doi:10.1038/nature16867

ECOLOGY

Biodiversity and productivity entwined

A systems-level analysis of grasslands across the planet provides stimulating insight into the interlaced pathways that connect species diversity and biological productivity in ecological communities.

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An abiding goal of ecology is to understand how the biological diversity of natural communities is linked to the rate at which those communities produce biomass, if it is linked at all[1–5]. Elucidating this connection and the processes behind it is useful, among other reasons, for anticipating how ecological communities may change in response to anthropogenic perturbations, such as alterations to the abiotic environment, the introduction of new species or the loss of established ones. Yet despite more than 40 years of study and debate, a comprehensive, mechanistic understanding of the relationship between biodiversity and ecosystem productivity remains elusive. In a paper online in *Nature*, Grace *et al.*[6] argue that the interplay between these factors is more fully understood when both are placed in a rich network of cause-and-effect pathways, as opposed to being regarded as entities engaged in an isolated back-and-forth.

The authors considered data generated by the Nutrient Network[7], a global scientific cooperative that examined several dozen grass-dominated plant communities from across the planet. Grace and colleagues analysed these data using a structural-equation model — a statistical method that examines whether a hypothesized system of cause-and-effect pathways is consistent with covariation in a collection of variables. The starting point for this analysis was a putative network of cause-and-effect relationships for several aspects of ecosystems and their associated environments, devised from the authors' synthesis of the literature. The confrontation between data and model then occurred at two nested levels: between the sites of the Nutrient Network, and across replicate communities within each site.

Several provocative results emerge (Fig. 1). First, the authors find that the rate of biomass production increases with the number of species found at a site (its species richness). What is notable here is that this effect holds steady across the observed variation in species richness, instead of saturating in communities with greater richness, as a generation of experimental and theoretical work has suggested that it may[8]. Second, both between and within sites, a greater stock of accumulated above-ground biomass (live plant tissue and dead litter) decreases species richness. The authors suggest that this provides evidence that competition between species — primarily for light, at least at smaller spatial scales — is an important force in determining why communities contain as many species as they do. Again, the noteworthy aspect is that competition seems to be influential regardless of how productive a community is, contrary to the historical suggestion that competition is a stronger structuring force in more-productive communities[1,5]. Finally, the analysis identifies several pathways by which the abiotic environment, including temperature, precipitation, soil properties and the history of major anthropogenic influences, adjusts the ecological context in which species diversity and productivity interact.

Herbaceous-plant communities provide the empirical grist for much of what we know about the relationship between biodiversity and productivity[1–3,5], for the good reason that these are systems in which those two entities can be readily quantified (relatively speaking, of course!). However, it is natural to ask how the causal network posited by Grace *et al.* can apply to other major biomes, such as tropical forests, coral reefs or the human body's resident microorganisms. A more explicit integration of the authors' causal network with the mathematical theories of species coexistence and community dynamics would help to delineate the network's biological generality.

Also, although a structural-equation model can reveal whether data are consistent with a causal network, it is possible that other causal networks are consistent with the data as well[9]. The authors justify their hypothesized network extensively, but alternative readings of the literature could surely be made. Whether other ecologically plausible causal networks can be constructed that are consistent with these or comparable data remains an open question, and one that should be asked.

Perhaps Grace and colleagues' most stimulating contribution, however, is their forceful suggestion that ecologists' theoretical, experimental and statistical practices are sufficiently mature to allow a more holistic, systems-level view of the relationship between productivity and biodiversity. This suggestion challenges

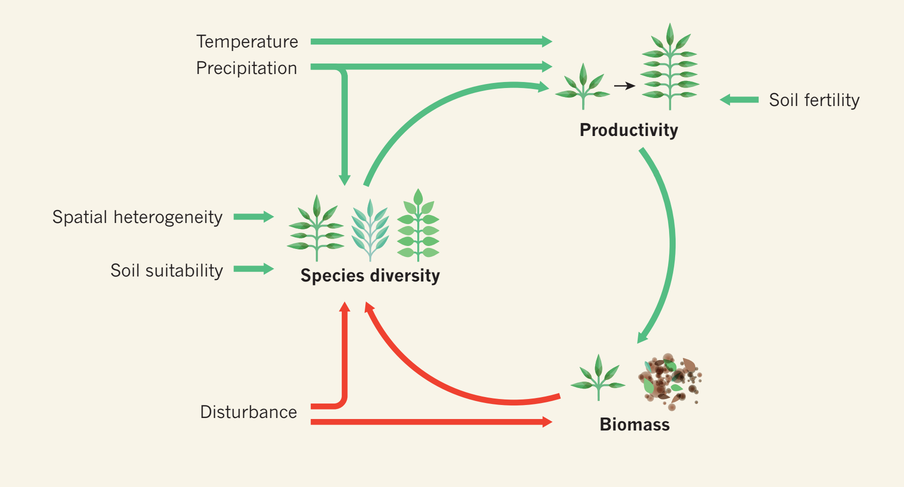

Figure 1 | A network-based view of biodiversity and biomass production. Using a structural-equation model and data from 39 herbaceous-plant communities across five continents, Grace *et al.*[6] show that variation in biological diversity and biomass productivity is well explained by a network of cause-and-effect pathways. Positive pathways (green) have an enhancing effect, such as soil fertility increasing plant productivity; an example of a negative pathway (red) is the suppressive effect of above-ground biomass (live plant material and dead litter) on species diversity. The network depicted represents patterns that are consistent with variation between the 39 communities; variation within the communities supports a comparable network.

the decades-old view that the biodiversity–productivity relationship can be characterized by a simple yet general bivariate curve[1,5]. This bivariate model has been remarkably durable, despite the severe and widely recognized weakness of its predictive power and disagreement regarding the basic shape of any such curve[1–3,5]. Mounting dissatisfaction with the bivariate model has inspired several alternative, more-nuanced models for how biodiversity and productivity are intertwined[4,10,11]. To this collection, Grace *et al.* have contributed a framework that is unique in its deep integration with data gathered from around the globe.

Nevertheless, the staying power of the bivariate relationship testifies to its appeal as a first handle on the daunting complexity of complicated ecosystems. As the dust settles, ecologists will ultimately gravitate to the conceptual framework that provides the best balance of transparency, predictive capacity and fidelity to data. The efforts of Grace *et al.* and others set the stage for a rigorous investigation and evaluation of more-nuanced conceptual models of ecological communities. In time, perhaps these models will emerge alongside the bivariate diversity–productivity model as cornerstones of ecological thought and inquiry, or may even supersede it. ■

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