Parasites lost

Keith Clay

Why do some plants and animals become pests when they are introduced to new areas? Part of the answer seems to be that they have left most of their parasites behind, gaining vigour as a consequence.

Invasive species can be a real bother. These are plants or animals that, when they are accidentally or deliberately moved from one region to another, flourish to the extent of getting out of hand and becoming pests in their naturalized environment. They tend to reduce biodiversity, and can have adverse effects on human well-being[1,2]. Much effort is devoted to controlling them after they are established, but a better understanding of why species become invasive offers the possibility of taking pre-emptive measures.

In companion papers on pages 625 and 628 of this issue, Mitchell and Power[3] and Torchin *et al.*[4] illuminate the biology of invasiveness. They report the results of surveying parasite loads of invasive plants and animals in their naturalized and native ranges. They find that parasitism is significantly reduced in organisms in the introduced range, so supporting the ‘enemy release hypothesis’ — the idea that species are more likely to become invasive when they are released from control by their natural enemies.

This hypothesis is one of several (not mutually exclusive) explanations put forward to account for why some species increase uncontrollably when introduced into new areas. In *The Ecology of Invasions by Animals and Plants*[5], Charles Elton favoured a more general form of this hypothesis, the ‘ecological resistance hypothesis’, which proposes that competition with native species and attack by native predators and pathogens keep invaders in check[6,7]. Island systems such as those of Hawaii or Australia may be particularly prone to invasion, for several reasons — their lower species diversity and population density; the absence of particular groups (placental mammals in Australia, for instance, and snakes in Hawaii); and the lack of coevolutionary history with invaders, in which host and parasite have had a long time to coadapt to each other and have reached a stable state[8]. This lack of coadaptation is dramatically illustrated by the lack of resistance of native species to introduced pathogens. More generally, communities with high diversity may be more resistant to invasions[9].

The ecological resistance hypothesis suggests why certain habitats might be more or less prone to invasion, but does not predict why certain species are more or less likely to invade that habitat. In particular, this hypothesis cannot provide explanations for continental habitats where species diversity is high and all ecological niches seem to be taken, yet where invasive species are numerous. A good example is the eastern United States, where nutria, an aquatic rodent, and purple loosestrife, a wetland plant, are just two of many introduced species that have had or could have adverse effects (Fig. 1). Mitchell and Power[3] and Torchin and colleagues[4] provide a more mechanistic explanation of why these species are problematic.

Figure 1 **Invasive species in the United States.** a, b, **Two species that have caused widespread ecological damage to native communities are the nutria, or coypu (*Myocastor coypus*), and purple loosestrife (*Lythrum salicaria*).** c, d, **Other species such as the Asian rice eel (*Monopterus albus*) and mile-a-minute weed (*Polygonum perfoliatum*) are limited in their distribution but threaten to become severe problems as they expand into areas to which they are well adapted.** e, f, **Examples of a worrisome group of species that could prove serious pests should they arrive are the brown tree snake (*Boiga irregularis*), which decimated bird life on Guam following its introduction from Indonesia but has not yet successfully invaded Hawaii, and witchweed (*Striga* spp.), which in parts of Africa has a highly adverse effect on cereal yields.**

(A) L. RICHARDSON/CORBIS; (B) E. CRICHTON/CORBIS; (C) MOLLUSCAN PICTURES; (D) M. C. PERRY/USGS; (E) RONENZILBERMAN/AP; (F) J. FRY/AA-Z BOTANICAL

Both groups compiled published information on parasitism of invasive species in their native and their naturalized ranges. Mitchell and Power[3] quantified the number of fungal pathogens and viruses infecting 473 plant species that are native to Europe but have become naturalized and invasive in the United States. They found that these species were infected on average by 77% fewer fungal and viral species in the United States than in Europe, strongly supporting the enemy release hypothesis. Interestingly, in their naturalized range, invasive plants were more likely to be released from control by fungal pathogens than by viruses.

Mitchell and Power also quantified the characteristics of each plant species from the frequency of reports naming that species as noxious (defined as a weed that poses a high risk to agriculture) or an invader of natural areas. Species that ranked higher on the scales of noxiousness and invasiveness showed greater release from their parasites. The authors found that invasive plant species do accumulate parasites from their naturalized range, but the overall parasite load tended to be less than in their original home. Finally, they also found that invasive plant species with higher rates of pathogen accumulation were less likely to be noxious, an observation that again supports the ecological resistance hypothesis. This provides a ray of hope: if invasive species accumulate parasites in their naturalized range relatively rapidly[10], the problems they cause may be temporary.

Torchin and colleagues[4] examined 26 invasive animal species ranging from mol-

Box 1 Tansy ragwort: a case history

The tansy ragwort (*Senecio jacobaea*, pictured) is native to Eurasia but has been introduced into North and South America and the Australian region. In the western United States it aggressively invaded range lands, where it displaced species of forage plant and poisoned livestock with its pyrrolizidine alkaloids. In 1976, aerial photography showed that the species covered more than 12,000 km^2 in western Oregon. But by 1988 the area infested had been reduced by 60–90% and more desirable vegetation was recovering, a change that can be attributed to the deliberate introduction of the cinnabar moth (*Tyria jacobaeae*) from France and the ragwort flea beetle (*Longitarsus jacobaeae*) from Italy. Cinnabar caterpillars feed on developing ragwort inflorescences and leaves, and can totally strip a plant of foliage; flea beetles chew holes in the leaves. The decline of ragwort populations clearly followed the establishment of these natural enemies from the ragwort's native range, and ragwort density has since remained low[12]. The same group has experimentally confirmed[12] that the introduction of the natural enemies from its home range was indeed responsible for controlling the ragwort. **K.C.**

NIALL BENVIE/CORBIS

luscs such as the common periwinkle, *Littorina littorea*, to the black rat, *Rattus rattus*. Like most of the cases examined, these species are native to the Old World but have been introduced to the New World. In addition to quantifying the number of parasite species hosted, the authors also analysed parasite prevalence (the percentage of individuals infected within a population) in the native and naturalized ranges. The parasites documented were exclusively helminths — flatworms or roundworms. There is a rich database on parasitic helminths, reflecting their great diversity and their ecological significance.

Torchin and colleagues' results are similar to those of Mitchell and Power, in that an average of 16 parasite species per host species occurred in the native range compared to seven in the naturalized range. On average, only three of the native parasites accompanied the host to the naturalized range. Hosts were also infected by four parasite species from the new environment, again showing that introduced species accumulate new parasites. But overall parasite prevalence was much lower in the host species' naturalized range.

Taken together, these studies[3,4] constitute further evidence for the enemy release hypothesis. Invasive species appear to suffer from fewer parasites and pathogens in their naturalized range than in their native range; so, presumably, they are more poorly regulated by parasites in their new environment. This provides conceptual support for one approach to biological control of such species, in which parasitic organisms from plants or animals in native habitats are identified and introduced into the naturalized environment (see Box 1). This strategy can, however, prove a double-edged sword when the biocontrol agent finds native species to be equally, or more, attractive.

Why are parasites and pathogens often left behind when their hosts migrate? There may be several reasons. The colonization of new habitats is often by just a handful of individuals, increasing the likelihood that all are free of infection. In addition, if parasite dispersal occurs independently of the host, two successful migrations are required. Similarly, for parasites with complex life cycles, their alternative hosts must also accompany the primary host into the new range, requiring migration of three or more species.

The new results[3,4] lend support to the idea that invasive species can be controlled by speeding up their accumulation of parasites. They may be less helpful for predicting which plant and animal species will prove invasive in the future[11]. But we can be sure that biological invasions will continue and that the actions of humans, the most successful invasive species of all, will remain their primary contributor. ■

Keith Clay is in the Department of Biology, Indiana University, Bloomington, Indiana 47405, USA.
e-mail: clay@indiana.edu

1. Pimentel, D. (ed.) *Biological Invasions: Economic and Environmental Costs of Alien Plant, Animal and Microbe Species* (CRC Press, Boca Raton, 2002).
2. Westbrooks, R. G. *Invasive Plants: Changing the Landscape of America* (Federal Interagency Committee for the Management of Noxious and Exotic Weeds, Washington DC, 1998).
3. Mitchell, C. E. & Power, A. G. *Nature* 421, 625–627 (2003).
4. Torchin, M. E., Lafferty, K. D., Dobson, A. P., McKenzie, V. J. & Kuris, A. M. *Nature* 421, 628–630 (2003).
5. Elton, C. *The Ecology of Invasions by Animals and Plants* (Univ. Chicago Press, 2000; orig. edn Methuen, 1958).
6. Maron, J. L. & Vila, M. *Oikos* 95, 361–373 (2001).
7. Keane, R. M. & Crawley, M. J. *Trends Ecol. Evol.* 17, 164–170 (2002).
8. Carlquist, S. *Island Biology* (Columbia Univ. Press, New York, 1974).
9. Tilman, D. *Ecology* 74, 2179–2191 (1993).
10. Strong, D. R. & Levin, D. A. *Proc. Natl Acad. Sci. USA* 72, 2116–2119 (1975).
11. Ehrlich, P. R. in *Biological Invasions: A Global Perspective* (eds Drake, J. A. *et al.*) 315–328 (Wiley, London, 1989).
12. McEvoy, P. & Cook, C. *Ecol. Appl.* 1, 430–442 (1991).

Applied physics

Solar cells to dye for

Michael Grätzel

The idea of producing electricity from sunlight is attractive, but in practice the technology to do so is expensive. A new device, moving away from the traditional silicon design, shows promise.

Photovoltaic conversion of solar energy — from photons to electrons — has so far been dominated by solid-state devices, usually made of silicon and profiting from the expertise of the semiconductor industry. That dominance is now being challenged by new generations of photovoltaic cells. On page 616 of this issue, McFarland and Tang[1] present an intriguing embodiment of a converter that is based on light harvesting by dye molecules on a metal surface. Contrary to expectation, their device shows a strikingly high internal quantum efficiency for electric-current generation.

The silicon used in most of today's solar cells must fulfil several tasks. It must absorb sunlight, converting photons into negative- and positive-charge carriers (electrons and holes, respectively); it must transmit an electric field to separate the electrons and holes; and it must then conduct these carriers to the current collectors. To achieve all this simultaneously, materials of very high purity are needed, and consequently silicon-based solar cells are too costly to compete with conventional means of producing electric power.

In contrast, the device developed by McFarland and Tang[1] has a multilayer structure that physically separates the processes of light absorption and charge-carrier transport (Fig. 1). Photons are harvested by dye molecules adsorbed on the surface of a thin gold film, which in turn rests on a layer of titanium dioxide (TiO_2). Spontaneous electron flow from the semiconducting TiO_2 layer to the metallic gold layer imparts a slight negative charge to the gold, leaving a slight positive charge on the TiO_2. The resulting local electrostatic field creates a potential