

clusters derived from gravitational lensing and x-ray data sometimes differ by up to a factor of 2 (17, 18), providing a further indication that our picture of these largest cosmological objects is not complete. Therefore, care should be taken before using the x-ray emission from the dark matter-dominated galaxy clusters to derive cosmological distances (19).

The astrophysical observations discussed here indicate that axions and neutralinos may have been abundantly produced in the early universe and/or inside stars. These two types of particles remain the favorite candidates for dark matter and other celestial phenomena. As ever more sensitive detectors are built, more defini-

tive evidence for or against neutralinos and axions should become available. Existence of one does not preclude existence of the other: The dark matter in the universe may contain both of these particles, as well as many other, as yet unforeseen ones.

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ECOLOGY

Oh the Locusts Sang, Then They Dropped Dead

Richard S. Ostfeld and Felicia Keesing

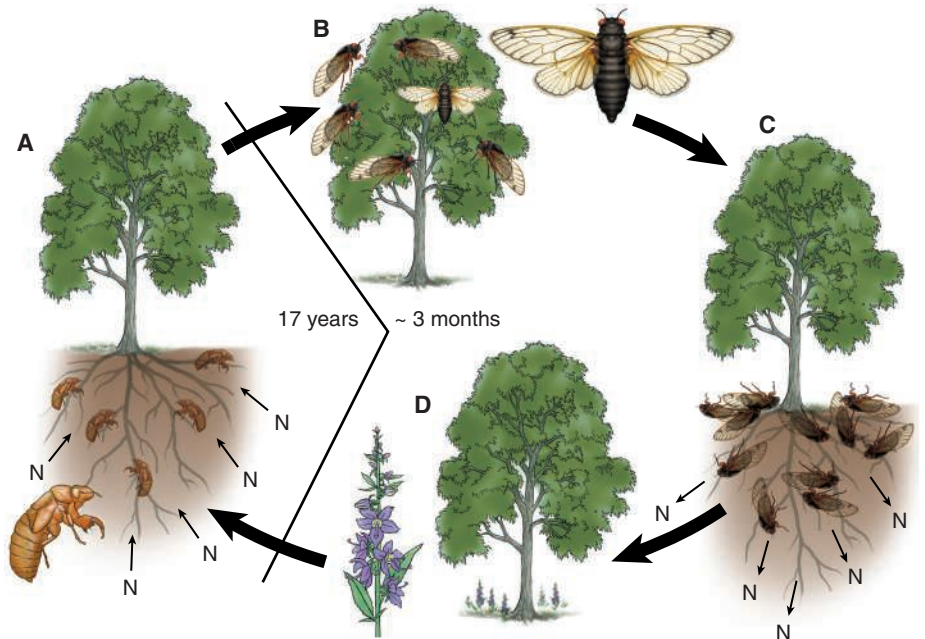
The Bob Dylan song “Day of the Locusts” refers to the cacophony from the 1970 emergence of 17-year cicadas (*Magicalicada* spp.), which happened to coincide with his acceptance of an honorary degree from Princeton University. These cicadas, which dutifully reappeared aboveground in 1987 and then again this year, are a quintessential case of a resource pulse—a transient, multiannual episode of resource superabundance. On page 1565 of this issue, Yang (1) describes the ramifying impacts that massive pulses of cicada carcasses have on forest soils, microbial biomass, nitrogen availability, and reproductive success of understory plants.

Resource pulses typically are associated with reproductive events in plants, such as synchronized heavy seed production (mast-seeding) within populations of oaks or bamboos, and even more spectacularly, across dozens of genera of paleotropical dipterocarp trees (2). Plant populations that synchronize seed production achieve high reproductive success because seed predators can only consume a fraction of the hyperabundant resource (“predator satiation”) (3), and most of the escapees ger-

minate. Similarly, so many periodical cicadas are involved in the dissonant mating swarms that their predators—principally birds—can consume no more than 15% of the peak numbers (4). The remainder die after reproducing and drop to the forest floor.

Although much is known about the evolutionary causes of synchronized reproductive events, only recently have ecologists begun to analyze the consequences of resource pulses for ecosystems (5). The predominant type of resource pulse—mast seeding—occurs in grasses, annual forbs, shrubs, and trees, across at least four continents and from deserts to tropical rain forests. Generalist consumers—often rodents—are the most immediate beneficiary of this superabundant resource, and they respond with population outbreaks of their own. These rodent irruptions, in turn, result in severe impacts on their alternate prey, such as songbird eggs (6), their avian

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A 17-year pulse of nitrogen from cicada carcasses. (A) For 17 years, cicada nymphs feed on tree xylem, slowly incorporating belowground nitrogen (N) absorbed by the tree’s roots. (B) Upon emergence, adult cicadas mate and lay eggs within a several-week period, and then die and drop to the forest floor. (C) The accumulated nitrogen in their carcasses is released after a burst of activity by microbial decomposers. (D) This spike of available soil nitrogen leads to increased nitrogen content and seed size of the American bellflower (*C. americanum*), an understory plant.

The authors are in the Institute of Ecosystem Studies, Millbrook, NY 12545, USA. F. Keesing is also in the Biology Department, Bard College, Annandale-on-Hudson, NY 12504, USA. E-mail: rostfeld@ecostudies.org

and mammalian predators (7), and their parasites and pathogens (5, 8). In these cases, the pulsed resource is quickly converted into consumer biomass, and the direct and indirect consequences for ecosystems follow this consumer pathway.

The research by Yang demonstrates a new pathway by which resource pulses can affect ecosystems—through the action of decomposers (1). Unlike seeds, which germinate following escape from predation, periodical cicadas die and rot. These insects are a high-quality fertilizer indeed (about 10% nitrogen), delivered at a rate of up to 0.5 kg m⁻². Within a month of a simulated cicada irruption, biomass of both fungal and bacterial decomposers in the soil increased dramatically, and this in turn resulted in a tripling of soil ammonium, and a more-than-doubling of soil nitrate concentration. As with other fertilizers, the cicada-induced flush of soil nutrients ultimately boosted nitrogen concentration and seed mass in the American bellflower (*Campanulastrum americanum*), an understory plant.

Periodical cicada nymphs spend 16-plus years attached to tree roots sucking on xylem (9), resulting in a persistent, long-term deflection of soil-derived nitrogen from leaves into insect biomass. Upon emergence, the cicadas then transport this stolen nitrogen aboveground. From there, a

little ends up in avian or mammalian consumer tissue, and another fraction goes to cicada egg production, but most becomes fertilizer, first for soil microbes and then for understory plants like bellflowers. Because the nitrogen-enriched bellflower tissues die and decompose themselves, the trees would seem to be the ultimate recipients of the prodigal nitrogen's return underground (see the figure).

Analyzing radial tree-ring growth of oaks within the geographic ranges of 13-year and 17-year cicadas, Koenig and Liebhold (10) found a ~4% decrease in tree growth during the year of emergence, which they attributed to the damage caused by oviposition wounds in twigs. However, some of Koenig and Liebhold's analyses also demonstrated a ~1% increase in tree radial growth during the first 4 years after emergence, for which they had no explanation. The fertilization effect of cicada carcasses reported by Yang might account for this apparently compensatory stimulation of growth after emergence.

Spectacular resource pulses like the emergence of periodical cicadas constitute one of the more obvious demonstrations that ecological systems rarely exist in equilibrium states, but instead are in constant flux. By tracing the responses of populations or entire trophic levels to resource pulses, ecologists can assess the extent to

which resources versus consumers control abundance or biomass—in other words, whether control is bottom-up or top-down. They can also determine the strength and nature of interconnections between species or trophic levels. A trophic cascade occurs when top-down effects permeate through three or more trophic levels (11), and we suggest that the cicada-decomposer-plant system, which represents the penetrance of bottom-up effects through three trophic levels, be considered a “trophic fountain.” The bottom-up metaphor, of course, refers to the effects of lower trophic levels on higher ones. In a more physical sense of the metaphor, Yang's work demonstrates how organisms and materials flow inexorably from bottom to top and back again.

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PLANETARY SCIENCE

Nothing Simple About Asteroids

Erik Asphaug

Twelve years ago, scientists obtained the first close look at asteroids, when the Galileo mission en route to Jupiter acquired high-resolution images of Gaspra and Ida (1, 2). Since then, much has changed but little has solidified. Even following a year-long rendezvous by NASA's NEAR Shoemaker orbiter at asteroid Eros (see first and second figures) (3), asteroid science remains at a crossroads. The surface remote sensing and imaging techniques applied to date have yet to resolve a single fundamental question of asteroid geophysics or chemistry. A detailed new model for asteroid seismology, reported by Richardson *et al.* on page 1526 of this issue (4), shows how acoustic reverberations from impacts can cause asteroid topography to flatten, diffusing small-scale features and erasing small craters. Like other recent

models (5), this work also illustrates how seismological experiments—akin to those conducted by Apollo astronauts on the Moon—may soon reveal information about the structure and evolution of comets and asteroids.

Asteroids are famously menacing, and the movie script requires them to be tamed or destroyed. The hazard posed by asteroids has focused minds, but their essence is the more interesting question. Asteroids are not mere rocks; their own self-gravitation, however minuscule, is central to their evolution (6). Nor are they planets: Most asteroids are undifferentiated (never melted) precursors to planets, or fragments of these. Others are

fragments of differentiated planet precursors that were catastrophically disrupted long ago. Most are very porous, spin rapidly, and are irregular in shape, suggesting a tumultuous history. Contradictory attempts have been made to correlate their visible and infrared colors to the confusing taxonomy of meteorites.

As for asteroid geophysics, the most basic terminology is undecided. Conflicting definitions exist for terms such as regolith,



Eros: the best studied asteroid. This image of the 33 by 13 by 13 km near-Earth object, with dimensions of 33 by 13 by 13 km³, was taken on 28 January 2001 by the NEAR Shoemaker orbiter.