Dynamics of Disturbed Ecosystems

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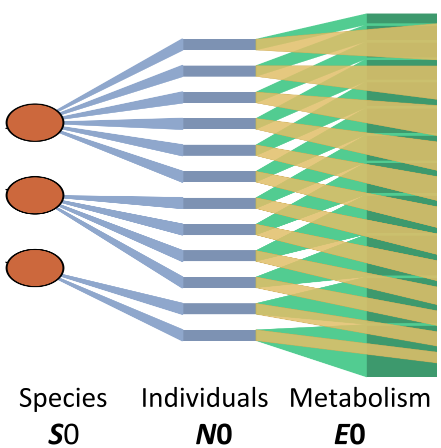
UC Berkeley

Static
Purely MaxEnt

Dynamic
Hybrid MaxEnt + Mechanism

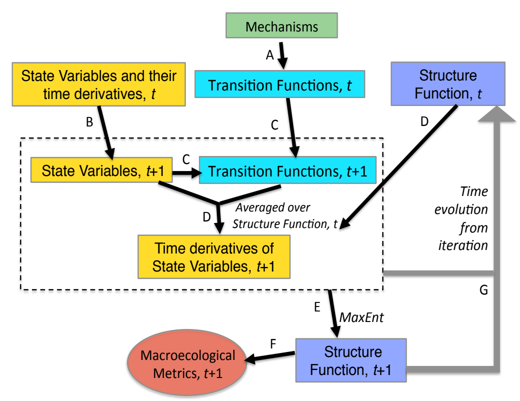
Architecture of METE



An allocation problem

Hybrid MaxEnt + Mechanism

Architecture of DynaMETE



A systems-dynamics problem

MaxEnt is a top-down (macro → micro) inference procedure

Prior knowledge

The knowledge sought

SYSTEM	State Variables (macro)	Probability Distributions (micro)
Thermodynamic	P, V, T	Molecular Kinetic energies, …
Network	Number of nodes and edges	Linkages across nodes, flow distributions
Economic	# sectors, firms, nations, people; total production	Individual incomes, inputs and outputs, …
Neural Net	# neurons and synapses	Neuron firing sequence correlations
Community structure in ecosystem	**Area, # species, # individuals, total metabolic rate**	**Individuals among species, metabolism among individuals, species and individuals over space …**

Maximum Entropy Theory of Ecology

State Variables

(Constraints)

S: # species (or families etc.)

N: # individuals

E: metabolic rate

Objective Function

$$H = -\Sigma\, R \log(R)$$

$R(n,\varepsilon|S,N,E)$ = ecological "structure function"

n = abundance of a species
ε = metabolic rate of an individual

Derivable from H_{max}

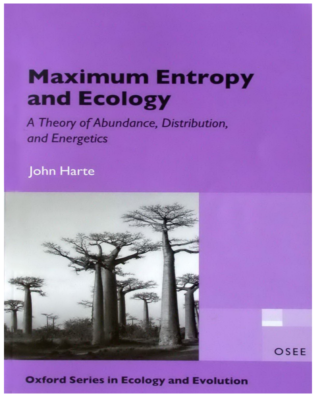
- **Abundance distribution over species**
- **Metabolic rate distribution over individuals**
- **metabolism-abundance correlations**
- **structure of taxonomic trees**

And with area as an additional constraint:

- **Spatial clustering and species-area relationships**

Predictions are applicable across all taxa, spatial scales, habitats,

with no adjustable parameters

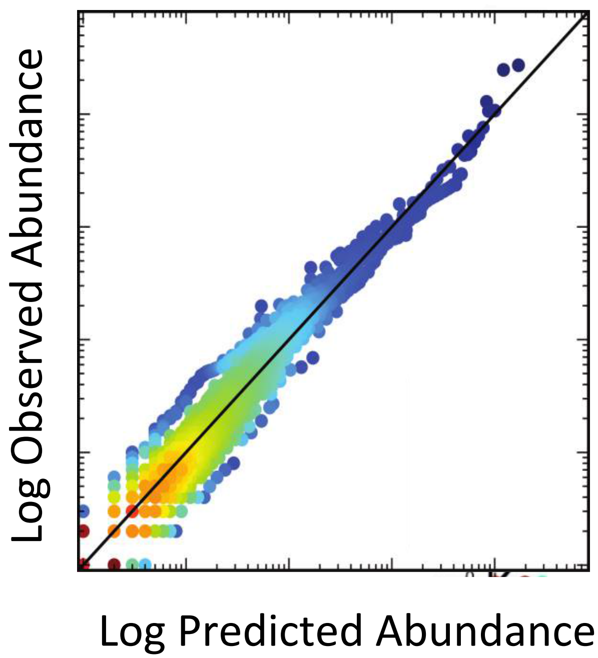


Numerous Tests of Predictions
At ~ 20 distinct habitats: ~ 10^5 Species, ~10^{14} individuals

36 serpentine meadow plots in CA
11 Smithsonian humid tropical forest plots
Dry tropical forest, Costa Rica
Plant census in Anza Borrego desert
Breeding bird censuses in southern Africa
Temperate Forest floor vegetation
Tree census data fom Western Ghats
Hawaiian arthropods
Panamanian arthropods
Human gut microbiome
Coastal pine forest at Pt. Reyes
Sierran and Rocky Mt. Meadow vegetation
Recovering erosion site vegetation

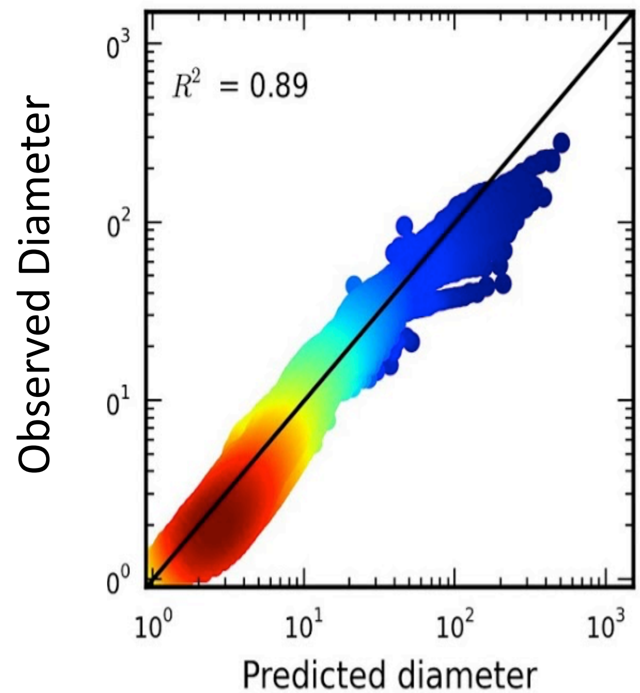
Tests of METE

Abundance distribution



15,848 plant, mammal, arthropod, and bird communities: *(White et al., 2012)*

Body-size distribution



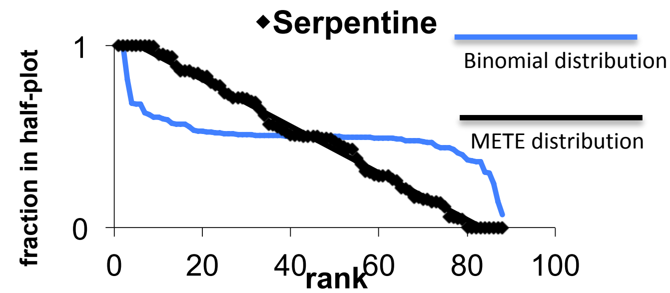
76 forest communities
(Xiao et al. 2015)

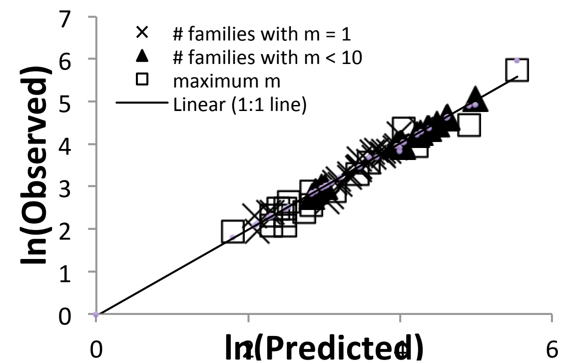
Three unexpected predictions are made by the Maximum Entropy Theory of Ecology

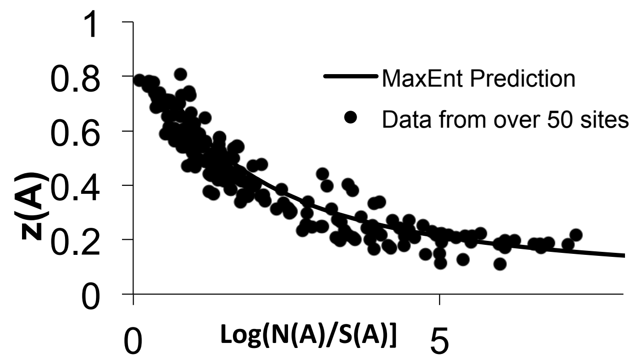
1. A counter-intuitive spatial distribution rule: Individuals obey the Laplace distribution, not the Poisson. (Like a Bose gas)
(Harte et al., Ecology, 2008)

2. Taxonomy influences Macroecology: The size-abundance rule is modified by the shape of the entire taxonomic tree.
(Harte et al., Ecology Letters, 2015)

3. Scale collapse of the species-area relationship: All SARs can be plotted on a universal curve.
(Harte et al., Ecology Letters, 2009)



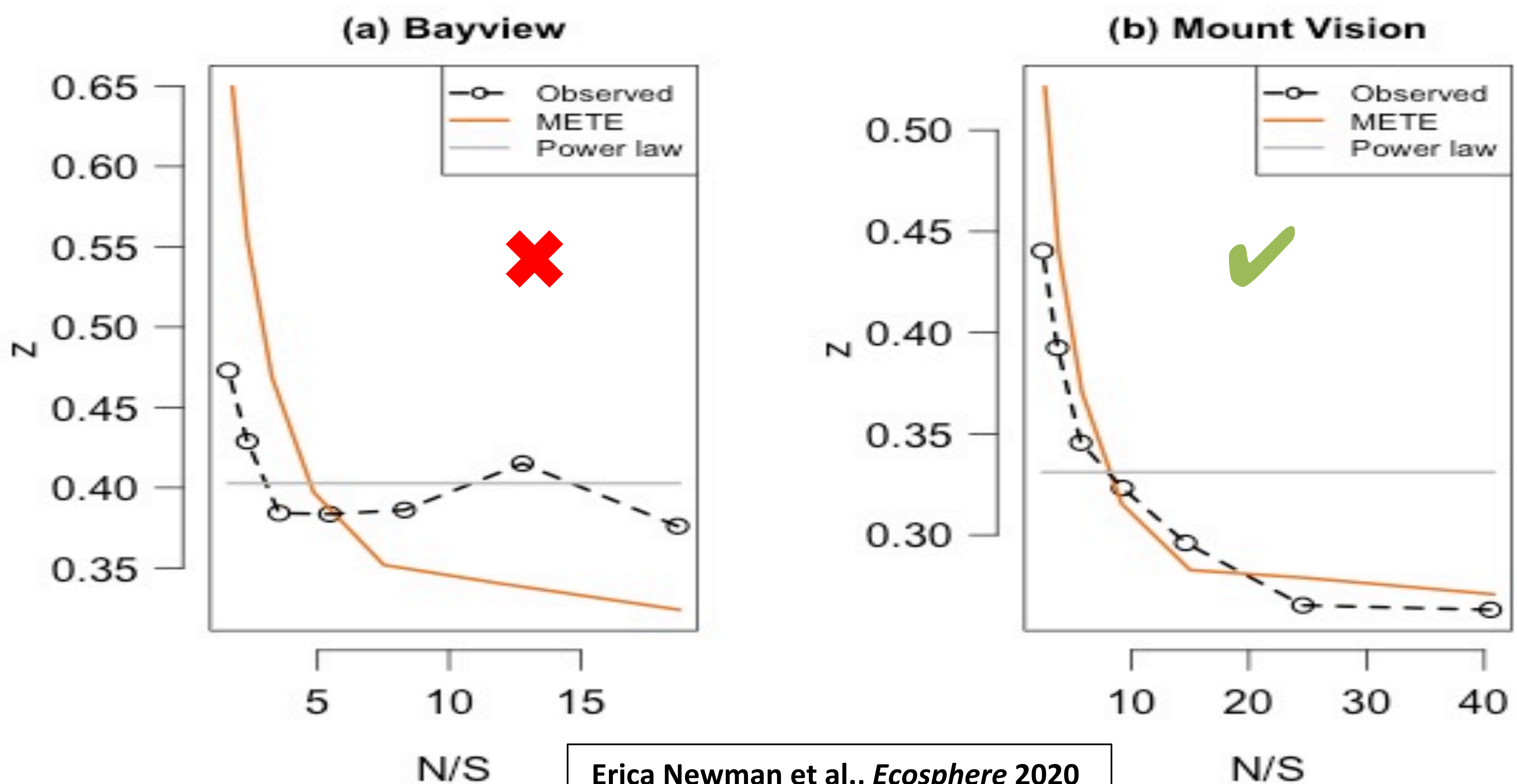




Disturbance: METE predictions fail for ecosystems in which the State Variables are rapidly changing!

E.G.: aftermath of fire in a fire-adapted Bishop Pine Forest

recently burned, rapidly changing **100y post fire, quasi-steady-state**

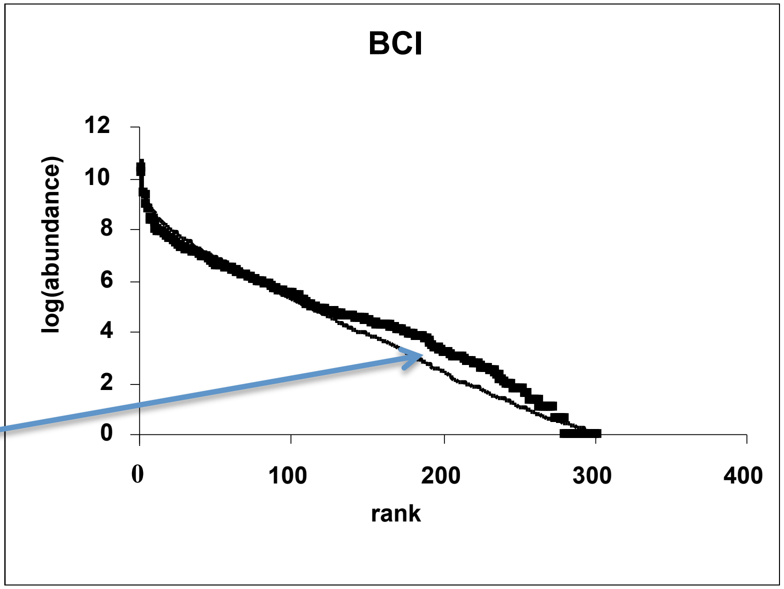


Erica Newman et al., *Ecosphere* 2020

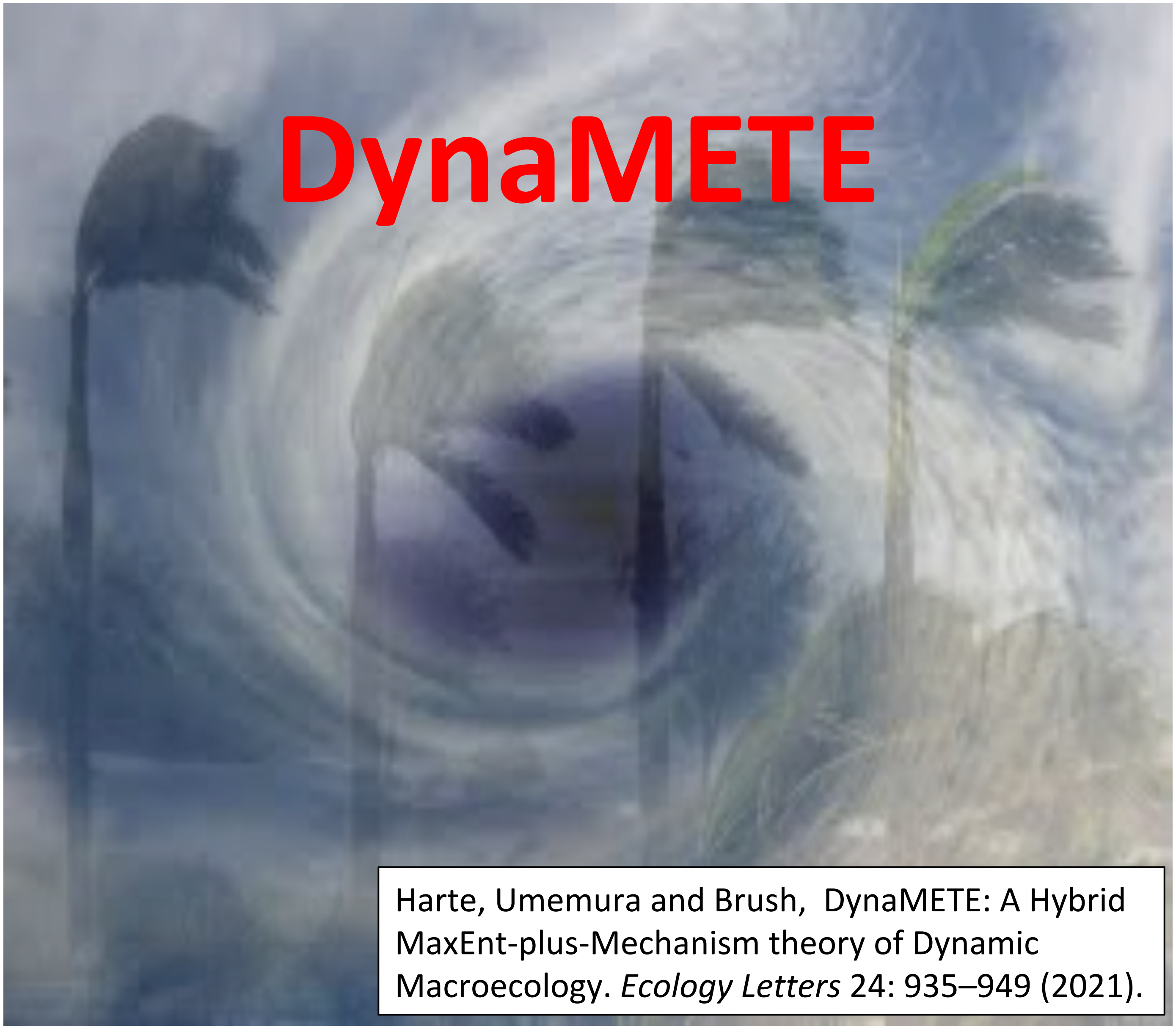
Another Example
The BCI 50 ha plot: A dynamic system

The creation of Gatun Lake isolated the plot from its immigrant source pool. It is losing species (Condit et al.; Egbert Leigh, pers. comm.)

Predicted log-series abundance distribution fails at BCI.



A Theory of Dynamic Macroecology



DynaMETE

Harte, Umemura and Brush, DynaMETE: A Hybrid MaxEnt-plus-Mechanism theory of Dynamic Macroecology. *Ecology Letters* 24: 935–949 (2021).

The Essential Idea

THE MACRO SCALE

Community State Variables:

S, N, E

+ their instantaneous rates of change!

Instantaneous
structure function
determined by
augmented
values of
state variables
using
MaxEnt

THE MICRO SCALE

Structure Function over *n* and *ε*:

plus **mechanistic transition functions**
that depend on *n*, *ε*, (and *S, N, E*)
and that give *dn/dt, dε/dt*

The updated
structure function
and
transition functions
update
the constraints

which then update the
structure function in
the next iteration,
etc.
.
.

DynaMETE is a **hybrid theory**,
with a **Mechanistic parent**
(the transition functions)
and an **Information-Theoretic parent**
(MaxEnt)

The Eqs. of DynaMETE

Notation: $W = S, N, E$; f_W = *transition functions* (e.g., $f_N = dn/dt = b_0 n - d_0 n(E/E_0)$)

Constraint equations:

$$N/S = \sum_{n,\varepsilon} nR(n,\varepsilon); \quad E/S = \sum_{n,\varepsilon} n\varepsilon R(n,\varepsilon); \quad dW/dt = S \sum_{n,\varepsilon} f_w R(n,\varepsilon)$$

Hybrid structure function: $R(n,\varepsilon) = Z^{-1} e^{-\lambda_1 n} \cdot e^{-\lambda_2 n\varepsilon} \cdot e^{-\sum_W \lambda_W f_W(n,\varepsilon)}$

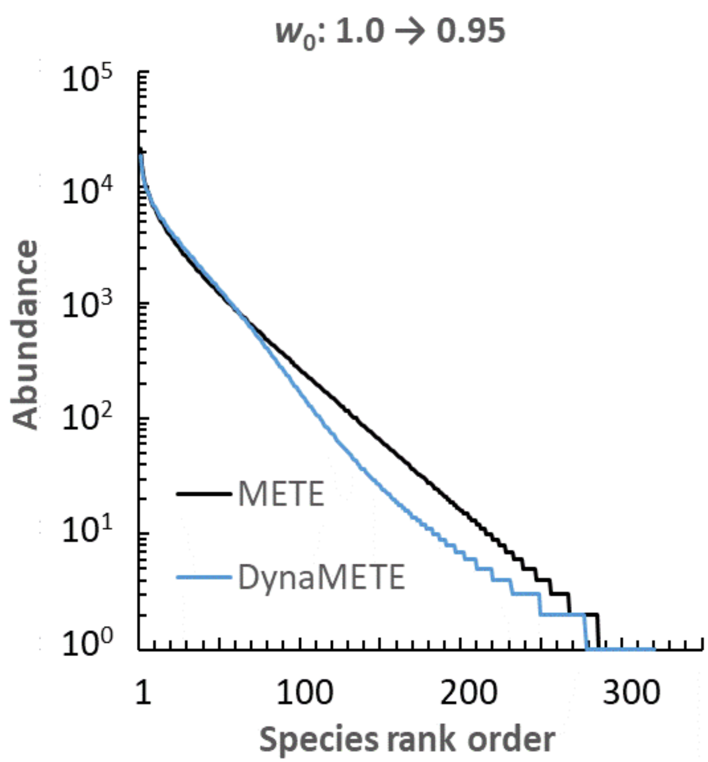
Specific mechanisms of disturbance (e.g., changes in growth or death or immigration rates) drive the state variables, *W*:

The structure function is updated in time by an iteration procedure, and from the *time-dependent R(n,ε)*, the time-dependent metrics of macroecology can be derived,

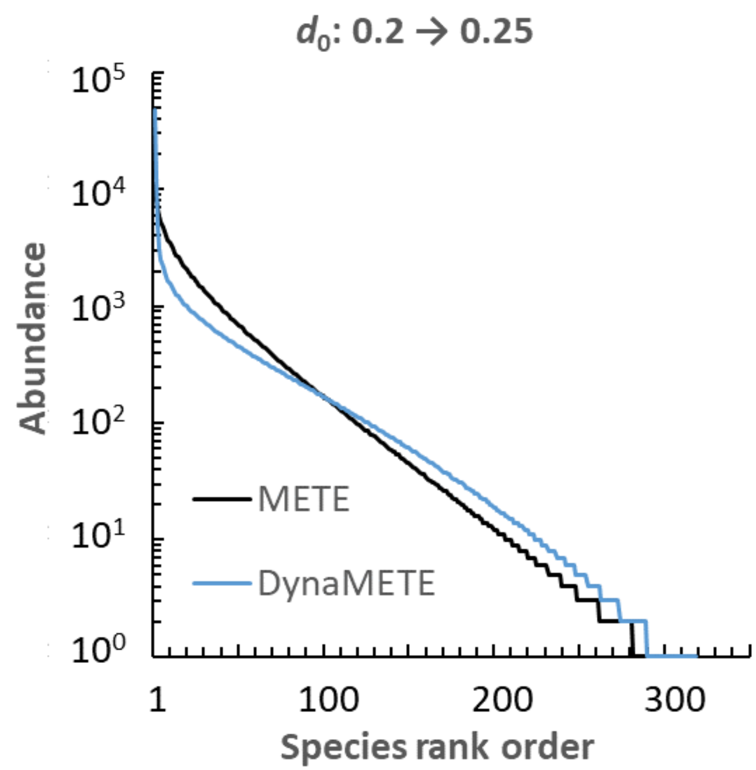
Harte, Umemura and Brush,
Ecology Letters 24: 935–949 (2021).

Different mechanisms of disturbance generate different macroecological patterns

A decrease in the growth rate of individuals

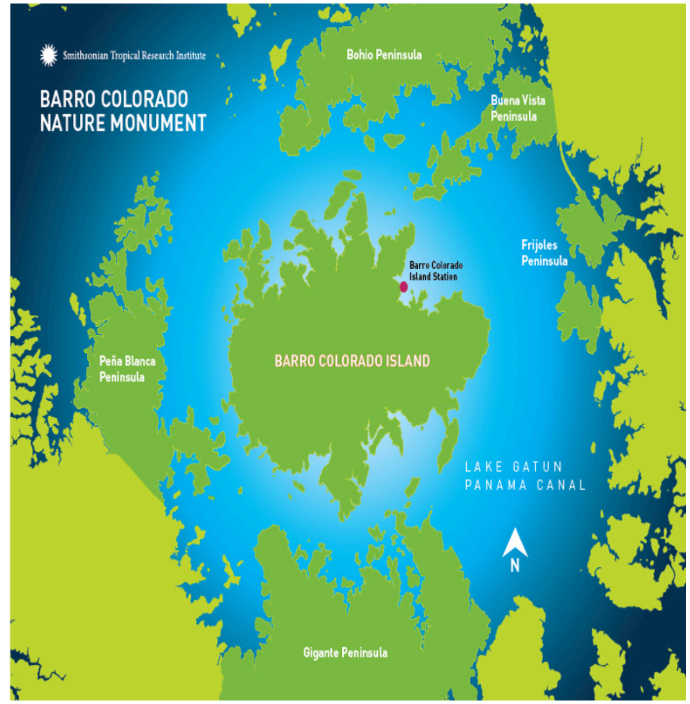


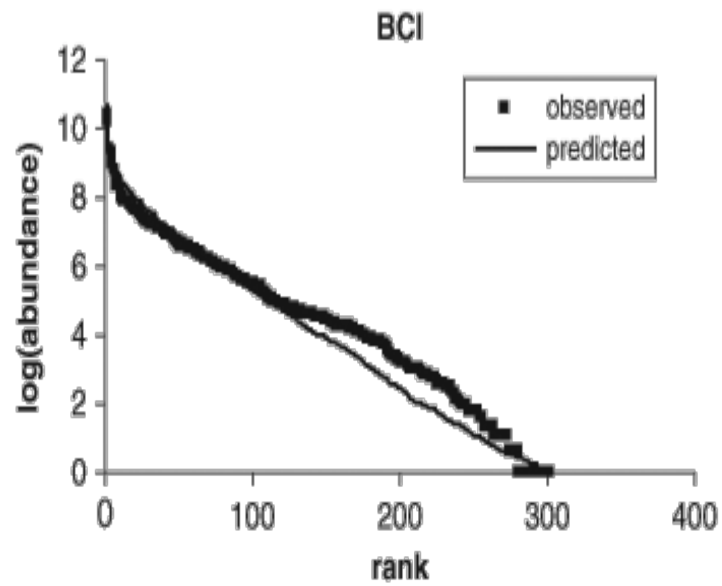
An increase in the death rate of individuals



Disturbance at Barro Colorado Island (BCI)

- Predicted log-series species-abundance distribution fails for forest data from BCI
- Possible sources of disturbance
  - Isolation and loss of immigrants
  - Increase in death rates
  - Change in growth rates



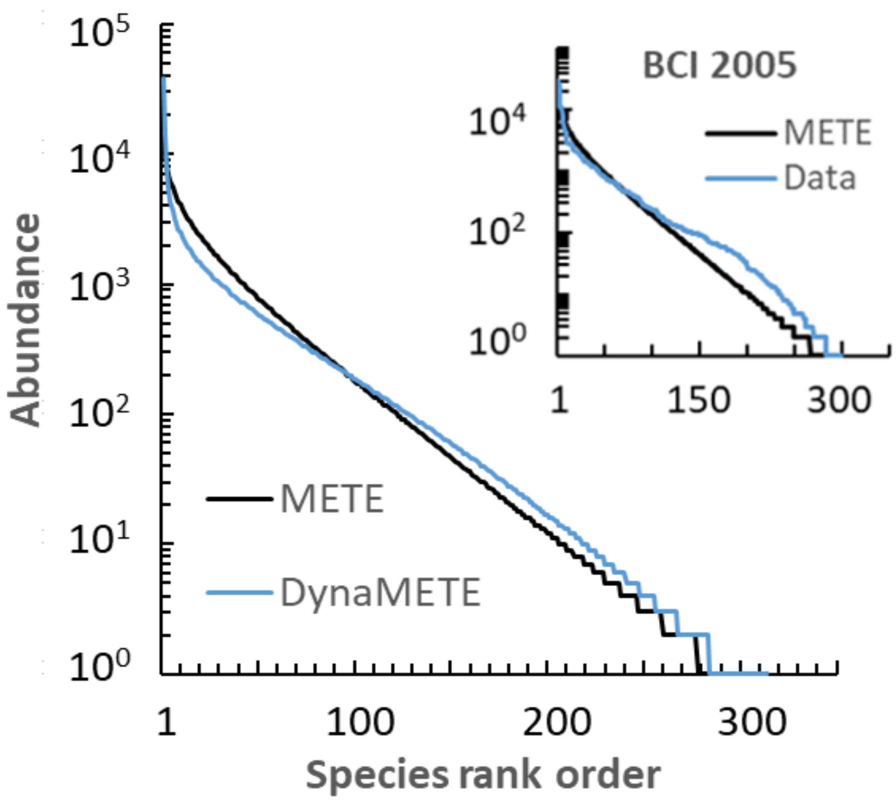


(Harte 2011)

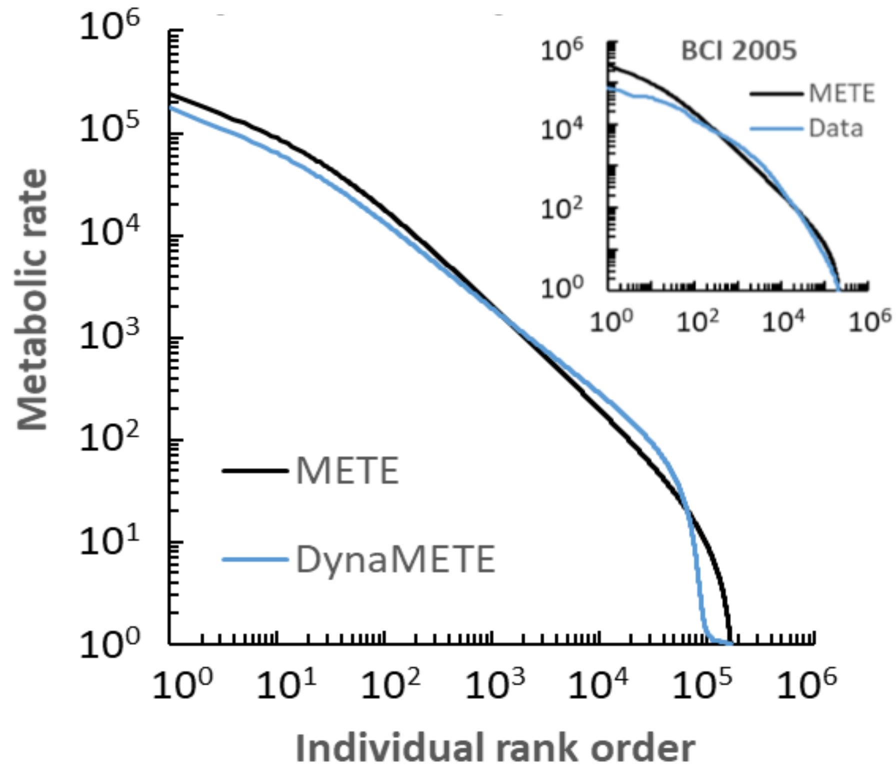
The Smithsonian 50 ha tropical forest plot at Barro Colorado Island looks like a disturbed ecosystem!

The immigration rate and ontogenic growth rate are decreased, and the death rate is increased:

Species-abundance distribution

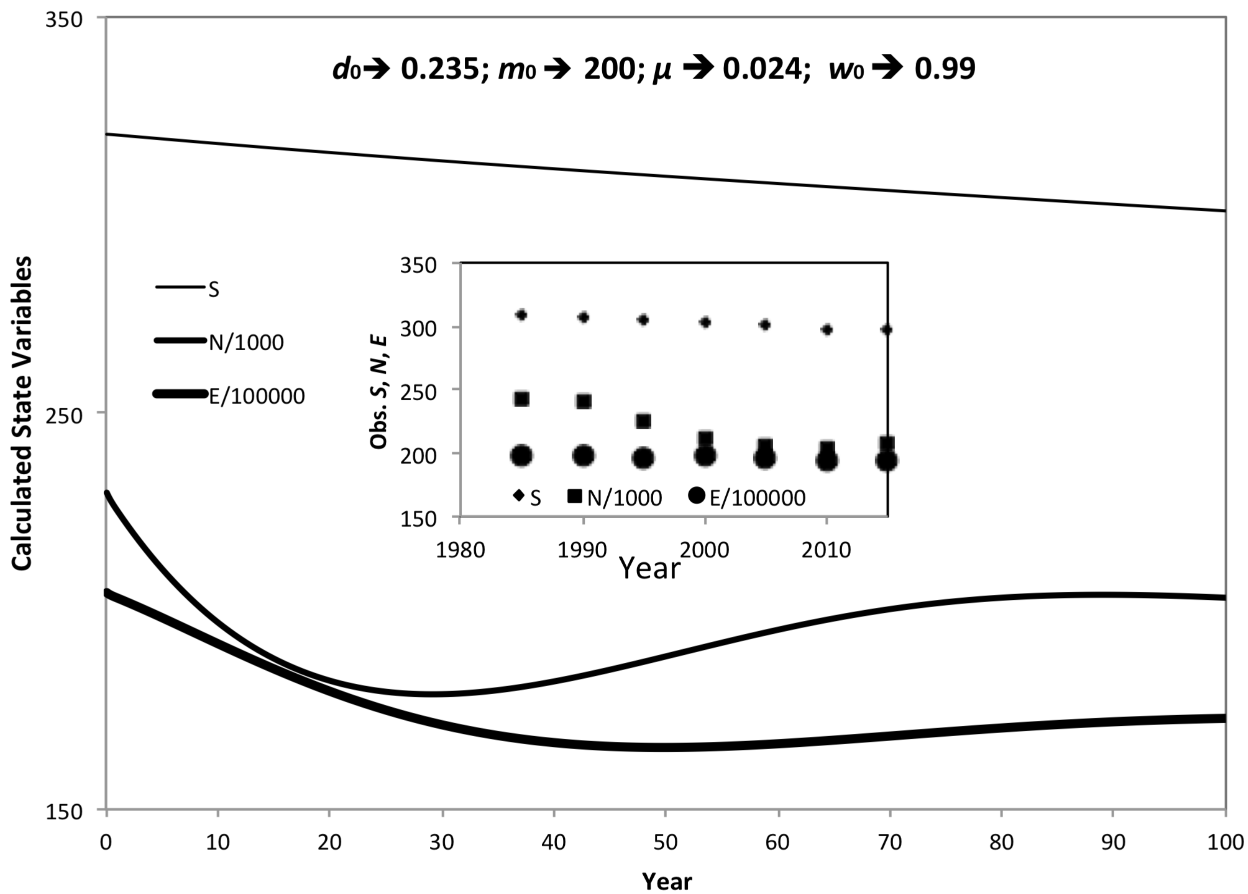


Metabolic rate distribution



DynaMETE also predicts the time trajectories of the state variables in response to a perturbation

Again, qualitative agreement with what is observed at BCI



The steady state limit of DynaMETE agrees with METE

But makes additional predictions:
in the steady-state,
DynaMETE predicts an “ideal biodiversity law”
analogous to PV=nRT

$$P = 0.343\ B^{3/4} S^{1/4} \ln^{3/4}(1/\beta)$$

P = community metabolic rate or productivity
B = community biomass
S = community species richness
1/beta ≈ $(N/S) * \ln(N/S)$
N = community abundance

A powerful New Analytical Method for Solving for the Time Evolution of the Lagrange Multipliers

Iterating DynaMETE entails solving for 5 Lagrange Multipliers at each time step.

That requires finding the location of the absolute maximum of a 5-dimensional surface at each time step. To run the model out 100 years ➔ 10^3 time steps for sufficient accuracy

Lambda Dynamics

We can derive five coupled equations for the five $d\lambda/dt$'s:

$$\Sigma_j C_{i,j} * d\lambda_j/dt = F_i$$

The F_i are function of the λ's and transition functions at time t.

The $C_{i,j}$ are covariances of the transition functions and n or $n\varepsilon$.
They are *easily* calculated from the structure function at time t.

The lambdas at time t+1 are then determined by inverting a 5x5 matrix of covariances to get their time derivatives at time t. Thus the λ's can be updated algebraically.

This is much faster and more accurate than searching for a maximum in 5-D.

SUMMARY

- The Maximum Entropy Theory of Ecology provides remarkably accurate predictions for the static shapes of numerous patterns observed in quasi steady-state ecosystems.
- But the predictions fail in rapidly changing systems.
- A dynamic extension of METE (DynaMETE) offers a possible approach to describing disturbed, rapidly changing ecosystems.
- With DynaMETE we can now predict the mechanism of disturbance from quantitative signatures of deviation from METE.
- DynaMETE also predicts the future trajectories of state variables and allows identification of system characteristics that result in resilience under different types of disturbance.
- With iterated MaxEnt, a new method of solving for the time dependence of the Lagrange Multipliers avoids having to find absolute maxima in 5-D.
- Hybridizing the Maximum Information Entropy method with explicit mechanisms of disturbance provides a foundation for the construction of a general theory of complex systems undergoing disturbance. Application may be possible to non-steady-state systems in economics, linguistics, thermodynamics and many other complex dynamic systems, where MaxEnt has proven useful in the static limit.

Thanks to my students and postdocs who collaborated in the development of METE and DynaMETE:

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Dynamic Maximum Entropy Theory

Thanks for Listening!

Questions?