

# Convergence or divergence?

Taxonomic, phylogenetic, and functional beta diversity during a 50-year old-field succession

**Shao-peng Li**<sup>1</sup>, Marc W. Cadotte<sup>2</sup>, Scott J. Meiners<sup>3</sup>, Zhichao Pu<sup>1</sup> & Lin Jiang<sup>1</sup>

*<sup>1</sup>School of Biology, Georgia Institute of Technology, Atlanta, GA, USA*

*<sup>2</sup>Biological Sciences, University of Toronto-Scarborough, Toronto, ON, Canada*

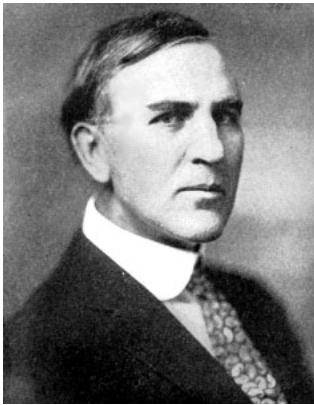
*<sup>3</sup>Department of Biological Sciences, Eastern Illinois University, Charleston, IL, USA*

100<sup>th</sup> ESA Annual Meeting

August 12<sup>th</sup>, 2015

# Is succession...

a deterministic process?



Frederic Clements  
1874-1945

a stochastic process?



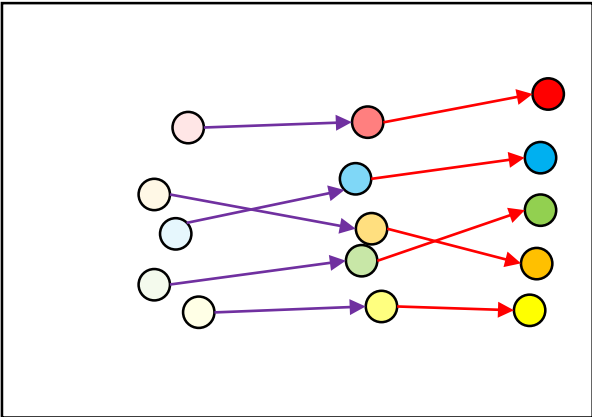
Henry Gleason  
1882-1975

## **Directionality, convergence, and rate of change during succession**

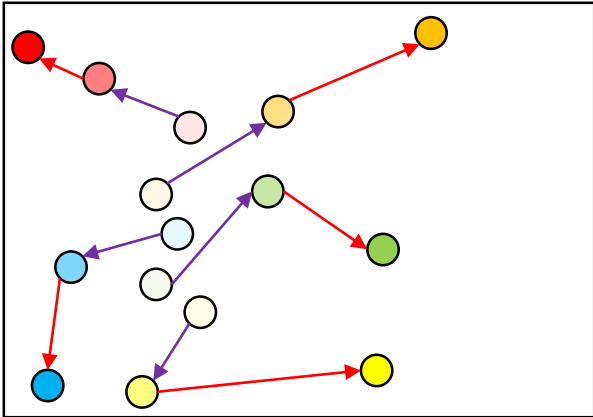
- Is succession directional or non-directional?
- Do different communities converge towards a similar composition (i.e., stable climax community)?
- Do successional rates decline over time?
- Do initial conditions matter (i.e., historical contingency)?

# The directions of succession

Directional

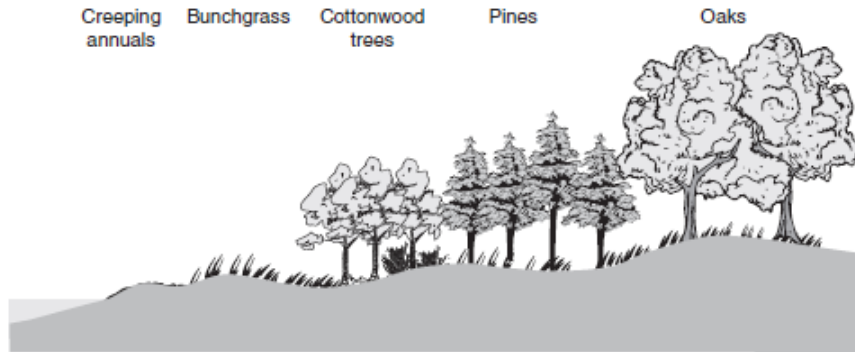


Non-directional



# The directions of succession

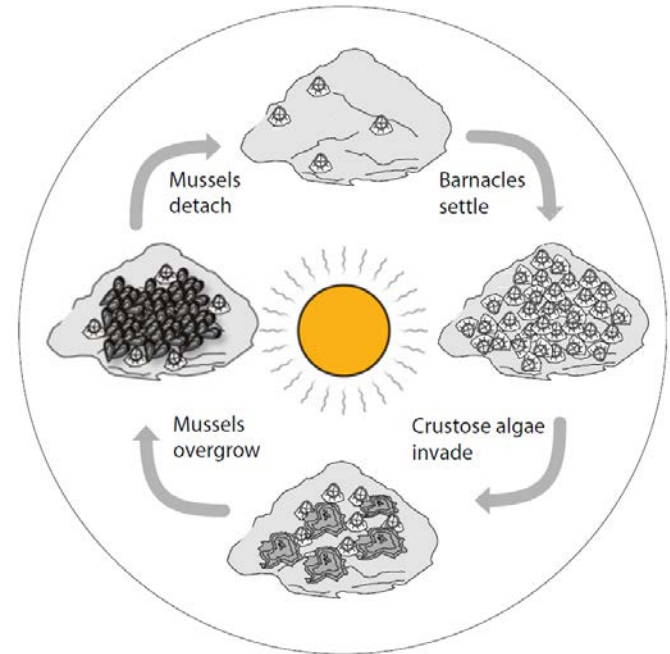
## Directional



Johnson & Miyanishi 2008, *Ecol. Lett.*

## Non-directional

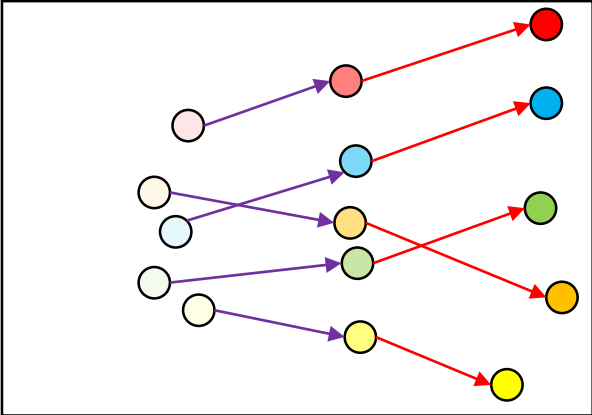
### Cyclic succession



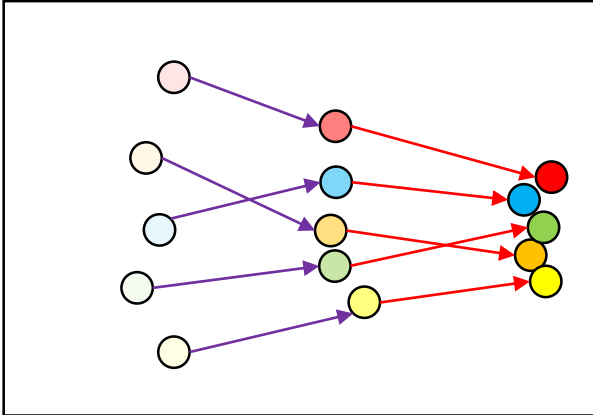
Benincà *et al.* 2015, *PNAS*

# Convergence or divergence?

Divergence

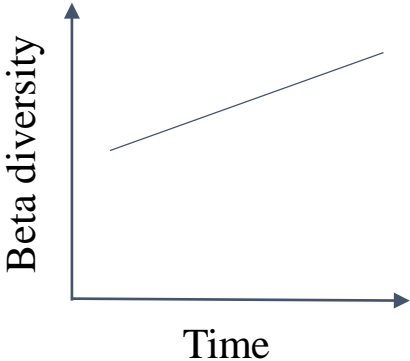


Convergence

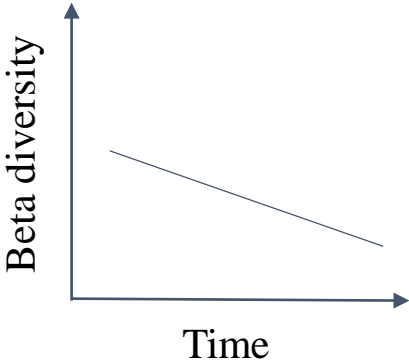


# Convergence or divergence?

Divergence



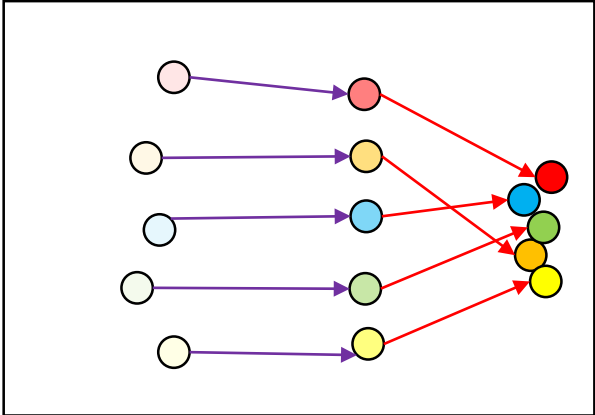
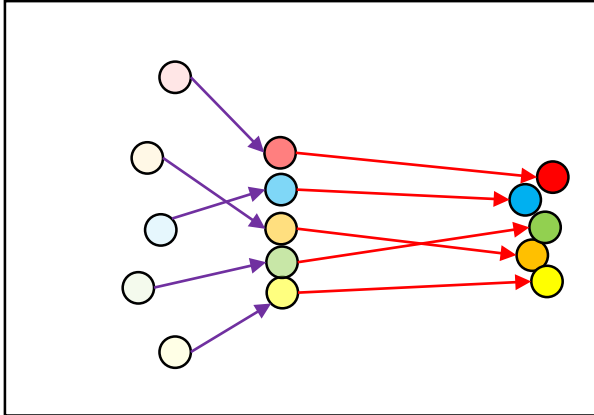
Convergence



# Temporal turnover rate

Decreased

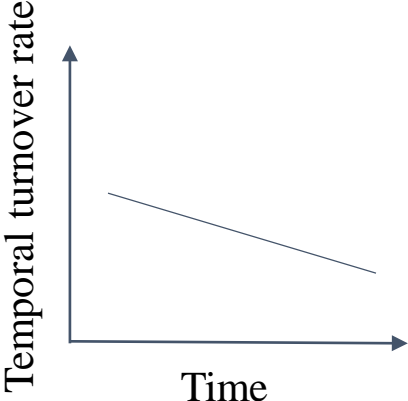
Increased



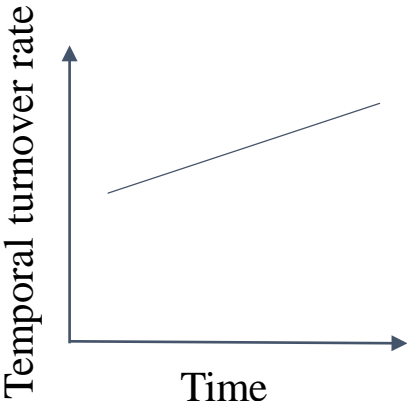


# Temporal turnover rate

Decreased



Increased

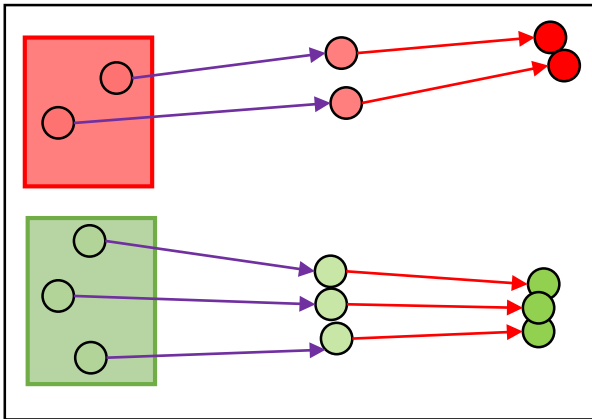


# Historical contingency

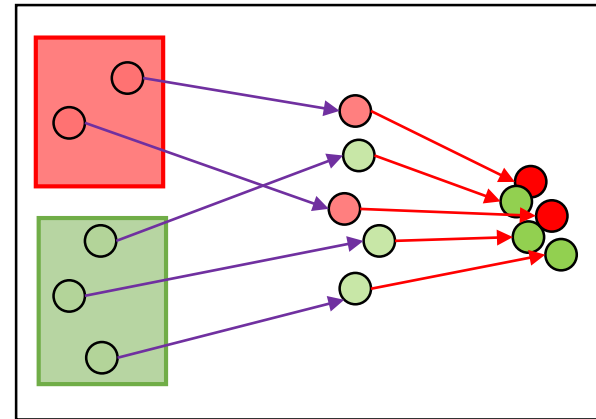
History includes the order and rate of invasion and colonization of a community, and **its initial conditions**.

*Myster & Pickett 1990, Am. Midl. Nat.*

Important



Not important



# Chronosequence vs long-term monitoring

- Space-for-time substitution

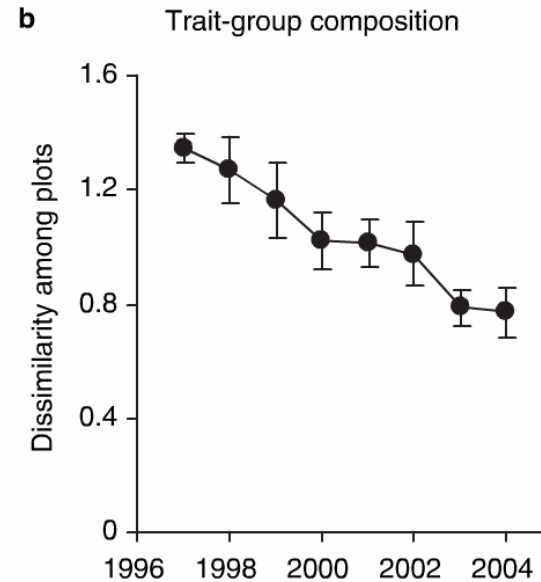
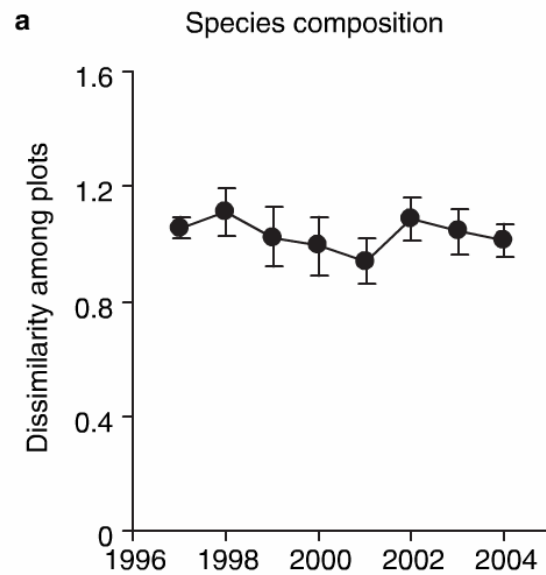
which is unlikely to reveal the trajectories and mechanisms of succession, and it is time to stop using them in ecology textbooks and course curricula (Johnson & Miyanishi 2008, *Ecol. Lett.*).

- Long-term demographic data

which could reveal the real patterns and mechanisms of succession, but the data are extremely rare.

# Taxonomic, phylogenetic, and functional approaches

- Taxonomic divergence and trait convergence

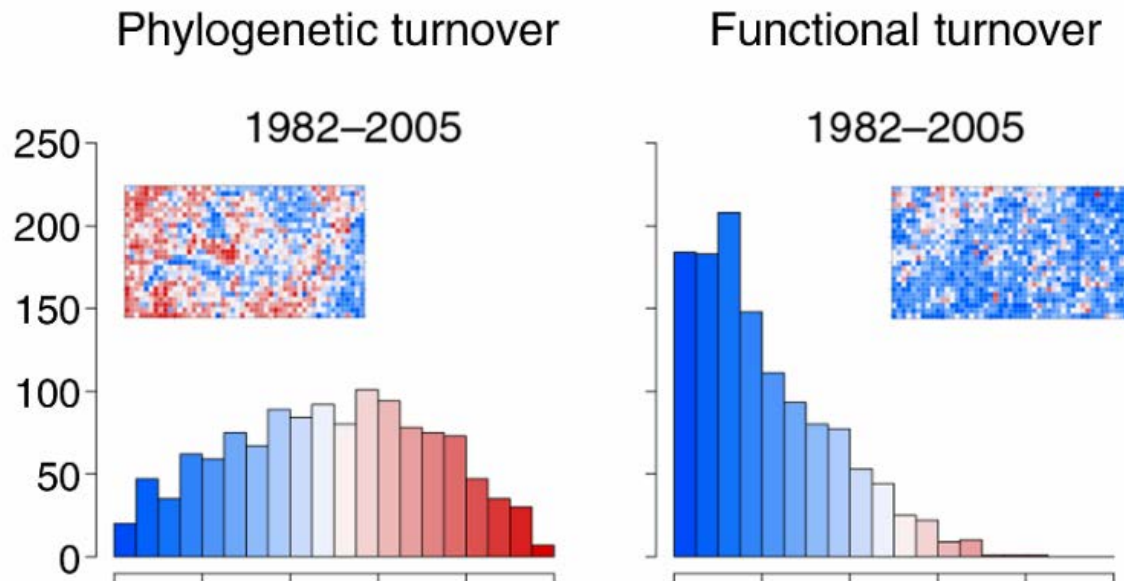


Fukami *et al.* 2005, *Ecol. Lett.*

# Taxonomic, phylogenetic, and functional approaches

- Functional determinism and phylogenetic stochasticity

## Barro Colorado Island



Swenson *et al.* 2012, *Ecology*

## **Directionality, convergence, and rate of change during succession**

- Is succession directional or non-directional?
- Do different communities converge towards a similar composition (i.e., stable climax community)?
- Do successional rates decline over time?
- Do initial conditions matter (i.e., historical contingency)?

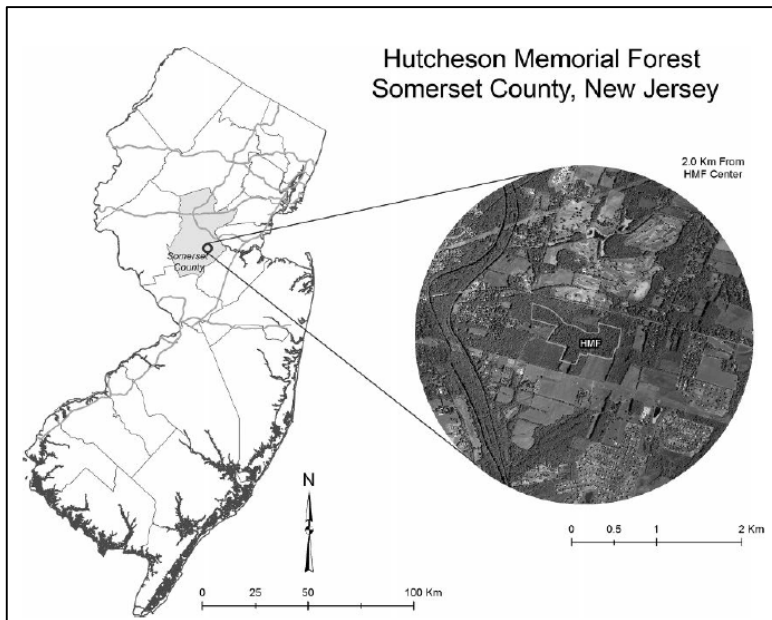
# Directionality, convergence, and rate of change during succession

**To answer these questions, we need:**

- Is succession directional or non-directional?
- Long-term experimental study on successional dynamics;
- Do different communities converge towards a similar composition (i.e. stable climate community)?
- Unifying taxonomic, phylogenetic, and functional measures and appropriate statistical analysis;
- Do successional rates decline over time?
- Directly manipulate the initial conditions of different communities, to assess their contribution on community structure;
- Do initial conditions matter (i.e., historical contingency)?
- ...
- ...

# The Buell-Small Succession Study

The longest continuous study of post-agricultural secondary succession in the world.



Hutcheson Memorial Forest Center  
(40°30' N, 74°34'W)

Figure from Meiners *et al.* 2015

Photo taken by Jon Moulding in 1973



# The Buell-Small Succession Study

The longest continuous study of post-agricultural secondary succession in the world.

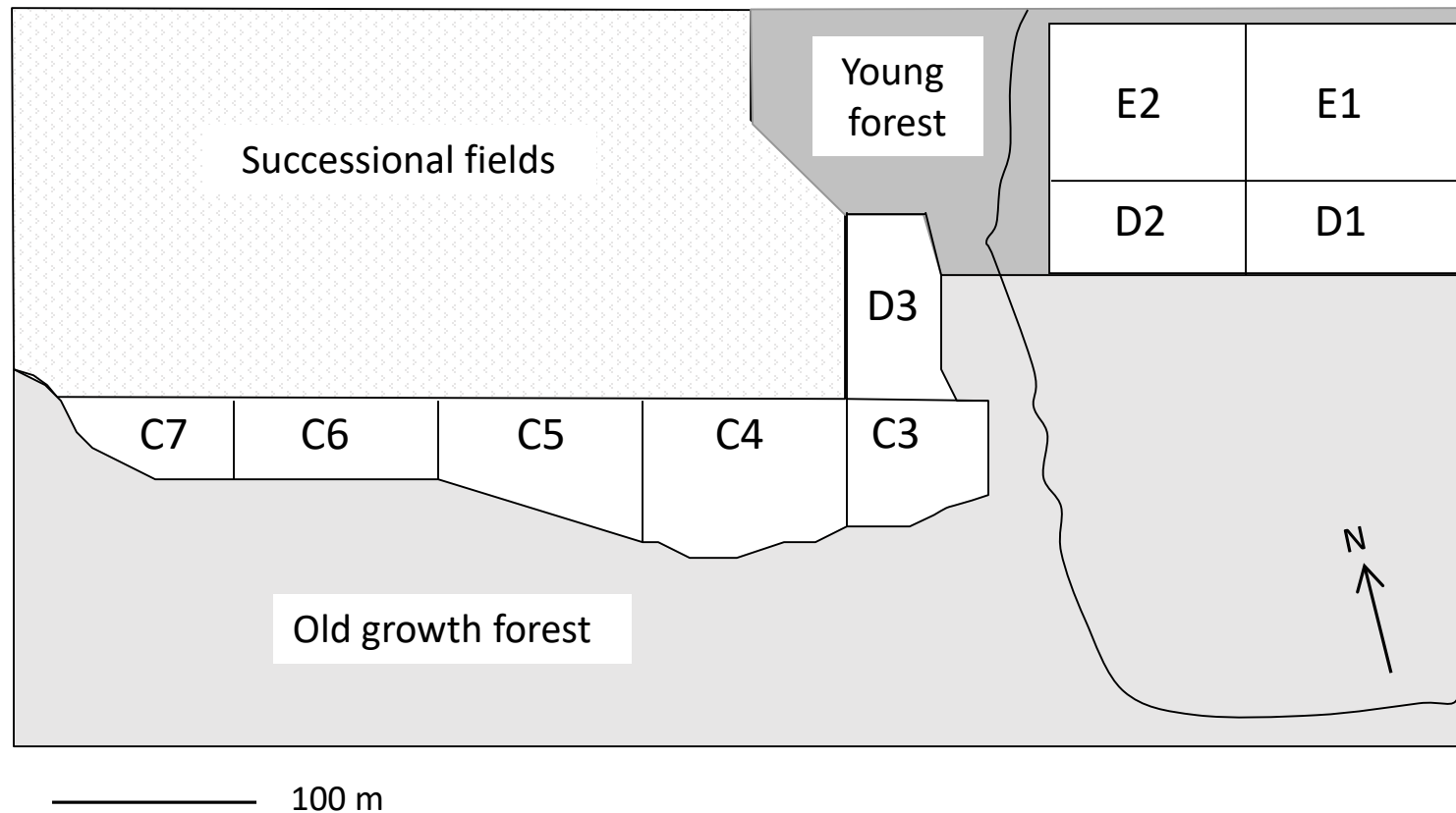
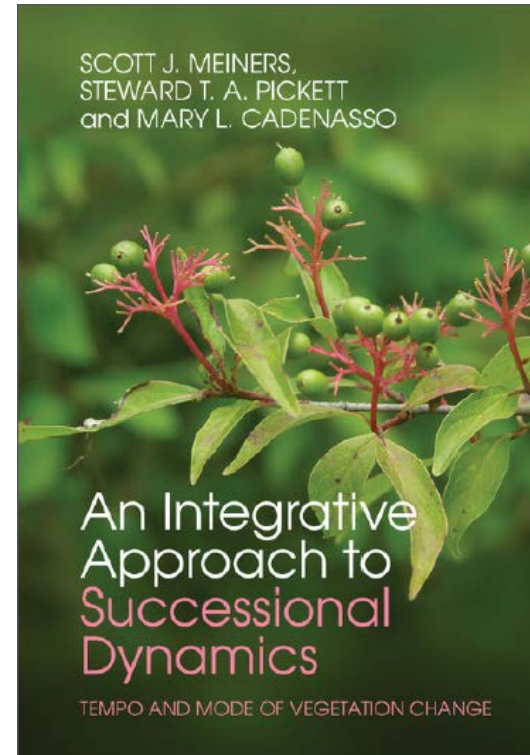


Figure from Meiners *et al.* 2015

# The Buell-Small Succession Study

The longest continuous study of post-agricultural secondary succession in the world.

Field	Year abandoned	Season of abandonment	Last crop type before abandonment	Mode of abandonment
C3	1958	Fall	Row crop	Leaf litter
D1	1958	Fall	Row crop	Leaf litter
D2	1960	Fall	Row crop	Leaf litter
D3	1960	Spring	Row crop	Bare soil
E1	1962	Fall	Hay	Leaf litter
E2	1962	Spring	Hay	Bare soil
C6	1964	Fall	Hay	Leaf litter
C7	1964	Spring	Hay	Bare soil
C4	1966	Spring	Row crop	Bare soil
C5	1966	Fall	Row crop	Bare soil



Meiners *et al.* 2015

# Study site and data collection

48 plots, measuring  $2.0 \times 0.5$  m, were permanently marked in each of the 10 fields.

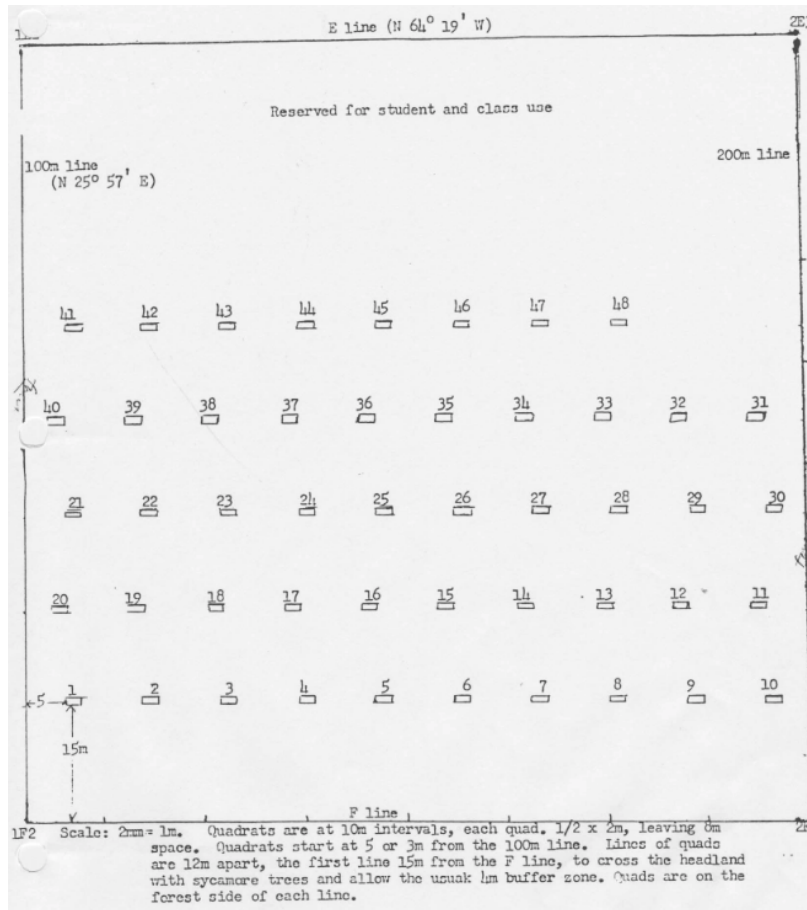


Photo of the BSS originators:  
Murray Buell, Helen Buell and John Small

Photo courtesy of Norma Reiners, 1963

Field E2

# The Buell-Small Succession Study

1<sup>st</sup> Year



Open agricultural land

5<sup>th</sup> Year



Short-lived herbaceous species

28<sup>th</sup> Year



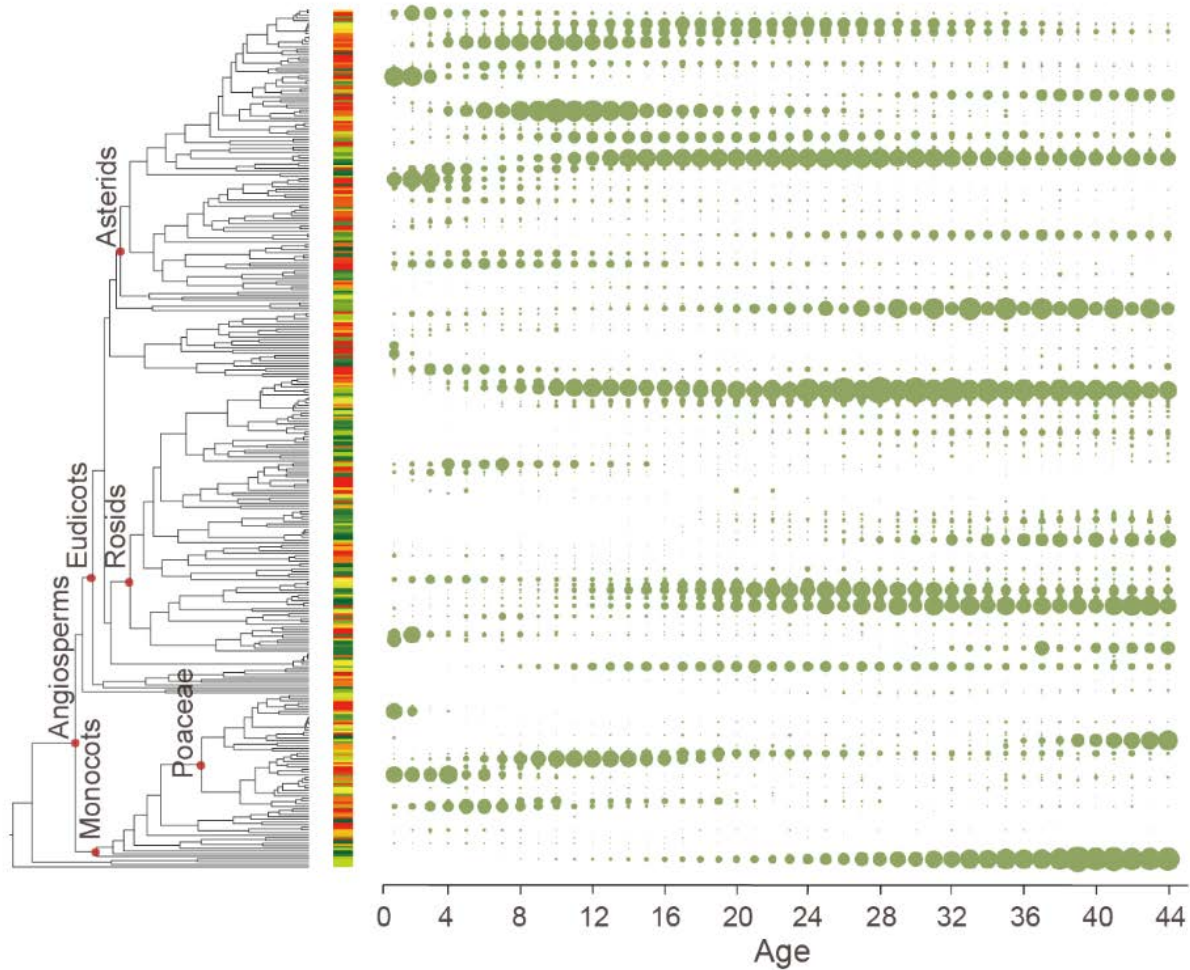
Young Forest

10<sup>th</sup> Year



Long-lived herbs and shrubs

# Phylogeny and the cover of the 325 species from 1958-2009



*Li et al. 2015, Ecol. Lett.*

# Functional traits and phylogenetic niche conservatism

<i>Continuous traits</i>	Blomberg's $K$	$P$ values	Pagel's $\lambda$	$P$ values
log maximum height (m)	0.13	0.001	0.87	<0.001
log leaf dry matter content (LDMC)	0.18	0.025	0.66	<0.001
log specific leaf area (SLA, cm <sup>2</sup> /g)	0.34	0.001	0.81	<0.001
log seed mass (g per 1000 seeds)	0.62	0.001	0.97	<0.001
<i>Categorical traits</i>	$P$ values			
Growth form (Graminoid, Forb, Vine, Shrub, Tree)	<0.001			
Life span (Annual, Biennial, Perennial)	<0.001			
Pollination (Abiotic, Biotic)	<0.001			
Seed dispersal (Abiotic, Biotic)	<0.001			
Clonal reproduction (False, True)	0.012			

Li *et al.* 2015, *Ecol. Lett.*

# Unifying taxonomic, phylogenetic and functional diversity measures through Hill numbers

## Unifying Species Diversity, Phylogenetic Diversity, Functional Diversity, and Related Similarity and Differentiation Measures Through Hill Numbers

Anne Chao,<sup>1</sup> Chun-Huo Chiu,<sup>1</sup> and Lou Jost<sup>2</sup>

<sup>1</sup>Institute of Statistics, National Tsing Hua University, Hsin-Chu, 30043 Taiwan; email: chao@stat.nthu.edu.tw, ceterfinder@yahoo.com.tw

<sup>2</sup>EcoMinga Foundation, Baños, Tungurahua, Ecuador; email: loujost@gmail.com

$${}^qD = \left( \sum_{i=1}^S p_i^q \right)^{1/(1-q)}$$

$q = 0$ , species richness

$q = 1$ , exp(Shannon index)

$q = 2$ , inverse Simpson index

Annu. Rev. Ecol. Evol. Syst. 2014. 45:297–324

First published online as a Review in Advance on September 29, 2014

The *Annual Review of Ecology, Evolution, and Systematics* is online at [ecobys.annualreviews.org](http://ecobys.annualreviews.org)

This article's doi: 10.1146/annurev-ecolsys-120213-091540

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### Keywords

beta diversity, diversity measures, diversity decomposition, doubling property, replication principle, trait diversity

### Abstract

Hill numbers or the effective number of species are increasingly used to quantify species diversity of an assemblage. Hill numbers were recently extended to phylogenetic diversity, which incorporates species evolutionary history, as well as to functional diversity, which considers the differences among

Chao *et al.* 2014, *Annu. Rev. Ecol. Evol. Syst.*



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# Directionality, convergence, and rate of change during succession

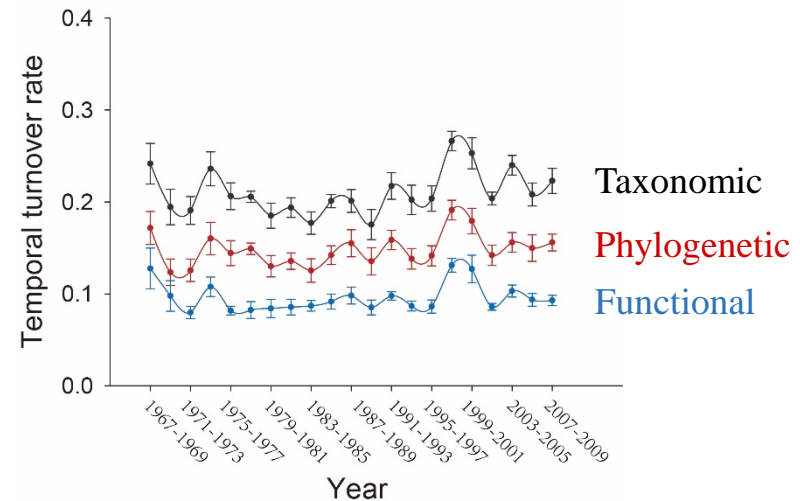
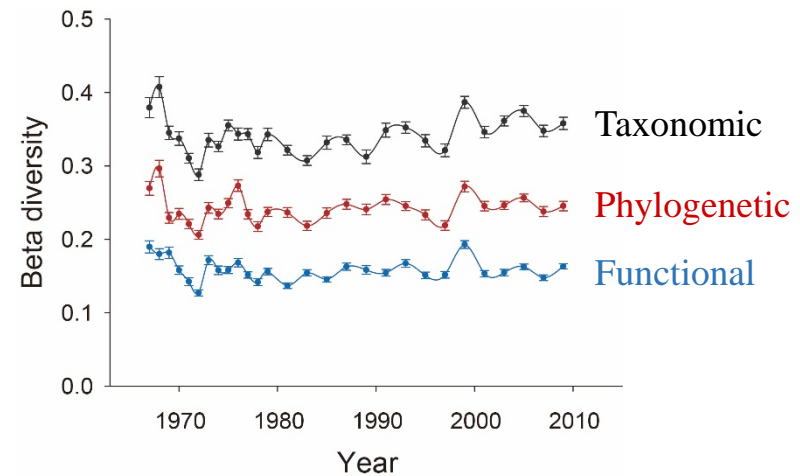
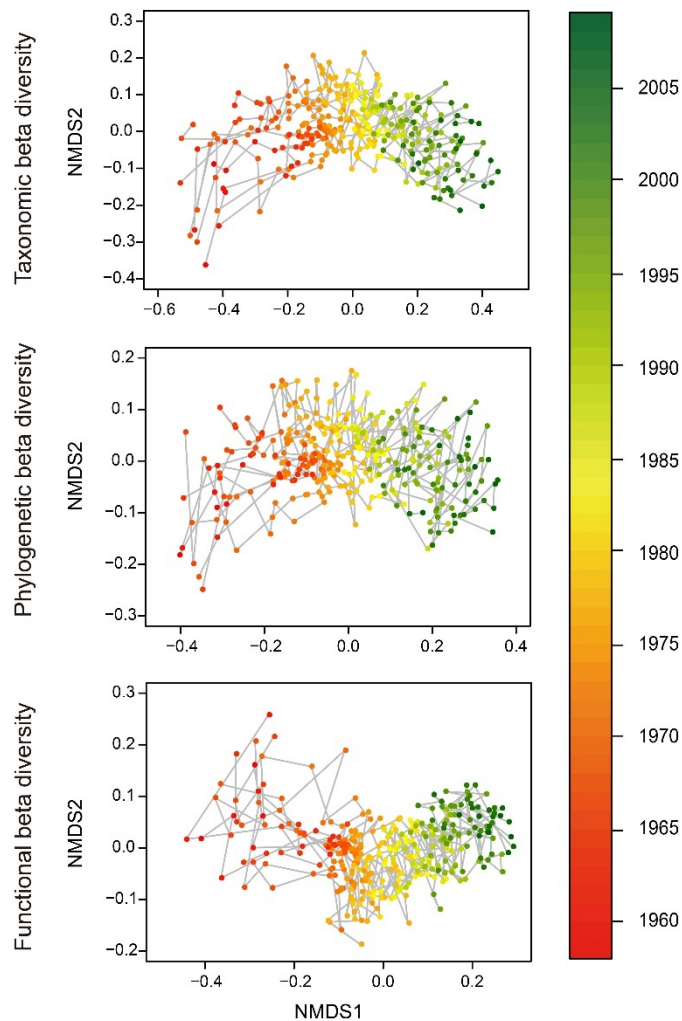
**To answer these questions, we need:**

- Is succession directional or non-directional?
- Long-term experimental study on successional dynamics;
- Unifying taxonomic, phylogenetic, and functional measures and appropriate statistical analysis;
- Directly manipulate the initial conditions of different communities, to assess their contribution on community structure;
- Do successional rates decline over time?
- Community patterns in different spatial scales (field level vs plot level);
- Do initial conditions matter (i.e., historical contingency)?
- The abundance of species (incidence- vs abundance based data).



The dissimilarity of rare species in each field did not decrease over time, with no sign of convergence among fields.

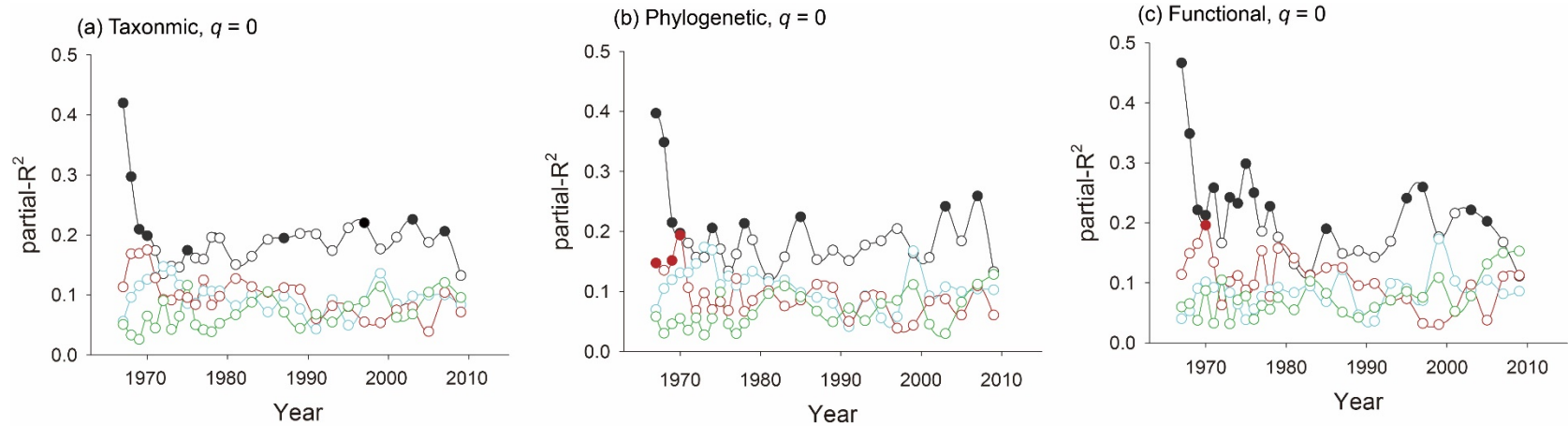
### Field level, Presence/absence metrics, $q = 0$



# Do initial conditions matter?

Field level, Presence/absence metrics,  $q = 0$

## PERMANOVA



● Year abandoned

● Last crop type before abandonment

● Season of abandonment

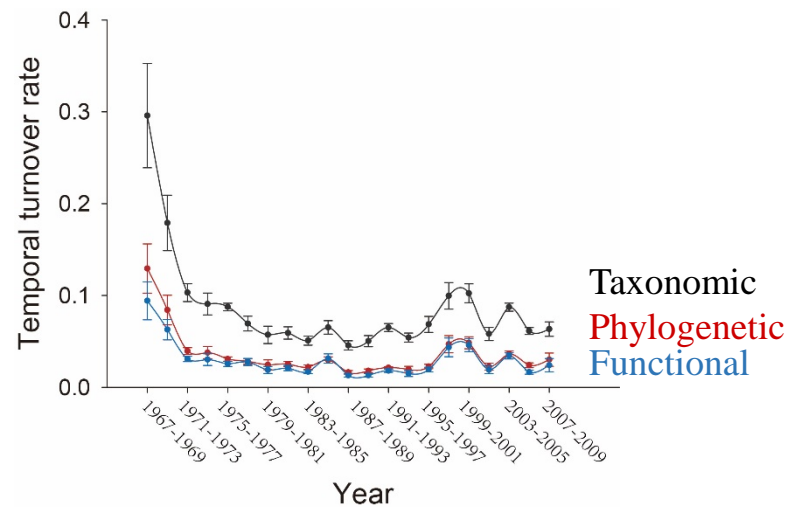
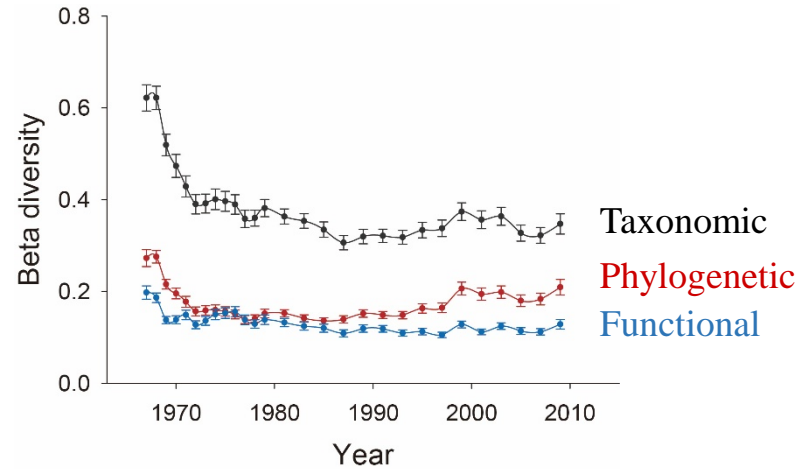
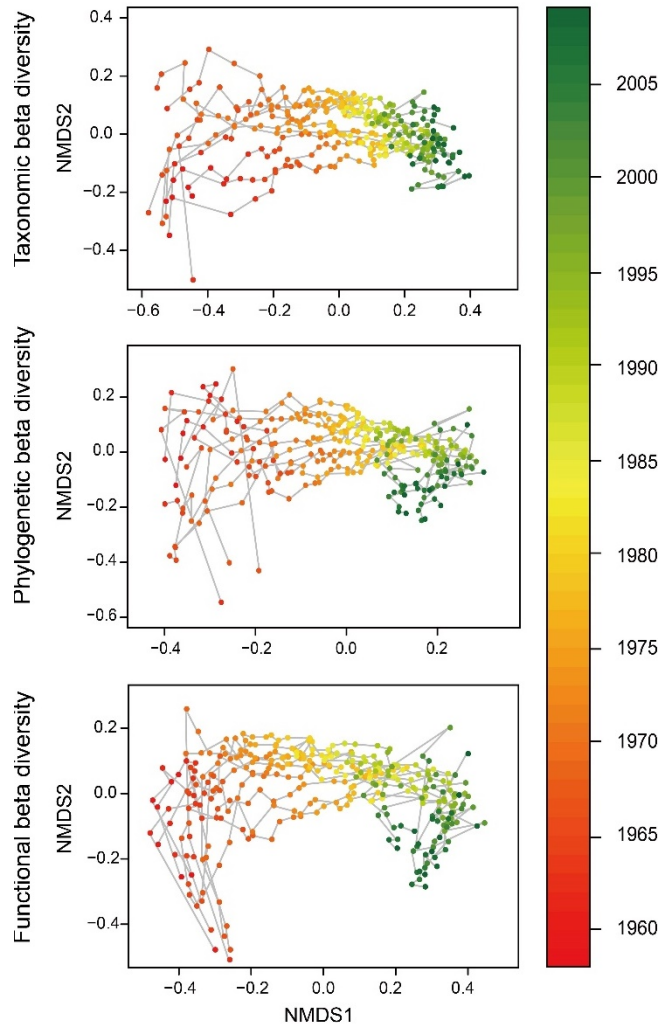
● Mode of abandonment

● Significant

○ Not significant

The taxonomic, phylogenetic and functional dissimilarity of common species among fields significantly decreased over time.

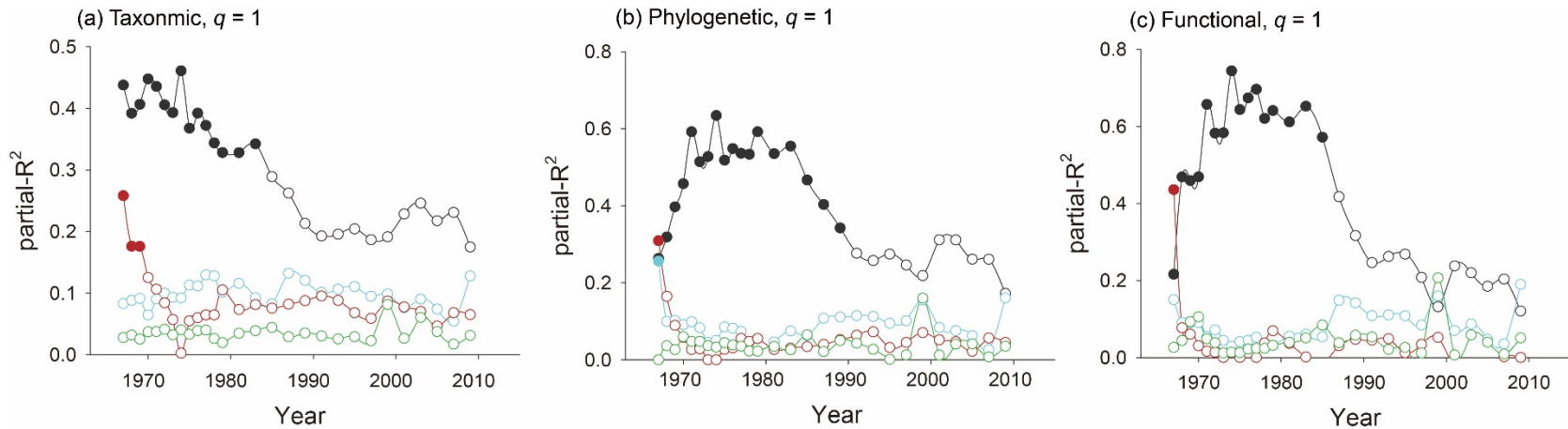
### Field level, abundance metrics, $q = 1$



# Do initial conditions matter?

Field level, abundance metrics,  $q = 1$

## PERMANOVA



● Year abandoned

● Last crop type before abandonment

● Season of abandonment

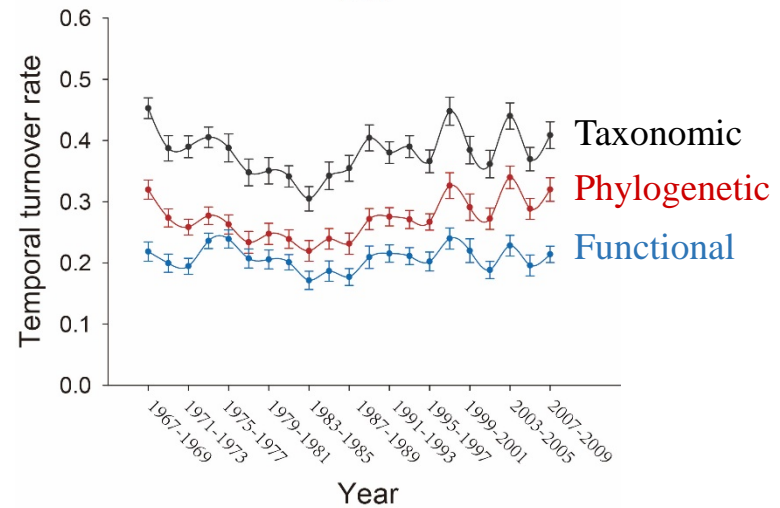
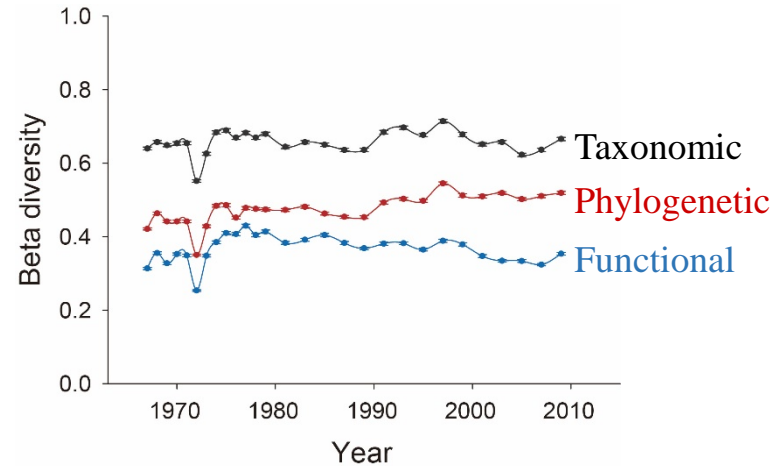
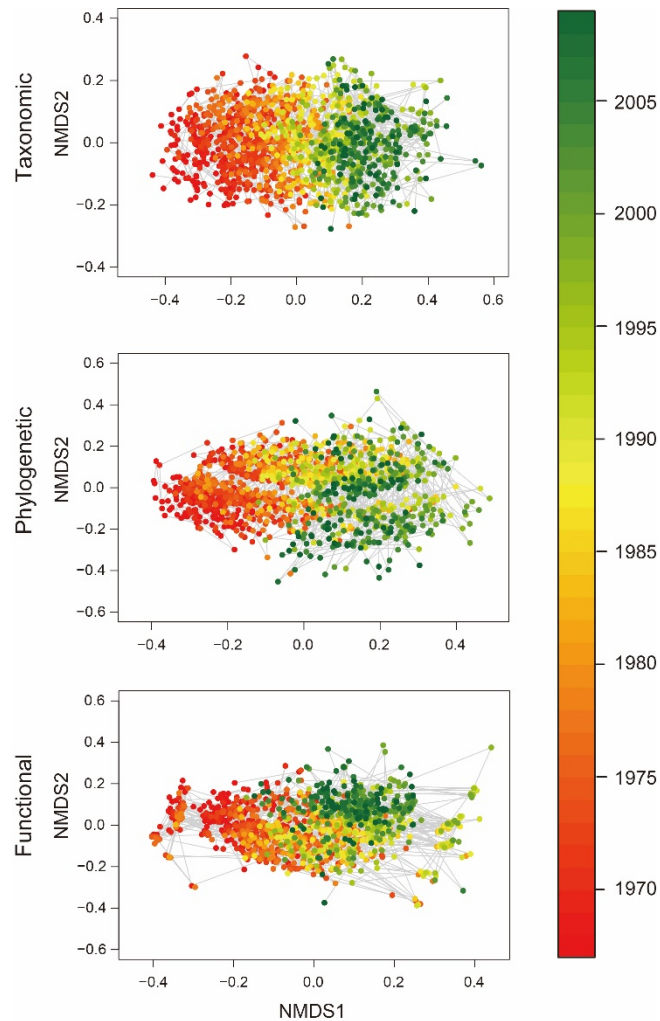
● Mode of abandonment

● Significant

○ Not significant

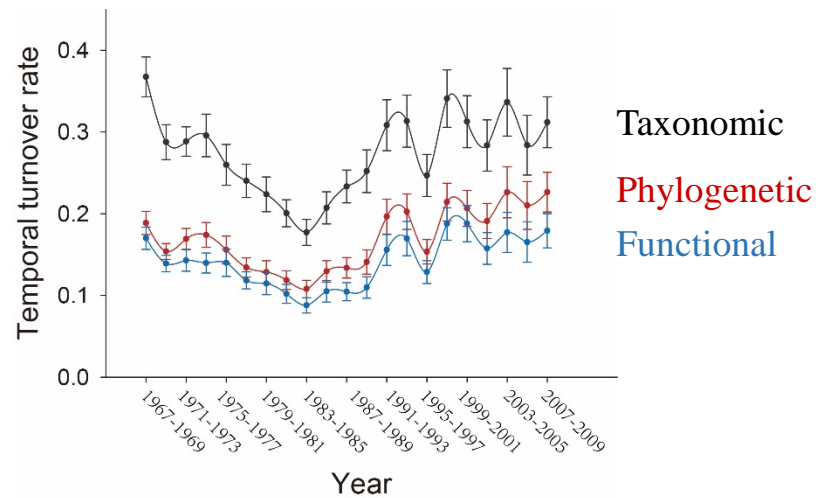
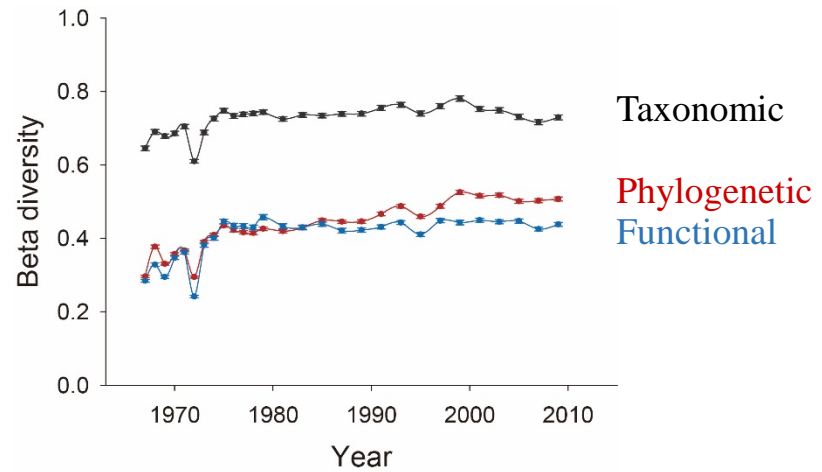
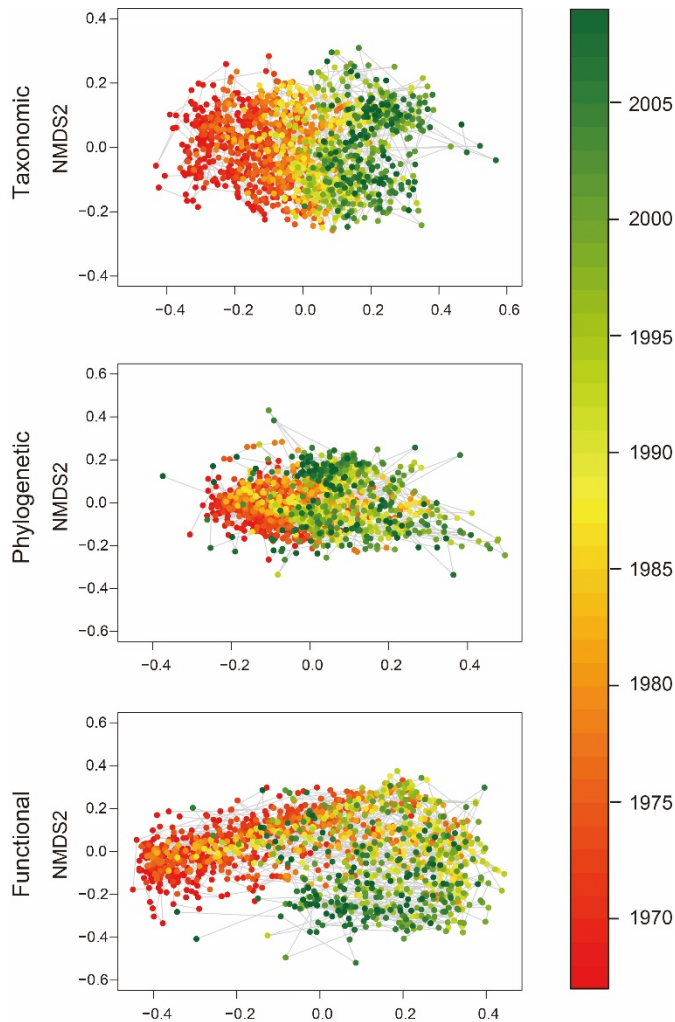
The taxonomic, phylogenetic and functional dissimilarity among plots within each field showed no significant decrease over time.

### Plot level, Presence/absence metrics, $q = 0$



The taxonomic, phylogenetic and functional dissimilarity among plots within each field showed no significant decrease over time.

### Plot level, abundance metrics, $q = 1$



# Take home message

- The old field succession in the Buell-Small Succession Study is **directional**.
- The trajectory of succession (**convergence** vs **divergence**) depended on the focal **spatial scale** and the **abundance** of the focal species.
- Taxonomic, phylogenetic, and functional beta diversity gradually showed consistent temporal patterns.
- The initial conditions of the fields (e.g. year of abandonment and last crop) significantly influenced the structure of the fields at the early stages of succession, but their contributions decreased over time and were no longer significant after 20 years of succession.

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Shao-peng Li

School of Biology  
Georgia Institute of Technology

Email: [shaopeng.li@biology.gatech.edu](mailto:shaopeng.li@biology.gatech.edu)