proton is now thought to lie between 0 and 32% (*5*, *6*) (the uncertainty is mainly caused by inconsistencies in the data and should be reduced by future experiments).

Second, deep inelastic muon scattering experiments at the CERN laboratory in Geneva in the 1980s revealed that only a small fraction of the proton's spin is carried by the quarks. These findings were such a surprise that they gave rise to the so-called spin crisis. The rest of the spin of the proton must be supplied by the gluon spins or by the angular momentum of the quarks and the gluons as they move around within the proton. The experiments further suggested that the polarization of the strange quark-antiquark pairs ($s\bar{s}$) is sizable and contributes considerably to the proton's total spin (*7*). Extensive work at CERN, Stanford (SLAC), and Hamburg (DESY) over the past decade has essentially corroborated the original results (*8*). A quantitative determination of the individual contributions of $s\bar{s}$ pairs, gluons, and angular momentum to the proton's total spin is in sight.

As pointed out by Kaplan and Manohar (*9*) and McKeown (*10*), there is a third way to get hold of the strange quarks in the nucleon. The method uses a unique feature of weak interactions: The weak force violates mirror symmetry, or parity. The mirror image of the experimental setup can simply be achieved by flipping the electron's spin in the beam from the accelerator. Electron scattering on a charged particle involves both electromagnetic and weak forces. Through interference effects, the tiny parity-violating weak part of the interaction is amplified by the much larger electromagnetic part, thus allowing the strange parts of the electric and magnetic form factors, G_{Es} and G_{Ms}, to be determined. Static moments, such as the strange magnetic moment μ_s [now determined in (*2*)], can be obtained from these form factors by extrapolation to zero momentum transfer. The drawback is that the asymmetries resulting from this type of experiment are expected to be very small, about 10^{-5}. Statistical and systematic errors must therefore be kept at or below the parts per million level—a formidable task.

Several collaborations in America and in Germany have taken up the challenge (*11*). Each experiment has a different setup and is therefore sensitive to different combinations of the strange electric and magnetic form factors. Preliminary results have been reported (*12*–*15*), but the contribution of strange quarks to the magnetic moment of the proton could not be deduced.

By combining new measurements on hydrogen and deuterium, Hasty *et al.* have now determined the strange part of the proton's magnetic moment to amount to $(-0.1 \pm 5.1)\%$ (*2*). The error margin is still rather large. Nevertheless, the study shows convincingly that the contribution of strange quarks to the magnetic moment is small. It is still an open question whether strange quarks influence other quantities, such as the nucleon's mass or spin, to a larger extent.

With the prospect of new data from ongoing and proposed experiments (*11*) the strange quarks' contributions to the proton's magnetic moment will soon be pinned down and, taking into account new information from pion and deep inelastic lepton scattering, we should know all about strangeness in the proton in the next decade.

References and Notes

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PERSPECTIVES: ECOLOGY

Species-Area Relations in Tropical Forests

Robert M. May and Michael P. H. Stumpf

One of the earliest accomplishments of theoretical ecology was the discovery of a relationship between the number of species (of plants, birds, beetles, or whatever) on a given island and the area of that island (*1*). For example, a 10-fold increase in island area approximately doubles the number of species. This species-area relationship (SAR) is often used by conservation biologists to assess the long-term effects of the fragmentation of tropical forests, or other reductions in habitat area, upon species diversity (*2*). The SAR, as first enunciated by MacArthur and Wilson in their influential book *Theory of Island Biogeography* (*1*) and by others [see (*3*) and references therein], was phenomenological, based on observations.

The islands described by the SAR may be real islands in the ocean, or virtual islands such as hilltops (where the surrounding lowland presents a barrier to many species), lakes, or wooded tracts surrounded by open land. In such island groups, plotting the number of species S in a particular taxonomic category against the area A results in a power-law relation of the form $S = cA^z$ (see the graph, next page). The constant c is characteristic of the taxonomic group, but the exponent z tends usually to lie between 0.2 and 0.3. Such a sweeping generalization inevitably requires qualifications. For example, the linear log S–log A relation tends to fail (the graph curves downward) if the island area is very small; on the other hand, the exponent z tends to have lower values if the islands are very large (particularly on the scale of a continent). But, despite occasional carping, this SAR with a $z \approx {}^1/_4$ applies to such a wide collection of taxa and island groups that a theoretical explanation is called for. Enter Plotkin *et al.* (*3*) with just such a theoretical explanation, reported in their new study of more than 1 million trees from five tropical forests on three different continents.

But Plotkin and colleagues are not the only investigators with a contentious theoretical explanation for SAR. The earliest explanation (*1*, *4*) was prompted by the observation that the distribution of numbers of individuals (N) among species (S) is likely to be influenced by the multiplicative interplay of many different ecological factors. This results in a lognormal distribution for the relative abundance of species within a particular area (see the graph, next page). Earlier, Preston (*5*) documented such lognormal distributions; he observed that they were commonly one particular or "canonical" member of this one-dimensionally infinite family, and that for a large number of species they corresponded to the numbers of species and individuals related by $S \approx (\text{constant}) \times N^{0.25}$.

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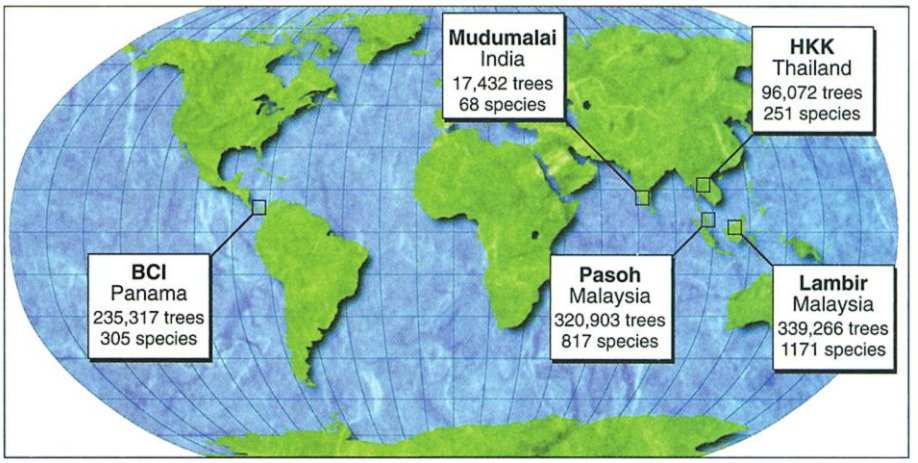
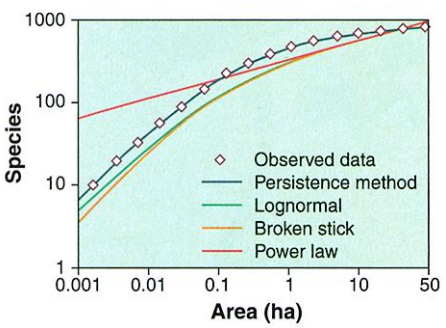
Later work (*4*) demonstrated that, for essentially all lognormal distributions with a sufficiently large number of species, this relation was roughly $S \approx (\text{constant}) \times N^z$, with z in the range 0.2 to 0.3. Add the further rough assumption that the number of individuals (N) is linearly proportional to the island's area (A), and you have the observed SAR power law. An additional refinement is that, although such lognormal distributions of relative abundance of species imply a power law for a large number of species, at lower values of N (and thus A) the curves turn downward. Sugihara (*6*) later argued that Preston's canonical shape with its exponent $z \approx 1/4$, is more accurate than May's (*4*) arm-waving can justify, and he proposed a "sequential broken stick" model (*7*) for the relationship between number of individuals (N) and abundance of species (S). This, I think, gives a better, although still debatable, explanation of observed SAR (see the graph). More recently, Harte *et al.* (*8*) have offered an explanation for a pure power-law SAR that assumes "self-similarity"—the fraction of a species found in an area A, which is also found in one-half A, is independent of A. This attractive assumption certainly supports the power law, but it has the disadvantage that it gives no reason for why the z exponent is so consistently in the range 0.2 to 0.3, nor does it agree with the observed departure from a pure power law at low values of A.

Now come Plotkin and co-workers with their new study (*3*). They begin with an especially valuable collection of data on the diversity of tropical tree species within each of five 50-ha study sites—in India, Panama, Thailand, and Malaysia (see the figure). Motivated by the work of Harte, Plotkin *et al.* calculate, for each plot, a spatial persistence function, $a(A)$, which describes the average fraction of species present in A that are found (or "persist") in one-half A. For Harte's self-similarity assumption, $a(A)$ is constant. To the contrary, Plotkin *et al.* find that the persistence function depends on A, in a way that is fairly similar for each of their 50-ha plots. From this analysis, they suggest that the plots have SAR patterns that roughly obey the relation $S = cA^z \exp(-kA)$, where the usual c and z, along with the additional parameter k, can be estimated from the empirical $a(A)$ curves. Interestingly, z and k estimated in this way from any one plot give a good description (to within 5 to 10%) of the shape of the SAR on any of the other plots. That is, the five SARs have similar shapes, although the absolute number of species for a given value of A, which depends on the parameter c, varies significantly among them.



Seeing the forest and the trees. The locations of five tropical forest plots, each 50 ha in size. In each plot, every woody stem greater than 1 cm in diameter was identified by species and counted in the census. Boxes show the total number of trees and the total number of species for each plot. [Adapted from (*3*)]



The diversity of species. The species-area relation (SAR) observed by Plotkin *et al.* (*3*) in the Pasoh tropical forest site in Malaysia compared with the predictions of four theoretical models. Specifically, all four models have a scaling parameter (c) that essentially depends on overall species richness. For the Plotkin "persistence method," the curve (which involves at least two adjustable parameters) is taken from their paper (*3*). The self-similarity assumption gives a pure power law, with an arbitrary exponent z; here, $z = 0.25$. The canonical lognormal and the sequential broken stick graphs have uniquely determined shapes (which asymptotically give power laws with $z = 0.25$), and thus have no adjustable parameters beyond c.

The data presented by Plotkin *et al.*—the outcome of a long-term research program coordinated by the Smithsonian Institution's Center for Tropical Forest Science—are immensely useful. As emphasized by the authors, their observed SARs on average roughly conform to a power law with $z \approx 1/4$, but such a simplistic statement underestimates the slope when the area is smaller (as noted by others) and overestimates the slope when the area is larger. The similarity in SAR shapes, despite the differences in overall species richness among the five plots, suggests that we can estimate the diversity of tree species in other unstudied tropical places, on the basis of sampling in just one relatively small area.

Turning from phenomenological usefulness to theoretical underpinnings, there are a number of nagging questions. First, it is not surprising that, with two adjustable parameters (z and k), Plotkin *et al.* can fit observed SAR observations better than the earlier theorists who used one-parameter models (z only). (Give me five parameters, and I will fit elephants.) Second, although Plotkin *et al.* (*9*) have begun to explore possible theoretical bases for their observed persistence functions, this work is itself phenomenological, based largely on observed clustering patterns of trees.

Third, as is true for other work oriented toward conservation biology, Plotkin *et al.* are not truly dealing with species-area relations, but rather with sampling effects (*4*). In the original body of work on SAR, which dealt with archipelagos of islands, the rough equilibrium numbers of plants or animals found on islands of different sizes were determined. This is clearly similar to asking about subplots within a larger tropical forest plot, but it is not exactly the same question. Before taking phenomenological rules and theoretical ideas about SAR (from real or virtual islands) and applying them to problems in conservation such as the fragmentation of tropical forests, I would like to see more careful discussion of the similarities and differences between these two ecological situations.

The new work certainly is important from the point of view of the empirical patterns it has uncovered and for the theoretical questions it raises. With the world's tropical forests currently disappearing at

an overall rate of between 0.8 and 2% each year—even the rate is uncertain—we desperately need ambitious projects, such as the Tropical Forest Science project on which this work is based, to ensure that effective conservation action is taken.

References and Notes

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PERSPECTIVES: MICROBIOLOGY

Action at a Distance—Bacterial Flagellar Assembly

Robert M. Macnab

The rapid rotation of a long helical filament called the flagellum propels bacteria such as *Escherichia coli* and *Salmonella*. The flagellum is composed of a reversible rotary motor comprising several different proteins; this is connected to a long filament (the propeller) assembled from subunits of the protein flagellin (*1*). The flagellar motor uses the proton electrical potential across the bacterial membrane as an energy source instead of hydrolyzing the energy-rich molecule adenosine triphosphate, which powers many other molecular motors. A molecular switch, set by incoming sensory information from the environment, determines the direction of motor rotation so that bacteria move toward positive stimuli such as food and move away from negative stimuli such as toxins. The flagellum extends far from the bacterial surface, presenting the bacterium with something of a problem—how are individual flagellin monomers added to the distal tip of the growing filament? In a report on page 2148 of this issue (*2*), Yonekura *et al.* describe the beautiful and subtle process of flagellin monomer assembly. By analyzing the tips of individual filaments under the electron microscope, they were able to observe how flagellin monomers that had diffused down the hollow interior of the flagellum became added to the filament tip with the help of a pentameric protein complex called the cap.

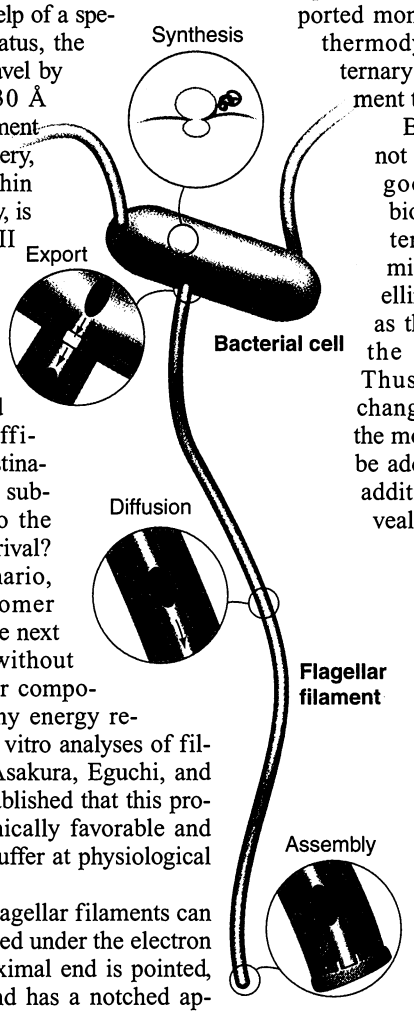
Assembly of the flagellum begins with components, such as the rotary motor, that are closest to the bacterial surface and ends with the filament, the most distal substructure. The filament is extremely long and slender and is composed of tens of thousands of flagellin subunits (*3*, *4*) that are synthesized in the cytoplasm and must be exported to the assembly site (see the figure). But how do the flagellin subunits arrive at their destination without getting lost? After translocation across the bacterial inner and outer membranes with the help of a specialized export apparatus, the flagellin monomers travel by diffusion down a ~30 Å channel inside the filament (*5*). The export machinery, probably located within the flagellar basal body, is similar to the type III protein complex that enables pathogenic bacteria to secrete virulence factors (*6*).

The channel ensures that exported flagellin subunits efficiently reach their destination, but how do the subunits get attached to the filament tip upon arrival? In the simplest scenario, each flagellin monomer would just settle in the next available position, without assistance from other components and without any energy requirement. Indeed, in vitro analyses of filament assembly by Asakura, Eguchi, and Iino (*7*) long ago established that this process is thermodynamically favorable and proceeds rapidly in buffer at physiological pH and temperature.

The two ends of flagellar filaments can be readily distinguished under the electron microscope: The proximal end is pointed, whereas the distal end has a notched appearance. However, when filaments grow in vivo, the notched shape of the distal end appears as a thin flat line, suggesting that there is a disklike structure that caps the filament tip (*8*). So, the assembly of flagellar filaments in vitro and in vivo is clearly different.

During the 1980s, biochemical analyses determined that the filament cap is a distinct structure made from the protein FliD (*9*); *fliD* mutant bacteria export flagellin subunits, but these are not added to the filament tip and instead pass out through the channel and are lost (*10*). This finding was interpreted to mean that the cap is a kinetic trap that gives the exported monomers time to settle into thermodynamically favored quaternary interactions with the filament tip.

But things turn out to be not quite that simple. There is good evidence (steric and biochemical) that the amino-terminal and carboxyl-terminal sequences of the flagellin monomers are unfolded as the monomers travel down the filament channel (*11*). Thus, large conformational changes would be required in the monomers before they could be added to the filament tip. In addition, structural studies reveal a mismatch in symmetry



When the cap fits. Monomers of flagellin (red) are synthesized by ribosomes (pale yellow) within the bacterial cell and are then exported by a specialized apparatus (green) at the base of the flagellum into a channel in the growing filament. The flagellin monomers diffuse down the filament channel toward its far end, where they assemble at the filament tip under the guidance of a pentameric cap (purple).

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