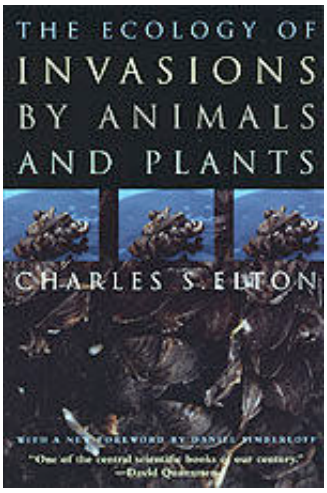

"History has caught up with Charles Elton's foresight, and *The Ecology of Invasions* can now be seen as one of the central scientific books of our century."—David Quammen, from the Foreword to *Killer Algae*

"A classic treatise on the subject of invasive animals and plants. . . . [T]he basic ecological lessons brought forth in this book provide a solid underpinning for our understanding of contemporary introductions of species."—*Science Books & Films*

"A book has to be really special to be republished 40 years after it first appeared. Elton's book is. The topic is even more important today than it was back then, because invasive species may now be the most important cause of species extinction. This book is a classic that I would like all of my students to read."—Stuart Pimm, Columbia University

An excerpt from

The Ecology of Invasions by Animals and Plants

Charles S. Elton

Ecological Explosions

Nowadays we live in a very explosive world, and while we may not know where or when the next outburst will be, we might hope to find ways of stopping it or at any rate damping down its force. It is not just nuclear bombs and wars that threaten us, though these rank very high on the list at the moment: there are other sorts of explosions, and this book is about ecological explosions. An ecological explosion means the enormous increase in numbers of some kind of living organism—it may be an infectious virus like influenza, or a bacterium like bubonic plague, or a fungus like that of the potato disease, a green plant like the prickly pear, or an animal like the grey squirrel. I use the word "explosion" deliberately, because it means the bursting out from control of forces that were previously held in restraint by other forces. Indeed the word was originally used to describe the barracking of actors by an audience whom they were no longer able to restrain by the quality of their performance.

Ecological explosions differ from some of the rest by not making such a loud noise and in taking longer to happen. That is to say, they may develop slowly and they may die down slowly; but they can be very impressive in their effects, and many people have been ruined by them, or died or forced to emigrate. At the end of the First World War, pandemic influenza broke out on the Western Front, and thence rolled right round the world, eventually, not sparing even the Eskimos of Labrador and Greenland, and it is reputed to have killed 100 million human beings. Bubonic plague is still pursuing its great modern pandemic that started at the back of China in the end of last century, was carried by ship rats to India, South Africa, and other continents, and now smoulders among hundreds of species of wild rodents there, as well as in its chief original home in Eastern Asia. In China it occasionally flares up on a very large scale in the pneumonic form, resembling the Black Death of medieval Europe. In 1911 about 60,000 people in Manchuria died in this way. This form of the disease, which spreads directly from one person to another without the intermediate link of a flea, has

"While Rachel Carson's 1962 classic *Silent Spring* launched the modern environmental movement by alerting the world to the perils of chemical pollution, Elton's book (written several years earlier) was largely ignored except among a few in the scientific community. Environmental groups and resource agencies are finally realizing that his was an equally important clarion call. Invasive species are clearly a form of global change, causing serial extinctions, decimating entire forests, transforming landscapes, and challenging human health. And while there is an avalanche of literature now being generated, Elton's book still stands as among the finest. Nice pictures, great maps, perky prose, low price, and a new foreword by Dan Simberloff makes this reprint a worthy addition to any library."—*Whole Earth*

mercifully been scarce in the newly invaded continents. Wherever plague has got into natural ecological communities, it is liable to explode on a smaller or larger scale, though by a stroke of fortune for the human race, the train of contacts that starts this up is not very easily fired. In South Africa the gerbilles living on the veld carry the bacteria permanently in many of their populations. Natural epidemics flare up among them frequently. From them the bacteria can pass through a flea to the multimammate mouse; this species, unlike the gerbilles, lives in contact with man's domestic rat; the latter may become infected occasionally and from it isolated human cases of bubonic plague arise. These in turn may spread into a small local epidemic, but often do not.

Most people have had experience of some kind of invasion by a foreign species, if only on a moderate scale. Though these are silent explosions in themselves, they often make quite a loud noise in the Press, and one may come across banner headlines like "Malaria Epidemic Hits Brazil," "Forest Damage on Cannock Chase," or "Rabbit Disease in Kent." This arrival of rabbit disease—myxomatosis—and its subsequent spread have made one of the biggest ecological explosions Great Britain has had this century, and its ramifying effects will be felt for many years.

But it is not just headlines or a more efficient news service that make such events commoner in our lives than they were last century. They are really happening much more commonly; indeed they are so frequent nowadays in every continent and island, and even in the oceans, that we need to understand what is causing them and try to arrive at some general viewpoint about the whole business. Why should a comfortably placed virus living in Brazilian cotton-tail rabbits suddenly wipe out a great part of the rabbit populations of Western Europe? Why do we have to worry about the Colorado potato beetle now, more than 300 years after the introduction of the potato itself? Why should the pine looper moth break out in Staffordshire and Morayshire pine plantations two years ago? It has been doing this on the Continent for over 150 years; it is not a new introduction to this country.

The examples given above point to two rather different kinds of outbreaks in populations: those that occur because a foreign species successfully invades another country, and those that happen in native or long-established populations. This book is chiefly about the first kind—the invaders. But the interaction of fresh arrivals with the native fauna and flora leads to some consideration of ecological ideas and research about the balance

within and between communities as a whole. In other words, the whole matter goes far wider than any technological discussion of pest control, though many of the examples are taken from applied ecology. The real thing is that we are living in a period of the world's history when the mingling of thousands of kinds of organisms from different parts of the world is setting up terrific dislocations in nature. We are seeing huge changes in the natural population balance of the world.

The larger ecological explosions have helped to alter the course of world history, and, as will be shown, can often be traced to a breakdown in the isolation of continents and islands built up during the early and middle parts of the Tertiary Period.

In order to focus the subject, here are three case histories of species which were brought from one country and exploded into another. About 1929, a few African mosquitoes accidentally reached the north-east corner of Brazil, having probably been carried from Dakar on a fast French destroyer. They managed to get ashore and founded a small colony in a marsh near the coast —the Mosquito Fathers as it were. At first not much attention was paid to them, though there was a pretty sharp outbreak of malaria in the local town, during which practically every person was infected. For the next few years the insects spread rather quietly along the coastal region, until at a spot about 200 miles farther on explosive malaria blazed up and continued in 1938 and 1939, by which time the mosquitoes were found to have moved a further 200 miles inland up the Jaguaribe River valley. It was one of the worst epidemics that Brazil had ever known, hundreds of thousands of people were ill, some twenty thousand are believed to have died, and the life of the countryside was partially paralysed. The biological reasons for this disaster were horribly simple: there had always been malaria-carrying mosquitoes in the country, but none that regularly flew into houses like the African species, and could also breed so successfully in open sunny pools outside the shade of the forest. Fortunately both these habits made control possible, and the Rockefeller Foundation combined with the Brazil government to wage a really astounding campaign, so thorough and drastic was it, using a staff of over three thousand people who dealt with all the breeding sites and sprayed the inside of houses. This prodigious enterprise succeeded, at a cost of over two million dollars, in completely exterminating *Anopheles gambiae* on the South American continent within three years.

Here we can see three chief elements that recur in this sort of situation. First there is the historical one:—this species of

mosquito was confined to tropical Africa but got carried to South America by man. Secondly, the ecological features—its method of breeding, and its choice of place to rest and to feed on man. It is quite certain that the campaign could never have succeeded without the intense ecological surveys and study that lay behind the inspection and control methods. The third thing is the disastrous consequences of the introduction. One further consequence was that quarantine inspection of aircraft was started, and in one of these they discovered a tsetse fly, *Glossina palpalis*, the African carrier of sleeping sickness in man, and at the present day not found outside Africa.

The second example is a plant disease. At the beginning of this century sweet chestnut trees in the eastern United States began to be infected by a killing disease caused by a fungus, *Endothia parasitica*, that came to be known as the chestnut blight. It was brought from Asia on nursery plants. In 1913 the parasitic fungus was found on its natural host in Asia, where it does no harm to the chestnuts. But the eastern American species, *Castanea dentate*, is so susceptible that it has almost died out over most of its range. This species carries two native species of *Endothia* that do not harm it, occurring also harmlessly on some other trees like oak; one of these two species also comes on the chestnut, *C. sativa*, in Europe. Even by 1911 the outbreak, being through wind-borne spores, had spread to at least ten states, and the losses were calculated to be at least twenty-five million dollars up to that date. In 1926 it was still spreading southwards, and by 1950 most of the chestnuts were dead except in the extreme south; and it is now on the Pacific coast too. So far, the only answer to the invasion has been to introduce the Chinese chestnut, *C. mollissima*, which is highly though not completely immune through having evolved into the same sort of balance with its parasite, as had the American trees with theirs; much as the big game animals of Africa can support trypanosomes in their blood that kill the introduced domestic animals like cattle and horses. The biological dislocation that occurs in this trypanosomiasis is the kind of thing that presumably would have happened also if the American chestnut had been introduced into Asia. The Chinese chestnut is immune both in Asia and America. Already by 1911 the European chestnuts grown in America had been found susceptible. In 1938 the blight appeared in Italy where it has exploded fast and threatens the chestnut groves that there are grown in pure stands for harvesting the nuts; it has also reached Spain and will very likely reach Britain in the long or short run. Unfortunately the Chinese chestnut will not flourish in Italy, and hopes are placed solely on the eventual breeding of a resistant variety of hybrid.

The third example given here concerns the sea lamprey, *Petromyzon marinus*, in the Great Lakes region of North America. This creature is a North Atlantic river-running species, mainly living in the sea, and spawning in streams. But in the past it established itself naturally in Lake Ontario, as well as in some small lakes in New York State. But Niagara Falls formed an insurmountable barrier to further penetration into the inner Great Lakes. In 1829 the Welland Ship Canal was completed, providing a by-pass into Lake Erie. But it was a further hundred years or so before any sea lampreys were observed in that lake. Then the invasion went with explosive violence. By 1930 lampreys had reached the St Clair River, and by 1937 through it to Lake Huron and Lake Michigan, where they began to establish spawning runs in the streams flowing to these lakes. In 1946 they were in Lake Superior. Meanwhile the lampreys were attacking fish, especially the lake trout, *Salvelinus namaycush*, a species of great commercial importance. The sea lamprey is a combination of hunting predator and ectoparasite: it hangs on to a fish, secretes an anticoagulant and lytic fluid into the wound, and rasps and sucks the flesh and juices until the fish is dead, which may be after a few hours or as long as a week. The numbers of lake trout caught had always fluctuated to some extent, and the statistics of the fishery since 1889 have been thoroughly analysed. But never before the recent catastrophe had the catch collapsed so rapidly: in ten years after the lamprey invasion began to take effect, the numbers of lake trout taken in the American waters of Lake Huron and Lake Michigan fell from 8,600,000 pounds to only 26,000 pounds. On the Canadian side things were little better. This was not caused by change in fishing pressure. Other species besides the lake trout have also been hard hit. Among these are the lake whitefish, burbot, and suckers, all of which declined in numbers. So, the making of a ship canal to give an outlet for produce from the Middle West has brought about a disaster to the Great Lakes fisheries over a century later. But in Lake Erie lampreys did not multiply, partly because there are not many lake trout there, but probably also because the streams are not right for spawning in.

These three examples alone illustrate what man has done in deliberate and accidental introductions, especially across the oceans. Some idea of what this can mean for the spread of animals can be got from the results of an ecological survey done by Myers, a noted tropical entomologist, while traveling on a Rangoon rice ship from Trinidad to Manila in 1929. He amused himself by making a list of every kind of animal on board, from cockroaches and rice beetles to fleas and pet animals. Altogether he found 41 species of these travelers, mostly insects. And when

he unpacked his clothes in the hotel in Manila, he saw some beetles walk out of them. They were *Tribolium castaneum*, a well-known pest of stored flour and grains, which was one of the species living among the rice on the ship.

A hundred years of faster and bigger transport has kept up and intensified this bombardment of every country by foreign species, brought accidentally or on purpose, by vessel and by air, and also overland from places that used to be isolated. Of course, not all the plants and animals carried around the world manage to establish themselves in the places they get to; and not all that do are harmful to man, though they must change the balance among native species in some way. But this worldwide process, gathering momentum every year, is gradually breaking down the sort of distribution that species had even a hundred years ago.

To see the full significance of what is happening, one needs to look back much further still, in fact many millions of years by the geological time-record. It was Alfred Russel Wallace who drew general public attention to the existence of great faunal realms in different parts of the world, corresponding in the main to the continents. These came to be known as Wallace's Realms, though their general distribution had already been pointed out by an ornithologist, P. L. Sclater. Wallace, however, did the enormous encyclopaedic work of assembling and classifying information about them. He supposed these realms to have been left isolated for such long periods that they had kept or evolved many special groups of animals. When one was a child, this circumstance was very simply summed up in books about animals. The tiger lives in India. The wallaby lives in Australia. The hippopotamus lives in Africa. One might have learned that the coypu or nutria lives in South America. A very advanced book might have speculated that this big water rodent was evolved inside South America, which we now know to be so. But nowadays, it would have to add a footnote to later editions, saying that the coypu is also doing quite well in the States of Washington, Oregon, California, and New Mexico; also in Louisiana (where 374,000 were trapped in one year recently); in south-east U.S.S.R.; in France; and in the Norfolk Broads of East Anglia. In the Broads it carries a special kind of fur parasite, *Pitrufquenia coypus*, belonging to a family (Gyropidae) that also evolved in South America. These fur lice have antennae shaped like monkey-wrenches, which perhaps explains how they managed to hang on so well all the way from South America.

But in very early times, say 100 million years ago in the Cretaceous Period, the world's fauna was much more truly

cosmopolitan, not so much separated off by oceans, deserts, and mountains. If there had been a Cretaceous child living at the time the chalk was deposited in the warm shallow seas at Marlborough or Dover, he would have read in his book, or slate perhaps: "Very large dinosaurs occur all over the world except in New Zealand; keep out of their way." Or that water monsters occurred in more than one loch in the world. In fact, zoogeographically, it would have been rather a dull book, though the illustrations and accounts of the habits of animals would have been terrifically interesting. There would have been much less use for zoos: you just went out, with suitable precautions, and did dinosaur-watching wherever you were, and made punch-card records of their egg clutch-sizes. But the significance of these dinosaurs for the serious historical evidence is that you couldn't then get an animal the size of a lorry from one continent to another except by land; therefore the continents must have been joined together, at any rate fairly frequently, as geological time is counted.

This early period of more or less cosmopolitan land and fresh-water life was about three times longer than that between the Cretaceous Period and the present day. It was in the later period that Wallace's Realms were formed, because the sea, and later on great obstructions like the Himalaya and the Central Asian deserts, made impassable barriers to so many species. In fact the world had not one, but five or six great faunas, besides innumerable smaller ones evolved on isolated islands like Hawaii or New Zealand or New Caledonia, and in enormous remote lakes like Lake Baikal or Tanganyika. Man was not the first influence to start breaking up this world pattern. A considerable amount of re-mixing has taken place in the few million years before the Ice Age and since then: two big factors in this were the emergence of the Panama Isthmus from the sea, and the passage at various times across what is now Bering Strait. But we are artificially stepping up the whole business, and feeling the manifold consequences.

For thirty years I have read publications about this spate of invasions; and many of them preserve the atmosphere of first-hand reporting by people who have actually seen them happening, and give a feeling of urgency and scale that is absent from the drier summaries of text-books. We must make no mistake: we are seeing one of the great historical convulsions in the world's fauna and flora. We might say, with Professor Challenger, standing on Conan Doyle's "Lost World", with his black beard jutting out: "We have been privileged to be present at one of the typical decisive battles of history—the battles which have determined the fate of the world." But how will it be

decisive? Will it be a Lost World? These are the questions that ecologists ought to try to answer.

Charles S. Elton
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