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The geographical distribution of insect pests

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ABSTRACT. By means of a divisive-monothetic program of numerical classification, the geographical patterns of 281 species of agricultural insect pests were analysed. A ten-division world map of agricultural insect pest distribution is presented, as well as a dendrogram explaining, step by step, the way in which the program selected the most representative species. An isoline map indicating the zones of maximum and minimum concentration of insect pests is also included.

Insect pests clearly show less cosmopolitanism than phytopathogens, and this is due to the presence of many locally-native species of insects on crops. The number of introduced insect species in a given country or region seems to depend on the intensity of commerce, the degree of agricultural and industrial development, internal transportation (that within the country's boundaries), isolation (insularity), climate, quarantine regulations and control programmes. A further analysis of the first variable, taking the intensity of commerce (X), expressed in thousands of USA \$ per km², between the state of New York and the rest of the world, and considering the proportion of insect pests shared by this state and the different countries (Y), shows that the relation may be expressed as $Y = 11.92 + 3.22X$. The correlation coefficient $r = 0.523$ for 3362 pairs of data.

Introduction

If one analyses the degree of species' cosmopolitanism, it can be seen that the viruses, bacteria and fungi which attack plants (phytopathogens) are among the best-distributed organisms. Phytopathogens are 30% more cosmopolitan than insect pests. This may reflect their greater dispersive ability or result from the fact that quarantine and port inspection services may detect or control an insect much better than a microorganism. A first analysis of the geography of phytopathogens (Rapoport, Ezcurra & Drausal, 1976) showed an astounding mixture of biotas, in which that of the centre of Canada may demonstrate similarities to those of Kenya, Peru or

Hokkaido. The objective of this present work is to apply the methods used in the above paper to an analysis of insect pest distributions. Among the fauna attacking cultivated plants and stored food, there are always native, non-cosmopolitan species, along with exotic species transported by man.

One of the first attempts to analyse the distribution of harmful insects in agriculture was by Filipjev (1929), who studied geographical patterns in the Palaearctic Region. He divided this region into twelve zones (i.e. in much greater detail than in our study), but used fewer species and was greatly influenced by their relationships with vegetational and climatic types.

In general terms, it is predictable that some

of the following factors may determine the distribution of insect pests: (i) the natural biogeography; (ii) the geography of crops; (iii) agricultural practices (extension of cultivated lands, monocultures, irrigation, fertilizers, pesticides); (iv) climate; (v) commerce; and (vi) cultural patterns, including not only gastronomic tastes, but also customs or ways of life. In respect of the latter, it may be noted as an example that the Spaniards introduced the viznaga, an invading weed (*Ammi visnaga*: Umbelliferae), into Peru at c. 1555 because of their custom of using its twigs as toothpicks, since when it has invaded practically all South American countries (Báez, 1952). Moreover, many phytopathogens and insects have become cosmopolitan or semi-cosmopolitan through the commercial exchange of living plants. Today this type of commercial exchange has been prohibited in most countries, but trade in fruit and flowers has not been interrupted. It is of course much more difficult to control the transport of goods within the borders of the same country, that is, between provinces, states or counties.

Methods

Several authors have used techniques of numerical classification in biogeographical problems (Jardine, 1972; Kikkawa, 1968; Kikkawa & Pearse, 1969; Rapoport *et al.*, 1976) as relatively objective methods for making primary classificatory divisions. Kikkawa & Pearse (1969) have used the numerical method employed in this study to analyse the distribution of 464 species of land birds in 121 selected sites, the groups obtained showing a remarkable similarity to the biogeographical areas suggested by other authors through classic, intuitive methods. We worked with 281 maps, which presented the distribution of agricultural insect pests, published by the Commonwealth Institute of Entomology. A grid of 10 368 contiguous quadrats (72×144 divisions), covering a world map, was superposed over the area map of each pest. In this way, the area occupied by each insect pest could be codified quantitatively, and the resulting matrix of qualitative information formed by 10 368 quadrats \times 281 species was stored in magnetic discs. Each quadrat repre-

sented a 'primary area' or Ordinary Taxonomic Unit (OTU). Those quadrats without insect pest species (oceans, deserts and polar regions) were not processed, so we really worked with 3565 OTUs. A full list of the insect pests used may be obtained from the authors.

The data were processed by means of a divisive-monothetic program of numerical taxonomy, based on the information statistic *I* (Clifford & Stephenson, 1975; Lance & Williams, 1965, 1968; Kikkawa & Pearse, 1969; Rapoport *et al.*, 1976). The method consists of a search for those species which, when dividing an area into two parts according to their presence or absence, produces two areas of maximum homogeneity. Once two or more areas have been formed, the most heterogeneous is selected for the next division until the desired number of groups is obtained. The heterogeneity, or information value, of each area corresponds to its hierarchic level within the dendrogram.

The classification program (MAMOTRETO) was written in FORTRAN with six central subroutines in B.A.L. in collaboration with the Centro de Cómputo of Fundación Bariloche. It was processed in a Honeywell-Bull 66 computer.

Results

The results given by the computer for each division are (i) heterogeneity values for each area or zone; (ii) the species selected as the optimal discriminant in the most heterogeneous zone; (iii) the number of discriminant species present in the considered zone (equivalent to degrees of freedom for the χ^2 test); and (iv) the printed world map with the different zones marked with different digits. Using the χ^2 approximation (Lance & Williams, 1968), we verified that all the divisions were found significant ($P < 0.001$), although we must point out that Bottomley (1971) considers that the bias of this approximation is in some cases too big to be used with a high degree of statistical confidence.

In order to avoid the very difficult interpretation of the digital map, we have redrawn the divisions produced by the species selected by the computer as being the most representative for each partition. This final map is

TABLE 1. Pests selected by the computer for zone divisions, in order of appearance

C.I.E. Map No. 9. <i>Cydia pomonella</i> (L.) (= <i>Carposcapsa pomonella</i> L., <i>Laspeyresia pomonella</i> L.) (Lep. Tortricidae) (Codling moth). Host plants: apple, pear, peach, quince, <i>Prunus</i> spp., walnut.
C.I.E. Map No. 27. <i>Nezara viridula</i> (L.) (Hemipt., Pentatomidae) (Green vegetable bug, Southern green stink bug). Host plants: many, especially legumes, cotton, tomato.
C.I.E. Map No. 39. <i>Lygus pratensis</i> (L.) (Hemipt., Miridae) (European tarnished plant bug). Host plants: wide range of field and garden crops.
C.I.E. Map No. 277. <i>Xyloborus ferrugineus</i> (F.) (= <i>X. confusus</i> Eichh.) (Col., Scolytidae). Host plants: cacao, coconut, rubber.
C.I.E. Map No. 237. <i>Sesamia inferens</i> (Wlk.) (Lep. Noctuidae) (Purple or ragi stemborer). Host plants: ragi (<i>Eleusine coracana</i>), rice, other cereals, sugar cane.
C.I.E. Map No. 20. <i>Thrips tabaci</i> Lind. (Thysanopt., Thripidae) (Onion thrips). Host plants: polyphagous; vector of virus diseases of tobacco, tomato, pineapple.
C.I.E. Map No. 38. <i>Lygus oblineatus</i> (Say.) (Hemipt., Miridae) (Tarnished plant bug). Host plants: lucerne, cotton, apple, peach; polyphagous.
C.I.E. Map No. 239. <i>Heliothis zea</i> (Boddie) (Lep., Noctuidae) (Cotton bollworm of U.S.A., Corn earworm, Tomato fruitworm). Host plants: cotton, maize, tomato, polyphagous.
C.I.E. Map No. 69. <i>Operophtera brumata</i> (L.) (Lep., Geometridae) (Winter Moth). Host plants: wide range of deciduous forest trees, fruit trees and shrubs.

shown as Fig. 1 (ten zones), and the corresponding dendrogram is displayed in Fig. 2. In order to follow all the divisions step by step, the reader must follow the dendrogram from top to bottom. The numbers appearing in each branch correspond to the species selected to make the division in that area (Table 1). The numbers at the bottom of the dendrogram correspond to the zone represented by that branch, and the height of the columns above each number indicates the remaining heterogeneity for that zone.

The first division is clearly related to climate, and type of agriculture. Species 9 (*Cydia pomonella*) separates areas of temperate agriculture from tropical areas with marginal agriculture. In the large area with temperate agriculture, remaining divisions are made by endemic species. Thus species 39 (*Lygus*

pratensis) separates the Palaearctic Region, that is the part corresponding to central and western Eurasia (regions 9 and 10), from the rest. Species 69 (*Operophtera brumata*), on the other hand, isolates the area of more intensive temperate agriculture within this region (zone 10). Species 38 (*Lygus oblineatus*), which is endemic to the Nearctic Region, separates this region from the other dispersed areas of temperate agriculture with European influence (Rio de la Plata and the South American Andes, South Africa, the eastern coast of China, Australia and New Zealand).

Outside the areal range of species 9 (*Cydia pomonella*), two large zones have been determined, namely those containing species 27 (*Nezara viridula*) (zones 4, 5 and 6) and those which do not have it (zones 1, 2 and 3). In these cases, the *N. viridula* is an indicator of moderately-intensive tropical and subtropical agriculture. Starting with this basic division, the remaining subdivisions are produced by endemic species. Thus species 237 (*Sesamia inferens*), which is endemic to the Oriental region, separates this region (No. 6) from others. Species 239 (*Heliothis zea*), which is endemic to the Americas, distinguishes those areas of tropical agriculture which form part of the Neotropical Region (zone 5). Zone 4 corresponds in large measure to the African continent (Aethiopic Region) with some 'residuals' in South America, Australia and certain islands. The remaining zones (1, 2 and 3) correspond to regions of less intensive agriculture, which have few pests. Zone 3 is defined by the presence of *Xyleborus ferrugineus* (species 277), a parasite of the cocoa tree, coconut palm and rubber. This zone corresponds to tropical regions with poorly-developed agriculture in America (Amazon), with some small associated areas in the African rainforest and on the Angolan coast. Zone 2 is defined by the presence of *Thrips tabaci* (species 20), a very cosmopolitan polyphagous species which, in this case, marks areas of marginal agriculture. Zone 1 corresponds to regions with a very small number of pests, comprising deserts, and high latitudinal areas in which agriculture is not practised. Due to the fact that the classification method adopted is symmetrical for presence and absence, the similarity of the scattered areas within this group (zone 1) is due more to the

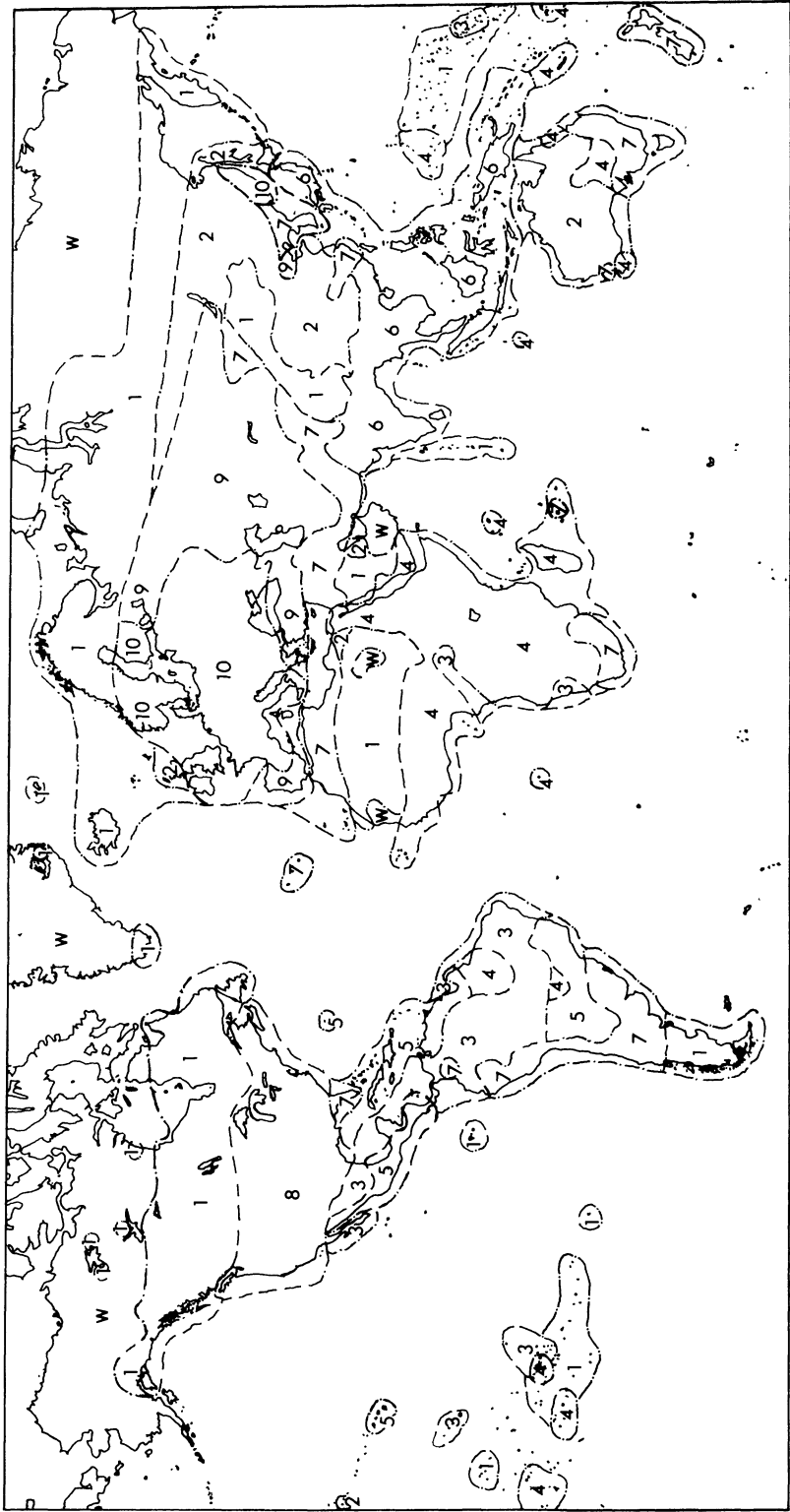


FIG. 1. World division into ten zones of maximum resemblance, based on the distributional patterns of 281 species of agricultural insect pests.
W = empty zones.

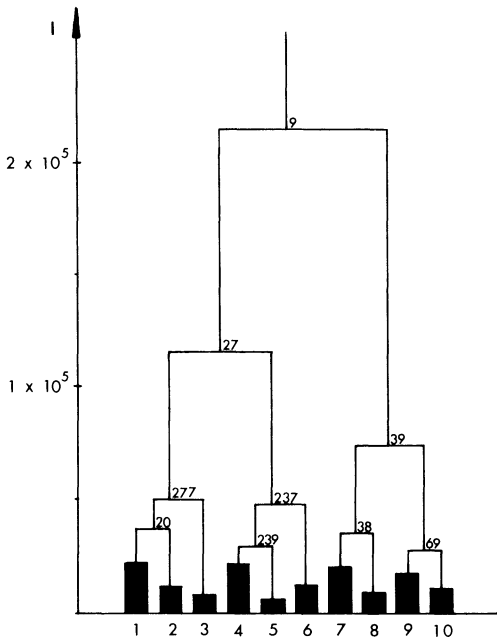


FIG. 2. Dendrogram corresponding to the division into ten zones. The I axis represents the heterogeneity (or information) values. The height of the columns represents the remaining heterogeneity within the groups. The species selected by the program as the most representative for each division, appear at each branching indicated by a number (see Table 1.). For further explanation, see text.

absence of species than to the presence of shared species (see Bottomley, 1971); thus the Sahara is viewed as being similar to tundra areas in that both have only one or two pests, although they do not share the same pests.

It should perhaps be emphasized that, in a ten-zones division such as that used in this paper, such marginal areas as zone 1 will of necessity demonstrate similar characteristics, but if we continue the analysis with further subdivisions, such likenesses will disappear. Our restriction in the number of divisions to be used was determined by available machine time. However, a brief look at specific papers on zone 1 will show that each of its geographically-segregated component parts contains its own distinct insect fauna, some of which may not have been mapped by the Commonwealth Institute of Entomology. For example, Filipjev (1929) has divided our extensive region 1, to the north of Eurasia, into two subregions: the West Siberian and the East Siberian taigas. The first of these is delimited

by insects harmful to agriculture and silviculture such as *Charaee graminis* (the grass cut worm), *Hadena secalis* (northern stem cut worm), *Phaedon cochleariae* which attacks cabbage, *Feltia segetum* (winter cut worm), and so on. The East Siberian region is characterized by different cut worms including *Euxoa tritici*, *E. islandica* (in gardens), *Dendrolimus sibiricus* (in forests), and others. (Filipjev's original taxonomic nomenclature was here respected).

It should also be noted that in the map of the Commonwealth Institute of Entomology which shows the distribution area of *Cydia pomonella* there is a notice stating that this species has been doubtfully cited in Japan. If Japan were to form part of the distribution area of this species, it would appear in our classification under zone 7, and not within zone 6 as at present.

Endemic areas in our classification are zone 5, which corresponds to a great part of the Guyano-Brazilian subregion; zone 6, which corresponds to the Indomalayan Region; and zone 8 which corresponds to the U.S.A. and southern Canada. It is interesting to note that the Indomalayan Region excludes practically all of Borneo and Taiwan, but includes islands which are generally considered to be Australian (the Celebes, Sumbawa, Timor) in faunal affinities; it also includes Kyoto Island (Japan). The strong Indomalayan influence on the entomofauna of the islands to the northwest of Australia is a fact which already has been noticed by Gressitt (1956).

We can also distinguish two semi-endemic zones: No. 9, which comprises central and western Asia and a small isolated portion in China (Shantung); and No. 10, which comprises Europe and an isolated portion of the eastern coast of the U.S.S.R. close to the Sakhalin Island.

The partition of zones 9 and 10 is also due to the type and intensity of agriculture, as much as to patterns of classical biogeography. The influence of commerce is noted particularly in zone 7 which, although relatively homogeneous, is scattered in the temperate zones of all continents, representing places which have assimilated European agriculture and many of its pests.

If we compare Fig. 1 to data published previously on the geography of phytopatho-

TABLE 2. Comparative number of zones in which the natural regions are divided

Region	Insect pests	No. zones	Phytopathogens*	No. zones
Nearctic	1, 2, 7, 8	4	0, 1, 2, 3, 7, 8, 9	7
Neotropic	1, 2, 3, 4, 5, 7	6	1, 2, 3, 4, 5, 6, 7	7
Aethiopic	1, 3, 4, 7	4	0, 1, 5, 6, 7	5
Palearctic	1, 2, 4, 6, 7, 9, 10	7	0, 1, 2, 3, 4, 5, 7, 8, 9	9
Oriental	1, 2, 4, 6	4	1, 3, 5, 6, 7	5
Australian	1, 2, 3, 4, 7	5	0, 1, 2, 3, 4, 5, 6, 7, 9	9
Mean		5.0		7.0
St. deviation		1.26		1.79

* Data on phytopathogens from Rapoport *et al.* (1976).

gens (Rapoport *et al.*, 1976), it is clear that the distributions of the latter are much more intermingled. These contrasts are further detailed in Table 2, which suggests that, on average, insects form five zones (as delimited by this paper) per natural biogeographic region, whereas phytopathogens form seven. The difference between means is significant at $P < 0.1$; in other words, we can say that insect pests show a higher degree of endemism than phytopathogens. While in the latter case there is no zone peculiar to or restricted to any given biogeographic region, this is the case for insect pests.

Figure 3 displays a series of isolines representing the zones with the same relative frequency of insect pests, on a world-wide basis. Data for this were accumulated by counting the number of species per quadrat on the square-hatched map (see Methods), and then calculating the total as a percentage of the total sample of the 281 analysed species. In some ways this map has the advantage over Fig. 1 in showing us certain weaknesses in our basic data. These weaknesses are demonstrated by the great bay formed by the 5% curve which transects Central Asia, Mongolia and China, running from Siberia to the Himalayas. This is probably indicative of a lack of data for that region. The same weaknesses occur in Australia, where the division of insect groups into zones (the three first divisions) leaves a gap in the south and not in the centre of the continent, in which the most desertic area is located. The extreme reduction of the gap (w) in the Sahara, and its absence in the Gobi and Amazon also is quite suspicious.

Figure 3 demonstrates further than the maximum frequencies of insect pests appear

in the agricultural regions, especially those of temperate areas, and also in Java (Indonesia).

Discussion: regionalism and universalism

Rarity and commonness, micro-areality and pandemism, endemism and cosmopolitanism are antonyms which are used to define abundance, geographical range and universality, respectively. All of these may be measured quantitatively (Preston, 1962; Rapoport, 1975; Rapoport *et al.*, 1976, respectively), and certain broad criteria appear to apply in any explanation of their relative importance.

First, polyphagy is rather uncommon because insect species generally reduce their food niches to one or a few plant species of the same genus. Thus Spencer (1965) has found that, in the case of food preferences by Diptera Agromyzidae, there are four oligaphagous and fourteen monophagous species for each polyphagous species.

Then, Southwood (1960) has noted that tree species consisting of large numbers of individuals tend to have a greater number of insect pests than species consisting of few individuals. The former house a specialized, monophagous fauna, which is not the case in the latter situation. When a tree species becomes abundant through cultivation, it tends also to support a greater number of pests which, in large measure, are transferences from other cultigens. This is encouraged by the fact that feeding habits of insect pests may change quickly. Thus many new pests became adapted to feed on cocoa plantations in less than 60 years. Strong (1974a, b) has calculated that 30–60 years is a significant

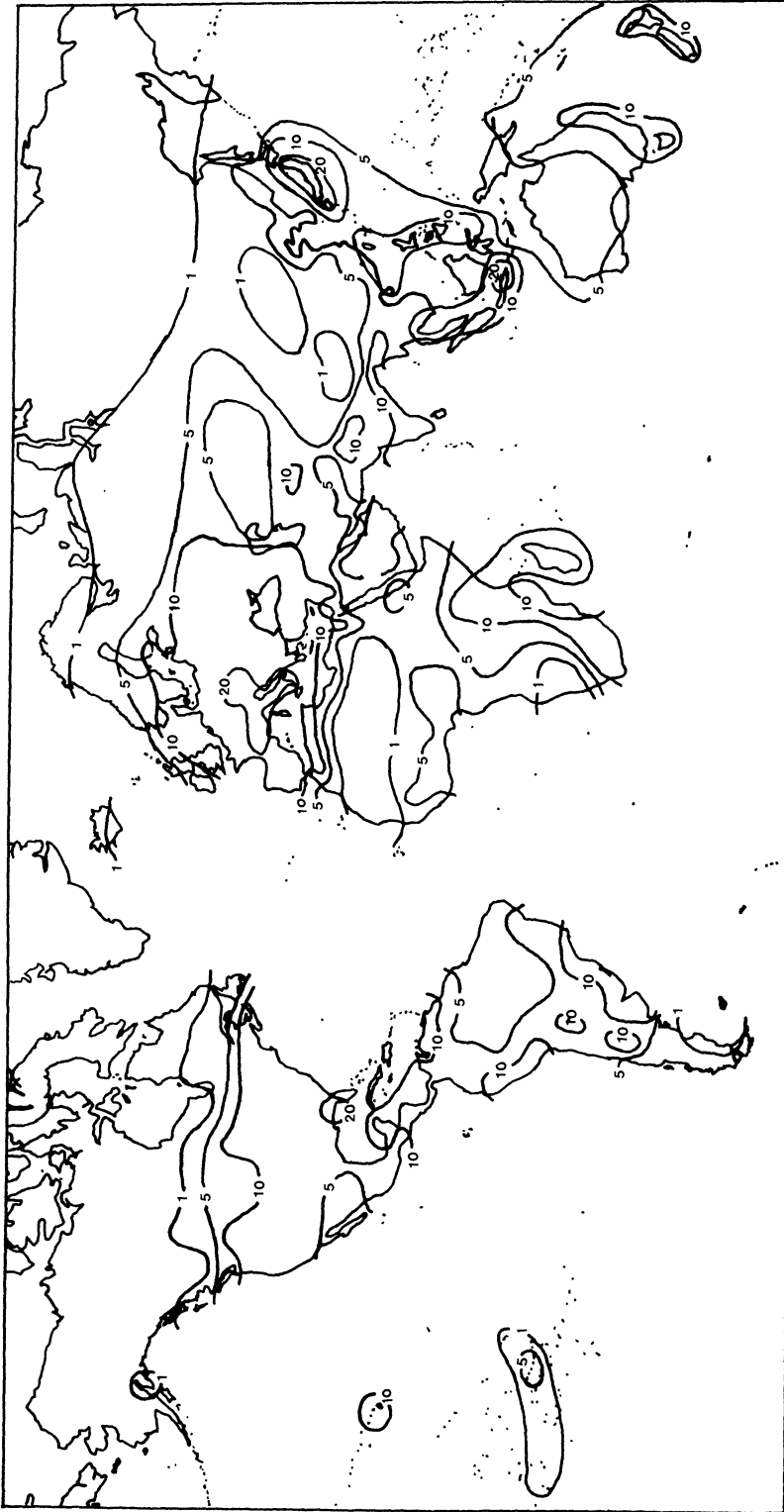


FIG. 3. Species isodensity lines. Figures represent percentages from the total number (281) of species considered.

period for a cultigen to become saturated with insect pest species: moreover, trees introduced into Great Britain have as many insect species associated with them as native trees, and the most important factor controlling the relative abundance of insects is not the antiquity of the tree in the region, but its abundance and overall geographical range. The relation is of the type

$$S = kA^z$$

in which S = number of insect pests, A = geographical range of the host plant, k = a constant for the biota (intercept), z = the ratio of log species change to log area change (slope). This equation describes the saturation of pest species, and it is equivalent to the species-area curve (Strong, 1974a, b).

Further, distance from source, transportation possibilities (commerce) and crop may also modify the numbers of insect pests found in particular areas. Undoubtedly, the closer two plots are to each other, the more similar will their faunas and floras be, except in special cases. Kellman & Adams (1970) have demonstrated this for weed floras, and it is also the case in classic biogeography, except when nearby localities are separated by a barrier. Distance *per se* is not an obstacle for the dispersion of invading species (Rapoport, 1975). Skellam (1955) has suggested that as long as there are no barriers, including interspecific competition, to prevent it, the wave of expansion of dispersing species will have constant velocity, and time alone will restrict species from occupying all available space. But the fact is that distance is in a certain way positively correlated with the probability of barrier appearance, and this has led some authors to erroneously consider distance as a major barrier in itself to species dispersal.

Technological advances in transportation have not of course shortened the distances themselves, but they have lessened the time involved in movement. Today it is not unusual to travel faster over long journeys than over short ones, and this has increased the probability that insects or pathogens of a short lifespan can be transported alive over considerable distances from one point to the other.

As the great majority of organisms are transported voluntarily or involuntarily by man, it is assumed that the intensity of com-

merce is in some way associated with the intensity of interchange of species. This is a very difficult relationship to evaluate, and due to difficulties of obtaining and processing the necessary information, we will present only one case, that of New York City, as an example (U.S.G.P.O., 1973).

In this instance, the value of imports and exports of New York City for 1973, was considered for each country (the rest of the U.S.A. was counted as one country), and then divided by the area of the corresponding country; thus we obtained a unit which indicates the intensity of commerce of each country with New York, in thousands of U.S.A. \$ per km². Using the computer, we noted the number of insect species present in the square of the map in which New York City lies, and then calculated the number of insect species in every other square which were shared with those present in New York City.

With these data, we could calculate the relationship between the intensity of commerce with New York (as expressed in thousands of U.S.A. \$ per km²) taken as an independent variable, and the number of insect species elsewhere shared in common with those present in New York (expressed as a percentage), taken as a dependent variable. The results showed a correlation coefficient $r = 0.53$ and a regression line $y = 11.92 + 3.22x$. * An analysis of variance showed that the regression line indicated a highly significant proportion of the variability in the 3362 pairs of data ($P < 0.001$ according to the 'F' test).

Restrictions of computer time meant that, in this analysis, we considered only the imports and exports of New York City for the year 1973, a decision which one may criticize. It would have been more correct to consider a long series of commerce data, which we did not possess. However, the results clearly suggest that the number of insect pests present in any part of the world are strongly influenced by the imports of that place, and that each area can influence the pest fauna of other places through its exports, thus acting as a dispersion centre.

* Readers interested in the raw data will be sent the information if requested.

Conclusions

In short, we can say that the number of introduced species in any country or region depends on a variety of factors, including the intensity of commerce; the level and development of agriculture, the degree of industrialization, and environmental alteration; history; the type and intensity of interior and exterior transport; distance and natural isolation with respect to other countries; climate; and official monitoring and control (legislation, quarantine services, eradication campaigns).

Although in the natural biogeography of plants and animals there is a tendency towards an expression of a very old ancestry, incorporating three zones, the Holarctic, the Holotropical and the Holantarctic (Rapoport, 1968), rather different trends exist today. If the mixing of all kinds of biotas continues, it is foreseeable that three new principal 'regions' will be established, which will be related to the ecophysiological limitations of invading species. These regions will be, broadly, 'cold', 'temperate' and 'tropical', and the first two of these will be separated further into two additional parts, one in the northern and the other in the southern hemisphere (Rapoport *et al.*, 1976). However, the distribution of insect pests does not yet seem to show this tendency in its entirety, and this is due to the fact that there still exists a high proportion of insect pests which are local in extent and which have had neither the time nor the opportunities to extend themselves outside of their endemic areas.

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