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Introduction: The ecological and social implications of changing biodiversity. An overview of a decade of biodiversity and ecosystem functioning research

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Biodiversity and ecosystem functioning

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Biodiversity and Ecosystem Functioning

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Outline

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Forecasts of ongoing biodiversity loss prompted ecologists in the early 1990s to question whether this loss of species could have a negative impact on the functioning of ecosystems. Ecosystem functioning is an umbrella term for the processes operating in an ecosystem, that is the biogeochemical flows of energy and matter within and between ecosystems (e.g. primary production and nutrient cycling). This first general phase of research on this topic addressed this question by assembling model communities of varying diversity to measure the effects on ecosystem processes. The results of the meta-analyses of this first wave of studies show that biodiversity generally has a positive but saturating effect on ecosystem processes which is remarkably consistent across trophic groups and ecosystem types. These relationships are driven by a combination of complementarity and selection effects with complementarity effects nearly twice as strong as selection effects overall. However, diverse communities rarely function

significantly better than the best single species, at least in the short term. In the longer term biodiversity can provide an insurance value similar to the risk spreading benefits of diverse portfolios of financial investments. The effects of biodiversity on ecosystem functioning may have been under-estimated by the first phase of research due to the short duration of many studies and due to the focus on single ecosystem processes in isolation rather than considering all important ecosystem functions simultaneously. The next phase of research will in part focus on whether the benefits of biodiversity seen in experiments translate to real-world settings.

Glossary

- Biodiversity: A contraction of biological diversity that encompasses all biological variation from the level of genes, through populations, species and functional groups (and sometimes higher levels such as landscape units).
- Ecosystem functioning: An umbrella term for the processes operating in an ecosystem.
- Ecosystem processes: The biogeochemical flows of energy and matter within and between ecosystems, e.g. primary production and nutrient cycling.
- Ecosystem service: An ecosystem process or property that is beneficial for human beings, e.g. the provision of foods and materials or sequestration of carbon dioxide.
- Selection effects: The influence that species have on ecosystem functioning simply due to their species-specific traits and their relative abundance in a community (positive selection effects occur when species with higher-than-average monoculture performance dominate communities).
- Complementarity effect: The influence that combinations of species have on ecosystem functioning as a consequence of their interactions (e.g. resource partitioning; facilitation, reduced natural enemy impacts in diverse communities).

Background and History

Darwin, in the *Origin of Species*, initially proposed that changes in biodiversity could affect ecosystem functioning if niche space is more fully occupied in more diverse communities than depauperate ones. We use ecosystem functioning as an umbrella term to embrace all the bio-geo-chemical processes that operate within ecosystems, primary production for example. This early work was apparently forgotten until the early 1990s, but the same reasoning was around in the mid-twentieth century where it was proposed that more diverse mixtures of fish species should lead to greater productivity: "Presumably fish production will increase as the number of niches increases…[and]…probably the proportion of occupied niches increases as the number of species of fishes increases". Indeed, both of these early studies even presented data in support of this relationship (Figure 1).

In the early 1990s, general concern about the impact of anthropogenic biodiversity was voiced at the Rio Earth Summit in 1992. At this the Convention on Biological Diversity (CBD) was launched with the signatures of 150 heads of government. This international treaty designed to promote sustainable development and the protection of biodiversity was evidence of political acceptance that anthropogenic biodiversity loss may have serious detrimental effects on humankind. Concerns highlighted at Rio and in the Convention also led to renewed scientific interest and a concerted effort by ecologists to understand the effects of changes in biodiversity on ecosystem functioning and the likely significance of such changes for humankind. More than a decade's worth of research has now been published, accompanied by a debate which focused in large part on the mechanisms underlying the relationship between biodiversity and functioning. Synthesis of the first decade of results through meta-analysis is helping to reveal both pattern and mechanism.

Biodiversity and ecosystem functioning relationships

The main approach that has been used to investigate the relationship between biodiversity and ecosystem functioning is the direct manipulation of biodiversity by the assembly of synthesized model communities in the laboratory or field. An alternative approach is to remove species from natural communities. A third non-manipulative approach is to infer the relationship between biodiversity and ecosystem functioning by seeing how they are correlated across habitats. All three approaches have strengths and weaknesses. In this piece we focus on the assembly of model communities of varying diversity.

Meta-analysis of the first decade's research clearly shows a positive relationship between biodiversity and ecosystem functioning (e.g. Figure 2); a pattern which is remarkably consistent across trophic groups (producers, herbivores, detrivores and predators) and present in both terrestrial and marine ecosystems. However, the relationship between biodiversity and ecosystem functioning is generally saturating suggesting that the effect of random biodiversity loss on ecosystem functioning will be initially weak but accelerating.

The first phase of research on biodiversity and ecosystem functioning was focused on identifying general patterns (whether biodiversity change can affect ecosystem functioning or not) and species were therefore removed at random to generate experimental diversity gradients. Another key result of these studies is that there is considerable variation among species or species assemblages in their impact on functioning. This suggests that the actual effect of biodiversity loss on ecosystem functioning seen in real-world situations will depend strongly on which species are lost. Moving from random to more realistic real-world situations is a key goal for the next phase or research.

Mechanisms

The early studies mentioned in the introductory background section only identify one way in which biodiversity changes can affect ecosystem functioning, namely by affecting the degree of species complementarity (basically by affecting the number of under-utilized or vacant niches). That is, more diverse communities utilise a greater proportion of available niche space. However, as mentioned above, biodiversity changes can also affect ecosystem functioning by the simple presence or loss of particular species with strong intrinsic effects on ecosystem processes (so-called sampling or selection effects); more diverse communities are more likely to contain those species or assemblages which strongly affect functioning. There has been widespread debate over the last decade about whether the positive relationships reviewed above were explained by complementarity or selection effects.

Additive partitioning methods are one approach which allows separation of the overall net effect of biodiversity on ecosystem functioning into complementarity effects that arise from species interactions and selection effects that are species-specific. Meta-analysis reveals that almost all studies are driven by a combination of these effects but that overall complementarity effects were nearly twice as strong as selection effects (Figure 2). However, even though complementarity effects have a greater effect than selection effects they are not strong enough to cause mixtures to do significantly better than monocultures in most cases (Figure 3). In summary, while the relationship between biodiversity and ecosystem functioning is positive, and complementarity effects contribute approximately twice as much as selection effects in generating these relationships, diverse communities do not generally perform better than the best individual species. However, this result is influenced by the short duration of many of the experiments performed to date since the relationship between biodiversity and ecosystem functioning grows stronger over time (Figure 3) due to increasing complementarity. Nevertheless, it appears that diverse communities are rarely able to do substantially better than a monoculture of the best-performing species that they contain. This appears to be due in part to the fact that communities are often not dominated by the most productive species but by species with a lower performance. In fact, in over 40% of the reviewed studies communities were dominated by a species with a lower-than-average monoculture biomass leading to a negative selection effect with a negative influence on the performance of the ecosystem as a whole. An important implication of this meta-analysis for future research is that studies must be longer-term if they are to reveal the full effects of biodiversity on ecosystem functioning; experiments to date have, if anything, underestimated the effects of random loss of species on ecosystem functioning.

Multi-trophic systems

Alongside the work on biodiversity and ecosystem functioning there has also been significant interest in the functional importance of biodiversity in the context of multi-trophic interactions. Here the focus has been more on the impact of diversity at one trophic level on the population density at the trophic level below. Most commonly this has involved studies of predator species diversity and impact on prey populations. Recently, attempts have been made to link the considerable bodies of work on biodiversity and ecosystem functioning and predator–prey interactions.

One striking difference between the predator–prey and biodiversity-ecosystem functioning perspectives is the relative importance ascribed to interspecific interactions among target species. Interactions among species are not explicitly considered in biodiversity-ecosystem functioning studies, whereas predator–prey theory has a long history of investigating direct and indirect interactions among predator species and how these affect the population size of the prey species. For example, intra-guild predation where one predatory species preys on another is a common interaction in nature which has the capacity to reduce the joint impact of the predator species on the original prey species. The opposite outcome can occur when facilitative interactions occur among predator species. One commonly reported example of this is when the avoidance behaviour of the prey to one predator makes them more susceptible to predation by a second. Aphids for example commonly drop from the plant when approached by a foliar predator, but this can leave them susceptible to ground foraging predators so that the functioning of ground and foliar predators together is greater than the sum of the functioning of each alone.

Facilitative and negative interactions among constituent species can occur in basal trophic levels, such as primary producers or detritivores. Plants are known to take part in allelopathic interactions in which they impact each other negatively via the production of toxic chemicals. There is also strong evidence that plant species may facilitate each other by enriching the soil by nitrogen fixation or by moderating harsh abiotic environments for example. A key question is whether the predictive power of biodiversity–ecosystem functioning theory would be improved by the incorporation of such species interactions. Generally, meta-analyses of biodiversity–ecosystem functioning reveal consistent positive effects of diversity on functioning, but results from terrestrial predator–prey systems are more equivocal, with almost half of the studies reporting negative or neutral effects of increasing species diversity on prey suppression. Where significant species interactions occur, it may be useful to think of observed relationships between biodiversity and ecosystem functioning as the net effect of co-occurring positive mechanisms (resource-use differentiation and facilitation) and negative mechanisms (intraguild predation, interference). Experimental evidence from predator–prey systems suggests that at least in some cases negative interactions among species outweigh the positive mechanisms causing reduced functionality in more diverse communities.

Diversity and stability

Ecological stability refers commonly to one of three general properties of ecosystems: the temporal variation in a property of the ecosystem (e.g. primary production) or the response (resistance) or recovery (resilience) of these properties following perturbation. One possible value of biodiversity to humans is its potential to increase stability by buffering ecosystem processes like production against environmental variation and in making them more resistant and resilient to perturbations. This insurance value of biodiversity has most often been considered in the context of fluctuations over time, where it has been likened to the risk-spreading benefits of diverse portfolios of investments in financial markets, but could also apply to spatial environmental variation. For this insurance effect to occur requires only that fluctuations in the abundances of a guild of species are not perfectly synchronised, because under perfect synchrony an entire guild or trophic level would effectively behave as one species. When species responses are not perfectly positively correlated changes in some species can be compensated by others and the averaging of their asynchronous fluctuations smoothes the collective productivity of the whole community (Figure 4).

One potentially confusing or counter-intuitive aspect of the insurance hypothesis is that diversity has a stabilizing effect on aggregate community or ecosystem properties (like primary productivity) at the same time as the fluctuations of the constituent species may be destabilized due to interactions with greater numbers of species (although destabilization is not inevitable). The key thing to understand is that it is the lack of perfect synchrony of individual species fluctuations that leads to the stabilizing effect of diversity on ecosystem processes. This asynchrony through independent or compensatory species responses can be interpreted as a form of temporal niche differentiation between species.

A recent review of the diversity-stability literature emphasizes its breadth and complexity due to the many different types of stability and the range of different variables that stability measures can be calculated for (e.g. stability of population abundance *vs* total community biomass as introduced above). For experiments where diversity was directly manipulated there are reports of two positive effects of plant species diversity on the stability of biomass production and three positive effects of microbial diversity on the stability of biomass or carbon dioxide production. There are no reports of negative or neutral effects of diversity on temporal stability of ecosystem processes from grassland experiments, but one negative effect of increased multitrophic diversity on the temporal stability of biomass production in seagrass beds, and one neutral and one negative effect of microbial diversity on the stability of microbial biomass production. Observational studies have also looked at stabilising effects of biodiversity on ecosystem processes producing five positive effects of plant diversity on temporal stability and one neutral effect. In summary, evidence from both natural and experimental systems of plants and microbes suggests that insurance effects of biodiversity on temporal stability may be relatively widespread.

Ecosystem multifunctionality

As summarised above, meta-analysis of the results of the first generation of experimental research on biodiversity and ecosystem functioning has revealed that individual ecosystem processes generally show a positive but saturating relationship with increasing diversity. The saturating relationship suggests that some species are redundant with respect to a single function. However, nearly all studies to date have been short-term and only address the effect of biodiversity on ecosystem functioning at a given point in time and under a relatively narrow set of conditions. Much of the other work reviewed above suggests that biodiversity can sometimes have an insurance value by buffering ecosystem-level processes in a way analogous to that in which diverse investment portfolios spread financial risk and improve average performance in the longer term. Nevertheless, all of the research to date considers ecosystem processes examined individually, despite the fact that most ecosystems are managed or valued for several ecosystem services or processes: so-called ecosystem multifunctionality. If it is the case that a single species, or group of species, controls ecosystem functioning, then the remaining species are functionally redundant. Although it seems unlikely that a single species could control all ecosystem processes, it is possible that a single group of species may. However, if there is appreciable lack of overlap in the groups of species that influence different ecosystem processes, then higher levels of biodiversity will be required to maintain overall ecosystem functioning than indicated by analyses focusing on individual ecosystem processes in isolation. Only one study of ecosystem multifunctionality exists to date, but this analysis of seven ecosystem processes measured in a network of grassland biodiversity experiments supports the ecosystem multifunctionality hypothesis: the greater the number of ecosystem processes included in the analysis the greater the number of species found to affect overall functioning (Figure 6).

Ecosystem service provision

The Millennium Ecosystem Assessment defines ecosystem services as the benefits provided by ecosystems to humans. Ecosystem services include the provision of materials (food, genetic resources, water etc.), cultural and psycho-spiritual well-being, supporting services (nutrient cycling, soil formation etc) and regulating services (pest and disease control, pollination, erosion control, climate regulation etc.). The ecosystem processes that we have covered in this chapter are closely aligned with both supporting and regulating services. The evidence from the meta-analyses discussed above suggests that, in general, we expect the provision of such services to be compromised due to anthropogenic declines in biodiversity. Direct evidence of impacts of biodiversity loss on ecosystem functioning is accumulating. For example, increased diversity of wild host species has been shown to lead to dilution effects that reduce the probability of human infection by zoonotic diseases. Loss of biodiversity is also implicated in causing reduced carbon sequestration and therefore a net release of carbon into the atmosphere where it contributes to global climate change. However, just as in experimental studies of biodiversity and ecosystem functioning, effects will depend strongly on which species are lost. The provision of ecosystem services has been of particular concern in agricultural systems both because of their spatial extent (they are estimated to cover a quarter of the terrestrial earth surface, rising to almost three-quarters in some developed regions) and the severe losses of biodiversity they endure. Intensification of production in many parts of the globe has resulted in extreme declines in biodiversity in agricultural systems, both in terms of homogenisation of production systems (simplified landscapes and fewer breeds/varieties grown) and declines in the wild species inhabiting agricultural ecosystems. Such simplification requires that compromised services such as pest regulation and maintenance of soil fertility and condition are replaced by synthetic pesticides and fertilisers, which are inherently unsustainable due to their reliance on externally derived energy and materials, and their negative impacts on non-target taxa, including humans.

Enhancement and utilisation of ecosystem services in agriculture is seen as one route to increased sustainability of food production.

The next phase of research

The first phase of research on biodiversity and ecosystem functioning primarily used experimental communities to investigate the effects of random species loss. Recent meta-analysis suggests that there generally are effects of species loss on ecosystem functioning in these experiments and that these effects are generally positive but saturating. Both complementarity and selection effects play a role in generating these relationships with the effects of complementarity being nearly twice as strong as selection. Nevertheless, diverse mixtures rarely perform better than the best-performing species, at least in the short term (complementarity effects grow stronger over time in these studies).

A key goal for the next phase of research is a move away from artificial experimental systems towards more realistic settings and to see if the biodiversity effects seen in the experiments translate to real-world situations. This will also necessitate a move away from the random loss of species used in the first phase of research towards more realistic scenarios of species loss and the incorporation of multiple trophic levels. The move from experimental to real-world settings will also require a move to larger field-scale study systems and, as suggested by the recent meta-analyses, to longer-term research. The first phase of research reviewed here has demonstrated the potential for biodiversity to have positive effects on ecosystem functioning. The question now is whether these experimental results will translate into positive effects of biodiversity on the provision of ecosystem services in the real world. The value of ecosystem services to humans is enormous [cross reference?] and it is now critical to find out what role biodiversity plays in the provision of these services to human societies.

Further reading

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Legends

Figure 1 Early evidence for a link between biodiversity and ecosystem functioning from (top panel) an early nineteenth century large-scale experimental garden at Woburn Abbey, U.K. mentioned by Darwin in *The Origin* (after Hector & Hooper 2002), and, (lower panel) “Relation between standing crops and numbers of species of fish present in Midwestern reservoirs” (after Carlander 1955).

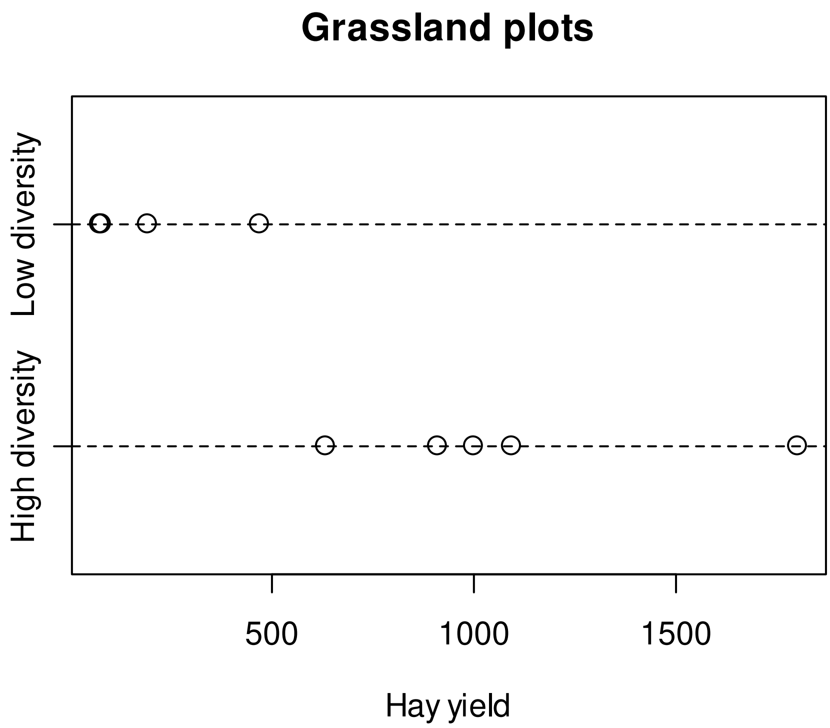
Figure 2 Effects of plant species richness on the production of above-ground plant biomass for 11 plant biodiversity experiments. Lines are linear regression slopes as a function of the number of plant species ($\log_2$ scale) for the eight BIODEPTH project experiments (black lines; see Hector et al. 1999) the Cedar Creek biodiversity experiment (dashed line; see Tilman et al. 2001) the Jena biodiversity experiment (dotted line; Roscher et al. 2005) and Van Ruijven & Berendse (2005; dotted-and-dashed line).

Figure 3 Meta-analysis results (Cardinale et al. 2007) for (top left) overyielding, (top right) transgressive overyielding, (lower left) complementarity effects and, (lower right) selection effects. The data for the upper and lower panels are for different (but overlapping) sets of studies. Note the different *y* axis scales in the two upper panels. Tukey box and whisker plots to the right of each scatter plot summarize the variation averaged over time (notches provide an approximate 95% interval for the medians).

Figure 4 Asynchronous population fluctuations buffer total community biomass. In this hypothetical example the total biomass of the three-species community (d) is less variable than the two-species community (b) due to the asynchrony of individual species biomasses (a and c).

Figure 5 Diversity increases stability (S) of ecosystem primary production (μ = mean and σ = standard deviation of biomass through time; reproduced from van Ruijven & Berendse 2007).

Figure 6 Positive relationship between the range of ecosystem processes considered and the number of species that affect one or more aspect of ecosystem functioning. The points (jittered for clarity) show numbers of species required for all possible combinations of ecosystem processes. Lines are average predictions based on the mean number of species required for a single process and the average overlap in the sets of species required for each pair of processes (after Hector & Bagchi 2007).


Grassland plots
Low diversity
High diversity
500
1000
1500
Hay yield

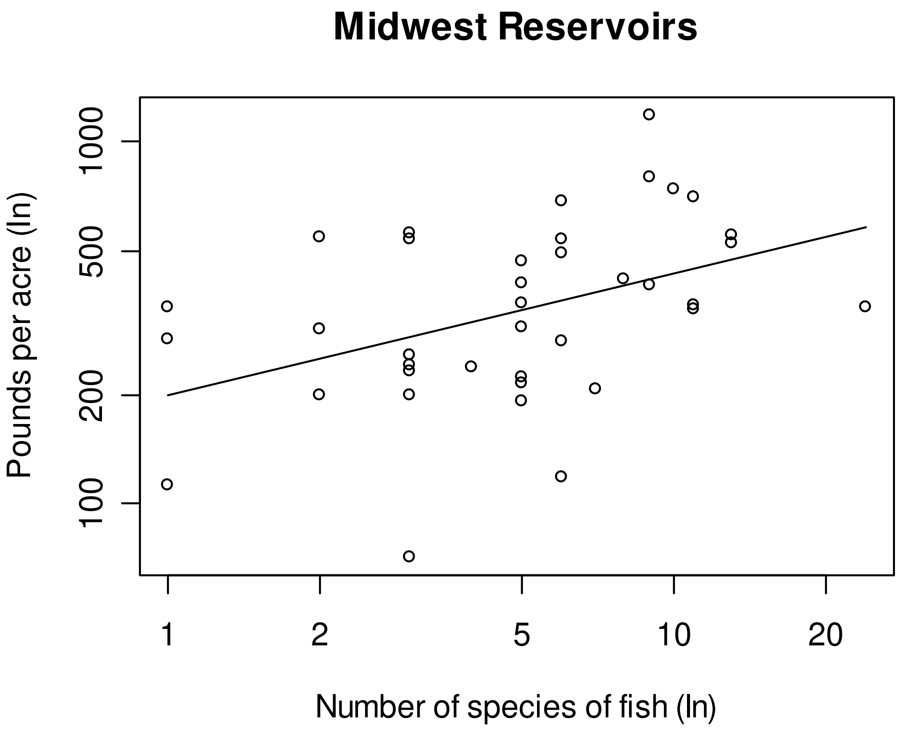

Midwest Reservoirs
Pounds per acre (ln)
1000
500
200
100
1
2
5
10
20
Number of species of fish (ln)

Figure 1

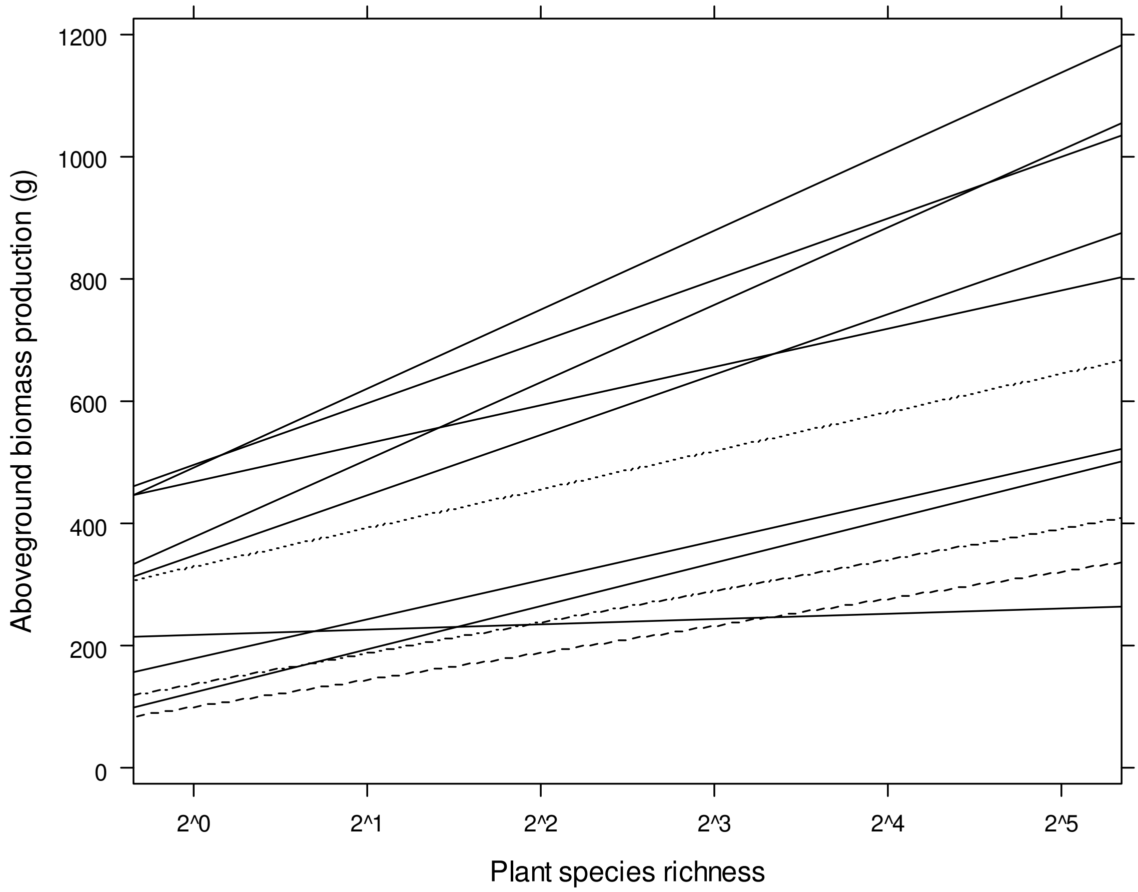

1200
1000
800
600
400
200
0
Aboveground biomass production (g)
2^0
2^1
2^2
2^3
2^4
2^5
Plant species richness

Figure 2

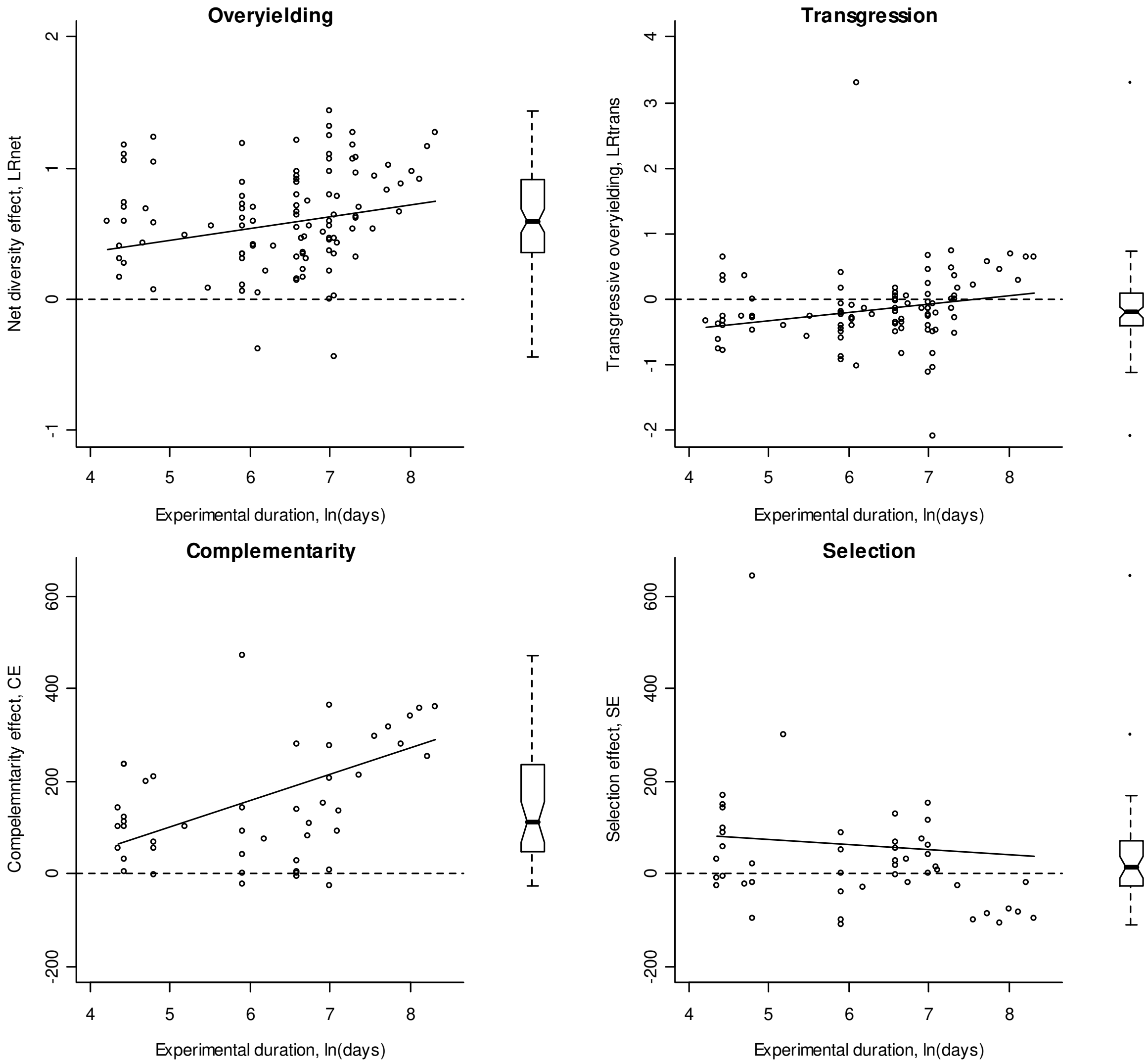

Overyielding
Net diversity effect, LRnet
Experimental duration, ln(days)
Transgression
Transgressive overyielding, LRtrans
Experimental duration, ln(days)
Complementarity
Compelemntarity effect, CE
Experimental duration, ln(days)
Selection
Selection effect, SE
Experimental duration, ln(days)

Figure 3

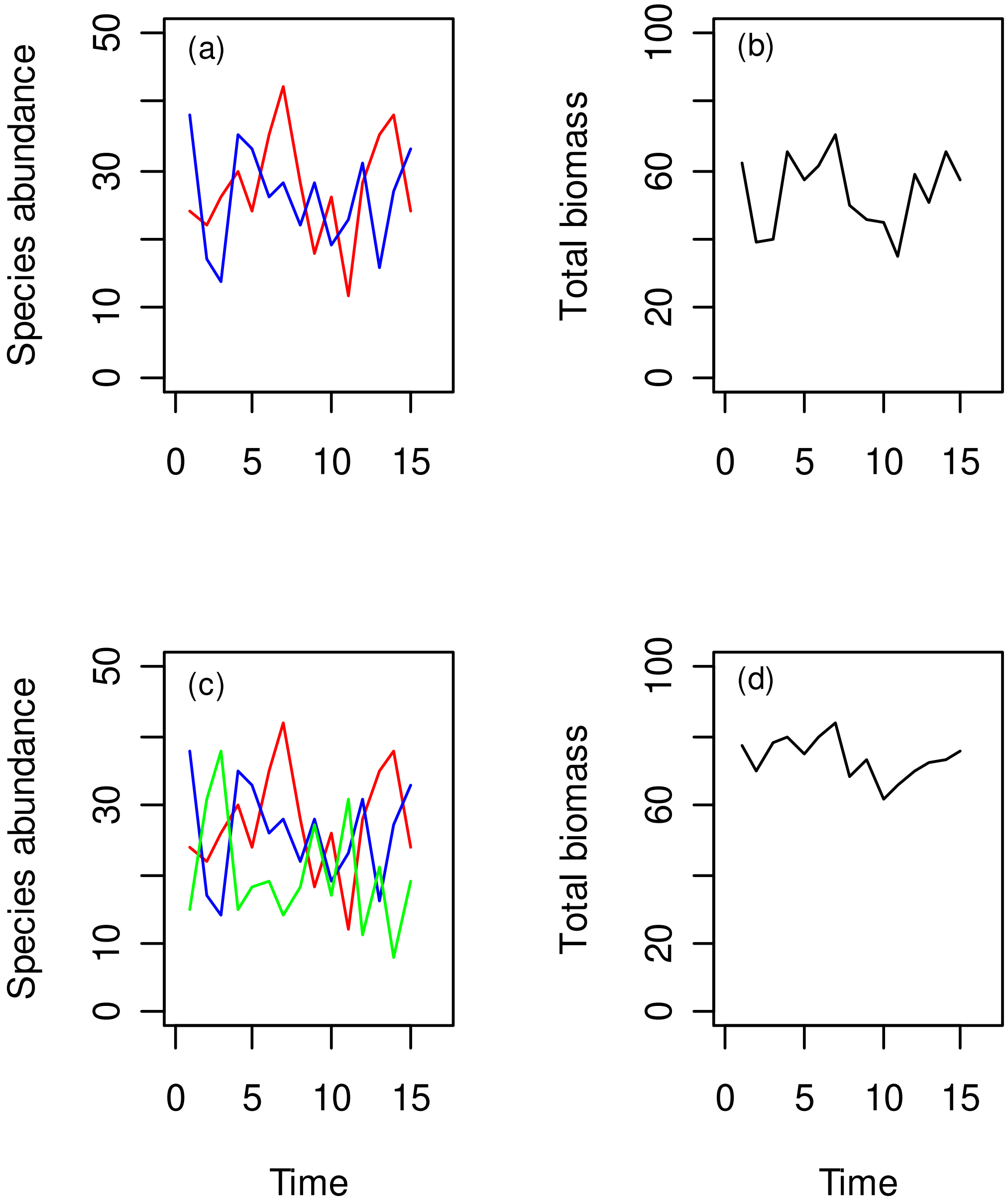
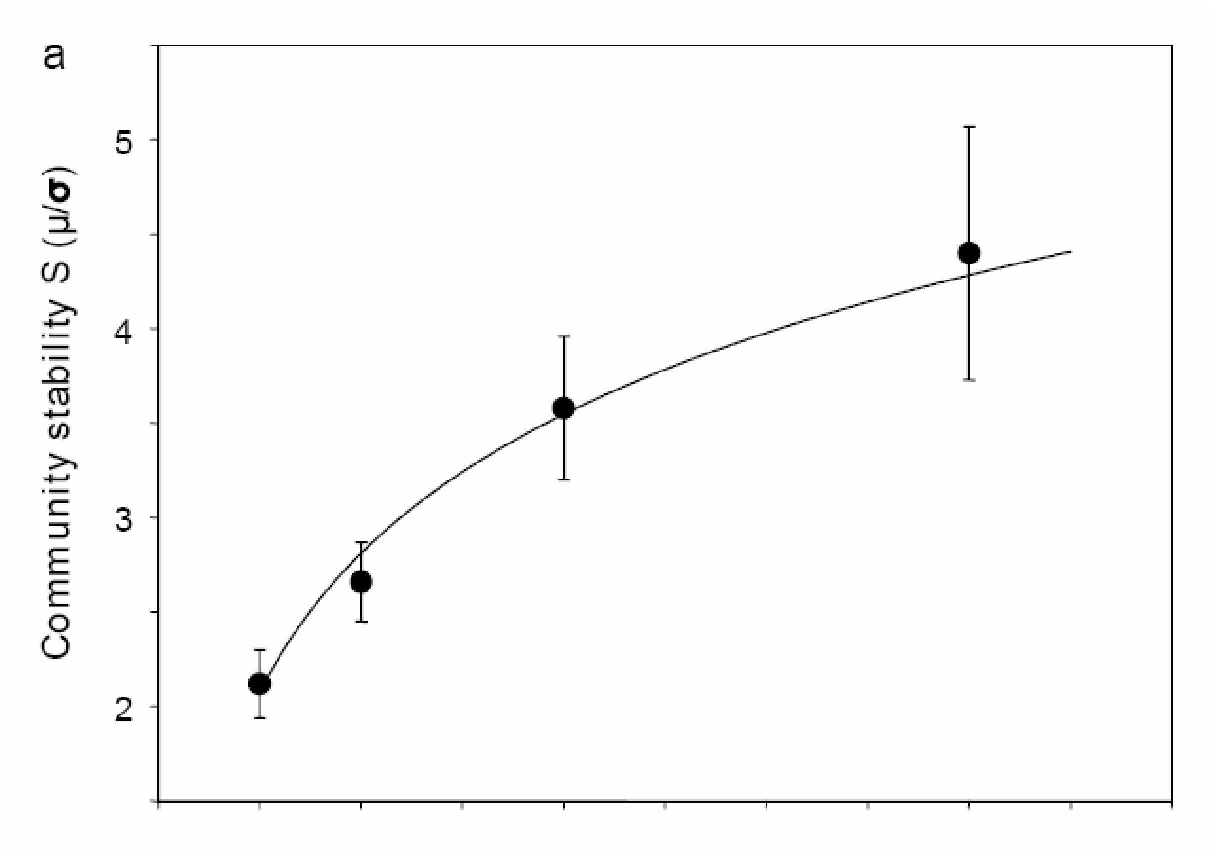

(a)
(b)
(c)
(d)
Species abundance
Total biomass
0
10
30
50
0
20
60
100
0
5
10
15
Time

Figure 4



Species richness

Figure 5

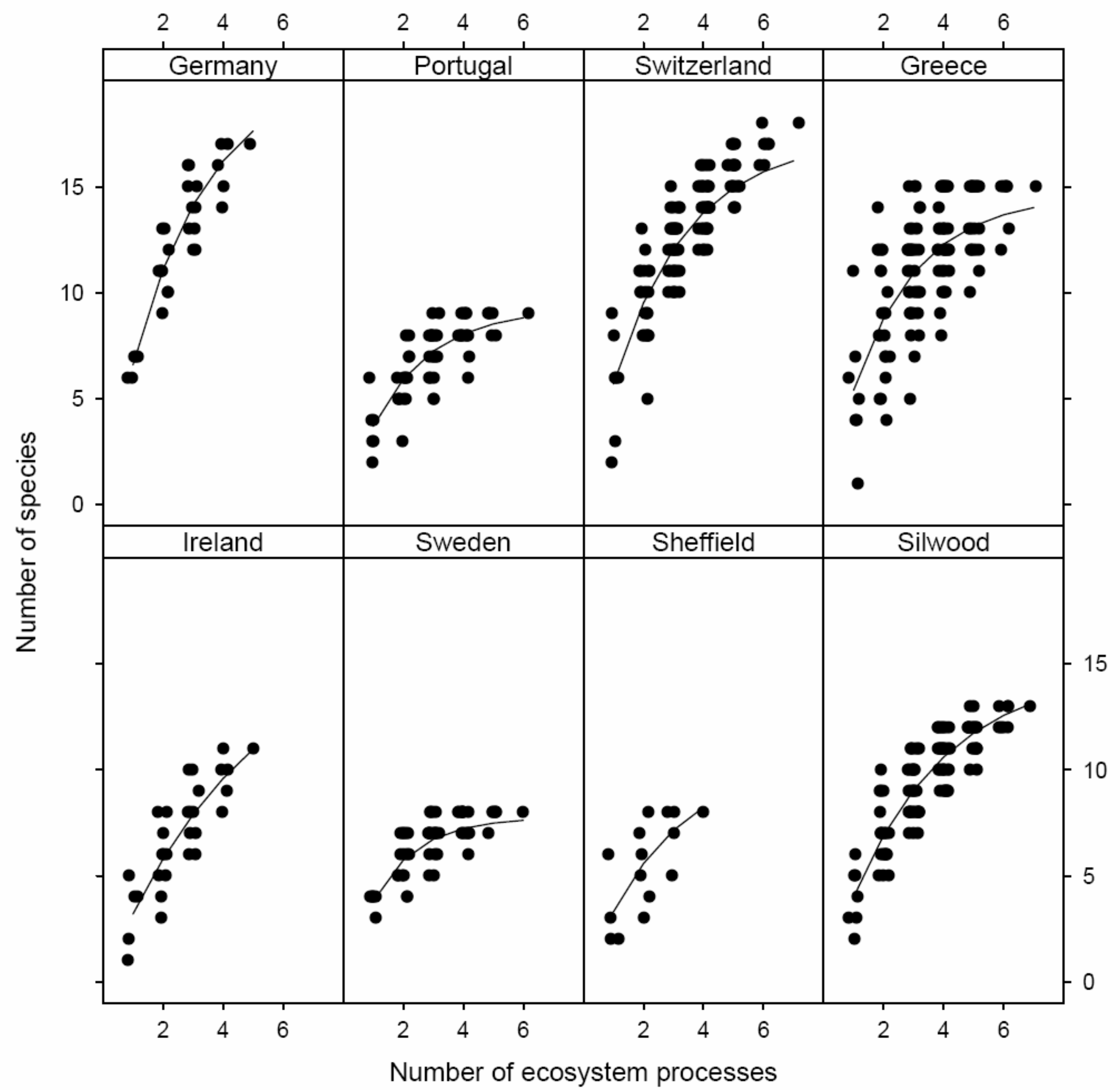

Germany
Portugal
Switzerland
Greece
Ireland
Sweden
Sheffield
Silwood
Number of species
Number of ecosystem processes
2
4
6
0
5
10
15

Figure 6