leads to rapid, seemingly random cycling between different kinds of motion. At the suggestion of Vitali Averbukh of the Technion in Israel, the Phillips group took pains to rule out the possibility that classical chaotic transport was heavily involved, thereby confirming that dynamical tunneling was taking place.

The experiments also raised the possibility of an even newer tunneling concept — chaos-assisted tunneling. Chaos can coexist with regions of stable, non-chaotic motion because some types of motion, called regular motion, can avoid getting mixed up in the chaotic fray. In this regime, chaos can assist tunneling by providing a ‘free ride’ over to another zone of regular motion once the system has tunneled out of the first regular zone into the chaotic region.

Any previous experiments have demonstrated quantum tunneling by individual atoms or molecules, but a nearly macroscopic system containing millions of atoms might be expected to behave more classically. Certainly near-macroscopic tunneling has been seen before, as in the Josephson effect in superconductors or in barrier tunneling by Bose-Einstein condensates, but such observations are rare, and physicists are always hungry for more examples. From a broader perspective, these and other recent experiments demonstrate that it is possible to exert quantum control over ultracold atoms with astonishing finesse and coherence. We can look forward to a continuing stream of mind-bending examples, perhaps leading to a better understanding of the implications of quantum mechanics.

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Ecology

**Price put on biodiversity**

Osvaldo E. Sala

The greater the plant diversity in an ecosystem, the greater the ecosystem’s productivity. A new analysis indicates that the higher productivity results from complementary patterns of species resource use.

Human activities are drastically altering Earth’s biodiversity. To get a handle on what the consequences might be, ecologists have been busily carrying out experiments. But interpreting such experiments has been confounded by the possible operation of two different causal mechanisms, with contrasting implications. This matter is tackled by Loreau and Hector on page 72 of this issue. They have devised a way of teasing apart the two effects, drawing upon a formulation — the Price equation — used...
in evolutionary genetics, and have tested their approach on a large body of data from European grasslands.

The continuing changes in biodiversity are of great concern. Some 5–20% of species in many groups of organisms have become extinct through human action, either direct or indirect. And given continuing changes—in land use, climate, nitrogen deposition and concentration of atmospheric CO$_2$, and increasing species invasions to the detriment of the existing inhabitants—such losses look likely to increase. Hence arises the pressing question of how changes in biodiversity affect the functioning of ecosystems and their ability to provide goods and services for humans. How will primary production and nutrient cycling be affected? And will the capacity of ecosystems to sequester carbon and provide food, fibre and clean water be impaired?

Several large, controlled experiments have shown that primary production seems to be higher with greater biodiversity. But ecologists have struggled to distinguish between two alternative hypotheses to account for the results. These are 'species complementarity' and the 'sampling effect'. The first is an ecological phenomenon, the second a statistical consequence of experimental design. What Loreau and Hector have done is to propose a way of telling the difference between the two.

The species-complementarity hypothesis is based on the idea of a trade-off between species traits. For example, different species may have deep or shallow roots, growth optima at high or low temperatures, or high or low relative growth rates with corresponding resistances to stress. Ecosystems that have a larger number of species will probably have a broader range of traits—and thus, for example, are more likely to draw on both shallow and deep layers of the soil, or to fix carbon at both low and high temperatures.

The sampling effect, in contrast, states that increased productivity with increasing diversity is an artefact of experimental design. It stems from the principle that different species are differentially adapted to a given environment. In most biodiversity experiments, the probability of a given sample containing the best-adapted species increases as diversity increases, because the species composition of each sample is a random draw from a finite pool of species.

Loreau and Hector's method is intended to distinguish between species complementarity and the sampling effect. It is based on the Price equation, which is used in evolutionary genetics to calculate changes in the frequency of a trait between individuals in one generation and the ancestral generation as a function of the covariance between fitness and trait value. Loreau and Hector's insight is to have identified parallels between the sampling effect in biodiversity experiments and the selection effect seen in the classic Price equation. Their new 'biodiversity equation' includes two terms that partition the 'biodiversity effect' into the distinct species-complementarity and sampling mechanisms. The biodiversity effect is the increase in yield with increasing biodiversity, yield in this case representing biomass, primary production or any other measure of ecosystem functioning.

The sampling effect is calculated as the covariance between species' yield in monoculture and its yield in mixed plots. The species-complementarity effect is calculated as a function of the increase in yield of a mixture of species relative to the expected yield based on the yield of the same species growing in monocultures.

A hypothetical example is depicted in Fig. 1. This shows how yields of mixtures of plants can be higher than the sum of their yields in monoculture as a result of either species complementarity (Fig. 1a, b) or the sampling effect (Fig. 1c, d), and also how the contribution of each mechanism can be quantified using the Loreau–Hector equation. An explanation that invokes species complementarity for the increase in yield might be that, in a water-limited ecosystem, two species use different water sources (say, shallow or deep soil layers). A sampling-effect explanation might be that species A is better adapted than species B, not only achieving a higher yield in monoculture but also dominating the mixed-species plots to the virtual exclusion of B.

Loreau and Hector applied their equation to results from BIODEPTH. This experiment, designed to assess the relationship between biodiversity and ecosystem functioning, had the same design (4 or 5 levels of plant-species diversity with 1 to 32 species) replicated in seven European countries. Loreau and Hector found that the main mechanism behind the increase in production with increasing biodiversity was species complementarity. This suggests that species losses, such as those expected in the near future, may result in lower production and less effective resource use. For example, reduced uptake of soil nitrogen may lead to higher concentrations of nitrate below the root zone; such an effect has been observed in North America, and could result in other environmental problems. Similarly, losses of biodiversity may hamper the ability of ecosystems to sequester carbon: it has been shown that a variety of ecosystems can be restored to a more productive state with a higher biodiversity.
shown\(^{12}\) that plant species diversity controls the magnitude of the increase in carbon fixation as levels of atmospheric CO\(_2\) increase. How general is species complementarity? I suggest that the strength of this mechanism is related positively to the length of evolutionary history, and negatively to the frequency and intensity of disturbances to an ecosystem. Complementary resource use and synergistic relationships are more likely to occur among species that have had a chance to coevolve over long periods of time\(^{14}\). Frequent disturbance will prevent the evolution of tight differentiation in resource use, and will perturb or destroy symbiotic relationships. BIODEPTH was carried out using grassland species, mostly at sites where the potential natural vegetation vegetation was forest. These sites were maintained as grasslands because of frequent human intervention; if they had not been mowed once or twice a year, they would have reverted to forest. Species complementarity may act even more strongly in ecosystems that have been disturbed less often and have a longer evolutionary history.

We clearly need a better understanding of the relationships between biodiversity and ecosystem functioning. There are two ways forward. The first is to apply this new tool, the Loreau–Hector equation, to other existing data sets, to see how general the species-complementarity principle is. The second is to gather — and then likewise analyse — fresh data for other ecosystems by carrying out experiments such as BIODEPTH in other areas of the world with different evolutionary and disturbance histories.

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**Climate change on Venus**

**Ronald G. Prinn**

Earth’s climate has changed significantly over the past several million years. New theoretical work suggests that the climate of our nearest neighbour, Venus, may have also changed on similar timescales.

**Venus** is a most inhospitable planet. Its average surface temperature of 735 K is some 435 K higher than that of Earth. It has a thick atmosphere of carbon dioxide that exerts a surface pressure about 92 times greater than Earth’s. Its craters and volcanoes are completely shrouded by thick clouds of sulphuric acid, and its surface features are revealed only in radar images. Not surprisingly, it has no oceans and no known life. But has this extreme climate always been the same, or does it change from millennium to millennium? In an article in Icarus, Mark Bullock and David Grinspoon\(^1\) describe a numerical simulation of venusian climate that suggests it has oscillated over the past billion years between periods of global cooling and global warming.

Bullock and Grinspoon\(^1\) have developed a new radiative-convective model of the venusian climate. It is based on recent data from spacecraft (particularly the 1990–1994 Magellan mission) and from ground-based telescopes, which together provide information on the geology, geophysics and atmospheric chemistry of Venus. Their model is the first to use high-temperature, high-resolution spectroscopic data on the absorption properties of the major greenhouse gases found on Venus (mainly CO\(_2\) with trace amounts of H\(_2\)O and SO\(_2\)). The authors also include data on the rates of reaction of these gases with surface minerals at high temperatures — reactions that limit their abundance in the atmosphere. They couple their climate model to models of cloud microphysics, volcanic outgassing of sulphur dioxide and water from the crust, surface chemistry, and water loss due to hydrogen atoms escaping from the high atmosphere into space.

The Bullock–Grinspoon\(^1\) model indicates that between 600 million and 1,100 million years ago, Venus was cooler than it is today. It was cooler because sunlight was reflected by thick clouds of sulphuric acid (H\(_2\)SO\(_4\)) produced during a geologically active period when erupting lavas from global volcanic activity resulted in the build-up of SO\(_2\) and H\(_2\)O in the atmosphere. This was followed by a period of warming as the SO\(_2\) responsible for creating the clouds was depleted by reactions with minerals in the surface, raising temperatures to 900 K. But the contribution of water vapour to greenhouse warming was subsequently lowered by the steady loss of hydrogen into space and the loss of oxygen through oxidation of surface minerals. This helped to cool Venus down to today’s temperatures.

I first became interested in climate change on Venus in the early 1980s, spurred on by the intriguing results from the Pioneer mission to Venus in 1978. My own studies were aimed at understanding the processes that maintain sulphuric acid clouds on Venus, and the possibility that the clouds, and hence climate, could change as a result of changes in the emission of sulphur gases through vulcanism and thermally driven surface chemistry\(^2–4\) (Fig. 1). Work in the laboratory indicated that SO\(_2\), the precursor of sulphuric acid, could be removed from the atmosphere by reactions with surface minerals in 1.9 million years\(^5\) — a relatively short timescale for geological processes. And because the removal rate of SO\(_2\) (and hence of H\(_2\)SO\(_4\)) increases with temperature, there is also the possibility of amplifying any warming or cooling trend.

The starting point for Bullock and Grinspoon’s study was the Magellan mission to Venus in the 1990s. Magellan used radar to penetrate the clouds to produce, among other things, the first extremely high-resolution spatial map of the surface of Venus. This map indicated that the density of impact craters, and hence the number of comet and asteroid collisions recorded on the surface of Venus, was fairly low, suggesting that the present surface is only 600 million to 1,100 million years old\(^6\). The previous surface must have been obliterated by erupting magmas from volcanic activity on a global scale.

Bullock and Grinspoon’s work indicates that H\(_2\)O and SO\(_2\) have both cooperative and competitive effects on the venusian climate. The climate on Venus today is controlled by two main processes: global warming, largely resulting from the greenhouse effect of CO\(_2\) and SO\(_2\), and cooling, owing to the reflection of solar radiation by the thick clouds of sulphuric acid. Large increases in H\(_2\)O above today’s levels could amplify the greenhouse warming effect and lead to thinning of the clouds through evaporation of their lowest layers. Overall, this could increase surface temperatures by 200 K. But large increases in SO\(_2\) could cool the planet by up to 40 K by thickening these same clouds and increasing their reflectivity.

The authors propose that global volcanic activity 600 million to 1,100 million years ago injected large quantities of H\(_2\)O and SO\(_2\) into the atmosphere. This thickened the clouds of sulphuric acid, and the resulting cooling was greater than any warming these gases contributed through...