

# A three-player solution

Lewi Stone

The seemingly unpredictable 'boom and bust' of insect-pest populations will be better understood with the advent of a deceptively simple model combining field and laboratory data with earlier theories.

Etienne Leopold Trouvelot, an astronomy professor at Harvard in the nineteenth century, had his scientific career "ruined by a moth"<sup>1</sup>. As it turns out, Trouvelot, an obsessive amateur entomologist, could not have chosen a more formidable opponent. In 1868, his experiments with the gypsy moth (*Lymantria dispar*) resulted in disaster after several of the insects escaped from his suburban Boston home. The moth was an alien species. It proceeded to multiply, only slowly at first, but some 20 years later it could be found in its millions, defoliating forests and causing major economic and ecological damage as it went on to invade North America (Fig. 1).

Enormously embarrassed, Trouvelot, the classic 'good man gone wrong', returned to France and to obscurity.

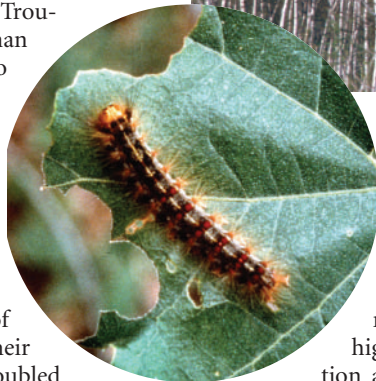
Alas, the same can't be said of the gypsy moth, which remains one of the most devastating forest pests to this day. Pinning down the ecological processes that give rise to outbreaks of this type of insect pest, and modelling their complex dynamics, has troubled theoretical ecologists for decades: in this issue Dwyer *et al.*<sup>2</sup> (page 341) present a mathematical model that might just crack the problem.

Broadly speaking there are two competing theories to explain insect outbreaks. The first argues that climatic factors, such as rainfall and temperature, set appropriate conditions for outbreaks. The other suggests that biotic interactions — competition and predation, for instance — are largely responsible. Mathematical models based on experimental data can provide insights about the extent to which these different factors are at play. Beyond this, however, there are some strange circumstances in need of an explanation. For example, of the approximately 80 different forest species of moths and butterflies (Lepidoptera) that exhibit large outbreaks, at least 18 are to some degree cyclical. That is, outbreaks recur in a regular fashion, and although not perfectly cyclical they have an average periodicity of 8–14 years<sup>3</sup>.

It is still not understood why these patterns have an underlying cyclicity, although one would expect there to be some basic



Figure 1 Bare birch — an upshot of the gypsy moth invasion of eastern North America. These grey birch trees would be in leafy splendour had they not been stripped of developing foliage. Inset, a gypsy moth caterpillar, the insect stage that does the damage.



force that drives it. The recurrent patterns, moreover, seem to be highly resilient to perturbation and do not break down with external manipulation: the cycling seems to possess some form of ecological stability. On top of all this, the insect outbreaks exhibit remarkable spatial synchrony, with populations rising and falling simultaneously, sometimes across millions of square kilometres.

Early theoretical explanations for insect outbreaks were based on the idea of multiple equilibria. According to the theory, density-dependent processes maintain the population at low levels for long periods. In the case of the gypsy moth, small-mammal predators such as the white-footed mouse regulate the population at low density until such time as the predators themselves drop in number because of the random failure of other food sources. The gypsy moth population then bursts into outbreak mode and rapidly jumps to the higher equilibrium level. At these higher densities, pathogens, especially a nuclear polyhedrosis virus (NPV), rapidly infect the population, causing enough gypsy moth mortality to trigger the collapse of the outbreak<sup>4</sup>. This, however, is only part of a complex story. A more comprehensive

description should also include the so-called induced-defence hypothesis, whereby the deteriorating quality of forest foliage due to defoliation has a negative impact on the gypsy moth population.

In the 1970s, insect-outbreak models were designed to mimic some of these features by incorporating multiple equilibria with alternative stable states at low and high densities. These models, however, did not include the critical ingredient of host–pathogen dynamics. In contrast, host–pathogen-type models of the 1980s and 1990s generally failed to take account of the density-dependent regulating effects of predation. Dwyer *et al.*<sup>2</sup> are the first to glue these two processes together, by careful and direct inclusion of the interactions between all three players — the gypsy moth, its predators and its specialist pathogen, NPV. In doing so, their model is able to reproduce long-term time series of gypsy moth outbreaks with greater success than any other so far. Moreover, the basic framework should prove equally applicable to modelling the dynamics of many other pests that defoliate forests.

The model of Dwyer *et al.* seems deceptively simple, but there is more to it than meets the eye. First, it is based on more than a decade of meticulous field and laboratory investigations of gypsy moth host–pathogen

transmission dynamics<sup>5</sup>. These studies not only provided well defined estimates of ecological parameters, but also identified an essential ingredient in outbreak dynamics, namely that gypsy moth larvae vary greatly in their susceptibility to the virus. Heterogeneity of this form has a known stabilizing effect and is a crucial contributing factor in ensuring the recurrence of outbreaks. Dwyer and colleagues' model takes this heterogeneity into account, along with the essential time delays that occur between larval infection and actual death, as well as inter-epidemic dynamics such as pathogen survival from one season to the next, and differences in mean susceptibility among larval stages. The version of the model analysed here is, in fact, the 'infinite epidemic/burnout approximation' of a more sophisticated set of equations<sup>5</sup>, but it elegantly captures all the main features.

Dwyer *et al.* note that their host-pathogen model inherits the multiple equilibria of the 1970s models. But, in addition, it generates even more complex, and sometimes chaotic, dynamics. With the inclusion of environmental stochasticity, to mimic the effects of weather, the model population jumps unpredictably between multiple attractors (different nonequilibrium 'attracting' states), producing time series of changes in population density that closely resemble those of real gypsy moth populations. Model outbreaks occur on average every 11 years, but with a variability from outbreak to outbreak that closely matches real data. Between outbreaks, the predator maintains the model gypsy moth population at relatively low levels. With time and stochasticity, however, the population slowly builds up to trigger the next outbreak. On inclusion of spatial structure, the authors show that different subpopulations synchronize their chaotic outbreak oscillations and remain relatively in phase with one another, which is in keeping with the coupled oscillator theory from nonlinear dynamics<sup>6</sup>. This result helps to explain the enigmatic spatial synchronization of many pest species.

Now that Dwyer *et al.*<sup>2</sup> have exposed the critical mechanisms behind gypsy moth outbreaks, it would be interesting to take their work further. For example, the model would allow assessment of the relatively new and effective natural enemy of the gypsy moth, the fungal pathogen *Entomophaga maimaiga*, present in North America since 1989. Unlike NPV, which triggers the collapse of a gypsy moth outbreak, the fungus can sometimes prevent outbreaks altogether. In some areas of North America, *E. maimaiga* has the potential to bring gypsy moth damage to a halt. Modelling work (see, for example, ref. 7) is currently under way to assess the dispersal dynamics of the fungus, its ability to become established and its overall impact. Modifications of Dwyer and

colleagues' model might help in this regard. Their model will undoubtedly prove of great value for studying the dynamics of many other pest species that cause episodes of ecological devastation. ■

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Imaging techniques

## Seeing single spins

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Combining the imaging power of magnetic resonance and the sensitivity of atomic force microscopy has created a hybrid technique that can resolve single spins beneath the surface of a sample.

Magnetic resonance imaging (MRI) and atomic force microscopy (AFM) are two of the most powerful imaging technologies available. MRI can provide, non-invasively, fully three-dimensional images from deep within an object. However, the spatial resolution of this technique is limited to the smallest volume that contains enough nuclear or electronic spins to generate a detectable signal. Sensitivity to a smaller number of spins is the key to improving spatial resolution.

Combining three-dimensional MRI with the excellent force sensitivity of AFM — in magnetic resonance force microscopy, or MRFM — opens the possibility of performing scanned-probe MRI with much improved spatial resolution. On page 329 of this issue, Rugar *et al.*<sup>1</sup> report the combination of MRI and AFM to achieve sensitivity to a single electron spin. Compare this with the 10<sup>8</sup>–10<sup>10</sup> spins required in a conventional electron-spin resonance experiment. This signal achievement will dramatically alter the horizons for high-resolution imaging.

But the ability to detect individual spins is about more than imaging — it implies the power to manipulate individual spins as well. Present-day information processing relies on the electron's charge, through manipulating and detecting voltages in electronic circuits. Exploiting the electron's magnetic moment, or spin, could lead to significant enhancements in electronic information processing, including nonvolatile memory, increased integration densities and reduced power consumption<sup>2</sup>. Furthermore, the spin of the electron is a natural two-state quantum system ('qubit') for quantum computing; the spin can also be isolated from its physical environment to achieve the long decoherence times needed for successful computation.

MRI exploits the proportionality between the easily measured frequency of a magnetic resonance signal and the value of the magnetic field at the spin's location. In

1. Liebhold, A., Mastro, V. & Schaefer, P. W. *Bull. Entomol. Soc. Am.* **35**, 20–21 (1989).
2. Dwyer, G., Dushoff, J. & Yee, S. H. *Nature* **430**, 341–345 (2004).
3. Myers, J. H. *Adv. Ecol. Res.* **18**, 179–242 (1988).
4. Elkinton, J. S. & Liebhold, A. M. *Annu. Rev. Entomol.* **35**, 571–596 (1990).
5. Dwyer, G., Dushoff, J., Elkinton, J. S. & Levin, S. A. *Am. Nat.* **156**, 105–120 (2000).
6. Blasius, B., Huppert, A. & Stone, L. *Nature* **399**, 354–359 (1999).
7. Weseloh, R. M. *Biol. Control* **29**, 138–144 (2004).

an applied magnetic field, the resonant frequency of spins increases steadily across a region, following the increasing field. Thus measuring the resonant frequency pinpoints the location of the spins responsible for the signal. And because magnetic fields penetrate samples easily, three-dimensional images can be constructed from signals from deep inside them. MRI has had a huge impact in the biomedical arena, but there is continuing demand for higher spatial resolution, below the 1 mm<sup>3</sup> currently achievable in medical settings.

A decade ago, John Sidles proposed<sup>3</sup> a radical approach to MRI, based on detecting the force exerted by the spins in a sample on a microscopic magnet, which is mounted on a flexible cantilever above the sample. This would offer the much improved sensitivity needed to reduce the imaged volume and to achieve atomic-scale nuclear MRI<sup>4</sup>. Rugar and colleagues' demonstration<sup>1</sup> of single electron-spin detection using Sidles' approach is a heartening milestone in realizing the dream of high-resolution MRI. Two elements are essential for the dramatically improved sensitivity: large magnetic-field gradients generated by micrometre-scale magnetic probe tips, and highly sensitive cantilevers. Rugar *et al.* engineered cantilevers with a state-of-the-art force sensitivity<sup>5</sup> of 10<sup>-18</sup> newtons specifically for this purpose.

The micromagnetic probe mounted on the cantilever tip generates a large field gradient (approximately proportional to its magnetization divided by its diameter). In this set-up<sup>1</sup> (Fig. 1), the gradient of the microscopic magnetic probe was approximately 2 gauss per nanometre, so that the force generated on the cantilever by an individual electron-spin was detectable, at 2 × 10<sup>-18</sup> newtons. The field gradient has a second, independent role: as in MRI, it causes spins located at different depths beneath the micromagnetic tip to resonate at different