number of micrometre-scale asperities, rough protrusions from the coin's surface. The weight of the coin, channelled through these tiny asperities, creates localized stresses so strong that the metal in the coin flows plastically at the asperities[2]. Thus the frictional mechanics of the coin is actually controlled by material phenomena at scales that are much smaller than the size of the coin. Amontons' laws ignore the existence of these complex phenomena at smaller length scales entirely, at the cost of introducing a highly nonlinear description at the macroscopic scale of the coin.

Granular physics, the science of assemblies of hard grains such as are found in a sand dune or an aspirin bottle, is complex and nonlinear for much the same reason[3]. The typical forces generated in granular flow and packings are not sufficiently strong to distort the particles macroscopically, so the particles are viewed as rigid. However, on the much smaller scale of the contacts between particles they can be highly distorted. This separation of scales again yields a highly nonlinear macroscopic description; indeed, there is still considerable controversy over precisely what macroscopic description appropriately encodes the microscopic physics.

Thus the science of mechanics becomes increasingly entwined with asymptotic analysis, the branch of applied mathematics dedicated to understanding the behaviour of equations at the limits where parameters become extremely small or large. Mechanics has moved to centre stage in our endeavour to understand in detail the links between microscopic and macroscopic dynamics. ■

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Ecology

Tail of death and resurrection

John Harte

Estimating the proportion of rare species in particular habitats is a big issue for ecologists. Hence the intensity of debate over whether 'neutral theory' has predictive value for species abundances.

First, the news. Earlier this year, Brian McGill[1] made an attempt on the life of the 'neutral theory' in ecology. That attempt has been thwarted by Volkov *et al.* (page 1035 of this issue[2]). But what is the neutral theory? How did the assassination attempt take place? And how has the theory been rescued from that attempt?

The neutral theory is the brainchild of Stephen Hubbell, one of the authors of the new paper[2]. It is a bold attempt to understand the influence of speciation, migration, birth, death, dispersal and extinction on the composition of ecosystems[3]. Its boldness lies not in the breadth of processes that it incorporates but in its manifestly oversimplified central assumption of neutrality. This assumption states that differences between traits that we really know differ from species to species — birth, growth and death rates, habitat preferences, dispersal abilities — can be neglected. In the theory, individuals in all species have the same probabilities of birth and death, but random outcomes of probabilistic demographic processes generate differences in species characteristics such as their abundance. Surely such a theory should be easy to slay?

C. ZIEGLER/STRI

Figure 1 **Ecological test site: Barro Colorado Island, Panama, on which a 50-hectare Forest Dynamics Plot is maintained by the Center for Tropical Forest Science of the Smithsonian Tropical Research Institute. Tree census data have been gathered here since 1982; it is these data that are used in the tests[1,2] of neutral theory discussed here.**

The attempt on its life was made by McGill in a paper entitled "A test of the unified neutral theory of biodiversity"[1]. McGill analysed a data set from Barro Colorado Island (BCI; Fig. 1) in Panama, which contains the location and species identity of all the trees on a 50-hectare plot of tropical forest. The neutral theory predicts a measure known as relative species abundance, which is expressed in terms of a probability distribution describing the fraction of species with any given abundance. The left tail of the probability distribution, which characterizes how many rare species there are, is of particular interest in ecology because it is rare species that are most likely to disappear under habitat loss. It is difficult to include rare species in census counts, so having a theory that reliably predicts how many there are is of enormous value.

McGill contrasted the neutral theory prediction of the relative species abundance with the lognormal distribution, an old standby function often used by ecologists to describe relative species abundances, and concluded that the lognormal fitted the BCI data better than the neutral theory prediction did. A hand-waving justification for the lognormal distribution is that it could arise from the central limit theorem, which in its more familiar form states that the distribution of a variable that is the sum of a collection of random variates is a normal (gaussian) function. If birth and death rates are governed by products of random factors, with a different product chosen for each species, then that same theorem states that those rates will be distributed lognormally from species to species. In contrast to the neutral theory, species differences will be built in from the outset. For many ecologists, the simple plausibility of that argument contrasts with what they feel is the unpalatable central assumption of neutrality, and so McGill's finding that the lognormal distribution fitted the data better was welcome news for many.

To the rescue now come Volkov and two other theoretical physicists, who have teamed up with Hubbell to perform a mathematical *tour de force* and a reanalysis of the data[2]. To calculate the predicted relative species abundance, McGill was forced to perform a computer simulation of the neutral theory, but the complexity of the theory resulted in numerical output whose accuracy could not be quantified. Instead, Volkov *et al.* derive an analytical solution of the neutral theory. When they compare that solution for relative species abundance against the lognormal distribution, the former fits the BCI data somewhat better. So reports of the death of the neutral theory were premature.

And now, the views. A look at Fig. 1 of Volkov and colleagues' paper, reproduced as

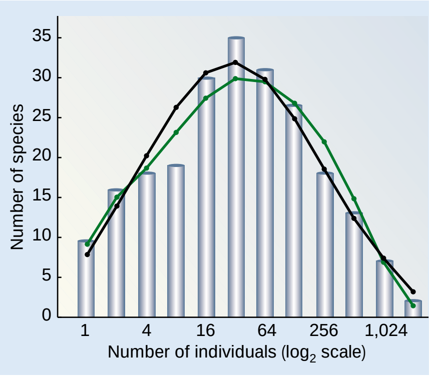

Figure 2 **Matching theory to data. Lognormal (black) and neutral (green) expectations against the data on 21,457 trees in 225 species from the 50-hectare plot on Barro Colorado Island. Here the data are grouped in 12 logarithmic intervals; note the slight asymmetry in the neutral theory prediction, favouring the bulged left-hand tail of the empirical distribution. Reproduced from ref. 2.**

Fig. 2 here, might leave readers perplexed. Both the lognormal and the neutral theory predictions look very good and at the tails of the distribution they are essentially indistinguishable. Surely when 21,457 individual trees, distributed among 225 tree species, are counted there will be measurement uncertainty, particularly given that very tiny young trees are not included. Should we really care whether one function fits slightly better than the other? More generally, how should theory-testing in ecology proceed?

Proposed theories are valuable when they make many falsifiable predictions, preferably about a variety of phenomena not previously recognized as being interconnected. Arguments about whether this or that function fits an empirical relative species abundance slightly better are unlikely to advance the field. Consider the lognormal distribution first. It is not really a theory, but rather a proposed mathematical function; its connection to relative species abundance has been motivated by a conceptual model of how growth and death are regulated in ecology. Advocates of the lognormal distribution would best serve their cause if they actually examined and modelled the dominant mechanisms of growth and death, checked for the applicability of the central limit theorem, and then made a swarm of testable predictions — not just about relative species abundance but about growth and death rates under different circumstances, about the relationship between body size and abundance, about the spatial distributions of species, and about time series of population fluctuations under different environmental conditions.

The ability of the neutral theory to make testable predictions about a wide variety of behaviours could also be more fully explored. One prediction of the theory pertains to what ecologists call beta diversity — the pattern of changing species composition in separated patches of habitat as a function of the distance between patches. In the neutral theory, species turnover with distance should result from dispersal but not from spatial variability in the different habitat niches. A test of this at the BCI plot found empirical patterns to be inconsistent with the prediction of the neutral theory[4].

Indeed, theories such as Hubbell's are valuable because they can and will fail some tests. In failing, they will tell us about the importance of the mechanisms that they assume away at the outset. Perhaps ecologists will some day develop a theory whose simplifications resemble that of the ideal gas assumption in thermodynamics and statistical physics: a seemingly preposterous assumption (point molecules, purely elastic collisions) that yields amazingly accurate predictions of a multitude of phenomena. No physicist would say that, because *PV* does not exactly equal *nRT*, the theory is wrong. Let's hope that ecologists heed that message. ■

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Quantum gravity

An astrophysical constraint

Sean Carroll

A quantum theory of gravity is proving elusive. Observations of radiation from the Crab nebula now place even stronger constraints on the likelihood of detecting the effects of quantum gravity.

For decades, physicists have been in search of quantum gravity, a theory that would encompass both general relativity and quantum mechanics. One of the difficulties in this quest is the paucity of detailed experimental data; direct effects of quantum gravity are generally thought to be out of reach of foreseeable experiments. But, if we are lucky, the effects of quantum gravity might cause small violations of spacetime symmetries, violations that could be directly observed through the behaviour of particles at high energies or over large distances. A new astrophysical test — reported by Jacobson *et al.*[1] on page 1019 of this issue — suggests, however, that we might not get lucky.

In the process of developing his theory of blackbody radiation in the late nineteenth century, Max Planck was forced to introduce a new fundamental constant into physics — what we now know as Planck's constant, *h*. Almost immediately, Planck realized that this number could be combined with the speed of light, *c*, and Newton's gravitational constant, *G*, to construct a set of natural units for quantities such as length, energy, mass and time (known as the Planck length, the Planck energy, and so on). He was happy to note that even extraterrestrials would understand these units, thus making quantitative communication between civilizations possible.

Planck's units combine the fundamental parameters of special relativity (*c*), general relativity (*G*) and quantum mechanics (*h*). We therefore expect that they should indicate the point at which quantum gravity begins to manifest itself. For example, if two particles collide with a total energy greater than the Planck energy, quantum gravity should have an important role in the outcome. Unfortunately, the Planck energy scale is approximately 10^{19} gigaelectronvolts — 16 orders of magnitude larger than the regimes being explored by our highest-energy particle accelerators. So it seems difficult, even impossible, to get any direct experimental data relevant to the reconciliation of gravity and quantum mechanics.

But our understanding of fundamental physics will not be coherent, much less correct, until quantum gravity is understood. It is therefore worth trying to think of clever ways to access phenomena at the Planck scale that we might at first think are beyond our reach. One possibility, common to several (but certainly not all) models of quantum gravity, is a breakdown of Lorentz invariance. This symmetry, a cornerstone of special relativity, says that there is no universal standard of rest; reference frames that are moving with respect to each other at constant velocities should be physically equivalent, and the speed of light looks the same to any observer. But perhaps this is only an approximation; if spacetime is discrete (rather than smooth) at small scales, for example, Lorentz invariance may break down at very short distances or very high energies.

Astrophysical phenomena provide a way of testing this idea. A phenomenological model[2] has been proposed in which Lorentz-