Biological Invasions (2005) 7: 99–106

Holocene turnover of the French vertebrate fauna

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Received 4 June 2003; accepted in revised form 30 March 2004

Key words: biological invasion, extinction, France, spatial scale, temporal scale, vertebrate

Abstract

Comparing available paleontological, archaeological, historical, and former distributional data with current natural history and distributions demonstrated a turnover in the French vertebrate fauna during the Holocene (subdivided into seven sub-periods). To this end, a network of 53 specialists gleaned information from more than 1300 documents, the majority never cited before in the academic literature. The designation of 699 species as native, vanished, or non-indigenous in France or in one or more of its biogeographical entities during the Holocene period was investigated. Among these 699 species, 585 were found to belong to one or more of these categories. Among the 154 species that fit the definition of non-indigenous, 86 species were new species for France during the Holocene. Fifty-one that were autochthonous vanished from France during this period. Among these 51 species, 10 (two birds and eight mammals) are now globally extinct. During the last 11 millennia, the turnover in the French vertebrate fauna yielded a net gain of 35 species. On a taxon-by-taxon basis, there was a gain in the sizes of the ichthyofauna (19 : 27%), the avifauna (10 : 3%) and the herpetofauna (7 : 9%) and a loss in the mammalian fauna (−1 : 1%). Values of a per-century invasion index were less than 1 between 9200 BC and 1600 AD but increased dramatically after this date. An exponential model fits the trajectory of this index well, reaching the value of 132 invasions per century for the last sub-period, which encompasses 1945–2002. Currently, the local ecological and economic impacts of populations of 116 species (75% of the 154 that satisfied the criteria for non-indigenous) are undocumented, and the non-indigenous populations of 107 vertebrate species (69%) are unmanaged. The delay in assessing the ecological and economical impact of non-indigenous species, which is related to a lack of interest of French academic scientists in the Science and Action programmes, prevents the public from becoming informed and hinders the debates needed to construct a global strategy. For such a strategy to be effective, it will have to be elaborated at a more global scale than in just France – definitely at least in Europe.

Introduction

From the beginning of the second half of the 20th century, many scientists have recognized the detrimental effect that biological invasions may have on the species and functioning of invaded ecosystems; Elton (1958) was a notable early example. Nevertheless, it was only during the 1990 Rio conference that the subject arose in an international political forum. Since then, many documents have been produced covering many aspects of the problem. One major issue concerns the causes of the recent increase in the number of biological invasions. Among identified causes, probably the main one is the great increase in the volume of international trade after World War II, accelerated by an international easing of trade restrictions (Jenkins 1996; Mack et al. 2000 i.a.).

Despite its political and international standing, the subject was not discussed much in public and

scientific forums in Europe during the 1990s; French governments, for example, never stressed the issue. What can account for this neglect? Taking France as an example, we can give two potential explanations (these may not be exhaustive). The first is structural, the second more cultural:

- The subject falls under the jurisdiction of many ministries (i.e., Ministry of the Environment, Ministry of Agriculture and Forestry, Ministry of Transport, Ministry of Foreign Affairs, Ministry of Health). Gathering the appropriate representatives of all these ministries in a single forum in order to formulate a general policy requires strong political leadership. The emergence of this issue implies that politicians clearly perceive the global risk posed by biological invasions. 'Global' in this sentence means that the risk surpasses the boundaries of traditional ministry jurisdiction and requires an assessment of the number, kind, and importance of impacts of non-indigenous species at a sufficiently large temporal and spatial scale.
- Many people, including scientists, perceive all European ecosystems, except for those few under protection, as having been influenced by humans for such a long time that they have lost their biological interest. This point of view implies a lack of concern for 'ordinary nature,' despite the fact that it comprises the major part of the country. A second point is that preventing introductions and managing populations of non-indigenous species appears to be impossible to many people. Moreover, when successful foreign examples of such prevention or management are presented, the response is often that local French circumstances lessen the relevance of foreign examples.

If accepted, these two explanations imply that pertinent data and knowledge about biological invasions in France are unavailable or uninterpretable for non-specialists. With the goal of clarifying perception of the issue, the French Ministry of the Environment ordered a synthesis of knowledge of the history, the biogeographical patterns, and impacts of invasions of France by vertebrates, as an exemplary taxon.

The aim of this paper is to summarize the reasoning and main results of this report (Pascal et al. 2003).

Methods

The area under study was restricted to the French European territory (including the Channel, West Atlantic, and French Mediterranean Islands), with the overseas departments (Martinique, Guadeloupe, and Reunion Islands, and French Guyana) and the French overseas territories excluded. As European France includes several biogeographical entities, it was divided into 11 biogeographical entities for terrestrial vertebrates (Tetrapoda) and six hydrogeographical basins for fishes. The 11 biogeographical entities include two insular ones (the Channel and Atlantic islands (1) and Corsica (2)), four mountainous ones (Alps (3), Pyrénées (4), Massif Central (5), Vosges, Jura and Ardennes (6)), three sets of plains (Atlantic plains, the northern limit is the Loire River and the southern limit is the Pyrénées (7), Paris Basin northward and eastward of the Seine River (8), Paris Basin southward of the Seine River, with Normandy and Brittany (9)), the French Mediterranean area (10) and the Rhone and Saone valleys, which were major ways of invasion (11). The six hydrogeographical basins are those defined by Persat and Keith (1997) and Keith (1998). Terrestrial and fresh and brackish water ecosystems were studied, but strictly marine ones were not.

The time interval considered was the Holocene period – 9200 BC to the present. This period starts with the end of the great modifications induced by the last climate warming. Among these modifications are the end of the last marine transgression and the stabilization of the west European vertebrate fauna, the majority of the cold-adapted species having migrated to the North, and the majority of the species of the Spanish, Italian and Dalmatian refugia having colonized at least the southern part of France. The Holocene was divided into seven sub-periods as follows:

1. 9200 BC–3000 BC: agriculture, animal-breeding, and the first villages appeared in western Europe.
2. 3000 BC–0: western European landscapes recorded the first strong anthropogenic influences of agriculture and animal-breeding. This sub-period ended with the *Pax Romana*.
3. 0–1600 AD: many events that strongly affected the landscape occurred, among them

being the Middle Age deforestation episode. This sub-period ended with the beginning of the global European Diaspora.
4. 1600–1800 AD: the European Diaspora was nearly complete and trade allowed many taxa to move between continents.
5. 1800–1914 AD: the advent of industry caused a dramatic evolution of the landscape because of new agricultural, silvicultural, and husbandry practices. The number of zoological gardens increased in Western Europe, promoting the introduction of non-indigenous species.
6. 1914–1945 AD: the two World Wars generated a large increase in the amount of international exchange and sped up the evolution of transport technology with substitution of a motor fleet for a sailing one, plus the development of roads, canals and railway networks.
7. 1945–2002 AD: during this half century, the western European landscape was dramatically modified by increasing urbanization, a rural exodus, and the further evolution of agriculture, silviculture, and husbandry. The perception of nature by citizens shifted as a consequence of the increasing fraction of the total population living in cities rather than farming communities. One consequence of this shift was the increasing number of non-indigenous pets.

We adopted a cladistic taxonomy, restricting ourselves to the species level for wild as well as for feral populations. The scientific nomenclatures used were those of Keith and Allardi (2001) for fishes, Gasc et al. (1997) for amphibians and reptiles, Dubois et al. (2000) for birds, and Wilson and Reeder (1993) for mammals.

For the purposes of this study, we defined a biological invasion as an event in which a species increased its distributional area during a specific period of time (whether or not because of human activities) and founded at least one self-perpetuating population in the newly invaded area.

This definition led to two corollaries:

– A species was regarded as autochthonous in France during the Holocene if it was believed to reproduce at the beginning of the Holocene in terrestrial, fresh, or brackish water ecosystems of at least one delineated biogeographical or hydrogeographical entity. If this species is allochthonous (non-indigenous) for one or more biogeographical or hydrogeographical entities, it satisfies the definition of biological invasion and was tallied as both autochthonous and allochthonous in France. At present, such a species may be present in France or it may be absent following a temporary disappearance. In the case of a temporary disappearance, the species accords with the definition of biological invasion and was tallied as autochthonous, disappeared, and allochthonous in France.

– A species was regarded as allochthonous in France during the Holocene period if it was believed not to reproduce at the beginning of the Holocene in the terrestrial, fresh, and brackish water ecosystems of France and is now represented by one or several self-sustaining populations. Self-sustaining means that the non-indigenous population does not require continuing recruitment from external sources in order to persist.

These three definitions share two features: history and *in situ* reproduction. Restriction to species with *in situ* reproduction resulted in discarding from the study all species that used French territories for various biological functions other than breeding. Among such species are birds using France for wintering or for migration, and amphihaline thalassotokous fishes. On the contrary, marine species such as sea turtles and seals were counted because they reproduce on the seashore. Lack of paleontological or archaeological data prevented us from adequately assessing the presence and reproduction at the beginning of the Holocene of many species belonging to the present French fauna; these are what Carlton (1996) calls 'cryptogenic' species, because their geographic origin is unknown. These species were considered as native unless we had proof to the contrary.

We used a simple typology of biological invasions. A first category included spontaneous biological invasions – that is, those whose arrival was not obviously related to human activities. The second category consisted of biological invasions that were inadvertently induced or facilitated by human activities but that were not transported by humans. The third category included both unintentional and intentional introductions transported by humans. This typology followed those elaborated by the Invasive Species Specialist Group (ISSG) of the IUCN (Anonymous 1999; Shine et al. 2000) and the

Invasive Species as defined by the ISSG were a subset of the third category.

For each tallied species, available paleontological, archaeological, and historical data were synthesized and compared to information on its natural history and past and present distributions. This synthesis was accomplished in order to classify the species as native, extinct, or vanished from France, or allochthonous based on all available information. For each non-indigenous species, we collected available data about the means and time of its arrival in France, its present numbers and distribution, and its impact on recipient ecosystems, including the role it may have played as a pathogen vector or reservoir. Data about management operations were also gathered wherever available.

Paleontological and archaeozoological information was extracted not only from the specialized literature, but also from the PTH database (PTH 1998; Vigne 1998) for mammals, the HAE-FAR (1993) database for birds, a Pleistocene synthesis (Mourer-Chauviré 1975; Vilette 1983; Laroulandie 2000; Louchart 2001) for both those taxa, and from Vigne et al. (1997), d'Hervet and Salotti (2000), and Bailon (2001) for the herpetofauna.

The present French fish distributions were gleaned from Keith (1998) and Keith and Allardi (2001). The present world, European, and French amphibian and reptile distributions were extracted from Anonymous (1987), Castanet and Guyetant (1989), Grossenbacher (1988), Hofer et al. (2001), Gasc et al. (1997), Parent (1981) and Delaugerre and Cheylan (1992), for birds from Voous (1960), Yeatman-Berthelot and Jarry (1994) and Dubois et al. (2000), and for mammals from Wilson and Reeder (1993), Mitchell-Jones et al. (1999) and Fayard (1984). Overall, the synthesis includes information from more than 1300 documents. Among them, some are academic papers, but the majority are reports, theses, or grey literature documents often issued during the last decade and never quoted before in academic literature. A network of 53 specialists amassed and verified all this information.

Results and discussion

We investigated the status of 699 species as native, vanished, or alien in France or one or several of its biogeographical entities during the Holocene period. Among these 699 species, 585 satisfied the definition of one or more of these categories. These 585 species include seven bird and three mammal species autochthonous in France that invaded the country after a temporary total disappearance and two allochthonous species that are presently absent after being present for several centuries.

Among these 585 species, 154, that is more than one-fourth, invaded France or at least one of its 11 biogeographical entities or six hydrogeographical basins during the Holocene period. Those species founded one or several populations that satisfied the criteria for a biological invasion.

Among these 154 species, 86, that is more than half, were species new to France during the Holocene if we consider France as a single geographical entity. Nevertheless, 68 species that were native in one or several French biogeographical entities invaded another entity during the Holocene. This result suggests that, as far as the topic of invasion is concerned, political or administrative entities are not adequate for an analysis of the subject.

Among the 585 species of the Holocene French vertebrate fauna, 51 autochthonous ones vanished during the Holocene (2 fishes, 1 amphibian, 1 reptile, 28 birds and 19 mammals). Among these 51 species, 10 (two birds and eight mammals) are now globally extinct.

A great discrepancy appears between the distribution of those 585 species among the four main vertebrate taxa and the sizes of those taxa in the world biota. With 308 species (53%), the French avifauna predominates, followed by the mammals (127 species; 22%), then the herpetofauna (80 species; 14%), and finally the ichthyofauna (70 species; 12%). This distribution differs strikingly from that of the world biota, in which herpetofauna are in the first place with 13,605 species (Frost 2002; Uetz et al. 2002) followed by avifauna (9968 species; Peterson 2002), freshwater ichthyofauna (9966 species among the 27,365 marine and freshwater species; Nelson 1994; Froese and Pauly 2003) and mammals (4629; Wilson and Reeder 1993).

The distribution of the 154 species that invaded the French biogeographical or hydrogeographical entities during the Holocene among the four main vertebrate taxa also shows a discrep-

ancy. However, the ranking of taxa calculated for the total 585 species changes dramatically if, for each taxon, we tally the ratio between the number of species that invaded the French biogeographical entities and the total number of native and alien species. Thirty one (44%), 17 (21%), 68 (22%) and 38 (30%) species of the ichthyofauna, herpetofauna, avifauna, and mammalian fauna, respectively, are or were represented by one or several allochthonous populations during the Holocene in France.

This last ranking remains if this analysis is restricted to species that are allochthonous for the entire French territory: 21 (30%), 9 (11%), 38 (12%) and 18 (14%) species of the ichthyofauna, herpetofauna, avifauna, and mammalian fauna, respectively, are new in the French vertebrate fauna. Consequently, the sizes of the French ichthyofauna and mammalian fauna were more affected by biological invasions during the Holocene than were the avifauna and herpetofauna.

During the last 11 millennia, the turnover in the French vertebrate fauna led to an increase of 35 species (86–51), thus 6% of the total number (585). In the future, this figure may be revised downwards because several species, mainly among the birds, probably disappeared from France during the first nine Holocene millennia but were not counted in this category, as their disappearance is not yet documented.

If we examine the results of the turnover taxon by taxon, we find an increase in the ichthyofauna (19 : 27%), the avifauna (10 : 3%), and the herpetofauna (7 : 9%) and a decrease in the mammalian fauna (−1 : 1%). If French vertebrates are typical, this result suggests the following hypothesis: the older the divergence date of a taxon, the greater is its capability to persist owing to a low rate of species disappearance and a high rate of successful invasion.

The number of vertebrate species that invaded France or one or several of its biogeographical entities during the seven Holocene sub-periods is shown in Figure 1. Except for a small Neolithic wave of invasion, the striking feature of this invasion process is, unsurprisingly, an acceleration at the beginning of the 19th century, with the number of invasions between 1945 and 2002 comprising 49% of the total.

This analysis does not account for variation among sub-periods in length. To compensate for this variation, we defined a century invasion index as the number of vertebrate species that invaded France or one or several of its biogeographical entities per century during each of the seven Holocene sub-periods (Figure 2). This

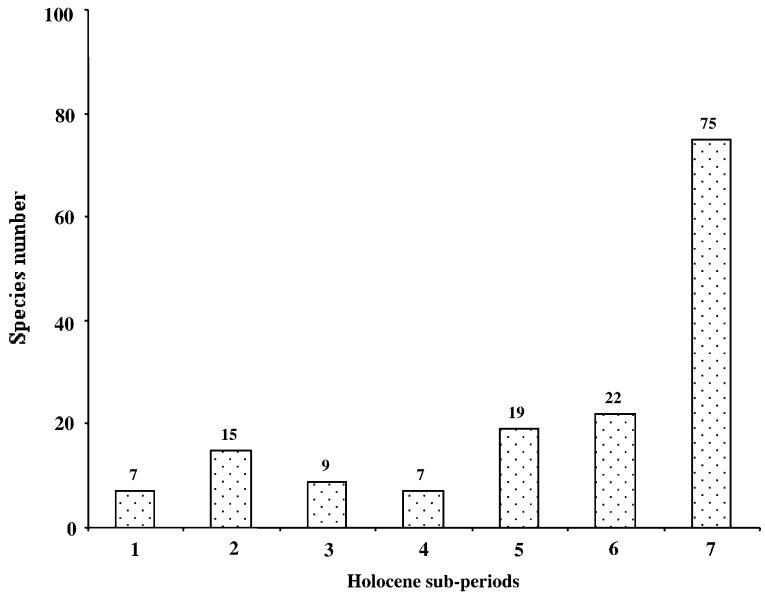

Figure 1. Number of vertebrate species that invaded France or one or several of its biogeographic entities during the seven Holocene sub-periods.

index value was less than 1 until 1600 AD, then increased dramatically. Its trajectory is well-fitted by an exponential model. It reaches the value of 132 invasions per century for the last sub-period, which encompasses 1945–2002. This last value may be overestimated because some of the new arrivals probably will not persist on French territory. The acceleration of the process may be also overestimated because past invasions are less well-documented than recent ones. Nevertheless, those two potential biases cannot by themselves explain the curve in Figure 2.

We compiled a list of all studies devoted to the assessment of impact for each species that invaded France or one or several of its biogeographical entities. We divided this dataset into four categories: no assessment, assessment of ecological impacts only, assessment of economic impacts only, assessment of both ecological and economic impacts. Studies devoted to ecological, economic, or both impact assessments were conducted for 11, 14, and 13 species, respectively. Consequently, at present, the ecological and economic impacts of 116 species (75% of 154) that are represented by allochthonous populations in France are completely undocumented.

We similarly compiled studies on management of allochthonous populations. Again, we constructed four categories: no management, management to reduce ecological impacts, management to reduce economic impacts, management to reduce both ecological and economic impacts. Allochthonous populations of 45 species are managed to reduce economic impacts and none are managed only for ecological purposes. Only *Rattus* populations (*R. rattus* and *R. norvegicus*) are managed for both economic (urban ecosystems) and ecological (insular ecosystems) purposes. Consequently, the allochthonous populations of 107 vertebrate species (69%) are currently not managed at all.

Conclusions

If the French vertebrate fauna is typical, these results show that national or administrative entities are not adequate to investigate the subject of biological invasions. Consequently, this subject must be investigated at the level of biogeographic entities.

The large discrepancy in the turnover among different vertebrate taxa shows that patterns for one taxon cannot always be generalized to others.

A sound understanding of the pace of biological invasions must account for time, not only to determine whether or not a species is allochthonous in a precise area, but also to grasp the changes in the tempo of the phenomenon. For this reason, paleontological, archeozoological, and historical data are of major interest despite difficulties in assessing their validity for comparison with recent data.

If allochthony alone does not justify managing populations, assessing the ecological and eco-

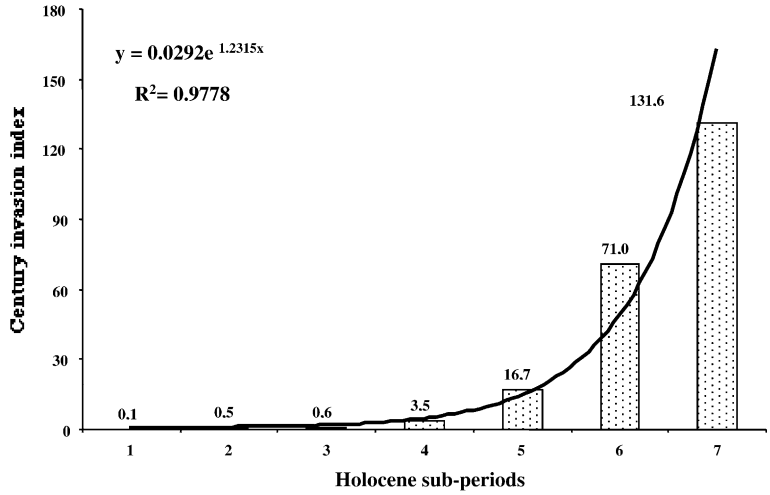

Figure 2. The century invasion index during the seven Holocene sub-periods.

nomic impact of non-indigenous species is a necessary precursor to development of an overall strategy. The exponential increase of the century invasion index, which reaches the value of 132 vertebrate invasions per century for the last 57 years, shows that France is not immune to the global flood of invasions. Further, the typical delay in assessing ecological and economic impacts of alien species hinders the dissemination of information to the public and thus delays the debates that must precede the development of an overall strategy.

This delay must be related to a lack of interest shown by French scientists in the Science and Action programmes. Although fundamental approaches to dealing with biodiversity and its recent evolution are promoted at the level of academic institutions (Anonymous 1995) and agencies (Fridlansky and Mounoulou 1996), no entity was devoted specifically to active management of and research on introduced species. As a consequence, for example, following two Environment Ministry calls for research projects on Biological Invasions (2000 and 2001), 30 projects were selected (Anonymous 2003), only four quoted the word 'management' in the title and two more the word 'control'.

Finally, to be efficient, such a strategy will have to be elaborated in Europe at least, as was proposed in the Convention on the conservation of European wildlife and natural habitats (Genovesi and Shine 2003).

Acknowledgements

We are grateful to Dan Simberloff who edited the English of this text and suggested several additions that clarified it. This research had financial support from the 'Sous-Direction de la Chasse, de la Faune et de la Flore Sauvage, Direction de la Nature et des Paysages' of the French Ministry of Environment.

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