# Balancing act: using balancing to measure transient dynamics across the animal kingdom

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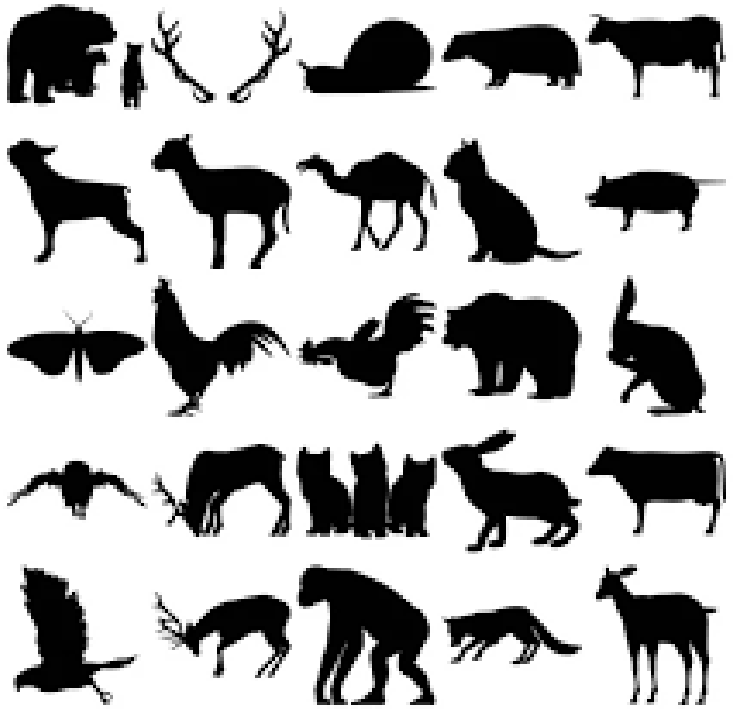
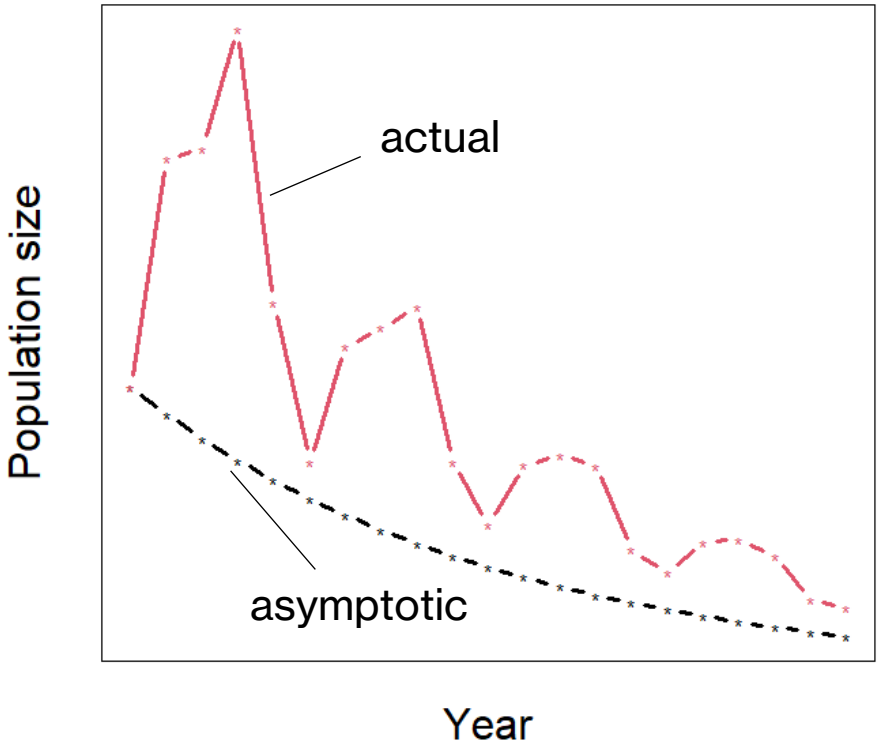


# Transient vs. asymptotic dynamics

- Because populations are at the mercy of random disturbances large and small, they rarely, if ever, converge on predicted long-term behaviors
- The population growth rate in a single time step can be much greater or much less than what is predicted by the usual asymptotic growth rate



# Population projection matrix model

- I examine transient dynamics of a population projection matrix model of the form

$$\boldsymbol{n}_{t+1} = \mathbf{A}\boldsymbol{n}_t$$

- $\boldsymbol{n}_t$ is the population vector at time $t$
- $\boldsymbol{A}$ is a population projection matrix

# Indices of transient dynamics

- Reactivity

$$\sigma_1(\boldsymbol{A}) = \max_{\boldsymbol{x}} \|\boldsymbol{A}\boldsymbol{x}\|_2$$

- Henrici metric

$$h(\boldsymbol{A}) = \sqrt{\sum_{i=1}^{n} \sigma_i^2 - |\lambda_i|^2}$$

# Disentangling transient and asymptotic dynamics

- It is customary to apply the indices of transient dynamics to a standardized population projection matrix instead of the projection matrix itself

$$\widehat{\boldsymbol{A}} = \boldsymbol{A}/\lambda_1$$

- Standardization does not go far enough

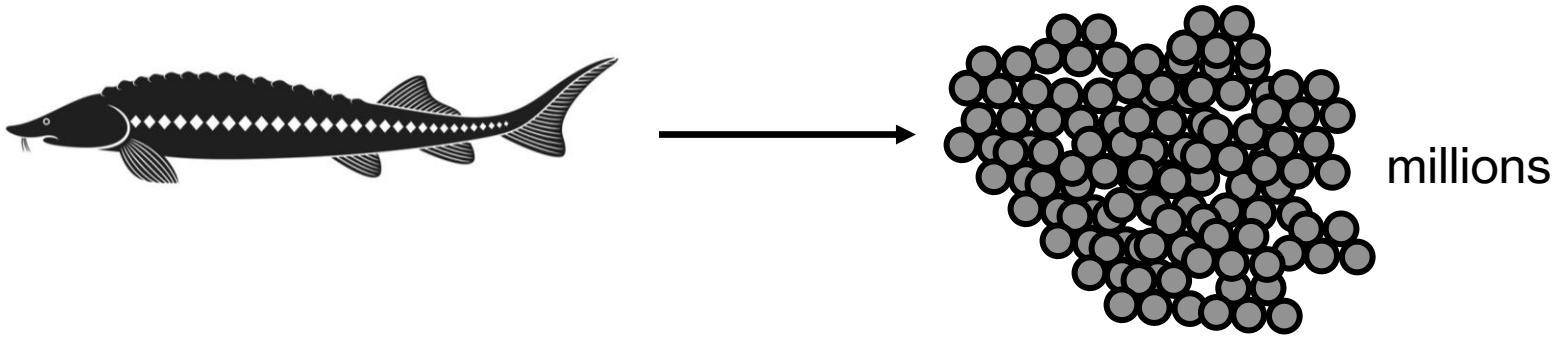
# Two problems with current indices of transient dynamics

- Classes that are exceptionally large have undue influence on the calculation of population growth rate (**Distortion**)

- Indices of transient dynamics are scale dependent
  - Counting a class such as eggs by the dozen, 100s, or by the molecule changes the value of an index of transient dynamics (but not the eigenvalues)

# Beluga sturgeon illustration

- Beluga sturgeon stable age distribution shows that the youngest class (eggs) is 4,355,878 times the number of 13 year-olds (Doukakis et al., 2010)
- Contributing to this skewed age distribution are the high fertility rates of the mature age classes, some in the millions, which pour eggs into the first age class in a single time step
- A single mature female can contribute millions of eggs to the youngest age class, making the reactivity quite large.



# Undue influence of eggs on population size

- A single egg is counted as the same as a mature adult even though an egg has a minute chance ($6.0 \times 10^{-7}$) of surviving a single year

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- The egg class has undue influence on the calculation of population size

# Indices of transient dynamics for beluga sturgeon

- Reactivity and the Henrici metric (applied to the standardized $\boldsymbol{A}$) are both 22,617,150 for the beluga sturgeon standardized $\boldsymbol{A}$
- Rescale the model so that eggs are counted as the number of 1-year-olds produced by those eggs
- This rescaling does not change the eigenvalues, but it has a profound influence on the indices of transient dynamics
- The rescaled model has reactivity 22.63 and Henrici metric 22.54

# Balancing

- Better would be indices of transient dynamics that are scale invariant
- *Solution*: rescale by the stable population distribution (balancing)

$$\tilde{\boldsymbol{n}}_t = \{\mathrm{diag}(\boldsymbol{w})\}^{-1}\hat{\boldsymbol{n}}_t$$

- Rescaling gives “large” and “small” a precise meaning (Murray, 1989)

# Balanced matrix

- The population projection matrix for the rescaled population vector becomes

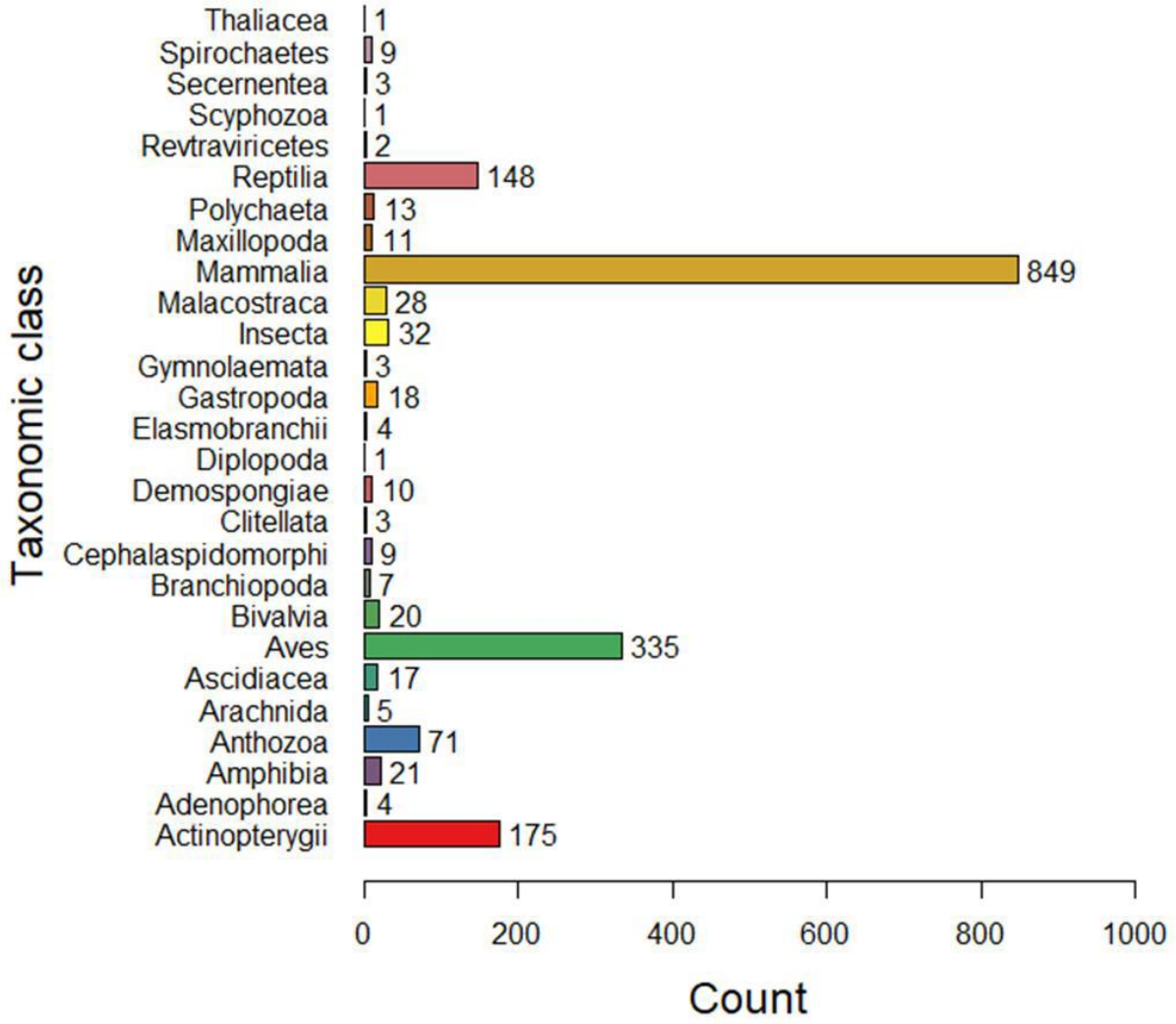
$$\widetilde{\boldsymbol{A}} = \{\mathrm{diag}(\boldsymbol{w})\}^{-1}\widehat{\boldsymbol{A}}\mathrm{diag}(\boldsymbol{w})$$

I call this the balanced population projection matrix. It has the same eigenvalues as $\widehat{\boldsymbol{A}}$

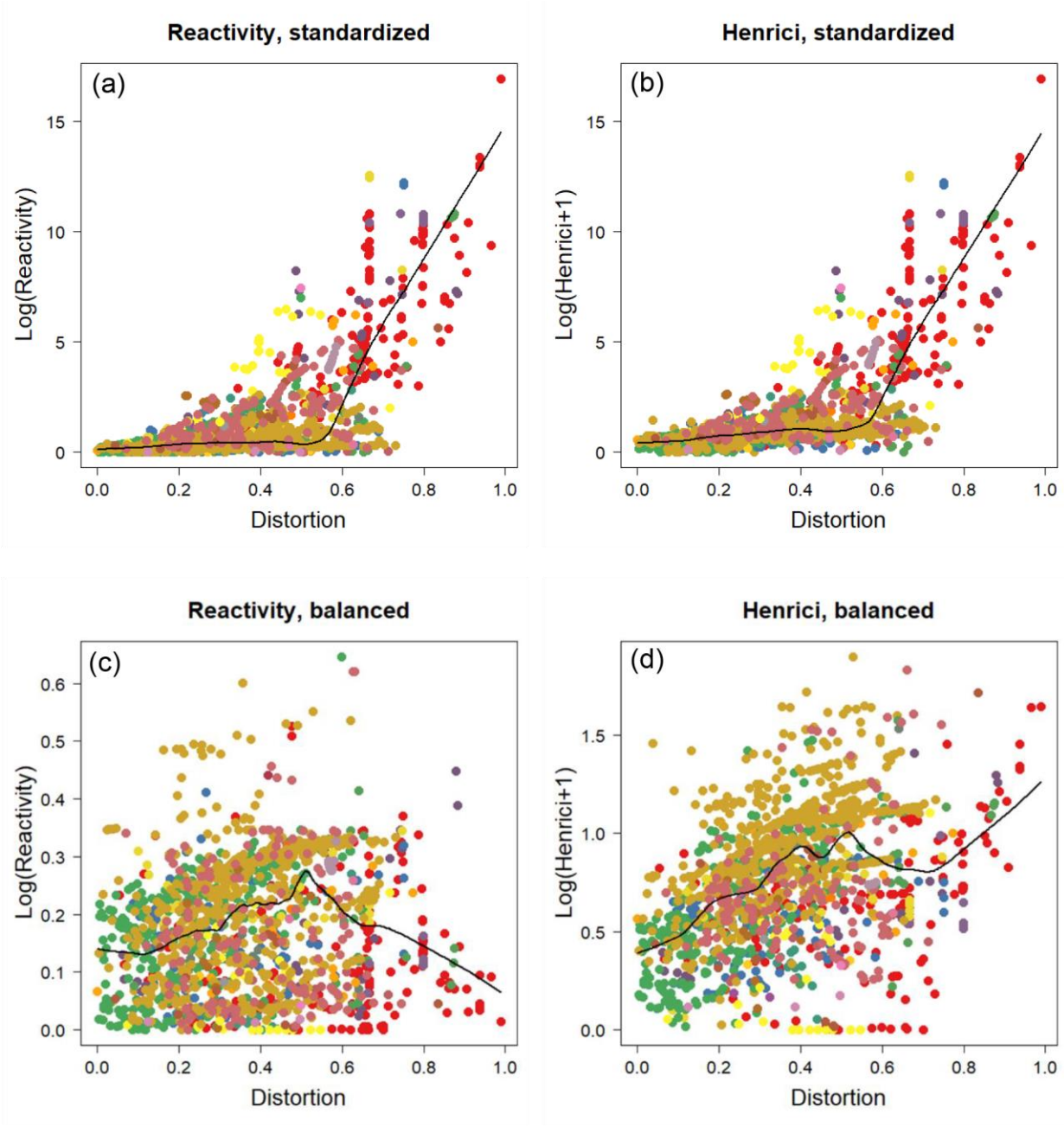
# Properties with balancing

- Indices of transient dynamics are scale invariant
- No undue influence of naturally large classes because the stable "balanced" population vector is a uniform distribution
- Balanced matrix is row stochastic (its rows sum to one)
- $1 \leq \text{reactivity} \leq \sqrt{n}$
- $0 \leq \text{Henrici metric} \leq \sqrt{n-1}$

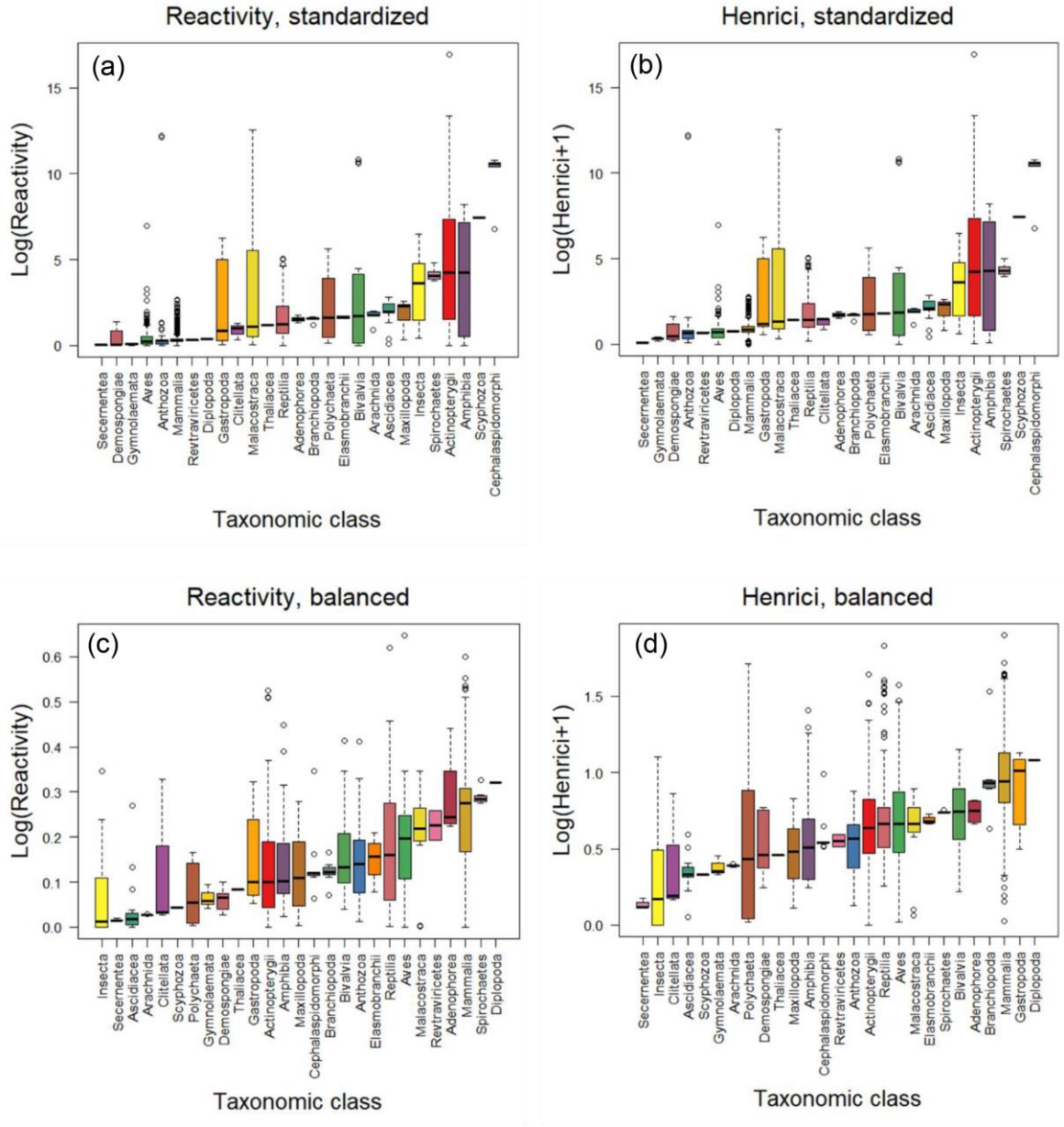
# Comadre Animal Matrix Database



# Index vs. distortion



# Box plots of indices by taxonomic class

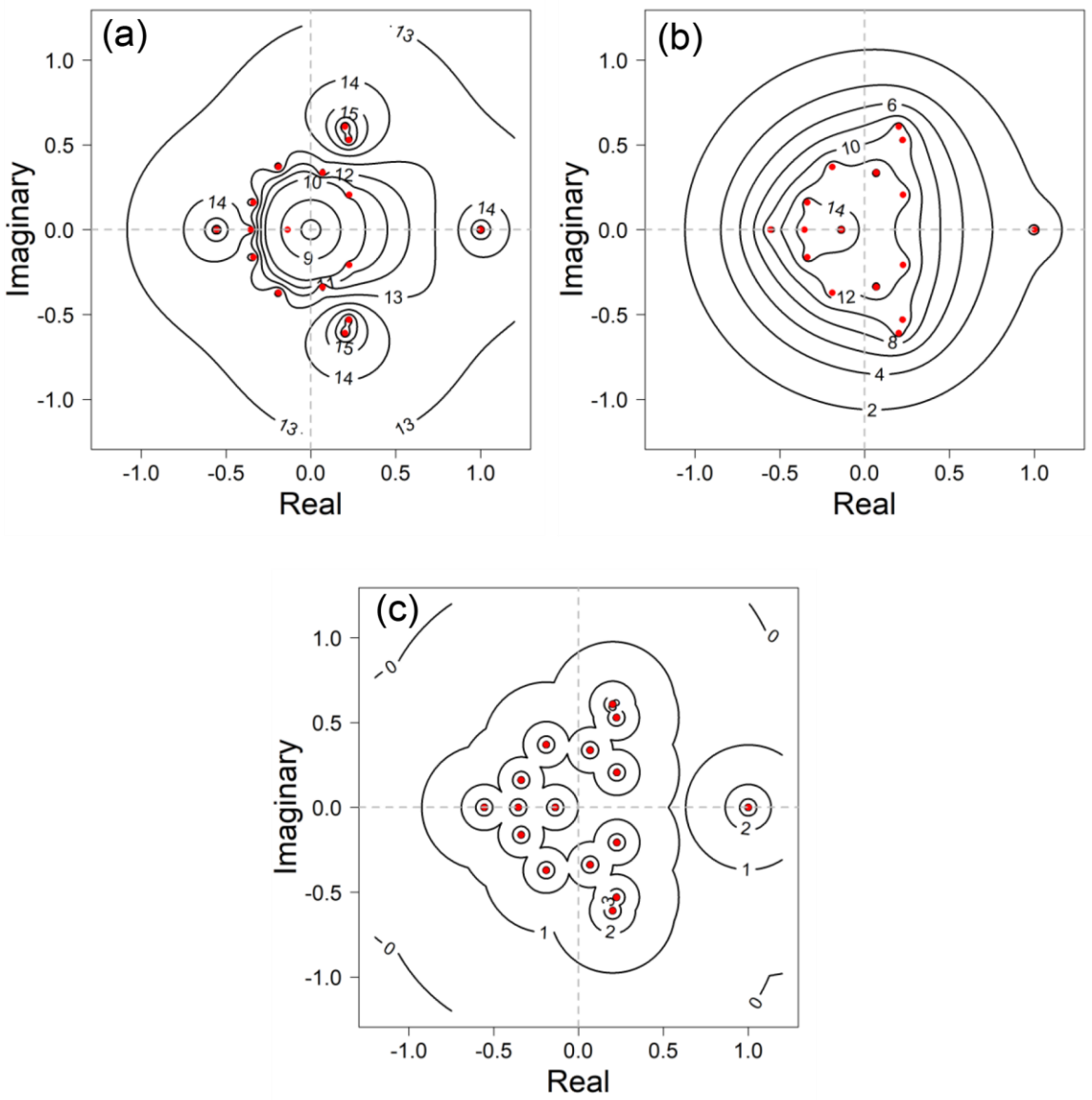


# Pseudospectra of population projection matrices (northern pike)

a) Standardized

b) Balanced

c) Normal (if Henrici metric = 0)



# Conclusions

- Indices of transient dynamics can be badly distorted by naturally large classes
- With balancing, the undue influence of outsized classes disappears, and indices become scale invariant
- By stripping away the effect of scale, balancing offers a clearer picture of transient dynamics, crystallizing what features of a creature’s life cycle foster transient growth