Biodiversity effects and underlying mechanisms in a large-scale field experiment in subtropical forest

Pascal A. Niklaus[1)]
Yuanyuan Huang, Helge Bruelheide, Keping Ma, Bernhard Schmid, et al.

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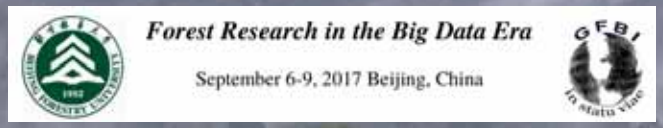
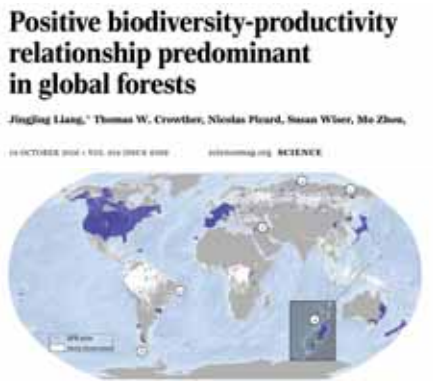
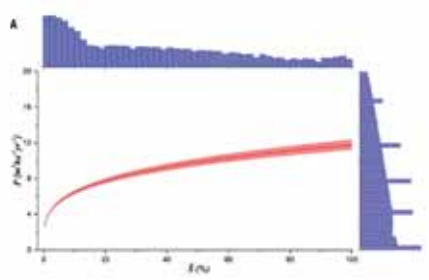


Approaches to Study BEF Relationships

Observational

natural ecosystems • high complexity • near equilibrium
confounded factors • biodiversity can be driver or response





Approaches to Study BEF Relationships

Experimental

highly controlled • low complexity • biodiversity is driver • traceable mechanisms
artificial • short-term • non-steady state • lacks large scale and environmental context

Impacts of Biodiversity Loss Escalate Through Time as Redundancy Fades

Peter B. Reich,[1,2] David Tilman,[1,3] Forest Isbell,[1] Kevin Mueller,[1] Sarah E. Hobbie,[1] Dan F. B. Flynn,[1] Nico Eisenhauer[1,2]

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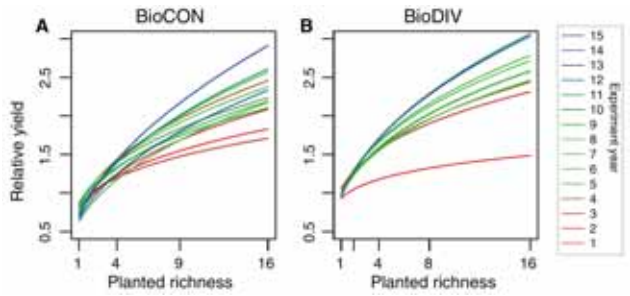
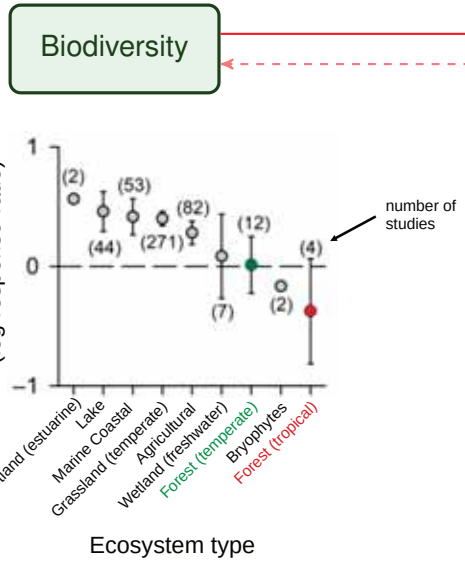


BioDiv

BioCON

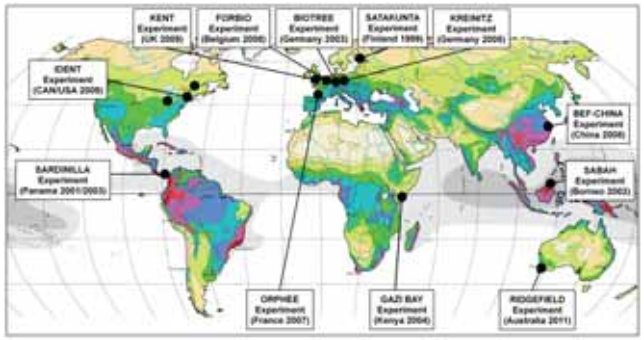
Biodiversity-Ecosystem Functioning Experiments



Cardinale et al. 2011 Am J Bot 98 572–592

(top: **Jena**; bottom: **Sardinilla** and **Biotree**)

BEF Experiments in Forest



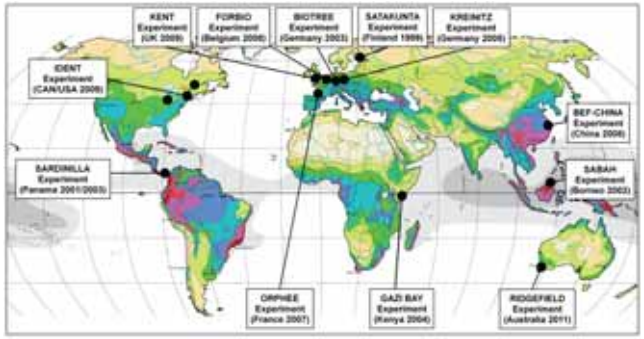
Map by Barthlott 2005; colors (yellow $\longrightarrow$ violet) indicate vascular plant diversity

BIOTREE, Germany

Sabah, Borneo

Sardinilla, Panama

BEF Experiments in Forest



Map by Barthlott 2005; colors (yellow $\longrightarrow$ violet) indicate vascular plant diversity

- Diversity is higher in low latitude forest
- Niche overlap may be lower in low latitude forest
- Mechanisms may differ
  (pathogens and herbivores more important)

BEF-China

- Joint Chinese-German-Swiss biodiversity-ecosystem functioning experiment in forest (`http://www.bef-china.de`)
- **Main Experiment**:
  Planted forest communities with 1...24 species
- **Comparative Study Plots**: $\longrightarrow$ Baruffol et al. 2013 PLoS ONE
  Natural subtropical forest plots in forest reserve
- **Pilot Experiment**:
  Short-term experiment with planted communities with 1...4 species


Main Experiment (2013)


CSPs


Pilot Experiment

Design of “Main Experiment”

- Extinction scenarios based on pool of 40 broadleaved tree species
  - Random (24, 16, 8, 4, 2, 1 species)
  - Directed Two trait based species removal (16, 8, 4, 2, 1 species)
    - rarity: rare species lost preferentially
    - SLA: high SLA species lost preferentially
- Reference plots: bare ground, economically important species
- Factorial treatments in a subset of plots (“VIP” plots):
  - BEFmod Insecticide and fungicide treatments
  - Shrubs Understory diversity treatment with shrubs

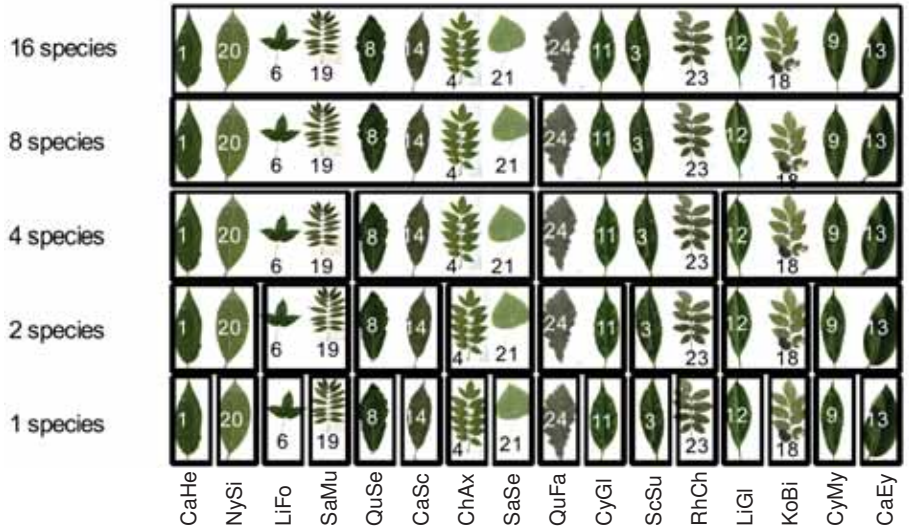
In total:

- 2 sites with a total of 566 plots
- 400 trees per plot
- $\sim$200’000 trees and 90’000 shrubs planted

Bruelheide et al. 2014 Methods in Ecology and Evolution 5:74–89

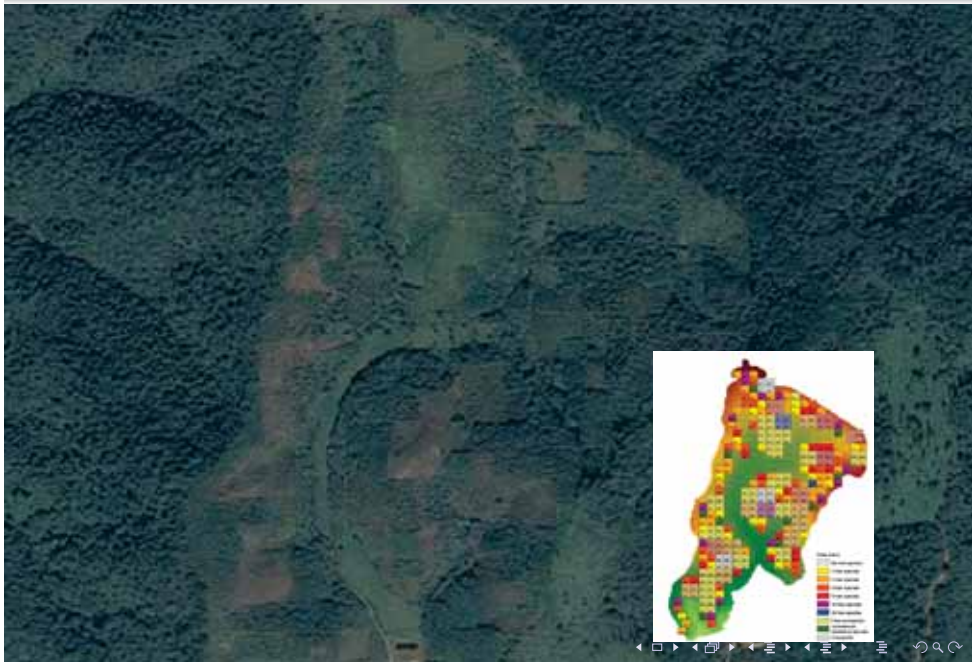
Random Extinction Scenario: Broken Stick Design

6 pools of 16 species; 1 shown below, 2 used in this study:



Bruelheide et al. 2014 Methods in Ecology and Evolution 5:74–89

Main Experiment

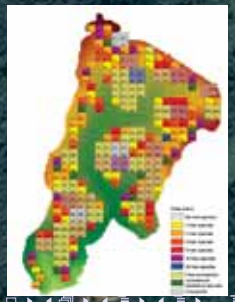


Main Experiment

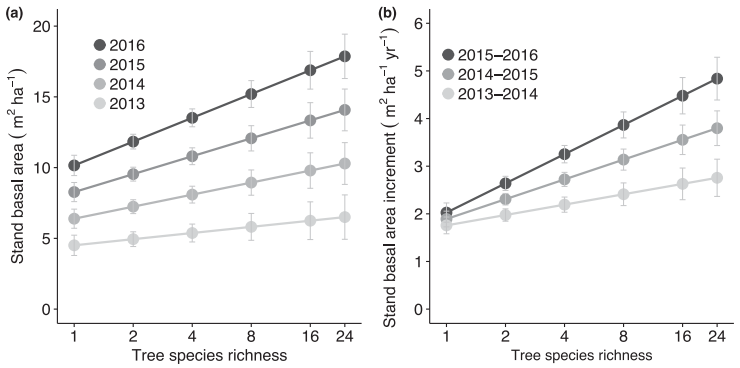
Main Experiment Site A in 2015

Main Experiment Site B in 2015

Ch. axillaris plot in 2015



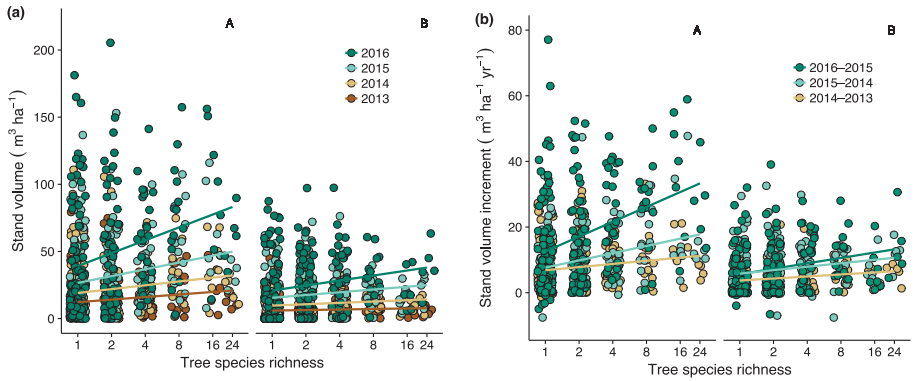
Stem Basal Area: Wood Production



- Experiment planted in 2008–2009
- BA increases with species richness
- BA growth increases with species richness
- Effects strengthen through time

Huang et al., in prep.

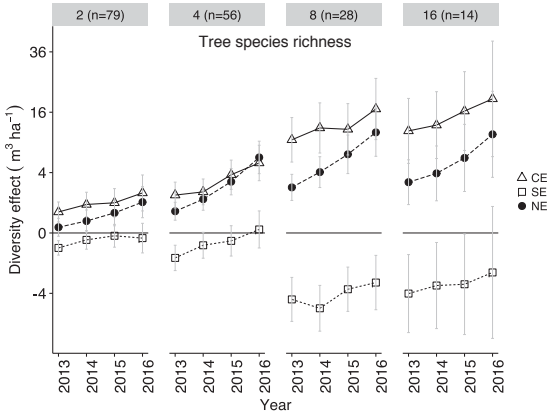
Stem Volume: Wood Production



- Two sites: “Site A” planted in 2008, “Site B” planted in 2009
- Tree volume responses follow BA responses
- Similar results for C stocks (calculated using harvested trees and site-specific allometries)

Huang et al., in prep.

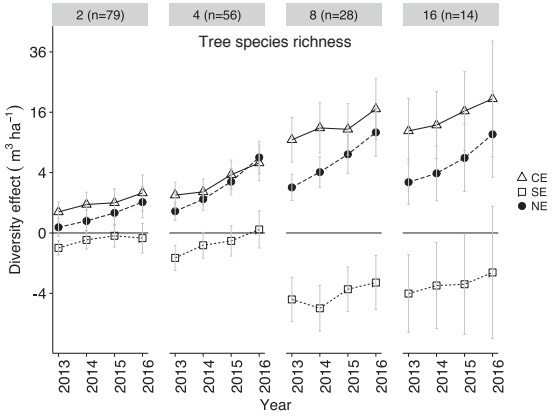
Mechanisms



- Loreau and Hector's (2001) additive partitioning method
- Complementarity effects drive biodiversity effects
- Complementarity effects increase through time

Huang et al., in prep.

Mechanisms

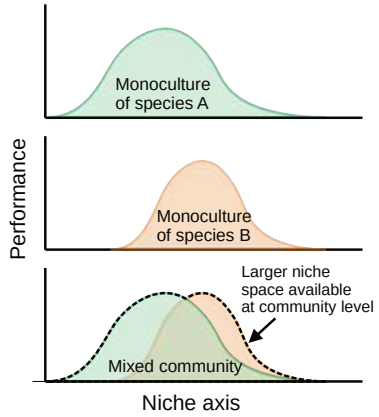


- Loreau and Hector's (2001) additive partitioning method
- Complementarity effects drive biodiversity effects
- Complementarity effects increase through time
- Statistical analysis of relative yield patterns...
- ...but what are the actual (ecological) mechanisms ?

Huang et al., in prep.

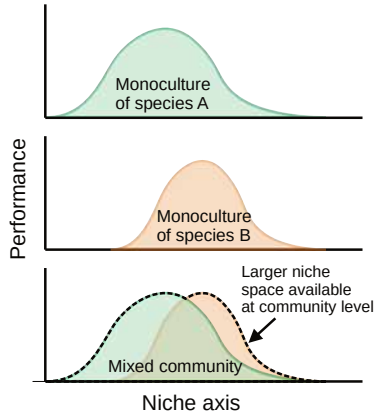
Mechanisms Promoting Complementarity

- It is evident that some sort of complementarity drives biodiversity effects



Mechanisms Promoting Complementarity

- It is evident that some sort of complementarity drives biodiversity effects
- Nature of complementarity rarely identified
  (e.g. von Felten et al. 2012 Ecology 93 2386-2396; Hoekstra et al. 2015 Plant Soil 394 21-34)
- Abiotic resources? Biotic interactions?



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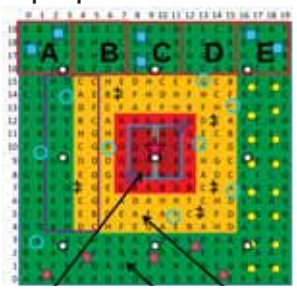
Negative Density-Dependent Effects of Enemies

Map of plot



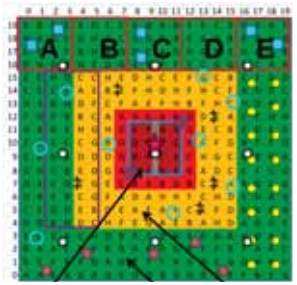
Subplot-level treatments

- Control
- Insecticide
- Fungicide

Huang et al., in prep.

Negative Density-Dependent Effects of Enemies

Map of plot



Subplot-level treatments

- Control
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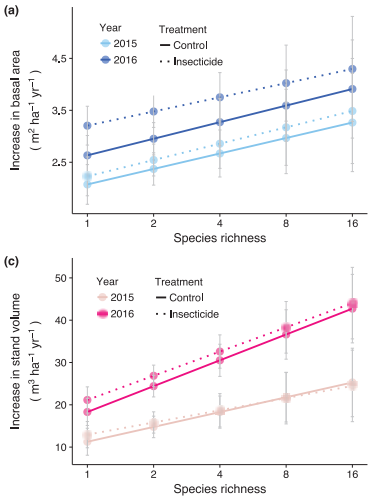
Huang et al., in prep.

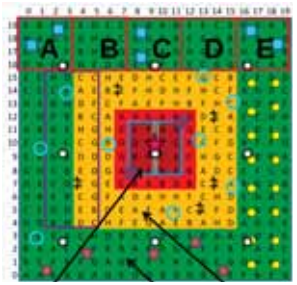
Insecticide



- Diversity effect remains

Negative Density-Dependent Effects of Enemies

Map of plot



Subplot-level treatments

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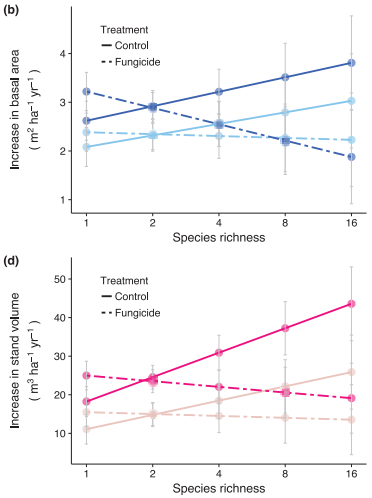
Huang et al., in prep.

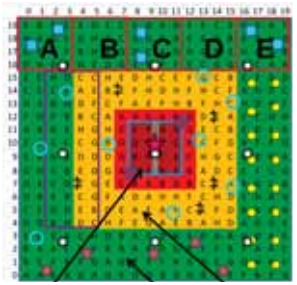
Fungicide



- Diversity effect weakened by fungicide

Negative Density-Dependent Effects of Enemies

Map of plot

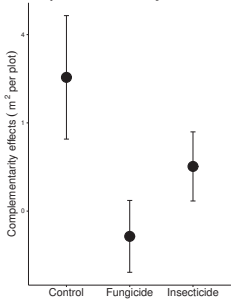


Subplot-level treatments

- Control
- Insecticide
- Fungicide

Fungicide

- Diversity effect weakened by fungicide
- Complementarity-effect decreases



- Fungicide-effect on diversity-effect is species-dependent
- We are currently analysing these patterns in relation to traits

Huang et al., in prep.

Complementary Canopies: Vertical Space Use

- Competition Experiment

3 Species pools $\times$ 11 Mixtures $\times$ 2 Treatments $\times$ 4 Repl. $=$ 264 Plots

Niklaus et al. 2017 Ecology 98 1104-1116; Schmid & Niklaus 2017 Nature Ecology & Evolution 1 0104

Complementary Canopies: Vertical Space Use

- Competition Experiment

3 Species pools $\times$ 11 Mixtures $\times$ 2 Treatments $\times$ 4 Repl. $=$ 264 Plots

	Species	Conifer	Evergreen
Pool 1	Castanea henryi	✘	✘
	Elaeocarpus decipiens	✘	✔
	Quercus serrata	✘	✘
	Schima superba	✘	✔
Pool 2	Cunninghamia lanceolata	✔	✔
	Cyclobalanopsis glauca	✘	✘
	Dalbergia hupeana	✘	✘
	Pinus massoniana	✔	✔
Pool 3	Cyclobalanopsis myrsinifolia	✘	✔
	Castanopsis sclerophylla	✘	✔
	Lithocarpus glaber	✘	✔
	Sapindus mukorossi	✘	✘

Niklaus et al. 2017 Ecology 98 1104-1116; Schmid & Niklaus 2017 Nature Ecology & Evolution 1 0104

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Mixture	Species richness	Composition
1	1	A
2		B
3		C
4		D
5	2	AB
6		AC
7		AD
8		BC
9		BD
10		CD
11	4	ABCD

Niklaus et al. 2017 Ecology 98 1104-1116; Schmid & Niklaus 2017 Nature Ecology & Evolution 1 0104

Complementary Canopies: Vertical Space Use

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Shade treatment implemented with mesh cover

- **"light":** open control plots
- **"shade":** reduced light

Niklaus et al. 2017 Ecology 98 1104-1116; Schmid & Niklaus 2017 Nature Ecology & Evolution 1 0104

Complementary Canopies: Vertical Space Use

- Competition Experiment

3 Species pools $\times$ 11 Mixtures $\times$ 2 Treatments $\times$ 4 Repl. $=$ 264 Plots

Replicated 4 times
(in blocks)

Niklaus et al. 2017 Ecology 98 1104-1116; Schmid & Niklaus 2017 Nature Ecology & Evolution 1 0104

Complementary Canopies: Vertical Space Use

- Competition Experiment

3 Species pools $\times$ 11 Mixtures $\times$ 2 Treatments $\times$ 4 Repl. $=$ 264 Plots

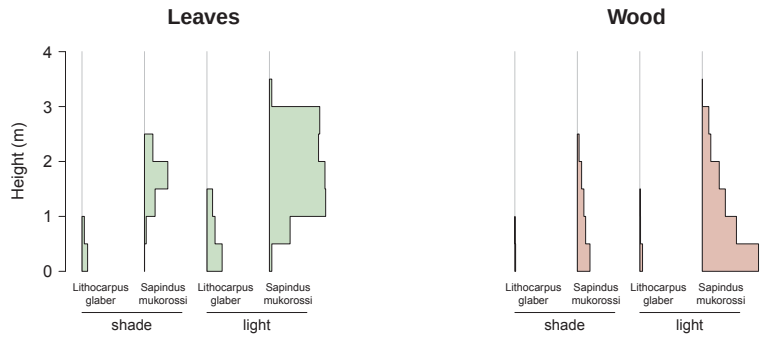
- Each 1m^2 plot consisted of 16 individuals, i.e. 4224 trees in total
- 4 × 4 grid, with full composition present in central 2 × 2 quadrat

Monoculture of *Elaeocarpus decipiens*

Destructive harvest

Niklaus et al. 2017 Ecology 98 1104-1116; Schmid & Niklaus 2017 Nature Ecology & Evolution 1 0104

Complementary Canopies: Vertical Space Use



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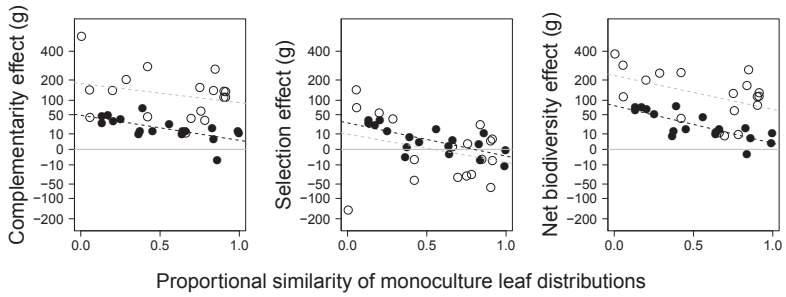
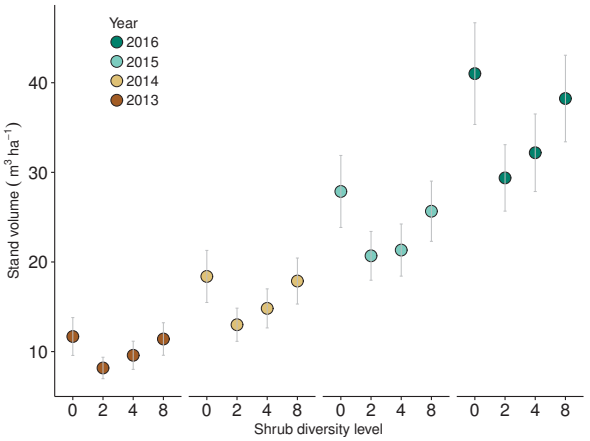
Complementary Canopies: Vertical Space Use



- Species with more different monoculture canopies are more complementary and produce more extra biomass in mixture

Niklaus et al. 2017 Ecology 98 1104-1116; Schmid & Niklaus 2017 Nature Ecology & Evolution 1 0104

Complementary Understory



Design

- Understory shrub diversity treatment
- Plots with 0 (no shrubs), 2, 4 or 8 shrub species

Results

- Shrubs compete with trees...
- ...but competition effect disappears with 8 shrub species !

Huang et al. in prep.

Summary & Conclusions

- Community-level productivity increases with diversity
  (BA, wood volume, biomass: Huang et al., in prep.
  LAI: Peng et al. 2017 JPE 10:129-135)
- Biodiversity effects increase through time
- Effects are driven by complementarity among species
  - Complementary enemy niches
  - Complementary canopy architecture
  - Complementarity between trees and understory

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Thank you for your attention !

Forest Research in the Big Data Era

September 6-9, 2017 Beijing, China

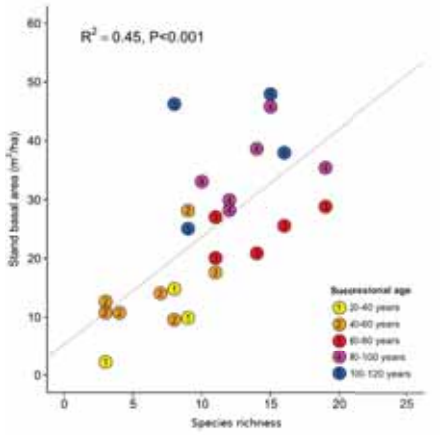
Comparative Study Plots in Nature Reserve

- Gutianshan Nature Reserve (near “Main Experiment”)
- Comparative Study Plots with natural vegetation
- 27 plots selected to span gradients in species richness and successional age

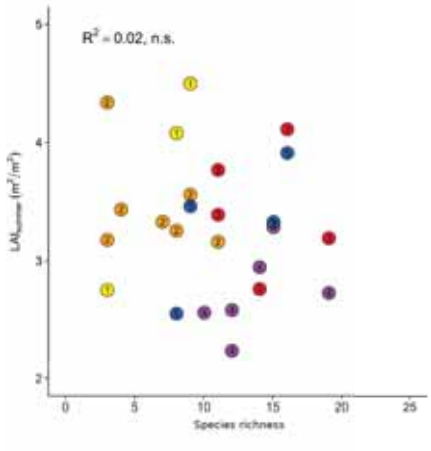
Baruffol et al. 2013 PLoS one 8 e81246
Bruelheide et al. 2011 Ecol Monogr 81 25–41

Comparative Study Plots in Nature Reserve

Basal area



Leaf Area Index

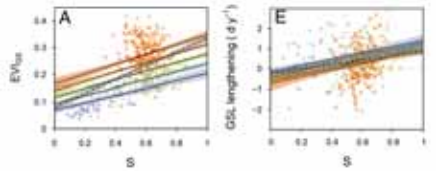


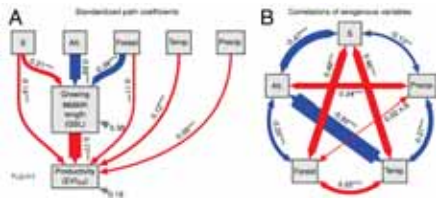
- Architectural complementarity among species likely contributed to increased BA in diverse plots

Castro et al. 2016 PLoS one 11 e0167771; Baruffol et al. 2013 PLoS one 8 e81246

Productivity Across Landscapes

Biodiversity promotes primary productivity and growing season lengthening at the landscape scale

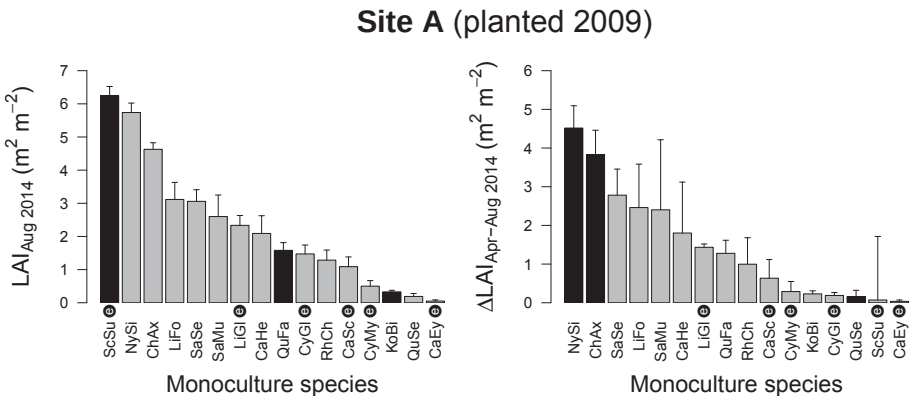




- 500 plots with species inventory data
- 16 years of MODIS satellite data

PNAS, in press, DOI:10.1073/pnas.1703928114

Leaf Area Index of Monocultures



Ailanthus altissima · Alniphyllum fortunei · Betula luminifera · Castanopsis eyrei · Castanopsis fargesii · Castanea henryi · Castanopsis sclerophylla · Celtis biondi · Choerospondias axillaris · Cyclobalanopsis glauca · Cyclobalanopsis myrsinifolia · Elaeocarpus chinensis · Elaeocarpus glabripetalus · Elaeocarpus japonicus · Idesia polycarpa · Koelreuteria bipinnata · Liquidambar formosana · Lithocarpus glaber · Machilus grijsii · Machilus leptophylla · Machilus thunbergii · Manglietia yuyuanensis · Meliosma flexuosa · Nyssa sinensis · Phoebe bournei · Quercus fabri · Quercus phillyraeoides · Quercus serrata · Rhus chinensis · Sapindus mukorossi · Sapium sebiferum · Schima superba

Peng et al. (2016) J Plant Ecol, DOI:10.1093/jpe/rtw016

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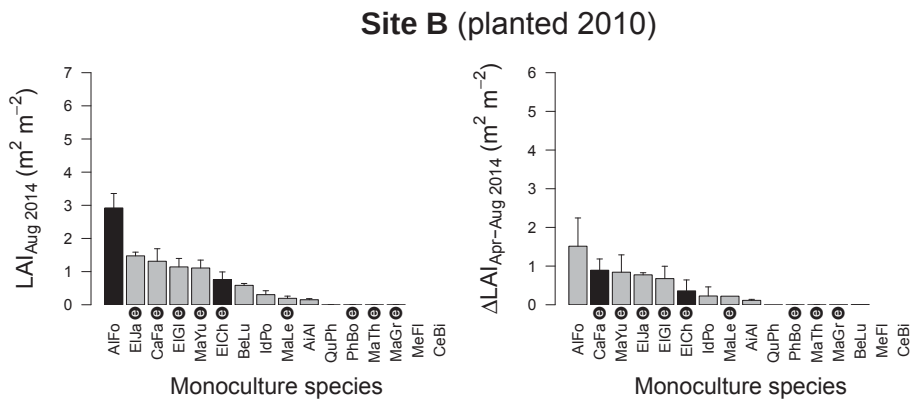

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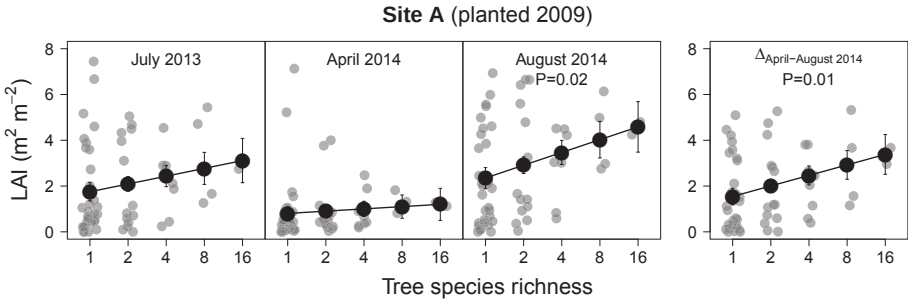
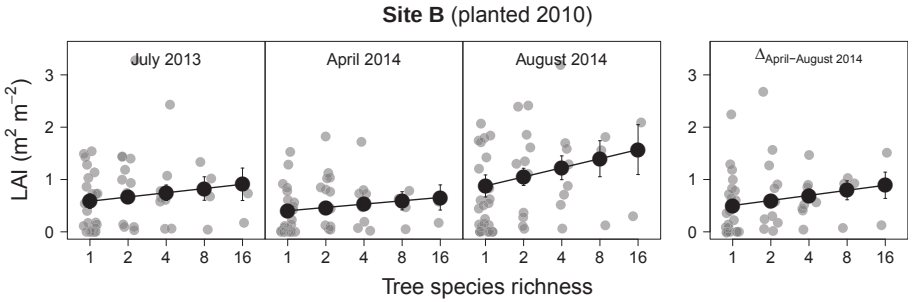
Diversity Effects on Leaf Area Index



- Positive effect of species richness on LAI after 5 years
- Positive effect on seasonal LAI increase
- Effect appears to develop with time

Peng et al. (2016) J Plant Ecol, DOI:10.1093/jpe/rtw016

Diversity Effects on Leaf Area Index

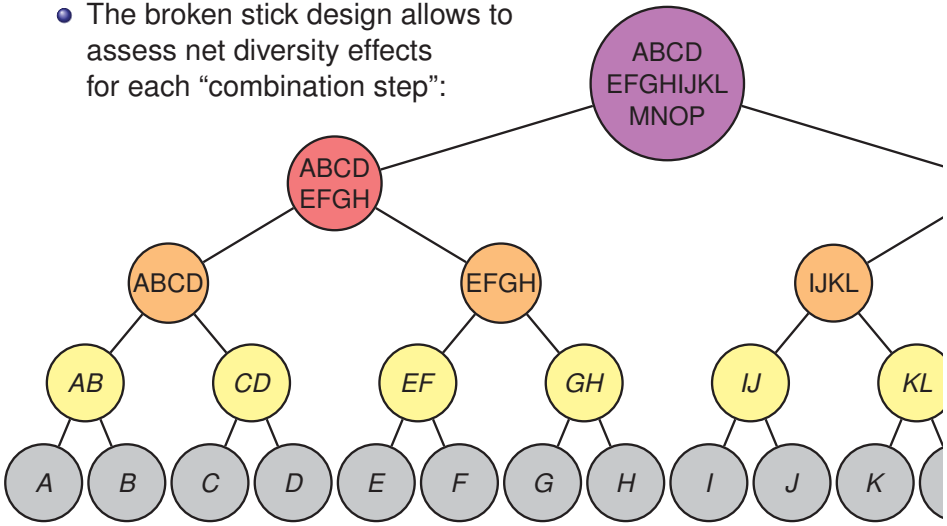


- Positive effect of species richness on LAI after 5 years
- Positive effect on seasonal LAI increase
- Effect appears to develop with time

Peng et al. (2016) J Plant Ecol, DOI:10.1093/jpe/rtw016

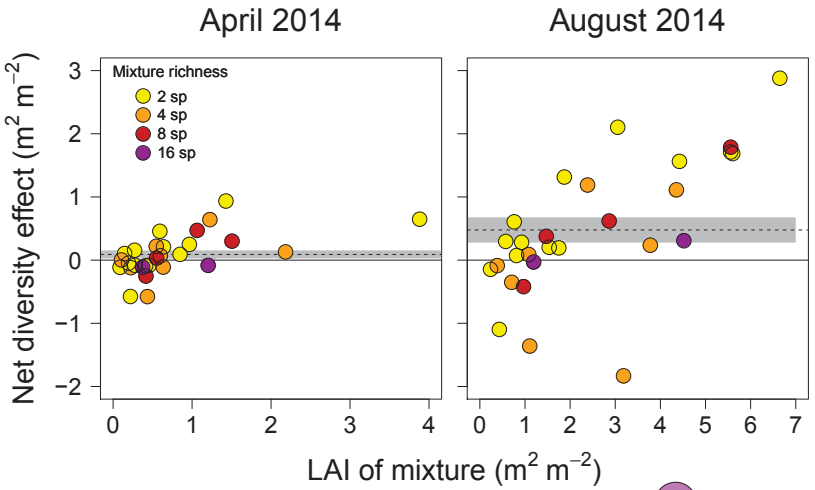
Biodiversity-Effects along Richness Gradient

- The broken stick design allows to assess net diversity effects for each “combination step”:

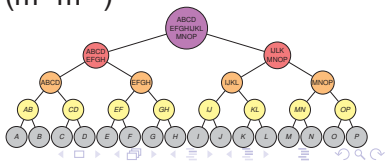


Peng et al. (2016) J Plant Ecol, DOI:10.1093/jpe/rtw016

Biodiversity-Effects along Richness Gradient



- Regular overyielding
- (but not transgressive)



Peng et al. (2016) J Plant Ecol, DOI:10.1093/jpe/rtw016

Architecture of Trees

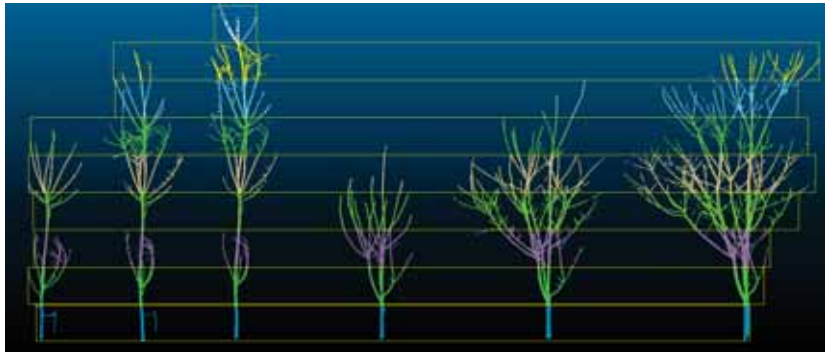
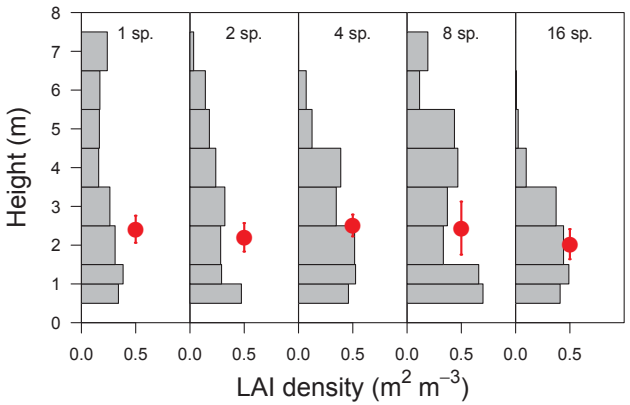


Figure by Goddert v. Oheimb

- Terrestrial laser scanning to determine shape of trees (Goddert von Oheimb, University of Dresden, Germany)

LAI distribution

- In 2015, layered LAI assessment by hemispheric photography, with camera mounted on pole



  - Height of gravity of leaf area

TOC