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Biodiversity and Ecosystem Functioning: The Mystery of the Deep Sea

Experiments performed in various ecosystems have shown a near-universal, saturating relationship between biodiversity and ecosystem processes. Analyses of deep-sea ecosystems challenge this generalisation and suggest that positive species interactions might be more widespread than previously believed.

Michel Loreau

Humans are altering the composition and diversity of biological communities through a variety of activities that increase the rates of species extinction and species invasion at all scales, from local to global. These changes in the Earth's biodiversity cause concern for ethical and aesthetic reasons, but in addition have a strong potential to alter the functioning of ecosystems and thus the goods and services they provide to humanity. 'Ecosystem functioning' is an umbrella term for the processes operating in an ecosystem, that is, the biogeochemical flow of energy and matter within and between ecosystems (e.g., primary production and nutrient cycling). The effects of biodiversity loss on ecosystem functioning have been the focus of an explosion of research over the past decade [1–4].

Most of the research relating biodiversity and ecosystem functioning has been performed using controlled field experiments that assemble model communities of varying diversity to measure the effects of changes in diversity on ecosystem processes. Recent meta-analyses of these studies show that species diversity generally has a positive but saturating effect on ecosystem processes that is remarkably consistent across trophic levels and ecosystem types [5–7] (Figure 1). A new study published in a recent issue of *Current Biology*, however, challenges the generality of this finding. In this study, Danovaro *et al.* [8] use

comparative data on a large number of deep-sea ecosystems across the globe to show that the relationship between species diversity and a number of ecosystem properties is exponential on the ocean floor. Since deep-sea ecosystems are the most extensive ecosystem type on the Earth's surface and are presumed to host a large fraction of the Earth's biodiversity — most of it yet undiscovered — non-saturating relationships between species diversity and ecosystem functioning might be more common than previously believed. This raises serious concerns that even modest reductions in deep-sea biodiversity might have significant impacts on the Earth's biogeochemical processes.

Are the Results of Comparative Studies Robust?
One key difference between the new study [8] and many previous studies is that it uses a comparative approach while saturating relationships between biodiversity and ecosystem functioning have been established using controlled experiments. A common problem with comparative studies is that correlation does not imply causation. Theory predicts that when environmental factors vary across sites, these co-varying environmental factors generally overwhelm the specific effect of diversity and thus drive the relationship between diversity and ecosystem functioning [9]. This explains why comparative studies often yield different results than

experimental studies: the former reveal the influence of environmental constraints, while the latter reveal the specific influence of diversity under controlled environmental conditions [1]. Could this difference in methodological approaches be responsible for the difference in the observed patterns?

Although this hypothesis cannot be rejected with certainty in the absence of controlled experimental tests, Danovaro *et al.* [8] provide convincing circumstantial evidence that covarying environmental factors are unlikely to fully explain the observed exponential relationships between biodiversity and ecosystem properties in the deep sea. Three of the main environmental factors that vary across deep-sea ecosystems are temperature, water depth and carbon inflow from the photic zone. Yet, the observed patterns still hold after controlling for these factors in the statistical analyses.

Despite their intrinsic limitations, comparative studies have great value in revealing patterns that would otherwise remain out of the reach of experimental studies when these patterns involve large spatial scales, long time scales or not very accessible ecosystems, such as in the deep sea. Controlling statistically for as many environmental factors as possible is then a useful approach to help formulate reasonable hypotheses about underlying causation and mechanisms. This approach has been followed in several other recent studies [10,11].

What Do Biodiversity–Ecosystem Functioning Relationships Tell Us about Underlying Mechanisms?
If the exponential relationships between biodiversity and ecosystem properties observed on the ocean floor are not caused solely by covarying environmental factors, what, then, explains them? Although a large number of specific biological mechanisms are likely to be involved in biodiversity effects on ecosystem functioning, these mechanisms are
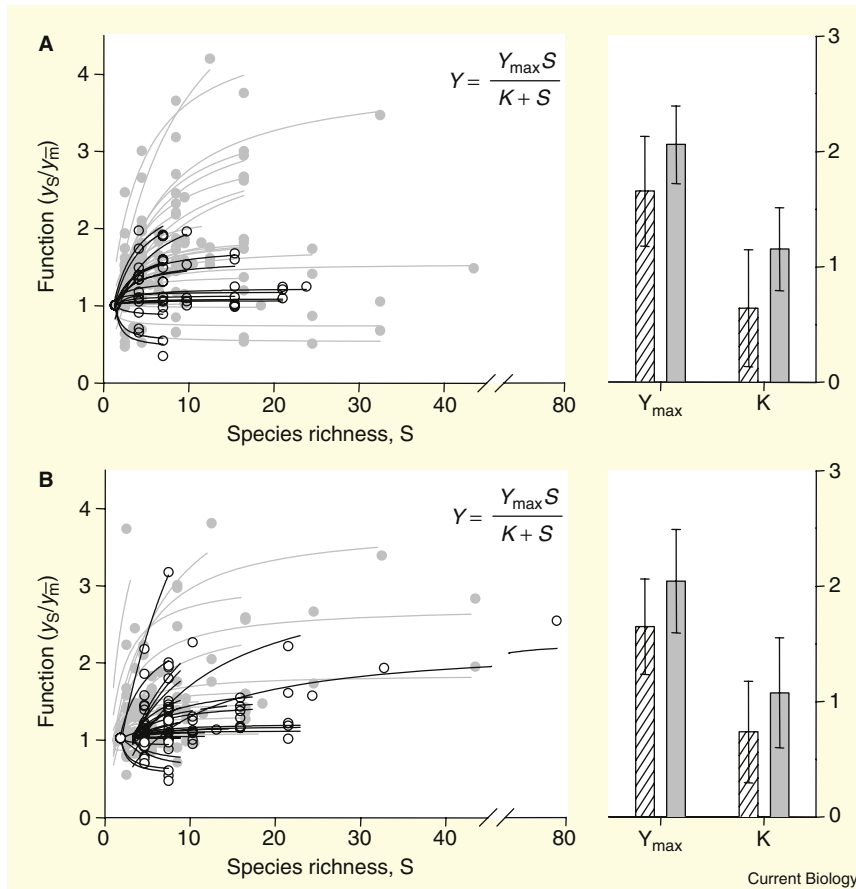
Figure 1. The general form of the diversity–ecosystem functioning relationship found in recent experiments.

Effects of species richness on the standing stock abundance or biomass of a trophic group (A), and the depletion of resources consumed by this trophic group (B), in aquatic (black circles and lines) and terrestrial (grey circles and lines) studies. Each curve corresponds to data from a single study fitted to the function $Y = Y_{max}S/(K + S)$, where Y is the proportional change in the dependent variable with increasing richness S, Y_{max} is the asymptotic estimate of Y, and K is the value of S at which $Y = Y_{max}/2$. Insets show the mean and 95% confidence interval for the maximum-likelihood parameter estimates (hatched: aquatic; grey: terrestrial). Modified with permission from [6].

generally grouped into two main classes of biodiversity effects: complementarity and selection [12]. Complementarity occurs when species in a mixed community perform better on average than expected from their performance in monoculture, thereby contributing to enhancing ecosystem processes. Selection occurs when species with particular traits or performance in monoculture tend to dominate mixed communities, thereby contributing to either enhancing or deteriorating ecosystem processes, depending on whether best-performing or worst-performing species dominate.

The relative contributions of these two effects to the results of biodiversity experiments have been highly contentious because the two effects have very different implications for the mechanisms that maintain diversity in natural communities as well as for ecosystem management. Selection effects involve mere competitive shifts in the relative contributions of the various species. By contrast, complementarity effects are indicative of resource partitioning or facilitation among species. A recent meta-analysis of biodiversity experiments concluded that the positive effects of species diversity on biomass production in temperate grasslands are driven by a combination of complementarity and selection effects, with complementarity effects nearly twice as strong as selection effects overall [13]. However, diverse communities appear to rarely function significantly better than the best single species, at least in the short term.

Surprisingly, this debate about mechanisms seems immaterial for deep-sea ecosystems. This is because, while different mechanisms can contribute to saturating biodiversity–ecosystem functioning relationships, only positive species interactions are known to yield accelerating relationships [14]. When species interactions are positive, species benefit from the presence of others, leading to mutual enhancement of their performance. Therefore, if the exponential relationships observed by Danovaro et al. [8] were to hold under controlled environmental conditions, this would mean that mutualistic interactions prevail in deep-sea communities. This is a stunning conclusion. Although positive species interactions are known to occur in plant communities [15], interspecific competition is strong enough to yield saturating biodiversity–ecosystem functioning relationships in these communities. Reworking of seafloor sediments by biological activity enhances ecosystem functioning through complex biogeochemical interactions [16]. Could this sediment reworking generate a prevalence of positive species interactions on the ocean floor? The new study by Danovaro et al. [8] raises a number of intriguing questions that could well change our understanding of species interactions, ecosystem functioning, and the threats of biodiversity loss.

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Plant Pathogen Effectors: Getting Mixed Messages

Plant pathogen effectors have now been shown to mimic plant transcription factors and turn on genes that help the pathogen. Some plants, however, have evolved to use these pathogen-derived transcription factors to turn on defence.

David L. Greenshields
and Jonathan D.G. Jones

The ability to live and reproduce within a plant has evolved independently several times in pathogens from different kingdoms of life. The apparent widespread success of this lifestyle suggests that it provides a comfortable living for organisms that have the right skill set. Although plants appear to be sessile nutrient reserves ripe for the plundering, inside plant cells it is a different story: pathogens that attempt entry can be simultaneously encased in fortified barriers, subjected to potent oxidizers and toxic small molecules and even thwarted by the suicide of the targeted host cell. Thus, the road to the good life within a plant requires a lot of disguise and deception, and only the most cunning can enjoy what the plant has to offer.

In response to pathogens, plants have evolved sophisticated recognition capabilities that sense conserved molecules expressed by fungal, bacterial and oomycete pathogens. The bacterial flagellum protein flagellin is the best characterized of these pathogen signatures [1]. To evade plant recognition and encourage a suitable environment for growth and reproduction, pathogens secrete a range of protein effectors into plant cells that can block the recognition of these molecules and manipulate host machinery for the pathogen's benefit. In turn, plants have evolved surveillance systems to recognize the effectors themselves, thereby triggering another layer of the plant immune response [2].

To enable pathogen survival and growth within the host, effectors must turn on pathways to promote pathogen nutrition and turn off pathways leading to defence activation. Therefore, plants must be able to recognize these attempts at manipulation and mount a defence response. Two recent papers [3,4] describe an interesting twist on pathogen effectors and their recognition. They show that the bacterial spot-causing pathogen *Xanthomonas campestris* pv. *vesicatoria* (*Xcv*) secretes AvrBs3, a transcription factor effector that induces the plant cell-size regulator *upa20* in susceptible plants and the resistance gene *Bs3* in resistant plants. While activation of *upa20* leads to cell hypertrophy, which supports the infecting bacteria [4], activation of *Bs3* triggers a defence response leading to plant cell death [3]. These two different transcription factor activities account for the phenotypes seen in resistant and susceptible plants.

Bacterial pathogens of both plants and animals have evolved a syringe-like organelle called the type III secretion system that delivers effector proteins directly into eukaryotic cells [5]. AvrBs3 is the signature member of a family of conserved proteins in *Xanthomonas* that is injected into host cells through type III secretion and is characterized by a nuclear localization signal [6], a transcriptional activation domain [7], and a central repeat domain that determines resistance and susceptible responses in different plant genotypes [8]. To isolate direct targets of AvrBs3, Kay et al. [4] screened cDNAs from infected pepper plants impaired in protein synthesis, and this led to the identification of Upa20, a basic helix–loop–helix transcription factor related to the *Arabidopsis* petal-size regulator BIGPETAL. Silencing of *upa20* reduced cell hypertrophy in infected plants and expression of *upa20* led to hypertrophy in uninfected plants [4]. Mutation of the *upa20* promoter identified a so-called *upa* box that is the direct target of AvrBs3 [4]. Interestingly, there is also a *upa* box in the promoter of the pepper *Bs3* resistance gene, which recognizes *Xcv* isolates carrying *AvrBs3* [3]. Römer et al. [3] show that AvrBs3 activates the transcription of its cognate resistance gene *Bs3*, thereby triggering a defensive localized plant cell death (Figure 1). Another AvrBs3-like protein, AvrXa27 from *X. oryzae* pv. *oryzae*, also activates transcription of its associated rice resistance gene *Xa27* [9], suggesting a common mode of action for this protein family.

How does Upa20 promote hypertrophy and what benefit does host cellular hypertrophy provide the pathogen? Upa20 induces expression of *upa7*, which encodes a putative α-expansin [4]. Interestingly, expansin gene induction is also seen in the enlarged root cells that harbour plant