

It has been known for more than 40 years that a moon whose orbit is tidally evolving away from a planet can trap a more distant moon in an orbital resonance, pushing the exterior moon outward ahead of itself (5). As the inner orbit expands due to tidal forces, the satellites thereby maintain the commensurate mean motions and move outward together (6).

The ratio of energy to angular momentum required to expand an orbit without changing its eccentricity is just the orbital frequency. So if energy is transferred outward to a moon with a longer orbital period, not enough angular momentum is available to maintain the circularity of the orbits, and the eccentricity of one or both moons increases (7). In the case of Jupiter's large inner moons Io, Europa, and Ganymede, which are locked in a 4:2:1 resonance identified by Pierre-Simon Laplace two centuries ago, tides raised by Jupiter on the satellites damp this eccentricity, producing persistent volcanic activity on Io and a liquid ocean below Europa's thin ice crust. Pluto itself was pushed hundreds of millions of kilometers away from the Sun by Neptune, as this giant planet migrated outward (as a back reaction from throwing solid bodies sunward, however, not solar tides) (8). Pluto is still locked in a 3:2 resonance with Neptune, and its high eccentricity is evidence of this migration.

But what of Nix and Hydra, which travel on circular orbits and are too small and distant to have their orbital eccentricities tidally damped? The answer is that the resonances in which Pluto's tiny moons were trapped, both were maintained by and acted to enhance (albeit not by much) the eccentricity of Charon. Charon, being much larger as well as closer to Pluto, has its eccentricity damped in a time that is much less than the age of the solar system. Indeed, for this mechanism to work, Charon must have initially been on a highly eccentric orbit, which would be expected if it was captured nearly intact after an inelastic collision (3), rather than having accreted from a giant impact-produced disk (the preferred mechanism for the formation of Earth's Moon).

Ward and Canup have offered a model that explains the origin of the orbital configuration of Pluto's three known satellites via tidal expansion from a compact system that was produced by a giant impact. Their model requires the impact origin of an intact Charon, which previous models (3) suggest is likely only if the Pluto impactor was a homogeneous mixture of ice and rock. Hence, the model of Ward and Canup also predicts that Nix and Hydra are made of ice-rock mixtures. Pluto is by far the brightest and best known of the Trans-Neptunian Objects (TNOs). Once believed to be a planet-sized body, it is now viewed as one of

the larger members of a populous class of distant solar system bodies. Many other TNOs are known to have moons. Observations of the orbital characteristics of additional, smaller moons of such minor planets could indicate whether their observed large moons were formed by giant impacts or purely gravitational capture (9).

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6. Moons trapped in such orbital resonances always have conjunctions (pass one another) near the place where their elliptical orbits are farthest apart. If the outer moon is moving too fast, conjunction occurs where the radial separation of the orbits is decreasing. This means that the outer moon gets pulled forward after conjunction more than it was pulled back before conjunction, resulting in a net transfer of orbital energy and angular momentum from the inner moon to the outer moon, expanding the outer moon's orbit and thereby slowing its orbital motion. Consequently, the next conjunction occurs closer to the longitude where the radial separation is maximized. For further details, see S. J. Peale, *Ann. Rev. Astron. Astrophys.* **14**, 215 (1976), and especially his figure 1.
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ECOLOGY

Crafting the Pieces of the Diversity Jigsaw Puzzle

R. L. Kitching

After his encounter with the Atlantic rainforest of Brazil, Charles Darwin observed that "the land is one great, wild, untidy, luxuriant hothouse, made by Nature for herself" (1). Increasing knowledge of the forest fauna over the past 30 years has only underscored Darwin's point: 978 species of beetles from six trees in Venezuela, 160 species of grasshoppers in 60 trees in Amazonia, 218 species of ants from 19 trees in Sabah—the list goes on (2). Dobzhansky, with characteristic prescience, asked "why?" as early as 1950 (3). He suggested that the ani-

mals of the Tropics were fundamentally different from those of temperate regions: In general, tropical species were more specialized, with niche limits defined by interactions among species rather than by physical or chemical factors. This has proved very difficult to test; indeed, it moved surreptitiously from hypothesis to dogma without any very critical evaluation. This difficulty is nowhere more acute than in the case of tropical herbivores. Two reports in this issue, one by Novotny *et al.* (4) on page 1115 and the other by Wilf *et al.* (5) on page 1112 shed light on both old and new aspects of these issues.

The relationships between the diversity of tropical trees and that of the associated arthropods have been central in the exciting if some-

Herbivorous insect species are more numerous in tropical than in temperate forests. Studies of present-day forests and fossil leaf patterns show how plant diversity controls insect diversity.

what circular debates on global species richness. It is relatively easy to count the number of tree species in a forest and to extrapolate this count to a region, continent, or even planet. If each tree species supports a certain number of herbivorous insects, then we can extrapolate to a global estimate of herbivore richness. With a few further assumptions, we can obtain an overall number of all arthropod species. That the estimates range from 5 to 100 million (6) suggests that this is not an exact science.

The Novotny/Basset group based in Papua New Guinea has been one of only two or three groups that have measured tropical host specificity empirically by field collecting, larval rearing, and choice experiments. Based on

The author is at the Australian School of Environmental Studies, Griffith University, Brisbane, Queensland 4111, Australia. E-mail: r.kitching@griffith.edu.au

thousands of rearing records from almost 60 tree species, they have constructed a database that promises answers to many fundamental questions on herbivory and diversity. They showed previously (7) that host plant phylogeny plays a key role in determining levels of specialization in dominant groups of insect herbivores. But how to use this information to say something general about insect herbivory in tropical as opposed to temperate ecosystems?

The problem is the perennial one of just what is a legitimate comparison: how to line up insect responses to ecosystems that, on the one hand, exhibit a tree diversity of perhaps 200 per hectare with one with perhaps 20? This is compounded when host plant records from temperate forests have been accumulated by centuries of anecdotal observation rather than by the intense, controlled observation of the best current tropical studies. In a masterful piece of interdisciplinary work, Novotny and his colleagues have overcome these problems and come up with an utterly unexpected answer. First, they applied their “tropical” methods to a mature forest in central Europe. They then used the power of GenBank to produce a phylogeny for the 14 tree species studied in Moravia. In a stroke of remarkable originality they then extracted from their database from New Guinea the 14 tree species that presented a phylogeny most closely congruent with the central European data set. So they were able to make a legitimate quantitative comparison of herbivore host specificity in temperate and tropical forests. There was no difference in the distribution of host specificities between the two regions. The huge richness of herbivorous insects in tropical rainforests is driven by the phylogenetic diversity of the plant assemblage in those forests and not by any fundamental differences in the nature of the niches of the herbivores.

The Novotny *et al.* result supports the general idea of a post-Pleistocene equilibrium (setting aside the anthropogenic clearing of trees on a vast scale) and an explanation of the herbivore diversity that we observe in nature. Simply stated, the Novotny law becomes: “Herbivore richness in forests is related positively to the phylogenetic breadth of its supporting tree assemblage.”

In a fascinating contrast, Wilf *et al.* have used the vast deposits of leaves from Cretaceous

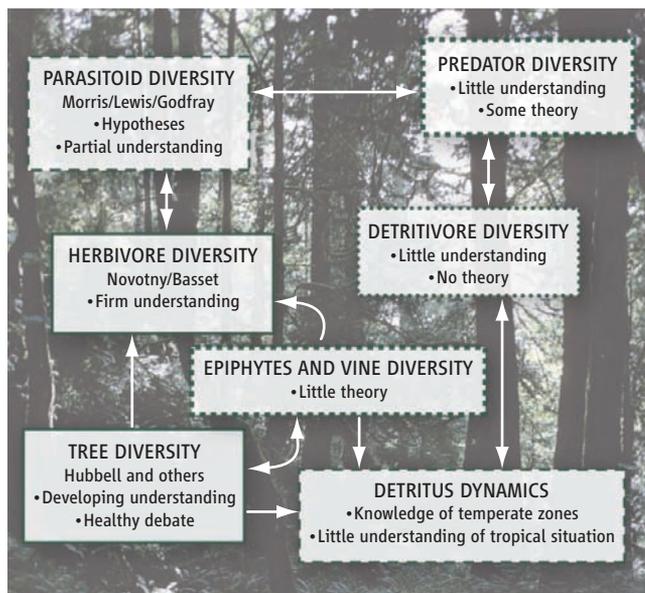
and Tertiary beds in North America to demonstrate that an equilibrium world is, geologically speaking, but a temporary end point rather than a constant property of ecosystems. Leaves carry with them species-specific patterns of herbivore activity. They show clearly that after the Cretaceous-Tertiary (K-T) mass extinction about 65 million years ago, recovery of herbivore richness was both slow and

of rainforest tree diversity. The initial proposition of equivalence across all trees of whatever species, melded with essentially random replacement processes (the “neutral” theory), produced results that mimicked well some commonly used species/abundance relationships. That such relationships could be generated with patently unrealistic assumptions has refocused attention on how we look at and

interpret diversity data. The heated debate that followed points now to a more deterministic theory focusing on the idea of rare species advantage. The generalizations that emerge from the work of Novotny *et al.* mean that we can extend our understanding of biodiversity-generating processes to the next trophic level—the herbivores. Their results make clear the “bottom-up” effects of plant diversity on the herbivore assemblage. There are undoubtedly “top-down” effects as well. Here the work of Lewis and Godfray (9) and Morris *et al.* (10) shows that apparent competition among host species is mediated through their assemblage of parasitoids—larval insects that prey on their hosts from the inside, so to speak.

In a simplified, general, rainforest food web (see the figure), the consensus (or at least the basis for a healthy debate) that we may now expect on tree diversity and the associated herbivores leaves several components requiring explanation: the third trophic level comprising the parasitoids and predators, and the externally maintained food chains based on decomposition processes (plus, incidentally, a general understanding of the interaction between herbivores and the epiphytes and vines so characteristic of tropical forests).

Processes determining the diversity of predators await their champions. Parasitoid assemblages are better understood as modifiers of herbivore diversity than as community-level objects in themselves. There has long been work on the top-down role of predators and parasitoids as modifiers of the assemblages of potential prey items, notably the idea that key predators can be the forces that flip whole food webs among different equilibria. We also have some controversial evidence of invariant or at least constrained predator-prey statistics within simple food webs (11), but mechanistic explanations are lacking. Finally, there are the chewers of rubbish—the “garbos” (if I may be permitted an Australianism). Arthropods that feed either on fungi or directly on detritus and its associated



Components of biodiversity in the forest. The diagram depicts a highly simplified rainforest food web. Dashed or dotted boxes indicate areas for which general explanations of diversity are either incomplete (dashed) or lacking (dotted) altogether.

more important, patchy. The rainforest-like faunas of the Castle Rock site in Colorado show a Paleocene herbivore signal more diverse than anything from the Cretaceous. In contrast, most other more temperate floras from the Paleocene show a dramatic reduction in herbivore signal. Bringing the two results together, Cretaceous assemblages should obey the Novotny law, whereas post-K-T ones may deviate from it significantly. With only a modestly richer database than the currently available one, this contention could be tested and so combine paleoecology and its modern counterpart in a productive way.

The firm basis of understanding as to just why herbivores are so diverse in tropical forests is part of a recent and welcome transition in tropical ecology. Over the past few decades, we have built up an impressive body of data that identifies biodiversity patterns in tropical rainforests. There remains much to be done, but there is enough information that we can look for general mechanistic explanations of the patterns. A recent flurry of activity followed Hubbell’s work (8), resulting in an active, firmly based debate on the generation

microorganisms make up as much as 30 to 40% of the rainforest fauna. General patterns for these components are few, and diversity-generating mechanisms are entirely conjectural at this time (12). There remains much to do, but this is an exciting time for rainforest ecologists. Encouraging progress toward a general theory has been made, and the field, laboratory, and statistical tools surely exist to maintain this drive.

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PHYSICS

Surface Transfer Doping of Semiconductors

Jürgen Ristein

“Doping” of semiconductors—that is, the local manipulation of their conductivity—is a key technology for electronic devices. Without doping, for example, a gallium nitride sample larger than the White House would be needed to host a single mobile charge at room temperature; for diamond, not even the volume of the globe would be sufficient. It is only through doping that semiconductors become useful electronic materials. Recent studies have revealed an unconventional way to achieve doping through surface engineering.

Doping of semiconductors is usually achieved by incorporating atoms of appropriate elements into the host lattice of the semiconductor. The dopants either release an excess electron as a free negative charge carrier to the semiconductor (n-type doping) or they consume one more electron for chemical bonding than they brought with them (p-type doping). In the latter case, the “stolen” electron behaves like a positive charge carrier—a hole—in the semiconductor.

The electrons or holes remain weakly bound to the dopants that carry their respective counter charge, and it takes a characteristic activation energy Δ to release them as free charge carriers. For effective dopants, this energy is rather small. At room temperature, it is easily supplied by the vibrations of the semiconductor atoms, and one ends up with free charge carriers of one sign and fixed ionized dopants with opposite charge. This situation is sketched for p-type doping in the figure (left panel).

The author is in the Lehrstuhl für Physik Universität Erlangen-Nürnberg, 91058 Erlangen, Germany. E-mail: juergen.ristein@physik.uni-erlangen.de

If the dopants are distributed homogeneously in the semiconductor lattice, then so will be the mobile charge carriers. Positive and negative charge cancel, and on average, no electric field acts on the mobile charge carriers. For electronic devices to function, the doping must therefore be inhomogeneous. Inhomogeneous doping results in local variations of electron and hole concentrations, which tend to equalize by diffusion. The result is a delicate equilibrium between charge separation and electric field that determines the electrical response of a device to externally applied voltages. The simplest such device is the p-n junction, which consists of a p-type and an n-type doped layer of the same semiconductor.

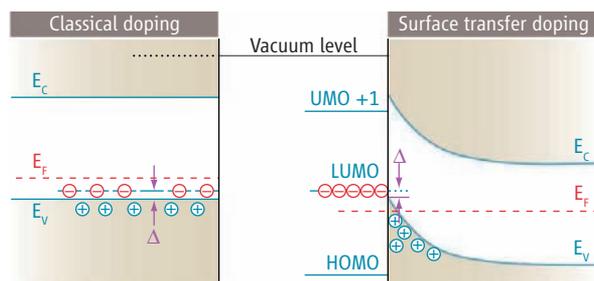
In all classical devices, the dopants are impurity atoms introduced into the bulk of the semiconductor. But doping can also be achieved by an electron exchange between a semiconductor and dopants situated at its surface. The surface dopants—below, we will use acceptors for illustration—possess unoccupied molecular orbitals for electrons (UMOs). If the energetically lowest of these orbitals (called LUMO) is close to the valence band maximum of the semiconductor, it will steal an electron from the semiconductor, just as classical acceptors do (see the figure, right panel). As a result, holes will form in the semiconductor, and negative charge will be localized on the surface acceptors (1). This charge separation will automatically establish an electrostatic potential that con-

The local conductivity of semiconductors can be changed by incorporating various atoms into the semiconductor material. New work shows that manipulation of the surface can produce the same effect.

finishes the holes in a perpendicular direction but leaves them free to move parallel to the surface.

This kind of p-type surface transfer doping has recently been demonstrated for fullerene (2) and fluorofullerene molecules (3) serving as surface acceptors on hydrogen-terminated diamond. The hydrogen termination leads to an exceptionally low ionization energy for the diamond; the fullerenes were chosen for their high electron affinities. For $C_{60}F_{48}$ (4), the activation energy Δ is even negative, and each molecule brought onto the diamond surface creates a hole (1).

The electronic states at the surface are not necessarily associated with molecular adsorbates. In fact, the first observation of p-type surface transfer doping of diamond involved a complex electrochemical system, in which hydrated ions acted as surface acceptors (5). These ions were usually created unintention-



Beyond conventional doping. This band diagram illustrates classical p-type doping (left) and p-type surface transfer doping (right), using the energy of an electron in free space as a reference (vacuum level). E_c and E_v are the energies of the conduction band minimum and the valence band maximum, respectively. The balance between electrons localized in acceptor states and free holes in the valence band is expressed by the constant Fermi energy E_f . The closer E_f is to E_v , the higher the local density of holes. LUMO and HOMO are the lowest unoccupied and highest occupied molecular orbitals of the surface acceptors, respectively.