



PERSPECTIVES: ECOLOGY

Diversity by Default

David Tilman

One of the mysteries of biology is how the estimated 5 to 50 million species on Earth coexist. Some of the diversity results from the separation of Earth into five continents and the somewhat parallel diversifications of each.

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Diversity within a continent is partly explained by large-scale gradients in climate, resource availability, productivity, and disturbance—in combination with interspecific trade-offs that cause each species to have optimal performance at a particular point on these gradients. The largest part of the world's diversity, however, may come from a poorly understood phenomenon—the ability of hundreds to thousands of species that seemingly compete for the same few resources to coexist in relatively homogeneous local sites in lakes, grasslands, rainforests, coral reefs, and intertidal habitats. A long-term study in a Panamanian rainforest, reported by Hubbell and colleagues on page 554 of this issue, has now provided important insights into how such coexistence may occur (1).

Almost 40 years ago G. E. Hutchinson noted that the coexistence of hundreds of species of algae in lakes was paradoxically high compared with the prediction of then-current theory that the number of species should not exceed the number of resources for which they competed (2). Comparably diverse assemblages of potential competitors occur in many types of ecosystems around the world. Four major classes of theoretical solutions to this paradox of diversity have since been proposed, all of which predict, as a first approximation, almost unlimited diversity. Given the appropriate trade-offs in species traits, high diversity can be caused by local spatial heterogeneity (3), by nonequilibrium conditions (4, 5), by interactions among at least three trophic levels (for example, plants, herbivores, and parasites) (3, 6), or by neighborhood recruitment limitation (local absence of young of superior competitors) (7–9). These theories solved the paradox, but the mystery remains: What actually explains high local diversity in nature?

Since 1980, Hubbell and collaborators have been studying the dynamics of a tropical rainforest on Barro Colorado Island, Panama, by mapping and periodically recensusing the locations of treefall gaps and of more than 300,000 individual trees. They used these data to test two hypotheses frequently cited as possibly accounting for high diversity in rainforests—the intermediate disturbance hypothesis (one of many variants of nonequilibrium coexistence) and the recruitment limita-



Rainforest diversity. The diversity of this Panamanian rainforest, and of other ecosystems, may hinge on spatially patchy dispersal. Local absence of a superior competitor can allow an inferior species to win by default.

tion hypotheses. The intermediate disturbance hypothesis (10, 11) states that disturbances, such as treefall gaps, lead to a predictable successional sequence in which one tree species replaces another, and another, culminating in dominance by a canopy tree species. If disturbances are rare, almost all sites are dominated by the late successional canopy species, and total stand diversity is low. If disturbances are frequent, almost all sites are dominated by early successional, pioneer species, and diversity is again low. However, at intermediate rates of disturbance, there are a range of sites, some newly disturbed, some of intermediate age, and some old enough to be dominated by late successional

canopy species. This would allow the full range of species traits to coexist and lead to maximal species diversity.

Hubbell's team also examined the importance of coexistence by recruitment limitation (8, 9). Plants compete only with individuals living sufficiently nearby that each could cast shade on or have roots that overlap with the other. Because of poor dispersal ability, low local abundance, or chance events, however, many plant species may be absent from such a neighborhood and thus have their abundance be recruitment limited. Like a team that fails to appear at a sporting event, a species that is locally absent has forfeited any chance of competitive victory at the site. This can allow inferior competitors to win by default. If there is recruitment limitation, the winners of local competition are not necessarily the best competitors that exist in the region, but the best competitors that happened to colonize a particular site. This can lead to essentially unlimited diversity (8, 9).

Much of the evidence that Hubbell and colleagues gathered supports recruitment limitation over the intermediate disturbance hypothesis. For example, they found that the composition of gaps was amazingly constant over the 12 years of their study. Because this suggests that little successional replacement was occurring, it fails to support the intermediate disturbance hypothesis. They also observed a significant positive correlation between changes in species abundances in gaps and those in non-gap areas, which further suggests that the changes in composition that did occur were not successional. They found a low diversity of seedling and sapling species in gaps. This seemed to result from the low number of seeds and of plant species in the seed that fell on a site, which they measured using a series of 200 seed traps spread throughout their plot. The absence of most species from any given gap is highly suggestive of recruitment limitation. In support of the victory-by-default hypothesis, they observed that pioneer species, which presumably are poorer competitors, persisted in gaps.

One of their assertions, however, and related tests, seems open to debate. They suggested that the intermediate disturbance hypothesis assumes higher diversity *within* gaps. Diversity within gaps, though, need not change during succession for the intermediate disturbance hypothesis to explain high diversity of a locality. All that is needed is for the species composition of gaps to change through time, and for intermediate disturbance to lead to the greatest range of gap ages.

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In combination with work in rocky intertidal (12), grassland (13, 14), and other habitats (15), this new work suggests that local recruitment limitation may be a universal feature of sessile species. The issue, now, is which of at least three alternative recruitment-limitation hypotheses actually explains the high-local diversity of such habitats. Is diversity maintained by a trade-off between recruitment ability versus competitive ability (8)? Or, does recruitment limitation allow local coexistence of species that already are capable of regional coexistence (9)? Or, does recruitment limitation so slow the rate of competitive displacement that high-local diversity can be maintained, without any such trade-offs, by a regional equilibrium between extinction and the evolution of new species (16)? Or, is there a diversity of explanations for diversity?

The growing consensus on the impor-

tance of recruitment limitation puts us a significant step closer to understanding the mystery of Earth's high diversity. This mystery was of only academic interest 40 years ago, but the preservation of Earth's diversity is an increasingly important societal goal. Habitat destruction and fragmentation, invasions by exotic species, and nutrient pollution all cause loss of local diversity and species extinctions. Our ability to preserve maximal diversity in the face of this increasingly great human domination of the world's ecosystems, however, requires a much more complete understanding of diversity. The causes and conservation of Earth's diversity remain one of the greatest challenges facing ecology and society.

References and Notes

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PERSPECTIVES: NEUROSCIENCE

Energy on Demand

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How does the coordinated activity of neurons translate into a sensation or a thought? Experimental methods to address this central question of neuroscience range from characterization of the molecular and cellular basis of neuronal activity to noninvasive studies of the living animal. Recent techniques that can image the functioning brain offer a promising bridge between the cells and molecules of neuroscience and the complexities of the mind.

Through positron emission tomography (PET) and functional magnetic resonance imaging (fMRI), it is now possible to see “the brain at work,” to visualize which brain areas are activated (and in certain cases inhibited) by specific tasks. The spatial and temporal resolution of PET and fMRI provide an intermediate step in linking neuronal activity to behavior: The signals detected reflect the activity of neuronal ensembles in $\sim 1\text{ mm}^3$ with acquisition times as short as seconds. Until recently, however, it has not been clear exactly what neuronal activity is measured in PET and fMRI experiments.

The basic principle of brain imaging

was formulated by Sherrington more than a century ago, when he suggested that neuronal activity and energy metabolism are tightly coupled. Indeed, PET and fMRI do not detect brain activity directly but rather measure signals that reflect brain energy consumption. How then is neuronal activity related to these measures of energy consumption? Energy is delivered to the brain by the oxidation of glucose from the blood. PET monitors changes in blood flow, glucose usage, or oxygen consumption, while fMRI signals reflect the degree of blood oxygenation and flow.

Thus, the metabolic signals detected by functional brain imaging techniques bring us part way to understanding how neuronal processes such as action potentials and neurotransmitter release lead to a given brain activity and its resulting behavioral state. To make further progress, it has been essential to identify and quantitate the specific cellular and molecular mechanisms of neuronal activity that are coupled to energy metabolism.

New data obtained in vitro and in vivo have identified the neurotransmitter glutamate and astrocytes, a specific type of glial cells, as pivotal elements in the stoichiometric coupling of energy-requiring neuronal activities and energy metabolism. These results have related functional imaging signals and brain energy metabolism to specific neurotransmitters and thereby suggest novel solutions to a wide range of questions about brain activity.

Glutamate, by far the dominant excitatory neurotransmitter of the brain, is released by $\sim 90\%$ of the neurons during excitation, after which it diffuses across the synaptic cleft and is recognized by receptors on the postsynaptic neuron (see the figure). Glutamate released from neurons must rapidly be removed from the synapses to set the stage for the next transmission. This is primarily accomplished by a highly efficient uptake system in the astrocytes that surround every glutamatergic synapse (see the figure). Glutamate is taken up by astrocytes via specific transporters that use the electrochemical gradient of Na^+ as a driving force, resulting in a tight coupling between glutamate and Na^+ uptake (1) (see the figure). The astrocyte is then confronted with a dual task: disposing of glutamate and reestablishing the Na^+ gradient. The gradient is maintained by activation of the Na^+ - and K^+ -dependent adenosine triphosphatase (Na^+, K^+ -ATPase), and glutamate is converted into glutamine, a reaction catalyzed by glutamine synthetase. Glutamine is subsequently released by astrocytes and taken up by neuronal terminals, where it is enzymatically reconverted to glutamate to replenish the neurotransmitter pool of glutamate (see the figure). Both glutamine synthesis and the Na^+, K^+ -ATPase require adenosine triphosphate (ATP). There is no mechanism for ATP exchange between astrocytes and neurons, so each cell must supply its own energy.

Astrocytic end-feet, enriched in glucose transporters, cover virtually all capillary walls in the brain (see the figure). Thus, the morphology and cytological relationship of astrocytes with the vasculature and the neu-

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