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The distribution of plant diseases: a look into the biogeography of the future

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Abstract

Since the sixteenth century predominantly, man has been modifying the geography of plants and animals, and this process has been accelerated in the last few decades. Plant pathogens such as viruses, bacteria and fungi are among the most cosmopolitan organisms, and can provide interesting information concerning the ways in which biogeographical regions become intermingled.

A quantitative measure of cosmopolitanism is proposed through making comparisons between different taxa. By means of a divisive-monothetic computer program, the geographical distribution of man-transported phytopathogens is analysed, and a world division into five and ten zones is depicted. A map of equal-percentage pest isolines is also included.

Introduction

A few instructive cases of increasing cosmopolitanism may first be considered. The opening of the Suez Canal has triggered the passage of species from the Red Sea into the Mediterranean Sea, a phenomenon known as the Lessepsian migration, and involving 'several hundred' species (Por, 1971; Kimor, 1972). Some marine species can be carried widely from one place to another, adhered to ship keels (Bishop, 1951). One rice ship trading between Burma and the West Indies carried forty-one species of insects (Myers, 1934), an illustration of one of the ways in which pests may move from one continent to another (Elton, 1958). Some agricultural pests may be dispersed by aircraft (Adamson, 1941; David, 1949).

There is a great resemblance between the arthropod fauna of eastern Canada and Great Britain, and this is largely due to the fact that fishing vessels leaving England sailed in ballast. This ballast has been brought ashore in eastern Canada since the seventeenth century, giving opportunities for colonization to animals and plants (Palmén, 1958; Lindroth, 1968). All the cosmopolitan staphylinid beetles have been spread by commerce (Moore & Legner, 1974). European introductions into North America are about ten times as numerous as those carried the opposite way, a feature which has been described as the 'Europeanization' of the North American fauna (Lindroth, 1968). All Rhode Island earthworm species are European (Reynolds, 1973).

About 250 to 300 plant species have been introduced into Poland to become adventitious; this represents 11–13 % of the country's total flora. At the same time, about 10% of the native plant species have become extinct in some regions of this country during the last hundred years (Kornaś, 1971).

The mean number of weed seeds per m^2 in cultivated fields of Finland is 35 220. In other regions of the world this number is even higher (Paatela & Erviö, 1972).

In 1968, at least 129 520 mammals belonging to 302 species were imported into the United States (Jones, 1970). Four years later 569 000 birds and more than 100 million fishes were imported into the same country (Courtenay & Robins, 1975). A considerable number of species have been liberated in this country in the last few decades to become invaders in natural ecosystems.

We have selected above a small sample from among the thousands of known cases of species taken from one biogeographic region to another by man in order to emphasize the incontrovertible fact that mankind is, intentionally or otherwise, greatly modifying the geography of plants and animals. Oceans, mountain ranges, and rivers have ceased to be great geographical barriers and have been transformed instead into routes of dispersal or the interchange of species. New roads have been opened across mountains, rivers or deserts, and people, cattle, agricultural products and diverse merchandise with all their respective parasites, pathogens, phoresics and their associated fauna and flora are being distributed more widely. The long-term transportation of seeds which has taken place for centuries (in some continents for millennia) has led to the general formation of extensive agricultural regions which have a very high degree of biological uniformity, and accordingly a low species diversity. Indeed, great numbers of cultivated species now prosper in both tropical and extra-tropical regions, such as cabbage, beans, and pumpkin. Further, the trade in live plants has also produced a considerable number of cosmopolitan species among soil microfauna and microflora. Two other important human activities also need to be considered in this respect: first, the wide introduction of species—mainly arthropods—for biological control; secondly, the extinction of native species by agriculture, livestock, hunting, pollution and other factors. All these activities favour the colonization of cosmopolitan species which otherwise would not be able to prosper.

Degree of cosmopolitanism

Suppose we start by dividing the world into the six classical biogeographic regions: Holarctic, Ethiopic, Neotropical, Oriental, Australian and Antarctic. For every species, we may determine the number of regions covered by its range, and in this way species can be classified into endemic, characteristic, semicosmopolitan and cosmopolitan, depending on whether they are distributed in 1, 2, 3–4 or 5–6 regions respectively (Rapoport, 1975). The degree of cosmopolitanism of each taxon can be measured. If r is the number of regions occupied by each species, Y_r the number of species that occupy r regions, n the total number of species, and r_{max} = six regions, then the degree of cosmopolitanism of one taxon will be

$$C = \frac{\left(\sum_{r=1}^{r_{max}} r\, Y_r/n\right) - 1}{r_{max} - 1}.$$

The values of C range between 0 and 1, being $\sum_{r=1}^{r_{max}} r\, Y_r/n$ the mean occupation ($\bar{x}$).

In Table 1 we have included a sample of rather low cosmopolitan taxa (Tinamid birds and Hemiptera: Reduviidae) as well as others of greater dispersion (phytopathogens, insect pests). The first column is simply an example of a case in which 100% of species are restricted to only one region. The opposite case would be one in which 100% of the component species of a taxon inhabit all six regions, and in this case $C = 1$. The two columns on the right, unlike the others, consist of groups principally distributed by man, whose degree of cosmopolitanism is high. This is especially true in the case of the phytopathogens, whose distributional patterns are now analysed further.

Table 1. Number of regions occupied by species, and the degree of cosmopolitanism (C)

No. of regions	Tinamid birds	Reduviidae Emesinae (1)	Plants (2)	Collembola (3)	Birds (4)	Insect pests (5)	Phytopathogens (viruses, bacteria and fungi) (6)
1	40	744	462	165	204	74	45
2	0	4	15	12	45	43	31
3	0	5	6	5	25	24	38
4	0	1	5	4	12	28	41
5	0	1	3	1	8	51	67
6	0	0	0	1	0	0	0
n	40	755	491	188	294	220	222
$\bar{x}$	1·00	1·03	1·11	1·23	1·55	2·72	3·24
C	0	0·006	0·022	0·046	0·110	0·344	0·448

Sources: (1) Wygodzinsky, 1966. (2) Meusel, Jäger & Weinert, 1965. (3) Salmon, 1964. (4) Voous, 1962. (5) Commonweath Institute of Entomology. (6) Commonwealth Mycological Institute.

This table should be interpreted in the following way. For example, there are 462 species of plants restricted to one biogeographical region, fifteen species are distributed in two regions, . . ., three species are widely distributed in five regions, and there is no case of a plant species spreading over the six regions.

Mapping plant pests: methods

A grid of 10 368 contiguous quadrats (72 × 144 divisions) was superposed upon a world map showing the areas occupied by each phytopathogenic species (viruses, bacteria and fungi). The quadrats occupied by each of the 203 considered species were annotated. The result was a matrix of qualitative data (presence-absence) with 2 104 704 elements (203 species × 10 368 quadrats). The original information was obtained from maps published by the Commonwealth Mycological Institute.

The main problems in the processing of this large matrix arose from limitations of machine time and memory, more than the complexity of the calculations. For this reason we rejected agglomerative methods as a form of analysis, although we found good clustering programmes in the literature, some of which were adapted to the use of qualitative information (Bonham-Carter, 1967; Grigal & Goldstein, 1972; Hall, 1967).

With divisive-monothetic methods, on the other hand, one can attain an adequate number of data groups in a shorter period of time, with fewer memory requirements and with the additional advantage of no chaining effects between groups produced by imperfect data. Due to the fact that the division of each area is defined according to the presence or absence of only one species, the disadvantage of the method lies in the fact that the division does not consider all the possible attributes. However, if species are associated and are not distributed in a continuous way, the error is minimized (Lance & Williams, 1965, 1968; Pielou, 1969).

In this present analysis, the divisive-monothetic method based on the Information Statistic (I) was used in which, given an area consisting of n quadrats with a total of s species so that a_j of the quadrats contains the jth species, it can be shown the total heterogeneity of the area with respect to all the species is:

$$I = sn \log n - \sum_{j=1}^{s} [a_j \log a_j + (n - a_j) \log (n - a_j)]$$

If an area (i) is divided into two subareas (g) and (h), we can define the heterogeneity fall as:

$$\Delta I_{(gh,\, i)} = I_i - I_g - I_h$$

The method involves searching for a species which, when dividing an area into two according to its presence or absence, produces a maximum ΔI. Once two or more groups are formed, the most heterogenous is divided until the required number of groups is reached. The heterogeneity value (I) of each area corresponds to its hierarchical level within the dendrogram (Lance & Williams, 1968). It is considered that $2\Delta I$ is a biased estimator of χ^2 with as many degrees of freedom as attributes (Lance & Williams, 1968), but the bias is too large to test correctly the significance of each division (Bottomley, 1971). Bottomley (1971) has shown that the method's symmetry for presence or absence results in quadrats with a small number of species being kept in the same group, although the quadrats need not necessarily share the same species. As a result, a set of residual quadrats with a very low number of reported species is produced. These quadrats are grouped as zones 1 and 2 on the resulting map. Their resemblance is due to the absence of the vast majority of the species, although they do not necessarily share the few species present.

Results

The classification programme was designed also to print the corresponding distribution map of species after each division. Planispheres divided into 2, 3, 4, etc., regions of maximum cohesion were obtained. Figure 1 shows a world map of *phytopathogenic species* divided into five such regions. Up to this level, the grain size allows one to make some inferences about the possible reasons that determine such a mixed biogeographical pattern. The search for a division into more than five regions leads into such entangled divisions that it becomes difficult to interpret. We have an example of this in Fig. 2, which indicates a division of the world into ten regions, based on a sample of fifty phytopathogens. In Fig. 3 the dendrogram, from which the division into five regions was calculated, is shown.

The region of maximum cohesion in Fig. 1 is formed by the U.S.A. and the south of Canada, in that it resists partitioning when all the other regions have been subdivided. Only in the ninth division does this region tend to divide into two parts, but instead of them producing an eastern and a western region—as would be the case if the natural biogeographic patterns were followed—it divides into a northern region shared with Western Europe and a southern area that is probably linked to the Sonoran Region. This case seems to be governed by the effects of agricultural geography as well as by those of temperature.

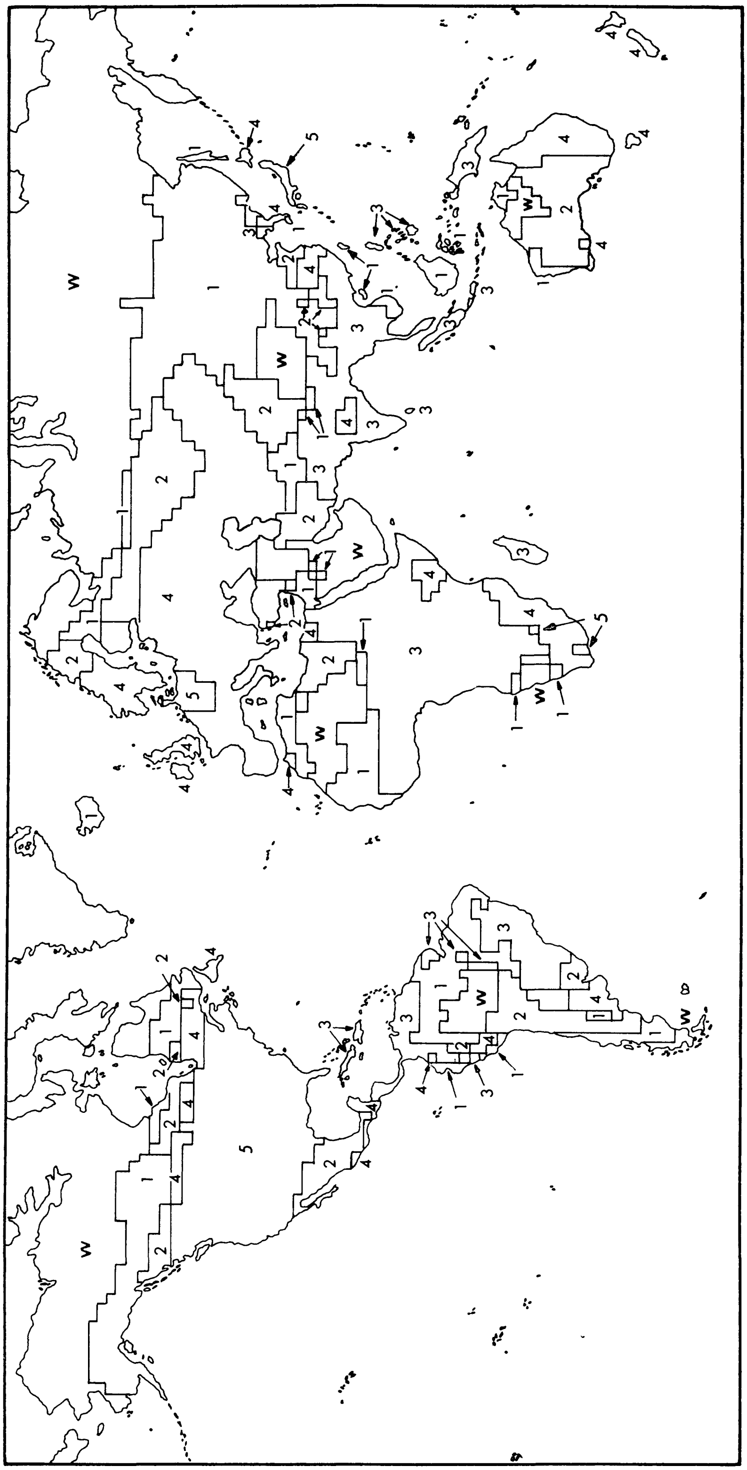

Fig. 1. World division into five zones of maximum resemblance based on the distributional patterns of 203 phytopathogen species. w = empty zones. Results were obtained through the computer's line printer.

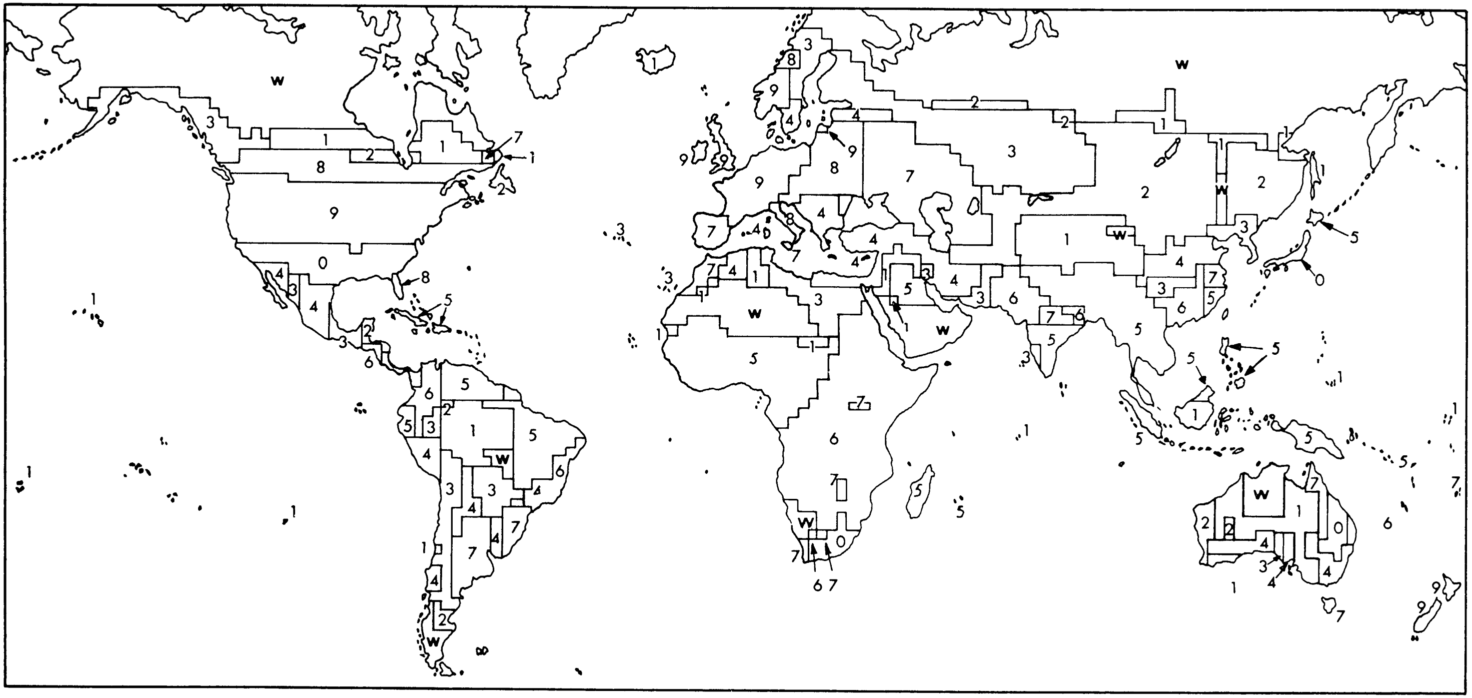

Fig. 2. World division into ten zones, based on a sample of fifty phytopathogen species.

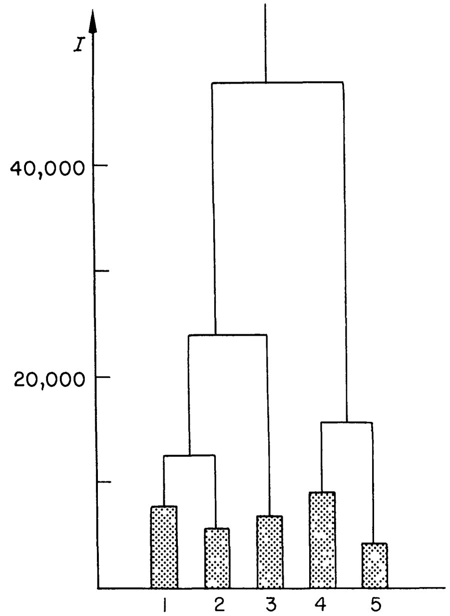

Fig. 3. Dendrogram corresponding to the division into five zones. The *I* axis represents the heterogeneity (or information) values. The height of the columns represents the remaining heterogeneity within the groups. The next division will take place in zone 4.

A first glance at Fig. 1 would suggest that region 5 might correspond to those areas of intensive agriculture with a high degree of mechanization, a wide use of herbicides and biocides, and a large number of pests; it might also indicate regions of great invasibility. Region 4 might correspond to areas of extensive agriculture, also with a great number of pests. The distribution of region 3 seems to be governed by a dominant climatic component because, in great part, it overlaps areas of tropical and subtropical agriculture, with a moderate number of pests. Region 2 appears to be comprised of areas of relatively intensive use of natural ecosystems, with small and isolated patches of cultivated land; and region 1 seems to correspond to areas with marginal agriculture, and with occasional phytopathogens and/or areas with pasturing and livestock. Region *w* corresponds to zones without agriculture and/or without reported pathogens (the Arctic tundra, and the deserts of Gobi, Sahara, Arabia, Kalahari, Australia, Patagonia; also, the Amazon basin).

The apparent relationship between the results of this classification and the diversity of pest species is displayed in Fig. 4, in which isolines join points with an equal number of pests. This map was drawn from the same data as those used for Figs. 1–3, and the curves express percentages with respect to the grand total of species considered.

Conclusions

Man has established communication channels between the different biogeographic regions to create species mixing. Initially we would tend to think that, if this mixing continues, a time will come when all the regions of the Earth will be species-similar, and a complete homogeneity of the species mix might be obtained. The results of this study suggest however that, in the future, although such homogeneity will be greater than at present, it will not be complete. Although climatic differences impose certain restrictions on mixing it is foreseeable that in the long run at least three major biogeographic regions will exist (polar, temperate and tropical), probably with less specific diversity but perhaps in some cases with a higher density and biomass than at present. There is a current tendency to consider that ecosystems are saturated with species, so the introduction of a new species might produce the extinction or at least the reduction in numbers of some pre-existing species. However, this need not happen since not all the introduced species prosper in the same manner. Thus an introduced new crop may become saturated in a short time (30–60 years) (Strong, 1974) with imported and native pests, but it is the latter which ultimately give local character to the crop.

This first computerized look into the biogeography produced by man needs to be augmented by data on human and animal epidemiology, introduced plants and animals, and crop-attacking insects. We are dealing with the latter problem at the present time.

Finally, to clarify the apparent disorder present in the geographical distribution of phytopathogens, several principal propositions can be made: (1) there are pathogens that exclusively attack cultivated plants, whose distribution accordingly is related to the geography of crops; (2) there are pathogens that attack native species within their ecosystems, whose distribution consequently is related to the natural phytogeography; (3) there exists a combination of environmental factors (including not only climate but also the degree of invasibility and the degree of euryoecity of the invading species which affect these distribution patterns; (4) there

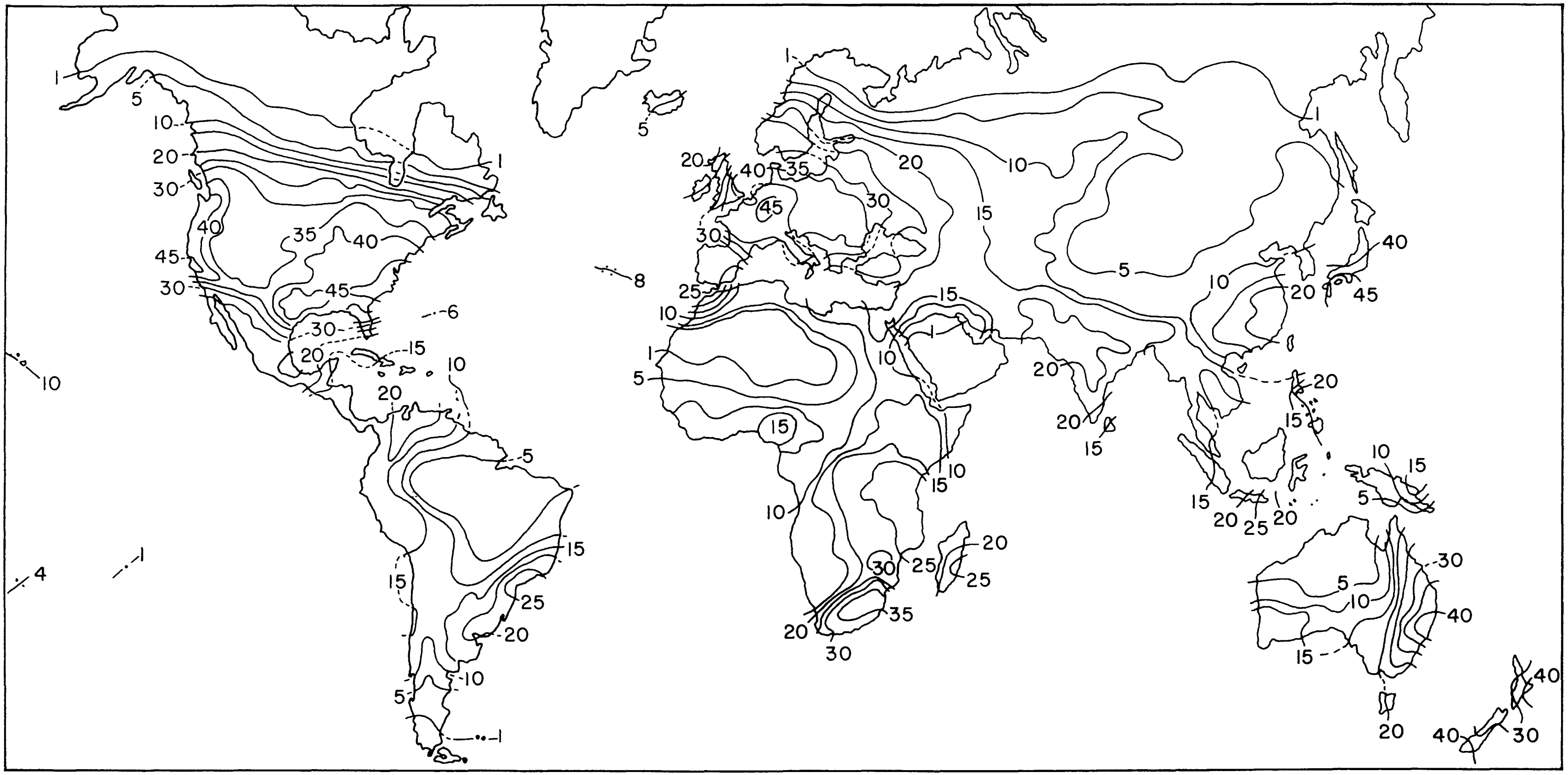

Fig. 4. Species isodensity lines. Figures represent percentages from the total number (203) of species considered. Note that the maximum richness does not occur in the tropics, but rather in temperate countries.

is a relationship between the degree of economic development and the prevailing agricultural practices on the one hand and the composition of the phytopathogenic flora on the other; (5) we can detect the influence of present and past geopolitical events in the distributions of phytopathogens. These latter include not only commercial relations and the intensity of traffic between countries but also the imposition of tastes, and aesthetic and culinary traditions, a feature which may be called 'cultural imperialism'. From the available evidence, it is clear that geopolitical barriers can delay, but not impede, the penetration of phytopathogenic invaders in that, if two countries do not have direct commercial relations with each other, pests will disperse indirectly, that is, through other countries with which they do trade and which act like intermediate 'hosts'.

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