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animal viruses, parasites, and other pathogens to their cellular hosts, binding of bacteria to plants and of pollen to the plant stigma, binding of amphibian and marine sperm to eggs, and sexual agglutination in yeast. All of these events are considered to be mediated by glycans (6).

The results reported by Pang *et al.* raise a number of questions. The functional analyses were carried out with SLeX from total human ZP, not with SLeX from individually purified ZP glycoproteins. It is thus unclear whether sperm bind to all human ZP glycoproteins (ZP1 to ZP4) containing SLeX or whether binding is restricted to one or more of them. In this context, the finding that SLeX that is covalently linked to BSA is orders of magnitude more effective than SLeX alone as an inhibitor of sperm binding to eggs suggests that the oligosaccharide's orientation may be affected by the polypeptide to which it is linked (10, 12). Indeed, the binding of mouse sperm to egg ZP oligosaccharides is influenced by the polypeptide to which they are

linked (13). Because Pang *et al.* conclude that the effectiveness of SLeX in sperm binding depends on the presence of a terminal sialic acid, it is uncertain whether the monosaccharide's negative charge is responsible for binding. It is likely that SLeX does not inhibit binding of mouse sperm to eggs because of the negative charge introduced by sialic acid (10). Whether SLeX can block the binding of other species of mammalian sperm to homologous eggs also remains unanswered; this would bear on the issue of species specificity during mammalian fertilization.

Another issue concerns the nature of the egg-binding proteins on human sperm that recognize and bind to SLeX. Perhaps derivatives of SLeX could be used as effective probes to tag the proteins. Even in the well-studied case of the binding of mouse sperm to the egg's ZP, the nature of the egg-binding proteins remains contentious (14). Despite these lingering issues, the study by Pang *et al.* should stimulate considerable interest in the molecular basis of sperm-egg interaction in

humans and may ultimately lead to development of new contraceptives.

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ECOLOGY

Biodiversity and Productivity

Michael R. Willig

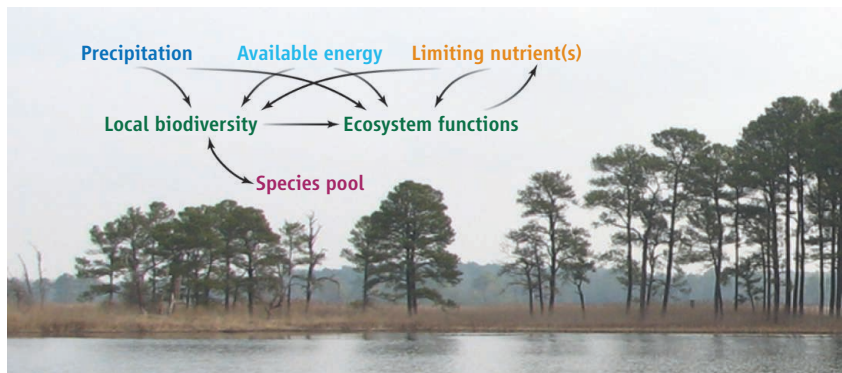
Researchers predict that human activities—especially landscape modification and climate change—will have a considerable impact on the distribution and abundance of species at local, regional, and global scales in the 21st century (1, 2). This is a concern for a number of reasons, including the potential loss of goods and services that biodiversity provides to people (3, 4). Exactly how biodiversity relates to ecosystem function and productivity, however, has been a widely studied and highly controversial issue over the past few decades. Initially, for example, many researchers believed that the relationship between species richness and net primary

productivity (often expressed as the number of grams of carbon produced within a square meter of an ecosystem over a year) could be visualized as a hump-shaped or modal curve (5), with richness first rising and then declining with increasing productivity. However, subsequent theoretical and empirical research, including meta-analyses, seriously diminished acceptance of the modal pattern

The relationship between species richness and ecosystem productivity appears to be very complex.

as a canonical relationship (6–11). On page 1750 of this issue, Adler *et al.* (12) carry the critique a step further. In a multiscale assessment of 48 plant communities on five continents, they demonstrate that the modal productivity-diversity pattern is quite rare in nature, rather than the dominant relationship. Their findings suggest that ecological understanding may advance more rapidly if investigators focus on exploring a range of topics that are germane to the productivity-diversity relationship in a changing world, rather than continue the search for a dominant pattern.

One topic that merits attention is developing a better understanding of the concepts underlying gradients in species richness, over both space and time. In general, biodiversity gradients can appear (13, 14) if (i) one or more limiting resources differ in



Complex relationship. The relationship between biodiversity (e.g., species richness) and associated ecosystem functions (e.g., net annual primary productivity) is governed by a suite of abiotic and climatic characteristics, as well as biotic feedback. To fully understand the underlying mechanistic bases for the biodiversity-productivity relationship and to predict how it might respond to climatic change and land use change, an effective synoptic network must minimally estimate these characteristics at multiple sites and scales, and must do so over the long term.

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time or space; (ii) more individuals lead to more species, given a uniform environment of fixed area; (iii) the variance of an environmental characteristic increases with its mean within an area of fixed size or time of fixed duration; and (iv) nonmonotonic relationships require trade-offs in organismal, population, or species characteristics with respect to the environmental gradient (e.g., competitive ability versus stress tolerance or competitive versus colonizing ability). By identifying critical trade-offs, researchers can identify contexts, including both times and places, in which modal patterns may be most likely to occur in natural settings and distinguish them from places and times in which monotonic patterns may be expected. Alternatively, the absence of a modal pattern suggests the absence of defining trade-offs. Finally, for a modal pattern to emerge, the trade-offs must be strong and pervasive. If the biota is large, comprising many species of different physiology or life history, a single dominant trade-off may not be in operation, reducing the likelihood of detecting a modal pattern.

A second issue is that biodiversity has multiple dimensions; species richness is but one of its many attributes. Areas that are ripe for investigation include the way in which productivity varies with other components of the taxonomic dimension of biodiversity, such as species evenness, diversity, or rarity (15), or the way in which other dimensions of biodiversity (e.g., functional, phylogenetic, genetic, or trait) vary with productivity (16, 17). Such comparisons may be useful in identifying causal mechanisms affecting empirical patterns from both ecological and evolutionary perspectives.

A final topic is the role of multicausality in a complex world. For example, although variation in available energy may mold patterns of species richness (and other attributes of biodiversity), variation in species richness (and other attributes of biodiversity) may in turn mold patterns of plant productivity. Each of these attributes may also respond to other driving factors, both environmental (e.g., energy, temperature, and precipitation) and evolutionary (e.g., size and composition of species pools). It should not be surprising that the relationship between biodiversity and productivity is complex, scale dependent, and context specific in nature.

Understanding the consequences of changes in land use and species richness at multiple scales may be critical for long-term sustainability, because these changes will affect the relationship between biodiversity and ecosystem functions. In this regard, Adler *et al.*

are correct in arguing for the establishment of large-scale environmental networks or global biodiversity observatories. To address global patterns and overarching conceptual issues, such as the relationship between assemblage structure and ecosystem function, networks must be coordinated and synoptic in nature (18, 19), measuring similar characteristics in similar ways at a variety of spatial scales. They also must be supported by cyberinfrastructure and connected to other networks and evolving databases, such as GenBank (www.ncbi.nlm.nih.gov), TreeBASE (a phylogenetic data source at www.treebase.org), or TraitNet (a repository for trait characteristics at <http://traitnet.ecoinformatics.org>). The answers to some of the greatest challenges facing society may depend on sustained support of biodiversity observatories that are designed to address the relationships between the multiple dimensions of biodiversity and a suite of ecosystem functions that provide critical services of value to humans.

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ECOLOGY

Coexisting with Cattle

Johan T. du Toit

In East Africa, large wild herbivores both compete with and benefit cattle.

Many large plant-eating mammals have evolved to live in multispecies assemblages, with species competing for food and other resources. Through domestication and animal husbandry, however, humans have enabled a few species of livestock, such as cattle, to dominate such assemblages. One standard practice in livestock production on rangelands, espoused by commercial ranchers and subsistence pastoralists alike, is the eradication of large, indigenous herbivores that are believed to compete with livestock for food. These eradication efforts have increasingly problematic implications for biodiversity conservation (1). So it is timely that on page 1753 of this issue, Odadi *et al.* (2) report on a relatively simple experiment that tested the assumption that cattle and wildlife compete for food. Their study, conducted in an East African savanna

renowned for its large herbivore diversity, revealed that cattle do compete with herbivores such as zebras and gazelles during the dry season, when food quantity is low. In contrast, during the wet season, when food quantity is high, grazing by wildlife benefits cattle by improving the quality of forage. The findings highlight ecological processes that promote coexistence among large herbivores in grasslands and savannas, and hence could be useful for conservation.

Large herbivores (>5 kg) generally belong to either a grazing guild (eating mostly grass) or a browsing guild (eating mostly foliage on trees and shrubs); a few are “mixed feeders” that alternate in response to seasonal changes in food plants (3). This grazer-browser dichotomy is a key factor promoting resource partitioning, with coexisting herbivores feeding on different plants or plant parts in the same area (4). In addition, coexisting species within each guild often differ in body size and/or digestive

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