



The Invaders

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

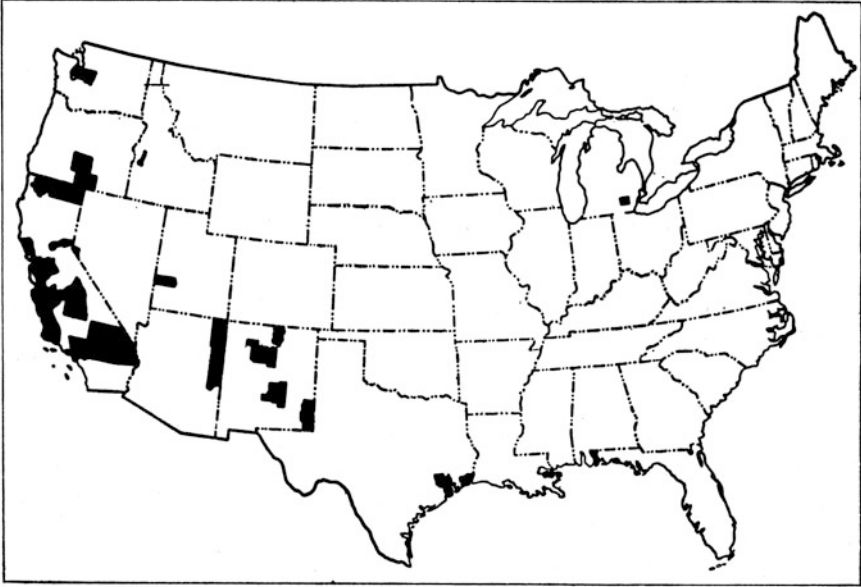


FIG. 1. Counties in the United States where plague has occurred in man. (From V. B. Link, 1955.)

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 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.⁴ These in turn may spread into a small local epidemic, but often do not. In the United States and Canada a similar underworld of plague (with different species in it) is established over an immense extent of the Western regions (Pls. 1-3, Figs. 1-2), though few outbreaks have happened in man.²² Here, then, the chain of

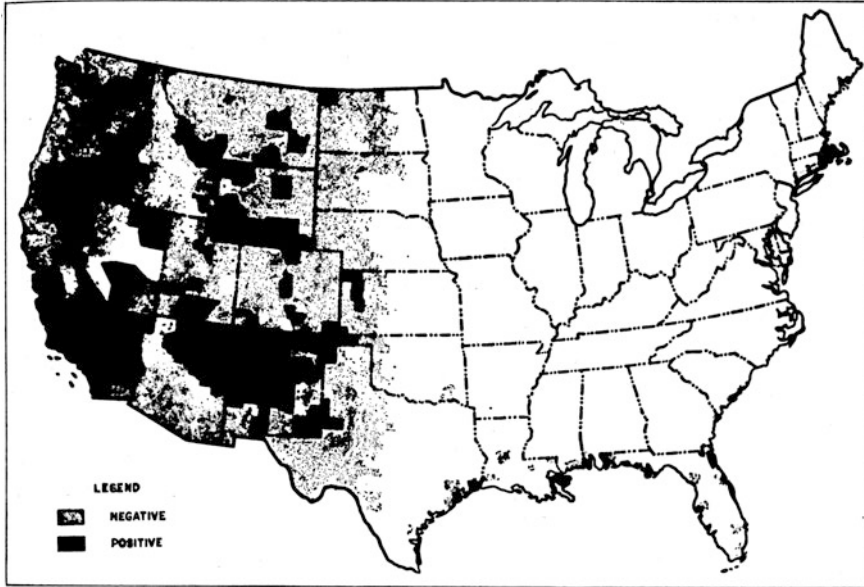


FIG. 2. Counties in the United States where plague has occurred in rodents.
(From V. B. Link, 1955.)

connexions is weaker even than in South Africa, though the potentiality is present. Although plague-stricken people and plague-infected rats certainly landed from ships in California early this century, it is still possible that the plague organism was already present in North America. Professor Karl Meyer, who started the chief ecological research on sylvatic plague there, says: "The only conclusion one can draw is that the original source and date of the creation of the endemic sylvatic plague area on the North American Continent, inclusive [of] Canada, must remain a matter of further investigation and critical analysis."²⁴

Another kind of explosion was that of the potato fungus from Europe that partly emptied Ireland through famine a hundred years ago. 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. Of course, pest control is very important, because we have to preserve our living resources and protect ourselves from diseases and the consequences of economic dislocation. But one should try to see the whole matter on a much broader canvas than that. I like the words of Dr Johnson: 'Whatever makes the past, the distant, or the future, predominate over the present, advances us in the dignity of thinking beings.'¹⁶ 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.

THE INVADERS

In order to focus the subject, here are seven 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 (Fig. 3). 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.

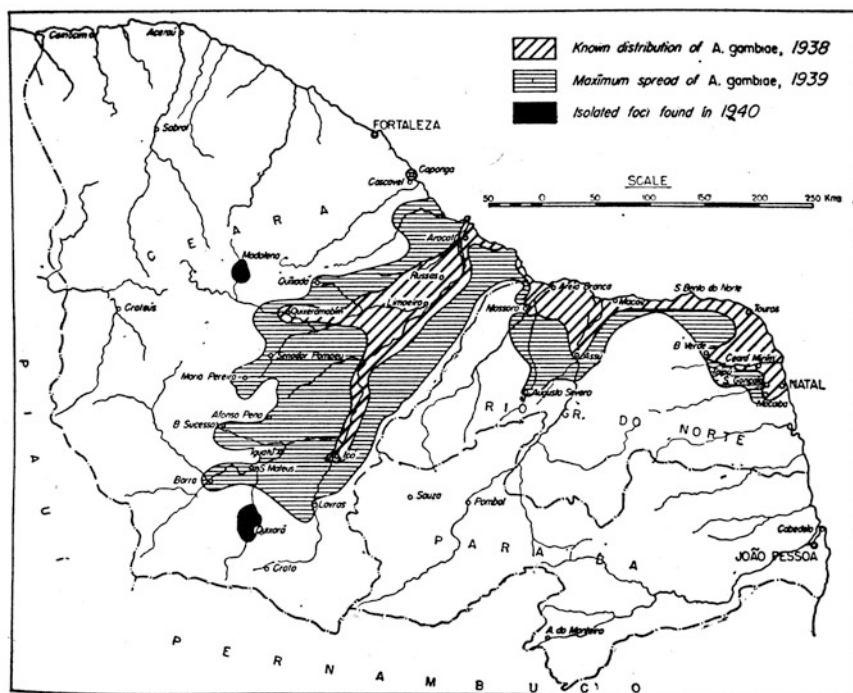


FIG. 3. Distribution areas of the African malaria mosquito, *Anopheles gambiae*, in Brazil in 1938, 1939, and 1940. Eradication measures had made it extinct in South America after this. (From F. L. Soper and D. B. Wilson, 1943.)

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.²⁸

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.²⁸

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 (Pl. 4). 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 dentata*, is so susceptible that it has almost died out over most of its range (Pl. 5). 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.²⁷ As the map shows (Fig. 4), 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.²³ 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,³¹ 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.²³ 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.⁸ Unfortunately the

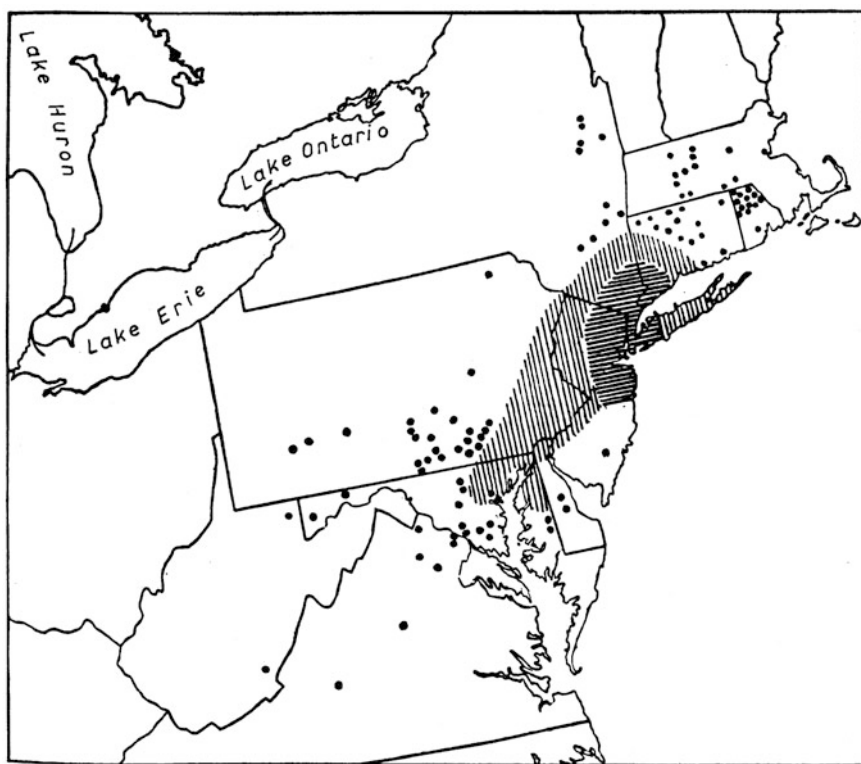


FIG. 4. Spread of the Asiatic chestnut blight, *Endothia parasitica*, to American chestnuts, *Castanea dentata*, in ten states. Horizontal hatching: majority of trees already dead; vertical hatching: complete infection generally; dots: isolated infections, many of which had been eradicated. (From H. Metcalfe and J. F. Collins, 1911.)

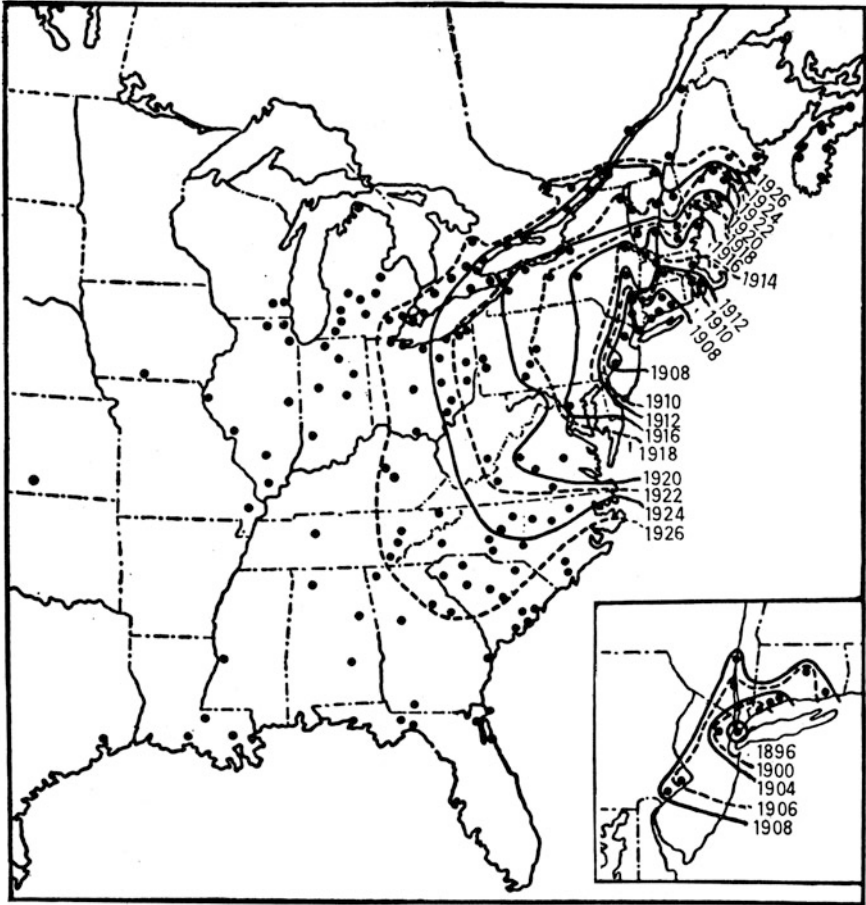


FIG. 5. Spread of the breeding range of the European starling, *Sturnus vulgaris*, in the United States and Canada from 1891 to 1926. Dots outside the 1926 line are chiefly winter records of pioneer spread. (From M. T. Cooke, 1928.)

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 is the European starling, *Sturnus vulgaris*, which has spread over the United States and Canada within a period of sixty years. (It has also become established in two other continents—South Africa and Australia, as well as in New Zealand.) This subspecies of starling has a natural range extending into Siberia, and from the north of Norway and Russia down to the Mediterranean. We should therefore expect it to be adaptable to a wide variety of continental habitats and

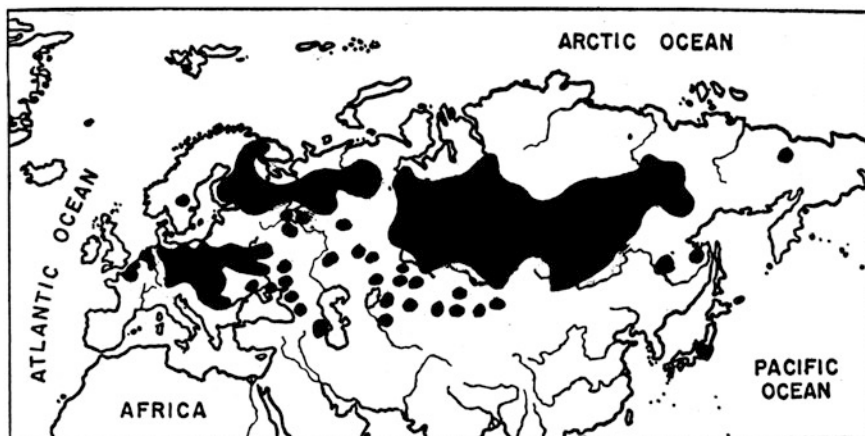


FIG. 6. Distribution of the North American muskrat, *Ondatra zibethica*, in Europe and Asia. (From A. De Vos, R. H. Manville and R. G. Van Gelder, 1956.)

climate. Nevertheless, the first few attempts to establish it in the United States were unsuccessful. Then from a stock of about eighty birds put into Central Park, New York, several pairs began to breed in 1891. After this the increase and spread went on steadily, apart from a severe mortality in the very cold winter of 1917–18. But up to 1916 the populations had not established beyond the Allegheny Mountains. Cooke's map of the position up to the year 1926 (Fig. 5) shows how the breeding range had extended concentrically, with outlying records of non-breeding birds far beyond the outer breeding limits, which had moved beyond the Alleghenies but nowhere westward of a line running about southwards from Lake Michigan.³ By 1954 the process was nearly reaching its end, and the starling was to be found, at any rate on migration outside its breeding season, almost all over the United States, though it was not fully entrenched yet in parts of the West coast states. It was penetrating northern Mexico during migration, and in 1953 one starling was seen in Alaska.¹⁷ This was an ecological explosion indeed, starting from a few pairs breeding in a city park; just as the spread of the North American muskrat, *Ondatra zibethica* (Pl. 8), over Europe was started from only five individuals kept by a landowner in Czechoslovakia in 1905 (Fig. 7). The muskrat now inhabits Europe in many millions, and its range has been augmented by subsidiary introductions for fur-breeding, with subsequent establishment of new centres of escaped animals and their progeny (Fig. 8). Since 1922, over 200 transplantations of muskrats have been started in Finland, some

originally from Czechoslovakia in 1922, and the annual catch is now between 100,000 and 240,000.¹ Independent Soviet introductions have also made the muskrat an important fur animal in most of the great river systems of Siberia and northern Russia, as well as in Kazakstan.¹⁸ In zoogeographical terminology, a purely Palaearctic species (the starling) and a purely Nearctic species (the muskrat) have both become Holarctic within half a century (Fig. 6).

The fifth example is a plant that has changed part of our landscape—the tall strong-growing cord-grass or rice-grass, *Spartina townsendii*, that has colonized many stretches of our tidal mud-flats.¹⁴ It is a natural hybrid between a native English species, *S. maritima*, and an American species, *S. alterniflora*, the latter brought over and established on our South coast in the early years of the nineteenth century. The strong hybrid, which breeds true, was first seen in Southampton Water in 1870, and for thirty years was not particularly fast-spreading. But during the present century it has occupied great areas on the Channel coast, not only in England but also on the North of France (Pls. 6–7). It has also been planted in some other places in England, and has been introduced into North and South America, Australia and New Zealand. The original American parent has largely been suppressed or driven out by the hybrid form. Here is a peculiar result of the spread of a species by man: the creation of a new polyploid hybrid species, from parents of Nearctic and Palaearctic range, which then becomes almost cosmopolitan by further human introduction. And it is on the whole a rather useful plant, because it stabilizes previously bare and mobile mud between tide-marks, on which often no other vascular plant could grow, helps to form new land and often in the first instance provides salt-marsh grazing. Its effects upon the coastal pattern are, however, not yet fully understood by physiographers and plant ecologists; but Tansley remarks that ‘no other species of salt-marsh plant, in north-western Europe at least, has anything like so rapid and so great an influence in gaining land from the sea’.²⁹

Changes of similar magnitude have been taking place in fresh-water lakes and rivers, as a result of the spread of foreign species. The sixth example given here concerns the sea lamprey, *Petromyzon marinus*, in the Great Lakes region of North America.⁷ 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,

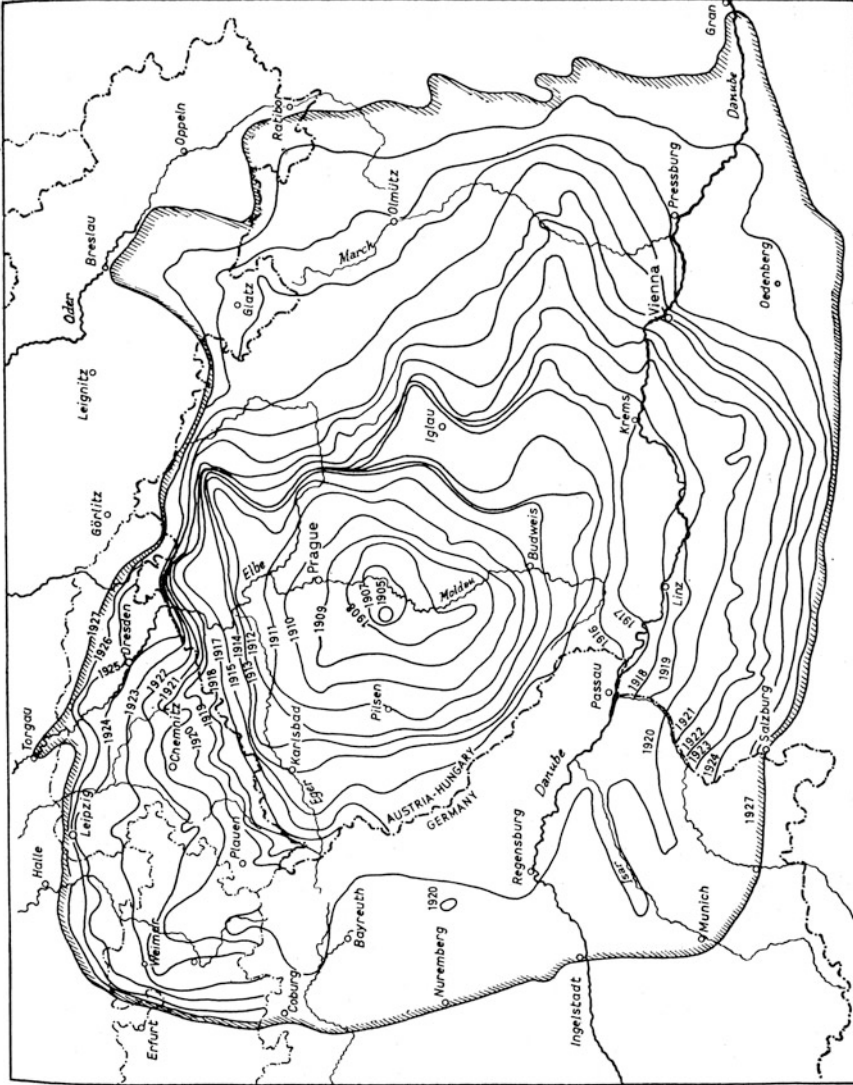


Fig. 7. Spread of the muskrat, *Ondatra zibethica*, up to 1927, from five individuals introduced into Bohemia in 1905. (After a coloured map in J. Ulbrich, 1930)

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 (Pl 9). 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 lb. to only 26,000 lb. On the Canadian side things were little better.¹² 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.¹⁹

The seventh example is the Chinese mitten crab, *Eriocheir sinensis*, a two-ounce crab that gets its name from the extraordinary bristly claws that make it look as if it was wearing dark fur mittens (Pl. 10). At home it inhabits the rivers of North China, and it has been found over 800 miles up the Yang Tse Kiang. However, it breeds only in the brackish estuaries, performing considerable migrations down-stream for the purpose. The females don't move so far away from the sea as the males, and they can lay up to a million eggs in a season, which hatch into a planktonic larva (Pl 11) whose later Megalopa stage migrates up-river again.²⁶ It is not really known how they got from East to West; they were first seen in the River Weser in 1912. The most likely explanation is that the young stages got into the tanks of a steamer and managed to get out again on arrival. Two large specimens were actually found in the sea-water ballast tanks of a German steamer in 1932, having, it is thought, got in locally from Hamburg Harbour. But these tanks are

normally well screened. In the last forty-five years, mitten crabs have colonized other European rivers from the Baltic to the Seine (Fig. 9). Those that invaded the Elbe have arrived as far as Prague, like Karel Čapek's newts. This crab has not yet taken hold in Britain, though it may very likely do so some day, as one was caught alive in a water-screen of the Metropolitan Water Board at Chelsea in 1935.

These seven examples alone illustrate what man has done in deliberate and accidental introductions, especially across the oceans. Between them all they cover the waters of sea, estuary, river, and lake; the shores of sea and estuary; tropical and temperate forest country, farm land, and towns. In the eighteenth century there were few ocean-going vessels of more than 300 tons. Today there are thousands. A Government map made for one day, 7 March 1936, shows the position of every British Empire ocean-going vessel all over the world. There are 1,462 at sea and 852 in port; and this map does not include purely coasting vessels. 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 travelling 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.²⁵ Altogether he found forty-one species of these travellers, 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 world-wide 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

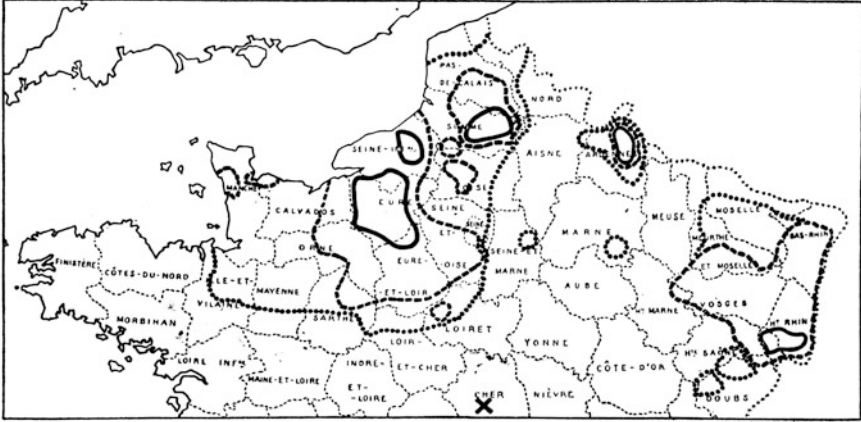


FIG. 8. Spread of the muskrat, *Ondatra zibethica*, in France. Unbroken line, 1932; dashed line, 1951; dotted line, 1954. Cross, one muskrat caught, extent of occupation unknown. (From J. Dorst and J. Giban, 1954.)

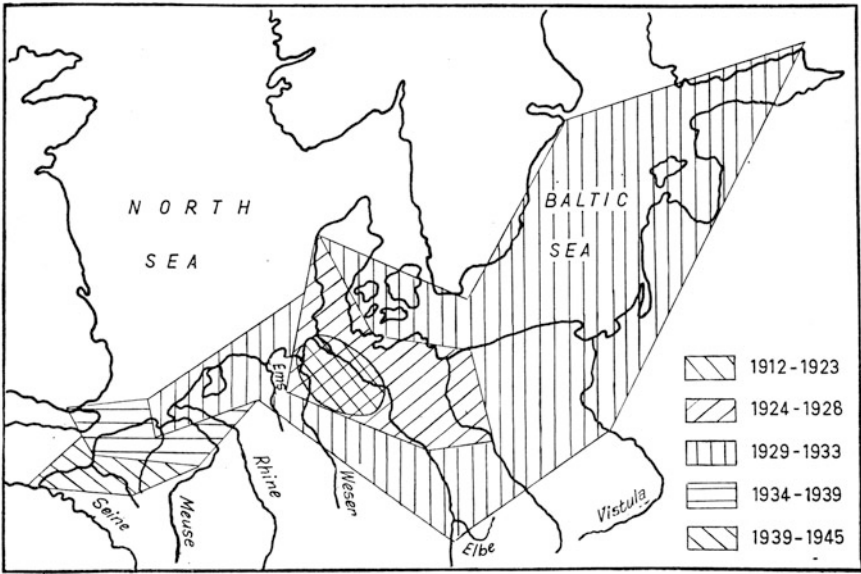


FIG. 9. Zones of spread of the Chinese mitten crab, *Eriocheir sinensis*, in Europe, 1912–43. (From H. Hoestlandt, 1945)

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 (Pl. 12). 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;¹¹ also in Louisiana (where 374,000 were trapped in one year recently); in south-east U.S.S.R.;³² in France;⁶ and in the Norfolk Broads of East Anglia (Pl 13).²⁰ In the Broads it carries a special kind of fur parasite, *Pitrufrquentia coypus*, belonging to a family (Gyropidae) that also evolved in South America.⁹ 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 questions that ecologists ought to try to answer.



1. Dr Karl Meyer explaining methods of field survey for sylvatic plague to public health students, near San Francisco, 1938. (Photo C. S. Elton.)



2. Dissecting ground squirrels to obtain organs for plague testing, near San Francisco, 1938. (Photo C. S. Elton.)



3. Ground squirrel, *Citellus beecheyi*: one of the wild hosts of plague in California. This one was in a plague-free part of the Sierra Nevada. (Photo C. S. Elton, 1938.)



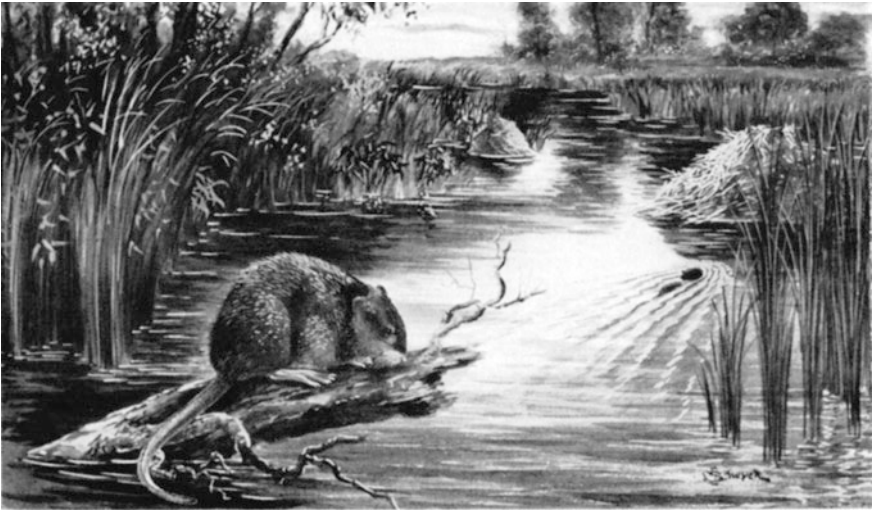
4. White or buff-coloured mycelial fans of the chestnut blight, *Endothia parasitica*, seen after peeling bark off a diseased American chestnut. (From G. F. Gravatt and R. P. Marshall, 1926.)



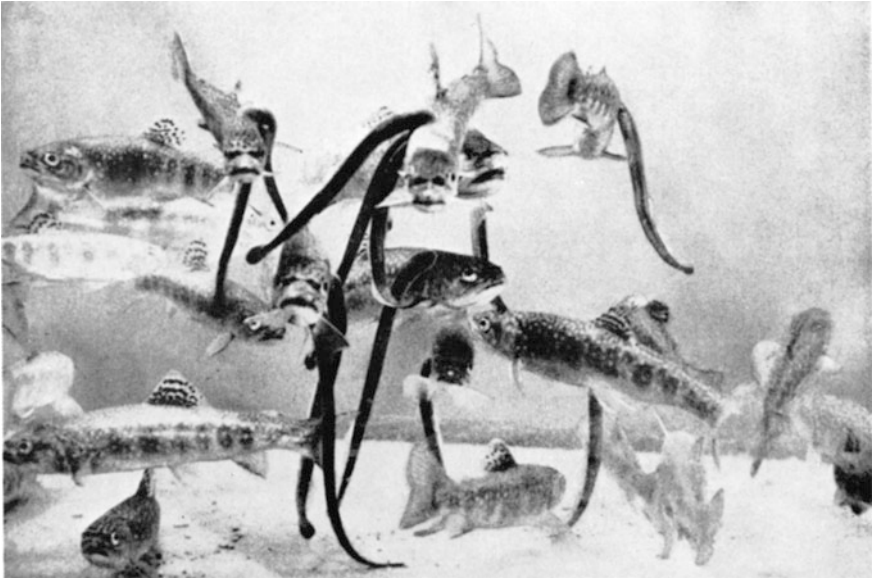
5. An American chestnut, *Castanea dentata*, almost killed by blight, *Endothia parasitica*, introduced from Asia. The new sprouts from the trunk would in turn become infected and die. (From G. F. Gravatt and R. P. Marshall, 1926.)



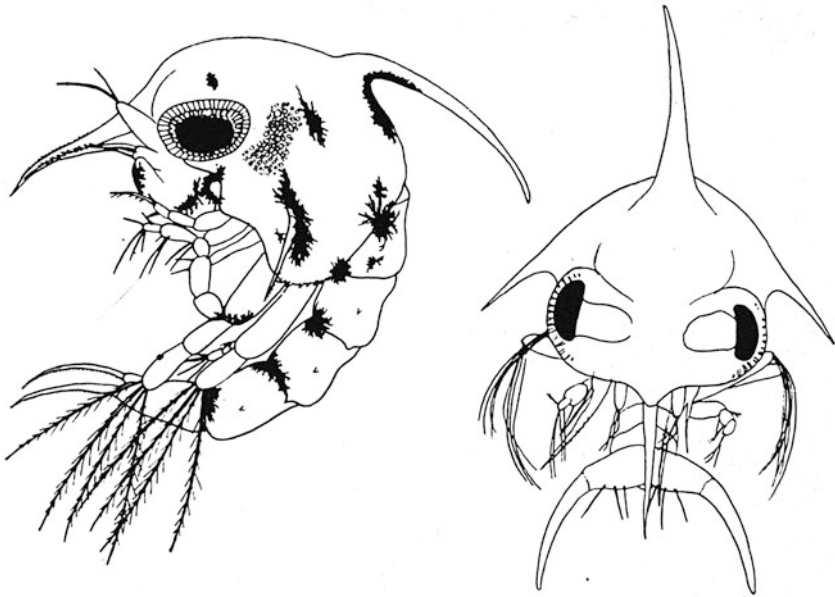
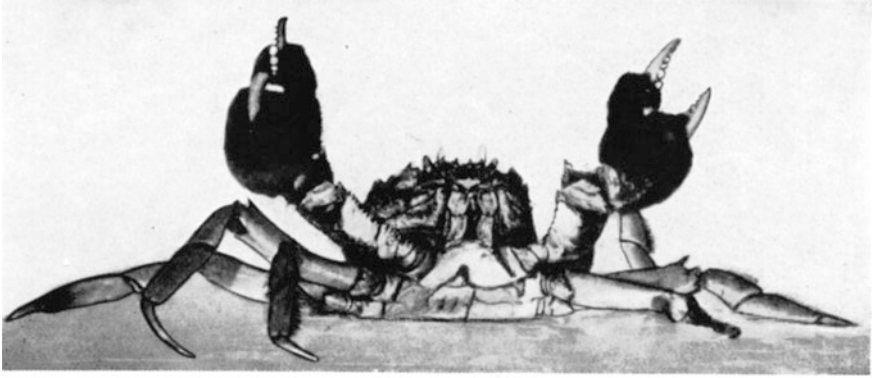
6 & 7. Muddy salt-marsh dominated by *Spartina townsendii*, at the head of a tidal inlet on the Sussex coast. Just off the lower area there was formerly a tidal watermill, which has disappeared through the growth of the *Spartina* marsh in the last fifty years. (Photo M. J. Thornton, 1957.)



8. Muskrats, *Ondatra zibethica*, in their natural habitat in Montezuma marshes, New York State. (By E. J. Sawyer, in C. E. Johnson, 1925.)



9. Young sea lampreys, *Petromyzon marinus*, attacking brook trout in an aquarium. (From R. E. Lennon, 1954.)



10 & 11. Above: Male mitten-crab, *Eriocheir sinensis*, with claws raised. Below: Young planktonic stage. (From N. Peters and A. Panning, 1933.)



12. A family of coypus, *Myocastor coypus*, at home in South America. (From coloured painting by C. C. Wiedner in A. Cabrera and J. Yepes, 1940.)



13. Habitat of the South American coypu, *Myocastor coypus*, in the channel of an East Anglian broad. Cover and food are given by the luxuriant fen vegetation, in this photograph chiefly the reed-grass, *Glyceria maxima*. (Photo C. S. Elton, 1957.)