Biodiversity-Ecosystem Function

EXPLORING NEW DEVELOPMENTS IN THE B.E.F. DEBATE, IN RELATION TO EXPERIMENTAL VS OBSERVATIONAL APPROACHES

BIOL470 - FEB 6 2015 - MARY TOEWS

Review of a few key definitions

Biodiversity: “The variability among living organisms from all sources including terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems” (Convention on Biological Diversity, 1993, as seen in Week 3 class)

Most BEF research has focused on functional and species diversity

- **Ecosystem Function**: This can include the ecosystem properties (pools of resources and rates of processes), ecosystem goods (market value) and services (directly or indirectly beneficial to humans, such as hydrologic cycles, water and air cleansing, pollination) (Hooper et al., 2005)

Most BEF research has focused on biomass and productivity

Current trends: Where is the debate at now?

- Although this has been a prominent theme in ecology for +20 years, there are still exciting new developments and many unresolved debates.
- The general consensus, despite the many curves found, is that there is a **positive relationship** between biodiversity and ecosystem function, and at a certain point decreasing biodiversity decreases function. However, the **shape of curve varies** between systems, unit measures, trophic levels, methods, etc (Schwartz et al., 2000; Cardinal et al., 2006; Loreau et al. 2001).
- Much of the current research focuses on the **mechanisms behind these relationships**, and how the relationship is affected by adding complexity (e.g. multiple trophic levels, larger spatial and temporal scales, other variables affecting relationship)
- Two key mechanisms to explain this positive relationship is sampling effect (Huston, 1997) and the niche complementarily effect (Loreau et al., 2001).

Current trends in relation to observational and experimental approaches

As discussed in first week of course – Both approaches are important, but the way in which data is collected may have implications for the interpretation of the results.

Due to obvious limitations and constraints, **experimental approaches have been more common** (and mostly on plants in terrestrial ecosystems), and are thus may have contributed more to the debate so far

With recent technological advances and the increased collaboration to answer big conservation questions, **would expect that observational studies which look at a variety of factors on larger scales to become more prevalent, and thus contribute new ideas to the field**.

Three new developments in the BEF literature…

For each paper, we will explore these points:
- Research goals and questions
- Overview of methods
- Key findings
- What current hypotheses do they support or refute and/or how do they fit into the BEF debate

Plant Species Richness and Ecosystem Multifunctionality in Global Drylands

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Alternative hypotheses to explain why biodiversity-ecosystem functioning relationships are concave-up in some natural ecosystems but concave-down in manipulative experiments

Camilo Mora[1], Roberto Danovaro[2,3] & Michel Loreau[4]

Functional Ecology 2014, **28**, 1523–1533 doi: 10.1111/1365-2435.12267

Community assembly effects shape the biodiversity-ecosystem functioning relationships

Benoît Jaillard[*,1], Alain Rapaport[2,3], Jérôme Harmand[3,4], Alain Brauman[5] and Naoise Nunan[6]

Community assembly effects shape the biodiversity-ecosystem functioning relationships

Jaillard, B., Rapaport, A., Harmand, J., Brauman, A., and Nunan, N. (2014)

Research goals and questions

- Could a model based on the random sampling effect and simple species dominance rules explain the multiple shapes of the BEF curve?
- Does this mean that a suite of species are needed for full function, or one/several key species?

Overview of methods

- Authors create a model based on random sampling effects and on the assumption that species and communities can fit into three classes of dominance (in relation to effect on ecosystem function). They use actual data from a variety of experimental BEF studies to test the model.

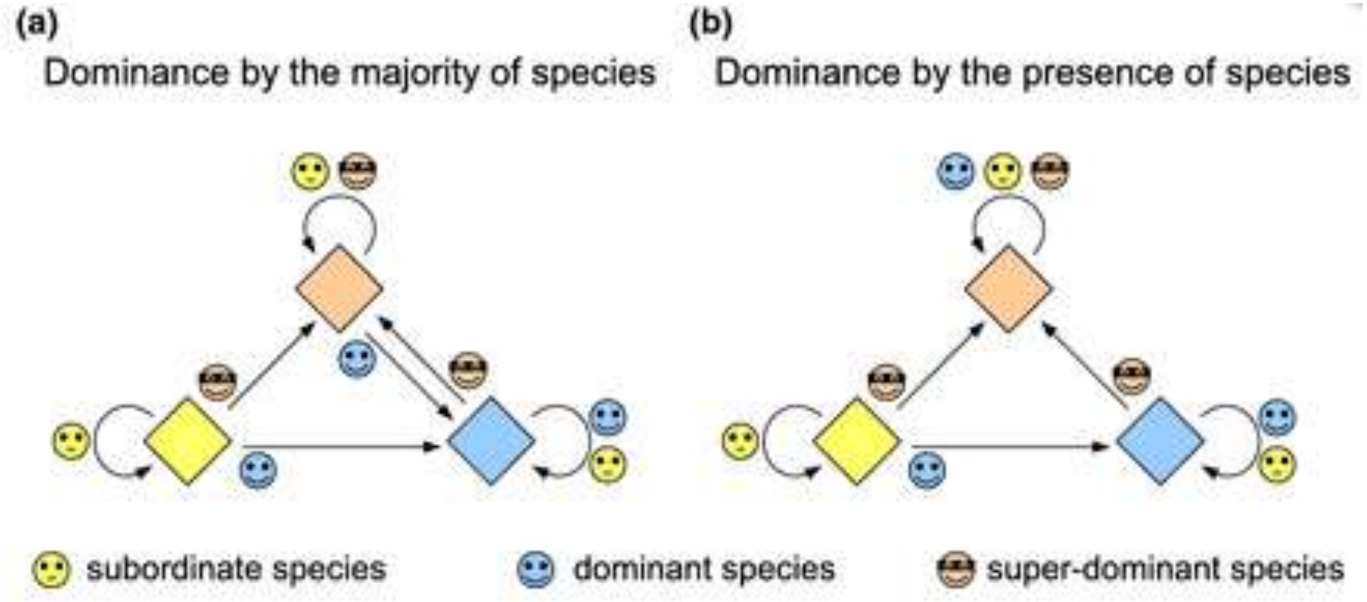
Community assembly effects shape the biodiversity-ecosystem functioning relationships
Jaillard, B., Rapaport, A., Harmand, J., Brauman, A., and Nunan, N. (2014)

Overview of methods

Used a three level dominance hierarchy of the effect of species on function:
- Subordinate – no direct effect on community function
- Dominant and superdominant – biologically the same, but superdominant>dominant

Obtained real data (experimental), then randomly sampled from each real dataset species pool, and got probability of obtaining each type of community, determined best fit model, and can infer the composition of species in the community (# s.d., sub., dom.)

Two dominance rules



Community assembly effects shape the biodiversity-ecosystem functioning relationships
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Key findings

The model fit all shapes of BEF curves! Linear increase, decrease, hump, u-shaped

“The model describes a real ‘assembly effect’ which owes only a bit to chance because it is mainly determined by the composition of the regional pool and the dominance rules that prevail in the communities.”

“The results suggest that the multi-faceted response of ecosystems to biodiversity may be nothing more than manifestations of random assembly effects and variation in species properties.”

Community assembly effects shape the biodiversity-ecosystem functioning relationships
Jaillard, B., Rapaport, A., Harmand, J., Brauman, A., and Nunan, N. (2014)

How this relates to the BEF debate

What current hypotheses do they support or refute?

In “sampling effect vs complimentarity” debate, they provide support for sampling effect, however also suggest that sampling effect can explain niche complimentarity and overyeilding.

Add a new dimension to the “key species vs multiple species” debate by adding third functional group, which is important aspect of the model.

Possible criticisms:

- The authors acknowledge that the model is simple, only 3 types of classes, minimal biological assumptions and also that it is static (only a snapshot) → Likely that niche complementarity will be overriding explanation further in time.

Alternative hypotheses to explain why biodiversity-ecosystem functioning relationships are concave-up in some natural ecosystems but concave-down in manipulative experiments.

Mora, C., Danovaro, R., & Loreau, M. (2014)

Research goals and questions

- What are some possible hypotheses to explain the difference found in the shape of the positive BEF curve between observational and experimental studies in the marine ecosystem?
- Is there theoretical support for the concave-up positive relationship found in observational studies?

→ Very different ecological implications

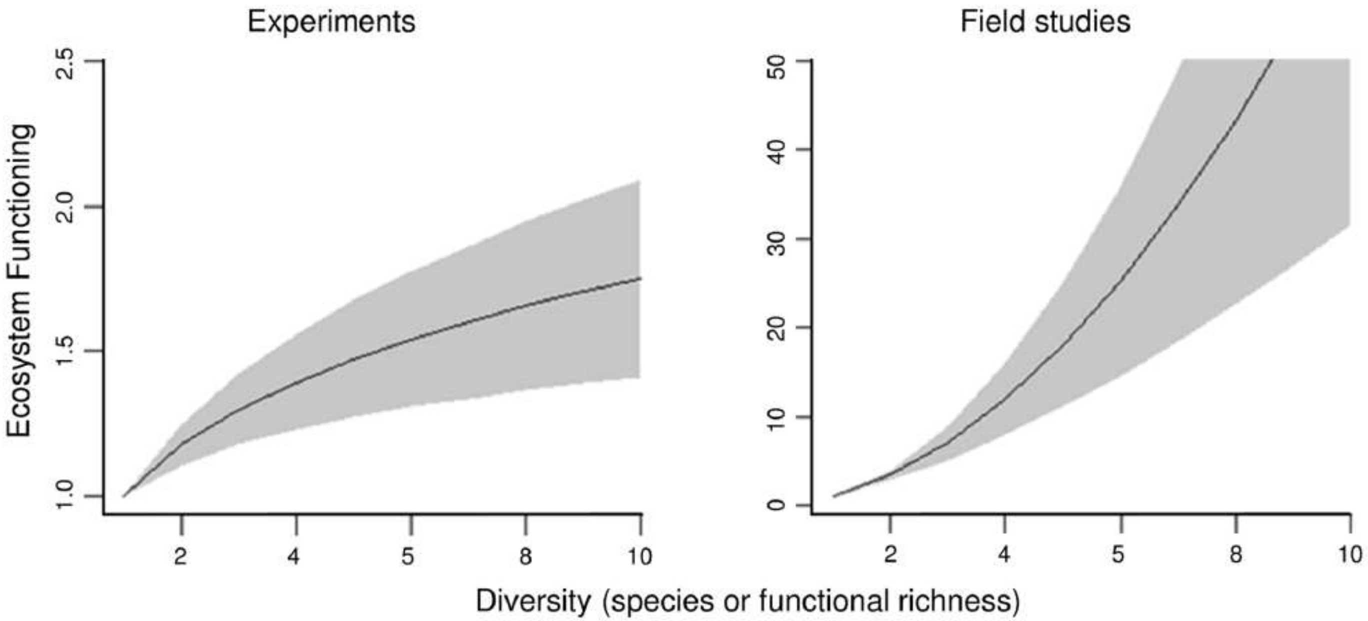


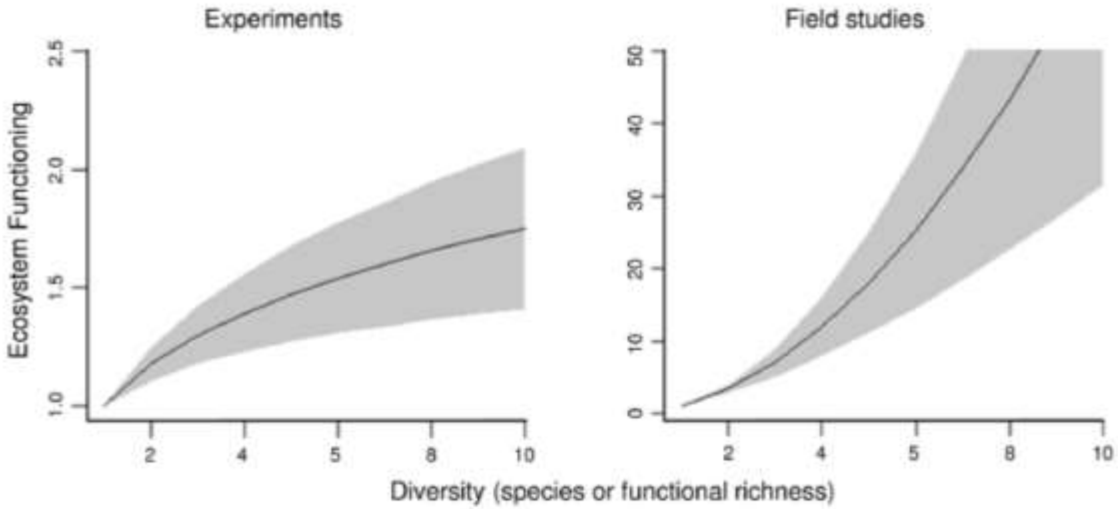
Figure 1 | Experimental (a) and natural (b) ecosystems relationships between biodiversity and ecosystem functioning. Plot a shows the 95% confidence limits of the log-log slopes yielded by 111 experiments analyzed[7]. Plot b show the range of slopes yielded by field studies on coral reef fishes and deep-sea nematodes (Table 1).

Is the BEF relationship concave-down (experimental studies) or concave-up (observational)

Not explained by confounding environmental variables

General methods

- Use models and equations to explain the mechanisms behind each hypothesis.
- The models are tested with data from previous observational and experimental studies.
- The data includes observational studies from four regions and three ocean basins, including two large ones for fish on coral reefs and nematodes in the deep sea (n=7), compared against a wide range of experimental studies (n=111). →Wide variety of data, considering limitations
- Explored three hypotheses to see whether functional groups, species interactions and patterns of succession may explain the different curves.



Mora, C., Danovaro, R., & Loreau, M. (2014)

Hypothesis 1:The use of functional richness in observational studies instead of species richness causes concave-up curve

Key findings
1. Functional richness in place of species richness – Get a steeper curve
2. The shape of the curve (concave-up vs concave-down) depends on the relationship between species and functional richness (e.g. relative number of species and functional groups)

Quick summary – Using functional richness instead of species richness *does* allow for the concave-up curve, whereas in previous methods it may not have. However, they get the *same concave-up relationship* even when using species richness – so this does not explain the true mechanism behind the concave-up curve

Mora, C., Danovaro, R., & Loreau, M. (2014)

Hypothesis 2: The increased biomass production that results from ecological interactions is more pronounced in observational systems due to complexity and longer establishment

In experimental studies, which are usually short time scales after establishment, the interactions are mostly driven by competition (tapering effect of adding species). Traditional population models and most experimental studies, had focused only on the changing **population size** leading to changes in interactions, and thus are not capable of obtaining the concave-up curve (unless the ecosystem dominated by mutualistic interactions)

In observational studies, a longer time scale of community adaptation and evolution can lead to specialization and increased function, and thus more **positive production efficiency effects**. Adding these effects, when positive, can give a concave-up curve.

→ Need a longer time scale

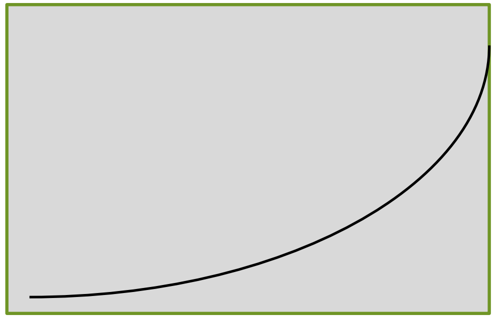
Mora, C., Danovaro, R., & Loreau, M. (2014)

Hypothesis 3: Based on the theory that communities are likely assembled in an order (low to high production efficiency), communities in early stages of succession may not account for increased efficiency with colonisation over time.

Theoretical studies have suggested ordered extinction of communities, where if least efficient go extinct first, then get concave-down curve, while if most efficient go extinct first get concave-up.

A similar theory, although with different mechanisms, is ordered colonisations, in which less efficient species (smaller, lower trophic levels) colonise ecosystems first, and over time get more complex (larger and more efficient species). Similarly, if order from least to most efficient colonizer, get concave-up relationship.

Communities in early stages of succession may not account for increased efficiency with colonisation over time.



Undetermined answer – yet to be studied!

Mora, C., Danovaro, R., & Loreau, M. (2014)

Alternative hypotheses to explain why biodiversity-ecosystem functioning relationships are concave-up in some natural ecosystems but concave-down in manipulative experiments.
Mora, C., Danovaro, R., & Loreau, M. (2014)

What are their key findings?

Key findings

- Found that all three hypotheses are possible, but that the difference is unlikely to be explained by biodiversity measure, but that it is more due to the short temporal span of experiments (insufficient time for full specialization and development, possibility of production efficiency outweighing negative competition effects)

What current hypotheses do they support or refute?

- Develop new hypotheses…
- IF hypotheses are correct, then shows evidence for niche complimentarity, role of succession, and temporal scale implications for experimental studies, and implies that conservation of all species is important for ecosystem function.

Plant Species Richness and Ecosystem Multifunctionality in Global Drylands

Maestre, F. T., Quero, J. L., Gotelli, N. J., Escudero, a., Ochoa, V., Delgado-Baquerizo, M., … Zaady, E. (2012)

Why this is a highly relevant paper…

- Study of natural ecosystems
- Global scale study (all continents except Antarctica)
- Drylands (few studies, 41% Earth's surface, supports 38% world's population)
- **Mutifunctionality** - The ability of an ecosystem to maintain multiple functions simultaneously
  - Previous two decades of BEF research have focused on one function, one measure biodiversity, and controlled small-scale experiments - but this is not necessarily how natural ecosystems work
  - Until several years ago, no papers on biodiversity-multifunctionality relationship, and still very few (<10?)
  - "…biodiversity is by no means the only, or even the primary, driver of ecosystem functioning, which is also influenced by other biotic and abiotic factors"

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Research goals and questions

- What is the relationship between biodiversity and multifunctionality of drylands at a global scale?
- What is the relative importance of biodiversity as a determinant of multifunctionality as compared to other variables?

Overview of methods

- Biodiversity = perennial vascular plant richness, “other variables” = climate, slope, elevation, soil texture, multifunctionality = “fourteen ecosystem functions related to the cycling and storage of carbon, nitrogen and phosphorus”
- Given the vast complexity of this question, required many sites that span a range of spatial variability (resource availability, abiotic variables, species richness, species composition).
- Surveyed 30m by 30m plots in 224 dryland locations, spanning a wide range of all the abiotic variables.

Overview of methods

- Calculated Z-scores for each measure of function separately, and then averaged them to get a measure of multifunctionality within the plot. This was done so that the measures are on a common scale of standard deviations from the mean (Z-scores).
- First, used two types of regression models, OLS and SAR (nonspatial and spatial), just to see if there is a relationship between species richness and multifunctionality or just function (C, P, N cycling).
- Second, they used a "multi-model inference approach based on information theory and OLS regression" to see how important species richness is, compared to abiotic variables (sand content, slope, elevation, four climatic component variables).

  Dependent variables = Ecosystem multifunctionality (average z-scores for each plot) and C, P, N function

  Independent variables = Seven abiotic variables plus species richness (Table headers)

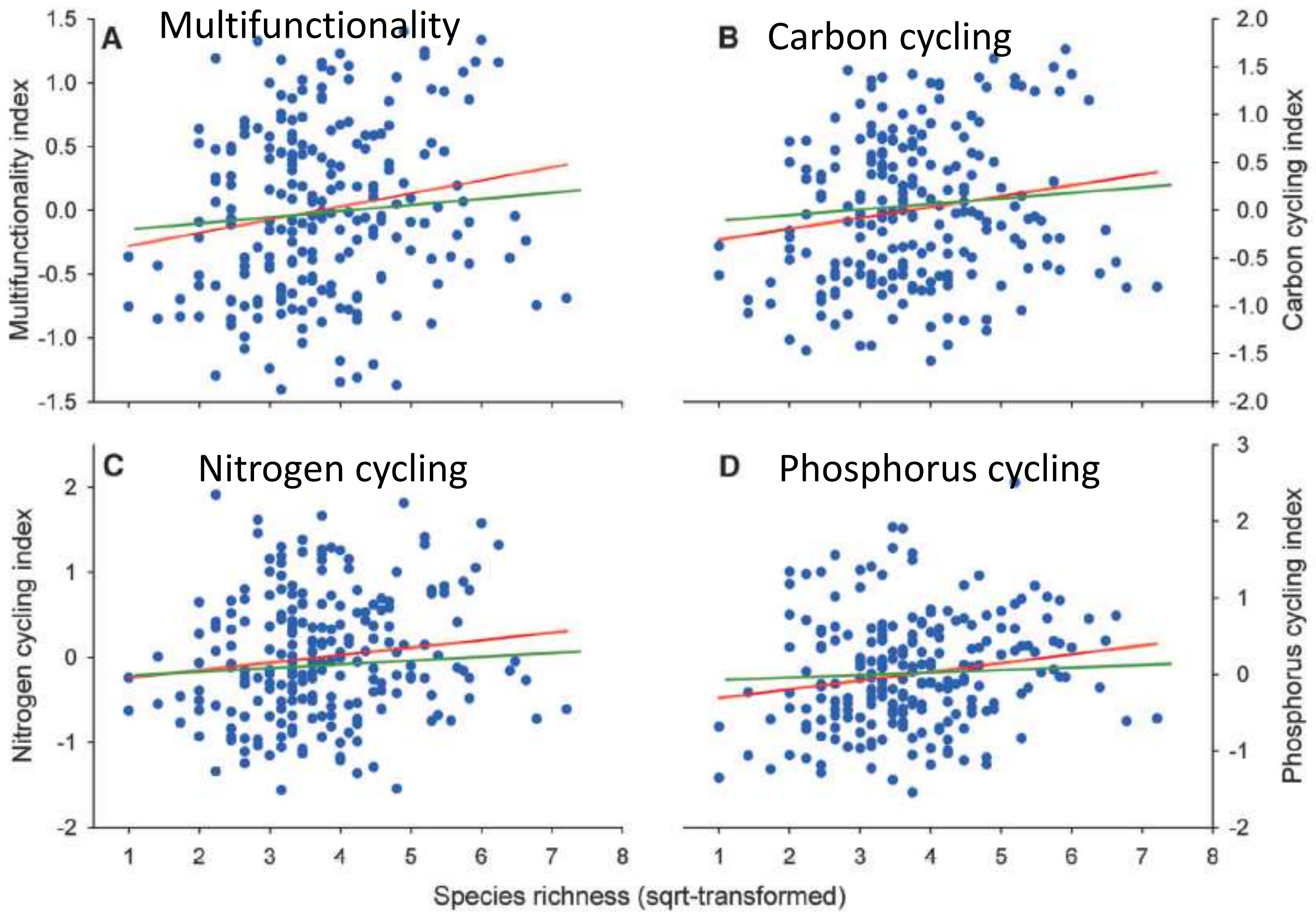
  255 possible combinations (models)

What are their key findings? Regression models

Despite all the “noise” in data from observational approach, still get a positive relationship between species richness and multifunctionality, as well as with individual functions with OLS model, and with multifunctionality and carbon cycling (A and B) in SAR model.

Although R^2 values are fairly low (<0.05; do not explain very much of the variability in the relationship), the p-values are <0.05 and thus significant (for all but SAR in C and D).

Red line = OLS
Green line = SAR



What are their key findings? Multi-model inference

Found that the two best models explain >55% of the variability found in multifunctionality

Both include species richness – and if remove this variable, then the model loses much of its fit.

Two most important predictors in models were mean temperature and sand content (similar importance to species richness); both negatively related to multifunctionality

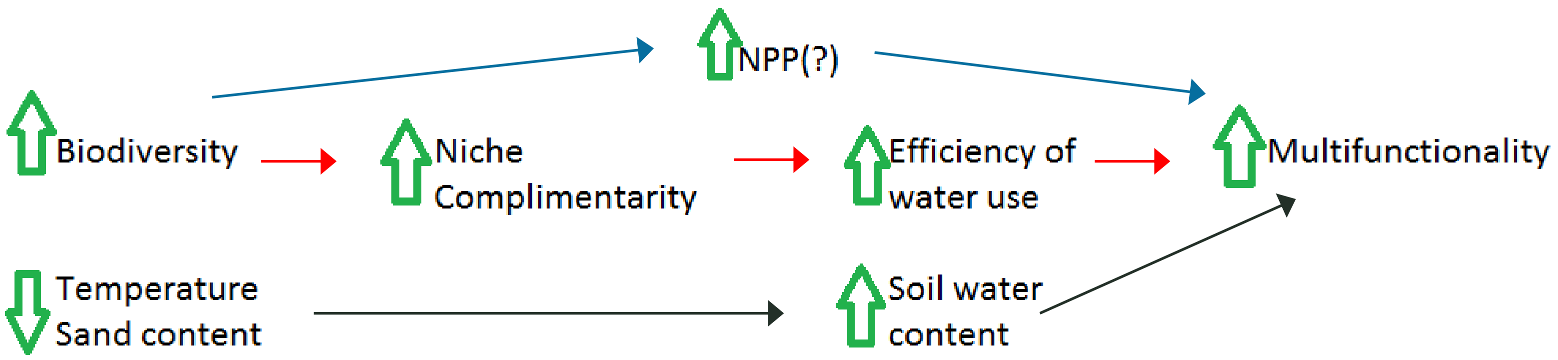
Species richness NOT the single most important predictor variable

Even with best models, some unexplained variation (maybe due to history land use, keystone/invasive species, soil fauna)

Species richness	Abiotic		Climatic				Geographic			R^2	AIC_c	ΔAIC_c	w_i
	SL	SA	C1	C2	C3	C4	LA	LO	EL				
■	■	■	■		■	■	■	■	■	0.564	282.750	0	0.217
■	■	■	■			■	■	■	■	0.559	283.226	0.475	0.171
■	■	■				■	■	■	■	0.554	283.595	0.845	0.143
■	■	■	■	■			■	■	■	0.558	283.862	1.111	0.125
■	■	■	■	■	■	■	■	■	■	0.565	284.502	1.751	0.091
■	■	■	■		■		■	■	■	0.556	284.637	1.887	0.085
■	■	■		■	■	■	■	■	■	0.561	284.677	1.927	0.083
■	■	■	■	■		■	■	■	■	0.560	285.035	2.285	0.069

Independent variables (shaded=included in model)

R2 = How much variation does it detect
AIC = lower value means more likely to be correct
ΔAIC = Difference between each model and the best model



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How does this fit into the debate?

- Quantitatively show that biodiversity is not the main or only driver of ecosystem function – Sand content and temperature were as important in this ecosystem.
- Show that all the previous studies on BEF may "scale up" to BEMF
- Suggest support for the niche complementarity theory. In relation to drylands this means that more plant species means more efficient C, N, P cycling, and a more efficient use of water conditions.

Before we get into the discussion…

…A quick summary

- There is still debate over the mechanisms behind the BEF curves. These papers represent new developments in the field, especially in relation to observational approaches.
- Despite all the biological and environmental reasons to assume a more complex mechanism, Jaillard et al 2014 suggest that all the curves, whether experimental or observational, multiple ecosystems, can be explained by the sampling effect and the assumption of dominance hierarchies.
- Although the general BEF relationship is positive, many variations in responses and curve types. Interesting that get a different relationship between observational and experimental in marine systems, and need new ways to explain it (Mora et al. 2014)
- The benefit of working with observational data is the ability to sample a range of environmental variables, and to consider all aspects of ecosystem function, including multifunctionality and other variables besides biodiversity which affect function.

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