will ultimately need to include this important and common type of interaction.

Brooker and Callaghan focus attention on important issues that will need to be resolved before we truly understand the nature and dynamics of plant communities. Their perspective on positive plant–plant interactions, however, also points to the role that an investigator's system plays in shaping the way they view nature and illustrates how the inability of plant ecologists to come to terms with how physical stress affects plant interactions influences general attempts to understand plant community organization. Field experiments across gradients of physical stress and natural disturbance, where stress and disturbance are independently and simultaneously manipulated, will be necessary to resolve these important issues.

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Transcending boundaries in biodiversity research

Neither species nor ecosystems recognize the borders of nations or the boundaries of scientific disciplines. Therefore, the development of effective research, assessment and management strategies for contending with the ecological consequences of global declines in biodiversity will require both international and transdisciplinary efforts. The Biodiversity and Ecological Complexity workshop held in Kyoto, Japan last November represents the most recent in a series of such international, multi-disciplinary efforts to foster exchange and collaboration among scientists studying declining biodiversity. Sponsored by Kyoto University's Center for Ecological Research (CERKU) and the Japanese Ministry of Education, Science, Sports and Culture, the workshop brought together 20 speakers and more than 20 additional participants from Japan, other Western Pacific and Asian countries, Europe, North America, and Australia to review key issues in the ecological dimensions of biodiversity. Masahiko Higashi (CERKU), the conference's principal organizer, assembled speakers to address key issues examined from both a theoretical and empirical perspective.

The importance of ecological heterogeneity

The multiplicity of roles ecological heterogeneity plays in the generation and maintenance of biodiversity was made clear by its recurrence as an important factor in many of the presentations. Higashi reviewed theoretical evidence for the importance of environmental heterogeneity in modes of speciation, while Simon Levin (Princeton University, NJ, USA), using similar theoretical approaches, showed the importance of spatial heterogeneity in coexistence among species.

Several different forms of ecological heterogeneity were discussed. Kuniyasu Momose (CERKU) discussed the importance of climatic variability (abiotic ecological heterogeneity) as a factor that accounts for the low degree of specialization among pollinators in Western Pacific dipterocarp forests. Norio Yamamura (CERKU) discussed how diverse strategies among plants for defense against herbivory (biotic ecological heterogeneity) leads to the evolution of diverse herbivore strategies for surmounting such defenses. Kazuyuki Mise (Kyoto University, Japan) presented a detailed example of such coevolutionary processes between plant viruses and their hosts. Finally, Moritaka Nishihira (Tohoku University, Japan) showed the importance of coral reef-dwelling organisms which modify microhabitats (biotically induced habitat heterogeneity) as a key factor in maintaining coral diversity. In contrast to these presentations, however, David Burslem (University of Aberdeen, UK) showed that long-term coexistence among tree species in the Solomon Islands can be remarkably constant despite environmental heterogeneity.

Species distributions are also associated with gradients in environmental heterogeneity. For example, Hiroshi Takeda (Kyoto University) showed that leaf-litter communities along a latitudinal gradient from subalpine/boreal forests in Japan to tropical forests in Thailand and Malaysia are organized by a gradient in shifting distributions of carbon and nitrogen from soils in the north to above-ground biomass in the south. Allen Herre (Smithsonian Tropical Research Institute, Panama) provided a picture of organization along a biotic gradient rather than an environmental gradient. Fig trees and their seemingly incomprehensibly complex nematode–wasp–mite–fungus–ant-and-bat communities reveal a strong pattern of organization along a biological gradient from small- to large-fruited trees. In contrast, Richard Law (University of York, UK), argued that some patterns in diversity reflect the result of intrinsic assembly rules independent of the influence of the environment, and he provided a detailed example using microbial microcosms.

Linking species diversity and ecosystems

A critical issue in contemporary biodiversity research is to understand how biodiversity loss may impair the functioning and stability of ecosystems. Five presentations reviewed this issue.

Michel Loreau (Ecole Normale Superieure, Paris, France) provided models for plant production in terrestrial ecosystems which, based on local nutrient depletion zones, predicted the well known asymptotic relationship observed between plant production and species diversity[1]. Using a different approach, Shigeo Yachi (Ecole Normale Superieure) demonstrated that when production responses of plants to environmental heterogeneity varies among species, variability in production decreases, while overall levels of production can increase. Shahid Naeem used still another approach, combining models and microbial microcosm experiments to demonstrate that when the numbers of species per functional group increases,

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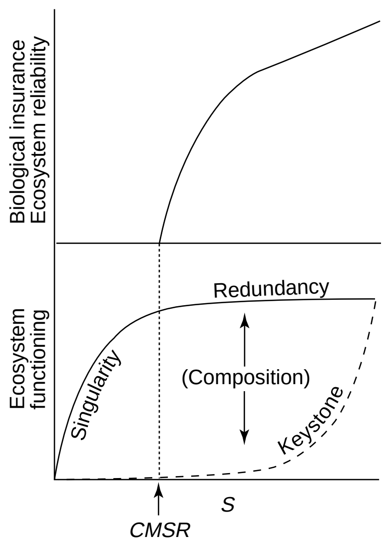

Fig. 1. This plot shows the relationship between ecosystem properties, such as functioning, biological insurance or ecosystem reliability, and biodiversity, plotted as the number of species (*S*). Singularity refers to the rapid rise in functioning obtained as genetically and functionally unique or singular species are added to a community. Once a critical minimum species richness is reached (*CMSR*), or when there are more than one species per functional group, an asymptote is approached. Additional species beyond the *CMSR* are considered redundant. (Increases in functioning may continue beyond *CMSR* in communities rich in redundant species, but these increases are likely to be minimal.) The upper plot shows that biological insurance and ecosystem reliability is lowest below the *CMSR*, but rises quickly even with small amounts of redundancy. The presence of keystone species or other species with strong impacts on ecosystem structure or functioning can cause dramatic declines in functioning if they suffer extinction. Thus, a range of possible relationships between biodiversity and ecosystem properties can occur, bounded by redundancy and keystone models[10].

predictability increases and variability decreases among replicate ecosystems. Matthew Liebold (University of Chicago, IL, USA), using results from an integrated program of observational, theoretical, and experimental studies of aquatic ecosystems, reminded us that the diversity and composition of the regional species pool, from which local ecosystems derive their species, is critical to ecosystem functioning, especially when keystone species are present. Finally, Shigeru Nakano (Hokkaido University Forests, Japan) showed that subsidization between land and water can have significant effects on ecosystem properties in riparian ecosystems.

Higashi provided a synthetic appraisal of this research. This synthesis in conjunction with the other contributions revealed that ecosystem processes can show almost any relationship with species diversity (from redundant to idiosyncratic) depending on such compositional properties as the presence or absence of ecological engineers[2], keystone species[3], and species with high community importance values[4] (Fig. 1). The array of possible patterns, however, is bounded by the pattern shown when redundancy is common and the pattern shown when species are predominantly singular in their contributions to functioning (Fig. 1). Biological insurance (constancy of functioning) and ecosystem reliability (predictability of functioning in the face of local extinction), however, show a consistent response once some critical minimal species richness (defined as one species per functional group) is reached (Fig. 1).

The human dimension

Human welfare is intimately connected to ecosystem functioning[5], but the human dimension of biodiversity issues remains unclear. Several presentations provided insights into this dimension.

Although aquatic ecosystems represent only a minor component of the biosphere, from the standpoint of human needs they are perhaps the most critical[6]. Jotaro Urabe (CERKU) noted that over 40 million people rely on Japan's lake Biwa alone for freshwater. Urabe showed, however, that the quality of lake Biwa water is strongly regulated by the community of organisms in the lake. Similarly, Zen'Ichiro Kawabata (Ehime University, Japan) provided evidence that pH buffering capacities of aquatic ecosystems may be a function of the level of diversity of organisms found in the water.

Measures of biodiversity may also serve as indicators of environmental quality. Roger Kitching (Griffith University, Brisbane, Australia) demonstrated that macro-moth diversity could serve as reliable indicators for 'rapid' biodiversity assessments of habitat disturbance. Finally, Katsyoshi Fukui (Kyoto University, Japan), provided a unique portrait of human cultural linkages with biological diversity with his studies on the Bodi of Ethiopia.

Whither biodiversity research?

Given the enormous scale of the issues, what directions should biodiversity research take? Takuya Abe (CERKU) and Eitaro Wada (CERKU) presented biodiversity initiatives in the region, in particular DIWPA (The International Network for Diversitas in Western Pacific and Asia) and CERKU's DIVER (Diversity and Ecosystem Relationships). Wada noted that these programs can trace their roots back as far as IBP (1965) on through MAB, WCRP, IGBP, Diversitas and GCTE, and most recently HDP[7]. Such programs are rapidly becoming the primary means for international evaluations of large scale environmental issues.

Such large-scale efforts may be an unfamiliar direction for ecology and evolution, which have traditionally emphasized the primacy of individual effort. Other disciplines of biology, however, have discovered the necessity of collaborating to address large-scale issues (for example, 150 researchers from 12 nations co-authored a recent paper describing the genome sequence of a single species of non-pathogenic bacteria[8]). Western nations have begun such large efforts such as BIODEPTH in Europe and the Ecotron in England[9]. With DIPWAS in the Western Pacific and the Symbiotron (a device like the Ecotron) under planning at CERKU, the Eastern nations are moving in a similar direction.

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