Biological Invasions: a Global Perspective
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CHAPTER 1

History of Biological Invasions with Special Emphasis on the Old World

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1.1 INTRODUCTION

It is admittedly an almost impossible task to collate, in a single short chapter, all the wealth of information on the history of biological invasions. History, indeed, should be considered in terms of both geological-evolutionary events and human-related factors; there is obviously a continuum as well as feedback relations between them. These interactions should be taken into account to understand trends and mechanisms of two processes: the species invasions across different biogeographical areas and the susceptibility to invasion ('invasibility') of the diverse ecosystems.

Proper attention to the historical background has been given in the previous regional or national syntheses on biological invasions, for instance of Australia (Groves and Burdon, 1986) and of North America and Hawaii (Mooney and Drake, 1986). In particular, Deacon (1986) presents a comprehensive historical profile of biological invasions in South Africa, and Coope (1986) refers to the palaeoecology of invasions of North Atlantic islands. As regards specifically the history of invasion of weeds, reference should be made to the syntheses of Foy *et al.* (1983) and Gwynne and Murray (1985), while the history of insect introductions is covered by Sailer (1983) and that of plant pathogen introductions by Yarwood (1983). Many chapters of this volume itself have quite understandably their own historical background. Finally, the symposium sponsored by SCOPE and held in Montpellier (France) from 21 to 23 May 1986 specifically addressed 'History and Patterns of Biological Invasions in Europe and the Mediterranean Basin'; the contributions of Le Floc'h *et al.* (1989), Marcuzzi (1989), Pons *et al.* (1989), Sykora (1989) and Vernet (1989) were among the most historically oriented articles.

Having discarded the possibility of compiling a real 'state of knowledge' report on the history of invasions because of the space limitations, and having considered it inappropriate to present too many unrelated episodic or anecdotal examples of invasions, I am compelled to go rather far towards a context of

generalization. This is in line with the objectives of this volume, but it may appear still premature at this stage.

Clearly, an analysis of the chronological steps of biological invasions within the Old World, from the Old World, and to the Old World, provides some of the best examples to propose a tentative framework for historical generalization. It must be stressed, however, that a cautious frame of mind is needed for a progressive conceptualization of a theory of biological invasions.

First of all, a number of concepts that ecologists use, namely those of resilience and disturbance, have very different meanings when applied to such different biota as plants, large animals, invertebrates, parasites and microbes, and terrestrial and aquatic organisms. These meanings are even more difficult to reconcile when different ecosystem types are considered.

Secondly, historical analyses—both the geological and human ones—are viewed at such a large scale of space and time that (in accordance with the hierarchical theory) they are more able to provide information on the relevance and constraints of a given process than explore the mechanisms of testable hypotheses. Experimental research on biological invasions is badly needed at this time.

Thirdly, a general interpretation of the invasion problem implies an inextricable mixture of ecological and genetic attributes of species from one side, and of chance, timing and human-derived opportunities from the other side (di Castri, 1989). If a geologically based analysis can provide insights on the emergence of genetic and ecological attributes, facilitating the invasion potential of species, human historical studies can provide the background to explain chance and opportunities for invasions.

Having already stressed the continuum between the geological and human dimensions of history, this chapter—nevertheless—emphasizes the latter dimension. A human historical approach is important, partly because it is inherent to the peculiarities of human occupation and migrations in the Old World, and partly because few attempts have been made in the previous workshops to explicate human history as a driving force of biological invasions. After all, the breakdown of natural biogeographical realms and their barriers, such is the cornerstone of the overall problem of biological invasions, is immediately imputable to unbounded economic and socio-cultural forces around the year 1500 AD rather than explicable on solely biological grounds.

In accordance with the objectives of this chapter, where generalities on the relevance of historical factors have to be combined with specificities related to the Old World, I will propose a few grossly defined steps as a framework to understand the relation between historical analyses and the invasion of species and the susceptibility of ecosystems to invasion. Later, I will reply in a preliminary way to such questions as: 'Do Old World organisms have a greater invasion potential in newly colonized ecosystems?', 'If so, is it because of intrinsic evolutionary-shaped attributes, or because of more opportunities provided by Old World men?', and 'Are the Old World ecosystems less susceptible to invasion

by alien species than New World ecosystems?' With this background, I will conclude by proposing another preliminary framework on human history as a driving force in the Old World in relation to biological invasions.

1.2 THE RELEVANCE OF AN HISTORICAL BACKGROUND TO UNDERSTANDING TRENDS AND PATTERNS OF BIOLOGICAL INVASIONS

The main aspects related to the above point are schematically presented in Table 1.1. The five steps along a time scale cannot be precisely defined, because of a time lag as regards the occurrence of similar events in different regions. This is particularly true in the pre-historical period, since there may be a difference of thousands of years regarding the presence and effects of early man, even within a given biogeographical area. Anyway, the duration of any given period decreases massively from millions of years as regards the geological one, tens of thousands of years for the pre-historical, a few thousands for the first historical period, a few hundreds from 1500 AD up to present. Presumably, a time span of only a few dozen years are considered in so far as the immediate perspective is concerned.

Admittedly, the selection for each period of the main events and of the lessons to be learned as regards invasion processes constitutes an arbitrary choice. Some of the points of Table 1.1 will be discussed in some length in this chapter, others are hopefully self-explanatory.

Geologically speaking, invasions of species from one continent to another are true evolutionary processes, somewhat like speciation and extinction. Classical examples are the rapid intercontinental expansion of the primitive horse, or the waves of migrations between the two Americas. This migration was more massive from North to South, when the broken isthmus of Panama in the Tertiary was bridged in successive times; invasions and extinctions—the latter concerning particularly South American mammals—are well documented processes. These processes can provide geological insights for a better understanding of the present-day phenomena of biological invasions (Elton, 1958).

In general, all large-scale climatic changes and geological crises—even very old ones like the Permian-Triassic crisis—are at the origin of massive exchanges of flora and fauna. At a smaller scale, it is well known that physical barriers such as oceans, mountains or deserts can be overcome by many organisms. These organisms move on rafts of vegetation carried by rivers and marine currents, long-distance wind transport, or phoresis (non-flying species tied up to, and carried by, birds or larger flying arthropods). The importance of these factors has probably been underestimated in the past by a number of biogeographers.

Nevertheless, the main lesson to be learned from studies of invasion processes, at the geological scale, may well be to understand whether or not, or to what extent, a given evolutionary and geological history has facilitated or undermined the potential of a species to become an invader. Additionally, one might ask how history has increased or decreased the susceptibility of an ecosystem and a region

Table 1.1. Historical steps as related to specific invasion processes

Time scale	Main events	Knowledge to be gained as regards the invasion of species and the invasibility of ecosystems
Geological	Climatic changes Tectonic proeesses	Understand the evolution of genetic and ecological attributes facilitating species invasion potential—as well as of ecosystem resilience—in relation to different disturbance regimes. Follow patterns of invasion of species from one biogeographical realm to another (e.g. from and to North America and South America) in the absence of man.
Pre-historical	Emergence of the human condition Synchronous climatic and tectonic changes	Pinpoint the concomitant effects on species of natural (endogenous) disturbance and of man-made (exogenous) disturbance, and in particular the interactions that may have led to positive or negative feedbacks increasing or decreasing the invasion potential of species.
Historical up to 1500 AD	Stronger and more extended man-made perturbations Migrations and 'shaking up' of human populations within a given biogeographical realm Improved marine transportation systems	Study patterns of success (and failure) of biological invaders closely associated with man's actions, within a given biogeographical realm. Follow the effects—as regards biological invasions and colonizations—of the first break-down by man of biogeographical realms (e.g. human migration from Southeast Asia to Pacific islands). Compare the effects of early biological invasions on the biota of islands of different size and located at different distances from continental masses.
Historical from 1500 AD to present	Opening of new man-made routes across biogeographical realms Intercontinental human migrations and colonizations, driven by strong economic and social pressures, and made possible by new transportation and communications systems	Highlight trends of species introduction and colonization (or their failure to colonize) from one biogeographical realm to another, due to intentional or inadvertent introduction by man. Compare the susceptibility to invasion of ecosystems, mainly those of the same type (tropical, savannas, mediterranean-climate, etc.) but

Table 1.1. (*Contd.*)

Time scale	Main events	Knowledge to be gained as regards the invasion of species and the invasibility of ecosystems
	Progressive globalization of trade and exchanges Enlargement of the scale of space and 'acceleration' of the scale of time	belonging to different biogeographical realms, and with different phylogenetic heritage and land-use history. Defect patterns of biological invasions as related to new large-scale uniform agricultural systems in 'colonized' territories.
Perspectives from present	Global interdependence of market economies and worldwide urbanization, thus implying further landscape uniformity and agricultural simplification, massive deforestation, and dramatically declining biological diversity New types of disturbance (e.g. pollutants, including nuclear fall-out) Genetic bioengineering Man-induced climatic changes	Monitor the changing behaviour of species or varieties that may have acquired an invader potential under new biologically simplified situations or thanks to new dispersal opportunities. Monitor the release, dispersal patterns and behaviour in natural 'free' conditions of genetically engineered organisms. Compare the invasibility of ecosystems submitted to increased human perturbations, from protected areas to strongly stressed ecosystems. Perceive the urgent need of a new generation of experimental predictive research on biological invasion of species and susceptibility of ecosystems to invaders.

to invasion. A subsequent question to be posed is whether the emergence of man-made ('exogenous') disturbance—as adding to or interacting with natural ('endogenous') disturbance—has had a synergistic or an opposite effect as regards the invasion problem of species and ecosystems. The concept of disturbance is used here *sensu* Fox and Fox (1986).

Once the human-history factor is taken into consideration, a major task is to characterize the kinds of disturbance caused by man and man's role in shaping new routes of dispersal, which facilitate colonization by invaders. In a similar way as for the geological crises, some human-history crises or breaking points are of particular importance: (1) for having 'fixed' the patterns of the 'man-biological invader' relationships (a kind of symbiotic relation *sensu lato*), (2) for having unlocked the biogeographic enclosures and triggered successive waves of invaders, and (3) for having changed the rules and rhythm of the natural evolutionary game.

The first of the three human-history crises outlined above can be placed in early

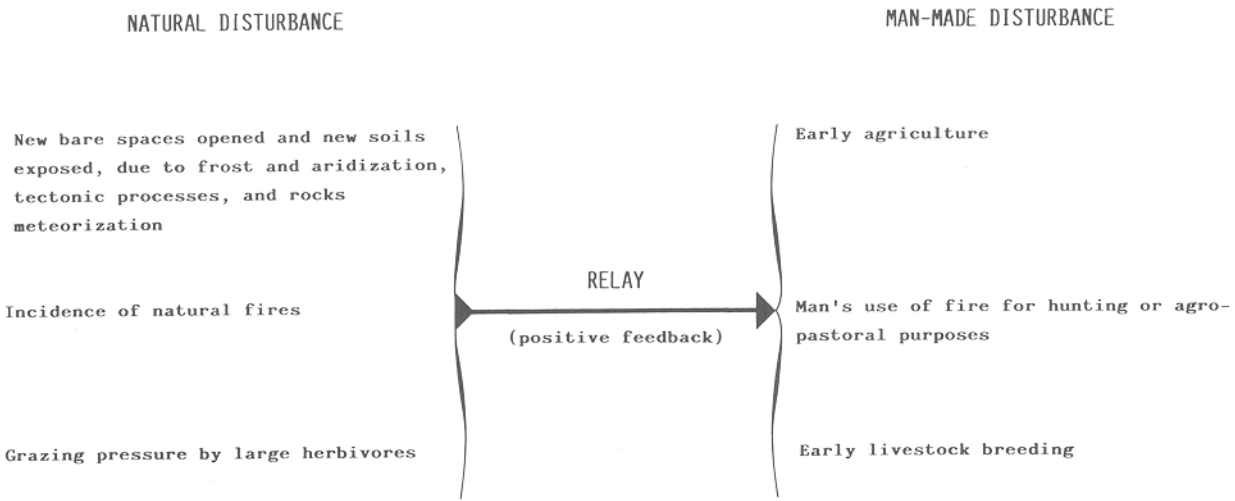

Figure 1.1. The 'relay' between natural and man-made disturbance

Neolithic times, when and wherein a sort of 'relay' took place between natural and man-made disturbance (as sketched in Figure 1.1). This relay may have synergistically strengthened some trends of natural selection, and created close ties between specific human actions and specific *potential* invaders. Under conditions of greater similarity between the effects of natural and man-made disturbance, of more ancient and more concomitant overlap of the two types of disturbance, and of more long-lasting association between man and an invader, one may assume that this relay should have been more efficient. These conditions seem to be particularly applicable to the patterns of early occupation by man of the lands around the Mediterranean Basin (Pons *et al.*, 1989; Vernet, 1989). Fortunately, these hypotheses can be challenged at present through a combination of the flourishing research on pollen analysis and profiles, on charcoal analysis, and on dendrochronology and archaeology.

The second, and more spectacular, historical crisis corresponds to the times of the 'great discoveries' and the ensuing European trade networks and 'colonization' (see Figures 1.8 and 1.9). Special attention to this aspect will be given in Section 1.5.

We are likely to face now the third crisis referred to above. Being able to act on a large scale, as the most impacting 'geological' agent (including inducing climatic changes), man has accelerated the pace of biological changes. In particular, man has genetically simplified many species. Other species have simply become extinct. Many 'surprises' may occur as new invaders and new trends and patterns of biological invasion emerge in a near future.

1.3 PECULIARITIES OF THE OLD WORLD AS RELATED TO THE INVASION POTENTIAL OF ITS SPECIES

The Old World covers the most extensive and continuous continental land mass. At least from East (Siberia) to West (Atlantic coasts) the physical barriers, represented by some mountain ranges (e.g. the Urals) and several large rivers, are not insurmountable for most organisms. Also because of the relative higher land/sea ratio, the extent and effects of the Quaternary glaciations have been greater in the Old World than anywhere else. Climate shows strong continental patterns (more than 20 °C difference between the mean temperature in summer and winter), and the occurrence of 'killing frosts' is frequent. This also happens—to a certain extent—in the Mediterranean Basin, so that this climate is the most 'continental' one (di Castri, 1981) as compared with those of other regions of the world with a mediterranean-type climate (California, Chile, Cape Province in South Africa, Western and southern Australia). The heterogeneity and roughness of the landscape have favoured the existence of several 'massifs de refuge' that have permitted recolonization by several taxa in interglacial periods. In addition, large open spaces exist (e.g. the Gobi desert, the Ethiopian plateaux, the Arabian, Persian and Turkmen deserts) together with large forested areas.

Man's impacts are detectable as long as 40 000 years before the present (BP)

(Verner, 1989), and strong human effects on the environment appear some 8000 years BP. Around the Mediterranean Basin, clearing by fire, pastoralism and primitive agriculture were the primary impacts (Pons *et al.*, 1989). In addition, frequent and sometimes massive migrations of human populations have taken place in Eurasia from the oldest periods up to the present times, more often—but not exclusively—from East to West.

From the practical point of view of biological invasions, I tend to limit the Old World to the zone situated north of the line (Figure 1.2, Braudel, 1979a) separating the areas with a hoe-based agriculture (towards the south) from those where the instruments for earth turn-over were the spade and particularly the plough (often using an animal-labour power). Deeply removing soil by ploughing has far-reaching effects on biological processes in soil, including germination. Tropical and South Africa (not eastern Africa), and part of south and South-east Asia, are therefore excluded from my considerations of the Old World.

Taking into account what has been said up to now, one could postulate that most of the species of the Old World have been and are submitted to frequent endogenous disturbances. Some of these disturbances (aridization, killing frosts) have been concomitant and analogous to some man-made disturbance that have led together to opening new spaces and creation of new habitats. Very frequent and extremely old biological invasions took place within the limits of the Old World itself. Expressed in a slightly caricatural way, the fact of having already been an invader and of still being submitted to high spatial and temporal variability, as well as to varied man's impacts, makes it easier for species to continue to have an 'invader destiny' when transported by man—intentionally or accidentally—to colonize new territories (Figure 1.3).

This statement on the invasion potential of species of the Old World is admittedly a speculation and an overgeneralization. If some species of the Old World have been and are 'good' invaders, others have been less resistant to invasion and prone to be displaced or extinct. For instance, all the original mammal faunas of Corsica have become extinct at the limit of the historical times because of the accidental introduction of new rodents, among them some *Rattus* originating from the Far and Middle East (see Figure 1.4, after Vigne, 1983). This provides a classical example of historical 'island biogeography' as applied within the Old World.

Furthermore, the condition for an invader to behave already like an invader in the region of origin is by no means a general law. For instance, *Pinus radiata* (Monterrey pine) does not exhibit an invasive behaviour in its original stands in California. However, it has become a strongly aggressive invader in South Africa, Australia and New Zealand (not so in the Mediterranean Basin, Atlantic France and Chile).

While keeping the pitfalls of generalization in mind, there are numerous facts in favour of a higher invasion potential—as an average—of Old World organisms

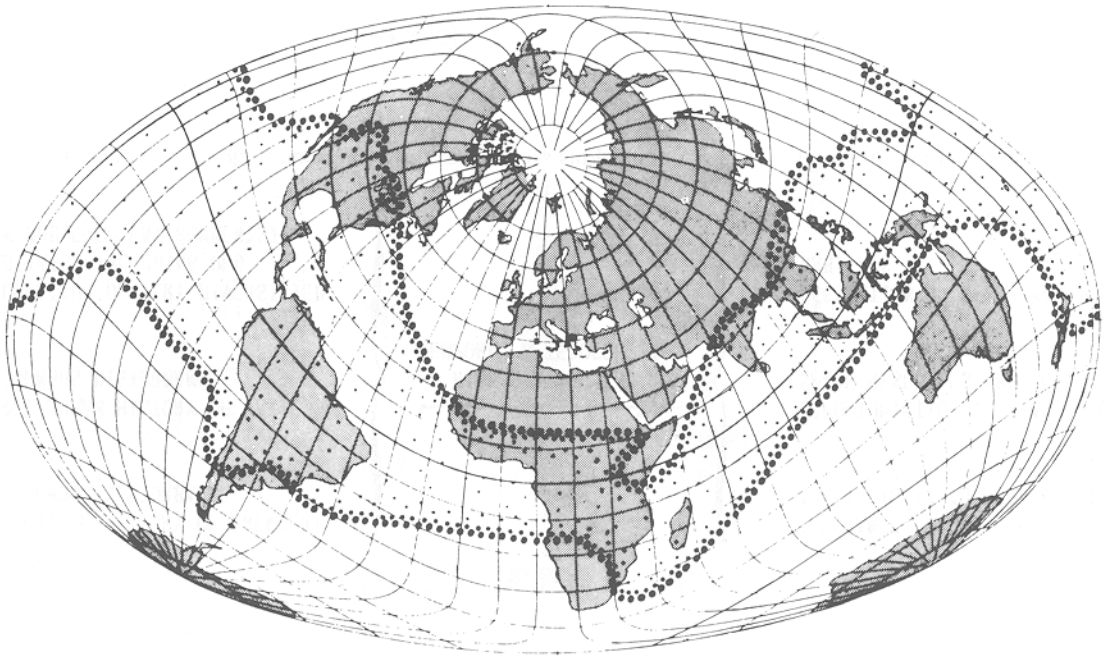

Figure 1.2. The central belt of 'hoe' cultivations (after Braudel 1979a; with permission of Armand Colin, Paris)

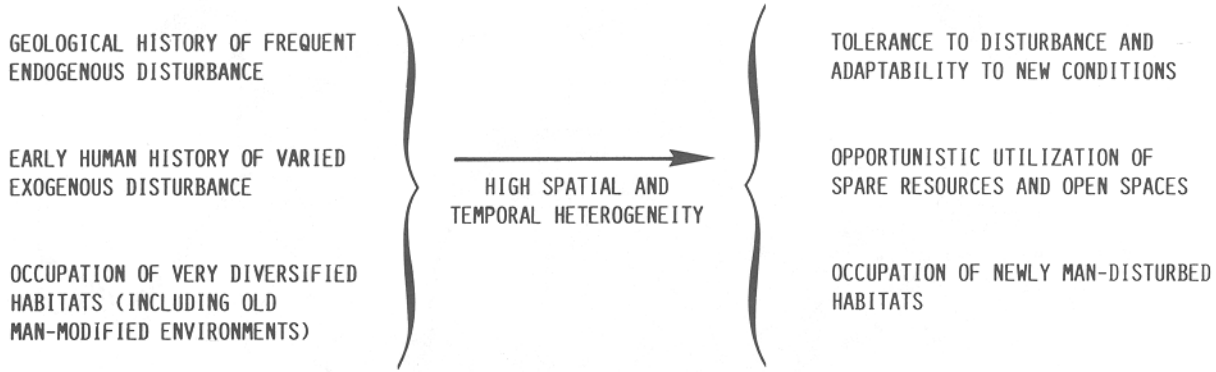

Figure 1.3. Evolutionary and historical factors supporting the invasion potential of Old World species

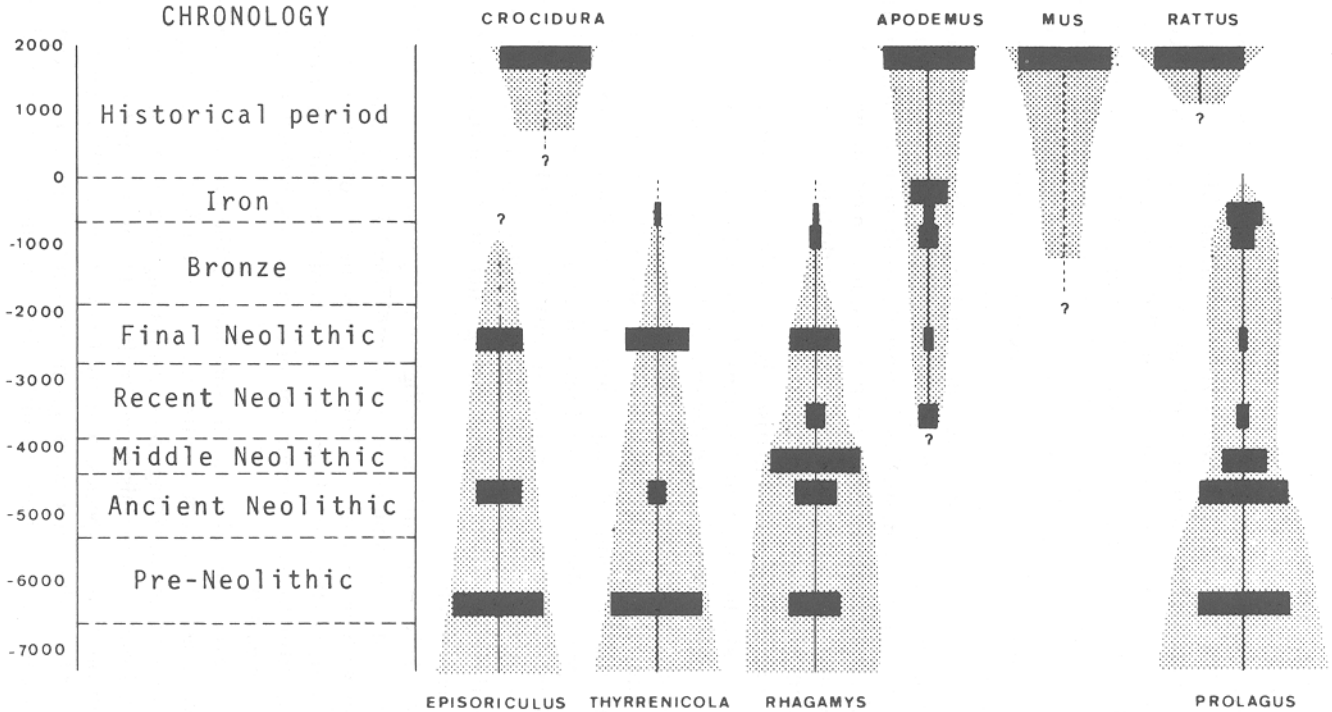

Figure 1.4. Introduction and extinction of mammals in Corsica (after Vigne, 1983) ■ fossil or present findings ▨ extrapolation

as compared with floras and faunas of other continents. Crawley's question (1985) on 'why has the trans-Atlantic "trade" in aliens been so one-sided?' is just one of many similar statements found in literature.

One is understandably impressed by the invasion ability of species such as the European rabbit (*Oryctolagus cuniculus*) in Australia (Myers, 1986) and Chile, *Rattus rattus* (an early invader even to South Africa, according to Deacon, 1986) and *Mus musculus* everywhere, *Rubus* in Chile, and *Pinus pinaster* in South Africa. Whole floras have also been virtually replaced. For example, the native species of the grazing lands of California, Chile, Argentina, South Africa, Australia, have been replaced by Old World species, particularly Mediterranean Basin annuals and herbs. A similar phenomenon has been the massive invasion of African plants into the South American savannas.

At least when vascular plants are considered (e.g. Allan, 1937; Frenkel, 1970; Raven, 1977), it appears that: (a) the proportion of alien species is lower in Europe and in the Mediterranean Basin than in most of the other regions of the world; and (b) most aliens in the other continents have a Eurasian origin, nearly 80% of the total of the adventive flora; annuals constitute the dominant group, followed by biennials and perennials, shrubs, and trees.

Taking as an example a comparison between the Mediterranean Basin and California—and admitting that the criteria followed for recording the nature and the origin of plant species may differ to a certain extent—Quezel *et al.* (1989) recognize over a total Mediterranean flora of about 20 000 species, no more than 400 'important' alien species, that is to say, some 5% (more likely 6–7% not considering the criterion of 'importance'). In California, more than 1000 introduced species (about 75% of Eurasian origin) were recognized in 1968 (certainly many more at present) as against about 5200 native species (see also Howell, 1972, and Spicher and Josselyn, 1985). The proportion of aliens would be therefore about three times greater in California than in the Mediterranean Basin.

There are likely to be intrinsic ecological and genetic attributes of Eurasian species that had been shaped by their geological history and by an early 'association' with man's activities. However, whether the difference in magnitude of invasion is due to these attributes or is a result of human-history driving forces is unknown (more likely a combination of both factors, but what is the relative importance of each?).

Only more experimental research, approaching the problem by formulating testable hypotheses, can hope to attribute cause to effect. Comparing as far as possible closely related invading and non-invading species can help resolve these issues singled out from the historical analysis. The works undertaken by Roy *et al.* (1989) on *Bromus* species, and by Cheylan *et al.* (1989) on the genera *Rattus* and *Mus*—the latter work giving particular emphasis to genetic and eco-ethological aspects—show already some promising insights in this direction.

1.4 BIOLOGICAL INVASIONS TO OLD WORLD ECOSYSTEMS

In spite of the so-called resistance to invasion of Old World ecosystems, even an incomplete list of real invaders is impressive. Obviously because of large oceanic barriers, the first invaders came from one region of the Old World to another. In addition, as far as the oldest invasions are concerned, it is almost impossible to determine whether or to what extent they have been favoured by the activities of primitive human populations. This is the case, for instance, of the slow migrations towards the northern Mediterranean Basin of tenebrionid beetles (a predominantly xerophilous family of Coleoptera). These species proceeded from the central Asian (Turkmenistan) deserts and North Africa northward since or before the Tertiary (Marcuzzi, 1989).

Conversely, species that are really indigenous may have had their distribution and their density increased largely due to different kinds of human impact on the environment. For instance, the Mediterranean species *Pinus halepensis* reached its largest distribution from the times of early man's activities up to those of the Roman Empire (Pons, personal communication).

The most common trend, in any event, is that of invasions from East to West. For example, annual plants moved from the east Mediterranean and the Irano-Turanian region towards the western Mediterranean. Rodents spread from the Far and Middle East to Europe and the Mediterranean. The black rat, *Rattus rattus*, probably indigenous to Indochina, and the house mouse, *Mus musculus domesticus*, from the Middle East reached the Mediterranean in the first or second millennium BC, while invasion by the Norway rat *Rattus norvegicus*, indigenous to southern China, seems to date only from a few centuries ago (but some recent fossil findings may prove the contrary). Also, *Cricetus cricetus* arrived in central Europe from central Asia in the late 19th century—but it was found as a fossil in central Europe (see Cheylan *et al.*, 1989, and Marcuzzi, 1989).

With the emergence of an agricultural civilization in the Mediterranean and later in central Europe, it is not surprising that most of the successful plant invaders came from the Mediterranean Basin. Kornas (1989) illustrates this trend in the Polish flora. The effect of these invasions has been an enrichment rather than a loss for the overall central European flora as exemplified in Figure 1.5 (after Kornas, 1982). An interesting case is that of rye; rye was apparently transported accidentally towards northern Europe as a weed of other cereals, but became a very useful crop under the new colder conditions.

Quite understandably, the discovery of the New World and Australia, and the increased communications with South Africa, opened a wealth of new possibilities of invasion of Old World ecosystems (and even more in the other direction). Interestingly enough, several succulents were introduced which became a most conspicuous and peculiar feature of Mediterranean Basin landscapes, such as *Agave americana, Yucca* and particularly *Opuntia* from

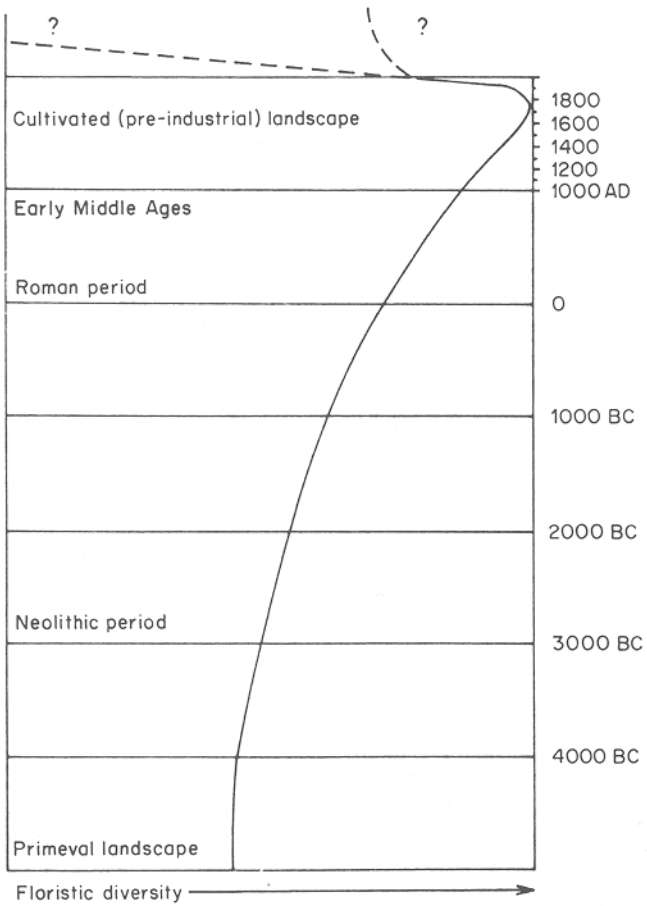

Figure 1.5. Changes in plant diversity in central Europe in pre-historic and historic times (after Kornas, 1982 and 1983, modified from Fukarek 1979)

southern North America, as well as *Mesembryanthemum* from South Africa. In addition, some notable shrubs or trees were successful invaders, including: *Nicotiana glauca* from South America, *Robinia pseudoacacia* from North America, *Acacia* and *Eucalyptus* from Australia. Incidentally, most of these succulents and some of the southern hemisphere trees have suffered so severely (including their total elimination in some regions) because of the 'killing frost' of the winter 1984–1985 in Europe that one can wonder to what extent they are really naturalized in this continental environment. This is particularly true for some species of *Mesembryanthemum* and *Acacia*.

As regards the Mediterranean Basin, it is worthwhile to point out that most of

the new invaders were indigenous to eastern North America. Surprisingly, few invaders came from the 'homoclimatic' California, Chile, South Africa and southern Australia (Quezel *et al.*, 1989). This undermines to a certain extent the value of the homoclimatic origin as a key factor for species invasions.

In spite of the relatively low percentage of true invaders, the Mediterranean Basin has undergone several alterations in the 'face' of its landscapes, because of the occurrence of many different waves of invasion of fruit and ornamental trees. As Braudel (1985) cogently said, if Herodotus (5th century BC), the father of history and a remarkable explorer and naturalist *ante litteram*, were able to revisit his eastern Mediterranean region (or even to visit it in Roman times), he would find himself in a very strange 'humanized' environment. Many of the most common and widespread plants introduced later by Mediterranean man such as citrus trees, peach tree, cypress, not to speak of the more recent introductions from the Americas, Australia and South Africa already mentioned, would be completely unrecognizable.

In highlighting the main historical events of biological invasions to the Old World, I would like to pinpoint three more recent cases of invasions. These invasions are well defined from a chronological viewpoint and represent three very distinct patterns of invasion.

The first one refers to the so-called Lessepsian migrations (Por, 1978), that is the migrations that took place from the Red Sea towards the Mediterranean Sea once the Suez Canal was opened in 1869. Most migrations of these marine organisms are one-sided (only recently some anti-Lessepsian migrations towards the Red Sea have been described), and concentrate on the eastern side. Most of the invaders have settled on the coasts rather than in the open sea. Furthermore, biogeographical explanations must take into account the distribution of the Tethys fauna and the characteristics of the Tethys Sea with a Tethyan Gulf having covered part of the present-day northern Red Sea. This is a further example of the significance of geological and evolutionary factors in understanding the present patterns of invasions (for a most comprehensive discussion of these topics see Por, 1978).

The second case points out a rather sudden change in the invasion behaviour of a Mediterranean plant, *Dittrichia viscosa*. This species has only recently begun invading ruderal habitats along roads, railways, and abandoned fields with a variety of different soil conditions as regards salinity and calcareous or siliceous substrate. This represents a testable case of an indigenous plant enlarging its ecological tolerance and poses quite interesting research questions on nutritional and genetic aspects (Wacquant, 1989).

A third classical case study is of the lepidopteran *Hyphantria cunea* (fall webworm). *Hyphantria* was accidentally introduced in central Europe from North America in 1940. A secondary introduction took place in 1978 on the French Atlantic coast. From the primary site of introduction, the trends and speed of this invasion have been followed. By the 1980s, this species had reached

the south of Italy and the Black Sea, and is further expanding—apparently more slowly—towards the north and the east (Marcuzzi, 1989).

Having shown—admittedly in a rather superficial and descriptive way—that Old World ecosystems are also prone to invasion by both Old World and exotic species, what is the degree of susceptibility to invasion ('invasibility') of different ecosystems and habitats?

There is no doubt that many new plant invaders initially become established by colonizing ruderal places and arable fields. In the ranking of central European ecosystems susceptible to invasion by plants proposed by Kornas (1983), it could be implied that openness and disturbance are the two main factors required for a successful colonization by a non-native species. Only very few introduced plants such as *Elodea canadensis* seem to be able to 'jump over' undisturbed and close sites (Kornas, 1983). There does not seem to be anything in the Old World comparable to the impressive invasions of apparently undisturbed habitats of South Africa by *Hakea* (from Australia) and *Pinus pinaster* (from Europe).

The problem is more complex when other taxa, life forms, ecological niches and habitats are jointly considered (animals, microbes, aquatic organisms, coastal and marine environments, urbanized environments, etc.). It is unquestionable that urbanized and densely populated sites favour the expansion of commensals and pathogens. In addition, while lacking precise statistics in this respect, I am impressed by the number and importance of invaders (intentionally or accidentally introduced species) in such environments as the coasts (including coastal dunes), and rivers and adjacent riverine habitats of Europe. It is more difficult to find real cases of biological invasions in the open sea, perhaps because there were few obstacles for a very old mixture of compatible species. On European coasts, where large engineering works or intensive culture of aquatic organisms have been developed, there is a wealth of invaders (molluscs and their numerous parasites, worms, sea-weeds, etc.; see Maillard and Raibaut, 1989). Classical invasions have taken place in and along most European rivers: fishes such as *Gambusia affinis* from southeastern North America, *Salmo gairdneri* (rainbow trout) from North America, *Ameiurus nebulosus* from the United States, several molluscs as well as parasites with complex cycles (Combes and Le Brun, 1989). Mammals such as the North American muskrat (*Ondatra zibethica*) and *Myocastor coypus* from South America, and even the water hyacinth (*Eichhornia crassipes*) in some thermophilous sites of south Portugal have also invaded riverine ecosystems. In some of these streams, the degree of disturbance was negligible at the moment of the introduction. However, it may be that the fact of introducing a species, even accidentally, represents in itself an exogenous disturbance.

In fact, I am not convinced that the resistance to invasion of these Eurasian aquatic and semi-aquatic ecosystems is really higher as compared with similar temperate-climate habitats in non-insular conditions. There are several reasons justifying this difference of invasibility between terrestrial and aquatic (or quasi-aquatic) ecosystems. First of all, the latter are very mobile environments (waves

on coasts, wind on sand-dunes, running waters, frequent flooding of riverine habitats), submitted therefore to an almost permanent disturbance regime. Secondly, as regards the marine environments, the possible barriers are not quite of the same kind as those commonly described to define biogeographical realms. Thirdly, it is unlikely that the same considerations already made on old 'man-invader associations' and on 'exogenous–endogenous disturbance overlaps' are applicable to these aquatic environments. Finally, as regards mainly Europe in the Old World, it is not yet known what the invasibility danger will be as related to strongly stressed ecosystems (as in forest die-back or in highly eutrophic waters) and the repercussions of invasions on the extinction rate of native species.

1.5 HUMAN-HISTORY DRIVING FORCES IN THE OLD WORLD AS RELATED TO BIOLOGICAL INVASIONS

The third section of this chapter has been rather speculative in trying to answer the question of why so many Old World species seem to be highly invasive. The fourth section has been of a mostly descriptive nature in mentioning some diverse types of invasions—in different times—within or towards the Old World.

I would now like to attempt a typification and categorization of the main human-history driving forces which originated in the Old World. These forces have had an effect in facilitating the introduction of alien species, either in direct relation to the Old World or—indirectly—by promoting exchanges. For instance, between North and South America, among regions of the inter-tropical belt, and between South Africa and Australia many exchanges have occurred, which are attributable to European economic expansion.

I am indebted to Fernand Braudel and his school of history which links and relates the patterns of the daily life with long-term historical trends, thus embracing different scales of space and time (as some modern approaches in ecology are also trying to do). Braudel's conception is free from the too common ethnocentric (Europocentric) distortions, and the different perceptions are presented in a very comprehensive and harmonious design. I have been particularly impressed, in preparing this chapter, by the relevance of his last monumental work in three volumes (Braudel, 1979 a, 1979 b, 1979 c) on 'civilization, economy, and capitalism' from the 15th to the 18th century. From another historical point of view, it is also worth reading Crosby's book (1986) on European 'Ecological Imperialism'.

Table 1.2 summarizes most of my preliminary thoughts. The columns are separated by 'breaking points' of high historical significance, at least as regards the chance and timing of species transportation to new territories. The general trend is certainly that of a progressive globalization of the problem, as well as of a very rapid acceleration of invasion processes.

Of course, an ideal presentation should have been to provide, for each one of

Table 1.2. Human-history driving forces in the Old World as related to biological invasions

Before 1500 AD	After 1500 AD	From last century in a worldwide perspective
Forest clearing	Exploration, discovery and early colonization by Europeans of other territories and continents	Improvement of transportation systems (roads, railways, internal navigation canals)
Primaeval agriculture	Establishment of new market economies and crossroads places (e.g. Amsterdam, London) favouring the 'globalization' of trade exchanges	Large engineering works for irrigation and hydropower
Sheep and cattle-raising	Large 'colonies' under the rule of Europeans, often entailing introduction of European-like agriculture and increasing *inter alia* intertropical exchanges	Opening of inter-oceanic canals (e.g. Suez, Panama, Volga-Don)
Migrations and nomadism	'Revolution' of food customs in wealthy Europe (e.g. increased use of tea, coffee, chocolate, rice, sugar, potatoes, maize, beef and lamb)	Aircraft transportation
Inshore coastal traffic	Increased demand in Europe of products such as cotton, tobacco, wool, etc.	World wars and displacement of human populations
Settlement of islands (e.g. Corsica)	Negro slavery; Indian and Chinese migrations	'Decolonization'; international aid to newly independent countries following 'western' patterns
Intensification of agriculture by ploughing	Missionary establishments	Emergence of multinational companies
Offshore traffic and trade	Occupation by Russians of northern and part of central Asia, up to Siberia	Tropical deforestation and resettlement schemes
Coastal 'colonies' (e.g. Phoenician and Greek colonies)	Intentional introduction into the Old World of exotic species through activities of acclimatization societies, botanical gardens and zoos, and for agricultural, forestry, fishery or ornamental purposes	Afforestation of arid lands with exotic species
Building up of large empires (e.g. Persian, Roman, Arab, Mogul) with considerable expansion of communication and transportation systems	Large-scale emigration from the Old World due to persecution during religious conflicts, civil and 'independence' wars, and to increased demography, unemployment and famine	Environmental impacts decreasing ecosystems' resilience
Long-ranging wars and military expansion		Increased urbanization and creation of ruderal habitats
Invasions of German and Asian people, mainly from east to west		International interdependence of markets
Long-distance shipping trade		Release of genetically engineered organisms
Establishment of 'market economies' (e.g. Venice) covering the 'known world' up to the Far East		

the historical driving forces mentioned in Table 1.2, a precise dating and a definition of a given set of parallel biological invasions. This is not feasible in this introductory general chapter, but more detailed work is underway towards these results. Furthermore, at least for the first part of the left column, a comparative dating is impossible, even within such a restricted region as the Mediterranean Basin. 'Neolithization' progressed slowly from east to west, and there may be a time lag of 4000 to 6000 years for the establishment, for instance, of the Bronze and Iron periods (Le Houerou, 1981; Vernet, 1989).

The left column covers a period of several millennia up to about 1500 AD, and refers exclusively to human historical events which favoured invasions and migrations *within* the Old World. For example, the existence of an extremely extended Persian Empire (500 years BC) with its imperial roads has conceivably promoted the expansion of Irano-Turanian and central Asian elements towards the Mediterranean Basin. The Phoenician and Greek colonies, far away from their eastern Mediterranean homelands, have certainly promoted the expansion of cereals (and their weeds) towards the western Mediterranean and the Black Sea. Later, the continuous movement of human populations in Europe and Asia at the end of the Roman Empire and in the Middle Ages—and in Asia up to very recent times—has produced a real biological 'brassage' ('shaking and mixing up' of species). It should be stressed that the so-called 'barbarian' invasions to Europe, and the migrations and wars in central Asia and the Far East (Figures 1.6 and 1.7) were not 'wars' in a modern meaning, but slow movements of populations with entire families, their domestic animals, seeds, parasites, pathogens and commensals.

During the last centuries of this period, Venice developed a quite modern market and trade economy. While its action in exchanging goods and products was not consistently different from the present-day patterns, its coverage was reduced to the 'known' world (see Figure 1.8, after Braudel, 1979c).

A historical turning point occurred around 1500 AD with the exploration, discovery and colonization of new territories. It also marked the beginning of the globalization of exchanges, while still keeping a very strong European focus. A comparison between Figure 1.8 (1500 AD) and Figure 1.9 (1775 AD) gives a fairly good idea of the enormous increase of communications and trades (and of the 'opportunities' for biological invasions) in a relatively short period. It is not a coincidence that the delimitating date between archaeophytes and neophytes as regards alien plants is also 1500 AD (see Kornas, 1983 and Sykora, 1984).

The second period (central column) has a much shorter duration that the previous one: some 350–400 years. Among the facts quoted here, the change in food and dressing customs, thanks to the unusual wealth of a part of the European people, may seem to be a most trivial one. On the contrary, in addition to prefiguring some of the most peculiar features of modern society, it has had far-reaching consequences as regards biological invasions; for example, through the importation of new products and species from other continents, or from poorer

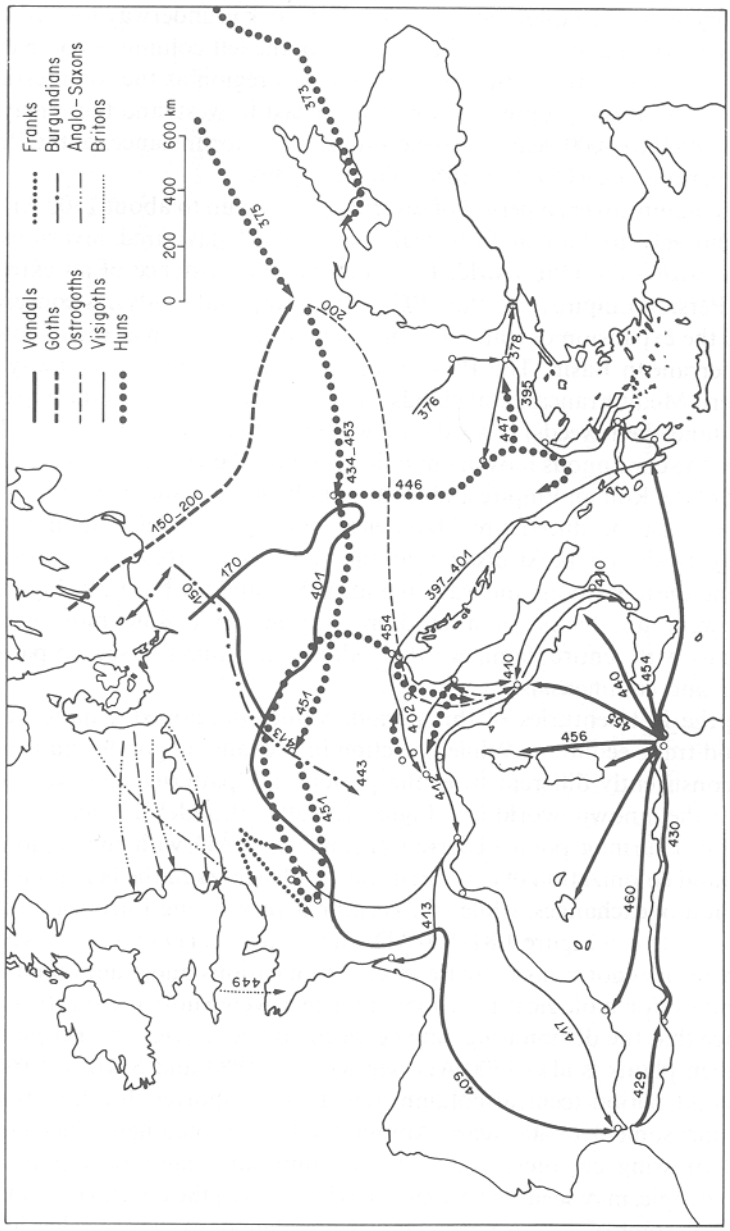

Figure 1.6. The German migrations around 500 AD

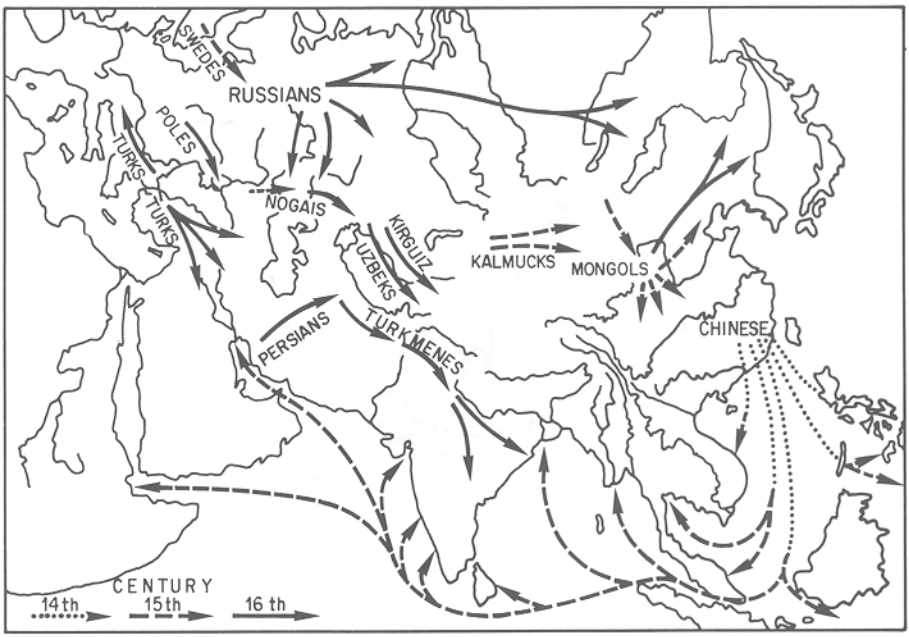

Figure 1.7. Eurasian migrations in the 14th to 16th centuries (after Braudel, 1979c; with permission of Armand Colin, Paris)

parts of Europe (e.g. cattle from eastern Europe), or by contributing to fundamental changes in tropical agriculture (including new human labour needs) and increasing intertropical exchanges. Consider the neotropical (South American) water hyacinth. It began to spread about a century ago, and is now found throughout the tropical world. It is worth pointing out the fate of water hyacinth, because it constitutes the case of a very harmful invader that has become a valuable resource in some invaded areas, such as in southern China, as a staple part of the diet of pigs and other domesticated animals (di Castri and Hadley, 1980).

Some of these historical factors, as for instance the increased demand for wool, have been analysed in a very detailed way from the viewpoint of the accidental introduction of alien plants. The very comprehensive and extremely stimulating monograph of Thellung (1908–1910) on the adventive flora of Montpellier was largely inspired by the expansion of aliens due to the import, hanging out and drying of wool at Port-Juvénal (near Montpellier). Similarly, very precise chronological steps can be established for the introduction of exotics to the botanical gardens of Europe at different times, and their intentional or accidental spreading out (see Sykora, 1984).

In spite of the fact that the last two examples are supportive of invasions towards the Old World, it is unquestionable that the period up to the middle of

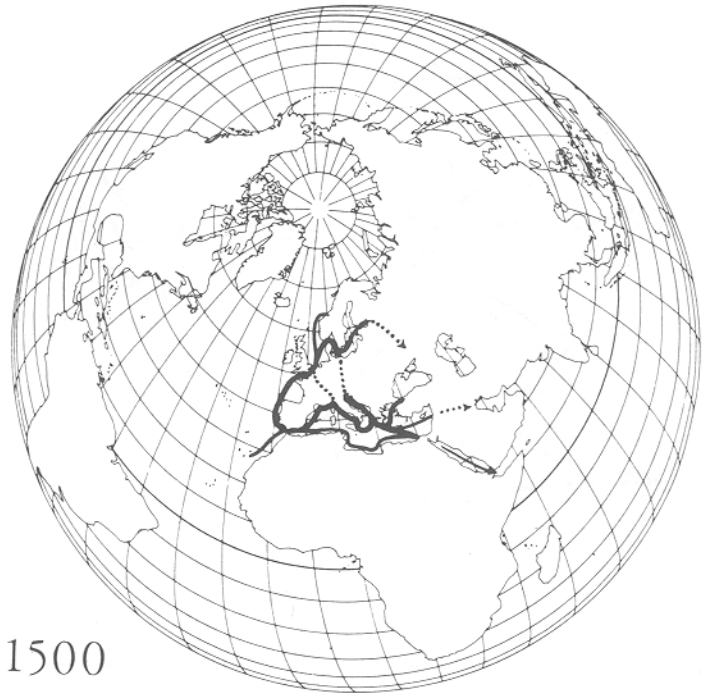

Figure 1.8. The expansion of the European trades and economies, with special emphasis on Venice as its centre, around 1500 AD (after Braudel, 1979c; with permission of Armand Colin, Paris)

the last century, has greatly facilitated opportunities for Old World invaders to colonize the other continents. As a matter of fact, at the turning time of 1500 AD when the main explorations and colonizations began, intensive agriculture was restricted to the Old World (including south and Southeast Asia, but occurring in very few parts of Africa south of the Sahara, and of central Asia). The rest of the 'unknown' world was populated mainly by nomads and hunter-gatherers, and by primitive agriculturists, while some more advanced agricultural practices—of a less perturbing nature as compared with the Eurasian ones—were applied mostly in Central and Andean America and in Madagascar. This does not imply a 'superiority' of European man vis-à-vis other extremely rich and diversified cultures and civilizations existing in the other continents. It means simply the 'implant' of a more aggressive technology.

Even the human emigrations from Europe at the end of this period—that have marked its political vicissitudes and a decline of the absolute economic predominance of Europe—further favoured the 'export' of culturally oriented agricultural practices. The waves of Germans, Greeks, Swedes, Italians, Irish,

Figure 1.9. The 'globalization' of the European trades (particularly of the British, Dutch, Spanish, Portuguese and French networks) around 1775 AD; London as the main crossroads of economies (after Braudel, 1979c; with permission of Armand Colin, Paris)

Spaniards, Poles, etc., that have shaped the cultivated landscapes of so many regions of the Americas or Australia, have tended to use their most familiar plants and animal breeds. Too often species were imported with insufficient (or badly applied) quarantine regulations.

As a matter of fact, even at present, any development scheme guided by another country (or by an international organization) is not 'aseptic', in the sense that a given technology carries with it a 'cortège' not only of cultural repercussions, but also of biological changes.

Accordingly, European man has not only greatly helped the introduction of Old World species (with their weeds and parasites), but also—by adopting his own original agricultural practices—he is likely to have facilitated colonization and naturalization processes (see Figure 1.10). Probably, the approximate mean rates given in Figure 1.10 for each successive process of invasion should be slightly increased, in the light of these considerations regarding the biological invasions from the Old World.

When one looks at the factors favouring invasion of new territories by Old

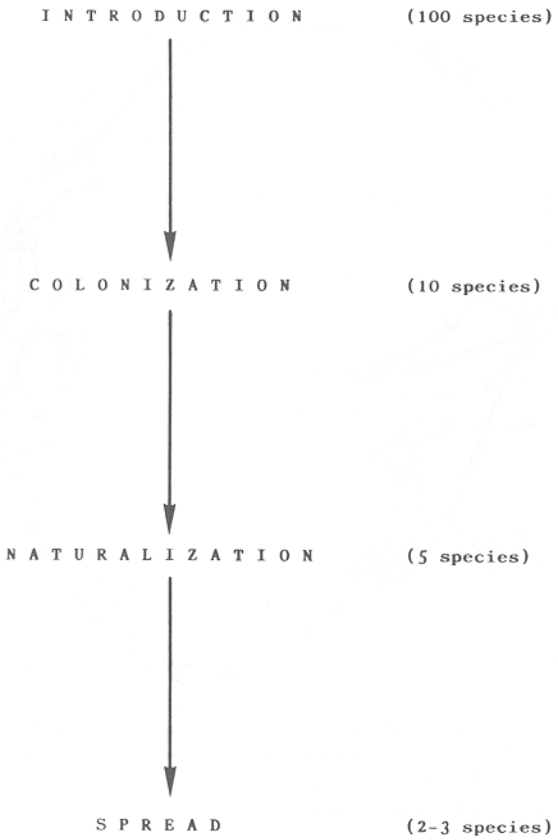

Figure 1.10. Main steps in the biological invasion processes

World species (Figure 1.11),—at least up to the end of the second historical period shown in Table 1.2—the first factors shown in Figure 1.11 and most likely the last one (the transformation of local conditions to resemble those of the original homeland) result in an incontestable advantage for Old World species compared with invaders from other continents. It is also true that several new territories colonized by Europeans had some biogeographical conditions of 'insularity' *sensu lato*, such as the southernmost tips of America and Africa, most of Chile, Australia, etc., being therefore more susceptible to invasion by alien organisms. The other factors mentioned in Figure 1.11 do not seem to be peculiar to invasion from the Old World.

The key place of the Mediterranean Basin should be stressed again. Having occupied a focal position as regards invasions within the Old World, due to its crossroads role in geological, evolutionary, biogeographical and human-cultural

Patterns of man's migration, invasion and colonization. Trade and market trends, transportation systems.

Leaving behind their own pathogens, parasites, predators, competitors.

Finding open spaces and spare resources in newly man-disturbed environments.

'Insularity' conditions in islands, southernmost tips of continents, western fringes of continents.

Homoclimatic regions.

Homocultural conditions.

Figure 1.11. Factors affecting the chance of invasion of new territories by Old World species

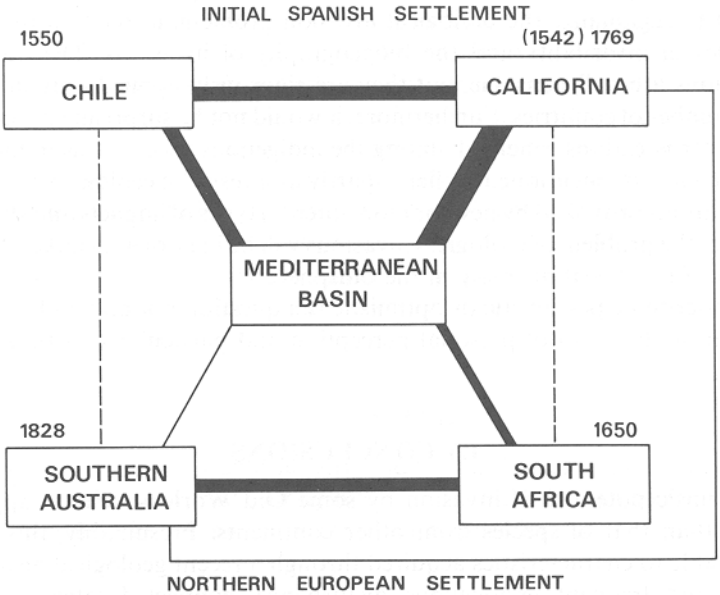

Figure 1.12. The similarities between the five regions with a mediterranean-type climate. The degree of similarity is proportional to the thickness of connecting bars and lines (simplified from Fox, 1989, on the basis of Figure 1.10. from di Castri, 1981)

terms, the Mediterranean Basin has maintained a similar role for invasions on a world-wide scale at least up to the 17th century or later. Figure 1.12, based on Fox (1989) on the basis of di Castri's (1981) typology of inter-mediterranean affinities, including here the affinities resulting from invasion processes, emphasizes the Mediterranean Basin focus. Furthermore, a 'homocultural' dimension is

added to the geological and ecological similarities. In fact, the degree of affinities increases between the mediterranean-climate regions settled by Spaniards on the one side, and between those settled by northern European people on the other side.

Finally, the right side column of Table 1.2 only covers the last 100–150 years, and is open towards the future. It is difficult to restrict here to simply Old World-based considerations, because a multifoci globalization of problems is almost completely achieved. This globalization, after vicissitudes like world wars and progressive cultural homogenization, is leading to a close international interdependence of markets and other exchanges. Together with an acceleration of the pace of changes, there is *de facto* a kind of increased 'smallness' of space because of the efficiency of new transportation and communication systems.

Most of the factors presented in this column are self-explanatory from an invasion viewpoint. It would be more interesting to foresee what the continuation of the present period would look like. It will certainly become more and more difficult to regionalize the biological invasion problem, in relation to both the processes of invasibility and the biogeography of invasions. The quarantine regulations are indispensable, but they are rigorously applied only in a rather small number of countries. Furthermore, it would not be surprising if a great deal of 'invader vocations' emerged among the indigenous species—as in the case of *Dittrichia viscosa* mentioned earlier—partly as a result of ecological and genetic modifications provoked by new (or more intense) types of impacts and stresses. In addition, the problem of biological invasions will be inextricably linked to that of the loss of biological diversity in the biosphere.

Whether to be pessimistic or optimistic is a question not only of background information, but also of personal perception and particularly of time scale of concern.

1.6 CONCLUSIONS

The intrinsic potential of invasion by some Old World species is apparently greater than that of species from other continents. Presumably, this skew is attributable to characteristics acquired through a recent geological history with diverse and frequent endogenous disturbance, connected later in positive feedbacks with the emerging exogenous disturbance of early man's impacts. Conversely, there is more evidence that human-historical events have really provided the Old World species with a greater wealth of opportunities for invading new man-colonized territories.

A broad historical overview from the geological past towards a perspective of possible future trends (Table 1.1) outlines three main 'crises' as regards biological invasions: the first, in pre-historical times, when the initial conditions of 'man-invader associations' were settled; the second, around 1500 AD, when the barriers of the biogeographical realms were broken owing to new transportation systems

of man (and the tied invaders); the third, at present, because of the breakdown of the previous 'scaling rules', with much more extended space available in a much shorter time.

Taking a stricter human-history viewpoint—and more specific to the Old World—three periods characterized by different human-driven forces as regards biological invasions are defined (Table 1.2). The first one, ranging from the Neolithic times up to 1500 AD only refers to human-history factors and biological invasions having taken place within the Old World. The second one extended almost up to the end of the last century. This period shows the occurrence of flows of invaders from, to and within the Old World. The progressive globalization of biological invasions has had, however, a decided Europocentric focus as regards the human-responsibility driving forces. The third period, covering the last 100–150 years, is leading to a complete multifocal globalization of the human-governed forces that promote biological invasions.

An historical analysis cannot provide testable elements to highlight the genetic and ecological attributes that give a species potential as an invader. Similarly, history cannot give us firm evidence on the reasons why some ecosystems are vulnerable to invasion while others are not. More experimental research is needed on these topics, particularly to understand not only why some species have been so successful as invaders, but also why closely relate species *are not* invaders. Furthermore, the 'invasion' approach can help in finding stimulating 'biological models' to study an 'evolution in march' through processes of genetic differentiation, ecological colonization, and extinction.

From both an historical and a biological viewpoint, the invasion problems may be considered as a play of chance and necessity, of human-derived opportunities and of evolutionary heritages.

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