



PERSPECTIVES: ECOLOGY

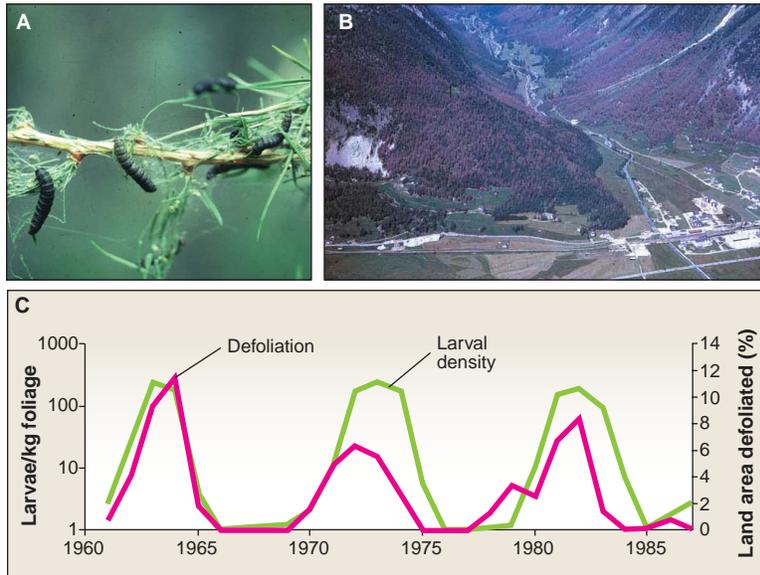
On the Crest of a Population Wave

Esa Ranta, Per Lundberg, Veijo Kaitala, Nils Chr. Stenseth

The biblical story of locusts sweeping across Egypt is a classic example of a traveling population wave. Periodically, an organism becomes so numerous that an outbreak emerges, which spreads not only across local areas but also over large geographical ranges. Such traveling waves are a special case of a more general ecological phenomenon: population dynamics synchronized in space and time across large areas (1, 2). On page 1020 of this issue, Bjørnstad *et al.* (3) use modeling to predict the speed and direction of moving waves of the Central European larch budmoth (*Zeiraphera diniana*). Larvae of this budmoth are major pests and defoliate large swaths of larch forests in the European Alps during periodic outbreaks that occur every 8 to 10 years (see the figure). For more than four decades, forest managers have kept detailed records of such outbreaks and the degree of defoliation that each caused.

Wavelike spatial patterns of outbreaks have been documented for other species (4). Elton described a similar phenomenon nearly 80 years ago (5) in snowshoe hare and Canadian lynx. Following Elton's paper, Butler (6) envisioned (on a rather weak empirical basis) hare-lynx periodic fluctuations as waves sweeping across Canada and the northern United States, with an epicenter located somewhere north of Lake Winnipeg. It has been notoriously difficult, however, to solidly document such phenomena empirically.

After the pioneering work of Elton and Butler, interest in population waves went dormant for decades. Researchers switched to investigating the mechanisms underlying the cyclic population fluctuations seen in lemmings, Canadian lynx, snowshoe hare, and the larch budmoth (see the figure).



Defoliation of Alpine larch forests. (A) Larvae (fifth-instar) of the larch budmoth (*Zeiraphera diniana*) cause severe periodic defoliation of larch forests. (B) A landscape view of forest defoliation in the Engadine Valley of the Swiss Alps. Areas of larch forest defoliated by larch budmoth larvae have a brownish coloration. (C) Estimates of larch budmoth density (green) and the percentage of land area defoliated by their larvae each year (pink) in the Engadine Valley, 1949 to 1989 (3).

Theoretical studies on population dynamics gradually evolved (1, 7), and during the 1990s mathematically inclined ecologists began to explore the consequences of dispersal-coupled population dynamics (1, 4, 7). Ecologists shifted from the traditional view of the world as being composed of large homogeneous areas inhabited by continuous populations. Instead, they started to view the world as being split into subunits where the redistribution of individuals among landscape elements ties local populations into a large-scale tapestry of population complexes (1, 2).

Using a combination of newly developed theory and sophisticated statistical tools, ecologists have achieved a reasonable understanding of the various mechanisms underlying large-scale temporal population

phenomena (1). In this respect, studies of traveling waves are unique in that they incorporate the features of the physical landscape into the models (8, 9). Bjørnstad *et al.* now show that a directional movement of the forest pest (in this case, the larch budmoth) or some gradient in habitat (forest) quality is required in order to understand the observed spatial-temporal pattern of periodic outbreaks (3). Their study makes a profound contribution not only to classical ecology but also to the more specialized field of landscape ecology.

Theoretical research has shown that coupling local populations through dispersal may generate a rich ensemble of spatial patterns that emerge beyond local areas.

With powerful statistical and mathematical techniques, Bjørnstad *et al.*'s model demonstrates that phases of population lows and highs of the larch budmoth pass as waves at a speed of about 200 km per year in an east-northeast direction through the forested areas of the European Alps. When the spatial redistribution of individual populations connects nearby units together, aggregated areas of population highs in matching phase may emerge. Aggregates of population highs may travel as waves through the landscape like ripples in a pond. When long-term population data from such areas are analyzed, one finds that populations tend to fluctuate in synchrony. The level of synchrony fades away with increasing distance between the localities from which the time series originated (2) and rises again when another wave crest is reached.

For logistical reasons, population data with sufficient temporal coverage and spatial resolution to reveal traveling waves are rare. Nonetheless, ecologists have been able to demonstrate the presence of traveling waves in outbreaks of small rodents (8, 10), Scottish red grouse (9), and human childhood diseases (11). A common denominator for these examples, including the larch budmoth, is the periodic population fluctuations (cycles) at any geographic site (typically assumed to be caused by nonlinear ecological interactions during population renewal). In theoretical population ecology, nonlinear interactions between prey and predator, or plant and herbivore,

E. Ranta and V. Kaitala are in the Department of Ecology and Systematics, FIN-00014, University of Helsinki, Finland. P. Lundberg is at the National Center for Ecological Analysis and Synthesis, University of California, Santa Barbara, CA 93101, USA. N. Chr. Stenseth is in the Department of Zoology, University of Oslo, Blindern 0316, Norway. E-mail: esa.ranta@helsinki.fi

or host and parasite (pathogen) have been invoked to explain periodic population fluctuations. In the case of the larch budmoth, there is a three-way trophic interaction between the larch tree, the moth, and a parasitoid of larch budmoth larvae. Bjørnstad and colleagues propose that strong nonlinear moth-parasitoid interactions explain the traveling waves of the larch budmoth outbreaks.

Related to these classic traveling waves are “tsunami waves,” which represent the spread of species into areas where they have not been previously found. A well-documented example is the invasion of Europe by the muskrat (*Ondatra zibethica*) after a few individuals escaped from a farm near Prague in 1905. Another classic example is the invasion of the United States by the European starling (*Sturnus vulgaris*): The first individuals were released in New York’s Central Park in 1880, and by 1954 the species’ range had reached the Pacific. These are archetypal

examples of a wave front passing through the landscape in all directions wherever the habitat is suitable (12). The modeling approach of Bjørnstad and colleagues should help us to better understand such tsunami population waves. This approach will help us to learn more about ecological invasions, an escalating problem as intercontinental travel and transport increases.

Data are now accumulating that support theoretical predictions of spatial-temporal behaviors in population models where individuals disperse between subpopulations. The close match between Bjørnstad *et al.*’s model and the larch budmoth outbreak data signifies a major step forward in understanding how complexity in nature works. This has far-reaching consequences for both theoretical and applied aspects of ecology, enabling predictions of the spread of pests (and diseases) over large geographical areas. If there is a larch budmoth outbreak in a given region, the foresters should exert controls at least 200 km to the

east-northeast beyond that area to mitigate defoliation. On the downside, it takes large-scale, long-term data to reveal emerging phenomena such as the traveling waves of pest populations or disease epidemics.

References

1. J. Bascompte, R. V. Solé, Eds., *Modeling Spatiotemporal Dynamics in Ecology* (Springer-Verlag, Berlin, 1997).
2. V. Kaitala, E. Ranta, P. Lundberg, *Proc. R. Soc. London Ser. B* **268**, 1655 (2001).
3. O. N. Bjørnstad, M. Peltonen, A. M. Liebhold, W. Baltensweiler, *Science* **298**, 1020 (2002).
4. J. Lindström, E. Ranta, H. Kokko, P. Lundberg, V. Kaitala, *Biol. Rev.* **76**, 129 (2001).
5. C. S. Elton, *Br. J. Exp. Biol.* **2**, 119 (1924).
6. L. Butler, *Can. J. Zool.* **31**, 242 (1953).
7. M. P. Hassell, H. N. Comins, R. M. May, *Nature* **353**, 255 (1991).
8. X. Lambin, D. A. Elston, S. J. Petty, J. L. MacKinnon, *Proc. R. Soc. London Ser. B* **265**, 1491 (1998).
9. R. Moss, D. A. Elston, A. Watson, *Ecology* **81**, 981 (2000).
10. E. Ranta, V. Kaitala, *Nature* **390**, 456 (1997).
11. B. T. Grenfell, O. N. Bjørnstad, J. Kappey, *Nature* **414**, 716 (2001).
12. N. Shikésada, K. Kawasaki, *Biological Invasions: Theory and Practice* (Oxford Univ. Press, Oxford, 1997).

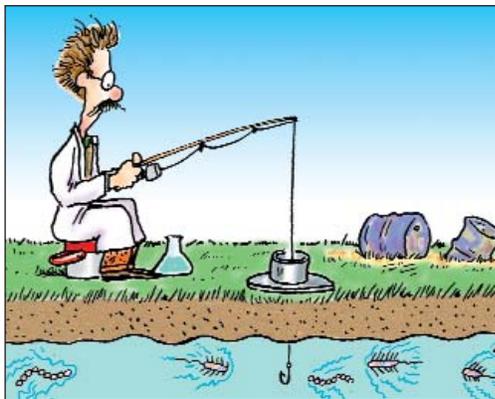
PERSPECTIVES: ENVIRONMENT

Fishing for Microbes

James M. Gossett

Chlorinated ethenes and ethanes are among the most common industrial contaminants of soils and groundwaters throughout the world. Most are suspected to be, and some are known to be, cancer-causing agents (carcinogens). Of 1233 hazardous waste sites on the U.S. Environmental Protection Agency’s Final National Priority List for 2002, 42% show contamination by tetrachloroethene (also known as perchloroethylene or PCE); 47% by trichloroethene (TCE); and 37% by 1,1,1-trichloroethane (TCA) (1). A representative sampling of 406 urban groundwaters in the United States (excluding areas of known point-source contamination) evidenced 17% of areas contaminated by PCE and 10% by TCA (2). One approach to tackling such contamination is bioremediation, which seeks to remove these solvents using bacteria that degrade them for energy.

Enter Sun *et al.* (3) on page 1023 of this issue with their discovery of a bacterium that derives energy by degrading TCA. This anaerobic microbe uses TCA as a respiratory electron acceptor to oxidize molecular hydrogen for energy production, in the same way that we use oxygen to oxidize our breakfast bagel. The valuable side



effect of this process is that TCA is reduced, just as we reduce oxygen during respiration. Taking a little anthropomorphic license, we can say that this bacterium “breathes” a chlorinated solvent (dehalorespiration). Sun *et al.*’s bacterium is the latest in an ever-growing list of bacteria that eke out a living by reducing chlorinated two-carbon solvents. This newly discovered TCA-degrading bacterium is particularly important because it is the first microbe found to degrade TCA.

Dehalobacter restrictus, isolated less than a decade ago by Holliger and colleagues (4), was the first bacterium discovered to couple growth to the reduction of a chlorinated aliphatic solvent acting as a respiratory electron acceptor. It was Holliger who coined the

term “dehalorespiration” to describe what *D. restrictus* does to PCE as it reduces it to *cis*-dichloroethene (cDCE). In the ensuing decade, many other chloroethene- and chloroethane-respiring anaerobic bacteria have been isolated [for example, see (5, 6)], as well as new aerobes that turn the tables on dehalorespiration by deriving energy through oxidation of chlorinated aliphatic solvents using oxygen as an electron acceptor (7).

Ironically, the new TCA-degrading bacterium reported by Sun *et al.* is a close cousin (or perhaps even the sibling) of Holliger’s *D. restrictus*. So, has science come full circle, in finding that this most recent bacterial isolate is akin to the first? No, because “full circle” implies that the process of discovery has somehow been completed. It has only just begun. The search for new contaminant-degrading bacteria continues at a feverish pace. Until recently, most microbe fishing expeditions followed a traditional sequence. First, contaminated soil or groundwater samples were obtained (presumably because they represented a likely source of contaminant-degrading microbes). Then these samples were subjected to enrichment strategies and different bacterial species were isolated and characterized. Now, characterization of bacterial isolates has been greatly aided by molecular biology. Molecular biology is also helping us to understand degradation genes and their expression, degradation enzymes and their regulation, and the evolution and adaptation of contaminant-degrading microbes. Intriguingly, many contaminant-degrading

The author is in the School of Civil and Environmental Engineering, Cornell University, Ithaca, NY 14853, USA. E-mail: jmg18@cornell.edu