LegumeLegacy

SS5 Data Science for biodiversity experiments

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Racines d'avenir
LABORATOIRE VIVANT

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Matthias Suter

18 - 19 June 2025

Legume Legacy event, Aarhus

«All things are of number» - but numbers are not things. Numbers are mental.

Pythagoras (~ 2500 b.p.) Greece

The design and analysis of biodiversity experiments

Overall aims:

- Understand basic principles of biodiversity experiments
- Gain deeper understanding of simplex designs and their analysis
- Critically reflect on concepts and their interpretation

With thanks to Olivier Huguenin-Elie and John Finn for feedbacks

The design and analysis of biodiversity experiments

Schedule

Day 1:

- Sampling effects in classical biodiversity experiments
- Additive partitioning approach and DI models

Day 2:

- Simplex designs, DI models, and related issues

Both days with lectures and lab sessions

Sampling effects in classical biodiversity experiments

Background

- Within vegetation ecology, *plant sociology* aims to systematically classify vegetation and to determine vegetation units.
- Basic unit: «Association». "Plant associations refer to a plant community of a specific species composition, uniform appearance, and similar site conditions. Each association has a specific species structure."
- Developed in early 20th century: Braun-Blanquet (CH), Heinz Ellenberg (D), …
- Originally for plant species, and extended to mosses, fungi, …
- Many transitions in natural habitats ⇨ description of «sub-associations»

de.wikipedia.org

Lowland grassland community

Arrhenatheretum typicum (Glatthaferwiese, Tall oat-grass meadow)

Grass species

- ***Arrhenatherum elatius***
- *Alopecurus pratensis*
- *Anthoxanthum odoratum*
- ***Bromus hordeaceus***
- ***Dactylis glomerata***
- ***Festuca pratensis***
- *Helictotrichon pubescens*
- ***Holcus lanatus***
- *Phleum pratense*
- *Poa pratensis*
- ***Poa trivialis***
- *Trisetum flavescens*

Legume species

- *Lathyrus pratensis*
- *Medicago lupulina*
- *Trifolium dubium*
- *Trifolium pratense*
- *Trifolium repens*
- *Vicia cracca*

Herb species

- ***Anthriscus sylvestris***
- *Achillea millefolium*
- *Campanula patula*
- *Cardamine pratensis*
- *Centaurea jacea*
- *Cerastium fontanum*
- *Crepis biennis*
- *Galium album*
- *Geranium pratense*
- *Heracleum sphondylium*
- *Knautia arvensis*
- *Pastinaca sativa*
- *Plantago lanceolata*
- *Ranunculus acris*
- ***Rhinanthus alectorolophus***
- ***Rumex acetosa***
- *Silene vulgaris*
- *Taraxacum officinale*
- *Tragopogon pratensis*
- *Veronica chamaedrys*

Lowland mesotrophic conditions

Herb: non-leguminous forb

bold: dominant species

Delarze & Gonseth (2015) Ott

Biodiversity – Ecosystem Function experiments

- Around 1970, intention to place vegetation ecology on a more experimental basis by adhering to statistical principles of randomisation and replication
- Aim: establish rules about the effects of species diversity on ecosystem functions - such as yield - by eliminating confounding factors inherent in records of natural communities
- Plant communities were constructed by randomly sampling from a local species pool, such as an *Arrhenatheretum*
- Replicate communities of 1, 2, 4, 8, 16, 32, 64 species (often geometric series)
- Sown into plots randomised on a local site

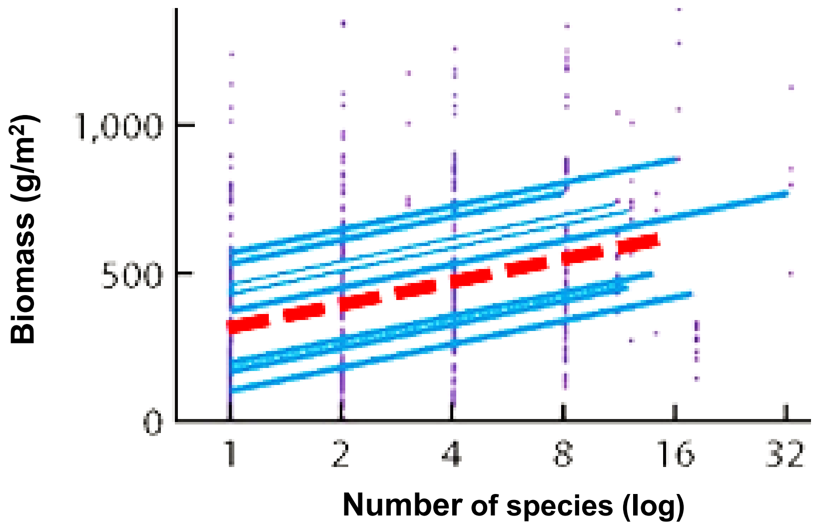
Diversity definitions

- Classically a function of species richness *and* relative abundance
  e.g., Shannon Diversity Index: $H = -\sum p_i * ln(p_i)$
- Biodiversity – Ecosystem Function experiments: used often only species richness
- Preferred: function of species richness, composition, and relative abundance

Agroscope

Biodiversity – **E**cosystem **F**unction experiments

BEF relationship



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«Plant diversity and productivity experiments in Europe»

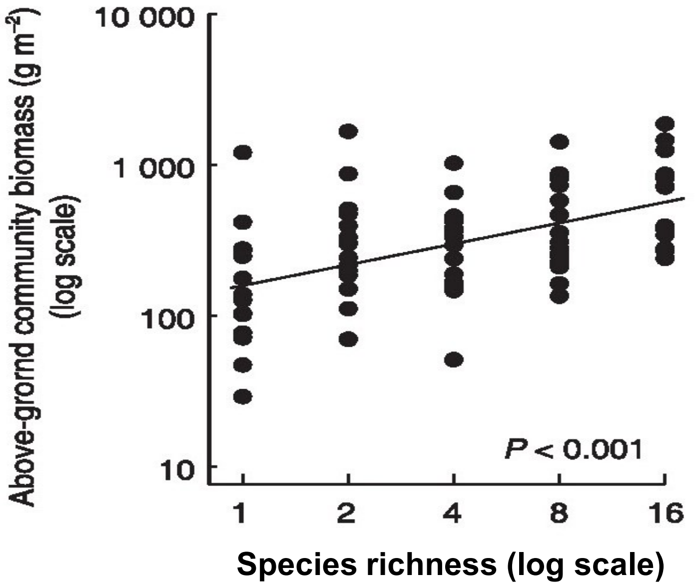
«We used constrained random selection from the local pool of grassland species»

(Figure from Tilman *et al.* (2014) Annu Rev Ecol Evol Syst)

Hector *et al.* (1999) Science

Biodiversity – Ecosystem Function experiments

BEF relationship



THE JENA EXPERIMENT

«Species compositions were determined by constrained random selection from a pool of 60 common Central European grassland species»

⇨ *Arrhenatheretum*!

Marquard *et al.* (2009) J Ecol

BEF experiments – Critique

Early critique:

- Plant communities are not assembled by random
- Plant species loss does not occur by random
- Positive relationship is due to:

  - greater probability of more diverse plots to contain highly productive species

  - presence of N_2-fixing species when N is limiting
- Positive diversity effects saturate at higher species richness

Huston *et al.* (1997) Oecologia

Thompson *et al.* (2005) Funct Ecol

BEF experiments – Critique

Critique: «*Plant communities are not assembled by random*»

- Plant communities develop over many years and are typically dominated by a few species, with many species present in (very) low abundance
- When plant communities are constructed by random sampling, the greater the species richness, the greater the likelihood that a highly productive species will be present and *dominate community biomass*
- Diversity effect measured is essentially an artefact from artificially constructed communities ⇨ not representative of natural conditions

Huston *et al.* (1997) Oecologia

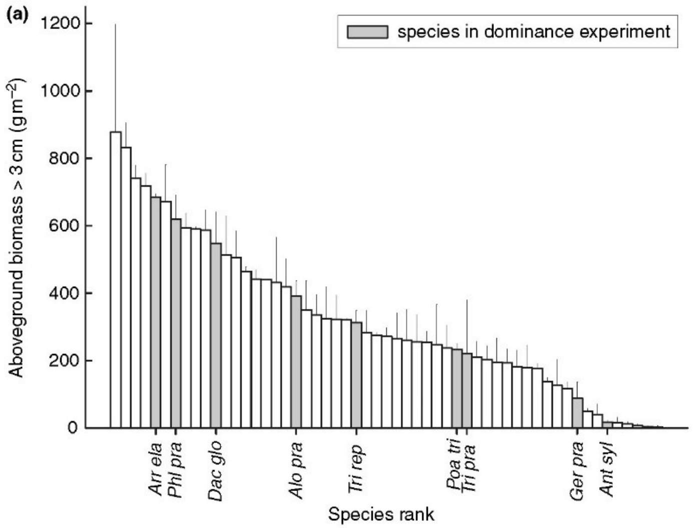
Thompson *et al.* (2005) Funct Ecol

BEF experiments – Rank-abundance relationship

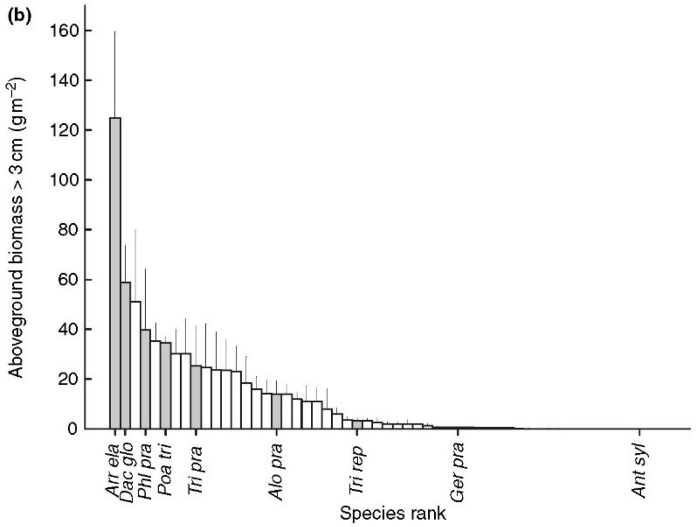
Dominance-diversity relationship

Biomass of plant species differs by a factor of 500

Monocultures



60-species mixture



Alo pra: *Alopecurus pratensis*
Ant syl: *Anthriscus sylvestris*
Arr ela: *Arrhenatherum elatius*
Dac glo: *Dactylis glomerata*
Ger pra: *Geranium pratense*
Phl pra: *Phleum pratense*
Poa tri: *Poa trivialis*
Tri pra: *Trifolium pratense*
Tri rep: *Trifolium repens*

⇨ Stronger dominance pattern in mixtures due to competitive suppression

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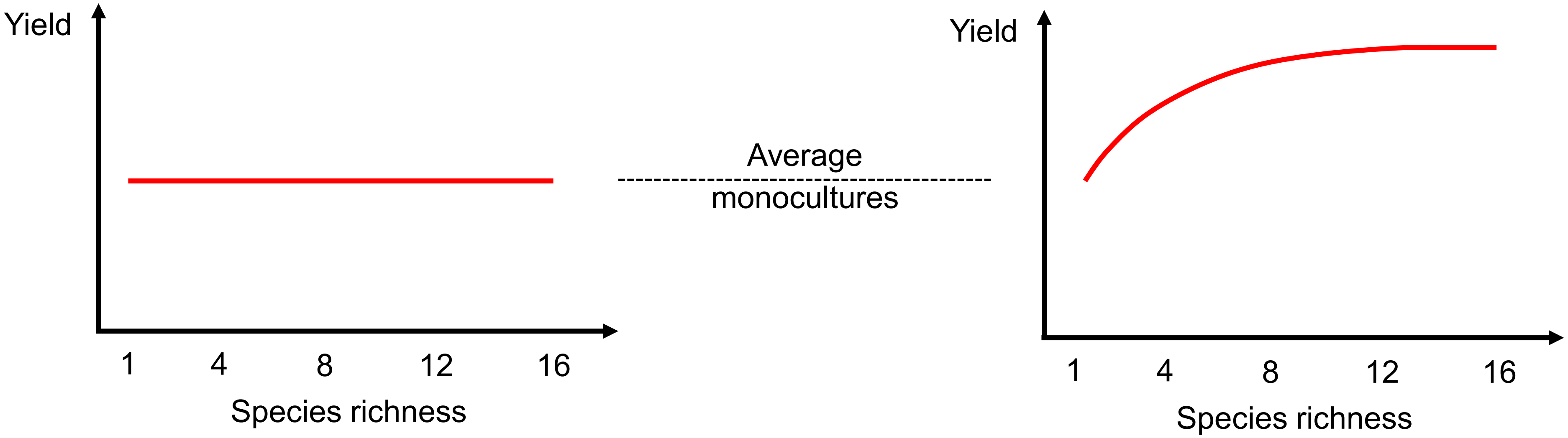
Roscher *et al.* (2005) Ecol Letters

BEF experiments – Sampling effect

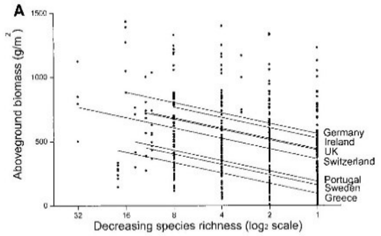
Expected patterns with random sampling

No sampling effect

With sampling effect

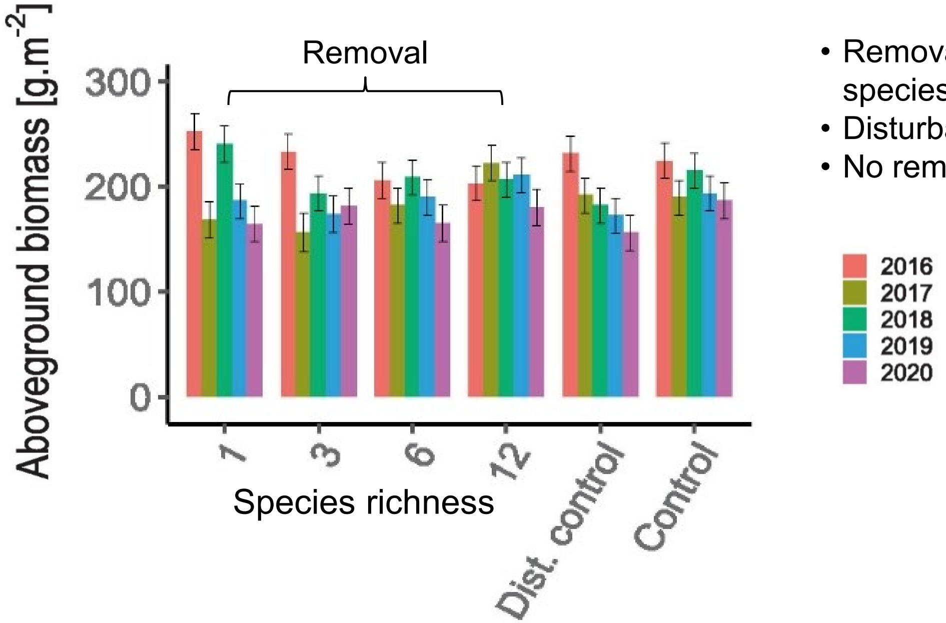


BEF experiments – Removal of least abundant

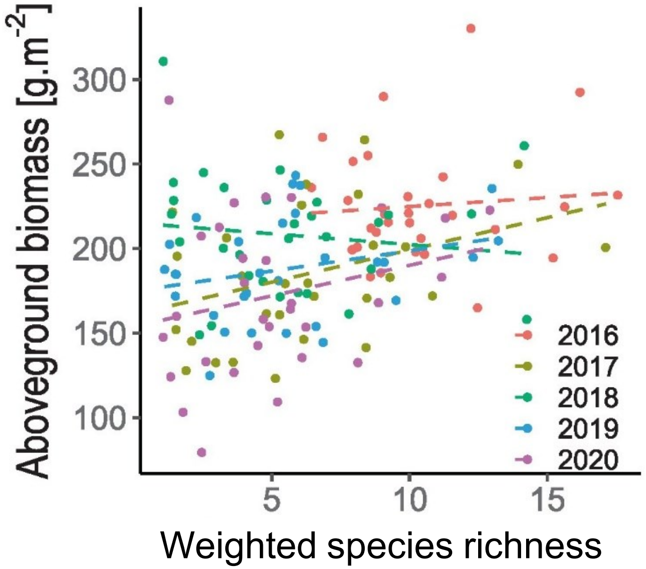


Hector *et al.* (1999)

Evidence



- Removal of least abundant species
- Disturbance (Dist. control)
- No removal (Control)



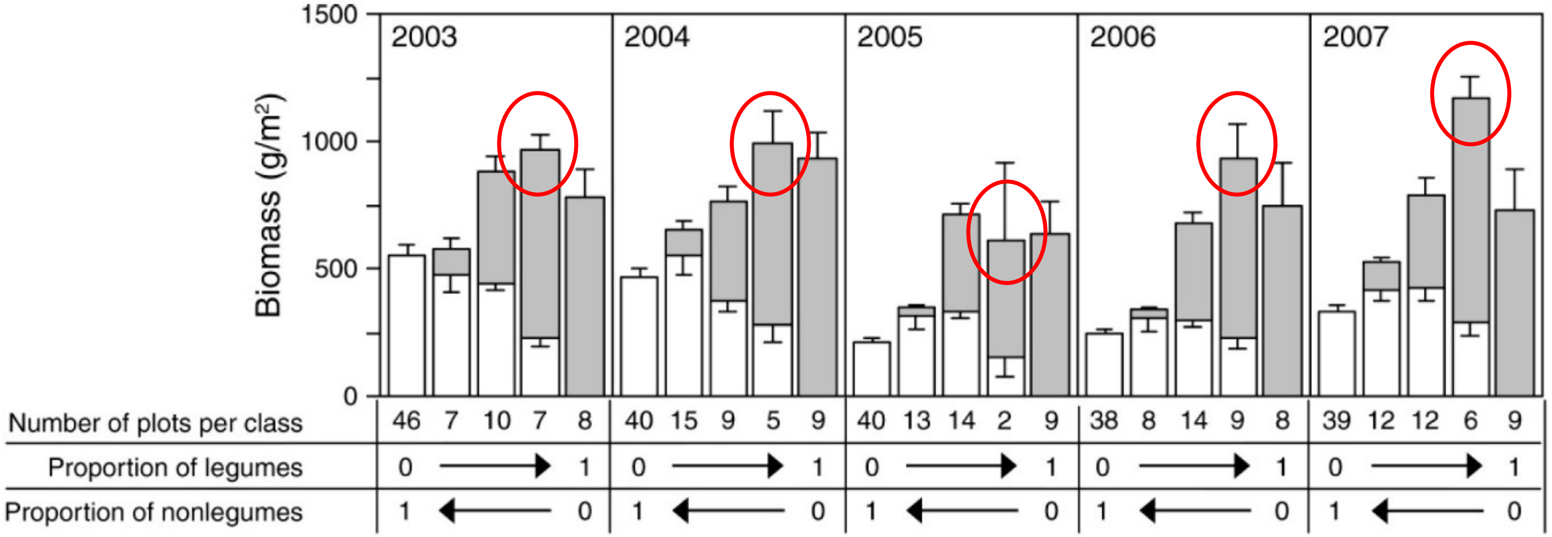
«Insignificant relationship in all the study years»

⇨ No effect of species richness if least abundant species are removed

Lisner *et al.* (2023) J Ecol

BEF experiments – Presence of N_2-fixing species

Critique: «*Diversity effect is mainly due to the presence of N_2-fixing species*»



⇨ Legume-dominated communities with highest yields

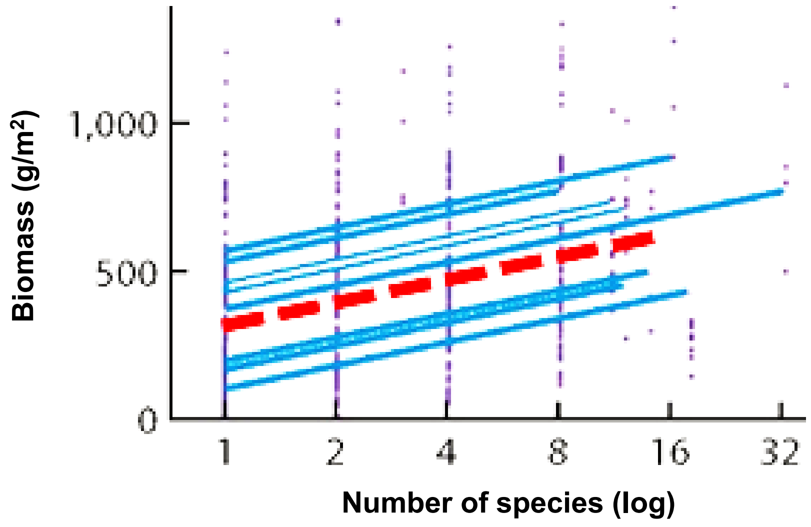
⇨ Variance explained by: presence of legumes: 48.9%

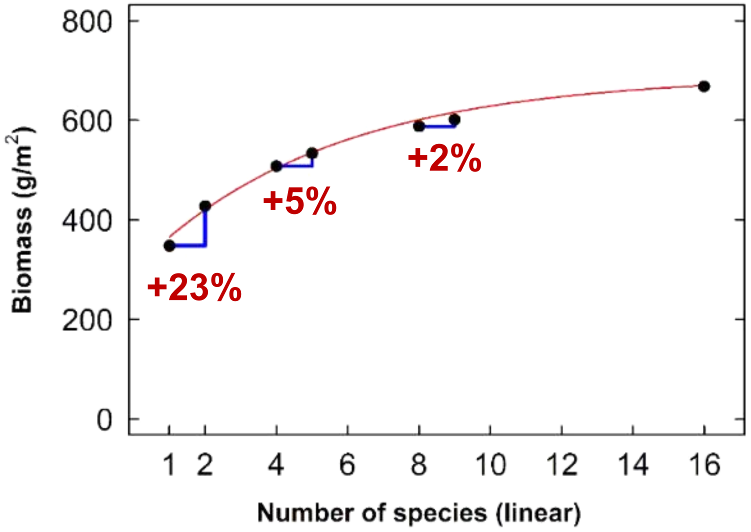
species richness: 9.4%

Marquard *et al.* (2009) Ecology

BEF experiments – Saturation

Critique: «*Positive diversity effects saturate at higher species*»





⇨ Saturation masked by log(species richness)

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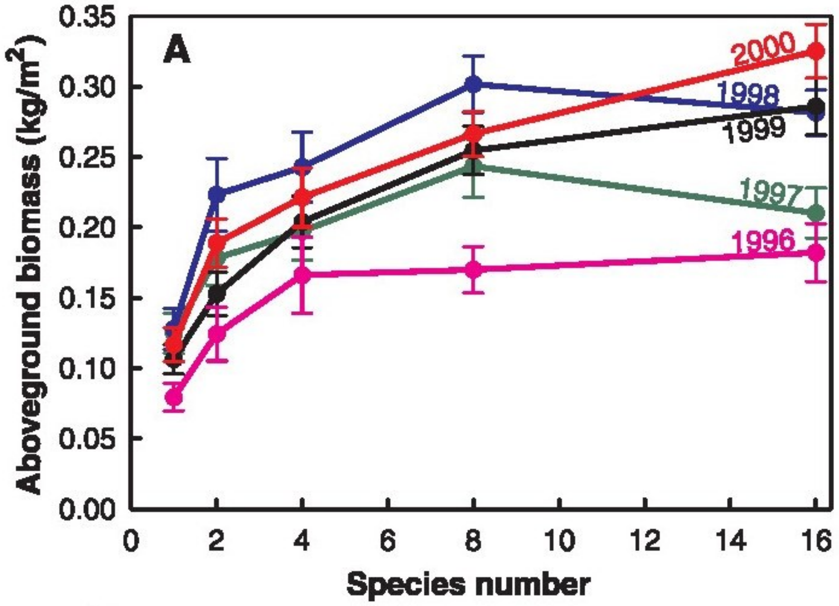
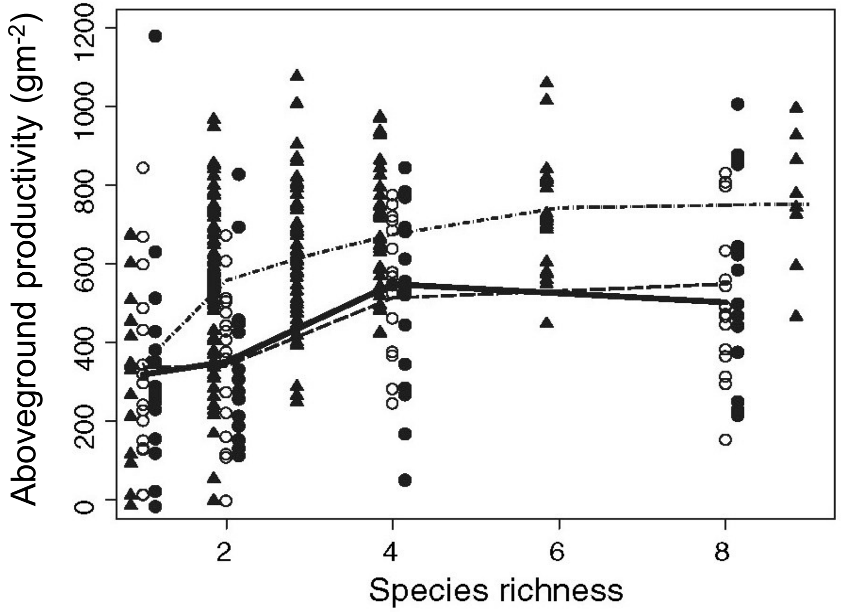
Hector *et al.* (1999) Science

BEF experiments – Saturation

Species richness on linear scale





⇨ Same results from the two largest and longest-running biodiversity exeriments

Cedar Creek

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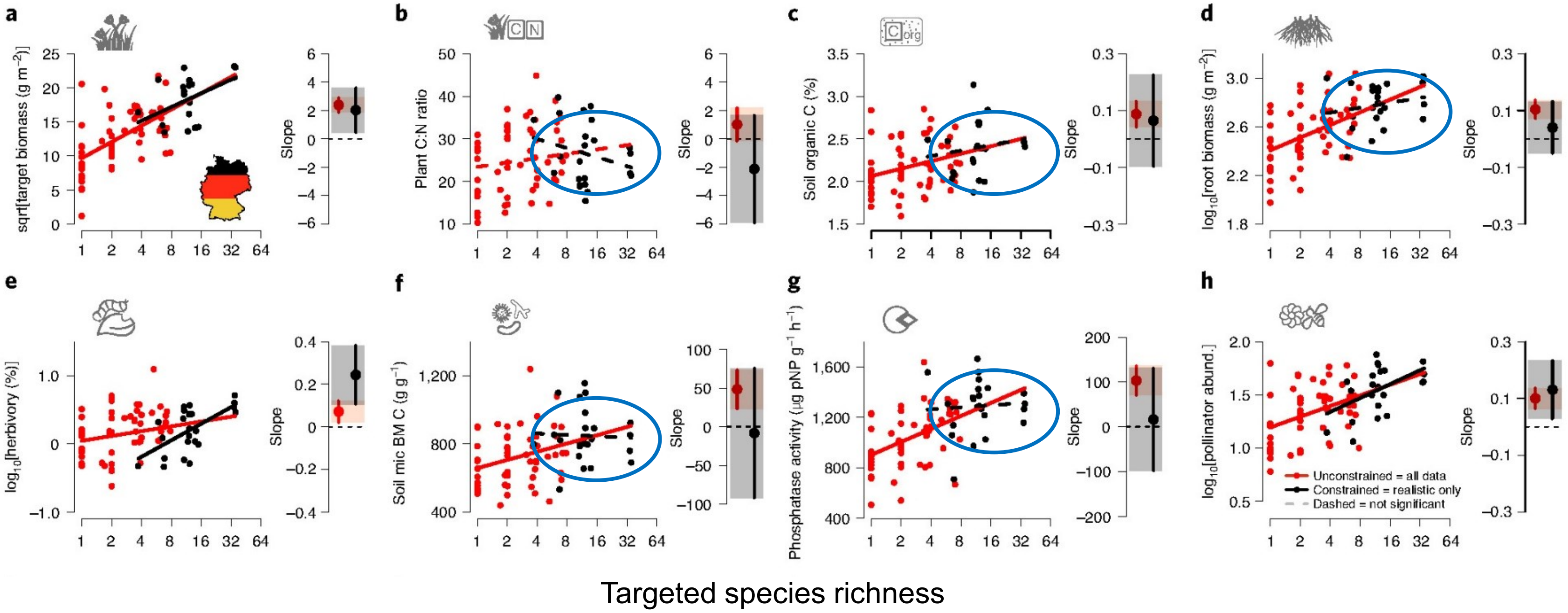
Tilman *et al.* (2001) Science

Roscher *et al.* (2005) Ecol Letters

BEF experiments – Weakend effects at richness ≥ 4

Indirect evidence for saturation

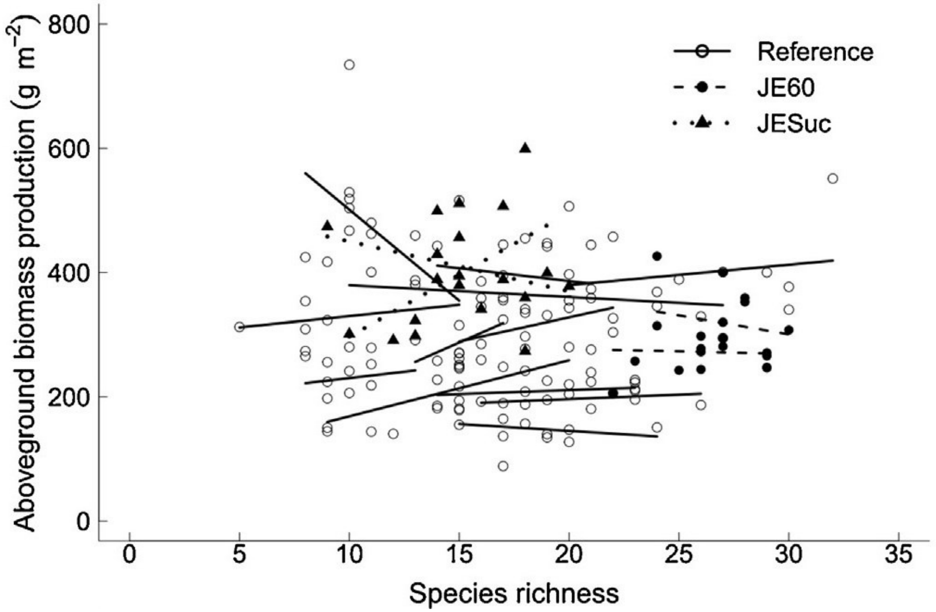


⇨ Effects in Germany weakened when considering only richness levels ≥ 4

Jochum *et al.* (2020) Nature Ecol Evol

BEF experiments – No effect at richness ≥ 10

Indirect evidence for saturation

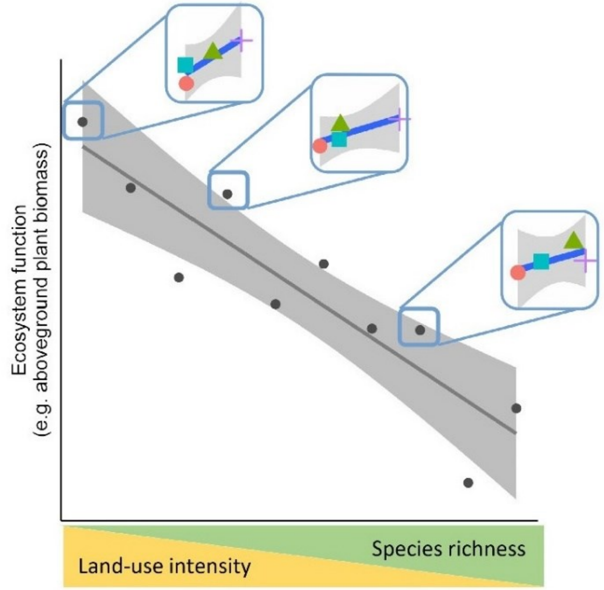


⇨ No effect of species richness on yield in diversity range of similar, permanent reference meadows

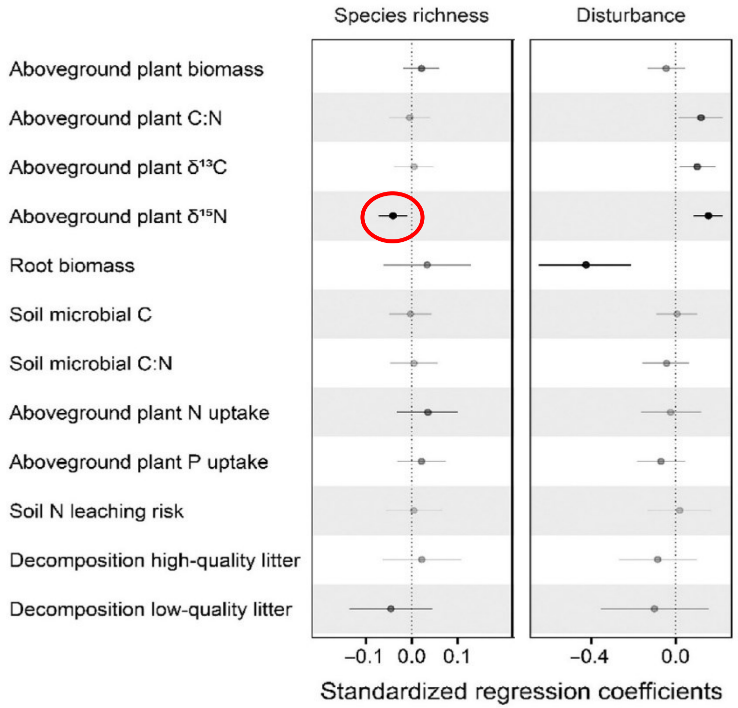
Buchmann *et al.* (2018) PPEES

BEF experiment with mature plant communities

«Increasing plant species richness by seeding has marginal effects on ecosystem functioning in agricultural grasslands»



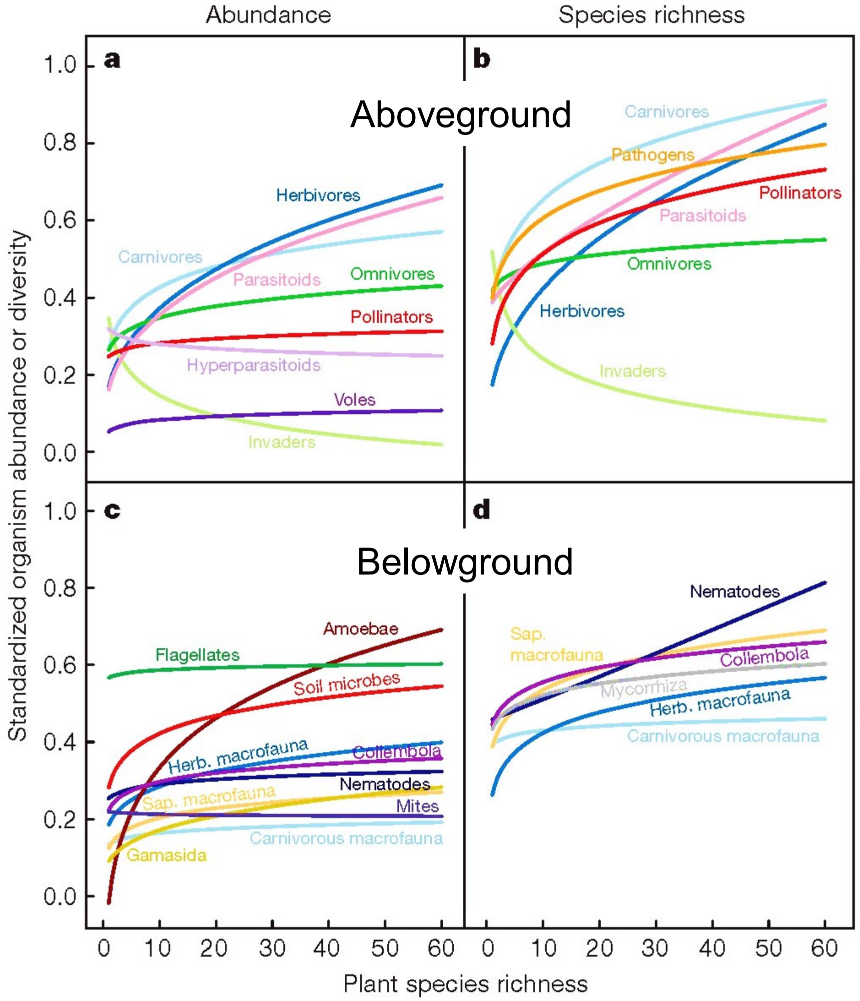
73 grassland sites



«Among sites, ecosystem functioning was mostly driven by environmental conditions and land-use intensity»

Freitag *et al.* (2023) J Ecol

BEF experiments – Less saturation with more functions

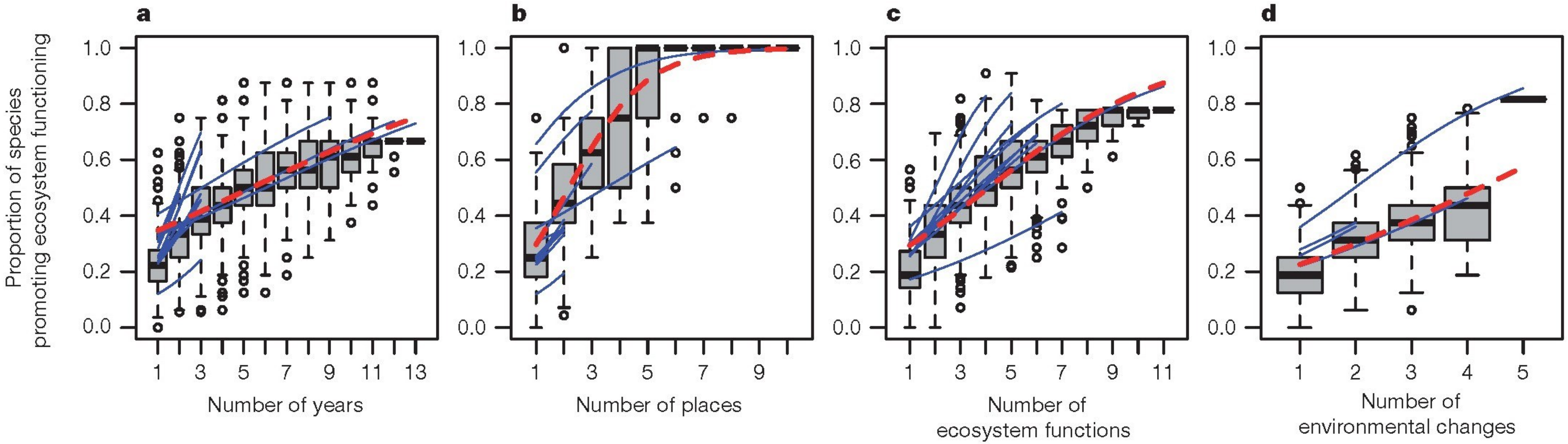


⇨ More species are likely to be needed if we consider more functions simultaneously!

Scherber *et al.* (2010) Nature

BEF experiments – Less saturation with more functions

147 species studied in 17 biodiversity experiments



⇨ More species are likely to be needed if we consider more years, places, functions, and environmental conditions

Isbell *et al.* (2011) Nature

Take home

- Randomly constructed plant communities do not necessarily reflect situations in natural vegetation
- Drivers other than species richness *per se* appear to be more important in explaining ecosystem functions (in particular yield)
- Important drivers: functional diversity *and* composition, species dominance, management incl. fertilisation (see LegLeg lecture Olivier)
- More species are needed for multiple functions, environmental conditions, years
- Think carefully about the implications of an experimental design – in terms of statistical *and* ecological/agronomic principles

Thank you for your attention

Matthias Suter

matthias.suter@agroscope.admin.ch

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