

1 of 1 DOCUMENT

NewScientist

New Scientist

May 1, 2004

One rate to rule them all;

Ecology has always lacked a strong overarching theory like those behind physics or chemistry. But no longer, thanks to the universal throttle inside every living thing, say ecologist James Brown and physicist Geoffrey West

BYLINE: James Brown, Geoffrey West; James Brown is an ecologist at the University of New Mexico in Albuquerque and the Santa Fe Institute in Santa Fe, New Mexico.; Geoffrey West is a physicist at the Santa Fe Institute and the Los Alamos National Laboratory in New Mexico

SECTION: Features; Pg. 38

LENGTH: 2327 words

IF YOU want to experience the diversity and complexity of life, walk into any forest anywhere in the world. Most revealing would be a tropical forest in Brazil, New Guinea or the Congo. Look at the birds, butterflies, ants and plants. Listen to the sounds of animals you cannot see. In just half a hectare there may be more than 1000 individuals of 100 different tree species and millions of individuals representing thousands of insect species. Is there any order to this jumble? It is hard to imagine learning the rules to the games all these organisms are playing.

Of course, any ecologist will tell you we can work out a few of the rules. This insect pollinates this tree; that one feeds on its leaves. Some plants are short-lived weedy opportunists; others grow slowly but live for centuries. But almost all such rules apply only to a specific collection of species in a particular place and time. Look elsewhere -- sometimes even just the next river basin -- and the rules are different. Despite a hundred years of research, ecology has little in the way of universal laws or principles like the laws of gravity and thermodynamics in physics or the Mendelian laws of inheritance in biology. Is ecology really devoid of universal laws?

We think not. The laws are there, just waiting to be discovered. In the past few years we have been leading a unique collaboration of biologists and physicists that has been investigating the forces behind a host of ecological patterns, and we have identified one factor that seems to have dramatic ecological consequences: metabolic rates, the rates at which organisms use energy and materials. Our developing "metabolic theory of ecology" has already provided powerful general explanations for how metabolic rate changes with the body size and temperature of animals, plants and microbes. It also predicts and explains many simple and regular relationships -- akin to the overarching laws in other areas of science.

One such regular relationship is found in forests throughout the world: there are always more saplings than mature trees, and this trend obeys a very simple mathematical relationship. Our colleagues Brian Enquist of the University of Arizona in Tucson and Karl Niklas of Cornell University in Ithaca, New York, have shown that for every tenfold increase in trunk diameter, the number of trees decreases a hundredfold (Nature, vol 410, p 655). Clearly, something interesting and important is going on here, and metabolic theory has much to say about it.

We are also finding that the metabolic approach provides general answers to many of the most important questions

One rate to rule them all; Ecology has always lacked a strong overarching theory like those behind physics or chemistry. But no longer, thanks to the universal throttle inside every living thing, say ecologist James Brown and physicist Geoffrey West *New Scientist* May 1, 2004

ecologists ask about the world -- from the growth and reproduction of individual organisms to the flows of energy and materials through ecosystems and the consequences of human-caused environmental change.

Metabolic rate is a good starting point because it is the fundamental rate of biology. Metabolism supplies the power organisms need for growth, maintenance and reproduction. It sets the pace of life at all scales, from the biochemical reactions within cells to the breakdown of litter in a forest and the global uptake of carbon dioxide.

Metabolic rates are governed primarily by two factors: body size and temperature. Scientists have known for over 70 years that as organisms get bigger metabolic rate increases, but not as fast as body size. A 200-kilogram elk, 10,000 times heavier than a 20-gram mouse, eats only 1000 times more food. Mathematically, this means that metabolic rate increases in proportion to body mass raised to the power $3/4$. Another way to express this is that metabolic rate per gram of body tissue is proportional to the body mass raised to the power of $-1/4$. Most other biological rates show the same pattern, while biological times such as lifespans increase with mass to the $1/4$ power. This means that each gram of mouse tissue uses energy at 10 times the rate of a gram of elk tissue, and the mouse's heart beats 10 times faster. But the elk lives 10 times longer and its gestation period is also 10 times longer.

The same quarter-power laws hold for plants and even for unicellular organisms such as bacteria and algae. In plants, for example, the number of leaves and the rate of photosynthesis scale as the $3/4$ power of mass, and lifespan as the $1/4$ power. In unicellular organisms metabolic rate scales as the $3/4$ power of cell mass, and cell generation time as the $1/4$ power. We have explained the origin of these quarter-power scalings in terms of geometric and physical constraints on resource distribution networks within organisms .

Beyond its effects on individuals, metabolic rate also has profound implications for ecology. Most directly, metabolic rate explains most of the variation in ecological rates and times, from how fast organisms grow and how long they live to how quickly nutrients such as carbon, nitrogen and phosphorus cycle through ecosystems. This is easiest to see in "microbe to monster" plots .

But the influence of metabolic rate extends much further than this. As we hinted earlier, it helps us understand how forests work as a function of plant size. Here's why. We know that plants of all sizes metabolise, produce new biomass and grow proportional to the $3/4$ power of their mass. In a forest at steady state, the resources needed for this growth must be freed by the deaths of other trees. When we work through the maths, we find that the number of trees of a given size must scale as the $-3/4$ power of body mass -- exactly the inverse. Putting the two together yields the striking conclusion that every size class of trees uses resources at exactly the same rate. Consequently, the many saplings use precisely the same share of resources as the few largest trees -- and we can predict this even before we set foot in the forest.

Moreover, knowing how the number of trees scales with their size allows us to correctly predict that the average distance separating trees of similar size is directly proportional to their diameter, and that probability of dying is approximately independent of size (except for seedlings and small trees, where the relationship is more complex).

Similar rules apply for the animals in an ecosystem: per capita birth and death rates scale as the $-1/4$ power of mass; population density scales as the $-3/4$ power. And each size class (lumping all species together, but keeping herbivores and carnivores separate) uses resources at the same rate -- a phenomenon that its discoverer John Damuth of the University of California at Santa Barbara in the 1980s termed the energy equivalence rule, and which metabolic theory can now explain.

When James Gillooly joined our group at the University of New Mexico in 2000, we investigated the important role of temperature. Biologists have long known that the pace of life accelerates about threefold for every 10 degreesC increase in temperature. We showed this is a consequence of basic biochemistry: as temperature rises, the rates of biochemical reactions increase exponentially (*Science*, vol 293, p 2248). But it has profound consequences in ecology, such as on competition for resources.

One rule to rule them all; Ecology has always lacked a strong overarching theory like those behind physics or chemistry. But no longer, thanks to the universal throttle inside every living thing, say ecologist James Brown and physicist Geoffrey West *New Scientist* May 1, 2004

In classic laboratory experiments at the University of Chicago in the mid-20th century, Thomas Park found that one of two species of flour beetle always outcompeted the other and drove it to extinction -- but which one won depended on the temperature and humidity. Ecologists have found no general rules that would predict the winner of such a contest based on the competitors' traits or the characteristics of the environment. Our research group asked a different question: does temperature predict the rate of interaction regardless of which species wins? Indeed it does. When Park decreased the temperature from 34 to 24 degrees C, the loser lasted more than twice as long -- 562 days, up from 247.

Temperature has other effects as well. For centuries scientists and lay people alike have marvelled at the amazing diversity of life in the tropics, especially in rainforests and coral reefs. Ecologists have shown that in most plant and animal groups, diversity increases from the poles to the equator. But they have been unable to agree upon the cause. In 1992 Australian ecologist Klaus Rohde of the University of New England in Armidale suggested that this latitudinal gradient is mostly due to temperature. Two years ago, Jim Brown's graduate student Andrew Allen, working with Gillooly and Brown (*Science*, vol 297, p 1545), showed that Rohde appears to be correct. Species diversity varies with temperature, whether as a result of latitude or altitude, almost exactly as predicted by our theory.

This puts a different spin on the factors behind biodiversity and raises exciting new questions. Most ecologists, supported by experiments such as Park's, have believed that the ecological interactions of competition, predation, parasitism and disease make it harder for species to coexist. Therefore, to explain the rich diversity of the tropics, they have assumed that the constancy and favourableness of tropical climates must slow down interactions among species and reduce rates of extinction.

Our theory and the data suggest just the opposite. Warmer temperatures in the tropics actively promote diversity by speeding up rates of metabolism, ecological interactions, speciation and extinction. The struggle for existence runs faster in warmer environments, and also in smaller organisms.

This implies that global warming is likely to have far more pervasive and dramatic effects on biodiversity than simply whether species can shift their geographic distributions to keep pace with climate change. By increasing each individual's rate of metabolism, and hence their consumption of resources, warming should decrease the number of individuals the ecosystem can support and so reduce population densities. Everything else being equal, global warming will exponentially increase rates of energy flow and the cycling of carbon and nutrients in ecosystems, but correspondingly decrease population sizes and the total biomass of organisms. It is hard to predict what effect this may have on the biodiversity and stability of ecosystems, but the exponential sensitivity to temperature suggests that even modest global warming is likely to have profound impacts.

Metabolic theory also has important implications for our own species. Most directly, it helps us understand the effect of global warming on ecosystem function and the evolutionary race between us and our many enemies. So, for example, human parasites and diseases, which have always been most diverse and damaging in the tropics, are likely not only to spread but also to evolve more rapidly as the planet warms.

But metabolism enters the picture in another way as well. Our species has attained an extraordinary degree of power and influence, unprecedented in the 4.5 billion year history of life. This reach comes in large part because our technology has allowed us to use a much wider array of resources -- especially the biologically generated energy stored in fossil fuels -- to do the work of creating the large, diverse structures and functions of modern human society. In short, fossil fuel use can be thought of as part of the "metabolism" of our species.

A typical human's biological metabolic rate of about 8400 kilojoules per day, or 100 watts, is just what you would predict for a mammal of our body size, evolving in a "natural" habitat. But our additional non-biological energy usage, chiefly from burning fossil fuels, ranges from about 300 watts per person in the poorest developing countries to over 11,000 watts per person in the wealthiest developed countries, such as the US, UK and Japan.

This variation in energy use affects everything from economics to reproductive biology. For example, metabolic

One rate to rule them all; Ecology has always lacked a strong overarching theory like those behind physics or chemistry. But no longer, thanks to the universal throttle inside every living thing, say ecologist James Brown and physicist Geoffrey West *New Scientist* May 1, 2004

theory appears to explain the so-called demographic transition -- the decrease in reproductive rates of human females that has accompanied economic development. Across species of wild primates, the birth rate per female per year declines with increasing body size. In fact it scales as the $-1/4$ power of mass, as predicted by metabolic theory. Brown and his graduate student Melanie Moses have shown that the same relationship also predicts how human female fertility declines with the additional "metabolism" of fossil fuel use. It means that a woman living in one of the most developed nations uses as much energy as a hypothetical primate weighing 30 tonnes. And metabolic theory correctly predicts the reproductive rate of this Queen Kong at less than two offspring per lifetime (*Ecology Letters*, vol 6, p 295).

Of course, our metabolic theory will never explain all of ecology. For example, for about a century ecologists have been trying to understand how similar species of nearly identical body size can coexist in the same environment. Metabolic theory can't answer such fine-scale questions about how similar species divide up resources, but it can answer the big questions of how much and how fast.

Even in the realm where metabolic theory holds sway, however, it would be naive to expect it to work perfectly. Life is just too diverse. There will always be unusual organisms or extreme environments that stray from the general pattern. We can learn a lot from such exceptions, because they highlight the influence of other factors, such as nutrient limitation, which we have now begun to incorporate into our metabolic theory. But we can only spot these interesting exceptions once we know the underlying pattern.

The power and scope of our new theory look promising. Metabolic rate affects biological rates and times at all levels of ecological organisation, from individuals to populations, communities and ecosystems. But it will take years, perhaps decades of further work before we truly understand just how far the pace of life controls the ecology of life on Earth.

LOAD-DATE: May 03, 2004

LANGUAGE: ENGLISH

Copyright 2004 Reed Business Information US, a division of Reed Elsevier Inc.
All Rights Reserved