Can coexistence theory fulfil its promise in real settings?

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The challenge:

"Explaining the distribution of species: now and into the future"

Environmental factors!

 \rightarrow Why isn't a species observed in all the areas we think it could live?

- Other environmental factors
- Dispersal limits
- Interactions with other species



'Modern' coexistence theory

Emphasises:

• Long term growth rate when rare (\bar{r})

i.e. 'invasion analysis'

 Partitioning into distinct processes



Terry et al (2022) *Synthesising the multiple impacts of climatic variability on community responses to climate change* Ecography

(29)

choice is $E_i = -m_i$ and $C_i = b_i F$. The per capita growth rates linear equations Eq. 21. For this model, there is a single then read

$$r_j(E_j, C_j) = \underbrace{b_j F}_{C_j} \underbrace{-m_j}_{E_j} = E_j + C_j. \tag{2}$$

We now determine the "equilibrium" values E_i^* and C_i^* . We can choose E_i^* to be the mean of $E_i = -m_i$; since the m_i are not fluctuating, $E_i^* = -m_i$. By definition, $r_i(E_i^*, C_i^*) = 0$, therefore $E_i^* = -m_j$ fixes $C_i^* = m_j$. The F^{*j} is defined to satisfy $C_i(F^{*j}) = C_i^*$ (Eq. 8); this equation reads $b_i F^{*j} = m_j$ for this model, from which $F^{*/} = m_i/b_i$. That is, $F^{*/}$ is equal to species *i*'s R^* value on that resource.

An alternative way of choosing the parameters is $E_j = b_j$ and $C_j = F$ with $E_i^* = b_j$, $C_i^* = F^{*j} = m_j/b_j$. See Appendix S4 for the model analysis using this parameterization. (Note that in Appendix S4, b_i is no longer constant, but here, an extra term for the storage effect also appears. Setting of the invasion growth rates reads the b_i to be constant recovers the result in this section.)

Step 2: Determine the standardized environmental and interaction parameters \mathcal{E}_i and \mathcal{C}_i .—We first need to calculate the Taylor coefficients of Eq. 3 for Eq. 27

$$\begin{split} &\alpha_j = \frac{\partial r_j}{\partial E_j} = 1, \, \alpha_j^{(2)} = \frac{\partial^2 r_j}{\partial E_j^2} = 0, \, \beta_j = \frac{\partial r_j}{\partial C_j} = 1, \\ &\beta_j^{(2)} = \frac{\partial^2 r_j}{\partial C_i^2} = 0, \, \zeta_j = \frac{\partial^2 r_j}{\partial E_i \partial C_j} = 0. \end{split}$$

We now evaluate Eqs. 4, 5

$$\begin{split} \mathcal{E}_j &= \alpha_j (E_j - E_j^*) + \frac{1}{2} \alpha_j^{(2)} (E_j - E_j^*)^2 \\ &= 1 \times (-m_j + m_j) + 0 = 0 \end{split}$$

$$C_{j} = \beta_{j}(C_{j} - C_{j}^{*}) + \frac{1}{2}\beta_{j}^{(2)}(C_{j} - C_{j}^{*})^{2}$$

= 1 × (b_{j}F - m_{j}) + 0 = b_{j}F - m_{j}. (30)

The C_i may also be written in the form of Eq. 9. From Eq. 10, we get $\phi_j = b_j$ and $\psi_j = 0$. We therefore have $\mathcal{C}_i = b_i F - m_j = \phi_j (F - F^{*j}).$

Step 3: Calculate the time-averaged growth rates .- The timeaveraged growth rates read

$$\bar{r}_j = \bar{\mathcal{E}}_j + \bar{\mathcal{C}}_j = b_j \bar{F} - m_i = \phi_j (\bar{F} - F^{*j}). \tag{31}$$

The covariance term $\gamma_i \text{cov}(\mathcal{E}_j, \mathcal{C}_j)$ is absent because ζ_j is zero (Eq. 28), and therefore so is $\gamma_i = \zeta_i / (\alpha_i \beta_i)$.

Step 4: Calculate the invasion growth rates \bar{r}_i .—This will still be given by Eq. 31, but it is understood that \overline{F} is evaluated at the level determined by whichever species is resident. This level cannot be computed without an extra equation determining the dynamics of F, but as we will see, this is not needed here.

Step 5: Form weighted sum of invader and resident growth *rates.*—The scaling factors d_i are solutions to the system of impact on coexistence. Those species that end up with a

equation with two unknowns, reading $d_i \phi_i + d_s \phi_s = 0$. The choice $d_i = 1/\phi_i$ and $d_s = -1/\phi_s$ satisfies the equation (and is (27) exactly what Eq. 22 recommends). Eq. 17 then reads, for two species, as

$$\bar{r}_i = \frac{1}{d_i} (d_i \bar{r}_i + d_s \bar{r}_s) = \phi_i \left(\frac{\bar{r}_i}{\phi_i} - \frac{\bar{r}_s}{\phi_s} \right)$$
(32)

where $\bar{r}_s = 0$. Using Eq. 31, we get

$$\begin{split} \bar{r}_i &= \phi_i \left(\frac{\bar{r}_i}{\phi_i} - \frac{\bar{r}_s}{\phi_s} \right) = \phi_i \left(\frac{\phi_i (\bar{F} - F^{*i})}{\phi_i} - \frac{\phi_s (\bar{F} - F^{*s})}{\phi_s} \right) \\ &= \phi_i (F^{*s} - F^{*i}). \end{split}$$
(33)

a function of time, which means that in addition to the results After substituting in $\phi_j = b_j$ and $F^{*j} = m/b_j$, the final form

$$\bar{r}_i = b_i \left(\frac{m_s}{b_s} - \frac{m_i}{b_i}\right) \tag{34}$$

recovering the result that only the species with the lower m/b_i (R*-value) will be able to invade and persist. As mentioned before, a useful aspect of the scaling factor approach is that it applies in the presence of multiple limiting factors. For instance, generalizing Eq. 25 to three species (28) competing for two resources, we have

$$r_j = \sum_{k=1}^{2} b_{jk} F_k - m_j$$
 $(j = 1, 2, 3).$ (35)

Applying Eq. 21, the d_i are solutions to the linear system of equations

$$b_{11}d_1 + b_{21}d_2 + b_{31}d_3 = 0$$
(36)
$$b_{12}d_1 + b_{22}d_2 + b_{32}d_3 = 0$$
(37)

whose general solution is

$$d_{j} = \begin{pmatrix} b_{22}b_{31} - b_{21}b_{32} \\ b_{11}b_{32} - b_{12}b_{31} \\ b_{12}b_{21} - b_{11}b_{22} \end{pmatrix} c$$
(38)

where c is an arbitrary constant. Partitioning the invader growth rates using Eq. 17, we get



which is independent of the resources \overline{F}_k , demonstrating yet again that fluctuations in resource levels have no



Theory often suggests responses are qualitatively indeterminate



Terry et al (2022) Synthesising the multiple impacts of climatic variability on community responses to climate change Ecography



Two classes of problems:

'Internal'

The MCT framework is hard to apply

(empirical uncertainty precludes clear answers)

◆ The MCT framework
 is inapplicable
 (its assumptions are too great a leap)

Empirical Coexistence Theory Recipe



20 -

Treat - CTRL - TREAT

20 **-**

Pérez-Ramos et al. (2019) Nature Communications

> Hart et al. (2019) PNAS

Hallett et al. (2019) Ecology Letters

Armitage and Jones (2019) Ecology

> Godoy et al. (2020) Nature Communications

Blackford et al. (2020) The American Naturalist

Terry et al. (2021) Journal of Animal Ecology

Kandlikar et al. (2021) The American Naturalist

Van Dyke et al. (2022) Nature

Johnson et al. (2022) Nature

Hess et al. (2022) Nature Ecology and Evolution

> Fragata et al. (2022) Ecology Letters

Bowler et al. (2022) Ecology Letters



Nature Mordecai (2013) Ecology Godoy et al. (2014) Ecology Letters Godoy and Levine (2014) Ecology Kraft et al. (2015) PNAS Germain et al. (2016) Proc B Rey et al. (2017) New Phytologist Wainwright et al. (2018) Journal of Ecology Petry et al. (2018) Journal of Ecology Matías et al. (2018) Journal of Ecology Lanuza et al. (2018) Ecology Letters Cardinaux et al. (2018) Journal of Ecology Bimler et al. (2018) Journal of Ecology

Levine and HilleRisLambers (2009)

Siefert et al. (2019) The American Naturalist

Biology is very noisy!







(vertical red line = predictive posterior)

Terry et al. (2021) *Natural enemies have inconsistent impacts on the coexistence of competing species* Journal of Animal Ecology







Van Dyke, Levine & Kraft, *Nature* **611**, 507–511 (2022).

1. Data quantity

- MCT is very data hungry
- Distribution of experimental effort (number of species vs replication) largely guesswork

6 species, all pairs:

6 population growth rates (λ)

+ directional competition all pairs: 36 $\alpha's$

 \times 2 treatments

= 84 parameters...

(+ error terms!)

× ~20 data points per parameter=

~1700 observations!



Number of Species 2

Shortcuts?

Various methods of interpolation from generalities:

- Use traits / phylogeny to find generalities?
- Sparse modelling to reduce parameter load

Still need a decently known core to build from...

2. We only have phenomenological models

Key estimates needed:

- Monoculture carrying capacity
- How much competitive pressure is exerted at that carrying capacity

Predictions depend on competition model choice



Not just competition...

...error modelling matters too

See review Terry and Armitage (In press, MEE) for a simulated and a real example

Model selection

$$\lambda_{i} - \alpha_{ii}N_{i} - \alpha_{ij}N_{j}$$

$$\lambda_{i}e^{\alpha_{ii}N_{i} + \alpha_{ij}N_{j}}$$

$$\lambda_{i}e^{-\alpha_{ii}\log(N_{i}+1) - \alpha_{ij}\log(N_{j}+1)}$$

$$\lambda_{i}e^{-\alpha_{ii}\log(N_{i}+1) - \alpha_{ij}\log(N_{j}+1)}$$

$$\lambda_{i}/(1 + \alpha_{ii}N_{i} + \alpha_{ij}N_{j})$$

$$\lambda_{i}/(1 + N_{i}^{\alpha_{ii}} + N_{j}^{\alpha_{ij}})$$

- AIC (for best prediction) or BIC (for best model)?
- Distribution of data influential.

3. Dealing with parameter uncertainty

- Propagating uncertainty increasingly common
- Given model, confidence in parameters
 - ... but as we've seen 'given model' is a big stretch!

Differential uncertainty

Competition coefficients (" α 's") almost always less precisely known than potential fecundities (" λ 's")

→ Less data (+ more assumptions)

→ Will change more by noise...

Example:



Figure S4.4 Posterior distribution of the two components of the fitness difference. The uncertainty in the 'competitive response ratio' $\sqrt{\frac{\alpha_{ij}\alpha_{ii}}{\alpha_{ji}\alpha_{jj}}}$ is much larger than the demographic ratio $\frac{r_j-1}{r_i-1}$ (mean coefficient of variation 32x larger).

Terry et al. (2021) Natural enemies have inconsistent impacts on the coexistence of competing species JAE

Differential uncertainty can generate spurious results

What is driving changes to coexistence?

→ Direct effects on raw fecundity, or the competition between species?

$$\left| \frac{\alpha_{ii}}{\alpha_{ji}} - \frac{\alpha_{ii}}{\alpha_{ji}} \right|$$
 VS $\left| \frac{\lambda_i}{\lambda_j} - \frac{\lambda_i}{\lambda_j} \right|$

Can also be framed as fitness differences vs niche differences (gets a bit more complicated)

Differential uncertainty can generate spurious results



inferences about coexistence Nature

4. Correlations in Uncertainty



Positive covariance between intrinsic growth rates and incoming competition effects

 α_{ii} α_{ii} α_{ii}





'Internal' problems summary:

- Data limitations imply inevitable large and influential uncertainties
- Model choice can impact results
- Recipes unreliable, but guidelines possible

Terry and Armitage Widespread analytical pitfalls in empirical coexistence studies and a checklist for improving their statistical robustness (In press at MEE)



Two classes of problems:

'Internal'

The MCT framework is hard to apply

(empirical uncertainty precludes clear answers)

◆ The MCT framework
 is inapplicable
 (its assumptions are too great a leap)

'Existential' problems

Should we be relying on the (standard) framework in the first place?

- 1. Breakdown beyond pairwise case
- 2. Assumption of infinite time and space horizons (demographic stochasticity)
- 3. Alignment of spatial scales
- 4. Challenge of positive density dependence (Allee effects)
- 5. No adaptation (plasticity / evolution)

Validation tests:

Need to step beyond comparing predictions based on single generation experiments

Possible tests:

- Plausibility of predicted equilibria densities
- Comparing to observed distributions (e.g. Armitage & Jones 2020)
- Analysing historical time series (e.g. Adler et al. 2006)
- Direct tests using mesocosms with fast life history

MCT in changing environments:



Breaks many assumptions (especially time scales!)

Actual validation tests:





PAL

D. pallidifrons 'PAL' (highland 'cold' distribution)
 D. pandora 'PAN' (lowland 'hot' distribution)









60 replicates per treatment = 240 total populations tracked

Each generation sexed and counted

- 37'826 PAL total
- 20'786 PAN total
- 1,255 usable transitions for PAL
- 613 usable transitions for PAN











Can coexistence theory make accurate predictions of time-to-extinction?

Step 1- Fitting a model...

Three key parts: $N_{t+1} \sim N_t \times B(T) \times C(N_{i,t}, N_{j,t}, T)$

- Fecundity Thermal Performance Curve B(T)
- Temperature dependent competition Kernel $C(N_{i,t}, N_{j,t}, T)$
- Error term (also possibly context-dependent)



Thermal Performance Curve

Taylor Sexton

$$B(T) = B_{pk} \times \frac{-(T - T_{min})^4 + 2 \times (T - T_{min})^2 \times (T_{pk} - T_{min})^2}{(T_{pk} - T_{min})^4}$$

Simplified Briere 1 $B(T) = a \times (T - T_{min}) \times \sqrt{T_{max} - T}$

Simplified β type

$$B(T) = \rho \times \left(a - \frac{T}{10}\right) \times \left(\frac{T}{10}\right)^{b}$$

Atkin

$$B(T) = B_0 \times (a - b \times T)^{T/10}$$

Competition

Lotka-Volterra (linear)

$$C(N_{i,t}, N_{j,t}) = 1 + \alpha_{ii}N_{i,t} + \alpha_{ij}N_{j,t}$$

Beverton-Holt

$$C(N_{i,t}, N_{j,t}) = \frac{1}{1 + \alpha_{ii}N_{i,t} + \alpha_{ij}N_{j,t}}$$

Beverton-Holt logged

$$C(N_{i,t}, N_{j,t}) = \frac{1}{1 + \alpha_{ii} log(N_{i,t} + 1) + \alpha_{ij} log(N_{j,t} + 1)}$$

Scaled BH

$$C(N_{i,t}, N_{j,t}) = \frac{1}{\theta + \alpha_{ii} log(N_{i,t} + 1) + \alpha_{ij} log(N_{j,t} + 1)}$$



$$C(N_{i,t}, N_{j,t}, T) = \frac{1}{1 + (\alpha_{0ii} + \alpha_{Tii} T) N_{i,t} + (\alpha_{0ij} + \alpha_{Tij} T) N_{j,t}}$$





Error Model

- Poisson
- Gaussian
- Negative Binomial
- Zero-inflated Negative Binomial

 $\lambda(T_t) = \lambda 0(T_t) \times (1 - inv.logit(Zi))$

- (Linear) Competition- dependent Zero inflated Negative Binomial
- (Linear) Temperature-dependent Zero inflated Negative Binomial (PAL)

$$\lambda(T_t) = \lambda 0(T_t) \times \left(1 - inv. logit(z_0 + z_T T)\right)$$

• (Linear) Zero inflated Competition-dependent-shape Negative Binomial (PAN)

brm(M, data = LaggedTotals_PAN, prior = PRIORS, chains=4,cores =4, iter=4000)



Same competition model, Poisson Error







all others (Tukey HSD of those comparisons all p<0.005) while others all p>0.7)

fluctuations and competition appears 'non-additive '

influential: (significance of random effect term for variability pathway = 0.011)

1.	Breakdown beyond pairwise case
2.	Assumption of infinite time and
	space horizons
	(No demographic stochasticity)
3.	Alignment of spatial scales
4.	Challenge of positive density
	dependence (Allee effects)
5.	Trait change

Is this any good?

- Better than I had assumed?
- Very low precision

Is this a fair test?

- Doesn't include spatial dynamics
- More data, in a more homogenous environment than realistic
- Tiny fraction of community

Outlook



Postmodernism Post-Modern Coexistence Theory ?

Article Tall

From Wikipedia, the free encyclopedia

Postmodernism is an intellectual stance or mode of discourse^{[1][2]} characterized by skepticism towards elements of the Enlightenment worldview. It questions the "grand narratives" of modernism, rejects the certainty of knowledge and stable meaning, and acknowledges the influence of ideology in maintaining political power.^{[3][4]} The idea of objective claims is dismissed as naïve realism,^[5] emphasizing the conditional nature of knowledge.^[4] Postmodernism embraces self-referentiality, epistemological relativism, moral relativism, pluralism, irony, irreverence, and eclecticism.^[4] It opposes the "universal validity" of binary oppositions, stable identity, hierarchy, and categorization.^{[6][7]}

Emerging in the mid-twentieth century as a reaction against modernism,^{[8][9][10]} postmodernism has permeated various disciplines^[11] and is linked to critical theory, deconstruction, and post-structuralism.^[4]

Critics argue that postmodernism promotes obscurantism, abandons Enlightenment rationalism and scientific rigor, and contributes little to analytical or empirical knowledge.^[12]



Thanks to collaborators past and present, but especially:

Owen Lewis, Jinlin Chen (Oxford) & Dave Armitage (OIST)



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Any further thoughts gratefully welcomed: christopher.terry@biology.ox.ac.uk

Outlook

- For a talk full of problems, I'm still fairly positive on the approach!
- Predictions certainly in right ballpark, which might be all that is needed.
- Extensions need to consider applicability
- Development of 'robust' theory lacking what can we say with confidence, what is probably too subtle to determine?
- Expect competition terms to appear to change between treatments – treat very sceptically any flat table of competition coefficients.
- Hard boundary of invasion analysis interacts poorly with very fuzzy reality – expected persistence time, or a more probabilistic approach may be more useful.



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