Species Co-occurrence

USGS
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Species co-occurrence: Single-season models

- Do some species tend to occur more (or less) often together than expected?

- A great deal of literature has been published during past 30 years on methods for assessing *patterns* of co-occurrence, but not accounting for detectability.

Species co-occurrence matrix

Species

		1	2	3	4	5
	1	1	0	0	1	0
	2	1	1	0	0	1
Units	3	0	1	1	1	0
	4	1	0	0	0	1
	5	1	1	0	1	0
	…	.	.	.	.	.
	s	1	0	0	1	1

Species co-occurrence matrix

Species

Units		1	2	3	4	5
	1	11	01	01	10	00
	2	10	11	00	01	11
	3	00	10	11	11	01
	4	10	00	00	00	10
	5	11	10	01	11	00
	…	.	.	.	.	.
	s	11	01	00	10	11

Species co-occurrence

- Direction of interaction may be correctly estimated, but the magnitude of the interaction underestimated, if probability of detecting a species is the same regardless of whether the other species is also present.

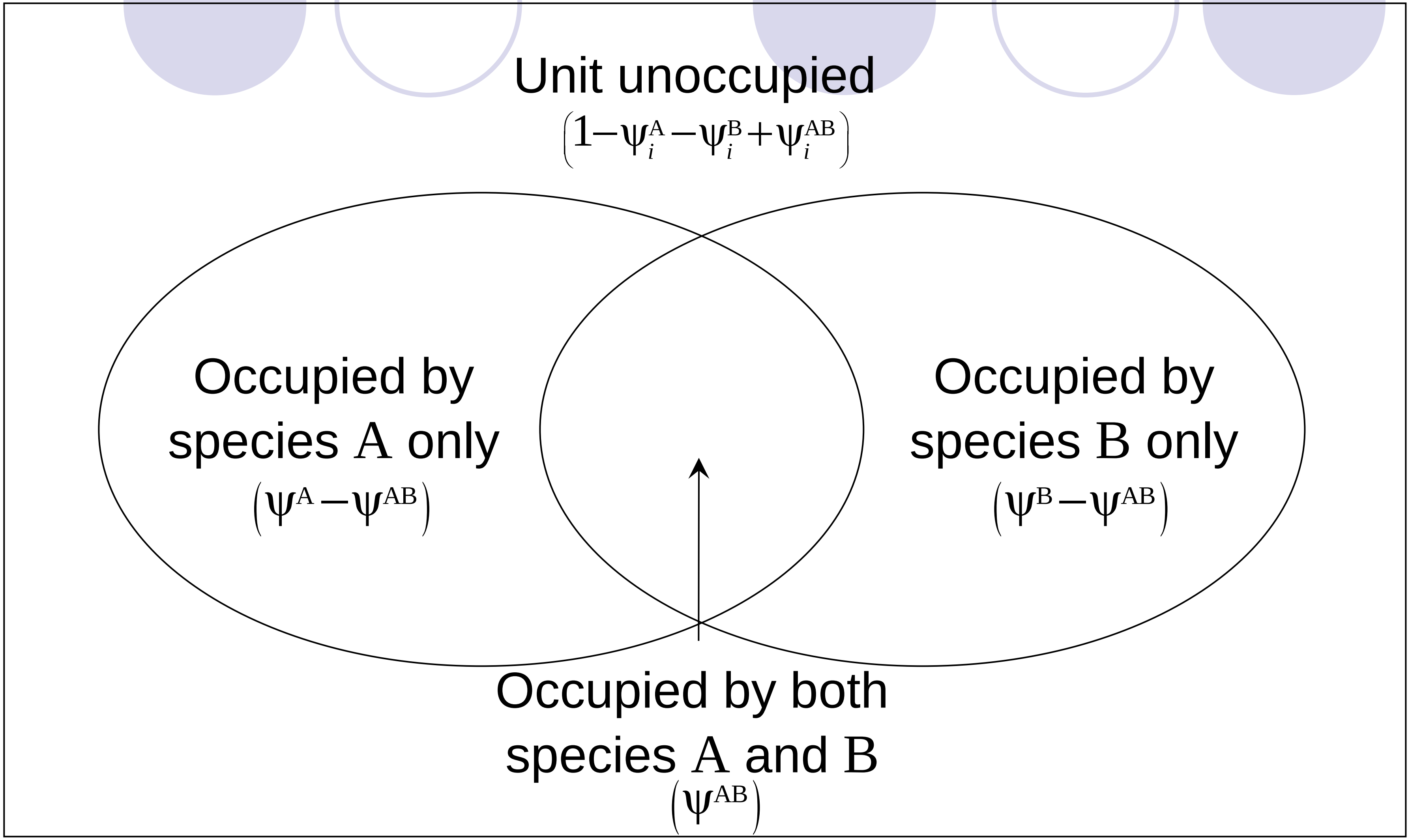
- If detectability of a species differs given the presence/absence of the other species, estimated interaction may be completely misleading.

Model parameters

ψ^{A} = probability unit occupied by species A

ψ^{B} = probability unit occupied by species B

ψ^{AB} = probability unit occupied by species A and B


Unit unoccupied
$\left(1-\psi_i^{A}-\psi_i^{B}+\psi_i^{AB}\right)$
Occupied by species A only
$\left(\psi^{A}-\psi^{AB}\right)$
Occupied by species B only
$\left(\psi^{B}-\psi^{AB}\right)$
Occupied by both species A and B
$\left(\psi^{AB}\right)$

Co-occurrence model (multistate)

- Consider units to be in one of 4 mutually exclusive 'states', or more generally 2^l states.
  - occupied by species A and B
  - occupied by species A only
  - occupied by species B only
  - occupied by neither species

$$\phi_0 = \left[\psi^{AB} \quad \psi^{A} - \psi^{AB} \quad \psi^{B} - \psi^{AB} \quad \left(1 - \psi^{A} - \psi^{B} + \psi^{AB}\right) \right]$$

Detection probabilities

Single species only present at site:

p^l = detection probability for species l, given only species l is present

Detection probabilities

Both species present at site:

r^{AB} = probability of detecting species A and B

r^{Ab} = probability of detecting species A, but not B

r^{aB} = probability of detecting species B, but not A

r^{ab} = probability of detecting neither species

Detection probabilities

- Define a detection probability vector

$$\mathbf{p}^{\{000\},\{101\}} = \begin{bmatrix} r_1^{\mathrm{aB}} r_2^{\mathrm{ab}} r_3^{\mathrm{aB}} \\ 0 \\ p_1^{\mathrm{B}} \left(1 - p_2^{\mathrm{B}}\right) p_3^{\mathrm{B}} \\ 0 \end{bmatrix}$$

Building a two-species model

- Define $\Pr\left(\mathbf{h}_i^{\mathrm{A}}, \mathbf{h}_i^{\mathrm{B}}\right)$ for each unit *i*

$$\Pr\left(\mathbf{h}_i^{\mathrm{A}}, \mathbf{h}_i^{\mathrm{B}}\right) = \boldsymbol{\phi}_0 \mathbf{p}^{\left\{\mathbf{h}_i^{\mathrm{A}}\right\}, \left\{\mathbf{h}_i^{\mathrm{B}}\right\}}$$

- The model likelihood is:

$$L = \prod_{i=1}^{s} \Pr\left(\mathbf{h}_i^{\mathrm{A}}, \mathbf{h}_i^{\mathrm{B}}\right)$$

Building a two-species model

- Consider $\mathbf{h}^{A} = 11$, $\mathbf{h}^{B} = 01$
  - Description: Both species present, only species A detected in survey 1, both detected in survey 2
  - Math: $\psi^{AB} r^{Ab} r^{AB}$

Building a two-species model

- Consider $\mathbf{h}^{\mathrm{A}} = 11$, $\mathbf{h}^{\mathrm{B}} = 00$
  - Description: Both species present, only species A detected in either survey,
    OR only species A present and was detected in surveys 1 & 2
  - Math: $\psi^{\mathrm{AB}} r^{\mathrm{Ab}} r^{\mathrm{Ab}} + \left(\psi^{\mathrm{A}} - \psi^{\mathrm{AB}}\right) p^{\mathrm{A}} p^{\mathrm{A}}$

Building a two-species model

- Consider $\mathbf{h}^{\mathrm{A}}$ = 00, $\mathbf{h}^{\mathrm{B}}$ = 00
  - Description: Both species present with neither ever being detected,
    OR only species A present and never detected,
    OR only species B present and never detected,
    OR both species absent
  - Math: $\psi^{AB}\left(r^{ab}\right)^2+\left(\psi^{A}-\psi^{AB}\right)\left(1-p^{A}\right)^2+\left(\psi^{B}-\psi^{AB}\right)\left(1-p^{B}\right)^2+\left(1-\psi^{A}-\psi^{B}+\psi^{AB}\right)$

1. Do the species co-occur more (or less) often than expected?

- If species occur at units independently then,

$$\psi^{AB} = \psi^{A} \times \psi^{B}$$

- The level of co-occurrence could be quantified as,

$$\hat{\varphi} = \frac{\hat{\psi}^{AB}}{\hat{\psi}^{A} \times \hat{\psi}^{B}}$$

1. Do the species co-occur more (or less) often than expected?

- Suggested reparameterization,

$$\psi^{AB} = \psi^{A} \times \psi^{B} \times \varphi$$

- Model φ directly

1. Do the species co-occur more (or less) often than expected?

- Another parameterization,

$$\psi^{AB} = \psi^{B|A}\psi^{A}$$

$$\psi^{B} = \psi^{B|A}\psi^{A} + \psi^{B|a}(1-\psi^{A})$$

- Estimated parameters are ψ^{A}, $\psi^{B|a}$ and $\psi^{B|A}$.

1. Do the species co-occur more (or less) often than expected?

- A third parameterization,

$$\nu = \frac{\psi^{B|A} \Big/ \left(\psi^{A} - \psi^{B|A}\right)}{\psi^{B|a} \Big/ \left(1 - \psi^{A} - \psi^{B|a}\right)}$$

- Equivalent to logistic regression with the presence of sp. A as a predictor variable for the presence of sp. B
- Estimated parameters are $\psi^{A}, \psi^{B|a}$ and ν (other sets possible).

2. Are the species detected independently?

- Redefine $r^{AB} = r^{A} \times r^{B} \times \delta$
- Detections are independent if, $\delta = 1$
- Or use similar reparameterizations as for occupancy

3. Is the probability of detecting species A affected by the presence of species B?

- Consider models with the constraint,

$$r^{\mathrm{A}} = p^{\mathrm{A}}$$

- Or similarly, $r^{\mathrm{B}} = p^{\mathrm{B}}$

Multiple-season species co-occurrence

- Single-season model only allows inference about the *patterns* of co-occurrence.
- To make inferences about the *dynamic processes* of change in co-occurrence need to survey the species at systematic points in time.
- Dynamic processes are probabilities of colonization and local extinction, given the presence or absence of other species.
- These processes *produce* observed patterns.

Multiple-season species co-occurrence

- Define a matrix that determines how the occupancy state of units may change between seasons t and $t+1$.

$$\phi_t = \begin{bmatrix} \mathrm{AB} \rightarrow \mathrm{AB} & \mathrm{AB} \rightarrow \mathrm{A} & \mathrm{AB} \rightarrow \mathrm{B} & \mathrm{AB} \rightarrow \mathrm{U} \\ \mathrm{A} \rightarrow \mathrm{AB} & \mathrm{A} \rightarrow \mathrm{A} & \mathrm{A} \rightarrow \mathrm{B} & \mathrm{A} \rightarrow \mathrm{U} \\ \mathrm{B} \rightarrow \mathrm{AB} & \mathrm{B} \rightarrow \mathrm{A} & \mathrm{B} \rightarrow \mathrm{B} & \mathrm{B} \rightarrow \mathrm{U} \\ \mathrm{U} \rightarrow \mathrm{AB} & \mathrm{U} \rightarrow \mathrm{A} & \mathrm{U} \rightarrow \mathrm{B} & \mathrm{U} \rightarrow \mathrm{U} \end{bmatrix}$$

Multiple-season species co-occurrence

- Define a matrix that determines how the occupancy state of units may change between seasons t and $t+1$.

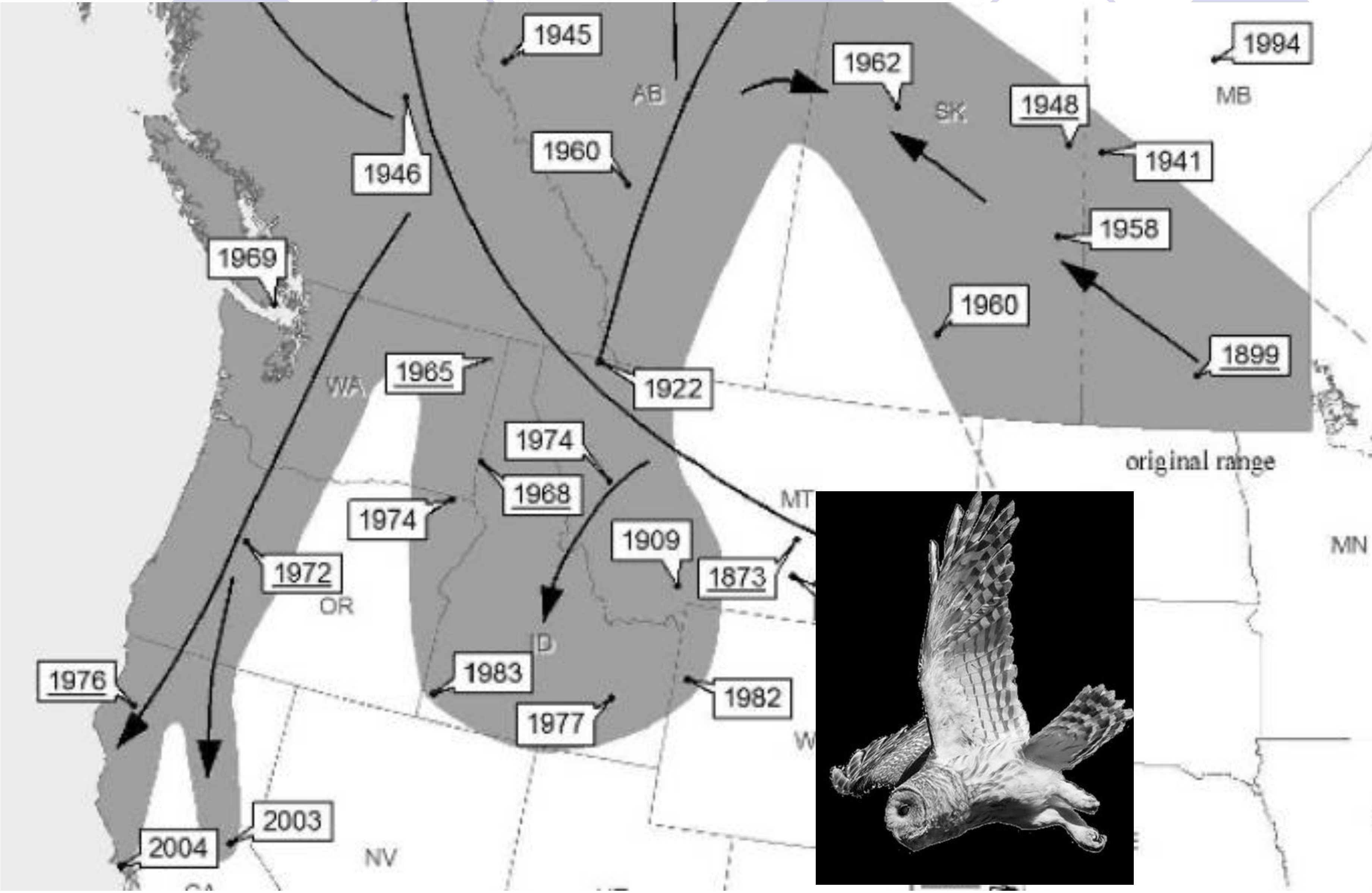
$$\phi_t = \begin{bmatrix} 1-\varepsilon_t^{A}-\varepsilon_t^{B}+\varepsilon_t^{AB} & \varepsilon_t^{B}-\varepsilon_t^{AB} & \varepsilon_t^{A}-\varepsilon_t^{AB} & \varepsilon_t^{AB} \\ \eta_t^{B} & 1-\omega_t^{AB}-\eta_t^{B}-\upsilon_t^{A} & \omega_t^{AB} & \upsilon_t^{A} \\ \eta_t^{A} & \omega_t^{BA} & 1-\omega_t^{BA}-\eta_t^{A}-\upsilon_t^{B} & \upsilon_t^{B} \\ \gamma_t^{AB} & \gamma_t^{A}-\gamma_t^{AB} & \gamma_t^{B}-\gamma_t^{AB} & 1-\gamma_t^{A}-\gamma_t^{B}+\gamma_t^{AB} \end{bmatrix}$$

Multiple-season species co-occurrence

- Observed data likelihood approach:

$$\Pr\left(\mathbf{h}_i^{\mathrm{A}}, \mathbf{h}_i^{\mathrm{B}}\right) = \boldsymbol{\phi}_0 \prod_{t=1}^{T-1} D\left(\mathbf{p}_t^{\left\{\mathbf{h}_{it}^{\mathrm{A}}, \mathbf{h}_{it}^{\mathrm{B}}\right\}}\right) \boldsymbol{\phi}_t \mathbf{p}_T^{\left\{\mathbf{h}_{iT}^{\mathrm{A}}, \mathbf{h}_{iT}^{\mathrm{B}}\right\}}$$

- Complete data likelihood could also be developed and used with EM algorithm or data augmentation


1945
1994
1962
AB
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1899
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1982
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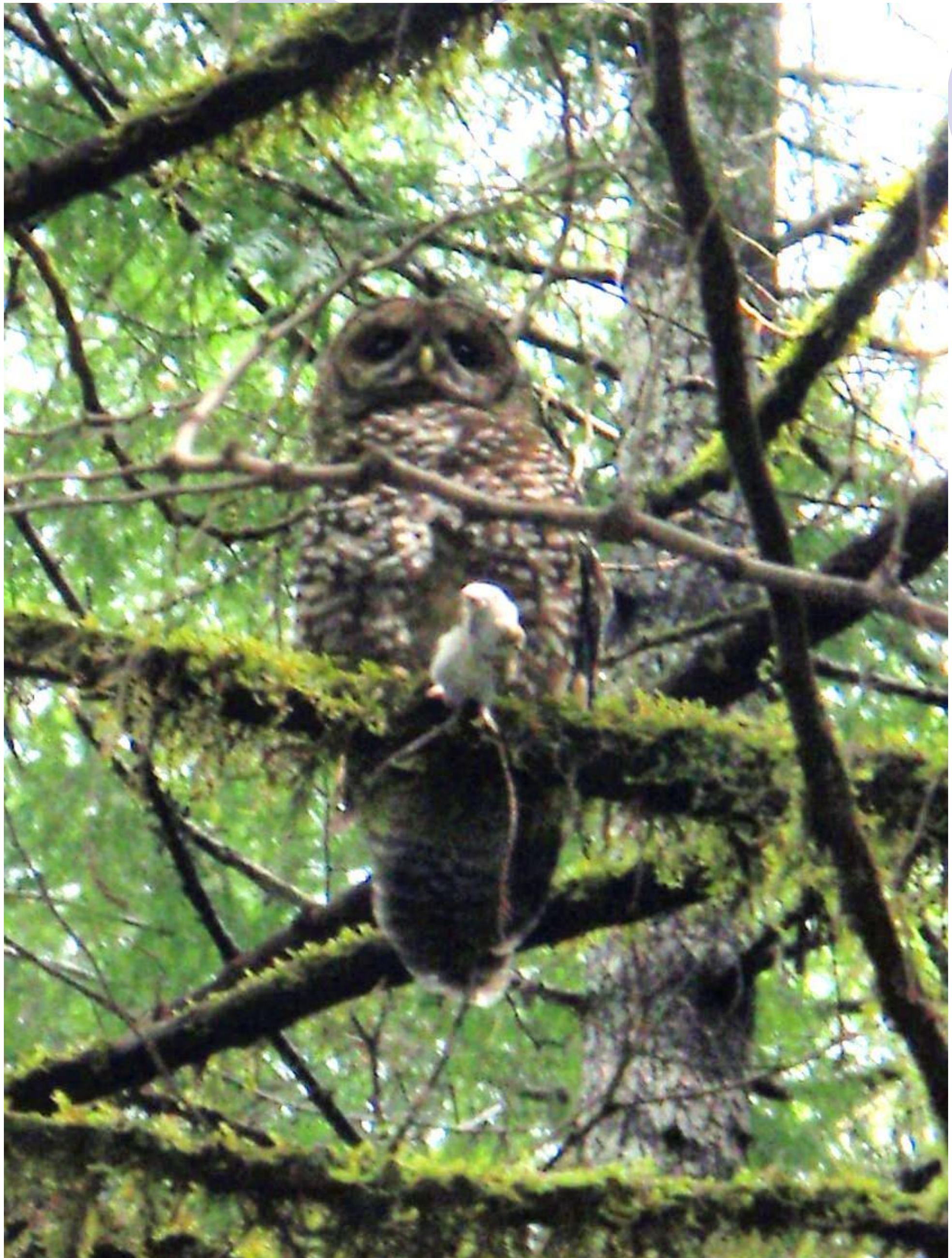
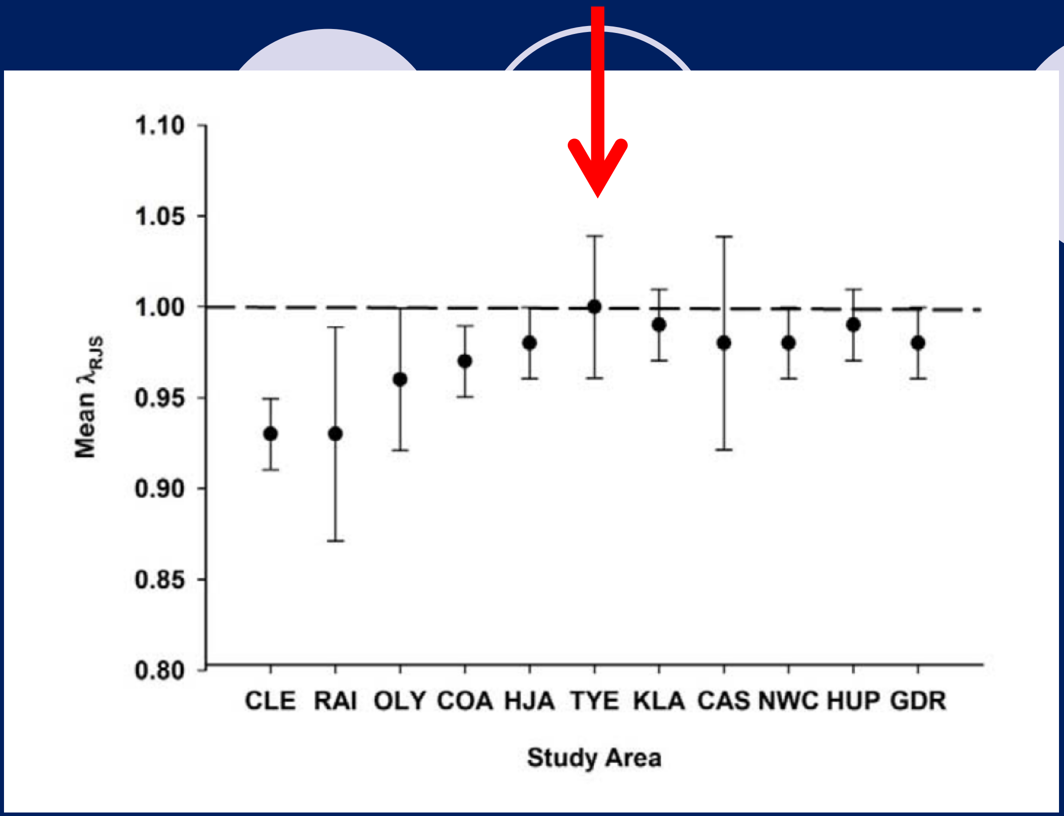
2004
NV

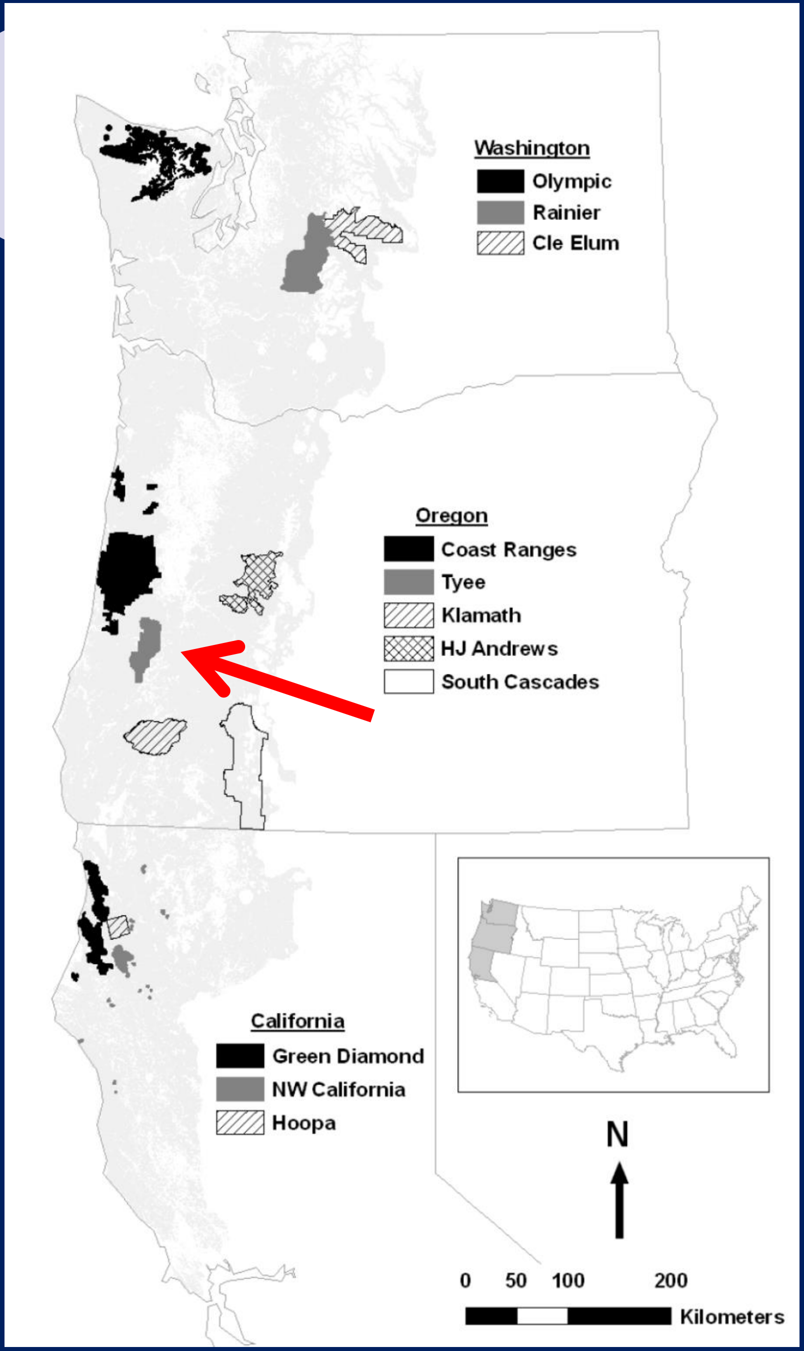



SAVE A LOGGER
UUPS
"EAT AN OWL"



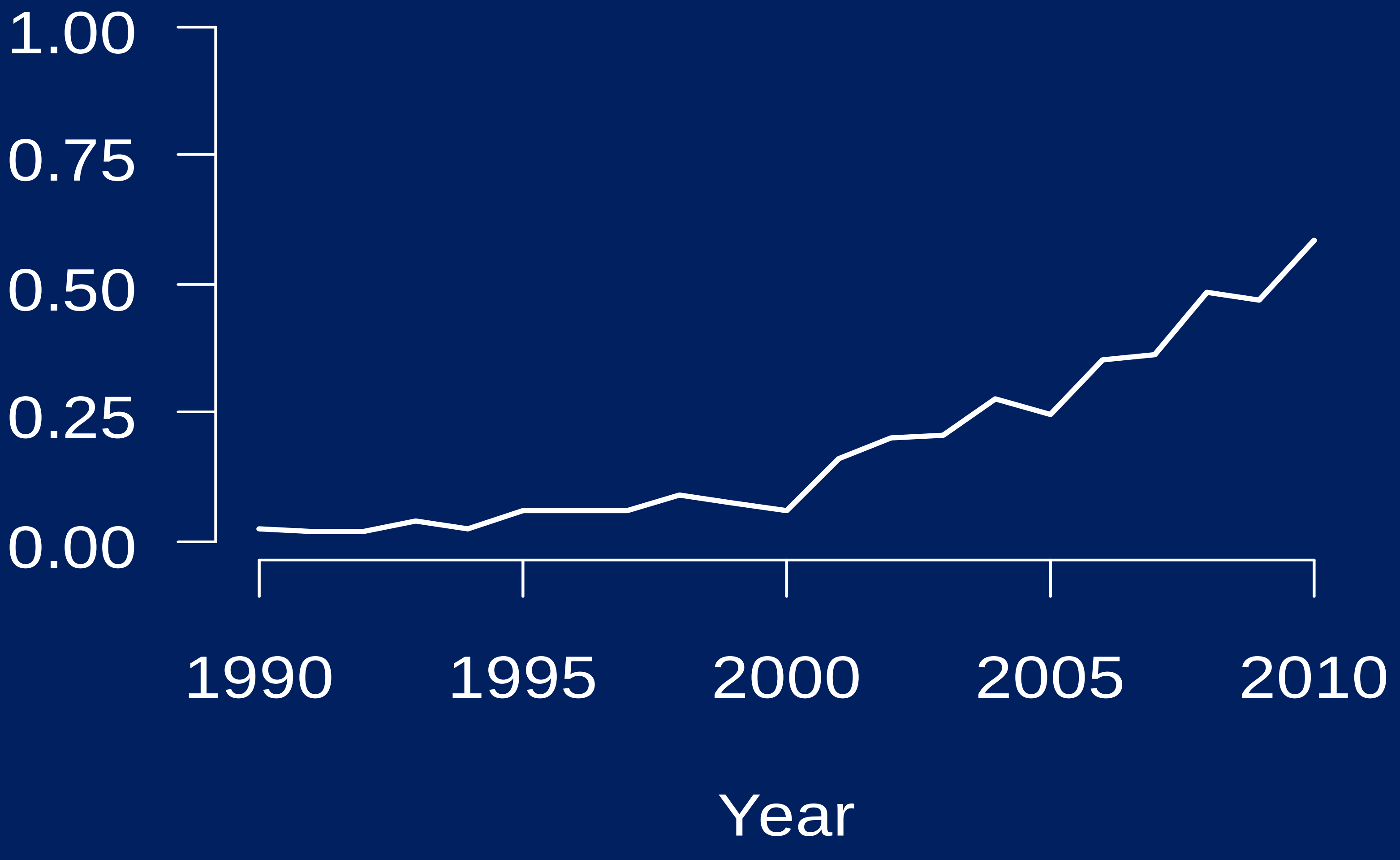
North

South



Forsman et al. (2011) Population demography of Northern spotted owl

Proportion of sites with barred owl detections



Detection (Bailey et al. 2009)

- Northern spotted owl
  - Time of day, method, barred owl presence
  - 0.05 – 0.57
- Barred owl
  - Time of day, method
  - Survey length or Northern spotted owl presence
  - 0.03 – 0.46

Multispecies dynamic model: Inferences and questions

- Detection
  - Is barred owl detection lower in jointly occupied territories for biological or methodological reasons?
- Species interactions
  - Is competition completely unidirectional?
  - What is the strength of competition (effect size)?
- Forest type
  - BO like riparian forest.
  - NSO like older growth forest.
  - Does this biological difference create a mechanism for coexistence?
- Forecast occupancy dynamics
  - Will Northern spotted owls persist at Tyee?

Multispecies dynamic model

- Detection
  - Is barred owl detection lower in jointly occupied territories for biological or methodological reasons?
- Previous result (Bailey et al. 2009)
  - BO showed lower detection probabilities when NSO was present
- Current analysis
  - strong evidence that survey length influenced BO detection
  - evidence is motivating change in survey protocol

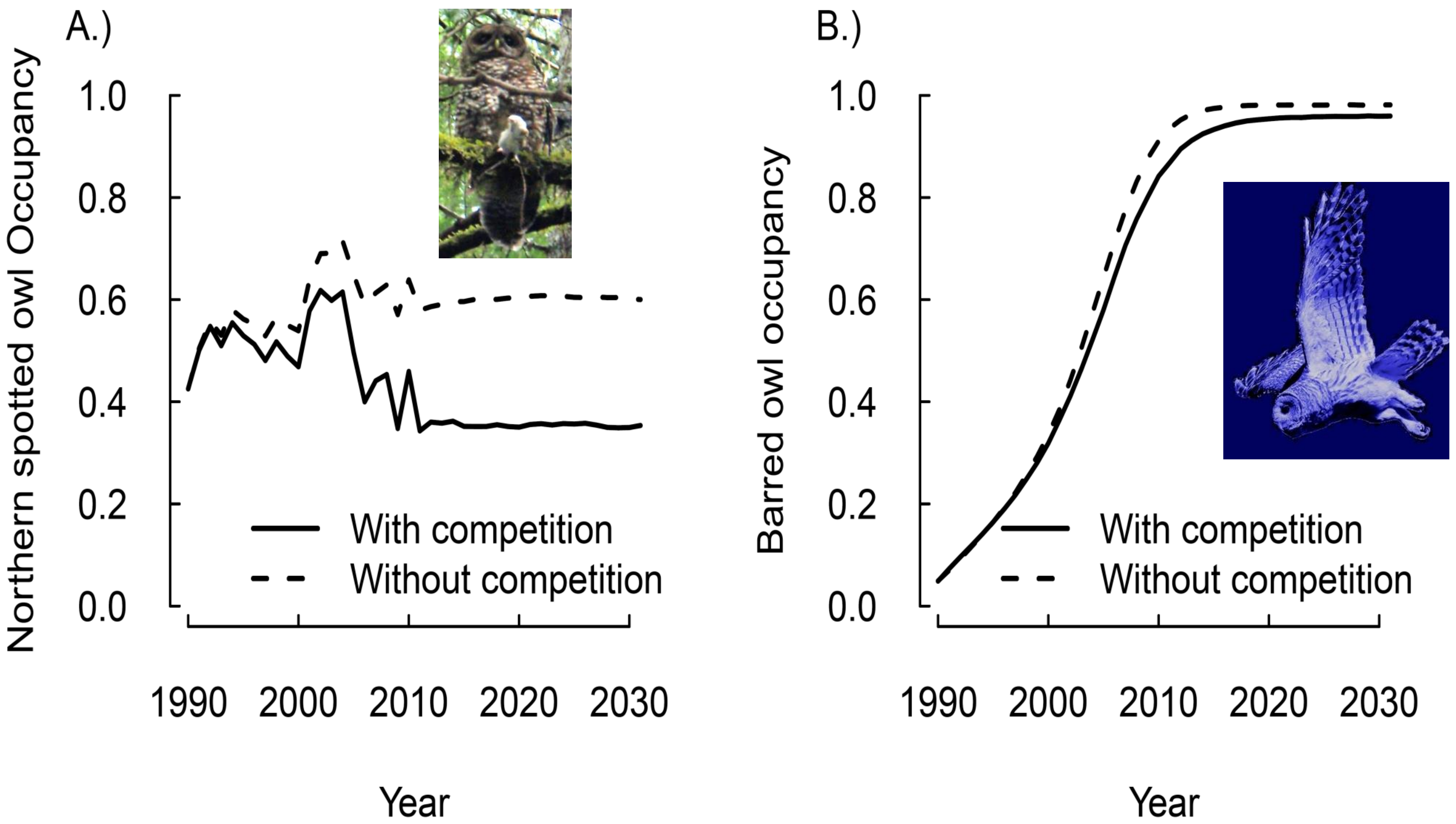
Multispecies dynamic model

- Species interactions
  - Is competition completely unidirectional?
  - What is the strength of competition (effect size)?

- Extinction probability
  - Higher each species when other species is present
  - Much larger effect of BO on NSO than vice versa

- Colonization
  - Some evidence of lower NSO colonization of patches inhabited by BO
  - Some evidence of higher BO colonization of patches inhabited by NSO

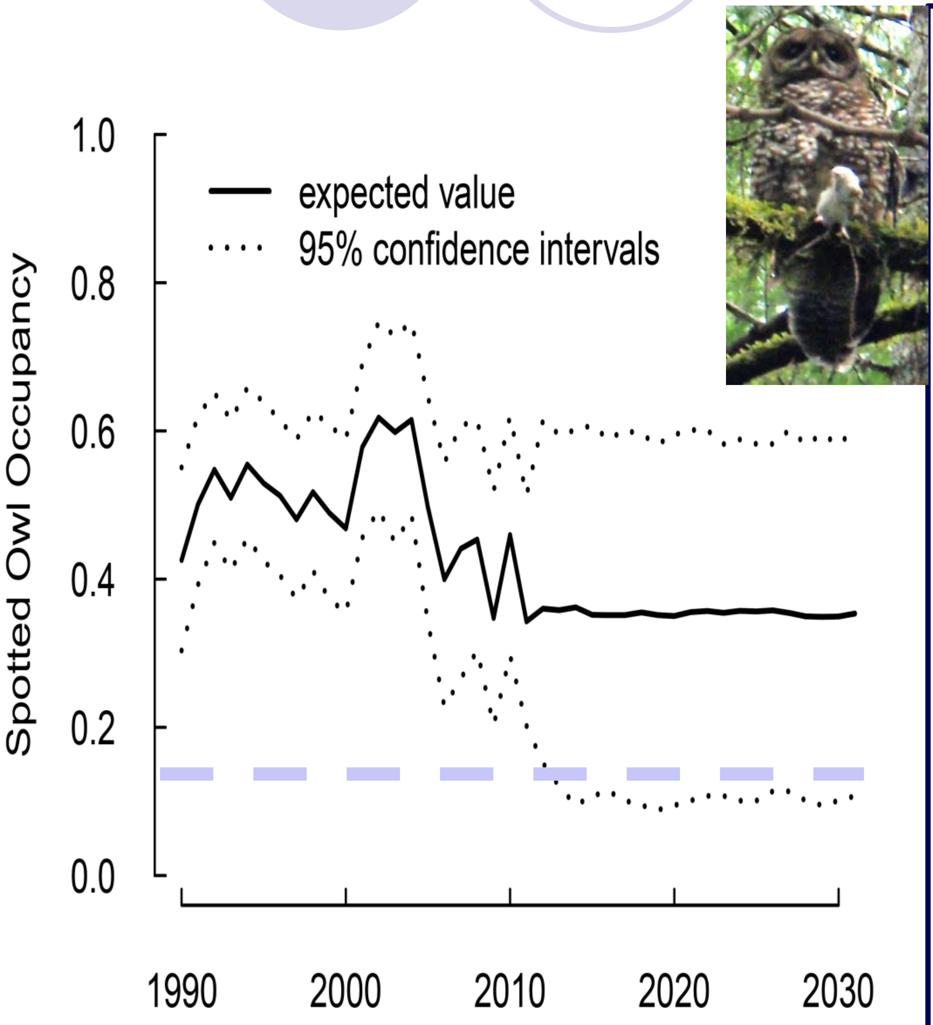
Species interactions

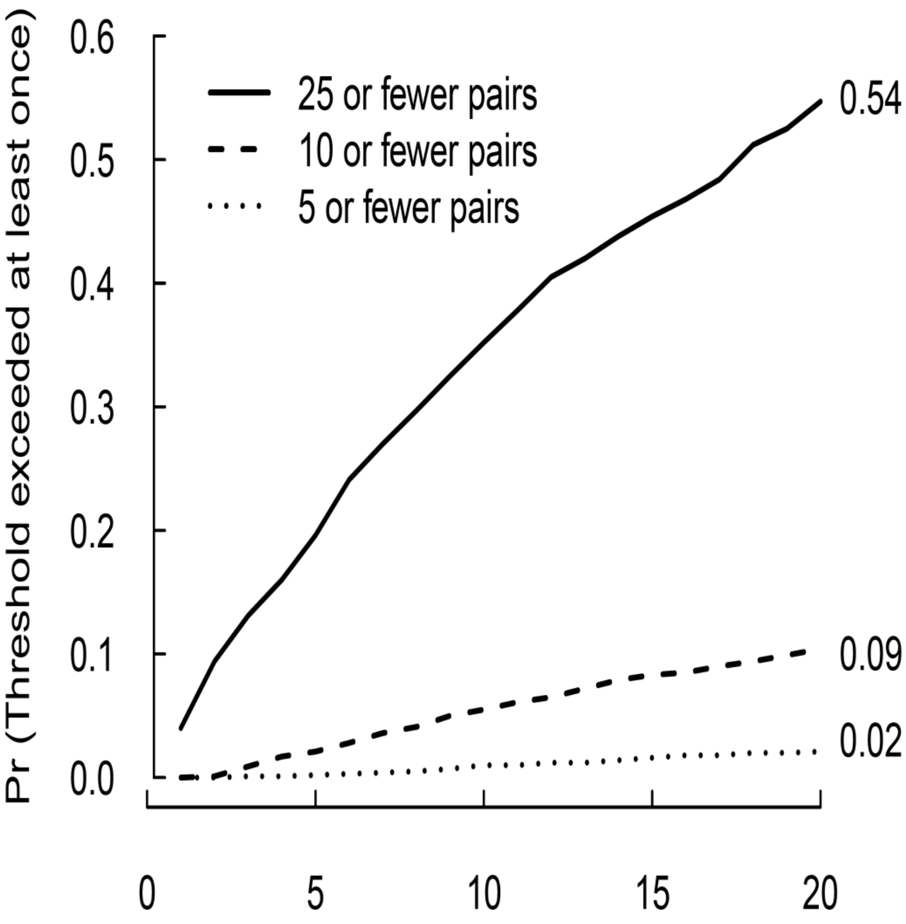


Multispecies dynamic model

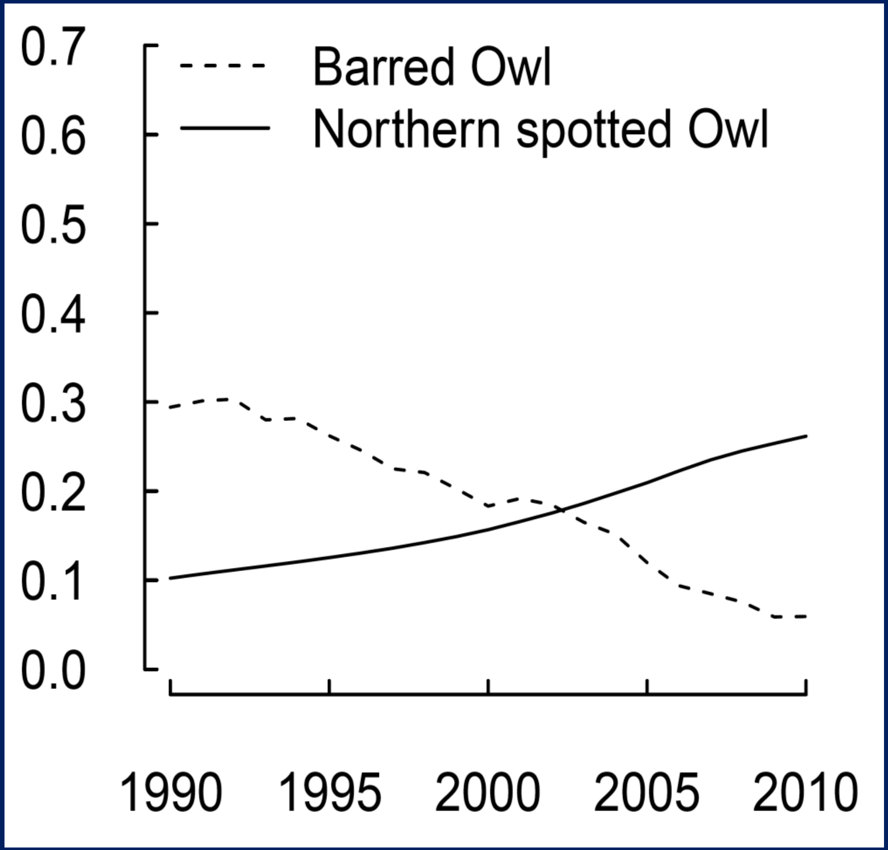
- Forecast occupancy dynamics
  - Will Northern spotted owls persist at Tyee?
- Uncertain, but not optimistic
  - Simulations/projections indicate NSO persistence on average
  - But NSO occupancy occasionally drops very low
  - “The future’s uncertain and the end is always near” (Doors/Morrison 1970)

Northern spotted owl persistence?

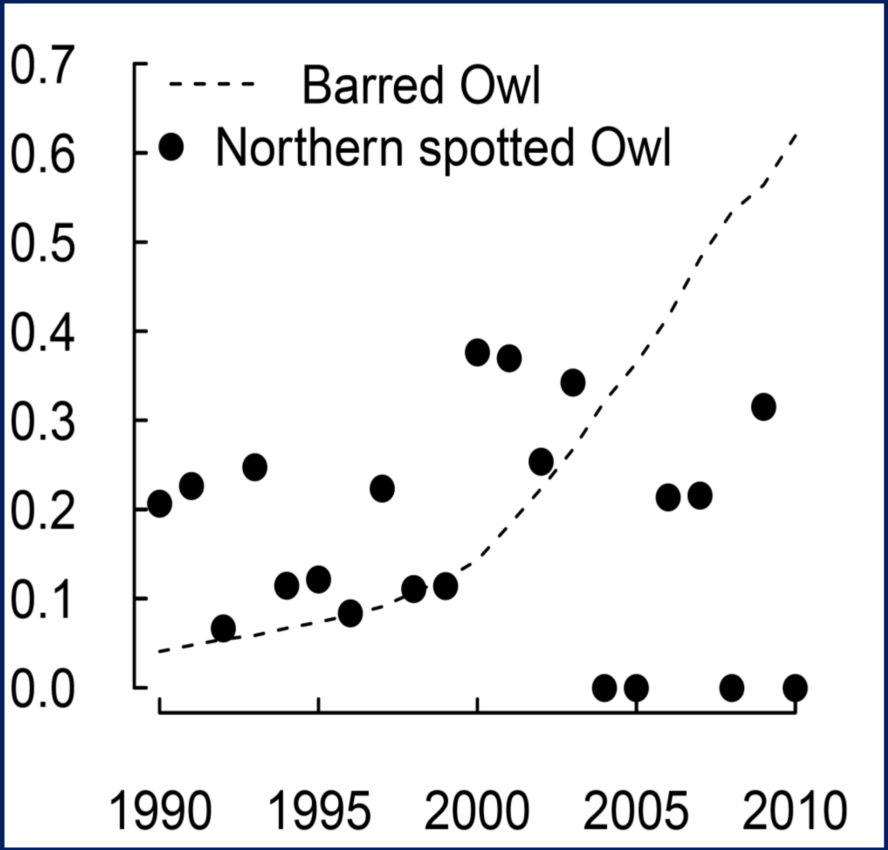




Population dynamics and uncertainty



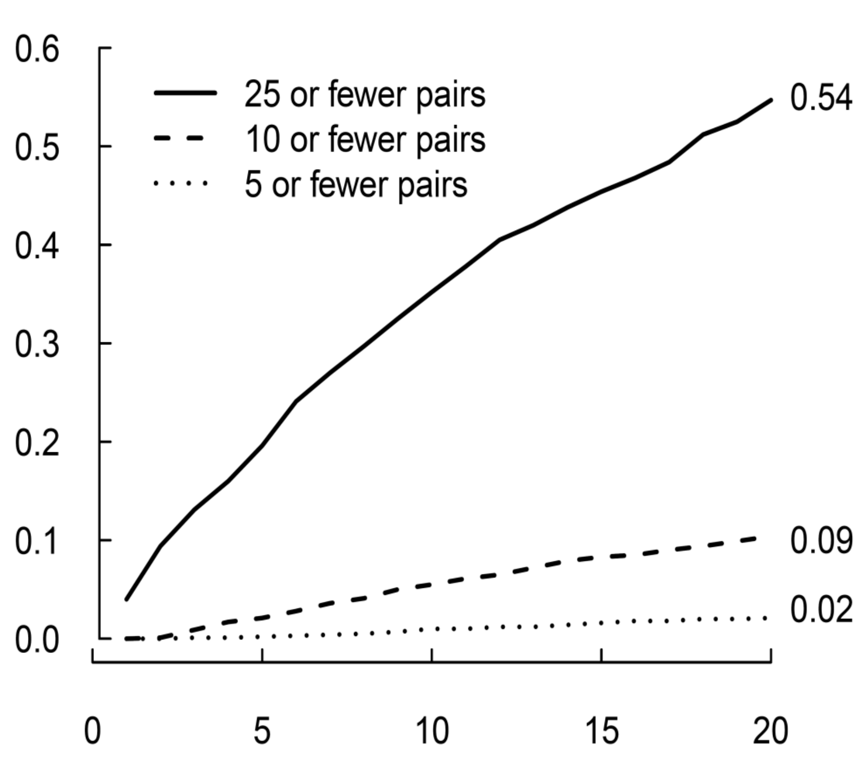
NSO extinction rates will remain high.



Will colonization eventually decline?

Take home messages I

- Dynamic modeling provides means of making inferences and projections (with and without management)
- Could add dynamic habitat modeling
- Autologistic modeling useful for BO invasion



Take home messages II

- Evidence for macroecological effects of competition: asymmetric competition with BO may be a factor associated with decreases in NSO occupancy
- Dynamic model projections indicate attainment of dynamic equilibrium for NSO, but with non-negligible probabilities of drops to very low levels of occupancy
- Dynamic model can be useful in projecting effects of various management options (e.g., BO removal)

Summary

- Imperfect detection of species may lead to misleading conclusions about species co-occurrence.
- Similarly, some apparent relationships may be explained by different habitat preferences or different responses to environmental changes.
- Reliable inferences about change can only be made by observing the system at systematic points in time.