of several Polycomb group (PcG)–related proteins in the E2F-6 complex. This group of proteins interacts with E2F-6 and has been implicated in the maintenance of inactive chromatin (*11*).

Perhaps one of the most tantalizing observations has been the identification of Max together with its protein partner Mga in the E2F-6 complex (*9*). Consistent with the presence of the Max-Mga heterodimer is the finding that the E2F-6 complex can bind not only to E2F sites but also to Myc sites in the DNA of target gene promoters. Moreover, Mga has a separate DNA binding domain, the T-box, which also dictates binding of the E2F-6 complex to unrelated T-box DNA binding sites. The E2F-6 chromatin-modifying complex therefore contains several distinct DNA binding activities that may allow its recruitment to the promoters of many different genes.

We are left with the overriding view that E2F-6 directs transcriptional silencing by modifying chromatin. It is likely that E2F-6 silences gene expression in quiescent cells in vivo because E2F-6, Max, and HP1γ preferentially occupy sites in the promoters of cell cycle–regulated genes during G_0. E2F-6 is replaced by other E2F family members including E2F-1 and E2F-4 as the cells move into G_1 (see the figure). Moreover, the presence of distinct DNA binding activities in the E2F-6 complex may allow for the coordinated regulation of diverse target genes through a common long-term gene-silencing mechanism that depends on chromatin modification.

The Ogawa *et al.* study represents a milestone in cell cycle research, with its revelation that E2F-6 is a key regulator of gene activity in quiescent cells. The new work has implications for tumor biology because cancer cells frequently harbor mutations in E2F and Myc. Intriguingly, as Ogawa and colleagues note, the E2F-6 expressed in HeLa cells and other tumor cells seems to be inactive. It is possible that abnormal E2F-6 is causally related to the reluctance of tumor cells to enter a quiescent state, and their continued drive toward proliferation. As the E2F-6 story continues to unfold with the characterization of other E2F-6 complexes and the identity of regulatory cues for E2F-6 control, we confidently anticipate a better understanding of the connection between chromatin modification, cell cycle progression, and tumorigenesis.

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PERSPECTIVES: ECOLOGY

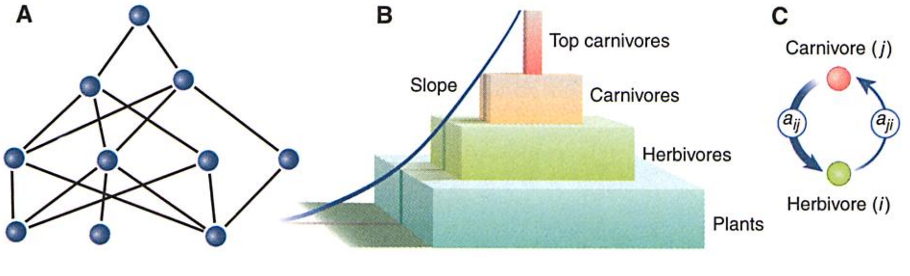
From Elton to Mathematics and Back Again

Dave Raffaelli

We live in a time when biodiversity is being lost at an alarming rate. There is growing pressure for community ecologists to deliver on basic questions about the consequences of biodiversity loss for ecological stability. But the true complexity of natural systems is overwhelming. Representing their dynamics and understanding the underlying processes is extraordinarily difficult; predicting their future states is even harder. Ecologists try to cope with this complexity by thinking in terms of food webs. Food webs can be represented as impressively complicated spider-web pictures (see the figure, A), but such diagrams conceal more than they reveal: Interesting patterns are obscured by the detail. However, by grouping species into feeding types (or trophic levels) and estimating the numbers or biomass at each level, early ecologists like Elton (*1*) and Odum (*2*) were able to show that pyramids are a consistent feature of natural systems (see the figure, B).

A quite different approach is to make abstract representations of food webs as mathematical models. Such models have revealed new and unsuspected behaviors in natural systems that would have been impossible to predict from simple observations (*3, 4*). Blending these different approaches has been a major challenge for food web ecologists, but Neutel *et al.* (*5*), reporting on page 1120 of this issue, demonstrate how this is possible. Their analysis brings us one step nearer to understanding how highly complex ecological systems retain their stability, contrary to theoretical expectations (*3, 4*).

Neutel *et al.* explore a concept called the trophic loop that was first described by Yodzis (*6*). Loops are closed chains representing interaction strengths between adjacent species in a food chain (see the figure, C). For each predator-prey link in a food web, two interaction strengths can be measured as simple coefficients: the effect of the predator on the prey, and the effect of the prey on the predator. Calculating these coefficients for all predator-prey links in a real food web involves highly detailed and painstaking estimates of population sizes, mortality rates, and energy conversion efficiencies (*7*). Un-



Staying connected. Food webs can be represented as species (blue dots) connected by trophic links (lines). Diagrams like these can be extremely complicated, and it is usually impossible to discern interesting patterns within such pictures. By grouping the species in a food web (**A**) into functionally similar types (trophic levels) and measuring the biomass of each of these levels, a pyramid of biomass can be constructed (**B**). The decrease in biomass between successively higher trophic levels is the slope of the pyramid, which may reflect system stability. Every trophic interaction between species in a food web can be described by two coefficients (**C**): The effects of the predator *j* on the prey *i* (a_{ij}) and the effects of the prey on the predator (a_{ji}). Usually, the former is larger than the latter. In the example shown of a two-species loop, the loop weight is the mean of the two coefficients. This can easily be extended to loops that include more than two species. Lower loop weights (that is, weaker species interactions), especially for longer loops, help to stabilize food webs.

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daunted, Neutel and colleagues have accomplished this for seven documented food webs in soil ecosystems. They find that the organization or architecture of these webs yields long loops that contain many weak links, a feature that enhances stability by reducing the average interaction strength of each loop. Longer loops are especially important in this respect because they are potentially destabilizing.

The groundwork for these ideas was laid by May's analysis of model systems (*3*). His analysis revealed that complex webs tended to be less stable than simple webs, a finding apparently at odds with the observation that real food webs are highly complex yet stable. One way in which this paradox can be resolved is if the average strength of interactions between species is low, and this is exactly what Neutel *et al.* have found. McCann and colleagues (*4*) came to similar conclusions, that is, a high proportion of weak interactions in webs contributes to their stability. However, Neutel and coworkers have gone a stage further by demonstrating that the organization of strong and weak linkages in food webs seems to be reflected in the shape of the biomass pyramid itself. This occurs because energy conversion efficiencies and body size depend on trophic levels. Thus, large long-lived animals with higher energy efficiencies, such as carnivores, are found in trophic levels near the top of the pyramid. It follows that the slope of the side of the pyramid may be a good indicator of web stability: Webs that give tall, thin pyramids are less likely to be stable than those with shorter, more squat pyramids (see the figure, B). A factor of 10 decrease in biomass with increasing trophic level would provide the patterns of interaction strengths necessary for stability, and these pyramids are not uncommon in nature.

The question remains as to how general these effects are. Fortunately, a compendium of food webs exists for exploring such ideas. Extending their analysis to systems across a range of habitat types and complexities has helped Neutel *et al.* to confirm the contention that observed biomass pyramidal shapes also have loops with weak links. However, several intriguing questions remain. For instance, not all systems have biomass pyramids, especially open-water marine and freshwater systems where the biomass of primary producers is typically low. Also, parasites can be considered the top consumers in most systems (*8*), and these species have life-history traits that are quite different from those of more traditional large and long-lived top predators. Doubtless these and similar considerations will stimulate extension and refinement of the ideas presented by Neutel and colleagues. I believe that the patterns they describe are likely to be sufficiently robust to accommodate such variants.

These authors have provided a valuable service for food web ecology by integrating early concepts of food web structure (biomass pyramids) with modern formal analyses to improve our understanding of the factors contributing to ecological stability. Hopefully, their findings will stimulate similar creativity in others.

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PERSPECTIVES: ASTEROIDS

Traces of an Unusual Impact

H. J. Melosh

Planetary scientist Peter Schultz was hailed as a public hero of Argentina when, in 1991, he and former Argentine air-force pilot Ruben Lianza announced that they had discovered Earth's most unusual meteorite impact crater (*1*). Ten elongated depressions near the small city of Rio Cuarto closely resembled the traces of a very oblique impact. The authors postulated that as recently as 10,000 years ago, a small, stony asteroid, 150 to 300 m in diameter, had grazed the Pampean plains at an angle of less than 7° and a velocity of about 25 km/s. After the impact, it split into fragments that ricocheted out of the first crater and gouged a series of smaller craters downrange.

Doubts about the impact origin of the structures were soon raised. Impacts at angles as low as 7° are very rare: Only 1 out of 67 impacts is this oblique. The occurrence of a low-angle impact by an asteroid of the required size in the past 10,000 years is thus extremely unlikely. Of all the thousands of fresh impact craters on the Moon, only one clear case of a ricocheting impact is known (see the figure).

But mere improbability is not proof that such an event did not occur. The discovery of meteorites and impact-produced glass in the craters swept away all criticism. A remarkably interdisciplinary investigation of the craters, reported by Bland *et al.* on page 1109 of this issue (*2*), now vindicates both the skeptics and Shultz and Lianza. The real story is both less and much more than the discoverers originally believed.

Bland and his associates became uneasy about the impact origin of the Rio Cuarto craters when satellite images revealed the nearby occurrence of nearly 400 elongated depressions of nearly identical morphology. The depressions seemed to be aligned with the prevailing wind direction, which gradually wraps around a nearby mountain range. Previous Argentine workers attributed the depressions to the action of the wind on the deposits of wind-deposited silt (loess) that mantles the Pampas, and many of their characteristics are consistent with such an origin.

Schultz and Lianza were aware of these problems. They even mentioned morphologically similar depressions in their original paper (*1*). However, the discovery of two fresh meteorites and impact-produced glasses in one of their craters convinced them (and most other workers in the field) that the craters were created by an impact.

Bland *et al.* also found meteorites in the craters. However, they are different classes of meteorite—a chondrite and an achondrite—and therefore seem unlikely to have been part of a single asteroid. Furthermore, ^{14}C dating revealed that the two meteorites fell at very different times, one 36,000 years ago and the other more than 52,000 years ago. They are thus much older than the craters, the age of which Bland *et al.* confirmed as about 4000 years. What are we to make of the conflicting data?

The presence of meteorites in the purported craters is consistent with the action of wind on the fine-grained loess of the Pampas. As wind blows away the loess, it leaves a residue of stones at the bottom of many of the depressions. Just as meteorites stand out on the ice fields of Antarctica, they are conspicuous on the Pampean

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