LegumeLegacy

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SS5 Data Science for biodiversity experiments

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Racines d'avenir
LABORATOIRE VIVANT

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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

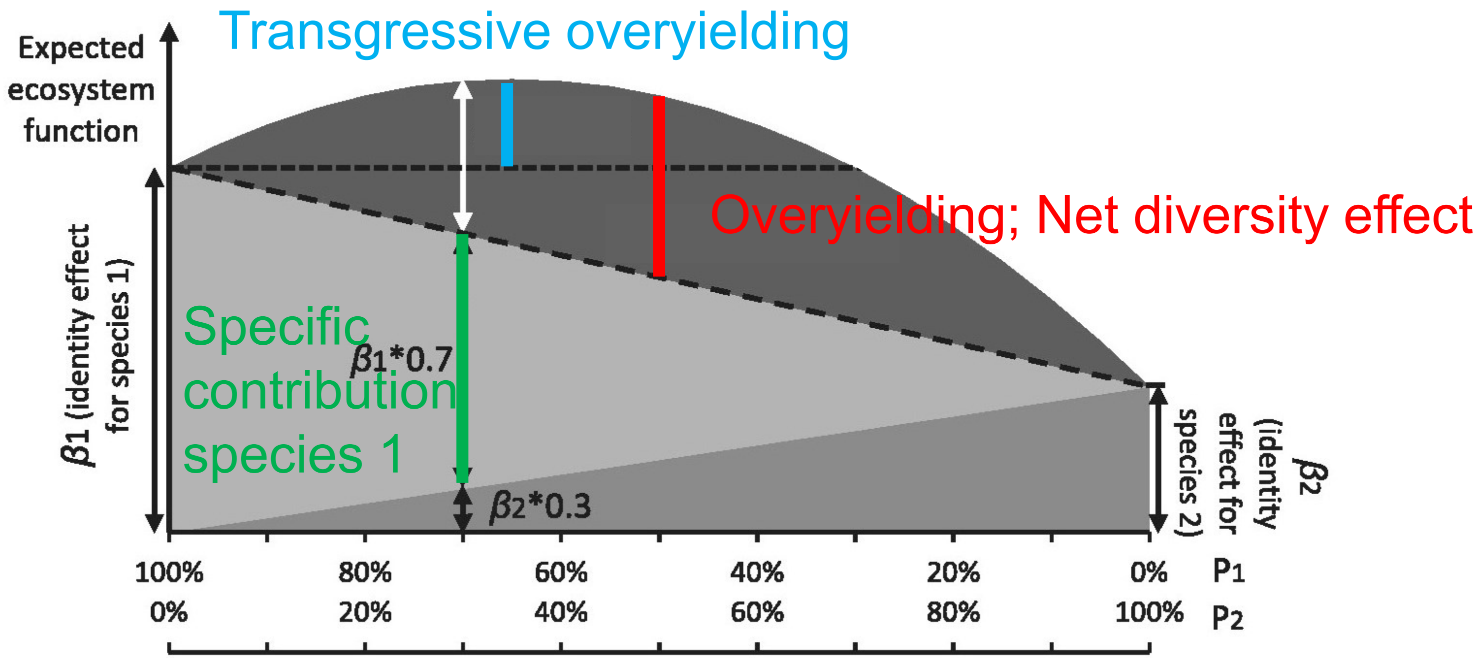
Definitions

- **Overyielding**: mixture performance that exceeds the performance expected from the *weighted* average of the constituent species grown in monoculture
- **Transgressive overyielding**: mixture performance that exceeds the best-performing monoculture
- **Selection effect**: dominance of most/least productive species in the mixture (relative to the species' monoculture performance); sampling effect *and* species dominance
- **Complementarity effect**: change in the average relative yield (relative to expected average monoculture performance)
- **Net diversity effect**: Selection effect + Complementarity effect. Synonym: Overyielding
- **Species identity and interaction effect**: estimated species contribution to ecosystem function from DI model

  - Species specific contribution: identity coefficients scaled by the species' proportions

  - Overyielding *or* transgressive overyielding: sum of interaction coefficients scaled by the species' proportions

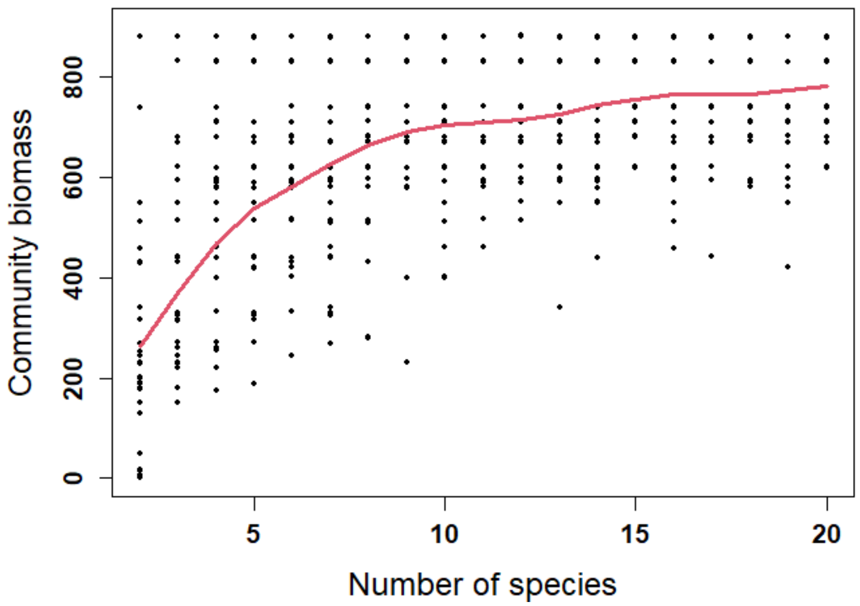
Definitions



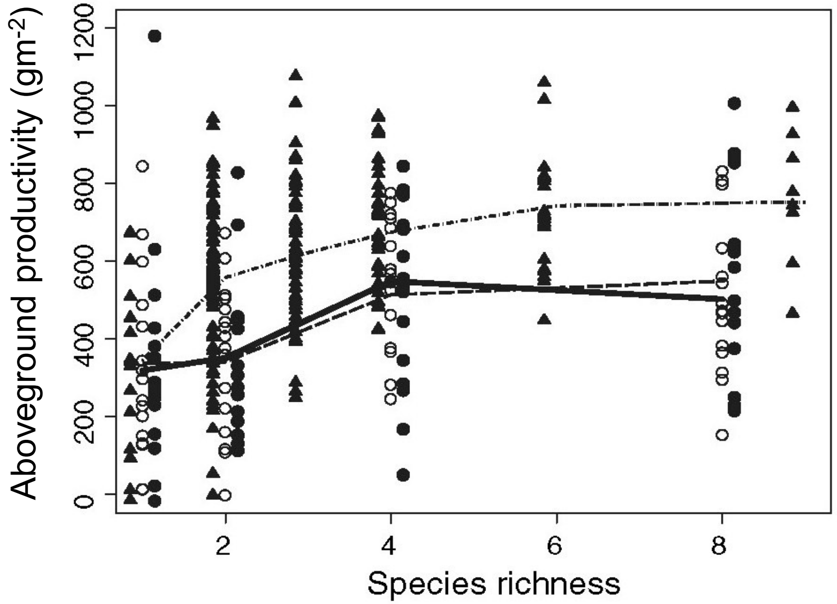
Modified from Grange *et al.* (2021) J Appl Ecol

Sampling effect in measured biomass?

Simulated



Measured



Not straightforward to assess the sampling effect in measured biomass

Roscher *et al.* (2005) Ecol Letters

Relative yield – Relative yield total

Concept

Relative Yield (RY) = $\frac{O}{M}$

$$\frac{\text{Observed yield in mixture}}{\text{Yield in monoculture}}$$

Relative Yield Total (RYT) = $\frac{O_1}{M_1} + \frac{O_2}{M_2}$

de Wit & van den Bergh (1965) Neth J Agri Sci

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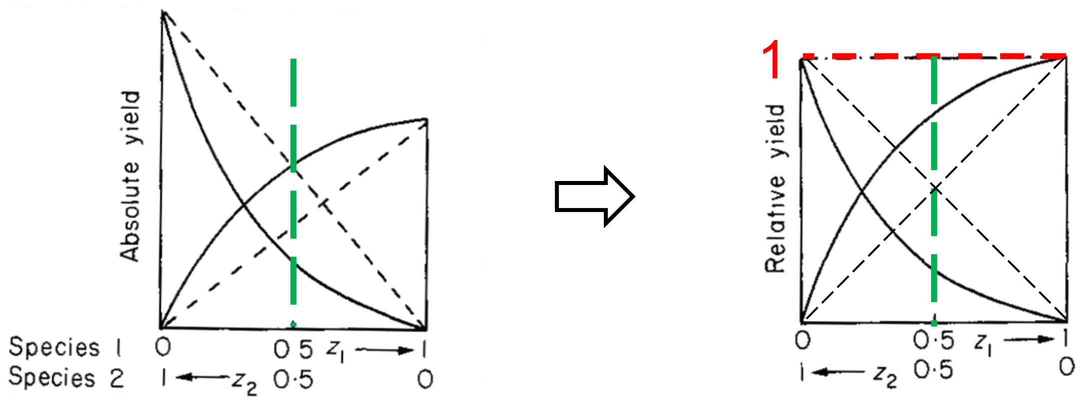
de Wit & van den Bergh (1965) Neth J Agri Sci

RYT = 1

--- expected
— observed



Berendse (1983) J Ecol

Relative yield – Relative yield total

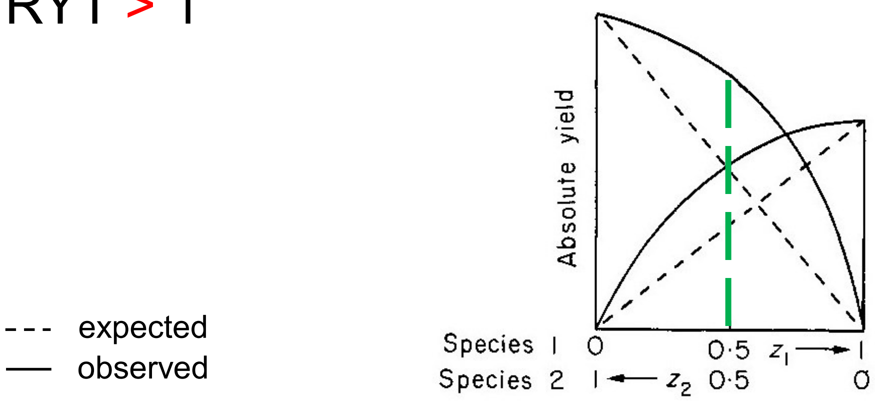
Concept

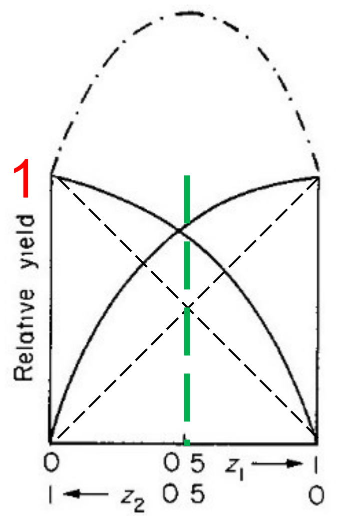
Relative Yield (RY) = $\frac{O}{M}$

Relative Yield Total (RYT) = $\frac{O_1}{M_1} + \frac{O_2}{M_2}$

RYT is a dimensionless index, *not* mixture yield

RYT > 1





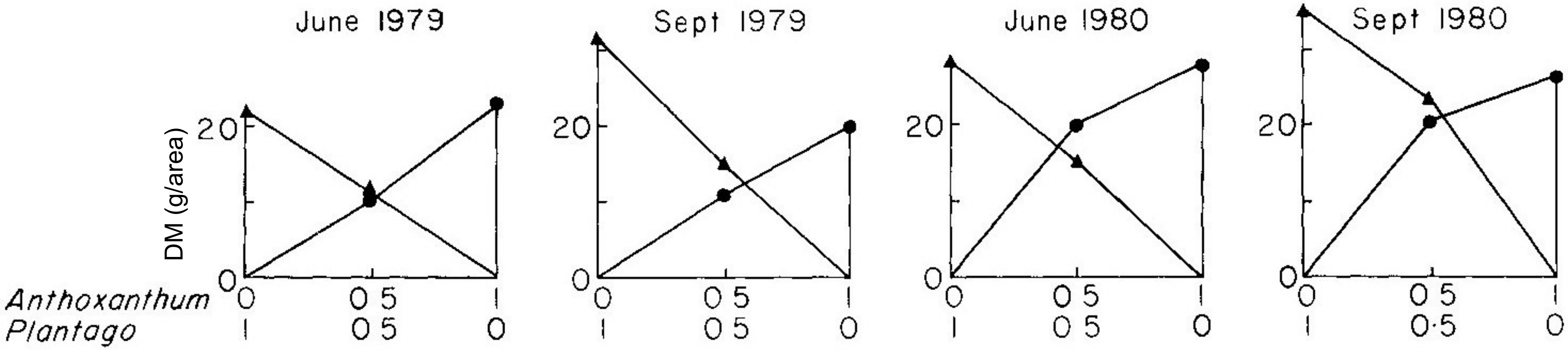
Following theory:
⇨ Implies some form of niche differentiation
⇨ Indicates more complete resource capture in mixture than in monoculture

Berendse (1983) J Ecol

Relative yield – Relative yield total

Applied

RYT 0.95 1.00 1.24 1.41



«The RYT reached values of about 1.5, which indicated a high degree of niche differentiation»

Berendse (1983) J Ecol

Additive partitioning

Concept

- Splits the net diversity effect of a mixture into:
  - a part assigned to species complementarity
  - a part assigned to species selection: sampling *and* dominance effects
- Based on relative yield (RY)
- Needs the realised species' proportions in the mixture
- Additive; both parts can be positive or negative, as can the net diversity effect

Net diversity effect

$$\Delta Y = Y_{\mathrm{O}} - Y_{\mathrm{E}} = \sum_i \mathrm{RY}_{\mathrm{O},i} M_i - \sum_i \mathrm{RY}_{\mathrm{E},i} M_i = \sum_i \Delta \mathrm{RY}_i M_i$$

$$= \underbrace{N\,\overline{\Delta \mathrm{RY}}\,\overline{M}}_{\text{Complementarity effect}} + \underbrace{N \operatorname{cov}(\Delta \mathrm{RY}, M)}_{\text{Selection effect}}$$

Complementarity effect

Average ΔRY *across all species* in the mixture

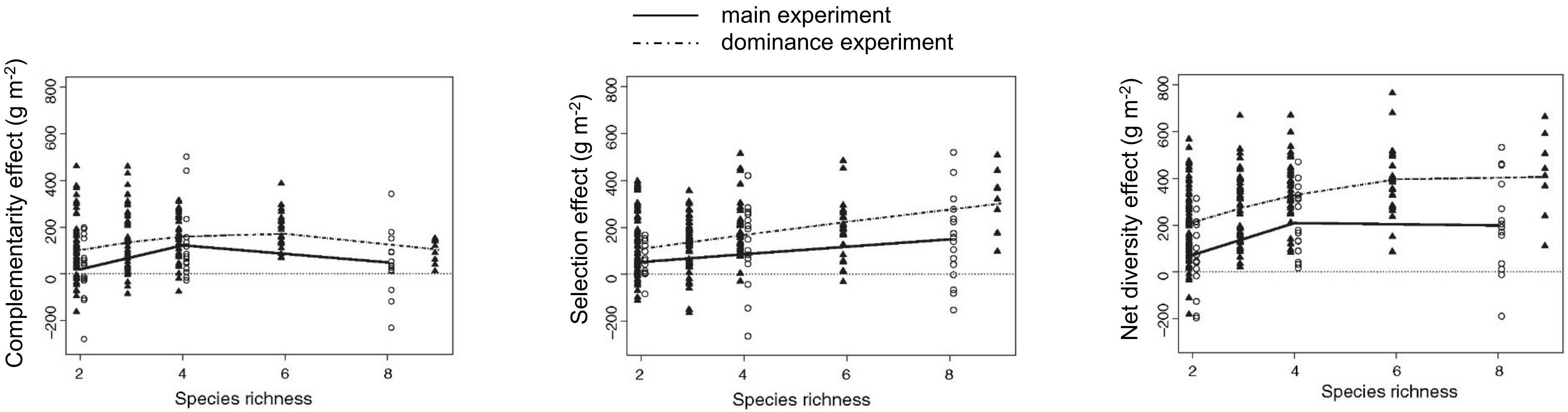
Selection effect

ΔRY *of each species* related to monoculture performance

Loreau & Hector (2001) Nature

Additive partitioning

Applied



⇨ Positive complementarity effect

⇨ Positive selection effect: increasing dominance of large species in more diverse plots *despite* stratified random sampling

THE JENA EXPERIMENT

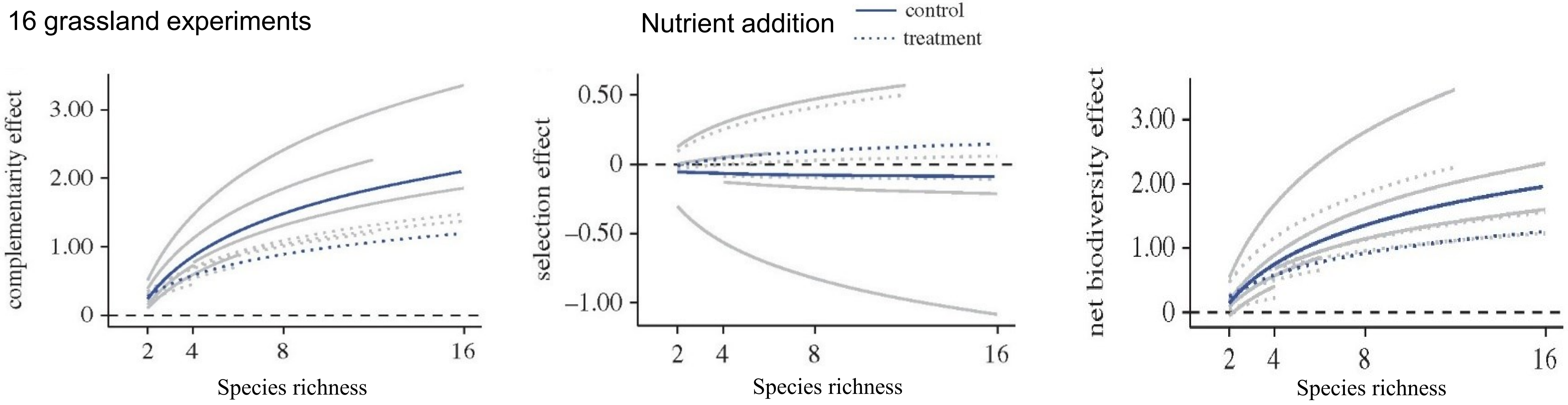
Roscher *et al.* (2005) Ecol Letters

Additive partitioning

Applied

16 grassland experiments

Nutrient addition



⇨ Positive complementarity effect, but reduced under nutrient addition

⇨ Negative selection effect switches to positive under nutrient addition

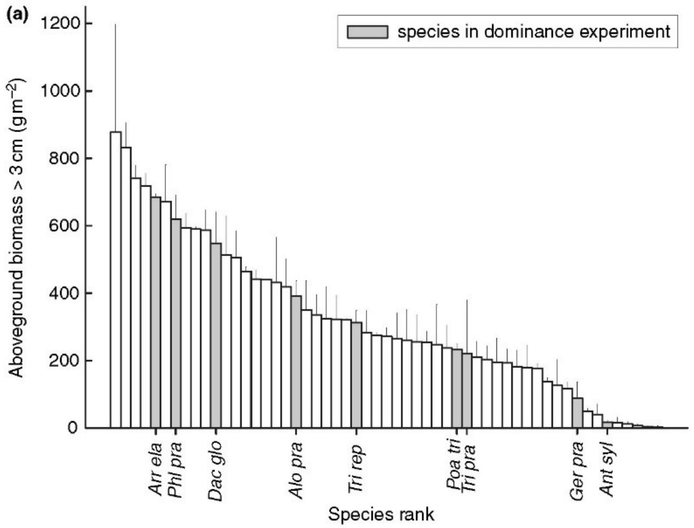
«Effects are dimensionless because they were standardised by the mean monoculture biomass of their corresponding treatment»

Craven *et al.* (2016) Philos T R Soc B

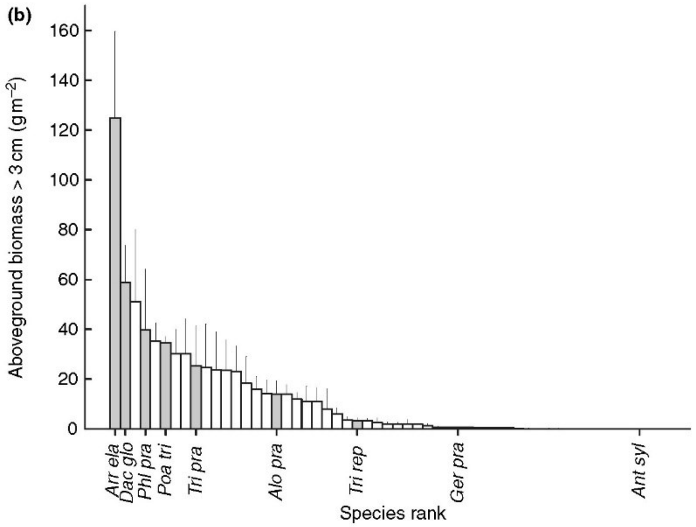
Rank-abundance relation indicates species dominance

Biomass of plant species differs by a factor of 500

Monocultures



60-species mixture



Alo pra: *Alopecurus pratensis*
Ant syl: *Anthriscus sylvestris*
Arr ela: *Arrhenaterum 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

THE JENA EXPERIMENT

Roscher *et al.* (2005) Ecol Letters

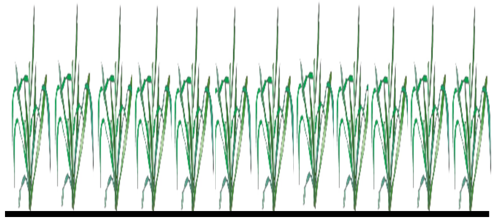
Species dominance

Monoculture 1 | 50:50 Mixture | Monoculture 2

Tall grass: DMY = 10 | Expected DMY = 6 | Small herb: DMY = 2

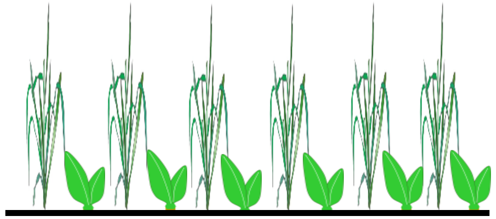
Species dominance in mixtures

Monoculture 1



Tall grass: DMY = 10

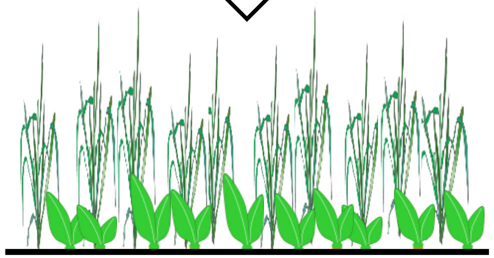
50:50 Mixture



Expected DMY = 6

Monoculture 2

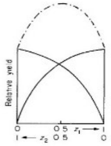
Small herb: DMY = 2



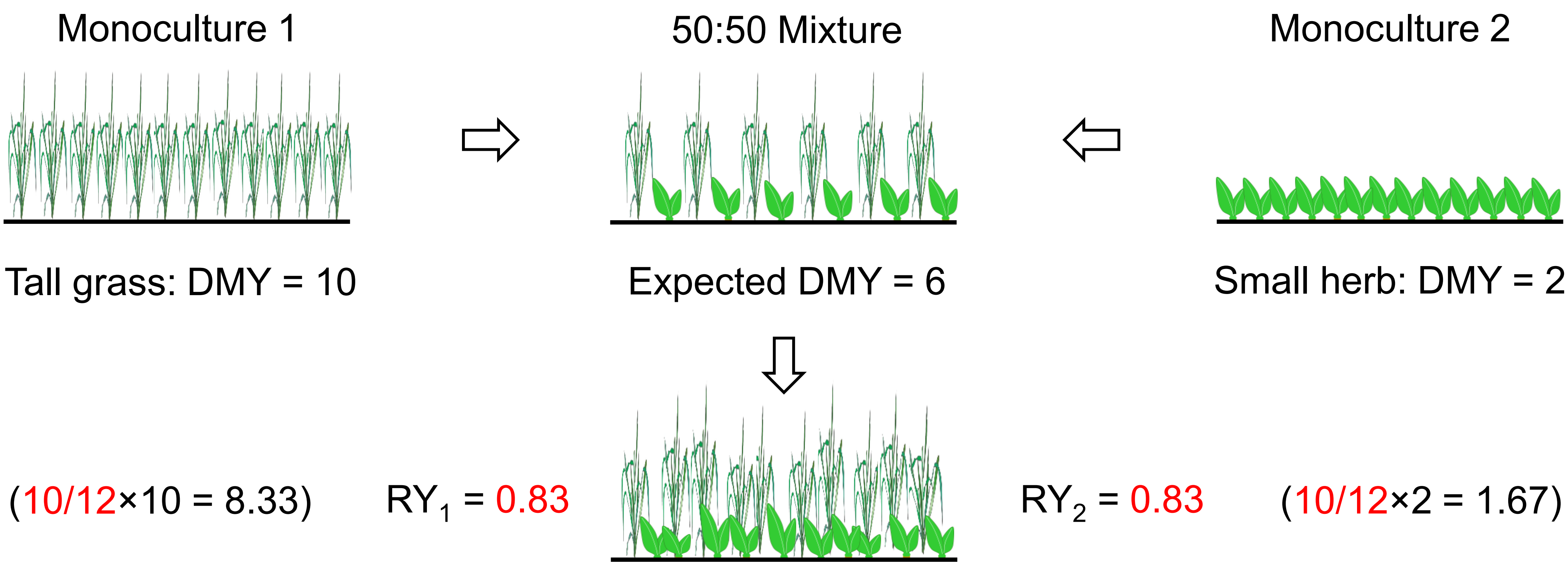
(10/12×10 = 8.33) RY_1 = 0.83

RY_2 = 0.83 (10/12×2 = 1.67)

RYT = 1.67



Species dominance in mixtures

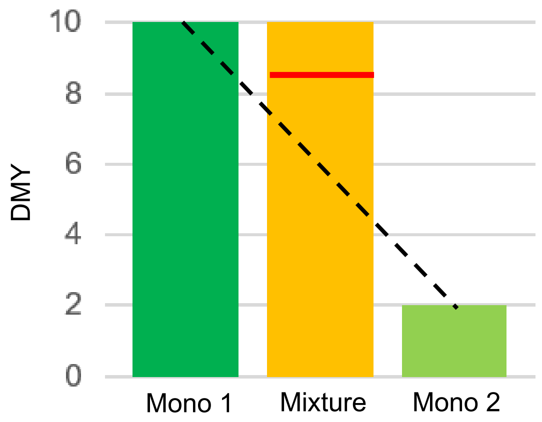


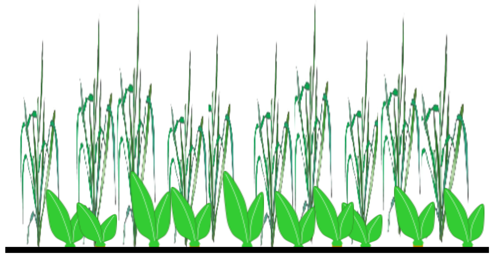
«The separate identity of species is submerged in a purely formal numerical equivalence»

Connolly (1988) TREE

Species dominance and realised proportions

Expected DMY = 6





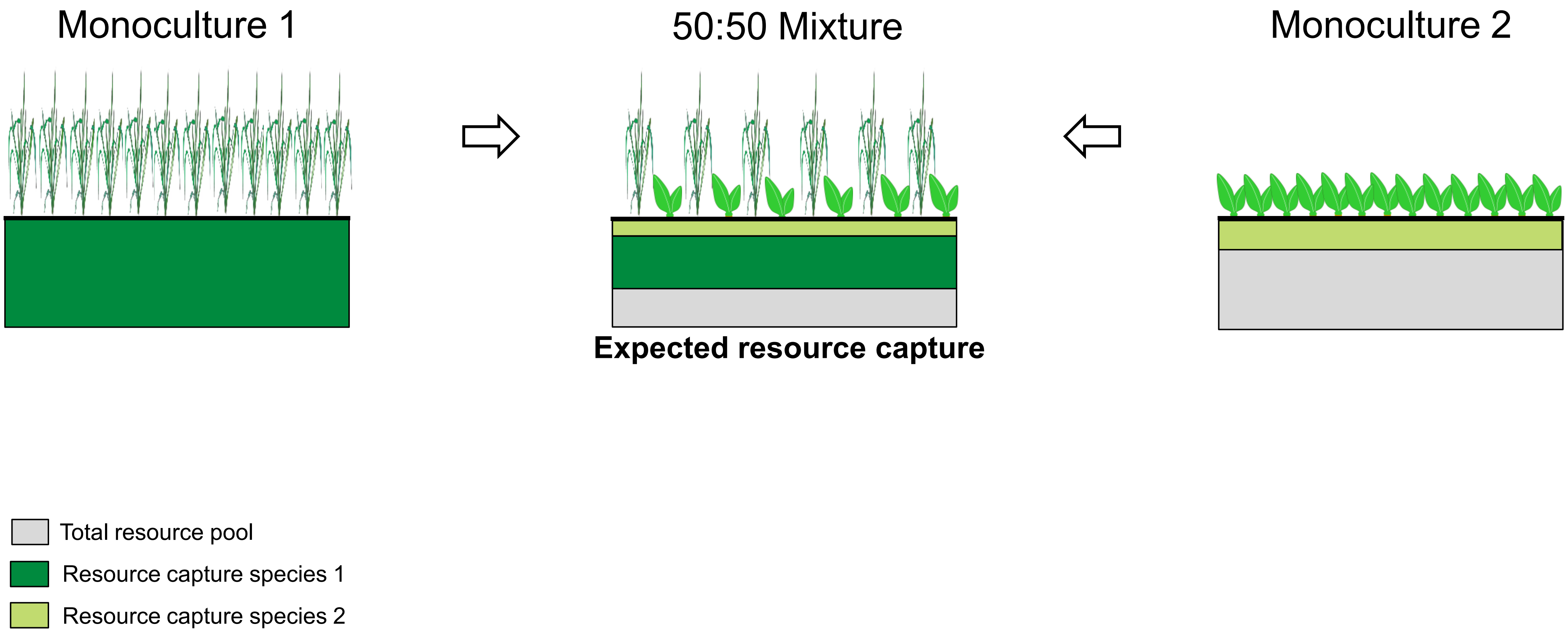
(10/12×10 = 8.33)

(10/12×2 = 1.67)

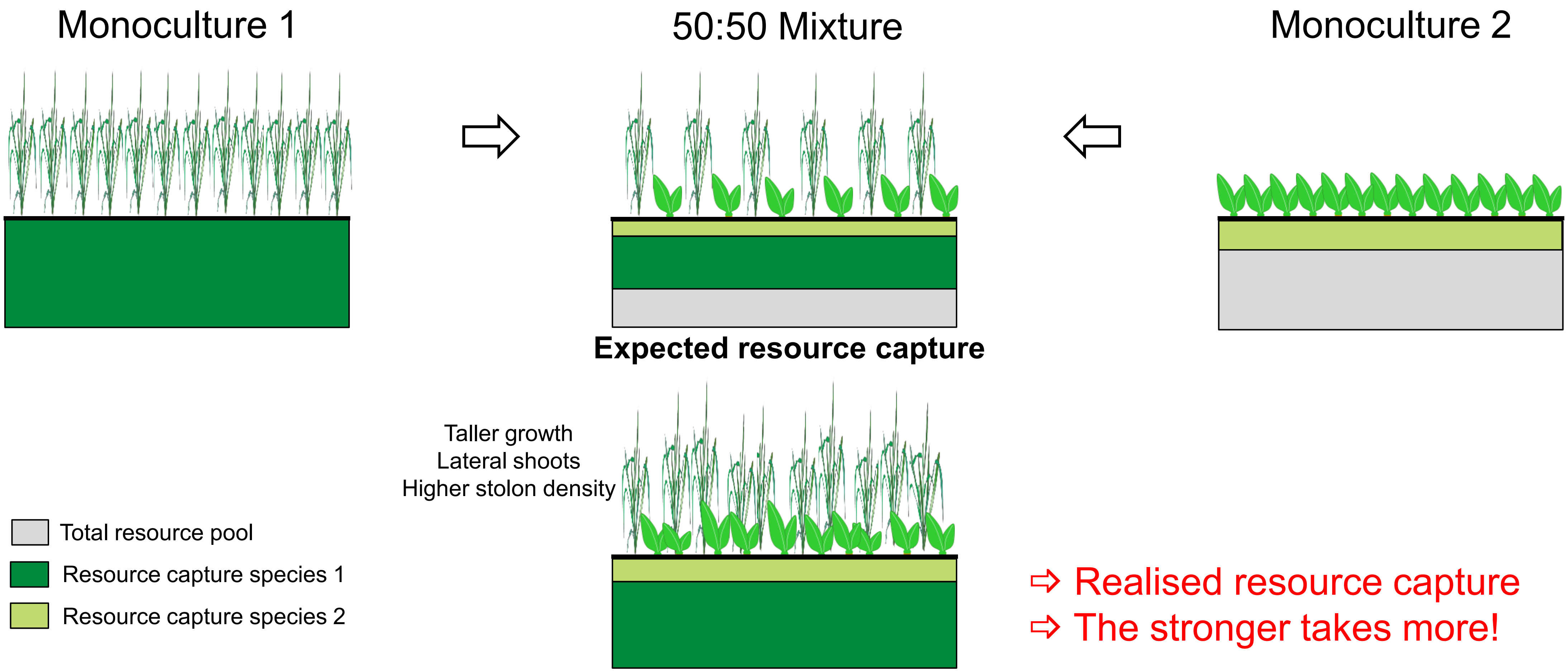
Realised DMY = 10

Realised proportions: 0.83:0.17 = 5:1

Species dominance – What happens?



Species dominance – What happens?



⇨ Realised resource capture

⇨ The stronger takes more!

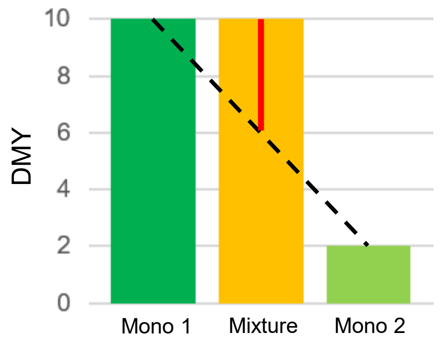
Species dominance and overyielding

Selection effect = 0

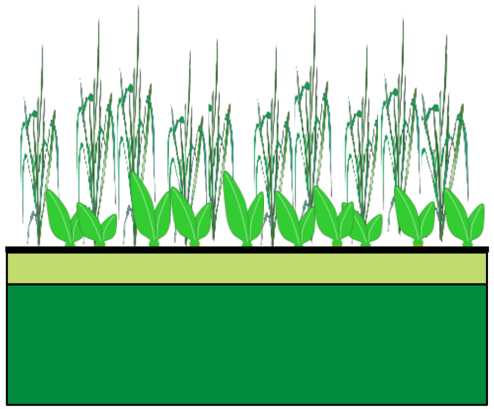
Complementarity effect = 4

⇨ Overyielding can occur through species dominance alone

⇨ Does *not* necessarily indicate direct species interference



Net diversity effect; Overyielding



(10/12×10 = 8.33) $RY_1 = 0.83$

$RY_2 = 0.83$ (10/12×2 = 1.67)

⇨ Selection effect zero, but species dominance

«The separate identity of species is submerged in a purely formal numerical equivalence» (Connolly, 1988, TREE)

Implicit assumptions of relative yield approaches

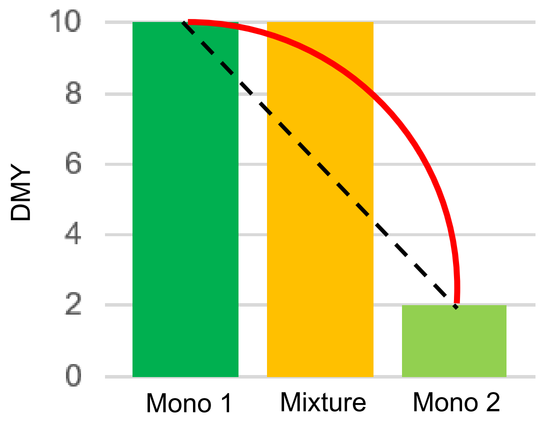
- Plants (can) occupy different niches
- The total initial (mass) density in the mixture is equivalent to that of the monocultures

However

- Plants generally compete for the same few resources: light, water, nutrients (N, P, K, Ca, …), space
- When plant species with different growth potentials are mixed, the total initial density between the mixture and the monocultures differs

Species dominance, overyielding, and DI model

- ⇨ «Species interaction effect» in a DI model does *not* necessarily indicate direct species interference
- ⇨ May be termed species interaction in the broader sense



Species interaction effect

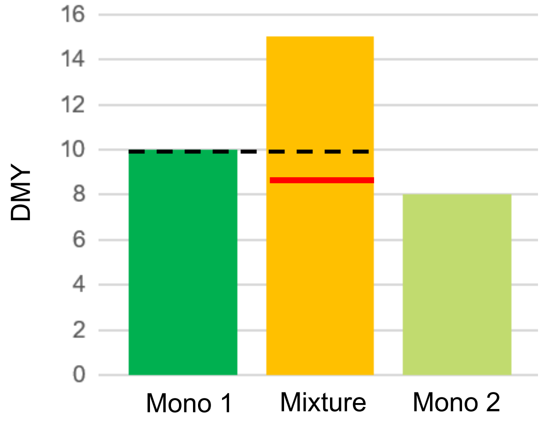
$$y = \beta_1 P_1 + \beta_2 P_2 + \delta P_1 P_2 + \varepsilon$$

Species identity

Species interactions

Transgressive overyielding

- ⇨ Transgressive overyielding implies direct interference between species
- ⇨ e.g., N transfer, stimulation of symbiotic N_2 fixation by grasses, (N sparing)



- ⇨ Species dominance less pronounced with approx. similar species identities
- ⇨ TO easier to achieve, when species have similar growth potential

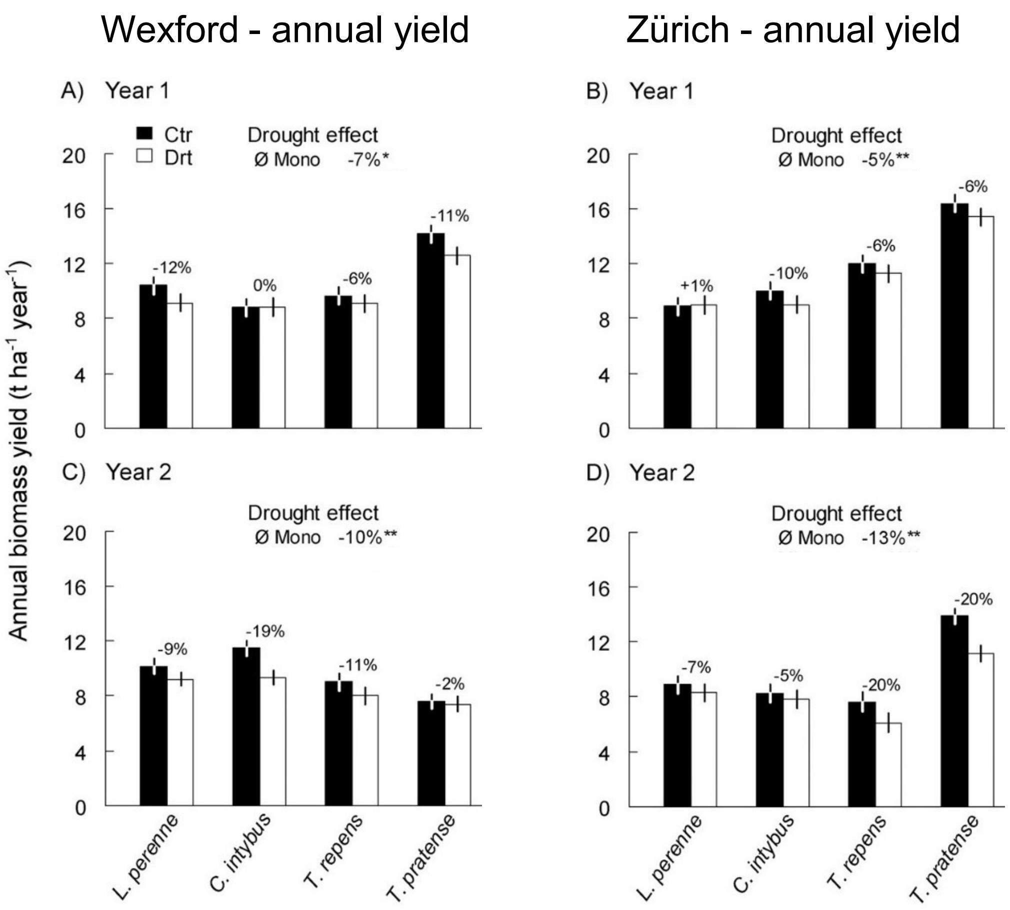
(10/12×**10** = 8.33)

Realised DMY = 15

Realised proportions: 0.56:0.44

(10/12×**8** = 6.67)

Ratio of species performances in forage mixtures



Finn *et al.* (2018) AGEE

Ratio of largest to lowest monoculture yield: often ≤ 2

See also:

Nyfeler *et al.* (2009) J Appl Ecol

Finn *et al.* (2013) J Appl Ecol

Helgadottir *et al.* (2018) Ann Bot

O'Malley *et al.* (2025) in revision

Extended resource pool belowground?

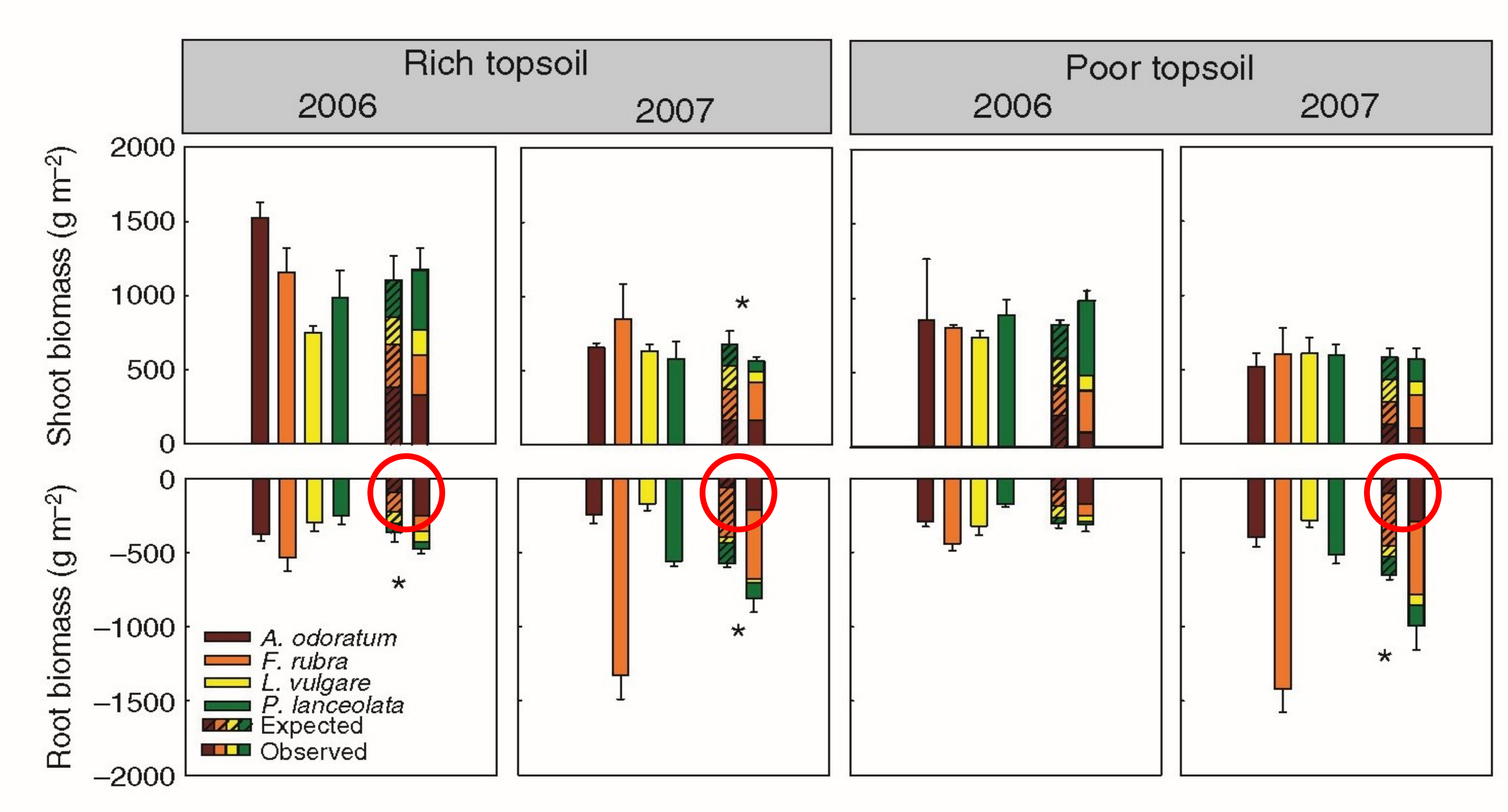
- This belowground overyielding appeared *not* to be the result of vertical niche differentiation, as rooting depth of the community tended to decrease, rather than increase in mixtures compared to monocultures. Mommer *et al.* (2010) J Ecol

- Plant community N uptake was *not* affected by species richness, …
- Our results suggest … that species composition was more important than species richness in determining community N uptake. van Felten *et al.* (2012) Ecology

- This positive plant diversity effect could *not* be explained by complementary soil ^{15}N-access of the different plant species from 0.4, 0.8 and 1.2 m soil depths, … Pirhofer-Walz *et al.* (2013) Plant Soil

- Clear evidence for spatial niche differences in resource uptake between shallow- and deep-rooted species did *not* translate into increased resource uptake in mixtures. Hoekstra *et al.* (2016) Plant Soil

Unveiling belowground species abundance



«The belowground overyielding was mainly driven by enhanced root invest-ments of one species, … without retarding the growth of the other species.»

Mommer *et al.* (2010) J Ecol

Unveiling belowground species abundance

Table 1. Biodiversity effects for root, shoot and total biomass (g m^{-2}), as well as shoot nitrogen (N) accumulation (g m^{-2}), in both treatments (rich topsoil and poor topsoil) in 2006 and 2007. Significant deviations ($P < 0.05$) from the intercept of the predicted model on square-root transformed values are given in bold. Data are mean ± SE, $N = 3$–4 plots

Rich topsoil treatment		Root	Shoot	Total	N $uptake_{shoot}$
2006	Overall net effect	**112.0 ± 27.7**	71.3 ± 124.3	183.3 ± 112.2	−3.61 ± 2.59
	Complementarity effect	**112.5 ± 24.8**	94.1 ± 118.2	179.9 ± 112.2	−3.45 ± 2.55
	Selection effect	**−0.5 ± 0.02**	**−22.8 ± 7.2**	3.4 ± 5.0	−0.15 ± 0.05
2007	Overall net effect	**232.3 ± 94.7**	**−114.0 ± 29.9**	118.3 ± 102.5	−1.28 ± 0.31
	Complementarity effect	**315.0 ± 104.4**	**−142.6 ± 32.6**	26.1 ± 100.8	−1.53 ± 0.29
	Selection effect	**−82.7 ± 9.7**	**28.6 ± 12.6**	**92.2 ± 24.2**	0.25 ± 0.06
Poor topsoil treatment					
2006	Overall net effect	5.5 ± 46.6	162.8 ± 69.3	**168.4 ± 73.1**	−0.21 ± 1.24
	Complementarity effect	7.6 ± 46.9	138.0 ± 64.6	171.5 ± 77.3	−0.61 ± 0.96
	Selection effect	**−2.1 ± 0.3**	**24.8 ± 6.07**	−3.2 ± 10.2	0.41 ± 0.31
2007	Overall net effect	**342.8 ± 158.6**	−13.0 ± 71.6	329.8 ± 150.6	−0.35 ± 0.55
	Complementarity effect	**390.8 ± 166.2**	−16.4 ± 68.6	281.6 ± 148.8	−0.48 ± 0.59
	Selection effect	**−48.0 ± 7.6**	3.4 ± 4.5	48.2 ± 25.8	0.13 ± 0.03

⇨ Selection effects negative because the species with fewer monoculture rootmass had on average greater relative rootmass gains in mixture

Mommer *et al.* (2010) J Ecol

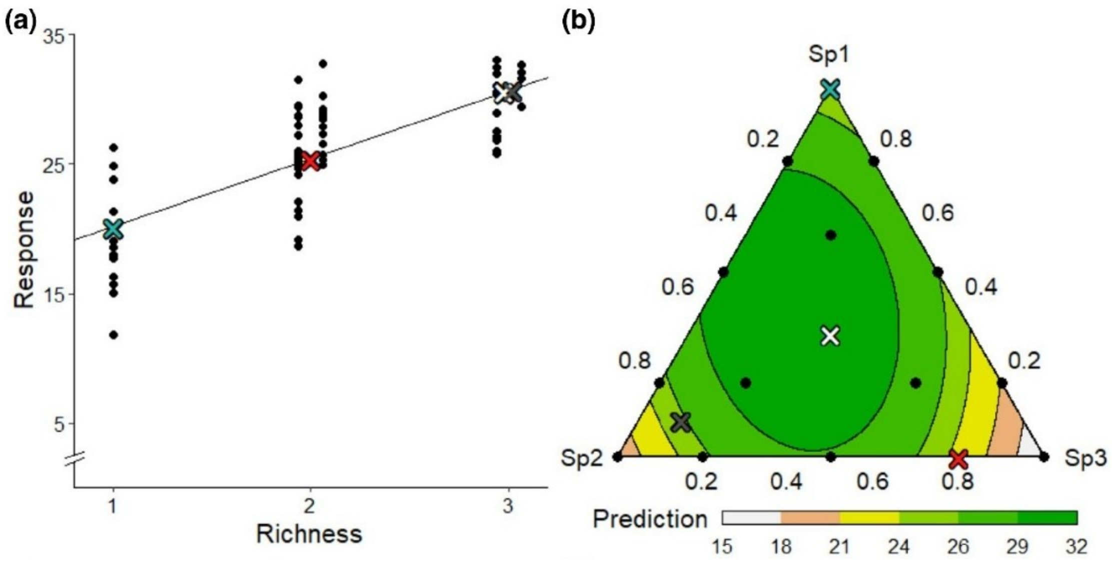
BEF relationship with DI-Models

Methods in Ecology and Evolution

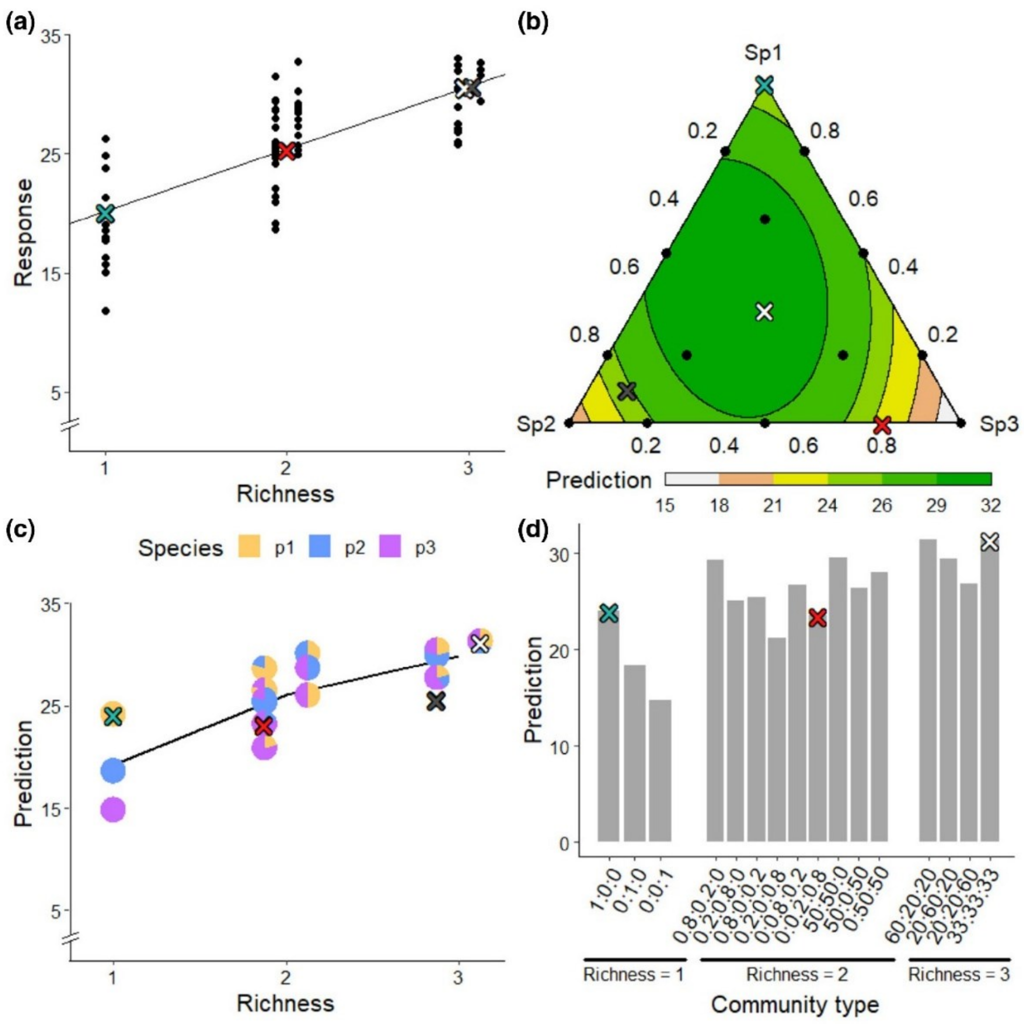
APPLICATION

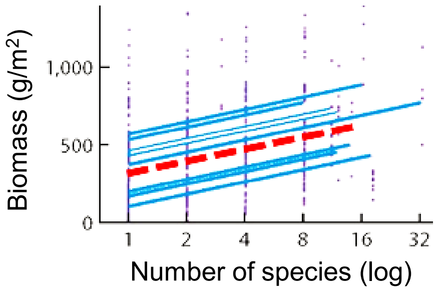
Going beyond richness: Modelling the BEF relationship using species identity, evenness, richness and species interactions via the DImodels R package

Rafael A. Moral[1] | Rishabh Vishwakarma[2] | John Connolly[3] | Laura Byrne[2] | Catherine Hurley[1] | John A. Finn[4] | Caroline Brophy[2]



BEF relationship with DI-Models





Hector *et al.* (1999) Science

⇨ More variation in performance explained by considering also composition and relative abundance

Moral *et al.* (2023) Methods Ecol Evol

Take home

- Overyielding does not necessarily indicate direct species interference; can also occur through species dominance
  ⇨ may be termed «species interaction in the broader sense»
- Overyielding through species dominance is more likely to occur when there are large differences in the species' inherent growth potentials
- Selection effect can be zero despite species dominance in mixtures
- Differences in species identities are much larger in natural plant communities than in sown forage plant mixtures
- Transgressive overyielding implies direct species interference, e.g., N transfer, stimulation of legumes' symbiotic N_2 fixation by grasses, facilitation by nutrient sparing
- «All things are of number» - but numbers are not things. Numbers are mental.
  Pythagoras (~ 2500 b.p.) Greece

Thank you for your attention

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