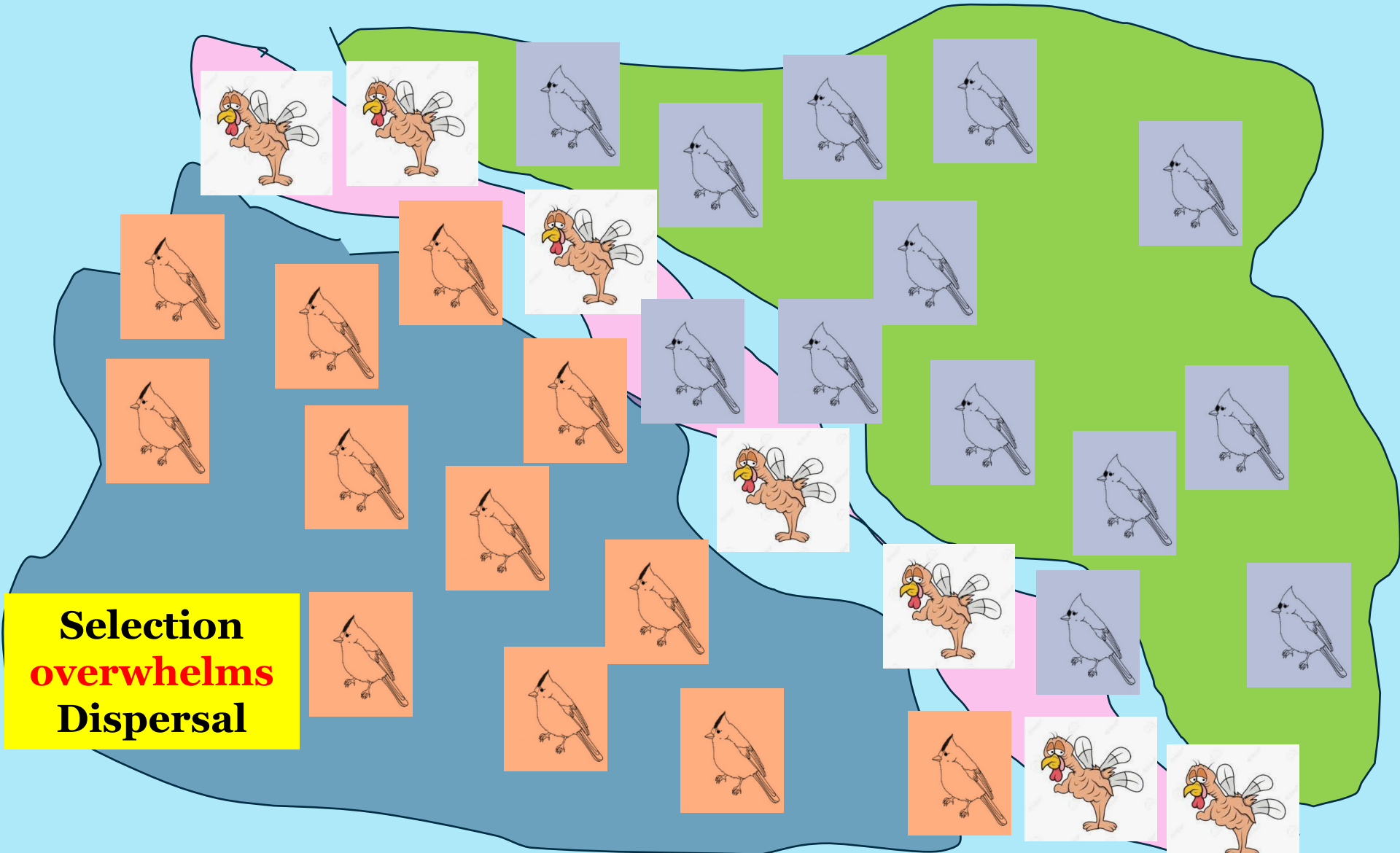
WHAT CAN HAPPEN AT SECONDARY CONTACT?

- Interbreed
  - Hybrid zone is created
    - **Ephemeral** – recent meeting of two divergent forms that blend back together
    - **Stable** – balance between **selection** & **dispersal**
    - **Expanding**

SECONDARY CONTACT

INTERBREEDING

Hybrids are unfit
(sterile, weak, unviable
or just less fit than parents)

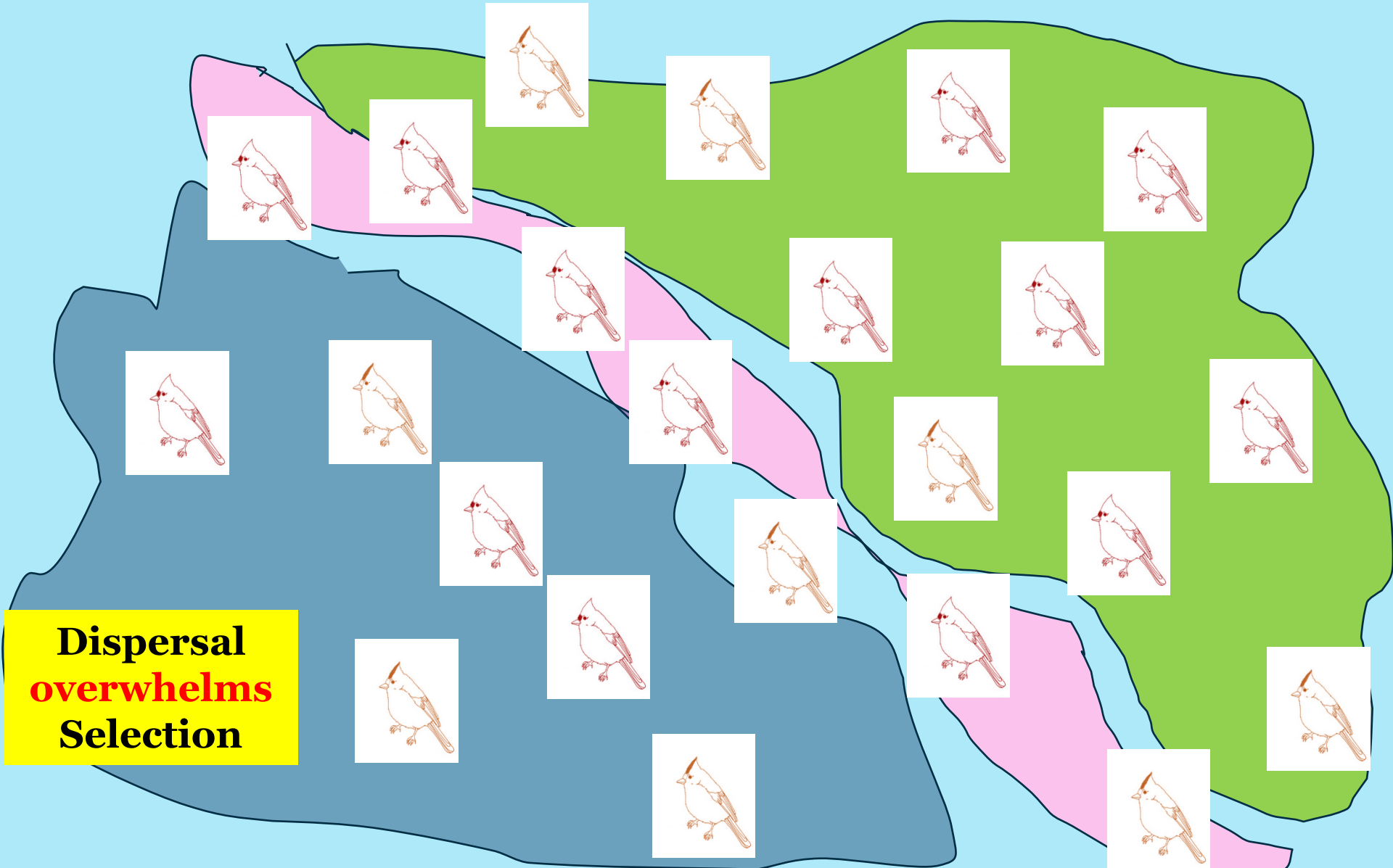


Selection overwhelms Dispersal

SECONDARY CONTACT

INTERBREEDING

Combine to form new species

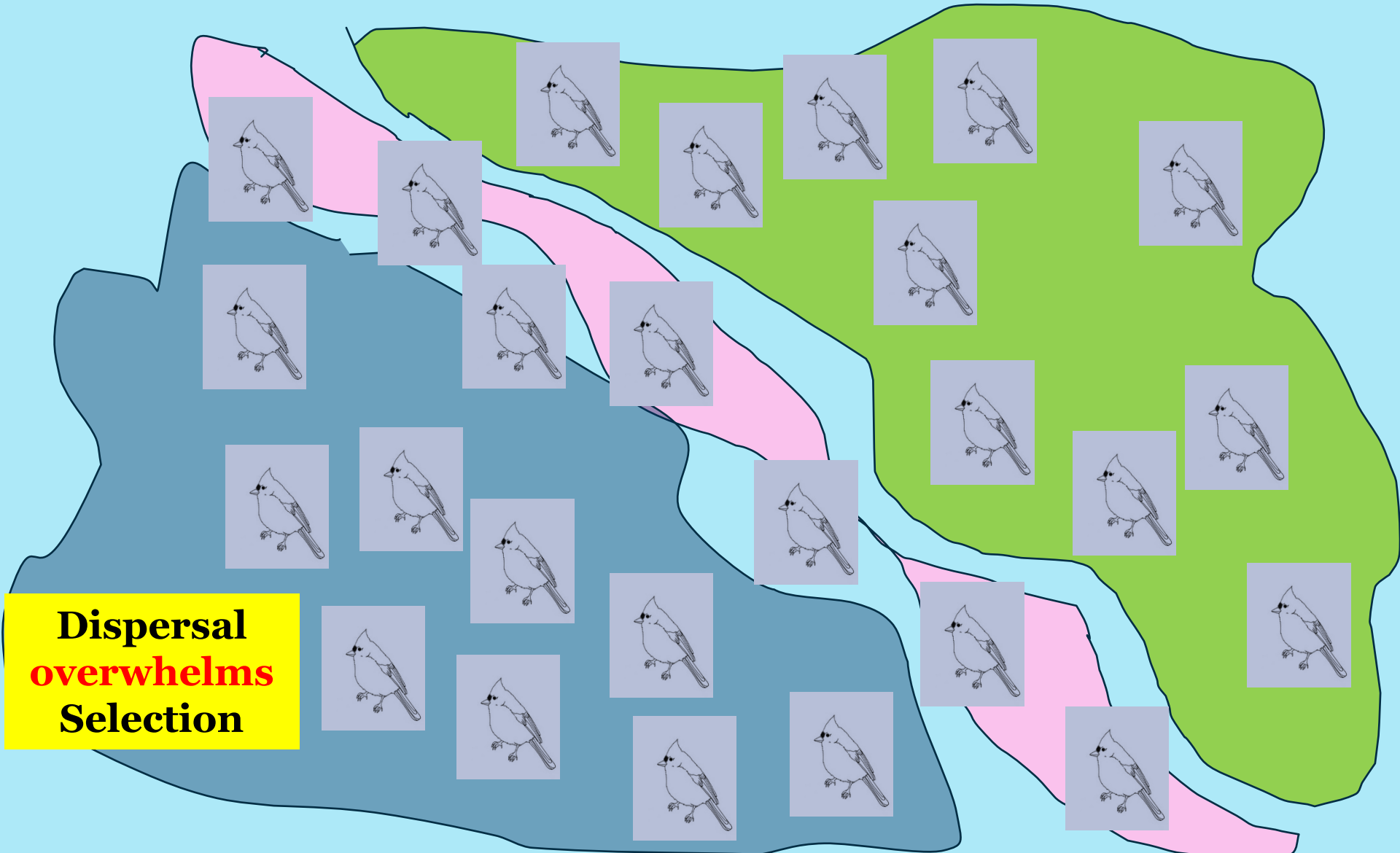


Dispersal overwhelms Selection

SECONDARY CONTACT

INTERBREEDING

1 species out-competes
Genetically

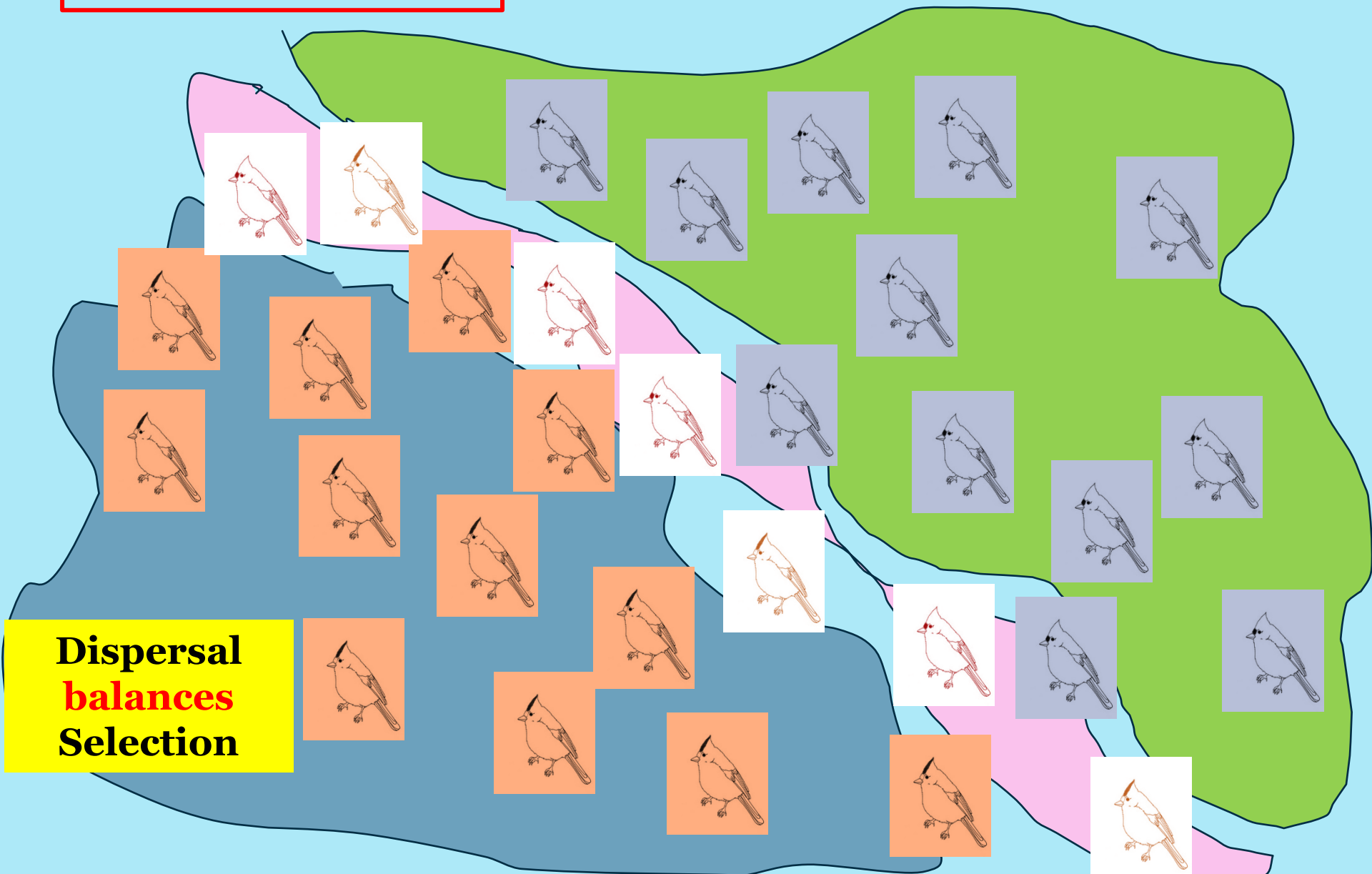


Dispersal
overwhelms
Selection

SECONDARY CONTACT

INTERBREEDING

Hybrid zone forms



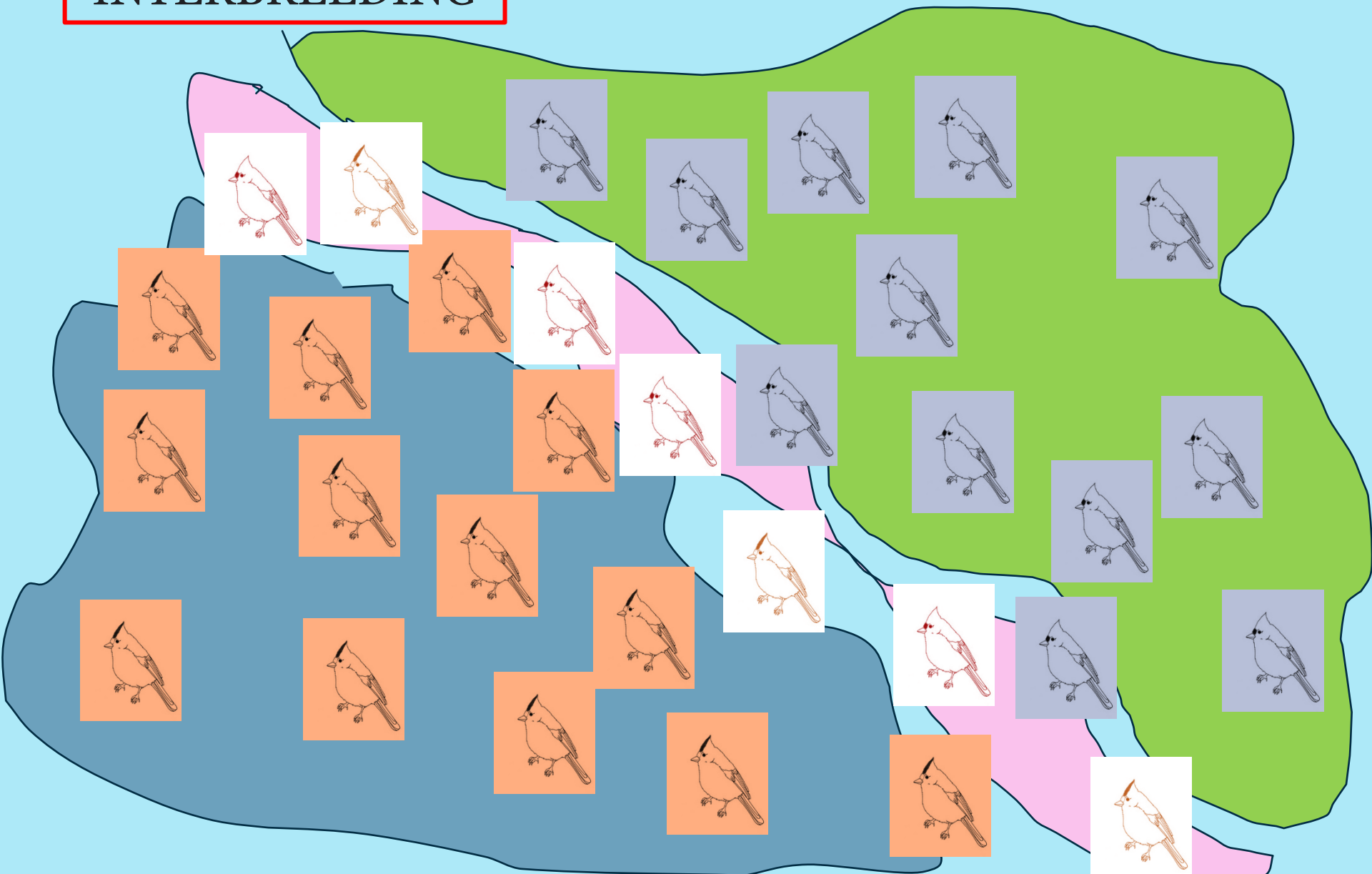
Dispersal
balances
Selection

TYPES OF HYBRID ZONES

HYBRID ZONE FORMS

INTERBREEDING

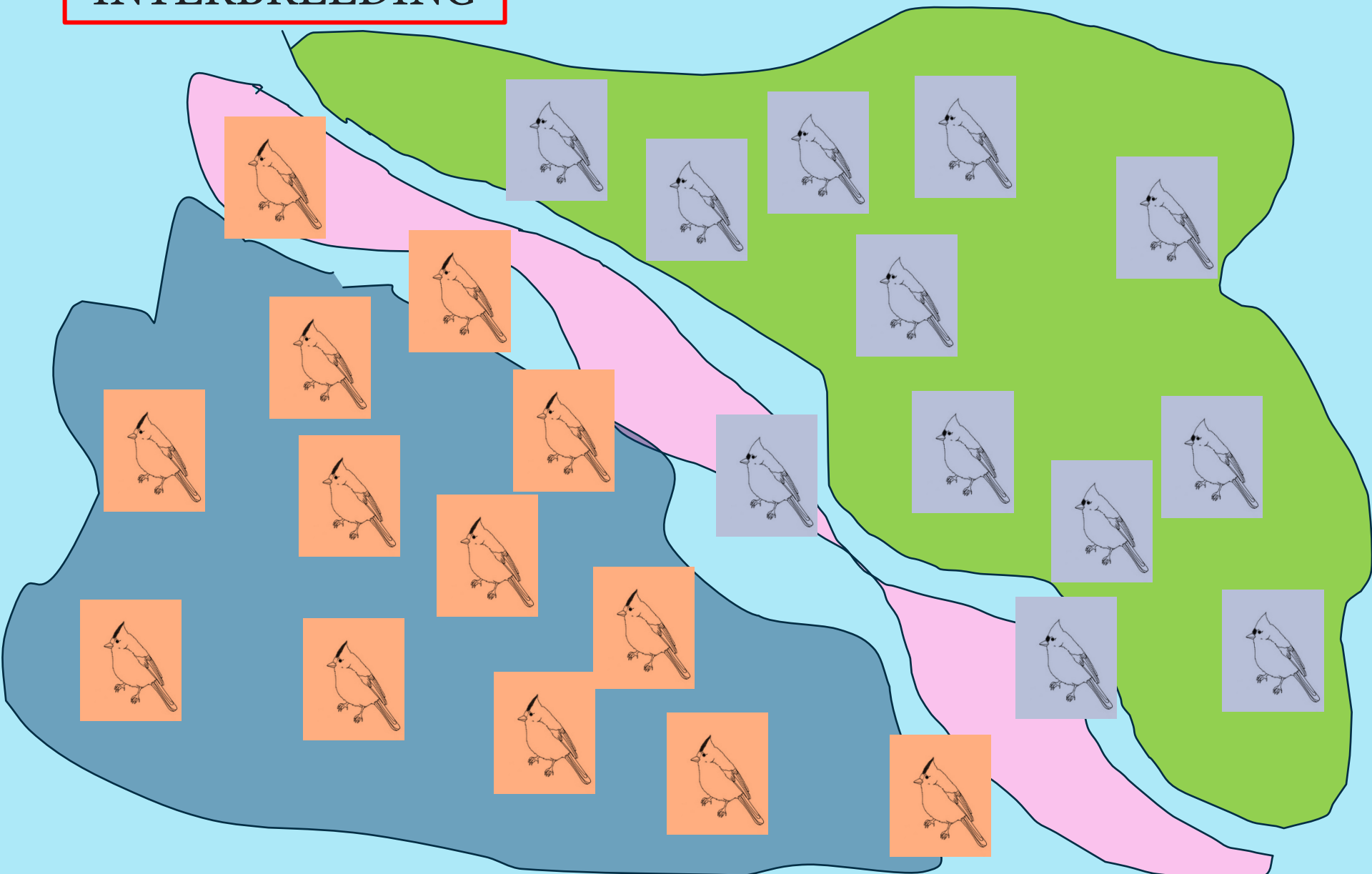
Ephemeral



HYBRID ZONE FORMS

INTERBREEDING

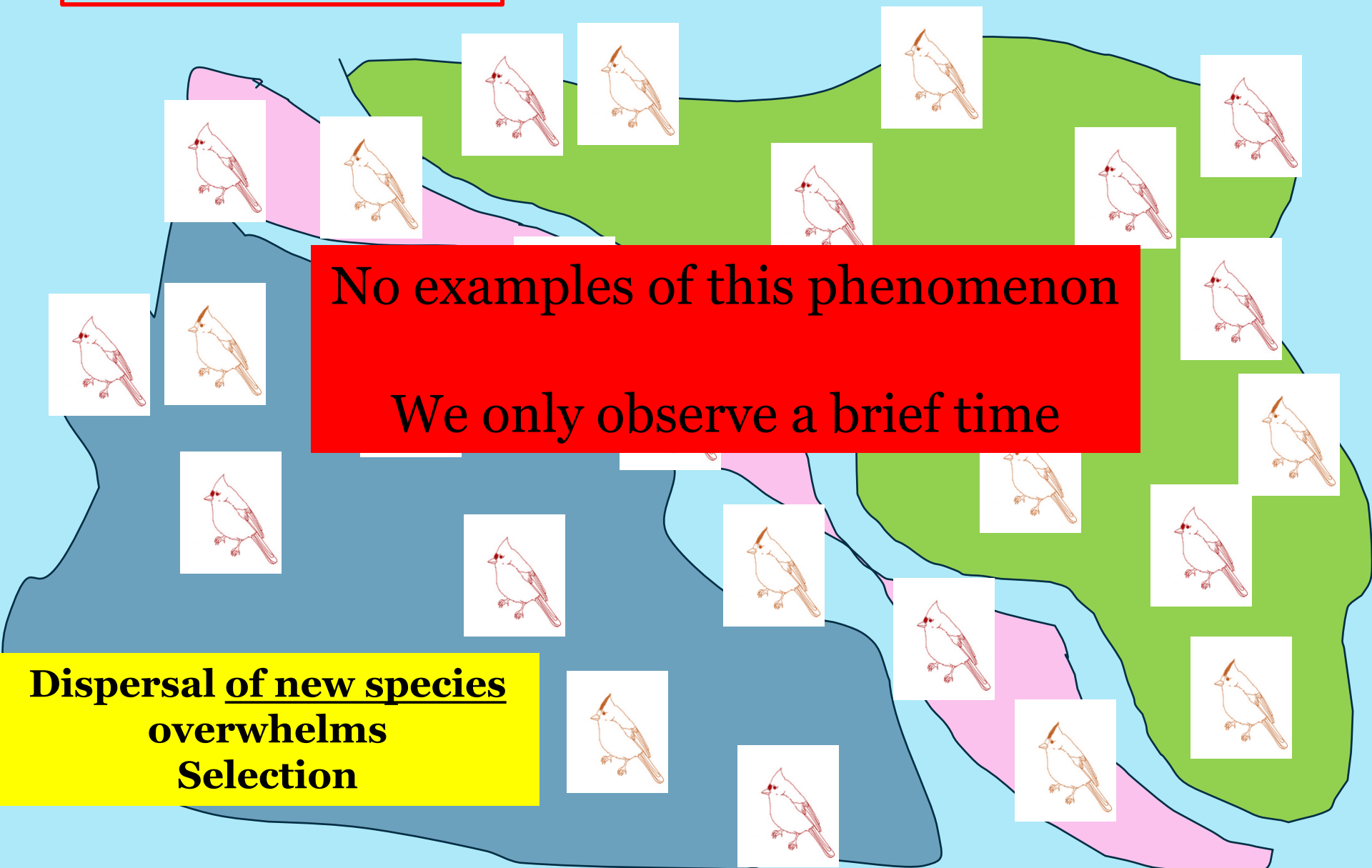
Ephemeral



HYBRID ZONE FORMS

INTERBREEDING

Expanding



No examples of this phenomenon

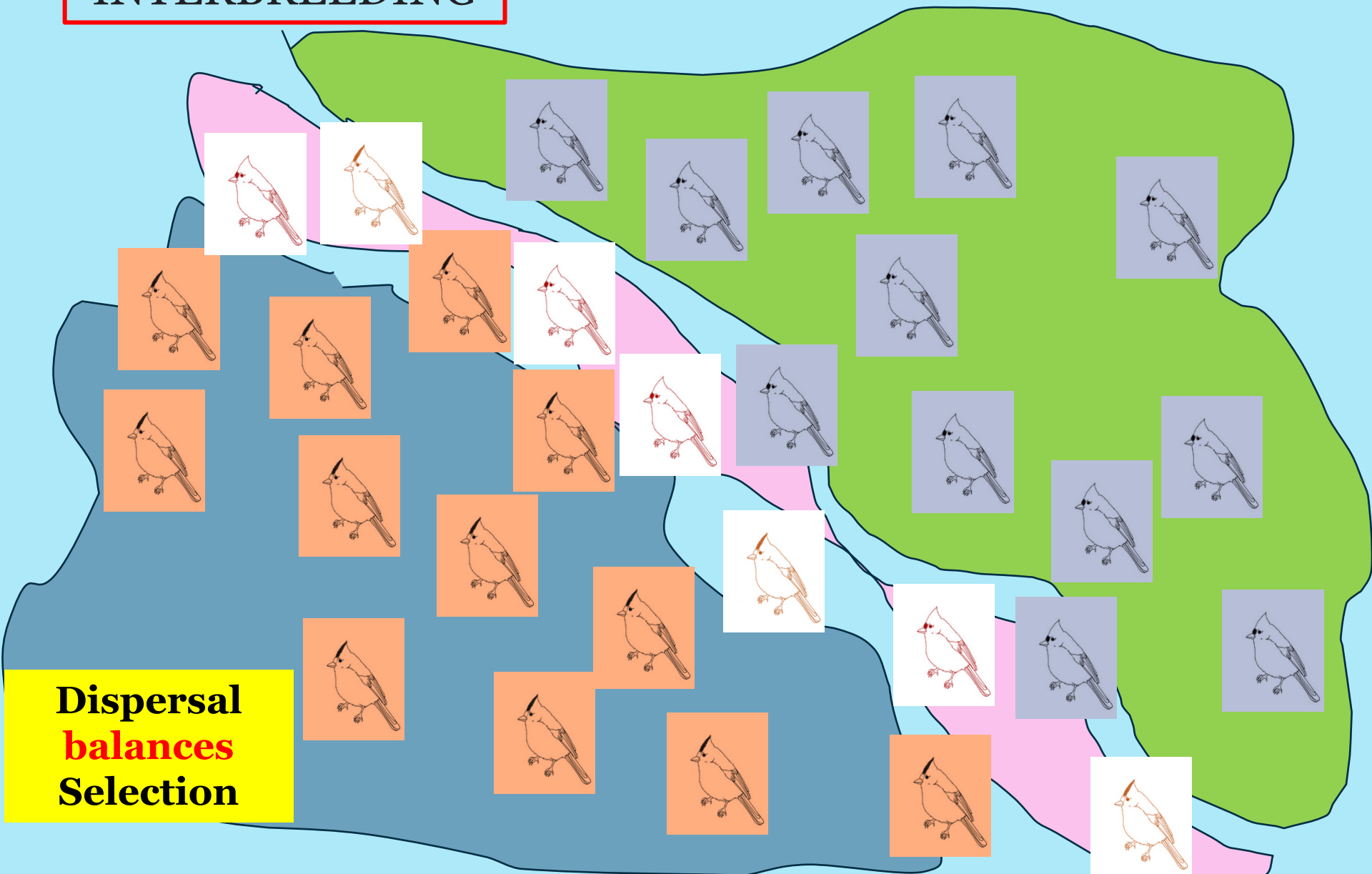
We only observe a brief time

Dispersal <u>of new species</u> overwhelms Selection

HYBRID ZONE FORMS

Hybrid zone is **Stable**

INTERBREEDING



Dispersal
balances
Selection

STABLE HYBRID ZONES

- Two species remain
- Continue to produce hybrids
- No net change

- **Selection** balanced by **dispersal**

- Hybrids slightly less fit than parent species
  - Less fit in specific habitat
  - Common with hybrids

FITNESS OF HYBRIDS IN THE HABITAT

- Hybrid fitness < Parent species fitness (usual)
  - Less fertile
  - Less successful in breeding
    - e.g. less able to attract mate
    - May be weird
  - Less competitive for food, survival….
  - Many examples
- Reinforces the original speciation (**reinforcement**)

- Hybrid fitness = Parent species fitness
  - May merge into a single new species (fusion)

- Persisting hybrid form
  - Must out-compete parent species in that habitat

OUR TITMICE

HYBRID ZONES

TWO HYBRID ZONES

- Texas ("old hybrid zone")
  - 2 populations interbreeding for several thousands of years
  - Meet at natural ecotone
  - Known to interbreed in Texas since 1880s (Ridgway (1887))

- Oklahoma ("young hybrid zone")
  - Until early 20th – no Black-crested in Oklahoma
  - Range expansion into SW Oklahoma
  - Should leave unique genetic footprint

- Multiple studies & 2 hybrid zones
  - See how hybrid zones change over time

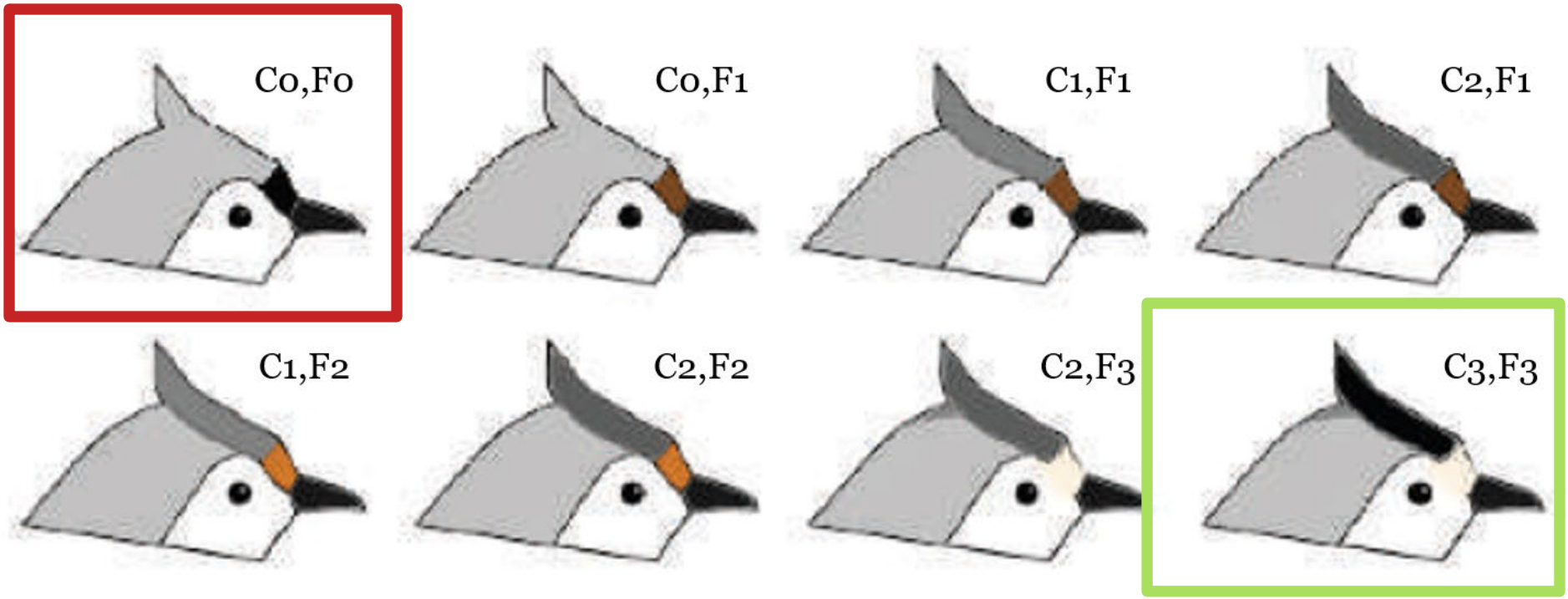
REFERENCES

- Dixon, K. L. (1955). An ecological analysis of the interbreeding of crested titmice in Texas. University of California Press.
- Braun, Kitto and Braun (1984) Molecular Population Genetics of Tufted and Black-Crested Forms of Parus bicolor (Early 2000s)
- Dixon, K. L, (1989). Contact Zones of Avian Congeners on the Southern Great Plains, The Cooper Ornithological Society 1989
- Dixon, K. L. (1990). Constancy of margins of the hybrid zone in titmice of the Parus bicolor complex in coastal Texas. The Auk, 184-188.
- Curry, C. M. & Patten, M. A. (2014). Current and Historical Extent of Phenotypic Variation in the Tufted and Black-crested Titmouse (Paridae) Hybrid Zone in the Southern Great Plains. American Midland Naturalist 171, 271-300.
- Vaughn, J. C., et. Al. Glucose Concentrations in Closely Related Titmice (Baeolophus) Species Linked to Regional Habitat Differences Across an Avian Hybrid Zone (2020)
- Tomasek, O., et. Al. Fuel for the pace of life: Baseline blood glucose concentration co-evolves with life-history traits in songbirds (2019)

Current and Historical Extent of Phenotypic Variation in the Tufted and Black-crested Titmouse (Paridae) Hybrid Zone in the Southern Great Plains,

Claire M. Curry; Michael A. Patten

Hybrid index is a sum of crest (0 to 3) and forehead (0 to 3) values.



STUDY METHODOLOGY "HYBRID INDEX"

		Crest Score			
		0	1	2	3
Forehead Score	0	0	1	2	3
	1	1	2	3	4
	2	2	3	4	5
	3	3	4	5	6

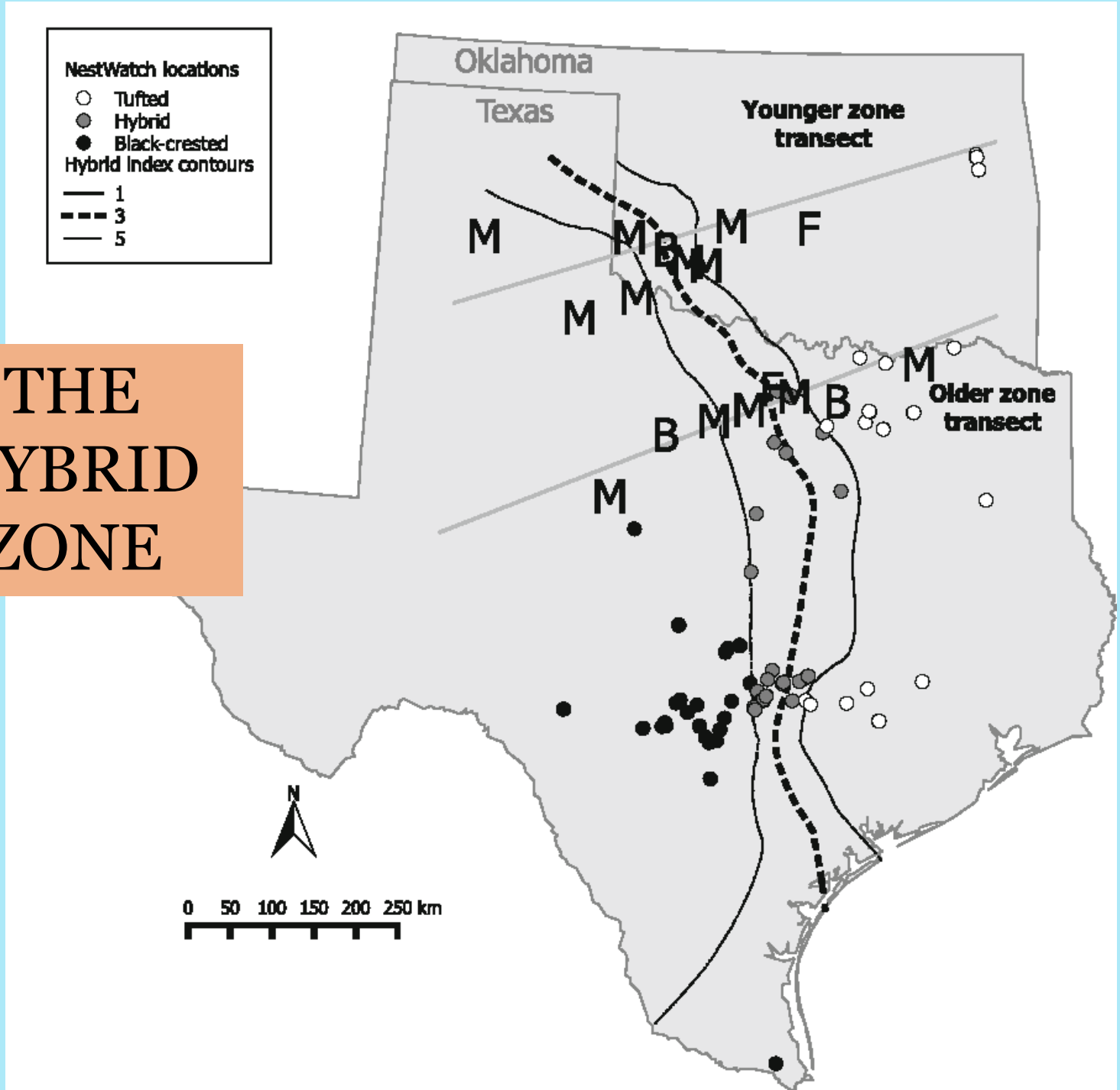
- Crest + forehead colors
- Crest (0 to 3) + forehead (0 to 3)
- Plumage scale from 0-6

Pure Tufted	Hybrids					Pure Black-crested
0	1	2	3	4	5	6

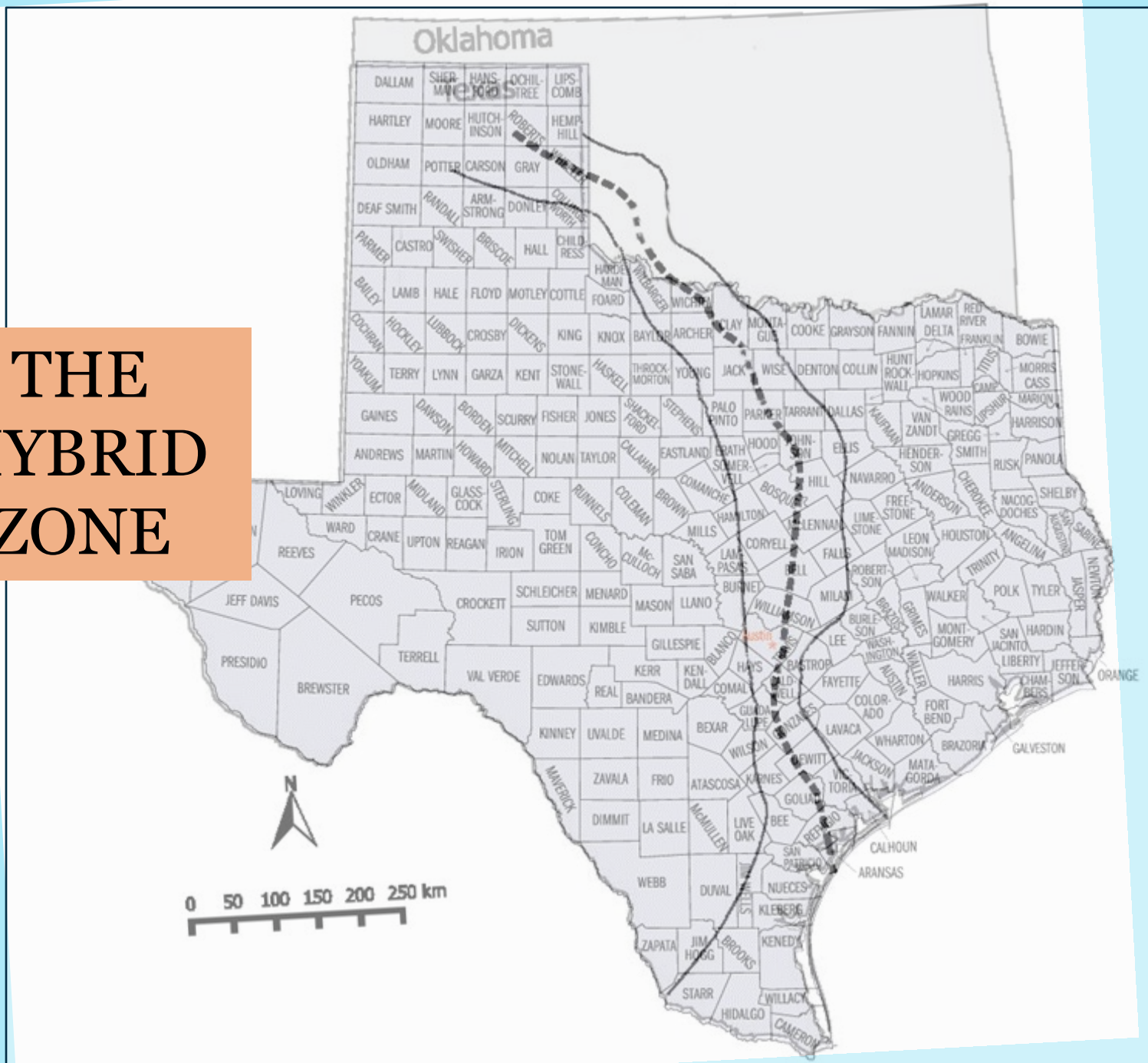
- Outside of hybrid zone:
  - 0–1 (Tufted) or
  - 5–6 (Black-crested)

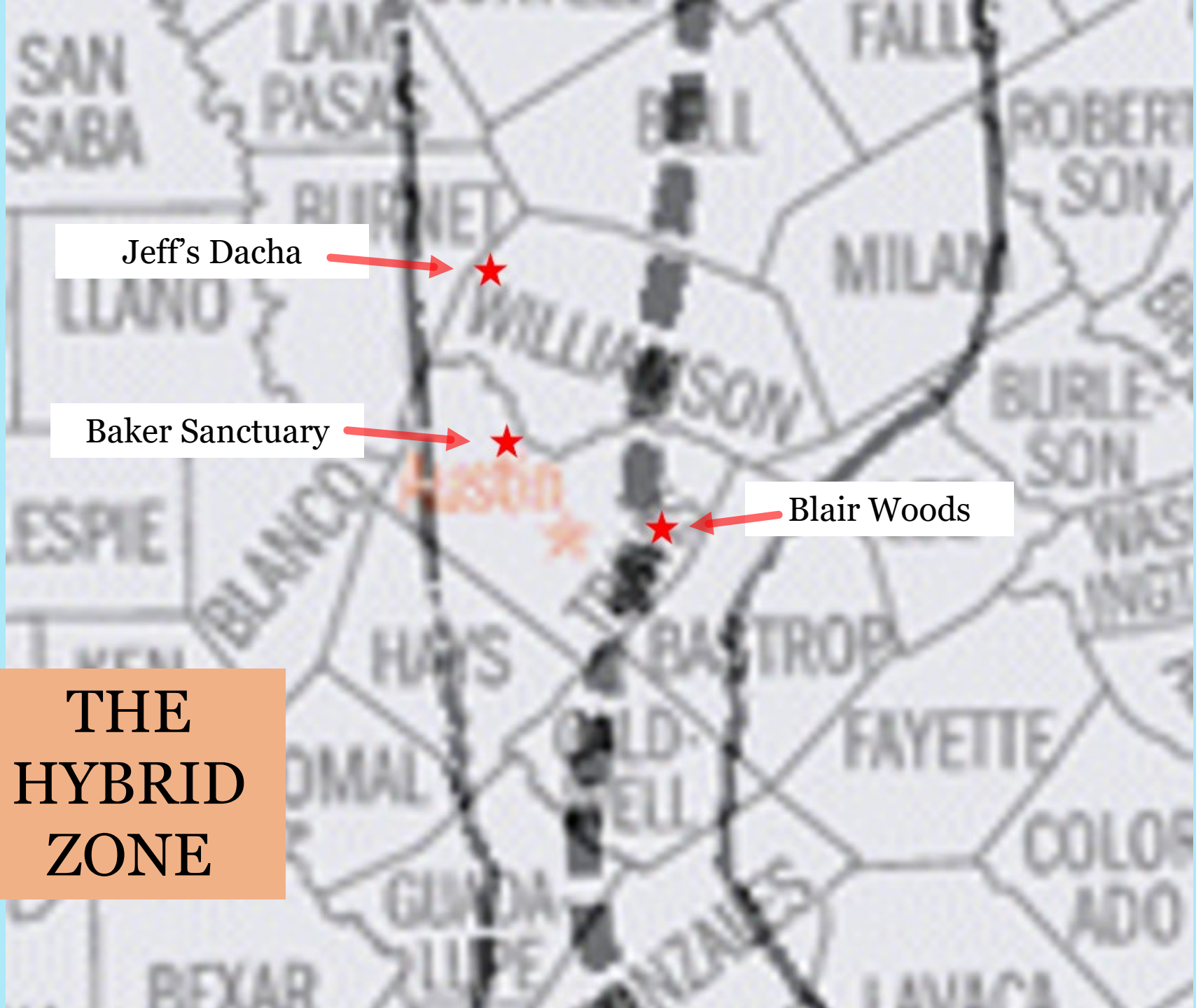
- Inside hybrid zone
  - Large range of intermediate plumages (0-6)

THE HYBRID ZONE



THE HYBRID ZONE

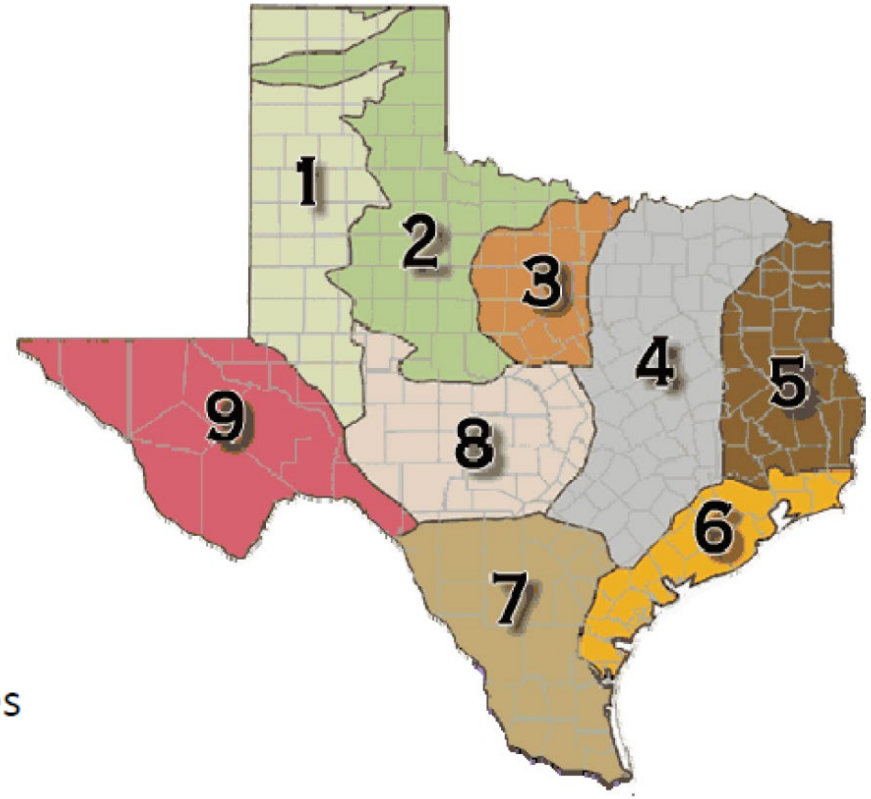



Jeff's Dacha
Baker Sanctuary
Blair Woods
THE HYBRID ZONE

DIDN’T JUST MEET ANYWHERE

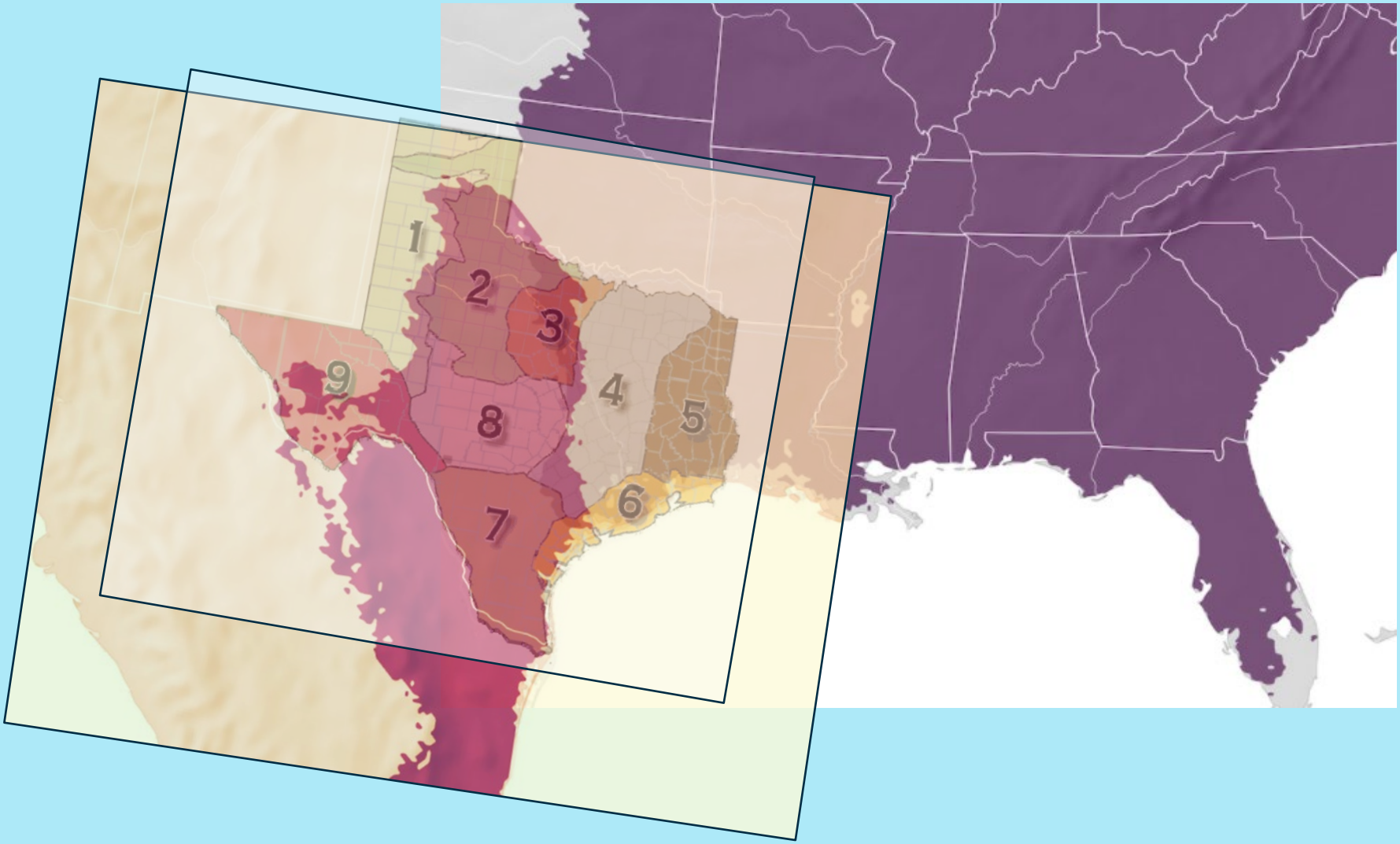
- Not at a bar !!!
- Not at work !!!
- Not on a dating app !!!

BIO GEOGRAPHICAL REGIONS OF TEXAS



1. High Plains
2. Rolling Plains
3. Osage Plains
4. Post-Oak Savannah and Blackland Prairies
5. Pineywoods
6. Coastal Prairies (and Coastal Sand Plain)
7. South Texas Brush Country
8. Edwards Plateau
9. Trans-Pecos

HYBRID ZONE



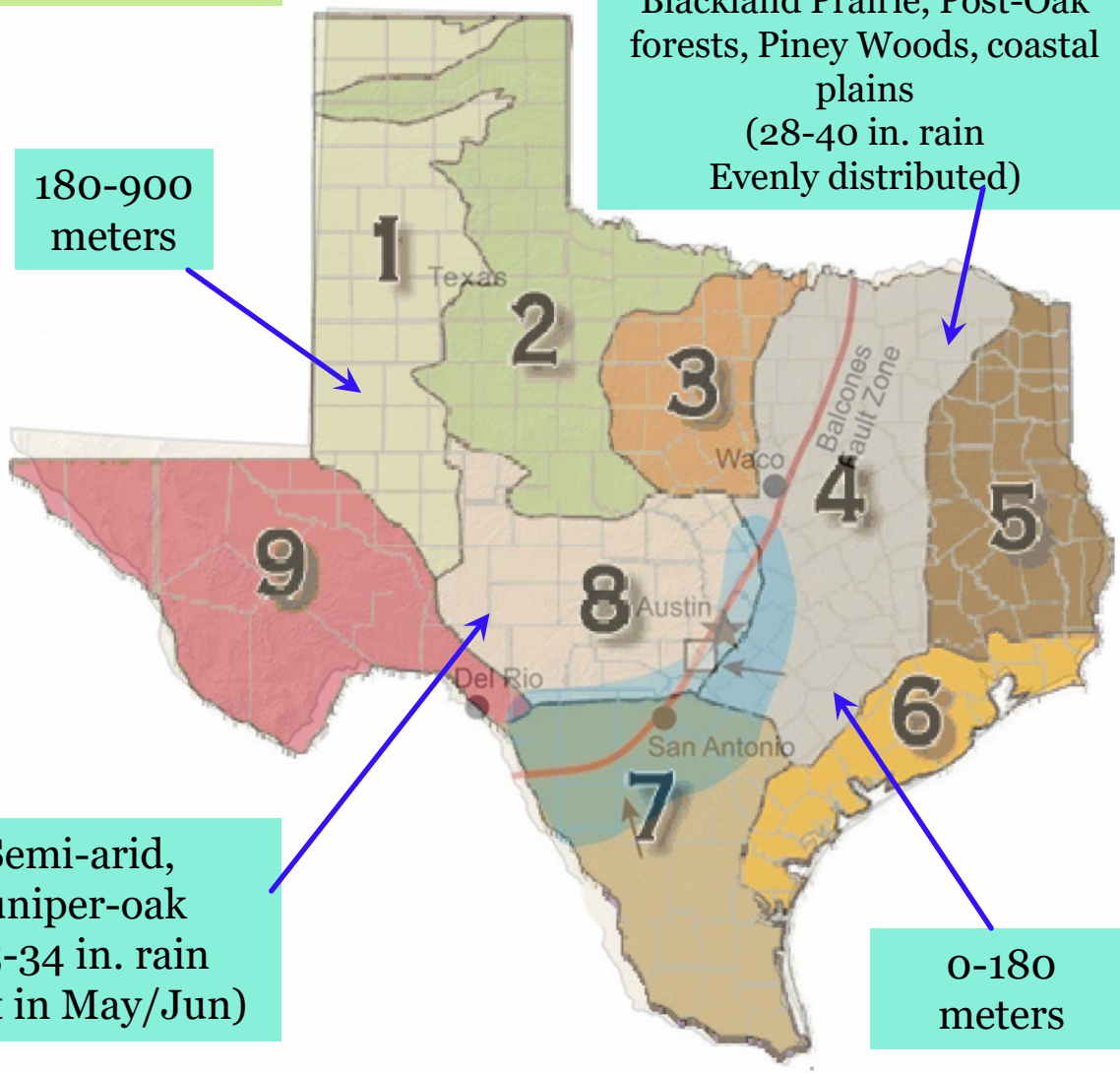
BALCONES ESCARPMENT

Strong ecological boundary **(Ecotone)**

Inactive fault line
Creates a strong W-E **ecotone**

Blackland Prairie, Post-Oak forests, Piney Woods, coastal plains
(28-40 in. rain
Evenly distributed)

180-900 meters



Semi-arid, juniper-oak
(15-34 in. rain
Most in May/Jun)

0-180 meters

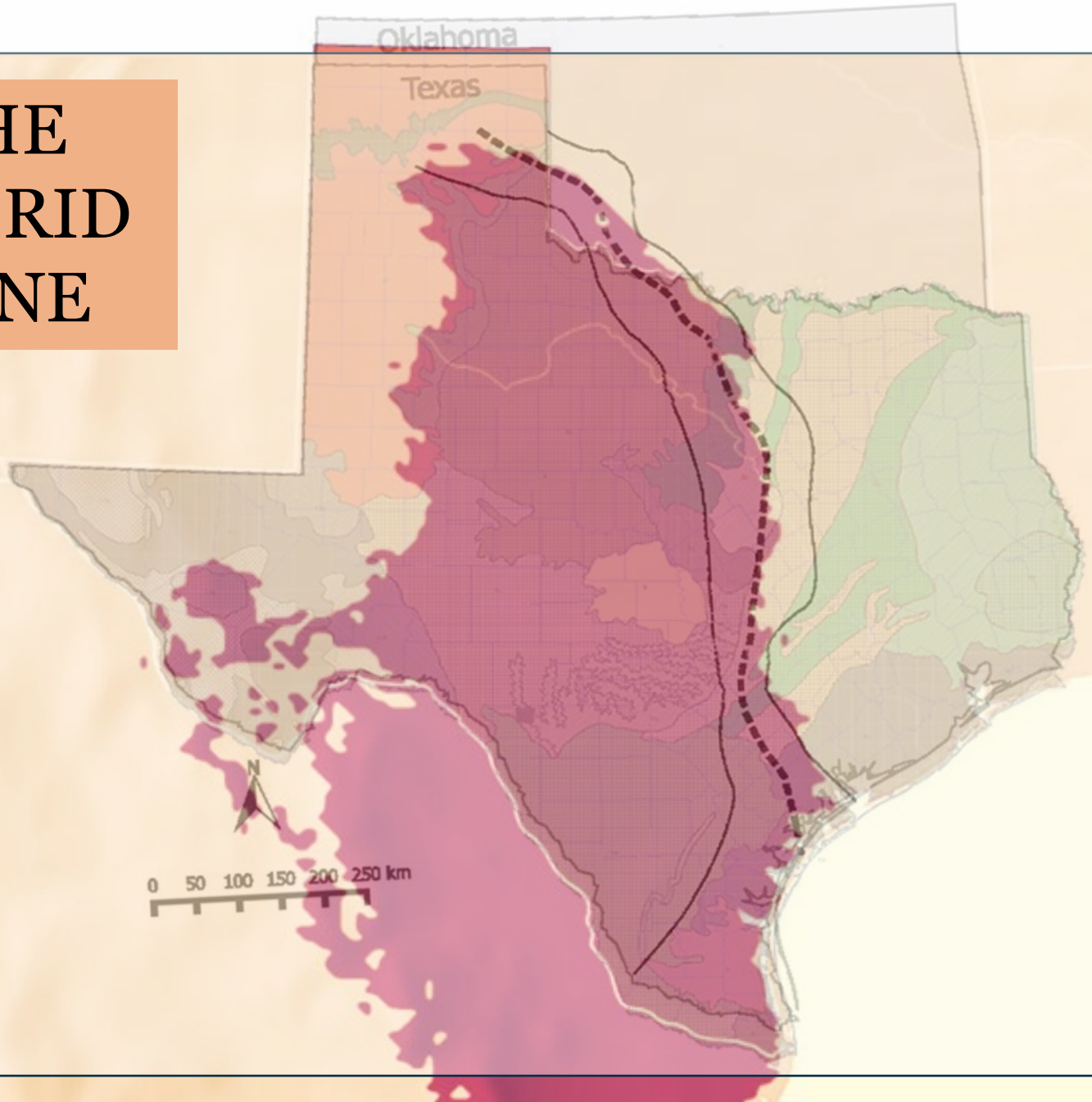
I-35

Hybrid zones cluster in “suture zones”

Eastern edge of Rockies – one of the most extensive suture zones

THE HYBRID ZONE

THE HYBRID ZONE



HYBRID ZONE WIDTH & CENTER (NATURAL LABS)

WIDTH OF HYBRID ZONE

- Measured over transects at several time periods
- Width can be:
  - Stable (width & location)
  - Expand
  - Contract
  - Center moves while remaining same width
    - Represents shifts in overall population density between species
  - No consistent pattern

WIDTH OF HYBRID ZONE

- Help determine what maintains species
- Stable width = stable hybrid zone
  - Balance between **selection** & **dispersal**
  - Allows estimation of dispersal and selection
- **Expansion – selection** & **dispersal** imbalanced
  - Requires sexual selection for hybrids (YOURE HOT),

  or
  - Adaptive advantages for hybrids

CENTER OF HYBRID ZONE

- Characteristics of individuals at center of zone
- Evaluate **selection** vs **dispersal**
- Resemble parents
  - Fewer generations of hybrid
  - = high **dispersal** & strong **selection**
- Different from parents
  - Many generations of hybridization & back-crossing
  - = low **dispersal** & weak **selection**

TEXAS HYBRID ZONE

- Secondary contact
- 2 populations interbreed 4-6 thousand years
- Stable hybrid zone forms
- **Selection** in equilibrium with **dispersal** (stable width)
- **Selection against hybrids** helps maintain 2 species
  - Black-crested (Texas hybrid zone)
    - Plumage under sexual selection
    - Parental species prefer **conspecific** song and plumage

OKLAHOMA HYBRID ZONE

- Recent secondary contact ~100 years
- Black-crested expanded range
  - Range fires became less frequent following settlement (~1870)
  - Woody plants invaded prairies

- Black-crested & Tufted
  - Few preferences by males or females for song or plumage

- Potential for continuing expansion
- Or other changes in hybrid zone

PHYSIOLOGICAL ADAPTATIONS

- During isolation sister lineages may develop physiological adaptations to differing environmental conditions

- Appears to be true here:
  - Blood glucose concentrations increase under stressful conditions

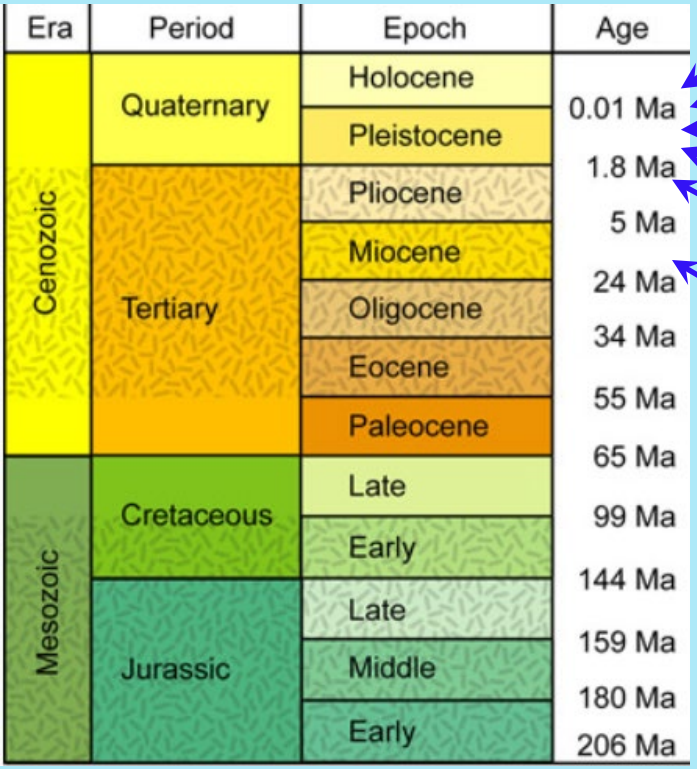
- Black-crested
  - Increased blood glucose concentrations
  - Lives in semi-arid environment = chronic stress
  - Unpredictable food & water & heat
  - Better able to deal with the stress

- Tufted
  - More aggressive
  - Physiological factors limit range expansion
    - Physiological adaptations to stress, aridity, heat
    - Less able to deal with different habitat

- Hybrids slightly less fit than parental species

THE TITMOUSE STORY

THE TITMOUSE STORY SUMMARY



Range expansion by Black-crested into Oklahoma creates younger hybrid zone (100 BP)

Secondary contact occurs (initially along forested river courses that connected ranges) creating older hybrid zone (4-6 thousand BP)

Titmice extend range via dispersal during a wetter period when woodlands extended into Mexico

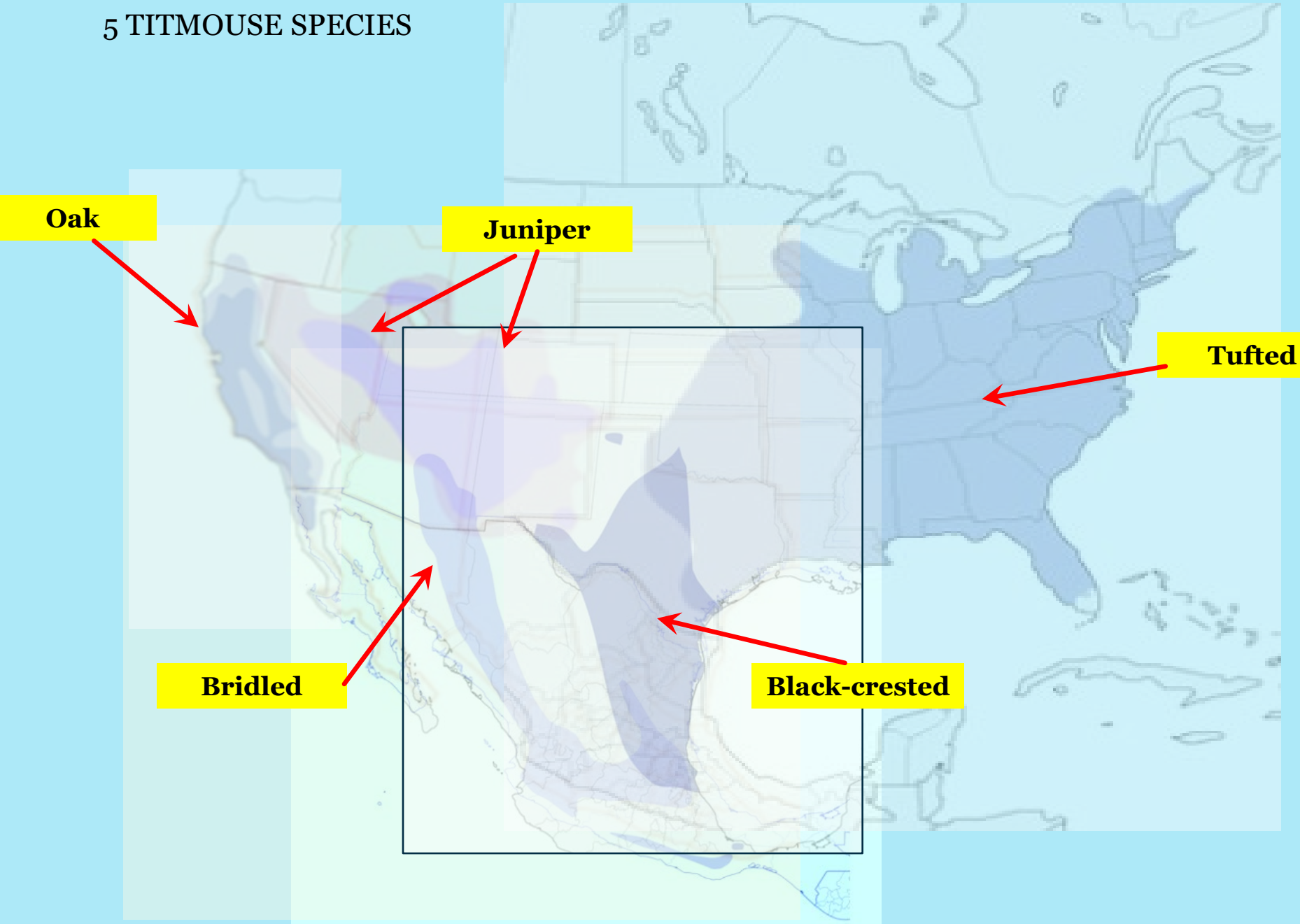
Woodland corridor broken during a less wet period, separating titmouse into 2 populations (200-250 thousand BP)

Baeolophus originates in New World (most other Paridae, originate in Asia)

Paridae colonize New World & Africa

1 Family Paridae & Family Remizidae diverge

5 TITMOUSE SPECIES



WHAT ABOUT THE
YELLOW-RUMPS ?

SPECIATION BY HYBRIDIZATION ?

Black-fronted

Myrtle

Audubon's

Anyone want to speculate?

Brelsford A., Hybridization and Speciation in the Yellow-Rumped Warbler Complex, Thesis