Of birds and benthos: on environmental variability, monitoring and community composition

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Note: Approaches to the classic question of how biotic and abiotic factors affect demography, driving life history evolution

Environment (space, time)

Demography (life history)

biotic

abiotic
Population and community dynamics and evolution in variable environments

- single-species data
- environmental variability (‘noise 1’) and other species (‘noise 2’)
- the irreducible uncertainty of the demography-environment interaction
- the community; interaction strengths and evolution
- the feedback environment

Note: A fundamental problem in biology is distinguishing noise from the signal in data.
Single-species data

Note: Example data of population trajectory

Moose on Isle Royale

- average population size
- range of fluctuations
- trends and extinction risk

What can we learn?

Note: Data like these show the average trends in population growth or decay over time. For example, they can be used for calculating extinction risk. However, more information is needed to make predictions.
Population dynamics

Note: These are the tools used to predict future population numbers. Models like these can be simple or complicated.

\[ N_{t+1} = N_t F(N_t, N_{t-1}, \ldots, \varepsilon_t) \]

Let \( R_t = \ln(N_t / N_{t-1}) \) and \( X = \ln(N) \)

\[ R_t = a_0 + a_1 X_{t-1} + a_2 X_{t-2} + \ldots + a_k X_{t-k} + \varepsilon_t \]

Null model (no feedback):

\[ R_t = a_0 + \varepsilon_t \] (random walk [biased if \( a_0 \neq 0 \)])

If \( a_1 \neq 0 \) – first order dynamics
If \( a_2 \neq 0 \) – second order dynamics
Consider a log-linear AR(1) model:

\[ x_{t+1} = ax_t + w_t \]  

(1)

where noise, \( w_t \), is autocorrelated such that

\[ w_t = bw_{t-1} + \varepsilon_t \]  

(2)

Setting \( t \equiv t-1 \) in (1), and rearranging,

\[ w_{t-1} = x_t - ax_{t-1} \]  

(3)

Substituting into (2) and back into (1);

\[ x_{t+1} = (a+b)x_t - abx_{t-1} + \varepsilon_t \]  

(4)

Eq. (4) is identical in structure to an AR(2) process!
Note: To include climate and density dependence, one needs to know more about the environment and how it affects demographic parameters.
Two data sets as examples

- Migrating passerine birds in Sweden
  standardized banding 1972-1999

- Soft-bottom benthos in the North Sea
  6 stations 1980-1998

Note: These data sets result from baseline monitoring programs of the Swedish government. This data is strong because it exists for a long time period. However, it is important to remember the worth of long term monitoring data is increased when you do the homework before beginning data collection.
Standardized ringing scheme (1963) 1972 – present
Part of Swedish EPA monitoring program

Note: Attempting to correlate banding data with NAO index supports idea that population responds to winter weather (NAO index can be used to indicate winter conditions in the North Atlantic).

Spring ringing figures, 17 passerine species.
European wintering areas.
Winter climate (NAO index) High: mild and moist winters in N. Europe
dry in the Mediterranean basin
? in sub-Saharan sahel
Remembering …

Note: Here we are trying to pick up the signal of previous population density.

\[ N_t = N_{t-1} F(\bullet) \]

\[ R_t = \ln(N_t) - \ln(N_{t-1}) = \ln(F(\bullet)) = g(\bullet) \]

the null model: \( g = a_0 + \varepsilon_t \)

the Gompertz approach:
\[ R_t = a_0 + a_1 X_{t-1} + a_2 X_{t-2} + \ldots + a_k X_{t-k} + \varepsilon_t \]

rearranging:
\[ X_t = a_0 + (1 + a_1) X_{t-1} + a_2 X_{t-2} + \ldots + a_k X_{t-k} + \varepsilon_t \]

This is an autoregressive process (AR) of order \( k \)

With covariate:
\[ X_t = a_0 + (1 + a_1) X_{t-1} + a_2 X_{t-2} + b NAO_{t-k} + \varepsilon_t \]

Note: This term allows climate variability to covary
Parameter estimates (with NAO as covariate)

\[ X_t = a_0 + (1 + a_1)X_{t-1} + a_2X_{t-2} \]

Note: Perfect compensation occurs where

\[ a_1 = -1 \]
\[ a_2 = 0 \]
How strong is the climatic effect?

Note: Here we can see in northern Europe, NAO data relates to annual variation. The effect is much weaker in the Mediterranean.
Model selection

Note: For example, we see the 3rd model is clearly the best for Linnet, the 4th for European Robin. We get a climate signal for some species but not all.

Fig. 4. The likelihood of each model given data normalised such that they sum to one (the Akaike weight) for each species. The 6 nested models are: (I) \( r_t = a_0 + a_1 x_{t-1} + a_2 x_{t-2} + b NAO_t + \epsilon_t \), (II) \( r_t = a_0 + a_1 x_{t-1} + a_2 x_{t-2} + \epsilon_t \), (III) \( r_t = a_0 + a_1 x_{t-1} + b NAO_t + \epsilon_t \), (IV) \( r_t = a_0 + a_1 x_{t-1} + \epsilon_t \), (V) \( r_t = a_0 + b NAO_t + \epsilon_t \), (VI) \( r_t = a_0 + \epsilon_t \). The black and white bars give the Akaike weight of models including or excluding NAO, respectively.
Conclusions

- Passerine birds respond differently to NAO variation
- Overwinter survival affects rate of change and partly explains population fluctuations
- Are all environmental factors included?
- Species interactions? Note: Species interactions are not included in the example model
- What is the “environment”? Note: In this case, environment is quantified as winter temperature
Inference of pattern and process from system level data?
Benthos (soft bottom macro)

Six stations selected for monitoring

> 400 species recorded

Note: The analysis only considered the few dominant species.
Time series data

Note: Time series data give lots of variability. The question: are the fluctuations in concert or out of sync?

In concert
Out of sync

the six stations
Analysis

- Linear regression of AR($k$) processes
- Temperature at 600 m as covariate (cold means upwelling of nutrient rich deep-water)

Do different species respond similarly to abiotic driver? Are the six locations similar?
Model selection

Note: The highest point is the best model (sometimes hard to determine)
Conclusions

- No consistent pattern in how temp. affects realized per capita rate of change
- No second order effects (species interactions)
- Temp. may synchronize entire community; ind. species respond differently indicating species substitutions (pre-emptive dominance)
- No strong biotic feedback environment

Note: ARII implies biological interactions are absent
Data largely uninformative

Note: Thinking back to the original problem: How biotic and abiotic factors affect demography (these data don’t give information in this area).
Remedies …

The statistical approach I (sensu stricto)

Construct a model such that all that is left is normally distributed, uncorrelated residuals. Note: this gets rid of noise, but may be complicated.

The statistical approach II (sensu Akaike)

Pick several alternative models and use information theoretical criteria to choose among them, given data.

The theoretical approach

Figure out what a model must look like and what the ’environment’ really is.
A study of species interactions

What do interactions look like in temporally variable environments?

U.S. Dept. of Interior aerial and ground surveys of breeding ducks 1955-1994
> 50 areas (‘strata’)

Only strata with all 7 dabbling duck (Anas) species present all years (= six strata)
The *Anas* guild

- 7 closely related species
- Co-occurring in same habitat
- Microhabitat and diet separation

Note: These species were chosen because they are closely related, share food resources, and co-occur. However, they are well separated into niches by food particle size preference.

Note: Fluctuations are in sync.
Some predictions:

- *clypeata* interacts with few
- *platyrhynchos* interacts with *acuta/americana*

↓↑*strepera/discors* interacts with many

Note: We estimate the coefficients, and expect linear relationship if niche theory holds. However, the nonlinearity suggests something else is going on...

Results:
Evaluation of ecological and evolutionary mechanisms require measures of **fitness**

Fitness *defined* as per capita rate of change (of a phenotypic strategy)

\[ r = f(\text{density } [\text{self/others}], \text{strategy frequencies}, \ldots) \]

\[ r = \varepsilon_t \]

*Note: Complicated term*

**Biotic decoupling** in heterogeneous environments

\[ \rightarrow \text{weak feedback} \]

\[ \quad \text{weak mechanisms of coexistence} \]

**Coevolution**

\[ \rightarrow \text{strong feedback} \]

\[ \quad \text{strong mechanisms of coexistence} \]
How sensitive is population growth rate (fitness) to changes in demographic parameters?

\[ N_t = \begin{bmatrix} f_1 & \cdots & f_n \\ s_1 & \ddots & \vdots \\ \vdots & \ddots & s_n \end{bmatrix} N_{t-1} \]

\[ \lambda = f(s_i) \]

\[ \frac{\partial \lambda}{\partial s_i} \cdot \frac{\partial \lambda}{\partial s_i} s_i \lambda \]

sensitivity (selection gradient)

elasticity

demography (A)
A two-species example

2 interacting species
- max. p.c. population growth rate $\lambda_i$
- strength of intraspecific density-dependence $\alpha_i$
- interaction coefficient $\beta_i$

\[
N_{t+1} = \frac{\lambda_N N_t}{1 + \alpha_N N_t + \beta_N P_t}
\]
\[
P_{t+1} = \frac{\lambda_P P_t}{1 + \alpha_P P_t + \beta_P N_t}
\]

Note: These are growth equations for each species. The strength of density dependence is the $\alpha$ term.

Fitness:

\[
W_N = \frac{\lambda_N}{1 + \alpha_N N_t + \beta_N P_t}
\]
Define interaction strength:

\[
\frac{\partial W_N}{\partial P} = -\frac{\lambda_N \beta_N}{(1 + \alpha_N N_t + \beta_N P_t)^2}
\]

Note: This is fitness over interaction strength.
Interaction strength in variable environment ($\lambda_N \text{ variable}$)

expected value $-0.25$

Note:
- Positive auto-correlation
- No auto-correlation
- Negative auto-correlation
Interaction strengths – additive noise

Note: Noise depends on environment
Selection gradients

in relation to $\lambda_N$

in relation to $N$
Are all links important in a food web?

Note: Varying environment results many changes in interactions. Some arrows may be weak and uninteresting.

Narragansett Bay food web (Kremer & Nixon 1978)
Typically, many links are weak and/or modified by variability
The web is not fully integrated, ‘community modules’ prevail
The evolutionary feedback environment is oligo-dimensional
Systems with

- near-compensatory dynamics
- noisy environments
- low degree of trophic specialization
- simple life histories (few degrees of freedom)

- over-compensatory dynamics (e.g., cycles)
- low noise/discernable spatial and temporal structure
- high degree of trophic specialization
- complicated life histories

... identification of the feedback environment
Evolution takes place in a feedback environment

Intra- and interspecific interactions determine the feedback environment

Interaction strength is affected by abiotic heterogeneity

Interactions → mechanisms of coexistence

Mechanisms of coexistence are trade-offs in trait space

Traits evolve under adaptive (strategy) dynamics

Adaptive community dynamics
Conclusions

• Data in itself uninformative
  Note: Monitoring is not enough: theory needed to interpret and guide

• Environmental variability must be identified and included sensibly
  Note: Not just dismissed as “white noise.”

• Trophic interactions are part of the environment

• Adaptive community dynamics must consider both biotic and abiotic feedback structure (although the separation of the two factors may not be trivial)