Connections between biodiversity and ecosystem functioning in large-scale natural ecosystems

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Doctoral thesis

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Svensk summering/English Abstract

Billions of years of evolution have given us a planet that supports a remarkable diversity of life. This *biodiversity* makes up the ecosystems that we, as humans, rely on to sustain almost every aspect of our lives. But, despite our reliance on these biodiverse ecosystems, we are eroding them at an alarming rate through habitat destruction, overexploitation and our transformation of the climate. How will this loss of biodiversity affect the functioning of ecosystems that we rely on? How much biodiversity do we need for healthy ecosystems? These are some of the questions that researchers began to address in the early 1990's. Based on hundreds of experimental manipulations of biodiversity, there is a general scientific consensus that biodiverse ecosystems tend to be more stable and more productive than depauperate ones. However, much of this work has taken place in artificial, experimental systems and at small scales of space and time. Thus, several questions remain. For example, if small-scale experiments show that biodiversity is important for ecosystem functioning, will the effects be the same at large scales? If ten species are required to maximise ecosystem functioning in a one square meter experimental grass patch, how many are required in a whole meadow, or in a landscape with many meadows? In my thesis, I attempt to extend our knowledge so we can better understand the consequences of biodiversity loss in natural systems and at larger scales of space and time. I did this through five different papers.

In **Paper I**, I re-examined experimental work on biodiversity and ecosystem functioning from the last 30 years through the lens of community assembly theory. The aim was to understand what these experiments may tell us about how biodiversity loss will impact ecosystem functioning in natural ecosystems. My analysis showed that there are probably many cases where the results of experiments will not easily transfer to natural ecosystems and how we might improve this transferability.

Many experiments performed over the last 30 years have shown that a high-diversity community of species is only rarely higher functioning than the highest functioning single species (i.e. monoculture). In **Paper II**, I used a set of theoretical simulations, an experiment in a bacteria-based model system, and a synthesis of previously published experiments to show that this may be because experiments have been performed in homogeneous environments. When environmental heterogeneity increased, we found that the functioning of diverse species mixtures increased relative to the highest functioning monocultures.

But, despite the general trend observed in **Paper II**, there were many experiments in the synthesis where a single species in monoculture was highest functioning across the range of environmental conditions. This contradicted many theoretical models for the effect of biodiversity on ecosystem functioning. Thus, in **Paper III**, I wanted to study species along an environmental gradient to see if we would obtain similar results. I did this using a transplant experiment with four common species of marine seaweeds on Swedish rocky shores which occupy relatively distinct depth zones on the shores. I hypothesised that the four species would grow best where they are most common. Counter to my predictions, only one species responded strongly to being transplanted to a different depth zone.

For **Paper IV**, I took the results obtained from **Paper III** and attempted to model what would happen to the biomass production of the seaweed communities if each of the four species went extinct. I found that the biomass production of these rocky shore communities would probably only be strongly affected if one of the seaweed species (*Fucus vesiculosus*) went extinct. This is because the four species showed high productivity outside of the depth zones where they are naturally found.

Arguably the most direct way to calculate an effect of biodiversity on ecosystem functioning is to compare a mixture of interacting species to a null expectation where species do not interact based on species' functioning in monoculture. However, in natural systems, this is generally not possible because we rarely have natural monocultures. In **Paper V**, I developed an analytical pipeline which enables comparisons of mixtures and monocultures in natural ecosystems. Combined with a previously developed statistical partition, I was able to show that a combination of local-scale species interactions, local-scale dominance by a few high functioning species and spatial niche partitioning all contributed to a positive effect of biodiversity on ecosystem functioning in two, natural marine ecosystems.

Based on these five papers, I conclude that the hundreds of experiments that have been done to date provide useful but imprecise information about how biodiversity loss may affect the functioning of natural ecosystems. To understand the ecosystem-level effects of biodiversity loss more thoroughly, we will need to carefully study how biodiversity is changing across multiple scales of space and time and use methods that can detect the consequences of these changes. **Papers IV** and **V** suggest avenues for how this may be done.