

quantifiable way to control the quantity of material deposited. Hence, the length of the gap-forming segment can be controlled with great precision. Furthermore, it is easy to prepare wires with more than one gap and with gaps of different lengths.

It would be pointless to have a dissolvable gap between two nondissolvable segments if, upon dissolution, the remaining segments fell apart. Qin *et al.* solve this problem by dispersing the segmented wires on a surface and then coating one side with a sheath of a nondissolvable material. This sheath holds the wire together after removal of the dissolvable segment. The authors show that these sheathed microwires can be placed between two much larger electrodes and that the gap can

be bridged with a test molecular-electronic material—a conductive polymer.

Challenges remain. The smallest gap reported by Qin *et al.* is 5 nm. There is no fundamental reason why smaller gaps cannot be prepared, but this remains to be demonstrated. Furthermore, the test material consisted of a collection of polymeric chains. The method has yet to be demonstrated on a single small-molecule conductor. Nevertheless, the ease with which the devices can be prepared, characterized, and manipulated bodes well for on-wire lithography to become an important tool in the molecular-electronics toolbox.

References

1. A. Nitzan, M. A. Ratner, *Science* **300**, 1384 (2003).
2. R. F. Service, *Science* **294**, 2442 (2001).

3. <http://public.itrs.net/Files/2003ITRS/Home2003.htm>
4. R. M. Metzger, *Chem. Rev.* **103**, 3803 (2003).
5. See the following Web sites for the efforts of these companies in molecular electronics: www.hpl.hp.com/research/qsr/, www.motorola.com/content/1,3306,284,00.htm, www.research.ibm.com/nanoscience/, and www.almaden.ibm.com/st/chemistry/me/index.shtml.
6. K. W. Hipps, *Science* **294**, 536 (2001).
7. L. Qin, S. Park, L. Huang, C. A. Mirkin, *Science* **309**, 113 (2005).
8. H. Park, A. K. L. Lim, A. P. Alivisatos, J. Park, P. L. McEuen, *Appl. Phys. Lett.* **75**, 301 (1999).
9. D. K. James, J. M. Tour, *Chem. Mater.* **16**, 4423 (2004).
10. M. M. Deshmukh, A. L. Prieto, Q. Gu, H. Park, *Nano Lett.* **3**, 1383 (2003).
11. C. R. Martin, *Science* **266**, 1961 (1994).
12. J. K. Klein *et al.*, *Chem. Mater.* **5**, 902 (1993).
13. S. R. Nicewarner-Peña *et al.*, *Science* **294**, 137 (2001).
14. J. K. N. Mbindyo *et al.*, *J. Am. Chem. Soc.* **124**, 4020 (2002).

10.1126/science.1114663

ECOLOGY

Food Web Ecology: Playing Jenga and Beyond

Peter C. de Ruiter, Volkmar Wolters, John C. Moore, Kirk O. Winemiller

Naturalists have long noted that the distribution, abundance, and behavior of organisms are influenced by interactions with other species (1). Motivated in part by Paine's (2) work in the rocky intertidal zone and May's (3) theoretical work on the relationship between the complexity and the stability of ecosystems, the study of food webs gained momentum in the late 1970s and early 1980s (4). These studies precipitated a convergence of different approaches—mathematical treatments, descriptive work, manipulative field studies, and a formal treatment of energy flow and matter. This in turn allowed mapping of the interrelationships among the structure of an ecological community, its stability, and the processes occurring within the ecosystem—that is, construction of a food web (5).

Over the past decade, new issues arising in ecology, such as environmental

change, spatial ecology, and the functional implications of biodiversity, require a different view of ecosystems and ecological research (6). The food web approach, with its focus on static structure and reliance on stability or persistence of species, seemed ill-equipped for analyzing these more dynamic topics.

Indeed, the often-used metaphor for the relationship among species, community structure, and stability was that of a stone arch with the loading forces among stones (species) representing interactions among species, and the “key-stone” representing the species that had the dominant role in regulating structure and stability of the community. But many ecologists now view such a static representation of biological communities as inappropriate. Moreover, food web descriptions have been criticized for incompleteness because they do not fully account for all the species and links that are present, and because they generally ignore spatial and temporal variability. For these reasons, food

web approaches have rarely been applied to current environmental issues.

The metaphor of the static arch might better be replaced with the metaphor of the structures built during a variation of the game Jenga (see the first figure, caption). Simple rules of balance and energetics govern the stability of both arch and Jenga structures, but unlike an arch, a Jenga structure is constantly changing, with additions and deletions of stones, and its stability at any moment depends on the importance of a given ingoing or outgoing stone's contribution to the structure. By realizing that dynamics are key to understanding complex

structures, we can see stable food webs not as static entities, but as open and flexible Jenga-like systems that can change in species attributes, composition, and dynamics. Recent food web studies have incorporated data on spatial and temporal dynamics. Here, we highlight a few examples of such studies and discuss their implications for environmental management.

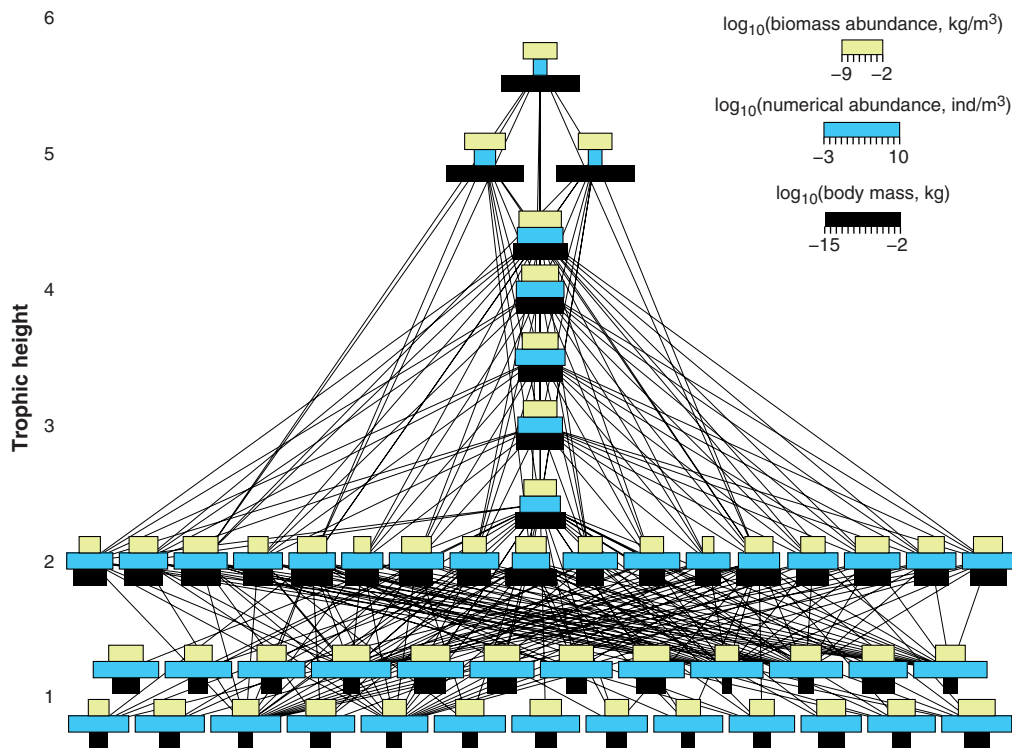
Over time, food webs change in species composition and in population life history parameters and abundances, and individual organisms within the web change in growth, size, and behavior.

Dynamic relationships among different levels of the biological hierarchy govern food web structure and stability. Field observations and theoretical models show that environmental heterogeneity creates subsystems



Jenga. In a game of Jenga, players successively take away parts and place them on top until the structure becomes unstable and crashes. Each part can thus be a key-stone. When parts are replaced at other positions, the stability of the Jenga structure can be maintained.

P. C. de Ruiter is in the Department of Environmental Sciences, Copernicus Research Institute for Sustainable Development and Innovation, Utrecht University, 3508 TC Utrecht, Netherlands. E-mail: p.deruiter@geo.uu.nl. V. Wolters is in the Department of Animal Ecology, Justus-Liebig-Universität, D-35392 Giessen, Germany. E-mail: Volkmar.Wolters@allzool.bio.uni-giessen.de. J. C. Moore is in the School of Biological Sciences, University of Northern Colorado, Greeley CO 80639, USA. E-mail: john.moore@unco.edu. K. O. Winemiller is in the Section of Ecology and Evolutionary Biology, Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843, USA. E-mail: k-winemiller@tamu.edu



The food web of Tuesday Lake, 1984. The width of the horizontal bars shows the body mass (\log_{10} kg), number (\log_{10} individuals per m^3), and biomass (\log_{10} kg/m^3), respectively, of each species. The vertical positions of the species show trophic height (20). Despite a major change in species composition, following a manipulation, this energetic setup of the food web remained roughly the same (19).

(compartments) of interacting species within food webs, especially at the lower trophic levels (7, 8). Organisms at the higher trophic levels act as integrators, linking the lower pathways in space and time, and stabilize the dynamics of their resources (prey) via density-dependent foraging (9, 10). This relationship explicitly supports MacArthur's idea (1) that community complexity buffers against perturbations and thereby overrides the inherent constraints on system stability imposed by complexity (3). Remarkably, this mechanism is similar to the way in which dynamics at the level of individual behavior influence food web structure and stability. For example, a predator switching to new prey affects population dynamics, because such dietary shifts inhibit rapid population growth of abundant prey while allowing rare prey to increase (11). Such shifts can be rapid; hence, when food web architecture changes (by changes in species composition or through fluctuating population abundances), web structure may quickly stabilize and may even result in a positive complexity-stability relationship.

Life history processes in structured populations also can influence community dynamics in extraordinary and even counterintuitive ways. Size-structured food web models, in which growth in body size is density-dependent, predict that size-selective predators decrease the overall biomass

of the prey as expected, but change the prey size distribution. This alters competition among prey individuals to such an extent that it actually leads to an increase in the abundance of the preferred prey stages. This positive feedback allows for large populations of predators to persist under conditions where small populations are likely to become extinct (12).

The trophic position of species in dynamic food webs may influence the risk of loss of that species, with possible consequences for ecosystem functioning (13). Experiments on pond food webs show that the effects of species on ecosystem processes depend on the interplay between environmental factors (such as productivity) and trophic position, whereby species at higher trophic levels tend to have larger effects (14). The risk of a given species' extinction and its consequences (in terms of secondary extinctions and ecosystem functioning) will be different in different ecosystems and will vary within ecosystems over space and time. Hence, a keystone species in one setting may have relatively little influence on community dynamics in another setting.

What does this research tell us? First, the performance and persistence of species and the role of species in biological communities should be examined in the context of a dynamic food web. The studies also show

how to go beyond playing Jenga by revealing the general rules of demography and energetics that tend to stabilize biological communities (15, 16). The stabilizing effect of flexible substructures imposed by environmental change and variability (9) echoes the notion of stabilizing trophic pyramids (17) occurring in food webs and food web compartments (10). When compartments are viewed as trophic interaction loops, we can even understand mathematically the stabilizing effect of pyramidal structures within loops on food web structure (18).

Dynamics and stability can be seen in the intensively studied food web of Tuesday Lake in Michigan, USA (see the second figure). Removal of three planktivorous fish species and addition of one piscivorous fish species changed the lake's community structure remarkably. Although this manipulation had almost no effect on species richness (56 in 1984, 57 in 1986), about 50% of the species were replaced by new incoming species within less than 2 years (19). The energetic setup

of the food web, in terms of distributions of body sizes and abundances over trophic levels, unexpectedly remained roughly the same. Apparently, the new web structure allowed the community to conserve key ecological features in the face of a major disturbance.

The notion of the ecosystem as a static arch has restricted our vision. In contrast, viewing food webs as open and flexible Jenga-like structures that accommodate changes in species composition, attributes, and dynamics reveals the features of the ecosystem that are critical to our understanding of community resistance and resilience to environmental change and disturbance. Recent theoretical advances in food web research must be accompanied by rigorous experiments and detailed empirical studies of food web modules in a variety of ecosystems. As food web science continues to develop, it surely will contribute new tools and new perspectives for the management of both natural and human-affected ecosystems.

References and Notes

1. R. MacArthur, *Ecology* **36**, 533 (1955).
2. R. T. Paine, *J. Anim. Ecol.* **49**, 667 (1980).
3. R. M. May, *Stability and Complexity in Model Ecosystems* (Princeton Univ. Press, Princeton, NJ, ed. 2, 1973).
4. H. T. Odum, *Systems Ecology: An Introduction* (Wiley, New York, 1983).
5. D. L. DeAngelis, *Dynamics in Food Webs and Nutrient Cycling* (Chapman & Hall, London, 1992).

6. G. A. Polis, K. O. Winemiller, *Food Webs: Integration of Patterns and Dynamics* (Chapman & Hall, New York, 1996).
7. J. C. Moore, H. W. Hunt, *Nature* **333**, 261 (1988).
8. A. E. Krause, K. A. Frank, D. M. Mason, R. E. Ulanowicz, W. Taylor, *Nature* **426**, 282 (2003).
9. K. S. McCann, J. B. Rasmussen, J. Umbanhowar, *Ecol. Lett.* **8**, 513 (2005).
10. J. C. Moore *et al.*, *Ecol. Lett.* **7**, 584 (2004).
11. M. Kondoh, *Science* **299**, 1388 (2003).
12. A. M. de Roos, L. Persson, *Proc. Natl. Acad. Sci. U.S.A.* **99**, 12907 (2002).
13. E. Thébault, M. Loreau, *Proc. Natl. Acad. Sci. U.S.A.* **100**, 14949 (2003).
14. A. Downing, M. A. Leibold, *Nature* **416**, 837 (2002).
15. U. Brose, A. Ostling, K. Harrison, M. Martinez, *Nature* **428**, 167 (2004).
16. R. J. Williams, N. D. Martinez, *Nature* **404**, 180 (2000).
17. C. Elton, *Animal Ecology* (McMillan, New York, 1927).
18. A.-M. Neutel, J. A. P. Heesterbeek, P. C. de Ruiter,

Science **296**, 1120 (2002).

19. T. Jonsson, J. E. Cohen, S. R. Carpenter, *Adv. Ecol. Res.* **36**, 1 (2005).
20. J. E. Cohen, T. Jonsson, S. R. Carpenter, *Proc. Natl. Acad. Sci. U.S.A.* **100**, 1781 (2003).
21. We thank T. Purtauf and A.-M. Neutel for discussion and comments.

10.1126/science.1096112

ASTRONOMY

Masers in the Sky

Moshe Elitzur

In 1963, radio emission from interstellar OH (the hydroxyl radical) was discovered. The emission patterns in the astronomical sources deviated considerably from expectations based on laboratory conditions.

Enhanced online at
www.sciencemag.org/cgi/content/full/309/5731/71

Two years later, researchers realized that some of the most peculiar emission properties of interstellar OH could only be explained in terms of maser amplification. (Maser is an acronym for microwave amplification by stimulated emission of radiation; masers operate on the same principles as lasers, except that they involve microwave radiation instead of visible light.)

Maser emission has now been detected from many different molecules in a variety of astronomical sources, from nearby comets to faraway galaxies. But the evidence for amplification is indirect in most cases. Observations from 18 pulsars, reported by Weisberg *et al.* on page 106 of this issue (1), provide direct evidence for an interstellar amplifier in the direction of one of these pulsars, B1641-45.

Every 0.455 seconds, B1641-45 emits a pulse of radio radiation toward Earth that passes through an OH cloud. Spectra of the four OH ground-state lines detected from the cloud display absorption features in three lines and an emission feature in the fourth [see figure 3 in (1)]. When the pulsar is on, passage of its radiation through the cloud deepens the absorption features, just like the shadow cast by an object in front of a bright light. But the emission feature in the fourth line becomes stronger after passing through the intervening screen, the equivalent of an object amplifying a background light instead of casting a shadow.

Almost 30 years ago, Rieu *et al.* observed a similar effect for an OH cloud in front of a distant radio galaxy when they switched the

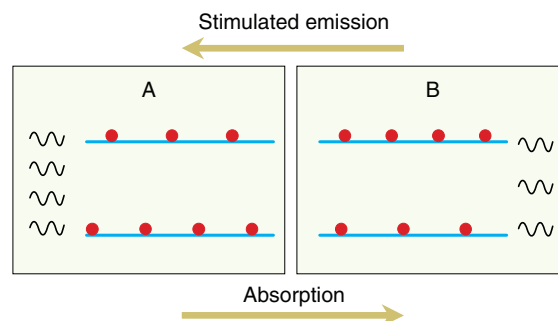
telescope between pointing directly at the source and pointing away from it (2). In both cases (1, 2), the input signals are amplified by only a few percent, but to date, these weak masers are the only unambiguous direct evidence for amplification. The pulsar method (1) increases confidence in the results, thanks to the repeated detection of signals that arrive more than twice every second.

The maser effect clearly occurs easily in interstellar space, even though it requires special effort on Earth. This disparity reflects fundamental requisites for laser and maser operation. Consider two states, A and B, of a system containing electromagnetic radiation (such as light or radio emission) and microscopic particles (such as atoms or molecules) (see the figure). The total energy is the same in both states; A contains an extra photon, whereas in B, one particle has moved from the lower to the upper level. The process that takes the system from A to B is called absorption and is the reason why the intensity of radiation is attenuated when it passes through matter. The process that takes the system from B to A is called stimulated emission—the interaction of radiation with particles leads to the emission of an additional photon. This process is the essence of the maser effect. As the reverse of absorption, stimulated emission amplifies the radiation.

In any given source, the net balance of absorptions and stimulated emissions depends on the particle population distribution between the two levels. Under most circumstances, this distribution follows the rules of thermodynamic equilibrium, and the population of the upper level is so small that stimulated emissions can be ignored; the material attenuates radiation. But when the number of particles in the upper level exceeds that in the lower level, a situation called population inversion, stimulated emissions outnumber

absorptions and the radiation is amplified. Such an extreme distribution can occur only at low matter densities, and interstellar space thus provides an ideal setting; its density is so low that its densest regions are comparable to the best laboratory vacuum. Thus, thermodynamic equilibrium is the rule in terrestrial circumstances but is the exception in interstellar space, making the latter a natural environment for maser operation.

Maser radiation can be extremely bright; the temperature equivalent of brightness sometimes exceeds 10^{15} K. These intense beacons enable radio imaging with an angular resolution of 0.0003 arc sec; if the human eye had this resolving power, these words could be read from a distance of ~3000



Absorption versus stimulated emission. Sketched are two states, A and B. Each state has two energy levels, with some particles populating each level. The frequency of the radiation (represented by waves) is matched to the energy separation between the levels, such that it can interact with the particles. The number of waves represents the radiation intensity, that is, the number of photons.

miles. Separations between neighboring maser spots are measured with the even higher accuracy of 0.00001 arc sec.

It was thanks to this resolving power that the existence of supermassive black holes at the center of galaxies was established. Miyoshi *et al.* (3) found that the galaxy NGC 4258 harbors a disk-like structure, with masers of water vapor revolving around the center just like the planets revolve around the Sun. From the orbital rotations, the authors determined that a central mass 7×10^7 times that of the Sun is contained in a region no larger than the solar system. No object other than a black hole can have such a high mass density.

Amplified radiation has distinct properties markedly different from those of ordi-

The author is in the Department of Physics and Astronomy, University of Kentucky, Lexington, KY 40506, USA. E-mail: moshe@pa.uky.edu