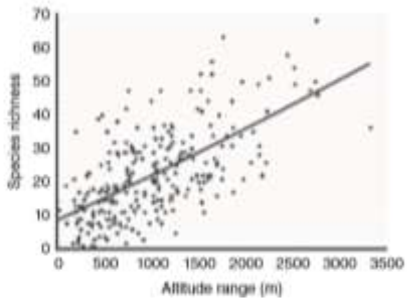
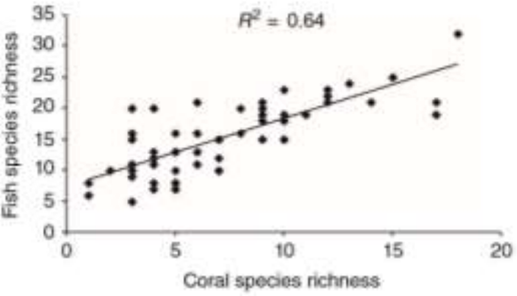
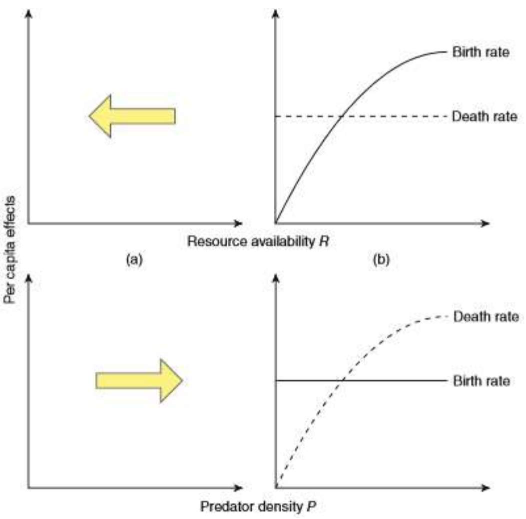
- Diversity gives rise to more diversity. Heterogeneity in space, time, abiotic and biotic environments creates diversity
- An example of special abiotic heterogeneity is fern's diversity as the altitude increases





- An example of special biotic heterogeneity is fish SR increasing with coral species richness
- In twig nesting generalist ants, the number of ant species nesting increase with the number of twigs in the sample bags, despite not being specialists
- In daphnia their environment has a high temporal heterogeneity, and their fitness varies accordingly. The persist in bad times so long as they have good years occasionally which buffer the population.
- Intermediate disturbance hypothesis – low and competitors dominate, high and ruderals (weedy) dominate, medium and a mixture survives
- Bristlecone pines might be the oldest organisms on earth and have very low diversity forests - because there is very low disturbance
- Top down control is a density dependant stabilising mechanism ((eg herbivory, disease, predation etc), including disturbance. Stabilises by having a heavier cost on common organisms (search image etc) and having less impact on rare individuals
- Janzen-Connell effects – distance dependent top down effects which promotes diversity. Seeds don't fall far from fruit trees, but the adults end up spread out. Animals disperse seeds. Seedlings directly below parents have a much worse survival – there is a soil borne pathogen present near to roots of adult trees which kills seedlings (restricted range).
- Herbivores can also be restricted range and control distribution

Summary: SAR is a general law. Local geography, environment, resources, isolation and regional SR all important. Congruence (of indicator taxa) is uncommon and unreliable. SR increases with the number of limiting resources, but the total amount of resources predicts little. Diversity begets diversity, and top-down control stabilises co-existence.

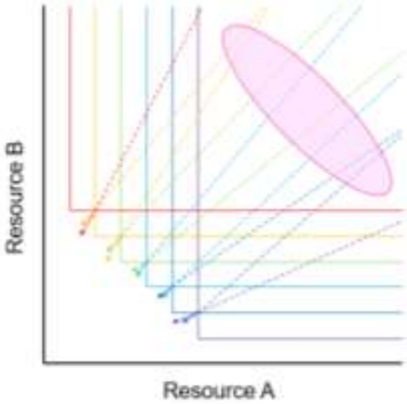


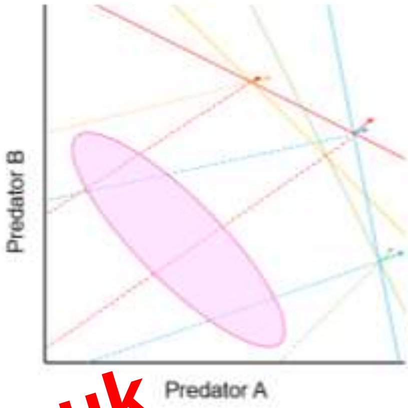
Niches

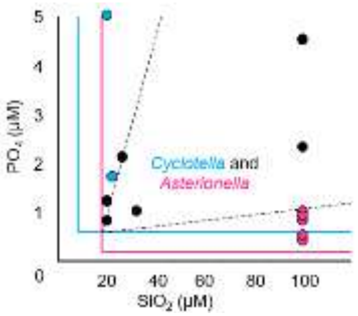
- Early definitions of the niche (like the fundamental and realised niches from earlier) focussed on the requirements for survival
- Elton's definition focused on the organism's impact on the environment
- MacArthur and Levins tried to show the joint effects of species
- Fundamental (never seen in nature) vs realised (implies competition).
- Niche packing works to try and limit overlap, predicting regular overlap – little support
- Liebig's law says that plant production is limited by light/water/nutrients, and that its most limiting resource is the most important. For animals this is nitrogen. Limiting factors can be predation stress, space etc, but it normally only comes down to one or two limiting factors
- The act of any organism on resources is to decrease them.
- The act of any prey on predators is to increase them

4 Outcome depends on supply and per capita impact
5 Coexistence along a gradient via tradeoffs
6 Peak SR at an intermediate ratio of resources

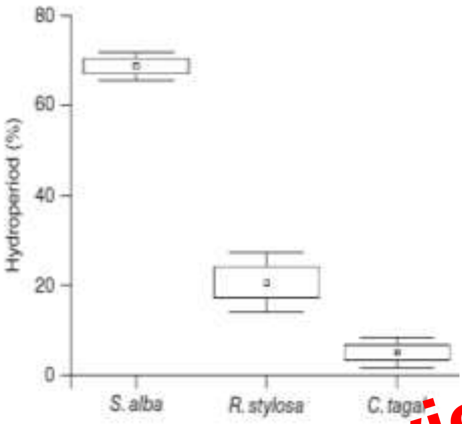
- 95% of tests support that R* determines the outcome
- Gause's theory that it is impossible for two species eating the same thing to coexist. Cyclotella and Asterionella both eat silica and phosphate. Tilman showed that they can coexist as long as there are tradeoffs.

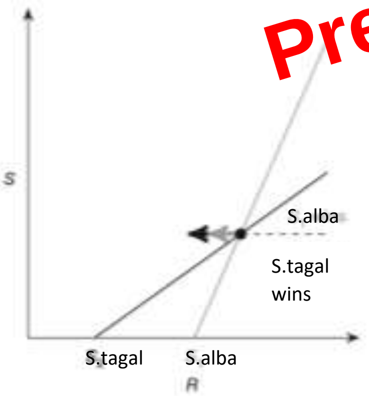




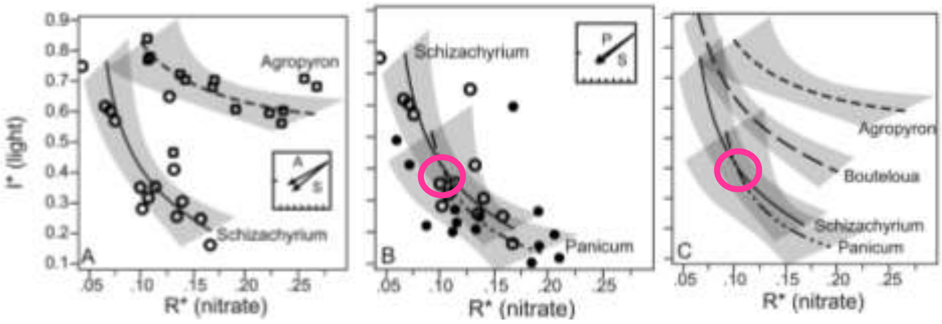


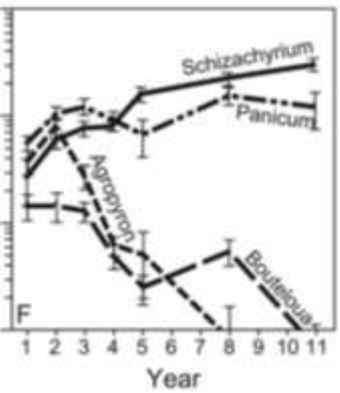
- Criteria for maintaining high SR:
  Multiple limiting factors
  Allow local coexistence
  Tradeoffs between requirements and impacts
  Habitat heterogeneity
  Spatial or temporal
- Heterogeneity in resources or predation actually leads to the most similar species winning, but can maintain multiple species
  - Variable predator and resource levels maintain multiple species (as no competitor has an advantage for long enough) -as long as the range is within the cloud
  - In Darwin harbour mangrove swamp 3 different mangrove species can be maintained due to having different hydroperiods (time they can be submerged) with tidal variation. The S. alba has the highest S* as it can tolerate the longest underwater, whereas S.tagal can tolerate the least submersion. If you look at the ZNGIs for these species though, you can see that there is a trade off: S.alba needs a lot of resources to cope with the stress – S.tagal has a lower R* for resources (is the best competitor for R)





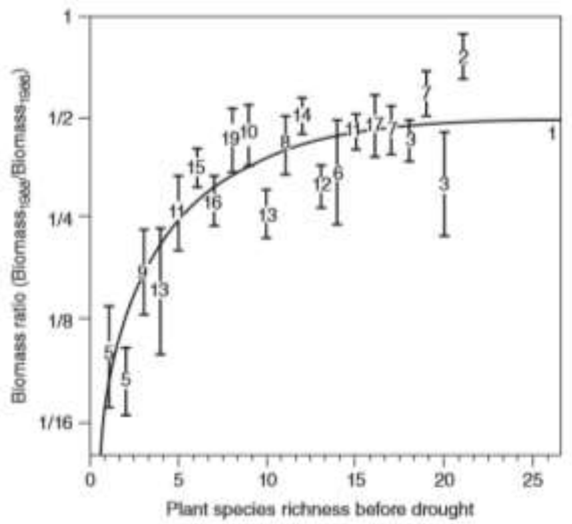
- Another real world example is in prairie plants – they compete for light (I*) and nitrogen (R*). In controlled trials there are a range of outcomes.



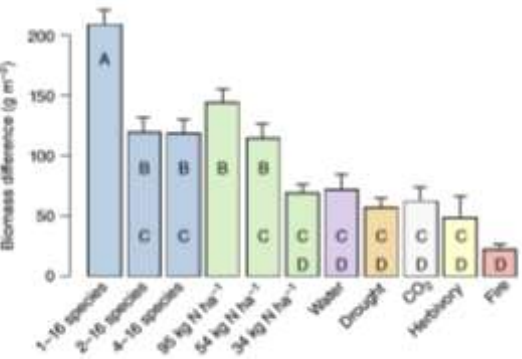


- In the first graph, the ZNGIs do not cross, so Agropyron is outcompeted by Schizachyrium (as it has a lower R* and I*). In the second graph, the ZNGIs cross, and the impact vectors are proportional – they can coexist. In the third graph, Schizachyrium and Panicum still cross, so out compete Agropyron and Boutella. These predictions hold true when tested, even if it takes a while to get there. The graph on the left shows S and P coexisting and slowly out competing A and B
- In real world systems all four of these species coexist, and the lowest R* species didn't dominate – shows that factors are missing from the model (such as herbivory,

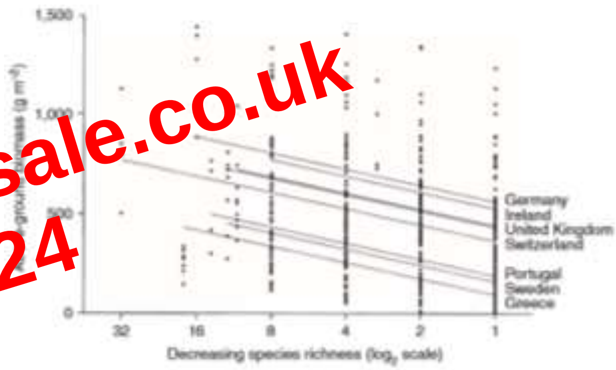
- Individual species can become more variable with the addition of more species, but it still makes the whole system more predictable. In an example with 207 grassland plots with manipulated SR, ↑ plant SR led to ↑ bacterial SR, increasing the number of nitrogen fixers, leading to an overall ↑ plant nitrogen (although individual species became more variable)



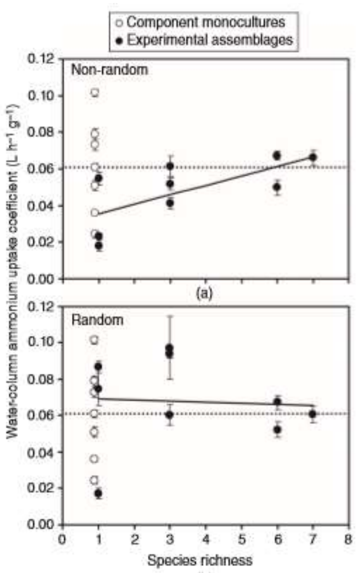
- SR has other benefits. In the graph on the right, the historical species richness of a plot before a two year drought increased the resilience of the plot (how much it could return to the old value)



- The graph to the right ranks diversity as more important than fertiliser in the productivity of a system. This does not mean that the extra biomass generated is actually useful biomass though
- The BIODEPTH project studied eight sites across Europe, with 1-32 random plant species and 11 variables (eg decomposition, fertiliser, etc) and found that the above ground biomass in every site increased with increasing species richness

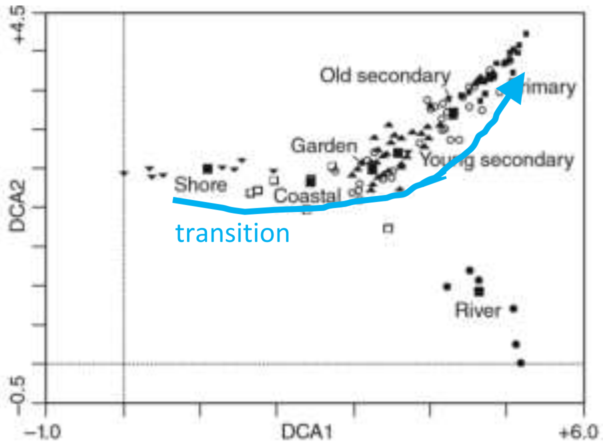


- Overyielding - how much more a plant produces when grown with other species, compared to growing in a monoculture. The yields are more than just the sum of the plants involved. Could be due to facilitation or mutualism, symbionts, complementarity (improve each other), or by having similar niches meaning that the resources are used in the most effective way.
- Overyielding does not occur in leguminous plants – but overyielding happens in so many other systems that its unlikely to just be an artefact
- More than just species richness, in BIODEPTH they found that increasing the number of functional groups (sets of similar species, eg grasses/forbs/legumes) increased biomass
- SR almost always has a positive effect on ecosystem processes, for productivity, nutrient cycling, diversity, stability etc



- BIODEPTH also found a 20-50% overlap species contributing to processes, meaning that they may trade off between them. It also found that whilst only 27% of species may be active in a process at a given time, 84% effected the ecosystem functioning at least once. As more years/sites/functions/environmental shifts were studied more and more species were found to be involved meaning that redundancy is unlikely
- All of these experiments use random species assemblies. When using a random assemblage of seaweed, the ammonium uptake becomes more predictable. However, with a non-random real world assemblage removing species also decreased the average uptake. This is because species tend to be removed in a predictable pattern.
- For example marine species disturb the sediment at the bottom of the ocean, adding oxygen to the sediment (bioturbation). Different species churn

- Communities depend on how you look at the environment, and what level of specificity you use. Eg, is a lake a community, or is it split into east and west, limnetic and benthic?
- Can use dissimilarity indices (like Sørenson's index) or ordination (statistical technique which shows similar things as close together on a xy graph) – looking at the degree of turnover



- Can do analysis to look at clusters etc, but can discern real groupings from them
- Cannot assume the same number of communities in two habitats which are similar, and more SR does not mean more communities
- Communities always made of the same things
- Functional groups – like plants or ground feeding predators etc (hard to get coexistence between multiple species in the same functional group)
- Dominant species (normally the most abundant by biomass), the basal species (bottom species which generates the energy going into the food chain – normally autotrophic plants/algae, but decomposition or chemosynthetic species in midnight zone of ocean)
- Ecosystem engineer – shapes the environment around it, creating the niche it needs (like a beaver knowing down a tree to form a dam for fishing)
- Californian kangaroo rats create large burrow mounds – grazes down the prairie and maintains the composition of vegetation and changes the habitats for other species – burrows used by other species. Presence totally alters vegetation and communities living on the prairie.
- Keystone species – a species which has an influence which outweighs its biomass (slightly different to ecosystem engineers and near impossible to test)
- Mistletoe in Australia – actually tested keystone concept, when totally removed bird diversity dropped 20% - but birds didn't interact with them. As were hemiparasitic (fed on tree branches), had very nutrient rich leaves which, when dropped, formed nutrient rich litter over the ground, improving vertebrate decomposer diversity – prey for the birds.

- Migrants – species which come and go (seasonally, or just pass through). Can be very important. Eg bats migrating to south America pollinate cacti even though are only there for a day – crucial.
- Food chains never have more than five levels, normally only 3-4 (not including decomposers or parasites as such small biomass, and start new food chains). Are rarely linear (not 1:1), and are very inefficient (on land transfer is only about 10%, better in the ocean as most things ectothermic and don't waste time heating themselves)
- The overall size of a system is the best predictor for food chain length
- At the lower nodes of food webs, it tends to be simplified into functional groups (big plants, insects etc) otherwise they would be huge (study in papa new guinea found 7000 links but estimated that it only comprised 20% of the total food web)
- Connectance – a measure of the number of links seen divided by the number of potential links – gives how many links there might be: $C = \frac{L}{[S(S-1)]}$. Can also look at how connected species are (within 1 link, 2 links etc)
- Natural systems are much more connected than you would expect by chance, because they are nested – generalists always