TraitsCape: Understanding the role of microrefugia in buffering fynbos from global change

Cory Merow University of Connecticut

Xinyi Shen University of Wisconsin-Madison

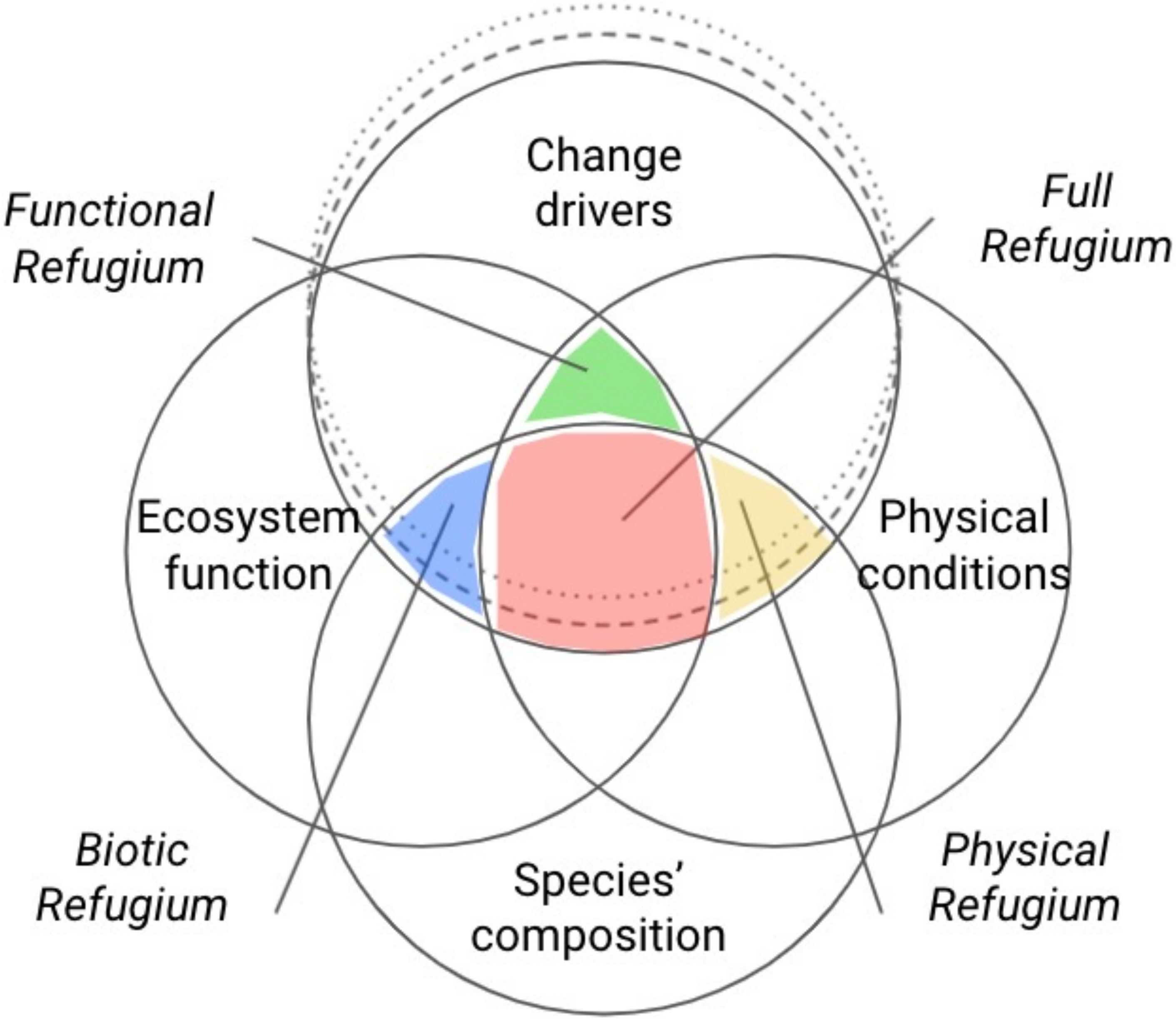
Pep Serra-Diaz University of Connecticut

Jasper Slingsby University of Cape Town

Wendy Foden SANParks

Nicola van Wilgen SANParks

Refugia



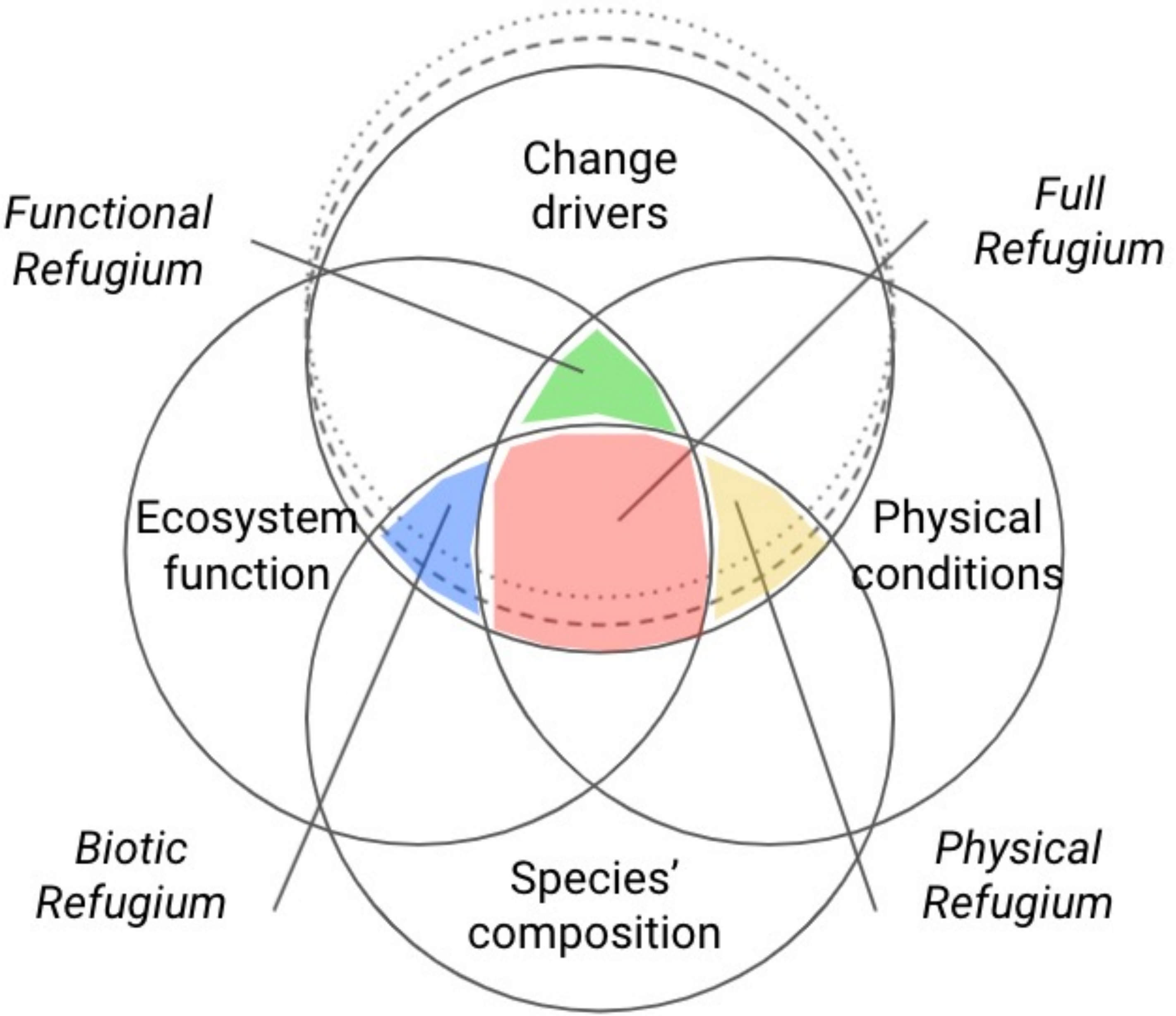
Change drivers
Functional Refugium
Full Refugium
Ecosystem function
Physical conditions
Biotic Refugium
Species' composition
Physical Refugium

Refugia

When are fynbos communities likely to be resilient to change?

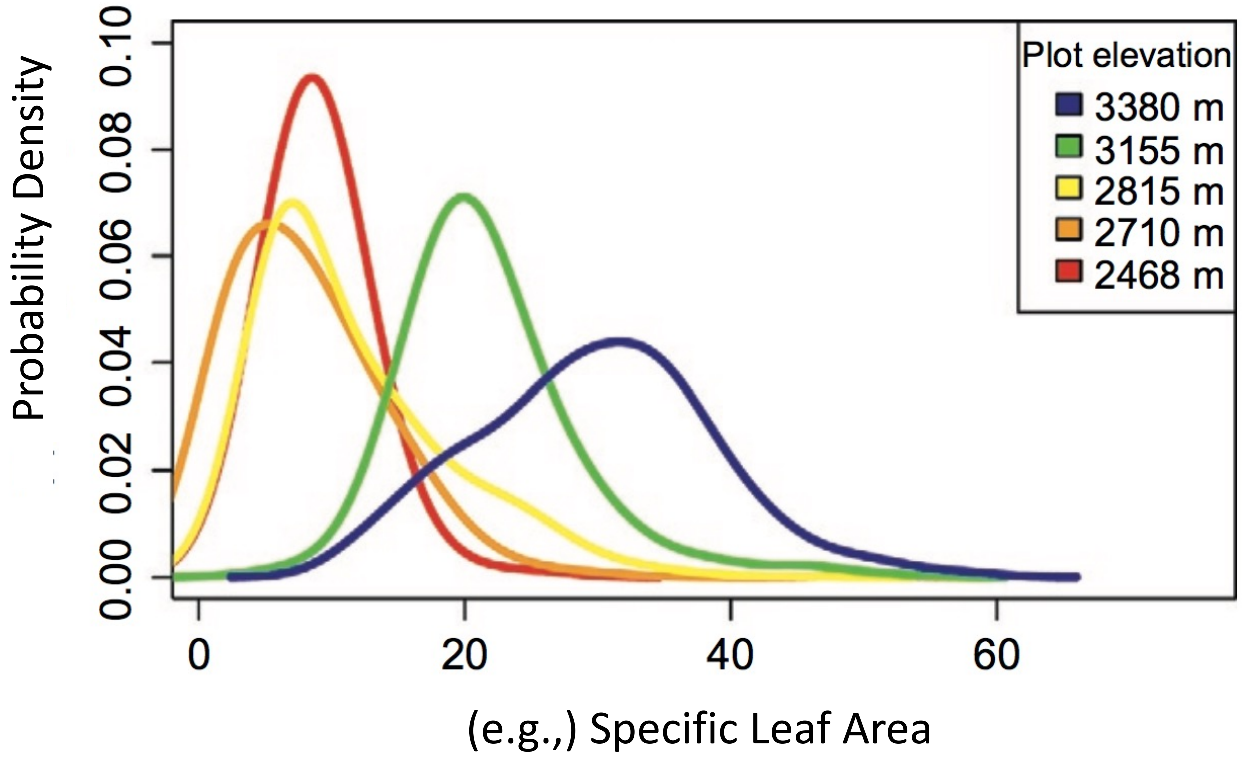
Will physical microrefugia maintain existing fynbos communities?

Will shifting abundance or immigration provide resilience in ecosystem function despite species composition change?



Trait Driver Theory

A general theory for trait-based ecology that can scale from individuals, to communities, and to ecosystems



Enquist et al. Adv. Ecol. Research 2015
Merow and Enquist, In prep

Trait Driver Theory

Moment of Community Trait Distribution, $C(z)$	Predictions for Rate of Community Response to a Changing Environment	Predicted Ecosystem Effects
I. Mean	**(a)** Will shift if environmental change alters value of z_{opt} and time scales are not too rapid and oscillatory **(b)** Lags z_{opt} by an amount that depends on rate of change in environment, rates of immigration, and the forces that influence the variance	**(i)** Will shift productivity according to form of growth equation, f
II. Variance	**(a)** Decreases with strong abiotic filtering **(b)** Decreases due to competitive exclusion by individuals with trait z_{opt} **(c)** Can increase with increased immigration, competitive niche displacement, and/or temporal variation in z_{opt}	**(i)** Increased variance implies lower productivity for fixed or stable environment **(ii)** Increased variance accelerates community response to environmental changes
III. Skewness	**(a)** Skewness values > or < 0 can reflect a lag between $\bar{z}$ and z_{opt} and a rapidly changing community due to an environmental driver or extreme limit to a trait value **(b)** Increases in skewness can indicate a response to rapid environmental changes or the importance of rare species advantages in local coexistence	**(i)** Depending upon kurtosis and variance value, productivity should be reduced compared with a community with similar variance but skewness equal to zero

Trait distribution moments scale with ecosystem function!

(i) Increased variance implies lower productivity for fixed or stable environment

(ii) Increased variance accelerates community response to environmental changes

Enquist et al. Adv. Ecol. Research 2015

Trait Driver Theory

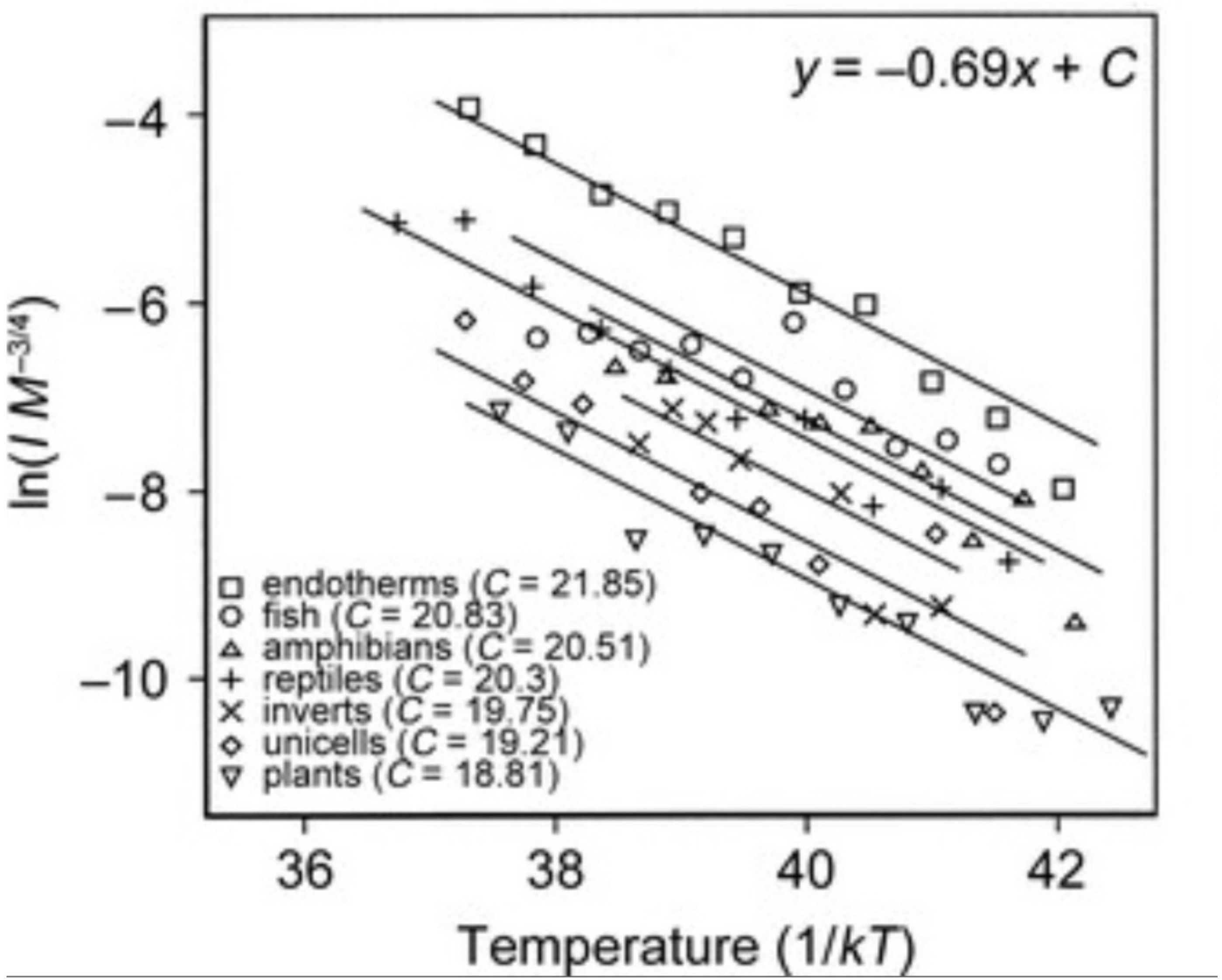
Moment of Community Trait Distribution, *C*(*z*)	Predictions for Rate of Community Response to a Changing Environment	Predicted Ecosystem Effects
I. Mean	**(a)** Will shift if environmental change alters value of z_{opt} and time scales are not too rapid and oscillatory **(b)** Lags z_{opt} by an amount that depends on rate of change in environment, rates of immigration, and the forces that influence the variance	**(i)** Will shift productivity according to form of growth equation, f
II. Variance	**(a)** Decreases with strong abiotic filtering **(b)** Decreases due to competitive exclusion by individuals with trait z_{opt} **(c)** Can increase with increased immigration, competitive niche displacement, and/or temporal variation in z_{opt}	**(i)** Increased variance implies lower productivity for fixed or stable environment **(ii)** Increased variance accelerates community response to environmental changes
III. Skewness	**(a)** Skewness values $>$ or $<$ 0 can reflect a lag between $\bar{z}$ and z_{opt} and a rapidly changing community due to an environmental driver or extreme limit to a trait value **(b)** Increases in skewness can indicate a response to rapid environmental changes or the importance of rare species advantages in local coexistence	**(i)** Depending upon kurtosis and variance value, productivity should be reduced compared with a community with similar variance but skewness equal to zero

Trait distribution moments scale with ecosystem function!

productivity should be reduced compared with a community with similar variance but skewness equal to zero

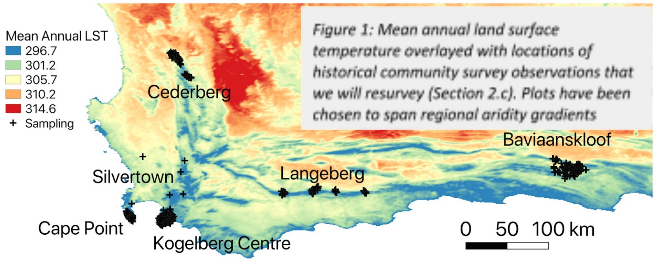
Enquist et al. Adv. Ecol. Research 2015

How do we test a theory?

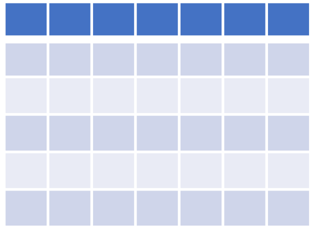


Brown et al 2007 Ecology

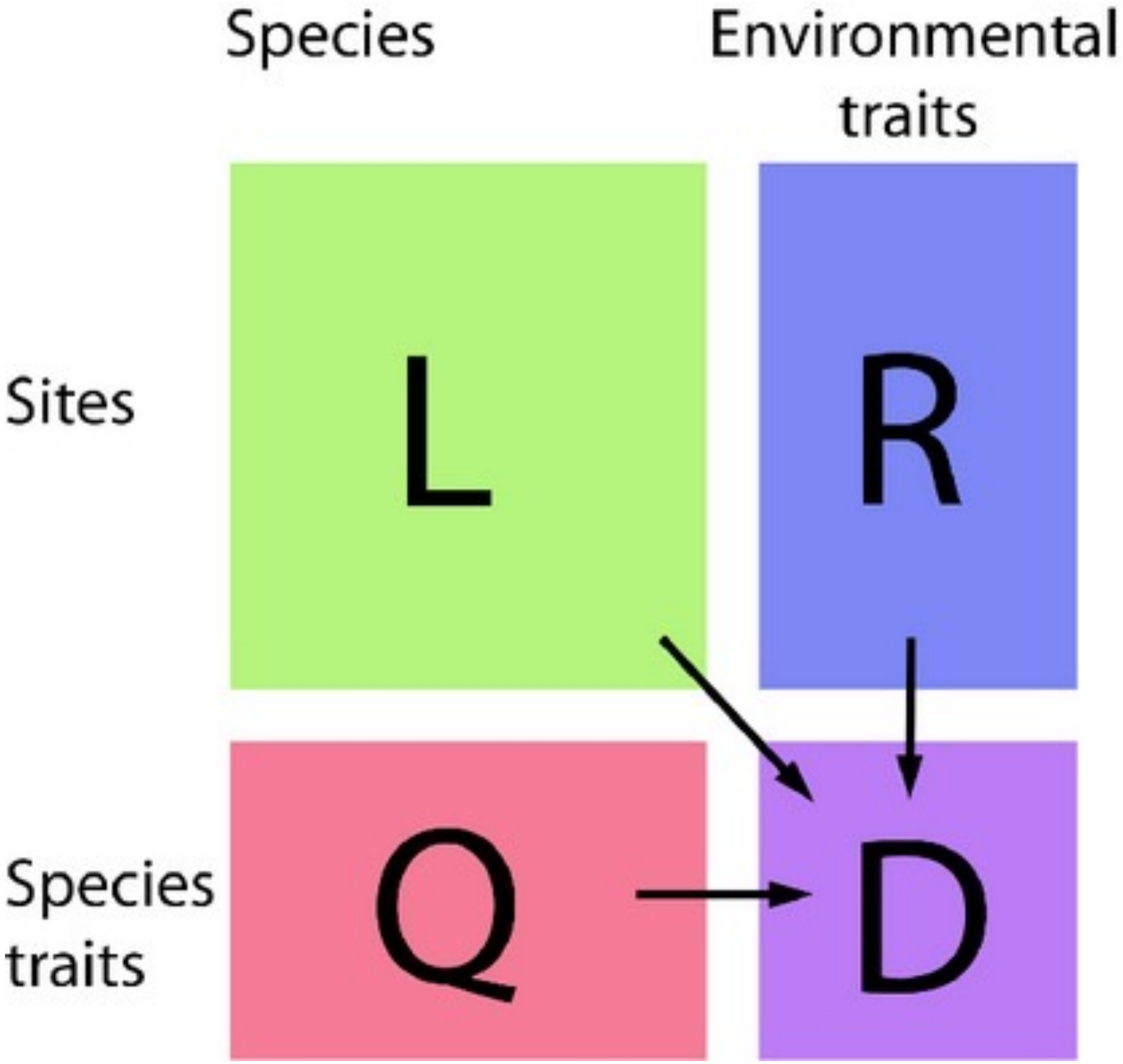
Ingredients : The fourth corner problem

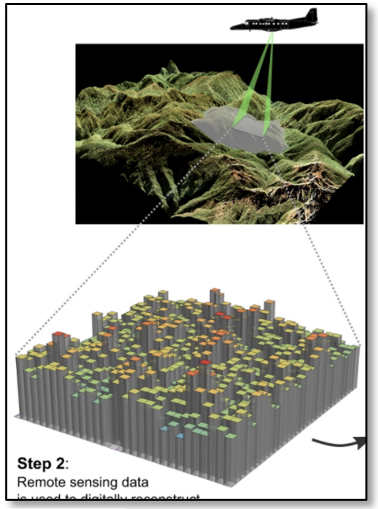


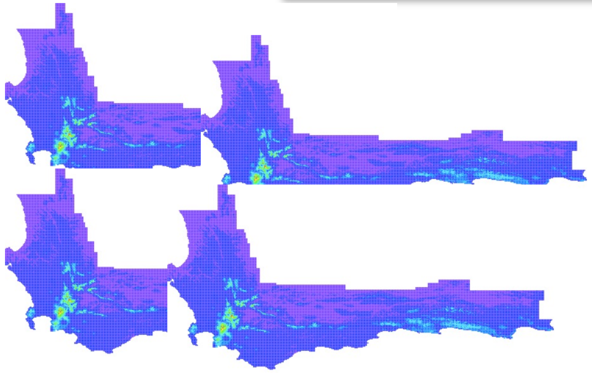
Releves



Trait Matrix







Environment

←Trait ~ Env

From Brown et al 2014 MEE

Model development (why this works)

BACKGROUND:

1. Maximum entropy models are used to estimate density functions, i.e., a **community trait distribution** (Shipley et al 2006, Science)
2. Maxent models can be inverted to **predict the relative abundance** of each species in a community based on their traits and the community mean traits (Merow et al. 2011, Ecology)
3. Maxent models applied to species distributions are constrained by the **moments** (mean, variance) of the niche for a species by including linear and quadratic features, respectively (Phillips and Dudik, 2008, Ecography)
4. Community Aggregated Trait models showed unified maximum entropy models of Shipley et al 2006 and Fourth Corner Problems (Legendre et al 1997 Ecology, Schleip et al 2018 MEE) **for trait-environment relationship in the GLM-based framework** (Warton et al 2013 MEE) enabling all the tools of regression to apply to entropy models. These focused just on community MEAN traits.

NEW:

1. Extend CATs to include **other central moments using additional polynomial terms**
2. Variable selection corresponds to testing for the **significance of mechanism** predicted by TDT
3. LASSO regression manages the slew of candidate variables. Adaptive LASSO distills further. This allows **big data and complex models to be interpretable.**
4. Combinations of significant variables help **isolate which TDT mechanisms operate**.

The model:

Poisson Point Process

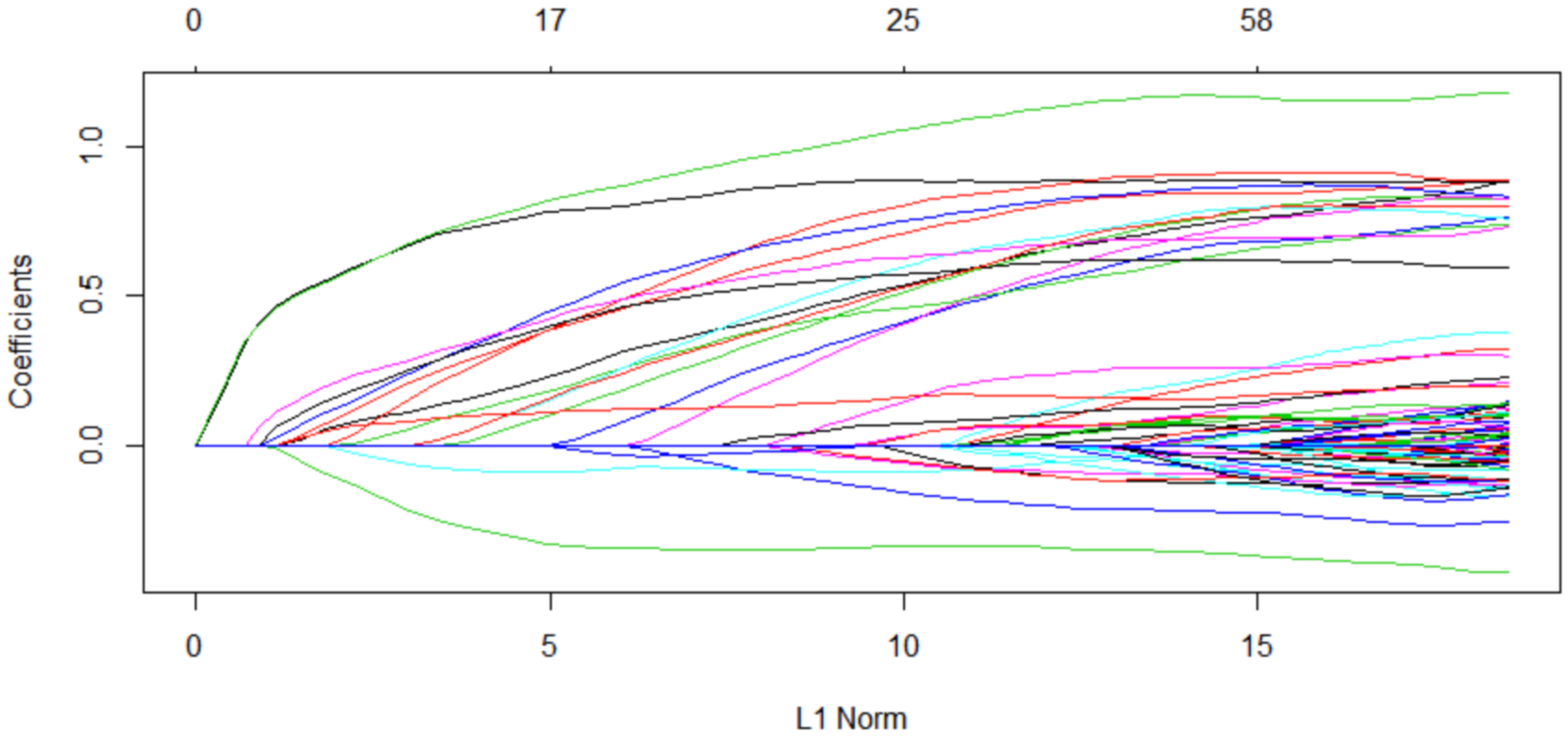
Trait Driver Theory

log(relative abundance) ~ trait + env + trait * env + trait^2 + trait ^3 + trait ^4 +
env* trait^2 + env* trait ^3 +env * trait ^4

+trait + env + trait * env + trait^2 + trait ^3 + trait ^4 + env* trait^2 + env* trait ^3 +env * trait ^4
+trait + env + trait * env + trait^2 + trait ^3 + trait ^4 + env* trait^2 + env* trait ^3 +env * trait ^4
+trait + env + trait * env + trait^2 + trait ^3 + trait ^4 + env* trait^2 + env* trait ^3 +env * trait ^4
+trait + env + trait * env + trait^2 + trait ^3 + trait ^4 + env* trait^2 + env* trait ^3 +env * trait ^4
+trait + env + trait * env + trait^2 + trait ^3 + trait ^4 + env* trait^2 + env* trait ^3 +env * trait ^4
+trait + env + trait * env + trait^2 + trait ^3 + trait ^4 + env* trait^2 + env* trait ^3 +env * trait ^4

The model:
Poisson Point Process fit with **LASSO regression**

Fewer parameters

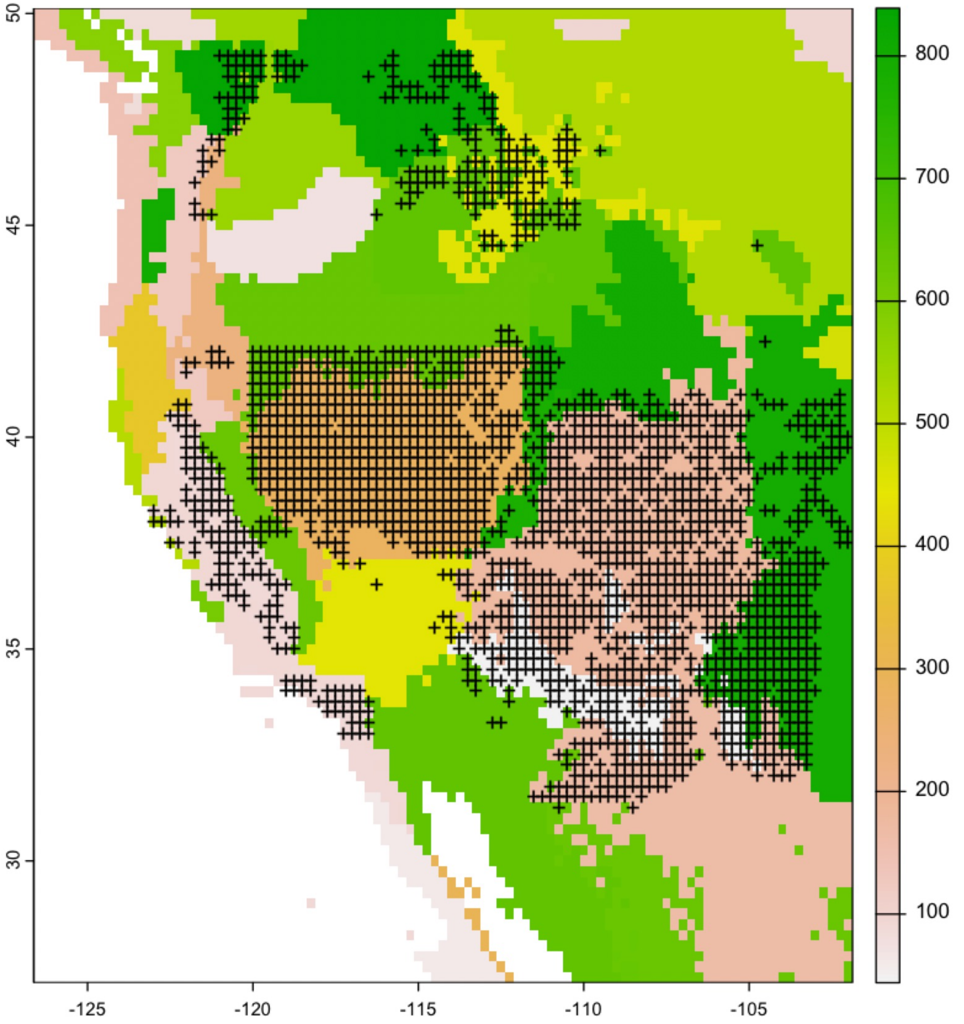


The Result (at this point, a prediction)

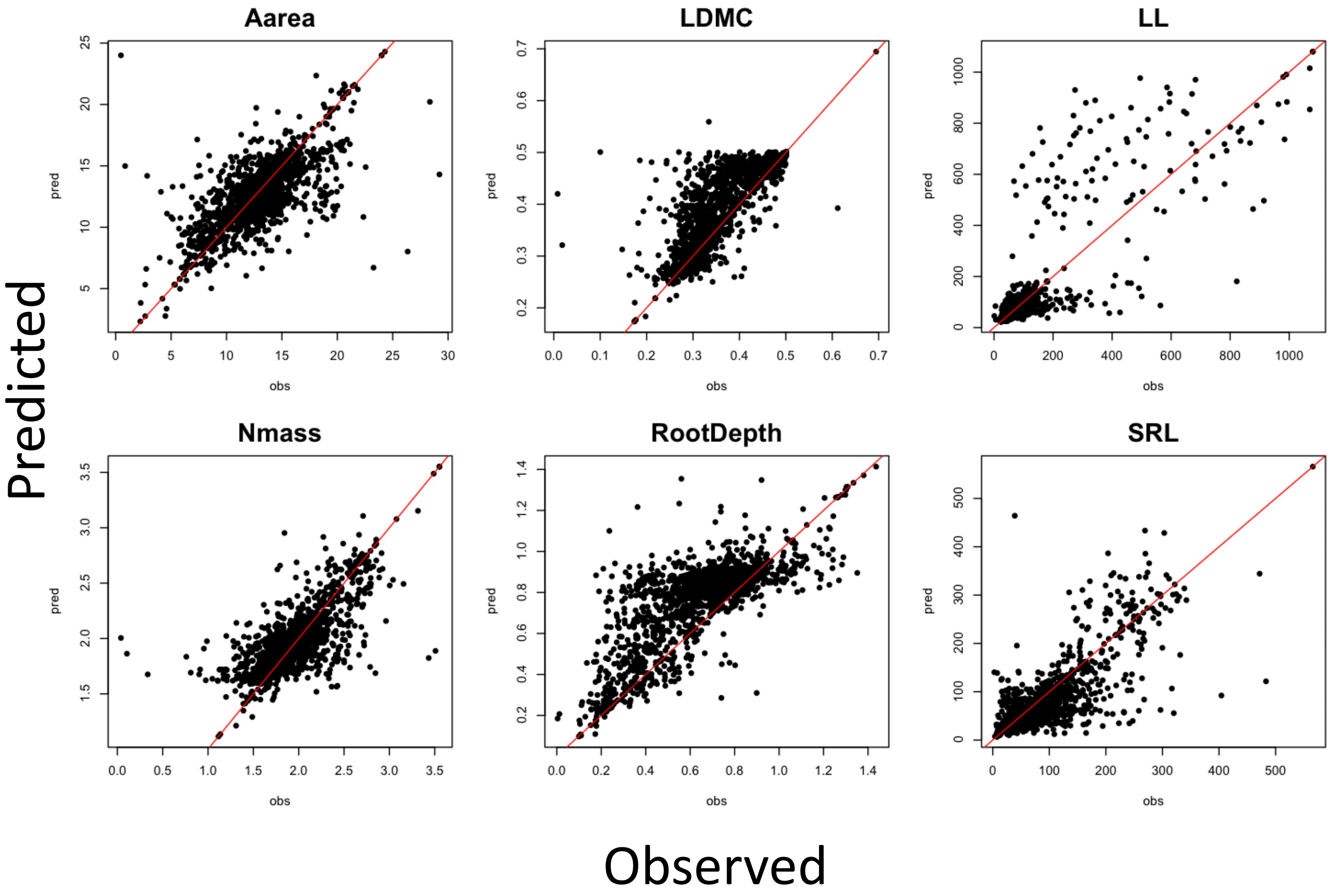
Coefficient	Value	Interpretation
Trait^2 * env	+5	diverse communities have higher productivity in variable environments AND Lower productivity in stable environments
Trait^3	- 5	lower productivity with higher skew due to community lagging env
TBD	---	---

Starting tests… California grasslands

Ecoregion classification



Community mean traits

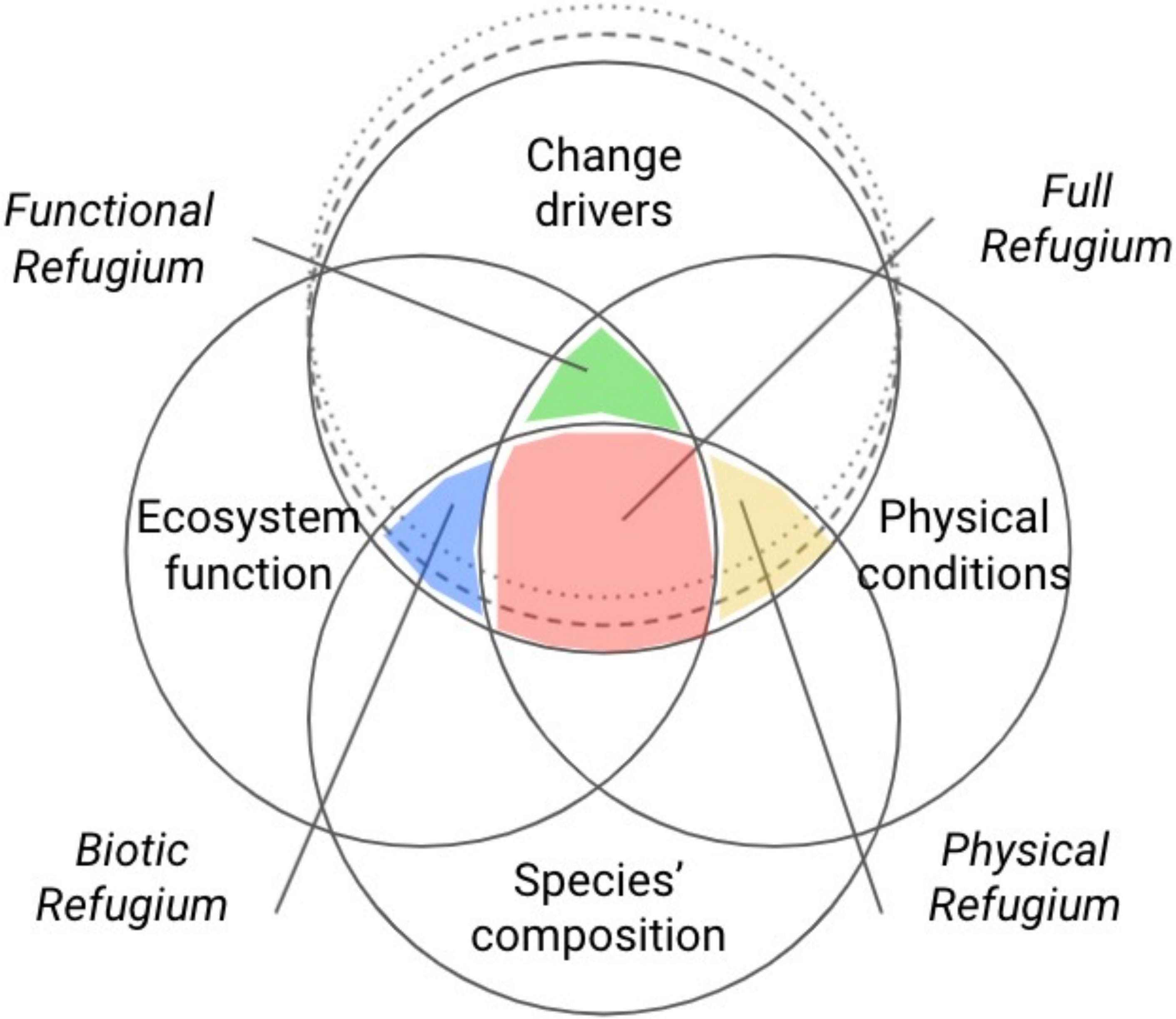


Refugia

When are fynbos communities likely to be resilient to change?

Will physical microrefugia maintain existing fynbos communities?

Will shifting abundance or immigration provide resilience in ecosystem function despite species composition change?



Thanks!

Pep Serra-Diaz

Mark Urban

Xinyi Shen

Pep Serra-Diaz

Jasper Slingsby

Wendy Foden

Nicola van Wilgen

Brian Enquist

Manos Anagnostou

Adam Wilson

Questions?

Bonus slides below

Dynamics of community trait moments

Decorative

Total biomass

$$dC_T/dt = C_T[f(\bar{z}) + f^{(2)}\bar{z})M_2 + f^{(3)}(\bar{z})M_3 + ...] + I \quad (6)$$

Trait mean

$$d\bar{z}/dt = f^{(1)}(\bar{z})M_2 + f^{(2)}(\bar{z})M_3 + ... + (I/C_T)(\bar{z}_I - \bar{z}) \quad (7)$$

Trait Variance

$$dV/dt = dM_2/dt = f^{(1)}(\bar{z})M_3 + f^{(2)}(\bar{z})(M_4 - M_2^2) + ... + (I/C_T)[(\bar{V}_I - V) + (\bar{z}_I - \bar{z})^2] \quad (8)$$

Trait Skew

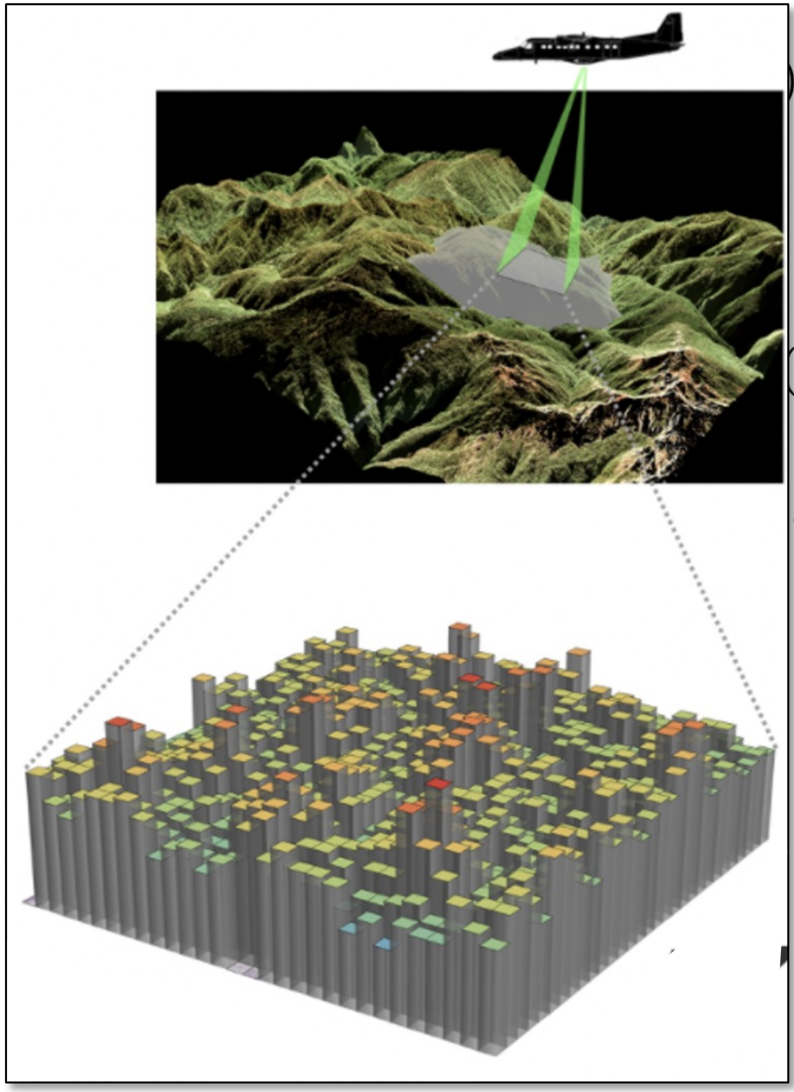
$$dS/dt = dM_3/dt = 3f^{(1)}(\bar{z})(M_4 + SV/B_T) + (I/C_T)[..] \quad (9)$$

f describes the per capita growth rate
M describes moments of the trait distribution

Turelli and Barton 1991
Norberg et al. 2001
Savage et al. 2007
Enquist et. al 2015

Trait Moment Dynamics

Growth function



Total biomass

$$) + f^{(2)}\bar{z})M_2 + f^{(3)}(\bar{z})M_3 + ...] + I \quad (6)$$

Trait mean

$$+ f^{(2)}(\bar{z})M_3 + ... + (I/C_T)(\bar{z}_I - \bar{z}) \quad (7)$$

Trait Variance

$$(\bar{z})(M_4 - M_2^2) + ... + (I/C_T)[(\bar{V}_I - V) + (\bar{z}_I - \bar{z})^2] \quad (8)$$

Trait Skew

$$3f^{(1)}(\bar{z})(M_4 + SV/B_T) + (I/C_T)[..] \quad (9)$$

Can parameterize with *high resolution* remote sensing pixels

Trait Moment Dynamics

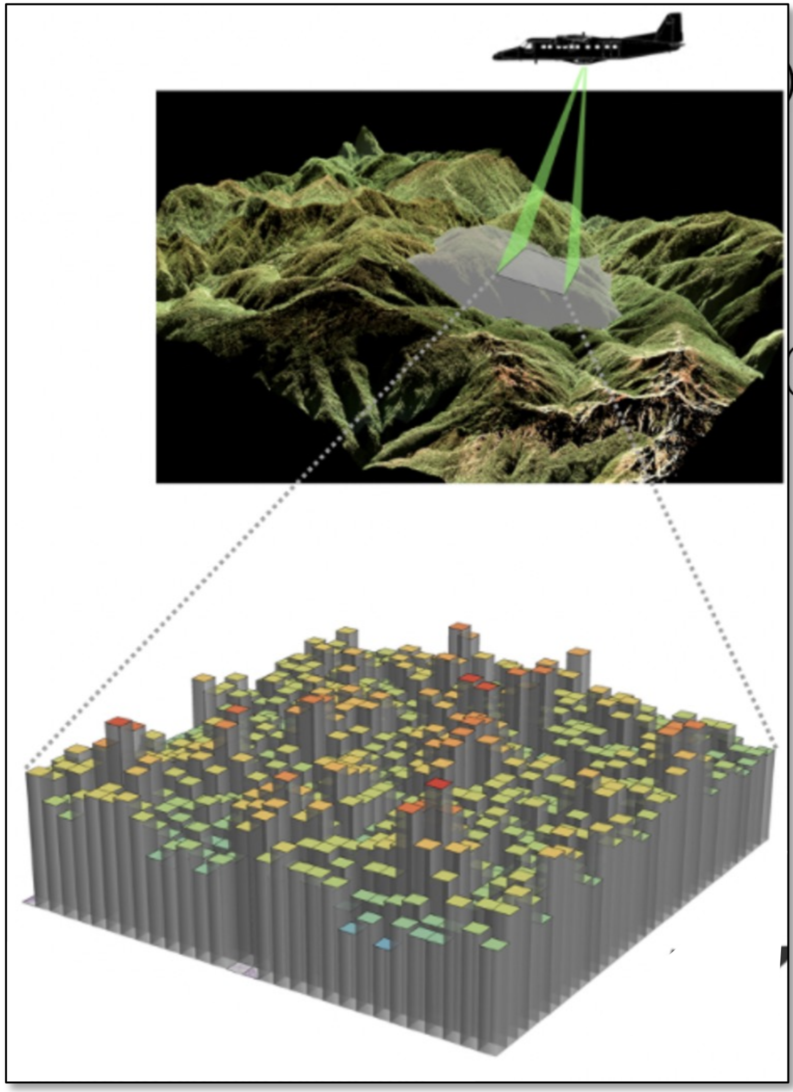
Growth function

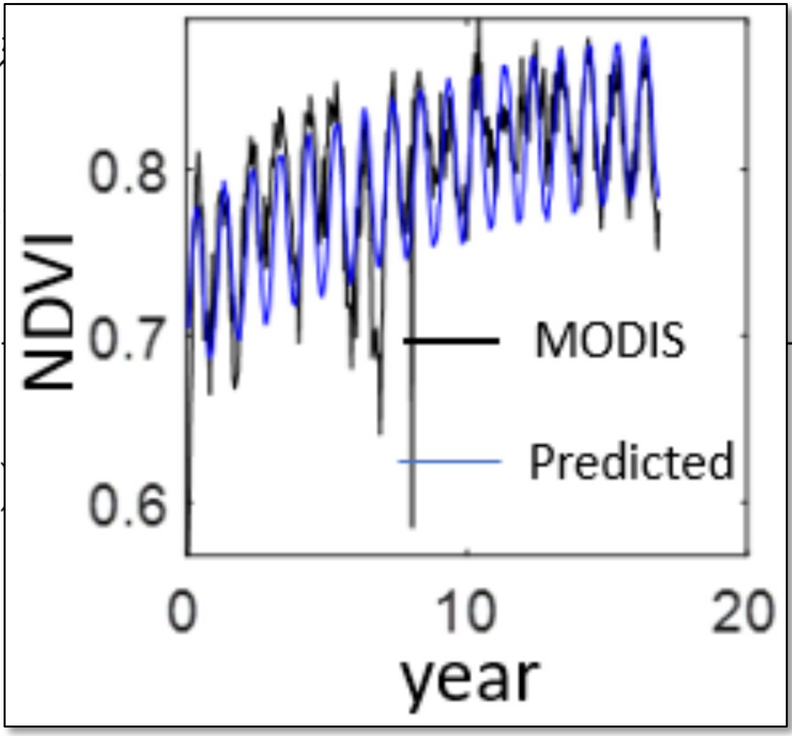
Total biomass $) + f^{(2)}$ (6)

Trait mean $+ f^{(2)}($ (7)

Trait Variance $(\bar{z})(M_4$ $\bar{z})^2]$ (8)

Trait Skew $3f^{(1)}(\bar{z}$ (9)





Can parameterize with *high resolution* remote sensing pixels

And a biomass growth as model (Wilson et al. 2010)

Adding more trait structure….

Decorative

$$recruit\ trait:\ r_q(q'|q, env) \sim \mathcal{F}(f(q, env), \epsilon_{q2})$$

Traits ~ Environment

$$growth:\ g(x'|x, q, env) \sim \mathcal{F}(f(x, q, env), \sigma_g^2)$$

$$survival:\ s(x, q, env) = f(x, q, env)$$

$$recruits:\ r(x, q, env) = f(x, q, env)$$

$$recruit\ size:\ r_x(x'|x, q, env) \sim \mathcal{F}(f(x, q, env), \sigma_r^2)$$

Individual Demography ~ Traits

$$n_{t+1}(x', q') = \int_{\Omega_z}\int_{\Omega_q} K(x', q'|x, q, env)\ n_t(x, q)\ dx\ dq + I(x', q', env)$$

$$K(x', q'|x, q, env) = P(z', q'|x, q, env) + F(z', q'|x, q, env)$$

$$P(x', q'|x, q, env) = s()\ g()\ t(); \qquad F(x', q'|x, q, env) = r()\ r_x()\ r_q()$$

$$I(x', q'|env) \sim \mathcal{F}(metacommunity(x, q), env)$$

Population Dynamics ~ Individual Demography

$$N(x, q) = \sum_i n_i(x, t)$$

$$K^*(x', q'|x, q, env) = \sum_i K_i(x, t, env)$$

Community Dynamics ~ Population Dynamics

$$\textbf{biomass} = \int_{\Omega_z}\int_{\Omega_q} N(x, q)\ dx\ dq$$

$$\textbf{NPP} = \lambda_1 \int_{\Omega_z}\int_{\Omega_q} N(x, q)\ dx\ dq$$

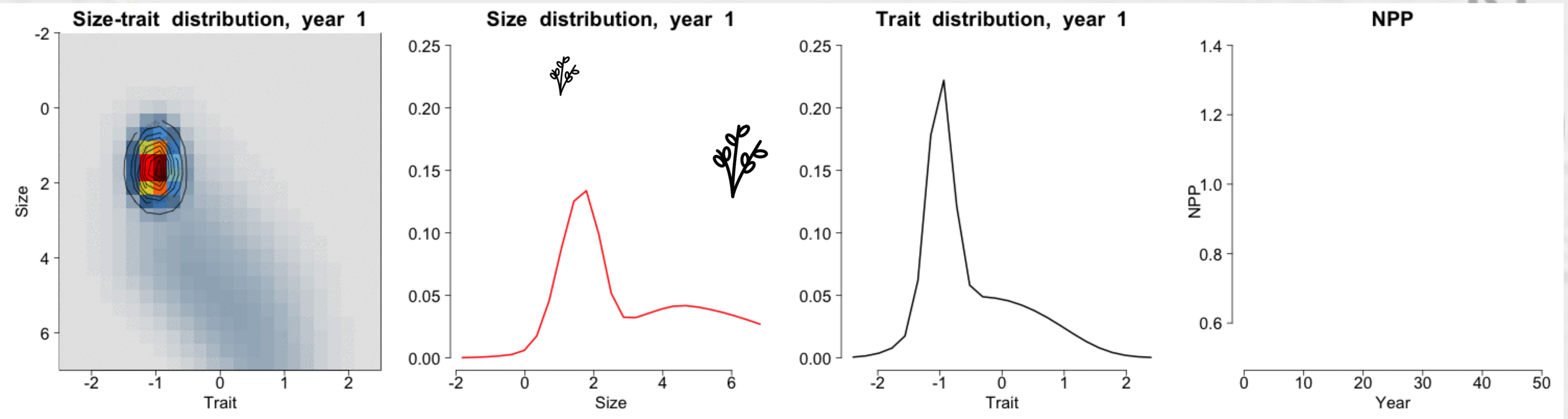
$$\textbf{time to recovery} = t_z = log(z)/log(\lambda_1/|\lambda_2|)$$

$$\textbf{trait life expectancy} = \eta = \sum_j^J (\mathbf{I} - \mathbf{P})^{-1}_{i,j}$$

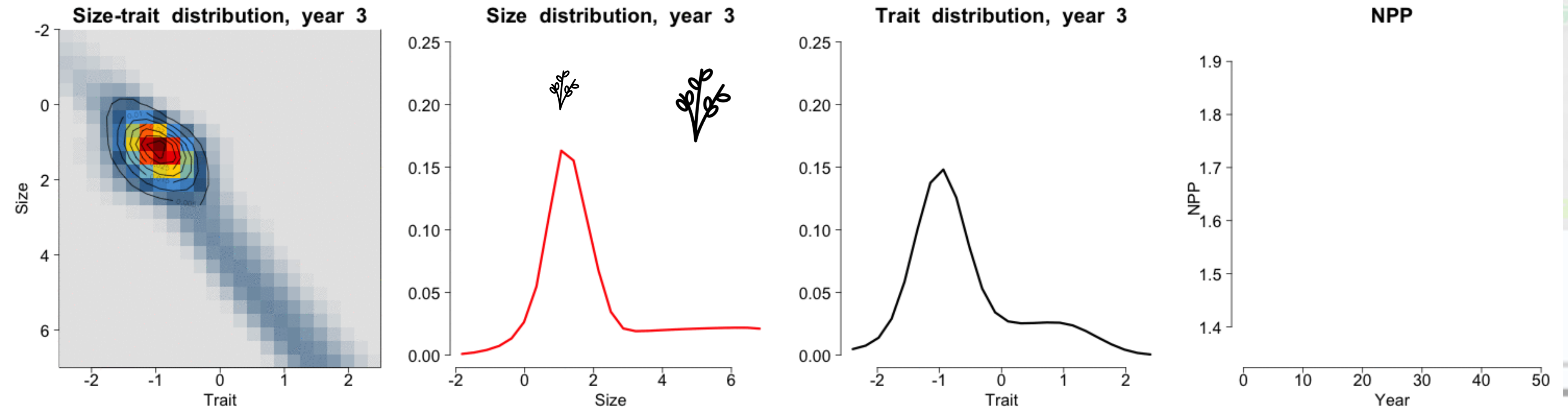
Ecosystem Function ~ Community Dynamics

Immigration is needed for resilience

Scenario 1:
Local Adaptation,
No dispersal

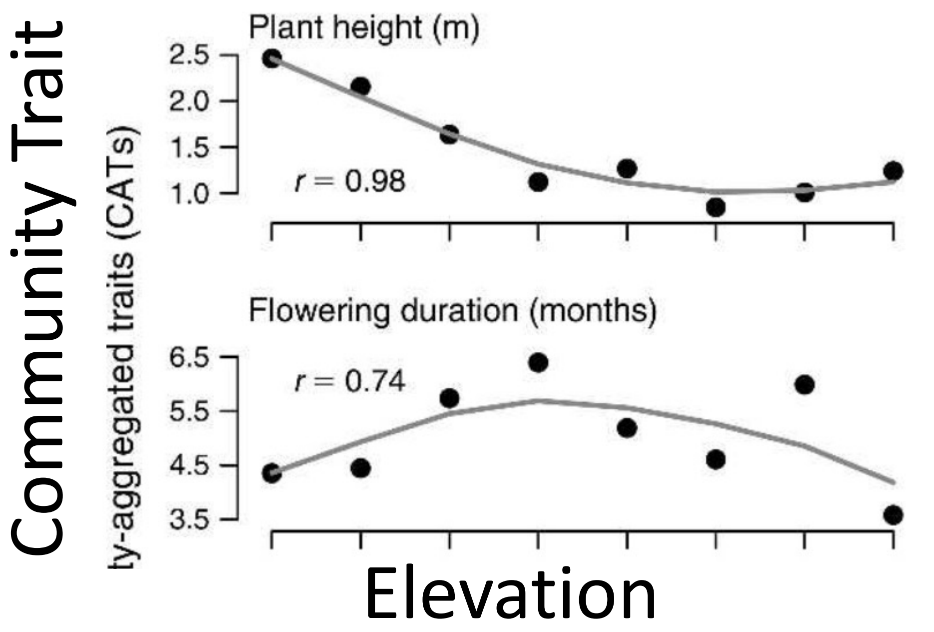


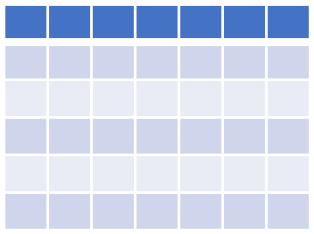
Scenario 2:
Immigration of
traits better
suited for new
climate



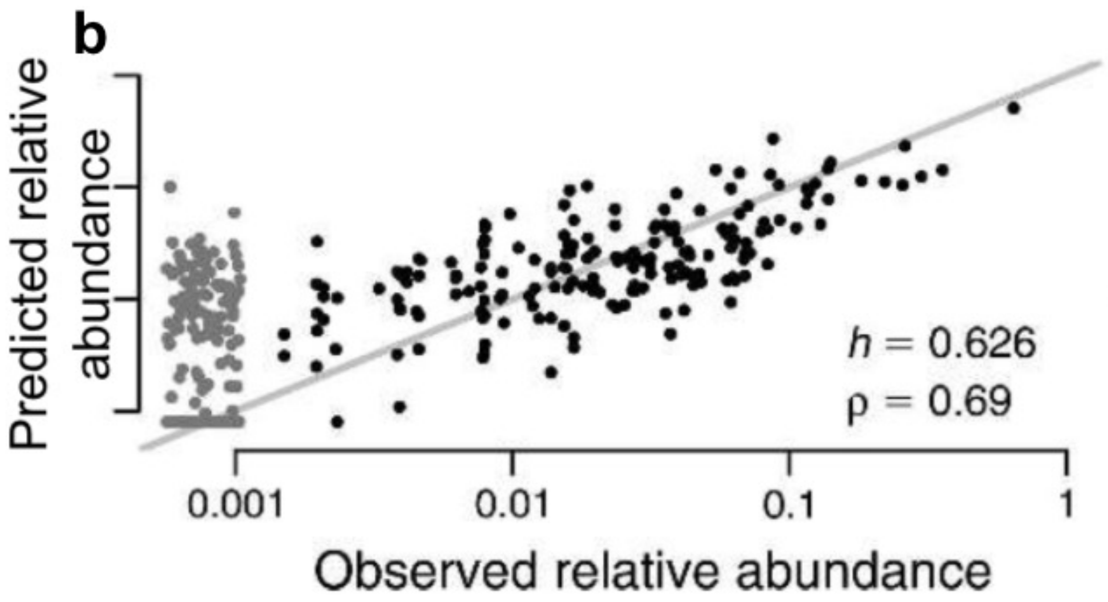
200 km

Recovering species composition from trait distributions

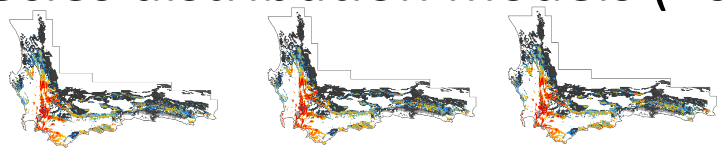




Trait Matrix

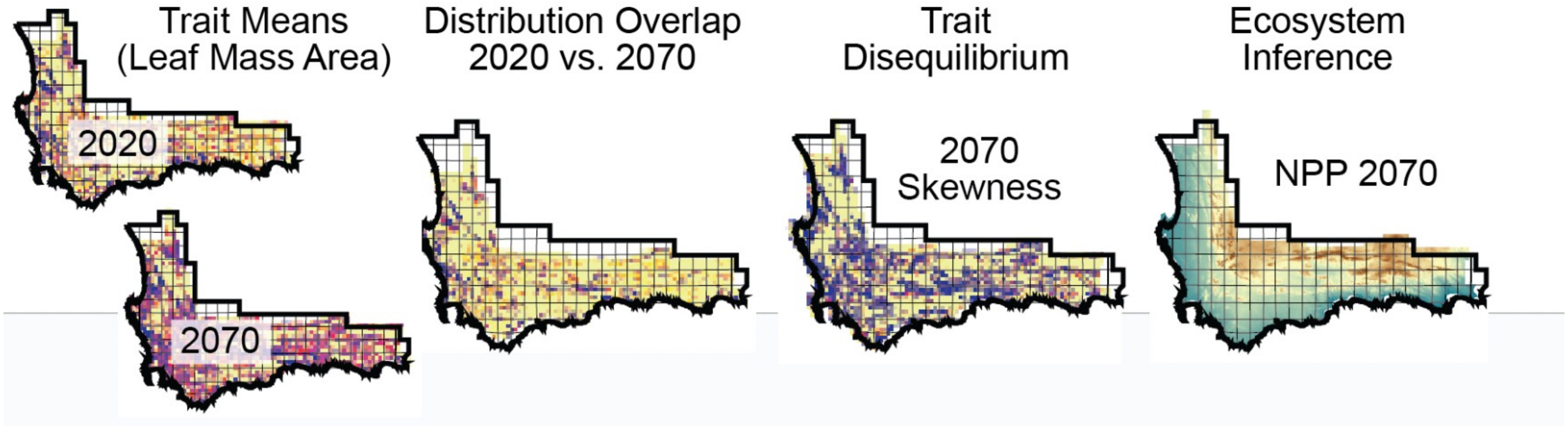


Species distribution models (~6k plants)



Merow et al 2011

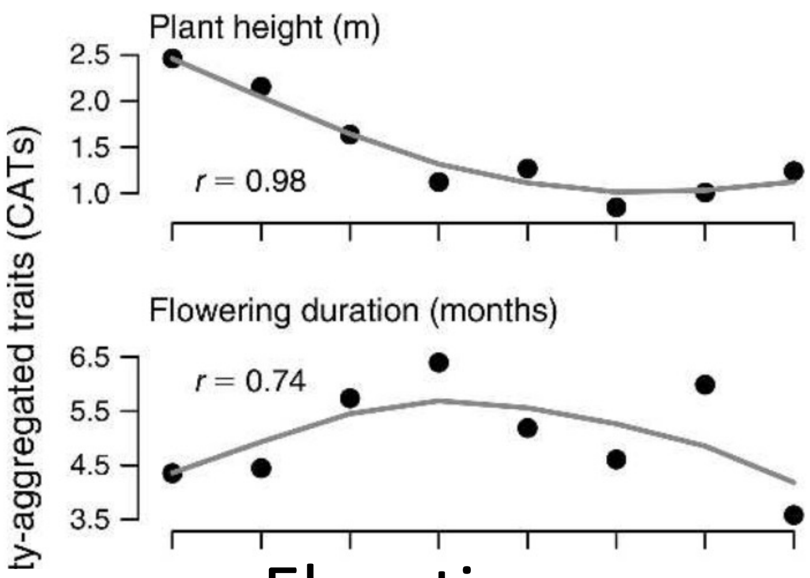
Products



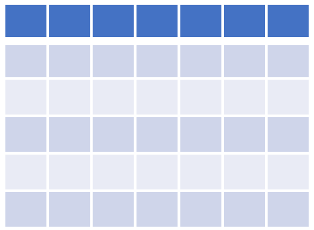
(Possibly only along flight paths, but we'll try using environmental covariates to extend to the CFR)

Recovering species composition from trait distributions

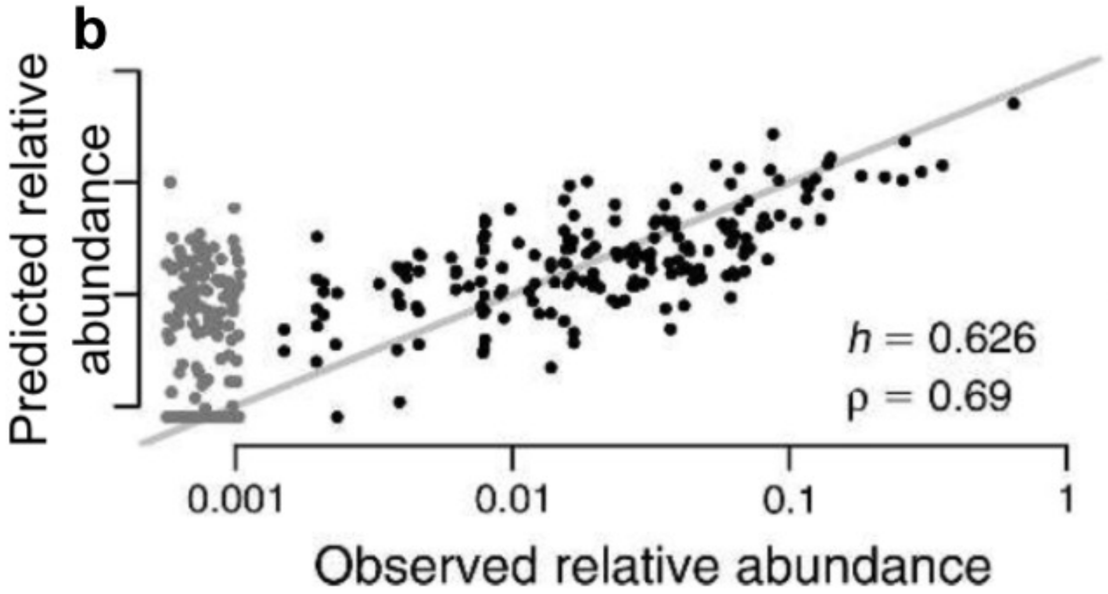
Community Trait



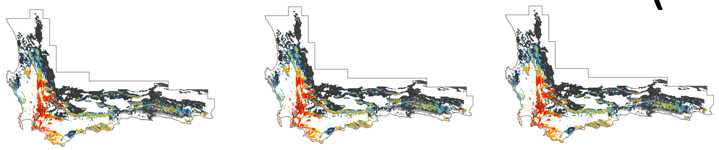
Elevation



Trait Matrix

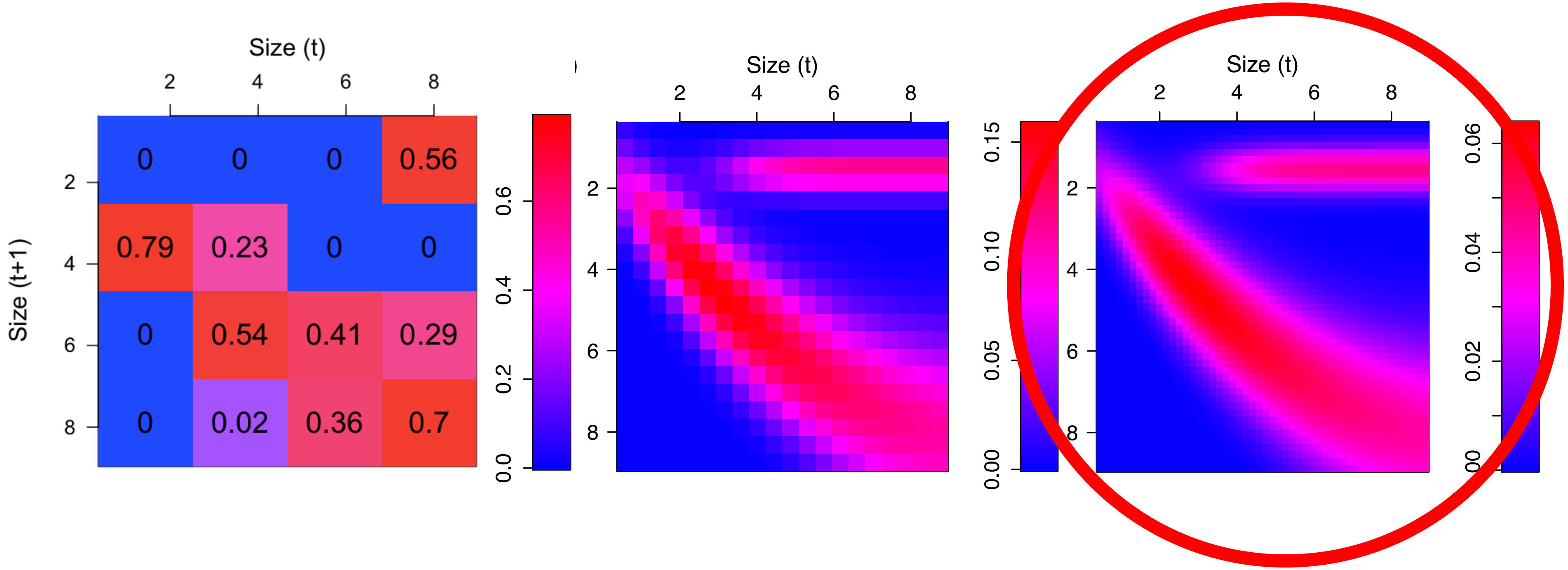


Species distribution models (~6k plants)



Merow et al 2011

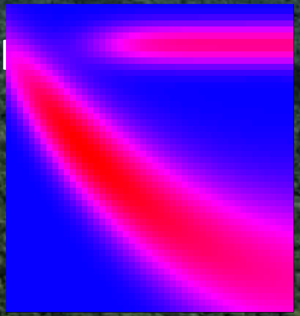
A step further with Integral Projection Models



Apply to communities,
rather than populations

Ecosystem Predictions

Reinterpreting population statistics in terms of comm
and ecosystem statistics



Ecosystem Quantity	Metric
Net Primary Productivity	Dominant right eigenvalue
Trait distributions	Dominant right eigenvector
Resilience	Damping Ratio
Duration of successional stages	Life Expectancy
Sensitivity/Elasticity	Eigenvectors

Amazon Rainforest © Jake Bryant

Merow and Enquist, In prep